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Crustacea (Decapoda, Cirripedia) z české křídové pánve

Crustacea (Decapoda, Cirripedia) from the Bohemian Cretaceous Basin

Disertační práce

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Prohlášení:

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyla předložena k získání jiného nebo stejného akademického titulu.

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Abstract

This thesis deals with systematic revision, evolutionary trends, palaeoecology and migration patterns of crustaceans (Cirripedia and Decapoda) from the Upper Cretaceous of the Bohemian Cretaceous Basin. Thesis is presented as a compilation of 9 papers that were published in scientific peer-reviewed journals and includes not only old museum material, but also numerous crustacean specimens which have been recovered in the last decade. Besides, short remarks on fossil crustaceans currently under study or in the process of being published (*Paraclythia*, *Oncopareia*, *Acrothoracica*) are also included in this thesis. In view of the fact that the fossil crustaceans from the BCB were most recently recorded in the turn of the 19th and the 20th centuries (and partially revised in the first half of the 20th century) and since the systematics and taxonomy have changed significantly, all papers presented here focus primarily on systematic revision and modern description. The essential part of the thesis thus deals with taphonomy and its bearing on the identification of fossil material. Thanks to a modern description, new species of *Ctenocheles fritschi* (axiidean shrimp), *Archaeochionelasmus nekvasilovae* (acorn barnacle), *Myolepas reussi* and *Capitulum sklenari* (pedunculate barnacles) were erected. *C. fritschi* is one of the oldest record of *Ctenocheles* and simultaneously the best preserved fossil material of the genus reported to date, *A. nekvasilovae* is the earliest known balanomorph barnacle, and *C. sklenari* represents the oldest record of *Capitulum*. Moreover, numerous species were re-examined, *e.g.* palaeocorystid crab *Ferroranina fritschi*, which represents the first record of *Ferroranina* for Europe. In addition, palaeobiogeographic distributions and palaeoecology reconstructions based on a correlation of both modern barnacle and decapod crustacean habitats with fossil situation were discussed.

Abstrakt

Předkládaná práce se zabývá systematickou revizí, evolučními trendy, paleoekologií a paleogeografií korýšů ze skupin Decapoda a Cirripedia pocházejících ze svrchní křídy české křídové pánve. Práce je prezentována jako soubor devíti samostatných článků, které byly publikovány v recenzovaných odborných časopisech. V jednotlivých článcích je popisován nejen materiál z muzejních kolekcí, ale i noví jedinci nasbíraní během posledních deseti let. Disertační práce navíc obsahuje i poznámky z článků v přípravě (týká se to rodů *Paraclythia* a *Oncopareia* a acrothoracidních svijonožců). Vzhledem k tomu, že korýši z české křídové pánve byli naposledy studováni na přelomu 19. a 20. století (poté částečně revidováni v první polovině 20. století) a od té doby se velmi změnily metody používané v systematice a taxonomii, jsou publikované studie zaměřeny především na moderní popis taxonů. Nedílnou součástí této práce je tak i kapitola o tafonomii a jejím významu při určování fosilních jedinců. Díky moderní revizi byly v článcích popsány nové druhy *Ctenocheles fritschi* (Decapoda: Axiidea: Ctenochelidae), *Archaeochionelasmus nekvasilovae* (Cirripedia: Thoracica: Balanomorpha), *Myolepas reussi* (Cirripedia: Thoracica: Myolepadidae) a *Capitulum sklenari* (Cirripedia: Thoracica: Pollicipedidae). *C. fritschi* je jeden z nejstarších a zároveň jeden z nejlépe zachovaných druhů v rámci tohoto rodu, *A. nekvasilovae* představuje nejstaršího balanomorfního svijonožce na světě, a stejně tak *C. sklenari* je nejstarším známým druhem rodu *Capitulum*. Mnoho dalších druhů bylo navíc zrevidováno, například krab *Ferroranina fritschi*, což je jediný známý zastupce rodu *Ferroranina* v Evropě. Diskutováno bylo také paleobiogeografické rozšíření jednotlivých druhů a paleoekologie založená na korelaci paleoprostředí fosilních korýšů s jejich analogiemi v recentu.

Contents

Introduction

The fossil crustacean fauna from the Bohemian Cretaceous Basin (BCB) has been documented since Reuss (1844, 1845-1846, 1854, 1859, 1864) provided brief descriptions and illustrations of cirripedes and decapods from the respective area. He was the first, who re-examined and described the occurrence of *Enoploclytia leachi* (Mantell, 1822) [originally classified as *Klytia leachii* in 1845 and *Clytia leachi* in 1854] from the BCB, one of the most common lobster in hemipelagic facies of this area, and erected new species of brachyuran crabs, both from Bečov near Bílina, *Secretanella buchii* (Reuss, 1845) [originally classified as *Podophthalmus buchii* in 1845 and *Reussia buchi* in 1859] and *Polycnemidium pustulosum* (Reuss, 1845) [originally classified as *Dromilites pustulosus* in 1845 and redescribed as *Polycnemidium pustulosum* in 1859]. Later, both Kafka (1885), and Fritsch and Kafka (1887) provided detailed study on cirripedes from the Ohře area, referring also to work of Darwin (1851, 1854), Reuss (1864) and Geinitz (1843, 1845, 1875a, 1875b). In the late 19th century, Fritsch (1867) described “callianassid” shrimps from the BCB and published his “Studien im Gebiete der Böhmischen Kreideformation” (1877, 1883, 1889, 1893), several lists of both invertebrate and vertebrate fossils, including crustaceans, from particular strata of the BCB. At the same time, Fritsch (in Fritsch and Kafka 1887) provided the first most compherensive study on decapod crustaceans from the BCB in which erected numerous new species.

Inevitably, the limitations of literature availability and international communication resulted in a proliferation of names, many of which were later judged to be synonymous. The first major attempt to sort out synonymous names and to catalogue the then-known species were that of Glaessner (1929) and Withers (1935), who provided ages, geographic distributions, classifications, and synonymies of all known fossils decapods and cirripedes, respectively. Glaessner (1929) recognized more than 1300 species, including specimens from the BCB, arrayed in about 317 genera (Schweitzer et al. 2010). Withers (1935) presented a modern revision of all Cretaceous cirripedes from Europe and elsewhere; he also studied and, in part, illustrated and examined cirripede species recorded by A. Frič [Fritsch], J. Perner and J. Šulc. One decade later, Mertin (1941) was the first, who recognized the importance taphonomy plays in the preservation of decapod crustaceans. He also dealt with decapods from the BCB and, among others, questionably synonymised *Stenocheles* Fritsch, 1887 with *Oncopareia* Bosquet, 1854, which was followed by Glaessner (1969).

Subsequent to Mertin’s work, many changes in nomenclature and systematics have occurred and additional material has been collected. Thus, the main purpose of all papers in this thesis was to review, illustrate, and revise the Cretaceous crustacean fauna from the BCB. Systematic methods in these papers encompass several levels, from basic species definitions to considerations of migration, palaeoecology or phylogenetic relationships among major taxa. The essential part of the thesis is taphonomy, because understanding of taphonomic influences on capitular cirripede plates, cuticle and individual body parts of decapod crustaceans plays the key role in appropriate interpretation of fossil crustacean remains and consequently in their correct taxonomic placement in a taxonomic framework.

List of papers

This thesis is based on the nine following papers, referred to in the text by Roman numerals:

I. **Kočová Veselská, M.**, Kočí, T., Buckeridge, J. 2013. A systematic revision of species *Stramentum* (*Stramentum*) *pulchellum* Sowerby, 1843 (Cirripedia, Thoracica, Stramentidae) from the Bohemian Cretaceous Basin (Czech Republic). *Acta Musei Nationalis Pragae, Series B (Historia Naturalis) 69(3-4)*, 151–158.

II. Hyžný, M., **Kočová Veselská, M.**, Dvořák, P. 2014. On the occurrence of *Ctenocheles* (Decapoda: Axiidea: Ctenochelidae) in the Bohemian Cretaceous Basin including a description of a new species. *Bulletin of Geosciences 89*, 245–256.

III. Kočí, T., **Kočová Veselská, M.**, Jagt, J.W.M. 2014. Barnacles (Crustacea, Cirripedia, Thoracica) from the Bohemian Cretaceous Basin described by Fritsch and Kafka (1887), with the exclusion of the family Stramentidae. *Acta Musei Nationalis Pragae, Series B (Historia Naturalis) 70(3-4)*, 223–234.

IV. **Kočová Veselská, M.**, Kočí, T., Kubajko, M. 2014. Dynomenid crabs (Decapoda, Brachyura) and stalked barnacles (Cirripedia, Scalpelliformes) from upper Cenomanian-lower Turonian nearshore, shallow-water strata in the Bohemian Cretaceous Basin, Czech Republic. *Scripta Geologica 147*, 49–81.

V. **Kočová Veselská, M.**, Kočí, T., Collins, J.S.H., Gale, A.S. 2015. A new species of scalpelliform cirripede (Crustacea, Cirripedia) from the Upper Cenomanian–Lower Turonian shallow-water facies at Velim (Bohemian Cretaceous Basin) and its palaeoecological implications. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 278(2),* 201–211.

VI. Kočí, T., **Kočová Veselská, M.**, Buckeridge, J.S., Jagt, J.W.M. 2016. A new barnacle, *Myolepas reussi* (Cirripedia, Scalpelliformes), from a near-shore, shallow-water facies in the Bohemian Cretaceous Basin, Czech Republic. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 280(3),* 299–313.

VII. Devillez, J., Charbonnier, S., **Kočová Veselská, M.**, Pezy, J.-P. 2017. Review of the Late Cretaceous erymid lobsters (Crustacea: Decapoda) from the Western Tethys. *Proceedings of the Geologists' Association 128(5-6),* 779–797.

VIII. Kočí, T., **Kočová Veselská, M.**, Newman, W.A., Buckeridge, J.S., Sklenář, J. 2017. *Archaeochionelasmus nekvasilovae* gen. et sp. nov. (Cirripedia, Balanomorpha, Chionelasmatoidea) from the Bohemian Cretaceous Basin (Czech Republic): the first bona fide Cretaceous neobalanoform. *Zootaxa 4294(2),* 181–196.

IX. **Kočová Veselská, M.**, Van Bakel, B., Kočí, T. (submitted). The palaeocorystid crab *Ferroranina fritschi* (Glaessner, 1929) from the lower-middle Coniacian of the Bohemian Cretaceous Basin (Czech Republic), the first record of *Ferroranina* for Europe. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*.

Aim of the thesis

The present thesis aims to give a new look on the Upper Cretaceous crustacean fauna with focus on taxa from the BCB, which benefit of new descriptions, and to compare with global fossil and related Recent crustacean fauna.

The main objectives of the thesis are the following:

a) A modern description of crustacean species, using appropriate imaging techniques (high resolution optical microscopy, scanning electron microscopy, X-ray tomography) and detailed biometrics. It is also necessary to take into sufficient account the taphonomy of cirripedes and decapod crustaceans and its bearing on the identification of fossil material. To better understand the taxonomic placement of fossils, and to evaluate convergency and inter- and intraspecific variation, the fossil material (if is complete enough including weak-part morphology) sould be compared with modern genera, because numerous Mesozoic crustacean taxa have modern relatives and a few of them even survived into the Recent (ghost shrimp *Ctenocheles* Kishinouye, 1926 in **paper II** or pedunculate cirripede *Capitulum* Gray, 1825 in **paper V**). Although this method is safer for Cenozoic specimens, many Cretaceous taxa exhibit very close morphological affinities and similar life strategies with extant forms, which could be observed in dynomenid crabs (**paper IV**), axiidean shrimps (**paper II**), clawed lobsters or in pedunculate (*e.g.* **paper V**) and sessile barnacles (**paper VIII**). However, it should be noted that modern classification of cirripedes and decapods is largely based upon characters of the anatomy that only rarely are preserved in the fossil record (soft body parts), such as the maxillipeds and the reproductive structures. Thus, it is necessary to employ morphological features that are preserved on fossils and relate those attributes to comparable features on extant forms (Schweitzer 2003, Schweitzer et al. 2010). We must also be careful when comparing morphological features among extinct and extanct taxa because potential similarities may be the result of convergent evolution. The convergence in decapods with pectinate claws is the main topic of **paper II** and the morhological similarities between extinct and extant nephropid lobsters (clade *Nephrops*-*Metanephrops*-*Paraclythia*), as a possible result of the convergent evolution, is discussed in the chapter about *Paraclythia* Fritsch, 1877 (paper in prep.). Finally, the evaluation of the implications for phylogeny of sessile barnacles by using fossil material is included in **paper VIII**.

b) The palaeoecology reconstructions based on a correlation of both modern barnacle and decapod crustacean habitats with fossil situation. Klompmaker et al. 2013 noted that the decapod groups that dominate today first became ecologically relevant in the Mesozoic Era, and simultaneously that the diversity partitioning across major groups of modern decapods may have been already established by the end of the Mesozoic. Thus, the correlation is possible, although this method is safer for Cenozoic than for Mesozoic interpretations.

Whereas many Cretaceous taxa had a comparable life strategies and inhabited similar environments as their modern relatives (**papers II, IV, V, VIII**), many lobster and cirripede species migrated (mostly during Cenozoic) from shallow waters to deeper environments due to the predacy and increased competition on inner shelves, and adaptated subsequently (*e.g.* the reduction or even complete loss of eyes in the extant, deep-water thaumastochelid lobsters) to continental slope where they occur today (Tshudy and Sorhannus 2000, Tshudy 2003).

Regarding barnacles, although they are permanently and irreversibly attached suspension feeders, they are not distributed uniformly; rather, they are zoned, firstly by depth and temperature, and then according to their response to a range of other factors, including exposure, siltation, pH, temperature, salinity, competition and predation (Foster and Buckeridge 1987). Collins and Mellen (1973), and Zullo (1982) recognised this potential and attempted to develop biostratigraphic zonations based on barnacle assemblages for Cretaceous and Cenozoic rocks of North America, respectively. Recently, many papers have focused on influences to dispersion of barnacle larvae along coastal margins (*e.g.* Pineda and López 2002, Pfeiffer-Herbert et al. 2007). Similar zonal stratification we may detect in cirripedes from the BCB where barnacles from shallow water deposits possess relatively heavily calcified capitular plates (in comparison to pelagic forms) as an adaptation to high-energy environment (*Myoleas* Gale in Gale and Sørensen, 2015b - **paper VI** and *Capitulum* - **paper V**).

c) Palaeogeographic and temporal distribution data based on fossil taxa rely on fine tuning of currently recognized species and their correct taxonomic placement in a taxonomic framework. Frequent migrations of marine animals during the Upper Cretaceous were possible due to the proximity of the continents to one another and the open communication among the basins during the Upper Cenomanian/Lower Turonian transgression (*e.g.* Fraaye 1996a, Schweitzer 2001, Feldmann and Schweitzer 2006). Numerous decapods were abundantly presented and cosmopolitan in this period (*Enoploclytia* in **paper VII**), whereas the occurrence of some genera was restricted to various parts of the world (*e.g. Paraclythia* Fritsch, 1877). Numerous taxa, despite their wide geographical range during the Cretaceous Period, retain sporadic regarding the number of the specimens (*Ctenocheles* in **paper II**, *Ferroranina* in **paper IX**). Their paucity in the fossil record is caused by their low fossilization potential (see more in the chapter *Taphonomy*).

Because barnacle adults are sessile, attached to hard substrata or to other organisms, their dispersion takes place mostly during the pelagic larval phases. Nevertheless, many extant barnacles settle on floating objects or nektonic animals, which allow them the long-distance dispersion (Southward 2008). The potential pseudoplanktonic mode of life in ancient cirripedes can be observed in stramentids, a distinctive group of Cretaceous pedunculate cirripedes usually found attached to ammonite shells or, more rarely, to the benthic bivalves (Wittler 1996, Hauschke et al. 2011, Ifrim et al. 2011, Gale 2015, **paper I**). Palaeogeography distributions and migratory patterns are included in **papers I-IX** of this thesis.

Material and methods

Material

The majority of the studied decapod crustaceans, except for dynomenid crabs, come from the Lower/Middle Turonian-Middle Coniacian hemipelagic sediments of the Bílá Hora Formation (Bílá Hora in Prague; **paper VII**, *Paraclythia*), the Teplice Formation-Rohatce Member (Oškobrh near Poděbrady; *Oncopareia*), and the Březno Formation (Březno; **papers II, IX**, *Paraclythia*). Dynomenids originate from the Upper Cenomanian-Lower Turonian (Peruc-Korycany Formation, Korycany Member) nearshore (rocky coast) deposits at Kamajka, Předboj and Kojetice, and additional, newly gathered claw remains come from Kaňk-Na Vrších, Velim and Chrtníky (**paper IV**). Cirripede specimens were collected in various areas within the BCB. The occurrences of *Myolepas reussi*, *Capitulum sklenari* and *Archaeochionelasmus nekvasilovae* are restricted exclusively to the rocky coast facies at Kaňk-Na Vrších, Velim and Předboj, respectively (**papers VI, V and VIII**, resp.). Analogously, *Stramentum pulchellum*, *Brachylepas fallax* and *Regioscalpellum maximum* are restricted to the Lower Turonian-Lower Coniacian hemipelagic deposits (**papers I and III**). Other studied cirripede species come from both nearshore and hemipelagic facies (**paper III**). For information about modes of preservation, see chapter *Taphonomy*.

All published material from the BCB is deposited in the collections of the National Museum in Prague (prefix NM), the Czech Geological Survey in Prague (prefix CGS), the Regional Museum in Most (prefix RMM) and the Krupka Museum (prefix KM). Further comparative cirripede material from Kaňk is held in the collections of the Natural History Museum in London (NHM).

Methods

In addition to the old museum collections, many specimens were gathered in the last two decades. Between 2001 and 2017 several fieldworks were conducted to rocky-coast facies in the BCB, during which more than 3000 kilogrammes were amassed and screened through a 1 mm-sieve for analysis. Obtained material yielded thousands of isolated capitular valves of scalpellid barnacles, and in excess of 50 crab claw remains, mainly isolated dactyls. Capitular plates were cleaned using hydrogen peroxide (*c*. 3-5%), and all newly collected material was subsequently transferred to the collections of the NM.

The standard procedure of using ammonium chloride sublimate was initially adopted to achieve a higher contrast when photographing specimen NM O3449 (in **paper I)** and decapods (in **paper IV**). For others, due to their fragility or clayey character of sediment, such procedure could not be used. The studied material was photographed under angled light using Canon EOS 550D digital camera (**papers II, VI, VII**, and decapods in **paper IV**); using the microphotography setting Olympus SZX-12 stereomicroscope with a DP70 camera (**papers I, II, V, VIII**), Keyence VHX-2000 3D microscope (**papers I, VIII**), or using scanning electron microscopes (SEM) Hitachi S-3700N at the NM and JEOL JSM-6380LV at the Institute of Geology and Palaeontology at Charles University in Prague (**papers II, V, VI, IX**, and cirripedes in **paper IV**). The specimens were left uncoated hence low vacuum was used instead. Stramentid specimen PA 1476 was photographed by museum curator Miroslav Radoň from the KM where material is deposited (**paper I**). Comparative cirripede material deposited in the NHM was photographed by Henry Taylor. Series of photographs taken with SEM were assembled into final images using the computer freeware Microsoft Image Composite Editor 1.4.4 (**paper II**). Plates were made using Corel Graphic Suite X4 (**papers I, III-IX**) and X5 (**paper II**).

All unpublished fossil material used for the purposes of this thesis is deposited in the NM and was photographed using Canon EOS 550D digital camera (nephropid lobsters) or scanning electron microscope Hitachi S-3700N (Acrothoracica). The Recent nephropid lobsters were photographed by Dr Denis Audo from the Université de Rennes.

Taphonomy

Although cirripedes and decapod crustaceans are highly successful group, both in number of species and abundance, in modern ecosystems (Newman and Abbott 1980), their known fossil record is described as sparse and heavily biased. It raises the question why the fossil record of these crustaceans is so scanty with comparison to other shelled fauna, such as gastropod, bivalve and cephalopod molluscs, or echinoderms. In general, cirripedes possess carapace which completely envelops the body and in most forms it secretes calcareous, phosphatic or chitinous plates. In many forms, these plates form the conspicuously armoured capitulum with high preservation potential (this is true especially for forms living in nearshore environments as an adaptation to high-energy environment), but soon after death, these plates tend to disarticulate, and thus only isolated capitular plates are available for study (**papers III–VI**). Besides, the insufficient numer of collected specimens is often caused by small sizes of their capitular valves (about 1–2 mm in *Cretiscalpellum* - **paper III**), and thus they can be easily overlooked. On the contrary, the fossil record of decapod crustaceans remains sparse and fragmentary primarily due to the low fossilization potential of their cuticle and due to the nature of their body plan, composed of discrete body and appendage segments (Schram 1982). It is clear that remains from dynamic rocky shore environments are affected by frequent transport and physical disturbance, but also remains which laid down under low-energy conditions are often scavenged and bioturbated, even after embedding, which leads to more destruction. The taphonomy potential of decapod crustaceans were studied in detail by several authors (*e.g.* Bishop 1986, Schram 1982, Stempien 2005, Krause et al. 2011, Hyžný and Klompmaker 2015, Klompmaker et al. 2015a).

Cirripede-like organisms have their origins in the Paleozoic, but until the Cenozoic, were represented primarily by pedunculate forms, such as the Scalpelliformes (Buckeridge 2012). It brings numerous problems in the fossil record. Their remains most often occur as dissociated plates of capitulum, because soon after death valves (plates) tend to disarticulate and become scattered, similar to modern lepadids and scalpellids (Hauschke et al. 2011, **paper I**). Moreover, valves from rocky coast facies are often abraded (**paper VI**). Due to such puzzling preservation, specimens may be misinterpreted and their taxonomic determination may easily be confused. The cirripede palaeontology thus rests on the ability to recognise and assign individual valves to taxa, and reconstruction of the whole shell rests partly on the basis of the few available whole fossil capitula but mostly on knowledge of living forms (Foster and

Buckeridge 1987). Species-level determination may commonly be achieved by the recognition of either some, or a combination of a few details of valve sculpture of single plates and growth patterns: conical or cylindrical plate, smooth or ribbed surface, shape of growth lines of inner and upper surface, or position of apex (Collins et al. 2014).

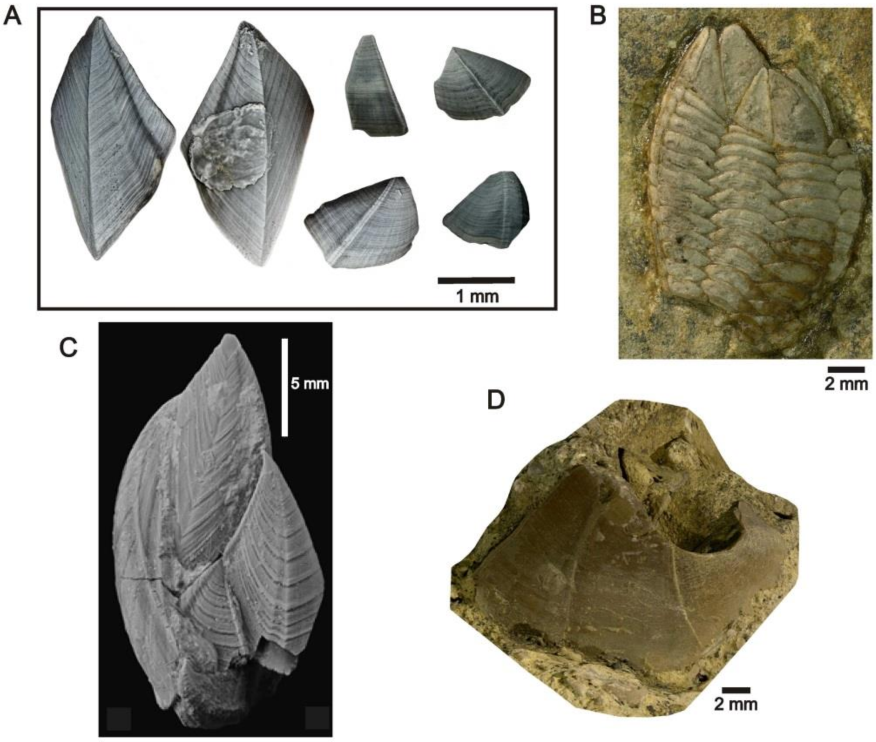

Figure 1 – Various modes of preservation of thoracican cirripedes. A – isolated capitular valves of *Cretiscalpellum glabrum*, CGS, the most common type of preservation of pedunculate thoracicans. B – near-complete *Stramentum pulchellum*, NM. C – exceptionally preserved complete capitulum of *Diotascalpellum angustatum*, CGS. D – near-complete sessile barnacle *Archaeochionelasmus nekvasilovae*, NM, the capitulum is formed to a rigid wall.

The mode of preservation depends on many factors. Sessile, non-pedunculate barnacles possess heavily calcified capitular plates, which became articulated to a rigid wall. This arrangement is generally considered better adapted to high-energy conditions, and thus there is the great chance to preservation of entire capitula even in rocky shore deposits (Newman and Abbott 1980). Regarding the BCB, a single specimen of near-complete balanomorph *Archaeochionelasmus nekvasilovae* Kočí, Buckeridge and Newman, 2017 was recorded in nearshore deposits at Přeboj near Prague (**paper VIII**). On the contrary, co-embedding of adjacent valves of pedunculate cirripedes, let alone more or less intact, complete capitula, is relatively uncommon (Foster and Buckeridge 1987). Such preservation requires a calm environment with rapid burial by very fine-grained sediment and absence of subsequent scavenging/burrowing. A beautiful example is the exceptionally preserved complete capitulum of *Diotascalpellum angustatum* (Geinitz, 1843) from the Upper Turonian at Křinec. The special occasion represents near-complete specimens of pedunculate *Stramentum* Logan, 1897, which were recorded as epizoans on shells of *Lewesiceras* and *Collignoniceras*, and thus remain articulated in the fossil record because ammonite shells provide them the protect against disarticulation during fossilization (**paper I**). Various modes of preservation of cirripedes from the BCB are shown in Fig. 1.

The lack of decapod fossil material has been attributed to the rapid decay of the cuticle. Decapod cuticle is composed of chitin and protein, often calcified. Whereas chitin is decomposited by fungi, bacteria or protozoans, the major factor in the destruction of decapod remains might be calcite dissolution from the exoskeleton. Axiidean (ghost) shrimps thus have a lower preservation potential than lobsters and crabs because of their fragile soft bodies (*e.g.* Stempien 2005, Jagt et al. 2015). These differences result in such anomalies of the fossil record as numerous axiidean claws but few intact bodies, because due to the delicate nature of most of the cuticle of these ghost shrimps, only heavily calcified chelipeds are usually preserved, and thus most fossil species are based on fragmentary material comprising propodi and dactyli only. This is a problem, because these elements can be subject to intraspecific and possible size-related variation (Schram 1982, Hyžný and Klompmaker 2015). Moreover, major chelae of these heterochelous ghost shrimps are more common in the fossil record than minor chelae. Minor chelae are rather rare because of their less calcified, thinner cuticle and their relatively small size, and thus can be easily overlooked (Hyžný and Klompmaker 2015). The same goes for the ghost shrimps from the BCB, which are mostly preserved as densely calcified isolated cheliped remains (*ca.* 93% of selected 50 specimens, and simultaneously more than two thirds of these remains exhibit major chelae only - unpublished data). But near-complete body fossils, showing carapace, legs and pleon, were also described. Such rare preservation is known in ghost shrimp *Ctenocheles fritschi* Hyžný, Kočová Veselská, Dvořák, 2014 from fine-grainded clayey sediments at Březno (**paper II**). Another reason why major chelae predominate in the fossil record was reported by Schäfer (1972), who found that the heavy claw of "*Callianassa*" separates from the exuvia and is left in the burrow, increasing the preservation potential of majors. The evidence of such preservation is known also from the BCB. A single specimen of an isolated major chela of the axiidean shrimp *Mesostylus* *faujasi* (Desmarest, 1822) placed in a single burrow come from the Upper Cenomanian of „Na Dolečkách“ near Kutná Hora (Fig. 2).

Figure 2 – A single specimen of an isolated major chela of the axiidean shrimp *Mesostylus faujasi* which is placed in a single burrow (Upper Cenomanian, Na Dolečkách near Kutná Hora), NM.

Because axiidean shrimps have been major bioturbators of muddy and sandy substrates, and simultaneously the preservation potential of axiidean shrimps is insufficient as mentioned above, the interpretations of the evolutionary history of these fossorial shrimps have been proposed based on indirect (and partly dubious) evidence of their trace fossils without taking into account the body fossil record. Moreover, indirect evidence of the trace fossils (permanent or semi-permanent burrow systems) are extremly valuable in areas without the body fossil record (Baucon et al. 2014).

The low taphonomy potential of axiidean shrimps is obvious especially when compared with, for example, taphonomy potential of the strongly calcified, clawed lobster *Enoploclytia* M’Coy, 1849. So, when I analyzed 50 well-preserved specimens of each group coming from the hemipelagic facies of the BCB, the result was not surprising. Whereas 93% of the total 50 specimens of axiidean shrimps is preserved mostly as more sclerotized distal cheliped elements (mainly propodi and dyctyli) and other 7% is represented mainly by pleons, *Enoploclytia* specimens retain carapaces, chelipeds, other appendages (mainly the 2nd and 3rd pereiopods) and abdomen in ratio of 34%, 40%, 14% and 12%, respectively. In general, the fossil lobsters [*Enoploclytia leachi* (Mantell, 1822), *Paraclythia nephropica* Fritsch, 1877)] from the hemipelagic deposits of the BCB are often very well-preserved, retain carapaces, pleons and chelipeds on the same matrix slab (although often disarticulated). Moreover, a few beautiful, relatively undeformed near-complete body fossils of *Enoploclytia* from the Bílá Hora Formation (Bílá Hora in Prague) were recorded, and although with no cuticle preserved because of the carbonate character of sediment, specimens retain even tail fan and carapaces associated with both chelipeds, which is not common in the decapod fossil record (**paper VII**). Nevertheless, the majority of fossil decapod crustaceans from the BCB is interpreted as decalcified moulted specimens with distorted carapaces. Beautiful specimen of such a damaged exuvia is that of ?*Rectaglyphea bohemica* (Fritsch, 1887) [NM O3490] from Bílá Hora in Prague (figured in Charbonnier et al. 2013, p. 205, fig. 455) which may be interpreted as scavenged moult. This phenomenon is very common because exuviae consist of minerals and nutrients, which were not resorbed during ecdysis, but can be used as a food source by a range of animals, such as cephalopods or fishes (Tshudy et al. 1989, Hyžný et al. 2015).

Regarding brachyuran crabs from the BCB, the situation is unsatisfactory. To date, only few poorly preserved carapaces and isolated chelipeds (belonging mainly to dynomenids and necrocarcinids) were described from both nearshore and hemipelagic facies (Fritsch and Kafka 1887, **paper IV**), and about another five carapaces were detected by private collectors in the hemipelagic deposits. Between 2001 and 2017, me and my colleague Tomáš Kočí conducted several fieldworks to rocky-coast facies and obtained more than 50 claw remains, mainly isolated dactyls of dynomenid crabs, but no carapaces. This is not surprising considering that claws are more durable than carapaces which were probably broken up under high hydrodynamic energy regime. To date, only three dynomenid carapaces of *Graptocarcinus texanus* Roemer, 1887 and one necrocarcinid carapace fragment (with associated, but unrelated dynomenid manus on the same matrix slab) have been known from the nearshore deposits in the BCB (**paper IV**). Unfortunately, carapaces preserving appendages are extremely sparse amongst graptocarcinines, and so far, such preservation is known only in specimens of *Graptocarcinus urbasaensis* Van Bakel, Guinot, Corral and Artal, 2012 from the Upper Cretaceous of northern Spain (Álava and Navarra). Recently, the taphonomy potential of brachyuran crabs was studied, for example, by Stempien (2005), who focused on the comparison between the fossilization potential of brachyurans and heavier calcified mollusks in modern tidal environments.

The successful preservation of delicate exoskeletal parts depends not only on rapidness of burial, chemical breakdown and dynamic environment (physical disturbance, destructive transport) but also on characters of sediment. In general, the more carbonate in sediment the lower chance to preserve the epicuticle (the uppermost layer of the decapod cuticle), whereas in lithographic limestones and claystones its preservation potential increase (Förster 1966). The best example from the BCB is the excellently preserved cuticle of *Ferroranina* from Březno, where fine-grained clayey sediments are exposed, and together with calm palaeoenvironment allowed such beautiful preservation (**paper IX**). We must also take into account the exfoliation of cuticular surfaces which may hinder identification of the specimens because ornamentation (as well as the strength of the grooves) is used as a diagnostic character for many decapod species. If exfoliation of the outer layers occurred, the surface morphology of the exocuticle and endocuticle might be different because the ornamentation, such as tubercles or spines, strongly depends on which cuticle layers are preserved and what appear to be tubercles on the internal mould are actually casts of the pits on the lowermost cuticle layers. Also erosion can alter the appearance of the cuticle, tubercles may break off the cuticular surface and leave a seemingly smoother carapace (Hyžný and Klompmaker 2015, Klompmaker et al. 2015a). Waugh et al. (2009) also referred to the need to apply the cuticle features in taxonomic classification because the cuticle microstructure (it means structures less than 1 mm in diameter) is generally similar within genera, but in successively higher taxonomic groups, greater variance is seen within and between groups. They simultaneously called for the careful examination of multiple specimens when using cuticle morphology for taxa designation because morphological features of the cuticle change both across a single carapace and during growth of the organisms, and cuticle morphology is also different in exuviae and in carcasses.

Finally, we must take into account following phenomena when examining fossil crustacean taxa:

1. *convergence*

Certain body forms appear in crustaceans and in other arthropod groups, despite the potential for diversity, were repeatedly and independently evolved in unrelated groups (Tshudy and Sorhannus 2000). Because isolated claws, which are generally more preserveable than the remainder of the body, are the most common remains of decapod crustaceans in the fossil record (as mentioned above), convergence in major claw forms may causes problems in the taxonomic classification. Numerous isolated chelipeds with bulbous palms and slender fingers armed with acicular denticles (pectinate, comb-like claws) belonging to several unrelated decapod taxa, namely *Enoploclytia leachi* (Erymidae), *Oncopareia esocina* (Nephropidae), and *Ctenocheles fritschi* (Ctenochelidae), have been reported from the hemipelagic deposits in the BCB. Whereas *Enoploclytia* is isochelous and *Oncopareia* is moderately heterochelous, *Ctenocheles* is strongly heterochelous and among permanent burrow-dwellers the sole known genus with pectinate claws. Because of confusing taxonomy of isolated pectinate claws, ctenochelid claw remains were mostly identified as that of lobster genus *Oncopareia* for a long time (Tshudy and Sorhannus 2000, **paper II**). But this problem is not merely restricted to single pectinate claws from the BCB. Numerous scholars in the late 1800s and early 1900s described several fossil species on the basis of isolated pectinate chelipeds, and most of these specimens were misidentified at the infraorder level (Tshudy and Sorhannus 2000).

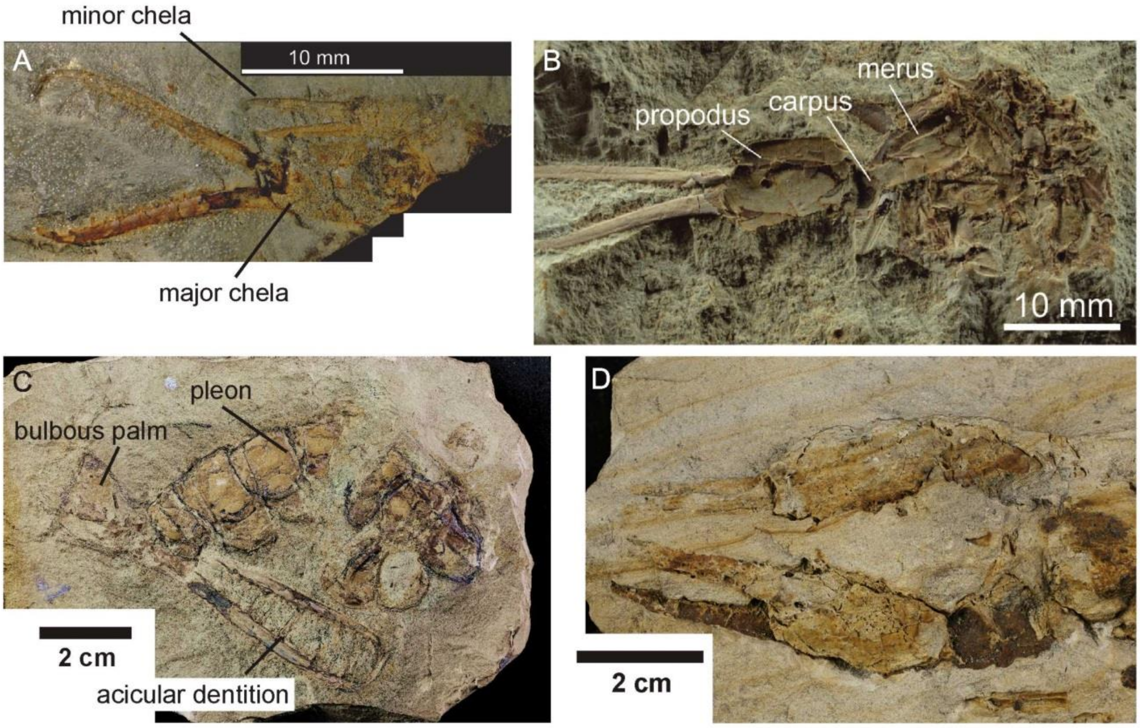

Figure 3 – Decapods with pectinate, comb-like claws. A – *Ctenocheles fritschi*, NM, originally described as *Stenocheles parvulus* Fritsch in Fritsch and Kafka, 1887. B – *Ctenocheles fritschi*, NM, nearly complete specimen. C – *Oncopareia esocina*, NM, originally described as *Stenocheles esocinus* Fritsch in Fritsch and Kafka, 1887. D – isochelous claws of *Enoploclytia leachi*, NM.

Tshudy and Sorhannus (2000) studied evolutionary trends in the occurrence of these chelipeds and discussed their various functions. They noted that close morphological similarities among these type of claws are result of the adaptation to environmental pressures (*e.g.* diet or burrow construction). Nevertheless, pectinate claws in mentioned genera from the BCB do not seem to represent adaptation to the same activity – whereas *Enoploclytia* was probably a relatively large epibenthic lobster (similar to homarine lobsters from recent environments), *Ctenocheles* was a tiny burrower (**paper II, VII**).

2. *Heterochely*

Heterochely is a condition in which the chelae of the first pereiopods, usually in lobsters and brachyurans, differ in size, shape, and often function, which usually occurs in both sexes of a species. In many decapod taxa heterochely becomes more evident in larger specimens, and is generally more obvious in males (Hartnoll 2012). Govind (1992) noted that initially, the paired claws and their closer muscles are symmetrical and both are slender but during a critical period of development, they become determined into a major (crusher) and minor (cutter) claw, and during subsequent development acquire their final form and behavior. The difference between the chelae in many crabs and lobsters is generally attributed to different functions in feeding, with the major chela operating as a crusher, and a minor chela as a cutter. The crusher is generally more heavily built, and has larger blunt teeth, adapted for breaking shells. The cutter is slender, longer, and the teeth are sharp, designed for shredding and manipulating soft tissue (Schweitzer and Feldmann 2010, Hartnoll 2012). As mentioned above, we can observe various degrees of heterochely in many crustacean taxa from the BCB: strongly heterochelous ghost shrimp *Ctenocheles fritschi*, moderately heterochelous lobsters *Paraclythia nephropica* (Fig. 4) or *Oncopareia esocina* (only a single major pectinate claw of this species is known, see fig. 3c; the minor claws of this genus have not yet been found in sediments of the BCB).

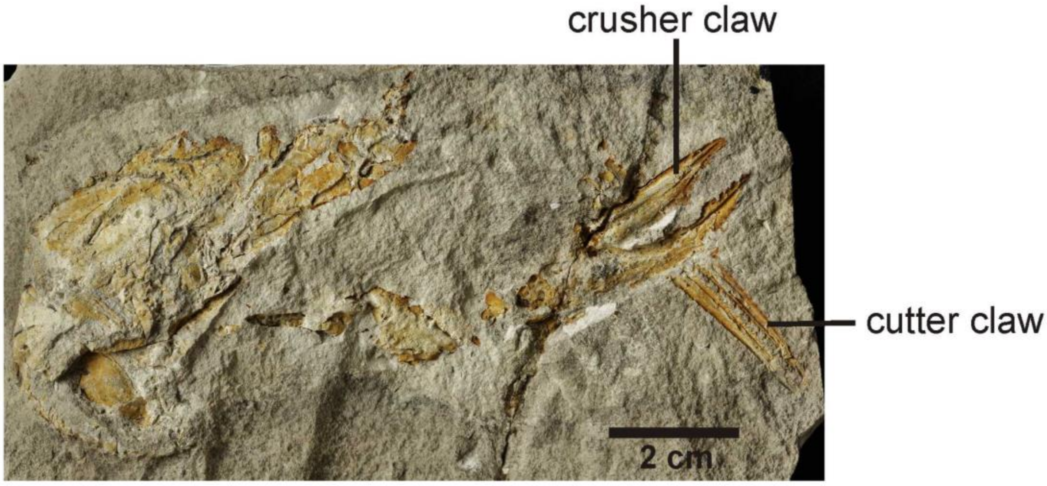

Figure 4 – Heterochelous nephropid lobster *Paraclythia nephropica* from the Lower-Middle Turonian, Bílá Hora Formation (Bílá Hora in Prague), deposited in the NM.

Sometimes heterochely does not involve a crusher and a cutter, but rather claws of differing shape or size. In these instances, the larger is called the major claw, and the smaller the minor claw (Schweitzer and Feldmann 2010). This is the reason, why we use terms „minor and major“ rather than „cutter and crusher“ claws in *Ctenocheles* (see fig. 3a). In the fossil record, the attribution of minor chelae to certain species is difficult unless they co-occur with major chelae in the same assemblage or based on morphological evidence from extant species (Hyžný and Dulai 2014, Hyžný and Klompmaker 2015). Regarding fossil decapods from the BCB, fragmentary fossil record causes difficulties especially in correct identification of heterochelous axiidean shrimps, because only heavily calcified chelipeds (mainly major chelae) are usually preserved (as mentioned above).

3. *Intraspecific variability*

Regarding the decapod crustaceans from the BCB, intraspecific variations can be observed, for example, in chelipeds of ghost shrimps. One of the most comprehensive study on this phenomenon was made by Hyžný and Klompmaker (2015). They noted that although the morphology of merus and carpus are usually quite consistent within the genus, the nature of the propodus and dactylus, especially the fixed fingers, can be variable and thus can cause major difficulties for the taxonomic interpretation of the isolated elements in the fossil record. Also growth has strong influence to the morphology of cheliped elements. Especially length / height ratios of the propodus and merus are prone to change with growth. Klompmaker et al. (2015b) observed that the propodal length / height ratios increased faster throughout growth in geologically older assemblages (suggesting possible heterochrony).

The ghost shrimp *Ctenocheles fritschi* from Březno possess a serrated ischium and an ovoid unarmed merus, but shows intraspecific variability on the length of major cheliped fingers (**paper II**) and simultaneously all studied specimens exhibit fingers to be approximately up to twice as long as the palm. Hyžný and Dulai (2014) concluded that *Ctenocheles* species cannot be distinguished from each other on the length of fingers alone and similarly, the angle of the major cheliped fixed finger to the long axis of palm is uninformative for the species identification. Nevertheless, combination of these intraspecifically variable characters (the shape of the propodus, the ratio between the length of the palm and fingers, dentition of fingers, and the angle of the fixed finger), can define the species (*e.g.* Schweitzer and Feldmann 2002).

An understanding of intra- and interspecific variations, heterochely, sexual dimorphism and ontogenetic changes of particular crustacean body parts can help placing new taxa, identifying misplaced taxa, and therefore improve the accuracy of taxon age ranges and biogeography which are ultimately the only available test of phylogenies or cladistic analyses. And thus caution must be taken when dealing with isolated crustacean remains only, especially with isolated cheliped elements, because it may lead us to the incorrect recognition of separate taxa (Hyžný and Klompmaker 2015).

Decapod crustaceans

Decapod crustaceans have an extensive fossil record that begins in the Middle Devonian (Schram et al. 1978). Although they are rarely the most abundant fossils in an assemblage, they are important elements in many marine, aquatic, and even terrestrial ecosystems. Most are opportunistic organisms, whose feeding patterns include scavenging, grazing, and predation. In addition to terrestrial and aquatic settings, modern decapods occupy nearly all marine habitats ranging from hydrothermal vent communities on the deep sea floor to intertidal and supratidal environments. Decapods are extremely rare in Paleozoic rocks, they increased in number and variety rapidly in the Mesozoic (starting from the Jurassic), and they exhibited great diversity in rocks ranging from the Eocene to the present day (Schweitzer et al. 2010). Whereas decapod diversity was still relatively low in the Triassic with the domination of lobsters and shrimps, during Jurassic decapod crustacean species and genus diversity increased markedly and a shift in dominance occurred with Anomura and especially with Brachyura which became the most diverse infraorder. The rapid diversification of true crabs coincided with a dramatic expansion of reefs in the Late Jurassic (Förster 1985, Müller et al. 2000, Krobicki and Zatoń 2008, Klompmaker et al. 2013). Moreover, Mesozoic decapods invaded variety of environments including deep waters, developed a burrowing lifestyle, and evolved durophagous predatory strategies (Förster 1985, Schweitzer and Feldmann 2010, Klompmaker 2013). Klompmaker et al. (2013) noted that the subsequent collapse of reefs near the end of the Jurassic was mirrored by a sharp drop in decapod diversity driven primarily by extinctions of numerous species of crabs. By the end of the Mesozoic, true crabs became the primary contributor to decapod diversity, a pattern that has persisted until the present time. Their adaptive radiation which led to extensive exploitation of various habitats undoubtedly lies in the compact morphology of their carapaces after progressive reduction of the abdomen (Förster 1985). In contrast to brachyurans and anomurans, lobsters and shrimps were rare in the Mesozoic reefs. A similar pattern is observed today, with the exception of the relatively abundance of shrimps in modern reefal environments (Klompmaker et al. 2013). The paucity of shrimps in sediments is caused by their low fossilization potential and collecting biases (for more about crustacean fossilization potential, see chapter *Taphonomy*).

Brief remarks on taxa re-examined in **papers II, IV, VII, IX** are given below. In addition, fossil decapod crustaceans currently under study or in the process of being published are also included.

Infraorder Astacidea Latreille, 1802

Family Nephropidae Dana, 1852 (*sensu* De Grave et al., 2009, inclusive of the former Thaumastochelidae)

Genus *Oncopareia* Bosquet, 1854

(paper in prep.)

Oncopareia Bosquet, 1854 is an extinct (Turonian–Paleocene), shelf-dwelling lobster easily identified by having short, quadrate pleura on the pleon and heterochelous chelipeds, which can be characterised as morphological analogues of the crusher and cutter claw of homarine lobsters. Cutter (catcher)-type claw exhibits short, bulbous palm and very long, slender fingers bearing acicular denticles of varying length, like those of recent *Thaumastocheles* Wood-Mason, 1874. Crusher-type claw is robustly constructed, like those of *Homarus* Weber (Mertin 1941, Tshudy and Babcock 1997, Tshudy and Sorhannus 2000, Tshudy and Saward 2012). Photos of Recent *Thaumastocheles* and *Homarus* are given in Fig. 5.

Morphologically, *Oncopareia* is considered to be the sister taxon to the extant most Indo-Pacific, deep-dwelling genera, *Thaumastocheles* (Neogene [Miocene], Chile–Recent), *Thaumastochelopsis* Bruce, 1988 (Recent) and *Dinochelus* Ahyong, Chan and Bouchet, 2010 (Paleogene [Eocene], England–Recent). All of these genera are characterized as having short, quadrate pleura and a major claw with a bulbous palm and acicular dentition. *Oncopareia* differs from these mainly in having a minor claw which is similar to crusher of *Homarus* and carapace that is laterally, not dorsoventrally, compressed (Tshudy and Saward 2012). For these reasons Tshudy and Sorhannus (2000), and Tshudy and Saward (2012) supposed that the geologically oldest known thaumastochelid genus, *Oncopareia*, is morphologically intermediate between the fossil *Hoploparia* M' Coy, 1849, which has a “mainstream” or “stem nephropid” morphology and the distinctive, recent thaumastochelids. The evolution history of this group has recently been assessed by cladistic analysis of morphological, molecular and combined data (Tshudy et al. 2007, Chan et al. 2009, Chang et al., 2017). Obtained data sources support thaumastocheliform monophyly (with the exception of *Thaumastocheles* which was recovered as paraphyletic in morphology-only analyses) and *Oncopareia* was recovered as a stem-lineage thaumastocheliform.

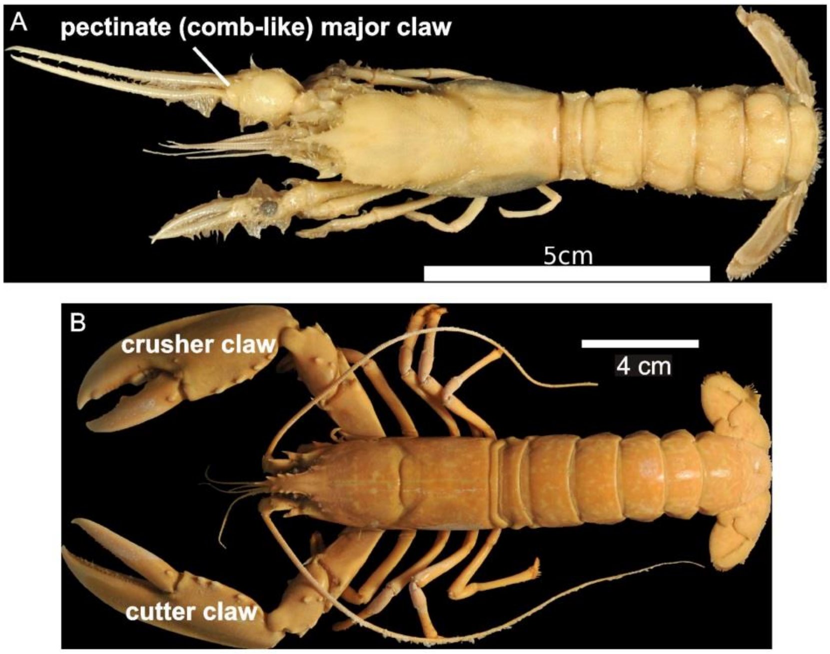

Figure 5 – Recent nepropid lobsters. A – *Thaumastocheles dochmiodon* Chan and de Saint Lauren, B – *Homarus gammarus* Linnaeus. Photographed by Dr Denis Audo, used with permission.

Oncopareia is known from shallow water deposits by five named species and 2 occurrences referred only to *Oncopareia* sp. ranging in age from the Lower-Middle Turonian and Lower Coniacian (the Czech Republic, Germany), through the Campanian (Germany, Belgium), the Upper Maastrichtian (Belgium, the Netherlands) to the Paleocene (Denmark). While the Upper Cretaceous members of thaumastocheliforms were typically inner shelf dwellers, during the Cenozoic lost shallow water environments, moved to the outer shelf and finally adapted to deeper water (continental slope) where they occur today. This led to the reduction or even complete loss of eyes in the extant, deep-water representatives. Thus, it seems clear that the thaumastochelids abandoned shelf depths in the Cenozoic Era (during the Miocene) (Tshudy and Sorhannus 2000, Tshudy 2003).

One of the oldest records of *Oncopareia* come from the BCB, where the genus is known by two species from different type of sediments and stratigraphic horizons:

O. esocina Fritsch (in Fritsch and Kafka, 1887) - Lower Coniacian, Teplice Formation, Rohatce Member at Oškobrh near Poděbrady: This species is known by a single specimen representing a pleon and associated major claw. Pleonal terga are wide and convex with lateral carina at tergum-pleuron boundary on each segment. Pectinate catcher claw with bulbous palm possesses long, slender fingers with acicular dentition. The material is flattened in fine-grained siliceous to calcareous claystones (see Fig. 3c).

O. lunata Fritsch (in Fritsch and Kafka, 1887) - Lower-Middle Turonian, Bílá Hora Formation at Bílá Hora in Prague: The species is known by a single specimen preserving part of carapace (without rostrum and anterior region) and the pleon in dorsal aspect. The thaumastochelid-like pleon with short pleura and convex pleonal terga is connected to the carapace (Fig. 6).

Figure 6 – *Oncopareia lunata* Fritsch, NM, carapace associated with pleon.

Note: The questions of close morphological similarities among pectinate (comb-like) major claws belonging to several unrelated decapod taxa as a result of the convergent evolution, and subsequent problems with their correct interpretation, are discussed in **paper II** and in the chapter *Taphonomy/convergence*).

Genus *Paraclythia* Fritsch, 1877

(paper in prep.)

The lobster genus *Paraclythia* is a rare nephropid genus, which was erected by Fritsch (in 1877) to accommodate the Upper Cretaceous carinate and spiny lobsters with the general form of recent *Nephrops* Leach. Mertin (1941) was the first, who provided a thorough treatment of the genus, described four species from the Upper Cretaceous of Europe and considered *Paraclythia* to be ancestral to recent *Nephrops*. Recently, McCobb and Hairapetian (2009) discovered another species from the Upper Cretaceous of Iran, and thus extended the previously known palaeographic range of the genus. In morphological cladistic analyses, *Paraclythia* is consistently determined to be a sister group to *Metanephrops* Jenkins, 1972; and, in turn, to *Nephrops* (Tshudy 2013). Nevertheless, molecular analyses argue that recent *Nephrops* is closer related to recent *Homarus* than to carinated, spiny *Metanephrops*. The phylogenetic relationships of *Nephrops* to other nephropid genera are thus unsettled due to conflicting results in morphological and molecular analyses (see Tshudy 2013 for discussion). Unfortunately, we cannot compare *Paraclythia* with fossil *Nephrops*, because the only known fossil *Nephrops* species, *N. kvistgaardae* Fraaije, Hansen and Hansen, 2005, is based only on single left cheliped specimen. Thus, the similarities between these two genera could be a result of the convergent evolution (Tshudy and Babcock 1997, Tshudy 2013).

Nephrops is known by a single recent and one fossil species (cheliped fragment) from the Upper Miocene, Denmark (Fraaije et al. 2005). The genus is characterised by its spiny carinate carapace with intercervical groove, with lacking of branchial carina (its absence is unique among nephropids), and moreover with long rostrum (longer that in *Metanephrops*) possessing three pairs of suprarostral spines. Chelipeds of the first pereiopods are spinose (Fig. 7a).

Metanephrops (Campanian-Recent) is the most diverse extant lobster genus, known by 18 extant and 3 extinct species. The recent species are mostly Indo-Pacific, deep-water (continental slope and deeper) dwellers (Tshudy et al. 2007, Tshudy 2013) which probably evolved in the southern latitudes, in shallow waters, and during the Lower Miocene radiated into lower latitudes, deeper setting (Jenkins 1972, Tshudy et al. 2007). *Metanephrops* strongly resembles *Paraclythia* in exhibiting three pairs of thoracic carinae, including branchial carina (absent in *Nephrops*), prominent spinose supraorbital carina extending to the postcervical groove, a long spinose rostrum, and isochelous long, slender chelipeds (Fig. 7b).

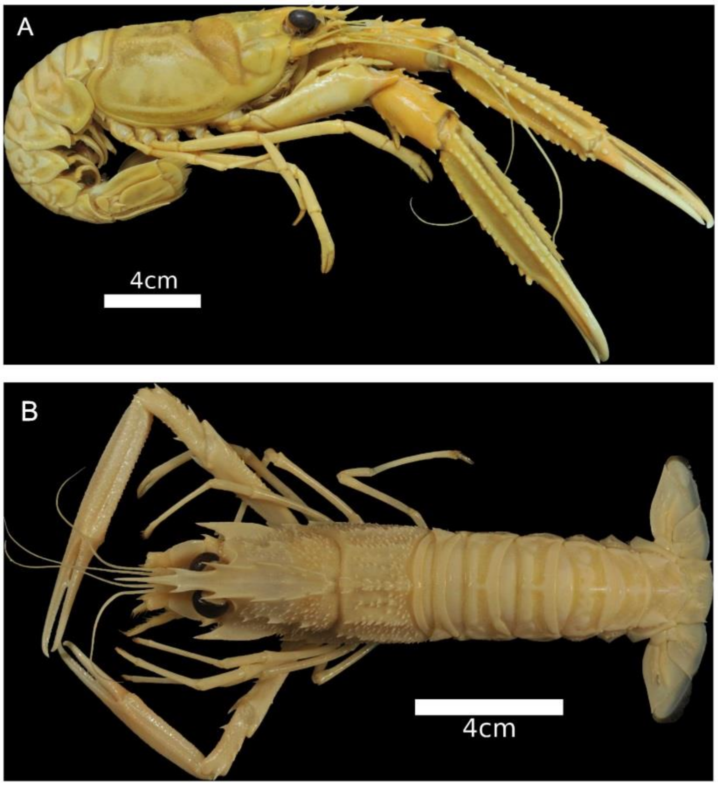

Figure 7 – Recent nephropid lobsters with carinate carapaces and carinate, spiny claws. A – *Nephrops norvegicus* (Linnaeus). B – *Metanephrops arafurensis* (de Man). Photographed by Dr Denis Audo, used with permission.

Paraclythia is known by 5 species restricted to Upper Cretaceous strata of Germany (Coniacian-Maastrichtian), the Czech Republic (Lower Turonian-Lower Coniacian, Fig. 8) and northern Iran (Campanian), where *Paraclytia* was able to spread through the shallow epicontinental sea (McCobb, Hairapetian 2009). *Paraclythia nephropica* from the Lower Turonian of Bílá Hora in Prague represents the oldest record of the genus. Regarding the morphological similarities between *Paraclythia* and *Metanephrops,* these two genera have very similar carapaces, but *Paraclythia* differs in possessing noticeably heterochelous chelipeds, which can be characterized as morphological analogues of the crusher and cutter claw of homarine lobsters, and in exhibiting a unique sculpture of the abdominal terga and pleura with deep transverse furrows and prominent longitudinal ridges (Tshudy and Babcock 1997, Tshudy et al. 2007, McCobb and Hairapetian 2009).

Figure 8 – *Paraclythia* from the Lower Coniacian at Březno, deposited in the NM.

Note: The designation *Paraclytia* Fritsch, 1887 has been largely used by several authors (*e.g.* Mertin 1941, McCobb Hairapetian 2009). Nevertheless, Karasawa et al. (2013) pointed out to incorrect spelling of this genus which was originally established by Fritsch (1877) as monotypic genus *Paraclythia* with *Paraclythia nephropica* Fritsch, 1877. Later, Zittel (1885) modified the generic name *Paraclythia* to *Paraclytia* without any reason and subsequently, Fritsch himself (in Fritsch and Kafka, 1887) adopted this generic name *Paraclytia*. Thus, although the designation *Paraclytia* is largely used, only *Paraclythia* Fritsch, 1877 is correct.

Erymida *sensu* Schram and Dixon, 2004

Family Erymidae Van Straelen, 1925

Genus *Enoploclytia* M'Coy, 1849

paper VII

The Erymidae Van Straelen, 1925 had a worldwide distribution during the Jurassic and the Cretaceous. The Lower Cretaceous erymids are reported from Europe, North America, South America, Australia, Antarctica, Madagascar and Japan, whereas the occurrences of the Upper Cretaceous erymids are almost exclusively concentrated in the northern hemisphere (Devillez et al. 2016). The only known Upper Cretaceous erymid fauna of the southern hemisphere was found in the Campanian deposits of Madagascar (Charbonnier et al. 2012).

Systematic revisions of the group show that the Lower Cretaceous erymid fauna (21 species in six genera) was currently more diversified than erymids during the Upper Cretaceous (13 species in four genera) (Devillez et al. 2016, **paper VII**). The phylogenetic position of Erymidae were much discussed recently (summary in **paper VII**). Many authors have included this family within the Astacidea Latreille, 1802 or to Glypheidea Zittel, 1885. However, results of phylogenetic analysis made by Charbonnier et al. (2015) suggest to remove Erymidae from Glypheidea. For now, the systematic position of the Erymidae is considered as uncertain (Hyžný et al. 2015) and according to Schram and Dixon (2004), we include the Erymidae in the separate clade Erymida, without listing taxonomic rank beyond superfamily (**paper VII**).

Enoploclytia with strongly calcified exoskeleton and isochelous chelipeds was probably an epibenthic lobster, similar to homarine lobsters from recent environments. The genus dominated the erymid diversity during the Upper Cretaceous by the number of its species: two of them were described from central-western Europe (Albian-Campanian), one species was reported from the Campanian of Madagascar and another one from the Campanian in Mexico, the four remaining species were found in the Maastrichtian deposits in North America. In contrast, only four species of the genus are known from the Lower Cretaceous (Devillez et al., 2016). It indicates that *Enoploclytia* has reached its higher diversity during the Late Cretaceous.

The type species, *Enoploclytia leachi* (Mantell, 1822), is known by numerous specimens from the Cenomanian to the Campanian of western and central Europe, especially from chalk formations of southeast England and hemipelagic facies of the Bohemian Cretaceous Basin. Regarding the quantity and distribution of *E. leachi* in the BCB, we may find its specimens abundantly in each stratigraphic horizon (excluding the Upper Cenomanian deposits and nearshore facies). To date, I counted more than 100 specimens coming from the Bohemian Cretaceous Basin (mainly from the Bílá Hora Formation), which are deposited in the collections of NM, MK, CGS, Institute of Geology and Palaeontology at Charles University as well as in private collections without inventary numbers. Moreover, many specimens are relatively undeformed, often near-completed, possessing even anatomical parts uncommonly preserved (abdomen, tail fan).

Infraorder Axiidea de Saint Laurent, 1979

Family Ctenochelidae Manning and Felder, 1991

Genus *Ctenocheles* Kishinouye, 1926

paper II

Ctenocheles Kishinouye, 1926 is soft-bodied heterochelous ghost shrimp exhibiting typically pectinate (comb-like) major claw and pleon distinctly longer than the carapace. Extinct and extant axiidean shrimps have been major bioturbators prefering soft siliciclastic muddy marine substrates predominantly in shallow intertidal and subtidal marine environments mainly in the tropics and subtropics (Dworschak 2000, 2005; Hyžný and Klompmaker 2015). They have elongated soft bodies with reduced integument because the burrow walls serve as a “skeletal” support and as protection from predation. Their burrow systems are complex tubular structures, extending one to five meters into the substrate, often with branches, and turn-around chambers (Bishop and Williams, 2005). Nevertheless, ghost shrimps are only rarely preserved *in situ* in burrows or in direct associated with them (e.g. Mertin 1941, Mourik et al. 2005, Hyžný 2011, Hyžný and Klompmaker 2015). This is also true for specimens from the BCB (**paper II**).

Generic fossil record spanning from the Upper Cretaceous (Cenomanian) to Recent. The fossil record of the genus consists almost exclusively of heavily calcified chelae due to the delicate nature of most ghost shrimps cuticle (see chapter *Taphonomy*). Even from extant environments only a handful of specimens are known and complete animals are rarely to be found (*e.g.* Holthuis 1967, Schweitzer and Feldmann 2001, Hyžný and Dulai 2014). Whereas the Upper Cretaceous ctenochelids are known by only three species (from Madagascar, the Netherlands, and the Czech Republic), since the Cenozoic, the genus has been widely reported from all over the world, and today, its generic distribution covers the marine part of the world except for eastern Pacific (summary in **paper II**).

As mentioned above, the interpretation of fossil material is difficult because the generic assignment of ghost shrimp remains is often hindered by their insufficient preservation (Hyžný and Klompmaker 2015) and several fossil species, such as *Ctenocheles cultellus* (Rathbun, 1935) or *C. dentatus* (Rathbun, 1935), were thus described on the basis of isolated cheliped fragments only (mainly propodi and dactyli). Nevertheless, the taxonomic identification on the basis of such elements causes numerous problems, because the shape of the propodus, the ratio between the length of the palm and fingers, dentition of fingers, and the angle of the fixed finger seem to be intraspecifically variable characters (which is usually phenomen in ghost shrimps) and only their combination can define the species (*e.g.* Schweitzer and Feldmann 2002). As concluded by Matsuzawa and Hayashi (1997), and Hyžný and Klompmaker (2015), the morphology of the ischium, merus and carpus of the major cheliped is taxonomically more important on the species level. Fortunately, a few well-preserved fossil ctenochelids are known. One of the best preserved species is *C. fritschi* Hyžný, Kočová Veselská, Dvořák, 2014 from the Lower-Middle Coniacian calcareous claystones at Březno in the BCB. This species was described on the basis of two nearly complete specimens exhibiting abdomen and both chelae, and several cheliped fragments including isolated major propodi. Due to such excellent preservation, we suppose no scavenging and/or subsequent physical disturbance for the depositional conditions, in which these ghost shrimps were preserved (**paper II**). As summarized by Hyžný and Dulai (2014), three cheliped morphotypes (based on more consistent distal elements - ischium and merus) can be distinguished in extant *Ctenocheles*; *Ctenocheles fritschi* 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 (**paper II**).

Infraorder Brachyura Latreille, 1802

Family Dynomenidae Ortmann, 1892

Genus *Graptocarcinus* Roemer, 1887

paper IV

Dynomenids are interpreted as one of the most basal brachyuran families, with an impressive record from the Upper Jurassic onwards (Van Bakel et al. 2012a). Like extant descendants, fossil dynomenids are found in reefal or non-refal deposits, with respect to modifications and adaptations of their claws. Their propodus/carpus and carpus/merus articulations have bulges, and thus there is no opening between these articles when bent (Jagt et al. 2010, Van Bakel et al. 2012a). Dynomenids are filter feeders and this modification probably protected the claws when they moved between coral colonies or during feeding, similar to extant dynomenids. Together with the possession of clumps of stiff setae at the inner and outer margins of fixed and movable fingers which close the space between both fingers, they may easily obtain food by sieving fine sediment (McLay 1999, Jagt et al. 2010). Jagt et al. (2010) also reported that these modifications are seen in all dynomenid species, but have not been observed in fossil dromiid or necrocarcinid crabs.

Unfortunately, the fossil specimens of these brachyurans consist almost exclusively of single carapaces and unassociated claws which cannot be matched with any carapace fragments. The fossil records of carapaces preserving appendages are extremely sparse amongst graptocarcinines, and so far, such preservation is known only in specimens of *Graptocarcinus urbasaensis* Van Bakel, Guinot, Corral and Artal, 2012 from the Upper Cretaceous of northern Spain (Álava and Navarra). This is the reason why these isolated chelae have been often misinterpreted and erroneously associated with carapaces of unrelated brachyuran taxa (and vice versa, necrocarcinid claws appeared invariably associated with dynomenid carapaces) throughout the Lower and Upper Cretaceous (Jagt et al. 2010). The same is true for dynomenids from the BCB. All specimens come from the high-energy environments, and thus are very rare and poorly preserved. Since 2001, during fieldworks at Velim, Kamajka, Chrtníky and Kaňk-Na Vrších, me and my colleague Tomáš Kočí collected only five dynomenid chelipeds and more than 50 isolated dactyls, but no carapaces, which were probably crushed due to high hydrodynamic energy regime. To date, only three carapaces of *Graptocarcinus texanus* and one necrocarcinid carapace fragment (with associated, but unrelated dynomenid manus on the same matrix slab) have been known from the nearshore deposits in the BCB. Thus, although these dynomenid claw remains and dactyls still not found connected with carapaces, they may be conspecific with the co-occurring, carapace-based species, *G. texanus* (**paper IV**).

Family Palaeocorystidae Lőrenthey in Lőrenthey and Beurlen, 1929

Genus *Ferroranina* Van Bakel, Guinot, Artal, Fraaije and Jagt, 2012

paper IX (submitted)

The family was extensively revised and diagnosed by Van Bakel et al. (2012b), who erected two new genera *Ferroranina* and *Joeranina*, and several new species. They also reassigned many genera previously placed within *Cretacoranina* Mertin, 1941 or *Notopocorystes* M'Coy, 1849. Depending on these new data of palaeocorystoidea, I examined a single specimen previously classified as *Cretacoranina fritschi* (Glaessner, 1929) from the Lower-Middle Coniacian clayey sediments at Březno. Interestingly, I found out that dorsal carapace of this specimen exhibits a unique set of characters which support its assignment to *Ferroranina*, rather than to *Cretacoranina* or any other palaeocorystid genus: typical fungiform and upright nodes on dorsal carapace, absence of medial carina, frontal furrows on rostrum slightly extended onto carapace, presence of distinct trilobate post-frontal terrace and medially defined cervical groove with V-shaped medial portion. All these carapace details clearly point to an identification of the material as a member of *Ferroranina* (**paper IX**).

The main interest of the present specimen lies in the fact that it constitutes one of the best preserved fossil material of *Ferroranina* (thanks to rapid burial by very fine-grained clayey sediment in calm environment, retains even cuticle) and simultaneously the sole known specimen of the genus from Europe to date. The spatial and temporal range of the genus would be marked by the *F. dichrous* (Stenzel, 1945) from the Upper Cenomanian of Texas and Mexico and *F. tamilnadu* Van Bakel, Guinot, Artal, Fraaije and Jagt, 2012 from the Middle Cenomanian of India, and its last appearance of *F. australis* (Secretan, 1964) from the Campanian of Madagascar which appears to be the youngest known member of the genus (Van Bakel et al. 2012b). Thus, the occurrence of *F. fritschi* in the Coniacian rocks of the BCB extends the geographic range and the Cretaceous diversity of the genus. Migratory patterns of the species are discussed in **paper IX**.

Cirripedes

The Cirripedia Burmeister, 1834 are marine crustaceans that as adults are usually sessile, attached to hard substrata or to other organisms by their first pair of antennas. The carapace completely envelops the body, and in most forms it secretes a calcareous shell, with an opening where they stretch out for food. The preferred habitats of modern cirripedes are widely diverse, ranging from the uppermost littoral to abyssal depths. Being principally filter feeders in the intertidal food chain, they modify the habitat structure and affect the abundance and population structure of other intertidal organisms, and are vital to the ecological balance of the nearshore marine system (Chan 2007).

Cirripedia encompasses three superorders: the conventional filter-feeding barnacles – Thoracica, the burrowing barnacles – Acrothoracica, and the parasitic barnacles – Rhizocephala. Thoracica and Acrothoracica feed by catching food particles from the surrounding seawater using their thoracic appendages (cirri) modified for grasping and rasping, while members of Rhizocephala are highly modified parasites, exclusively parasitic primarily on malacostracan crustaceans, and they are recognizable as cirripeds only by their larval stages (Newman and Abbott 1980, Glenner and Hebsgaard 2006). Because Rhizocephala are soft-bodied, they have no fossil record.

The Acrothoracica are generally very small. In the fossil record, they are recognized indirectly as ichnofossils from their borings in calcareous substrata (Tomlinson 1969). These burrowing barnacles, living permanently inside their boreholes, differ from the true barnacles (Thoracica) in having limbs situated at the end of the thorax rather than evenly distributed along it (Newman and Abbott 1980). A few specimens preserved as ichnogenus *Rogerella* de Saint-Seine, 1951 in serpulid tubes are known from the BCB.

The Thoracica (barnacles) live in virtually all marine and estuarine environments from intertidal pools to abyssal vents. They deviate from other crustaceans in being permanently and irreversibly attached suspension feeders (nonmobile adults) that have abandoned the normal arthropod growth pattern by being armed externally with mineralized plates that are never shed in molts but increase incrementally in size. They are important members of many marine habitats, such as the rocky intertidal zone (living attached on boulders or rocky bottom), and their sessile mode of life makes them the primary fouling objects on man-made structures in the sea (Southward 2008, Buckeridge 2012). Many cirripedes living in offshore and subtidal waters form intricate symbiotic associations with larger organisms such as whales, sea snakes, lobsters, medusae, corals, and sponges, which cirripedes, in earlier stages of their evolution, exploited simply for support or protection (Newman et al. 1969 in Newman and Abbott 1980).

Thoracica can be divided into two main groups: stalked (pedunculate) barnacles and sessile barnacles. Fossil representatives of both groups occur in the BCB.

1. group (Fig. 9a): In stalked (pedunculate) barnacles, the body is divided into a flexible peduncle by which the animal is attached to the substratum, and a crown of larger plates called the capitulum, containing cirri (as feeding appendages) and other organs. The peduncle

is usually armoured with large numbers of peduncular scales, and the capitulum is tall, laterally compressed and formed of two rings of plates. The upper ring comprises an unpaired carina, and paired scuta and terga. The lower ring is made up of a variable number of lateral plates, which have been classified as laterals (in contact with scuta and terga), including rostrum, rostrolaterals, carinolaterals, and in some taxa subrostra and subcarina. Whereas the homology of these plates, at least within the extant Calanticidae Zevina, 1978 and Scalpellidae Pilsbry, 1907, is well established and the pattern of overlap is consistent, the number and size of lateral plates are quite variable (Gale and Sørensen 2015a).

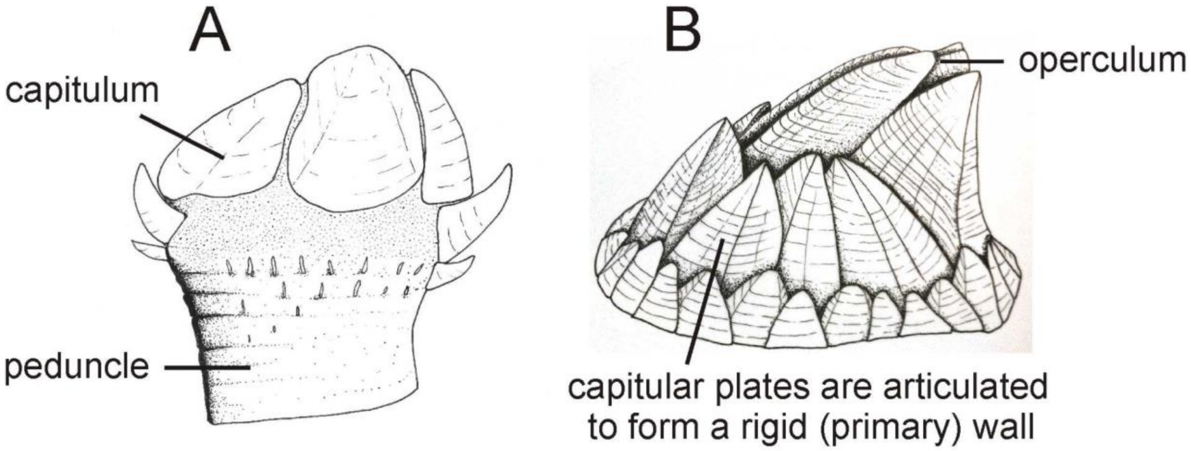

Figure 9 – Reconstruction of Thoracica. A – pedunculate scalpelliform *Myolepas reussi* Kočí, Kočová Veselská, Buckeridge, Jagt, 2016, Upper Cretaceous, Bohemian Cretaceous Basin (in **paper VI**). B – sessile neobalanoform *Waikalasma juneae* Buckeridge, 1983, Lower Miocene, New Zealand (in **paper VIII**).

2. group (Fig. 9b): In sessile barnacles (Verrucomorpha, Brachylepadomorpha, Balanomorpha) the peduncle is absent, and the capitulum is either attached directly to the substratum (*e.g.* derived balanomorphs, verrucomorphs) or elevated above it by whorls of smaller, imbricating plates (brachylepadomorphs, basal balanomorphs, basal verrucomorphs). Certain of the capitular plates became articulated to form a rigid (primary) wall; while the scuta and terga formed the movable lid or operculum. This arrangement is generally considered better adapted to shore environments, but radiation of sessile barnacles into a wide array of habitats indicates other advantages (Newman and Abbott 1980). Balanomorphs possess a primary wall made up of four to eight plates, which are thought to be homologous with the lateral plates of pedunculate cirripedes (Gale and Sørensen 2015a). In *Brachylepas*

Woodward, 1901, only the rostrum and carina are enlarged, and the gap between these is infilled by smaller plates. The homology of these plates with either lateral plates or peduncular scales of stalked cirripedes is litigious (Gale and Sørensen 2015a).

The earliest confirmed cirripede, a cyprilepadiform *Cyprilepas holmi* Wills, 1962, is Silurian in age. Its body was divided into capitulum and peduncle with a bivalved carapace, which contained little or no calcite, and found attached to the appendages of Estonian eurypterids (Schram 1982). But the evolutionary history of this group probably go further back to the early Paleozoic. In 1981, Collins and Rudkin described *Priscansermarinus barnetti* from the Middle Cambrian Burgess Shale, which has been identified as a lepadomorph cirripede. Most of the time since the Silurian, around 420 Ma, cirripedes have been represented as pedunculate forms (Buckeridge and Newman 2006). The oldest known scalpellid, *Arcuatoscalpellum* Gale, 2016, appears in the early Aptian, at approximately 125 Ma. This trend continued to the late Mesozoic, when the Cretaceous–Paleogene extinction event resulted in vacant niches that were rapidly occupied by opportunistic sessile acorn barnacles (Buckeridge 2012).

In general, the Mesozoic was the time of origins of the stalk-less condition when stalk flexibility and support off hosts and substrata was either unnecessary or a liability in the face of predators. This may be observed in sessile (acorn) barnacles, or in the Cretaceous pedunculate stramentids which retained the peduncle, albeit securely armoured and thus lost its flexibility (Newman 1987, Foster and Buckeridge 1987, Gale 2015, **papers I, VIII**). During the Paleogene, rapid radiation of cirripedes resulted in sufficient diversification for them to occupy most marine environments. That they survived both the Paleocene-Eocene Thermal Maximum and the Pleistocene glaciation is testament to their ability to rapidly adapt to opportunities (Buckeridge 2012).

The majority of cirripede material available in the BCB (including newly recovered specimens and material from old museum collections) consists of disarticulated capitular plates of scallpelid barnacles, which is the typical state of preservation for almost all Mesozoic cirripedes. On the contrary, only one specimen of sessile Balanomorpha is known from the BCB. This assemblage is very different in composition to cirripede faunas from comparable present-day environments. This can be attributed to the paucity of derived balanomorphs in the Cretaceous, during which time scalpelliforms and brachylepadid forms predominated. Today, Balanomorpha dominate intertidal and subtidal environments globally (Gale and Sørensen 2015a).

Cirripede assemblage from the BCB comprises specimens of Acrothoracia (preserved as ichnospecies *Rogerella* isp. in serpulid tubes) and Thoracica (pedunculate Scalpelliformes and sessile Brachylepadomorpha and Balanomorpha). Brief remarks on taxa re-examined in **papers I, III-VI, VIII** are listed below. In addition, fossil cirripedes currently under study (Acrothoracica) are also included.

Superorder Acrothoracica Gruvel, 1905

Although the tubes of alive and dead serpulid worms lying on the soft seafloor have been used as typical hard substrates (*sensu* Taylor and Wilson 2003) for settling by the larvae of different invertebrates, the Cretaceous fossil record of boreholes preserved in tubes of serpulid worms remains sparse compared to those in bivalves and gastropods (*e.g.* Taylor et al. 1983, Kelley 2008). The same is true for serpulids from the BCB. Regarding Acrothoracica, only ten acrothoracican non penetrative boreholes, recognized as *Rogerella* isp., have been detected in serpulid tubes of *Pyrgopolon* (*Septenaria*) cf. *tricostata* (Goldfuss) and *Placostegus velimensis* Jäger and Kočí to date. The boreholes are visible as very small elliptical slits (apertures) in the external surface of the tube. These eliptical apertures with horny knob (bourrelet) are very small, about only 1–2 mm in length (Fig. 10).

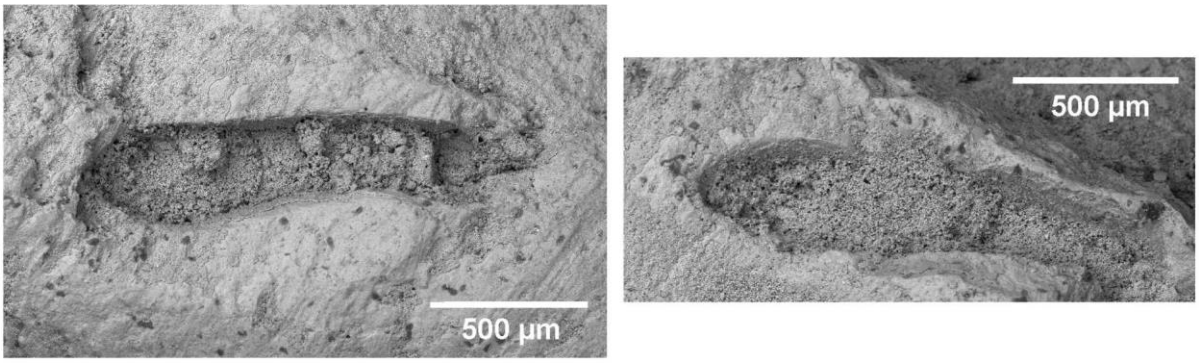

Figure 10 – Boreholes of acrothoracican cirripedes in the tube of serpulid worm *Placostegus velimensis* from rocky shore deposits (Velim).

We propose that these acrothoracicans infested the serpulids when the serpulids were still alive (in-vivo settlement; John Jagt and Tomáš Kočí, pers. com.), considering the possible commensal relationship between these animals (in accordance with Seilacher 1969). The commensal rather than parasitic relationship seems to be evident, because acrothoracicans are microfiltrators just as serpulids worms. In this case, acrothoracican cirripedes could used small rests of food during serpulid alimentation, and thus could gain another benefit in addition to skeletal support in boreholes.

Superorder Thoracica Darwin, 1854 - pedunculate barnacles

All studied pedunculate cirripedes from the BCB belong to the order Scalpelliformes Buckeridge and Newman, 2006. During the examination of these animals, two new species were erected:

Myolepas reussi Kočí, Kočová Veselská, Buckeridge, Jagt, 2016; family Myolepadidae Gale *in* Gale and Sørensen 2015b; **paper VI**

Capitulum sklenari Kočová Veselská, Kočí, Collins, Gale, 2015; family Pollicipedidae Leach, 1817; **paper V**

and numerous specimens were re-examined, and thus confirmed the occurrence of the following species in the BCB:

Titanolepas tuberculatum (Darwin, 1851); family Titanolepadidae Gale in Gale and Sørensen 2015b; **papers III, IV**

Cretiscalpellum glabrum (Roemer, 1841) and *Cretiscalpellum striatum* (Darwin, 1851); family Calanticidae Zevina, 1978; **papers III, IV**

Diotascalpellum angustatum (Geinitz, 1843); family Scalpellidae Pilsbry, 1907; **papers III, IV**

Regioscalpellum maximum (J. de C. Sowerby, 1829); family Scalpellidae Pilsbry, 1907; **papers III, IV**

Stramentum pulchellum (G.B. Sowerby jr., 1843); family Stramentidae Withers, 1920; **paper I**

Note: Gale (2016) studied the phylogeny of family Scalpellidae based on shell capitular morphology. Among others, he erected two new genera: *Diotascalpellum* to accomodate the basal scalpellines and *Regioscalpellum* includes *Arcoscalpellum maximum* group of Withers (1935). Because *Diotascalpellum angustatum* and *Regioscalpellum maximum* from the BCB were described before 2016, the generic designation "*Arcoscalpellum*" for *A. angustatum* and *A. maximum* were used in our papers.

The occurrences of *Myolepas* and *Capitulum* within the BCB are restricted to Kaňk-Na Vrších and Velim, respectively. They were typical dwellers of intertidal, high energy environments, similar to that of extant pollicipedid members of *Pollicipes* Leach, 1817 and *Capitulum* (**papers V, VI**). This assumption concurs with the observations made by Gale and Sørensen (2015b), who described the Upper Cretaceous species of the pollicipedids *Capitulum*, *Pollicipes* and the myolepadid *Myolepas* from Ivö Klack (Sweden) which are interpreted to have lived in the same way. These barnacles represented a group of short, squat pollicipedid-like forms with strongly armoured peduncles, and low, laterally flattened capitula; and thus better adapted to wave-exposed rocky shores (Gale and Sørensen 2015b). Regarding the cirripede assemblage at Kaňk-Na Vrších, the high abundance and low diversity of this group at this locality (only one taxon *Myolepas*) is similar to that of living intertidal calanticids, such as *Calantica spinosa* (Quoy and Gaimard, 1834) - see **paper VI** for more details.

Finally, the importance of *Capitulum sklenari* lies in the fact that represents the oldest record of *Capitulum*. The genus thus has encrusted rocky substrata in the intertidal and sublittoral zone, since at least the Cenomanian (**paper V**).

Although other scalpelliformes, namely *Cretiscalpellum*, *Titanolepas* and *Diotascalpellum,* were also detected in nearshore facies, we suppose them living in rather calm environments compared to *Myolepas* and *Capitulum*. They occupied the Lower Turonian deposits in pocket Václav at Velim, where is a higher distribution of these genera or the Upper Cenomanian/Lower Turonian microenvironments between larger boulders, where currents would be less turbulent. Besides, they inhabited not only wave-exposed rocky shores, but also hemipelagic facies and, for example, specimens of *Regioscalpellum maximum* are known only from hemipelagic sediments (**paper III**). Moreover, Gale and Sørensen (2015b) mentioned the occurrence of delicately constructed *Titanolepas* in deeper subtidal habitats (10-30 m water depth) of the Upper Campanian in Ivö Klack.

Stramentum was the Upper Cretaceous (Upper Cenomanian–Upper Turonian) highly derived, distinctive scalpelliform genus restricted to north-west and central Europe (Great Britain, northern Germany and the Czech Republic). Its securely armoured peduncle was covered by eight columns of strongly imbricating plates and lost its flexibility. Articulated stramentids are usually rare fossils (as well as other pedunculate cirripedes), preserved by rapid burial, or settling on ammonites or benthic bivalves (Wittler 1996, Hauschke et al. 2011, Ifrim et al. 2011, Gale 2015). All stramentids from the BCB (including even juveniles) were recorded as epizoans on shells of *Lewesiceras* or *Collignoniceras*, and thus remain articulated in the fossil record because ammonite shells provided them the protect against disarticulation during fossilization (**paper I**). Nevertheless, it is not possible to tell whether attachment took place on life, floating shells, or onto sunken shells of dead ammonites on the seafloor (Gale 2015).

Ifrim (2011) noted that the pseudoplanktonic mode of life of *Stramentum* may have been a response of a once benthic organism to repeated oxygen-deficient conditions on the seafloor of mid-Cretaceous oceans, *i.e.*, to oceanic anoxic events. Accordingly, we do not reject such life strategy in other barnacles from the BCB. However, because most of them are preserved only as disarticulated capitular plates, we remain unsure about their original substratum. Similar pseudoplanktonic lifestyle we can observe in many recent barnacles. Numerous balanids or lepadids choose to settle on living organisms, both animals and plants, and also on artificial objects. Spread via attaching to nektonic organisms confers an advantage to a barnacle in providing more propagules for establishment in a new habitat compared to natural drift of larvae, and has confused the original geographical range of several species (Southward 2008). In view of this fact, it is surprising that although species of *Stramentum* were found attached to cosmopolitan ammonites *Lewesiceras* and *Collignoniceras*, their geographical distribution is restricted only to north-east and central Europe (Gale 2015).

Interestingly, several ontogenetic stages of *Stramentum* have been identified in the fossil record. Gale (2015) described ontogenetic changes in *S. pulchellum* (in which ontogenetic changes are the best understood), *S. elegans* Hattin and also in *S. inconstans* Collins, and distinguished three distinctive stages in the development of peduncular plate rows. We can also observe varying numbers of peduncular scales amongst individuals from the BCB, including even the earliest ontogenetic stages of juvenile stramentids preserved as external moulds (**paper I**).

Superorder Thoracica Darwin, 1854 - sessile barnacles

Family Brachylepadidae Woodward, 1901

Brachylepas Woodward, 1901

paper III

Brachylepadids are sessile group of dominantly Cretaceous barnacles with two constituent genera: *Brachylepas* Woodward 1901 which is exclusive the Upper Cretaceous in age (Zullo et al. 1987) and *Pycnolepas* (Withers, 1935) ranging from the Upper Jurassic to the Miocene (Jagt et al. 2007). Both genera are identified as comprising a paraphyletic assemblage of taxa including basal sessilians, forms close to the base of the verrucomorphs, and basal balanomorphs. Brachylepadids lack a peduncle (with the exception of *Pycnolepas articulata* Collins), and the large capitular plates (rostrum, carina, 2 terga, 2 scuta, 2 upper latera) are surrounded by 3 whorls of small, imbricating plates (Newman 1987, Gale and Sørensen 2015a, **paper III, VIII**).

The fossil record of *Brachylepas fallax* (Darwin, 1851) spanning from the Turonian to the Maastrichtian of middle to northwest Europe. Numerous isolated capitular plates of this species has been recorded also from the Upper Turonian to the Lower Coniacian sediments of Úhřetická Lhota and Choceň in the BCB. Although all specimens are disarticulated, capitular plates were not displaced after decomposition of the capitula and were most likely covered by sediment immediately afterwards.

Gale and Sørensen (2015a) described the phylogeny of sessile barnacles on the basis of the morphological cladistic analysis, leading from pedunculate ancestors [*Pycnolepas articulata* from the Aptian of Antarctica which is the only known *Pycnolepas* clearly possessing a peduncle, in contrast to other, evidently non-pedunculate, *Pycnolepas* species], through the basal sessile forms [*B. naissanti* (Hebert), *B. guascoi* (Bosquet)], to taxa identified as basal balanomorphs. They noted that *Brachylepas fallax* resembles rather laterally compresed *Pycnolepas* and pedunculate calanticid *Calantica villosa* Leach than other *Brachylepas* species, in terms of overall form and plate development, retaining a tall rostrum, carina and opercular plates. They thus proposed that an extensive transition in the morphology took place between *B. fallax* and *B. naissanti*, and subsequently in basal balanoformes which led, among others, to development of a strongly imbricated, firmly articulated primary wall constructed of large, robust plates (as seen in higher balanoformes, neobalanoformes). This may indicate that

B. fallax represents the basal element of brachylepadid taxa and simultaneously stays on the basis of all sessile barnacles. Such idea may be also supported by its preservation. Whereas the rigid primary wall of neobalanoform *A. nekvasilovae* Kočí, Buckeridge and Newman, 2017 from high energy environment at Předboj retain articulated in sediment, the fossil record of all known specimens of *B. fallax* consists exclusively of disarticulated plates (Gale and Sørensen 2015a, **paper III**).

Family Chionelasmatidae Buckeridge, 1983

Archaeochionelasmus Kočí, Buckeridge and Newman, 2017

paper VIII

The exceptional fossil record of the sessile cirripede *Archaeochionelasmus nekvasilovae* from the Upper Cenomanian sediments of a nearshore/shallow water facies at Předboj near Prague plays an important role in study of sessile barnacles, because constitutes the earliest representative of the Chionelasmatidae and simultaneously the earliest known 6-plated neobalanoform barnacle to date.

Gale and Sørensen (2015a) mentioned a morphological and stratigraphical hiatus between the Cretaceous taxa which represent basal balanomorphs, and the Paleocene-present day Neobalanomorpha (= Neobalanoformes in **paper VIII**). Pérez-Losada et al. (2008, 2009, 2014) proposed that balanomorphs and verrucomorphs had diverged from the pedunculate barnacles by 147 Ma (Upper Jurassic, Tithonian) and the Neobalanomorpha (Neobalanoformes), dominant shallow water thoracicans in the Cenozoic, originated during the Upper Cretaceous (95-100 Ma). Their molecular and morphological analysis, which confirm the monophyly of sessile thoracicans (Balanomorpha and Veruccomorpha), suggest that 6-wall form is the ancestral condition with 8-wall taxa appearing as a derived state in at least four independent events. However, until now the earliest confirmed neobalanoform with IPs (whorls of basal imbricating plates) was *Chionelasma* from the Eocene (Buckeridge, 1983). The earliest known chionelasmatoid, *A. nekvasilovae*, thus supports previous assessment of the neobalanoform origin in nearshore environments during the Upper Cretaceous, albeit the extant chionelasmatines are known from bathyal-abyssal depths, including hydrothermal vents in the Indo-Western Pacific (Buckeridge 1996; Gale and Sørensen 2015a, 2015b).

A. nekvasilovae from the Upper Cenomanian nearshore facies, showing a moderately low profile similar to that of the "turtle barnacles", was supposedly attached to living substrates, such as ammonites or turtles. Although direct evidence is lacking, we suggest *A. nekvasilovae* may have lived as an obligate commensal with ammonites or marine reptiles rather than along the shore because of the absence of any other neobalanoform plates, conspecific or otherwise, at this locality (**paper VIII**). This is in contrast, for example, to the variety of forms known to have lived on hard substrates along the rocky coast at Ivö Klack (southern Sweden) during the Campanian (Withers 1935; Gale and Sørensen 2015b).

Note: The relationships of thoracican cirripedes, the discussion on the origin and phylogeny of sessile barnacles (including the process from the pedunculate ancestral stock through brachylepadomorphs leading to basal 4-plated configuration in balanoformes, 6-plated wall configuration in chionelasmatoids, and subsequently to crown group 8-plated neobalanoformes) by reduction, multiplication and reorganization of the plates have been well documented, for example, in Newman and Ross (1976) or **paper VIII**, in molecular analysis (Pérez-Losada et al. 2008, 2014; Herrera et al. 2015) and in a morphological cladistic analysis provided by Gale (2016), and Gale and Sørensen (2015a).

Conclusions

This thesis is the most comprehensive study on cirripedes and decapod crustaceans from the BCB since these groups were reviewed last (*e.g.* Withers 1935, Mertin 1941) and yields the interesting insights to our knowledge of shallow-water faunas of that time.

Major conclusions of this thesis involve (a) generic assignment of the fossil taxa and taphonomical aspects, (b) palaeoecology, (c) remarks on palaeobiogeography distribution and migratory patterns.

a) Thanks to a modern description, new species of *Ctenocheles fritschi* (axiidean shrimp) *Archaeochionelasmus nekvasilovae* (sessile barnacle), *Myolepas reussi* and *Capitulum* *sklenari* (stalked cirripedes) were erected, and numerous species were re-examined. Thus, we can confirm the occurrence of the following genera in the BCB: nephropid lobster *Oncopareia* and *Paraclythia* (papers currently under study), clawed lobster *Enoploclytia* (**paper VII**), axiidean shrimp *Ctenocheles* (**paper II**), brachyuran crabs *Graptocarcinus* and *Ferroranina* (**papers IV, IX**, respectively), sessile barnacles *Brachylepas* and *Archaeochionelasmus* (**papers III, VIII**, respectively), and stalked cirripedes belonging to the order Scalpelliformes: myolepadid *Myolepas* (**paper VI**), pollicipedid *Capitulum* (**paper V**), titanolepadid *Titanolepas* (**papers III, IV**), calanticid *Cretiscalpellum* (**papers III, IV**), scalpellids *Diotascalpellum* and *Regioscalpellum* (**papers III, IV**), and stramentid *Stramentum* (**paper I**). Moreover, ten acrothoracid non penetrative boreholes (*Rogerella* isp.) in serpulid tubes of *Pyrgopolon* (*Septenaria*) cf. *tricostata* and *Placostegus velimensis* were determined.

The essential part of the thesis is taphonomy and its bearing on the identification of fossil material. Capitular plates of pedunculate cirripede species from the BCB are heavily calcified with high preservation potential, but upon death, most thoracican cirripedes rapidly disarticulate and become scattered, similar to modern lepadids and scalpellids (Hauschke et al. 2011); and thus co-embedding of adjacent valves of pedunculate cirripedes, let alone complete shells, is relatively uncommon. It brings numerous problems in their identification and in the subsequent correct taxonomic placement in a taxonomic framework. The mode of preservation depends on many factors. Sediments of the rocky coast facies, due to the high energy of environment, have provided hundreds of isolated plates of stalked cirripedes only (**papers III–VI**). To date, only one complete sessile balanomorph *Archeochionelasmus nekvasilovae* have been known from such environment because possess heavily calcified capitular plates articulated to a rigid wall. This arrangement is generally considered better adapted to high energy conditions, and thus there is the great chance to preservation of whole capitula even in nearshore facies. Moreover, the discovery of this remarkable barnacle has been considered pivotal to our understanding of the origin of balanomorphs, because *Archaeochionelasmus* constitutes the earliest representative of the Chionelasmatidae and simultaneously the earliest known neobalanoform barnacle to date (**paper VIII**).

The successful preservation of entire capitula of stalked cirripedes depends primarily on rapid burial in fine-grained sediment without subsequent physical disturbance, as shown the exceptionaly preserved complete capitulum of *Diotascalpellum* from the Upper Turonian of Křinec (unpublished data), or near-complete stramentids (including juveniles) attached on ammonite shells which provided protection against disarticulation during fossilization (**paper I**).

The quality of preservation of fossil decapod crustaceans depends on various factors, such as the level of cuticle calcification, nature of remains (corps or moults), type of sediment and its grain size, depositional environment, type of fossilization (phosphatic, calcitic, concretions), rate of burial, and others. Regarding decapods from hemipelagic facies, fossil specimens of heavily calcified *Enoploclytia* often retain carapaces associated with chelipeds and even tail fans (**paper VII**), whereas only heavily calcified chelipeds of ghost shrimps are usually preserved due to the delicate nature of their cuticle. Nevertheless, very fine-grained clayey sediments, together with calm conditions of the sea in which they were deposited, allowed beautiful preservation even of poorly calcified exoskeleton parts. The best examples are the excellently preserved cuticle of brachyuran crab *Ferroranina*, or partially flattened, near-complete specimens of ghost shrimps *Ctenocheles fritschi* from Březno near Louny (**paper IX, II**, respectively). The importance of *C. fritschi* lies in the fact that represents one of the oldest record of *Ctenocheles* and simultaneously one of the best preserved fossil material of the genus reported to date.

On the contrary, conditions of nearshore, rocky coast facies are characterized by frequent sediment reworking where only the most robust parts of the skeleton survive (Jagt et al. 2015); and thus, during fieldworks between 2011–2017, we gathered hundreds of fragmentary remains of crab cheliped only, but no carapaces or even articulated specimens. To date, only one complete carapace and two carapace fragments have been known from rocky coast facies within the BCB (**paper IV**).

b) The palaeoecology reconstructions based on a correlation of both modern barnacle and decapod crustacean habitats with fossil situation, because many Cretaceous taxa had a similar life strategies as their modern relatives. Fossil dynomenid crabs, like their extant descendants, are found in reefal or near-reefal deposits, with respect to modifications and adaptations of their claws (Jagt et al. 2010, Van Bakel et al. 2012a, **paper IV**). Extinct and extant axiidean (ghost) shrimps have been major bioturbators prefering soft siliciclastic muddy bottoms. Specimens have elongated soft bodies with reduced integument because the burrow walls serve as a “skeletal” support and as protection from predation (Bishop and Williams 2005, **paper II**). Extinct and extant specimens of the cirripede genus *Capitulum* have been adapted to wave-exposed rocky shores and are mostly intertidal in distribution (Gale and Sørensen 2015b, **paper V**).

On the other hand, we may observe changes in habitats of many lobsters caused by migrations from shallow waters to deeper environments (due to predacy and increased competition on inner shelves). So, while the Upper Cretaceous thaumastochelids, including the Cretaceous genus *Oncopareia*, were typically inner shelf dwellers, during the Cenozoic lost shallow water environments, moved to the outer shelf, and finally adapted to deeper water (continental slope) where they occur today. This migration led to the reduction or even complete loss of eyes in extant, deep-dwelling genera *Thaumastocheles* and *Thaumastochelopsis* (Tshudy and Babcock 1997, Tshudy and Sorhannus 2000). Similar migration to deeper waters we can also observe in sessile chionelasmatid or calanticid barnacles. The extant chionelasmatines are known from bathyal-abyssal depths, including hydrothermal vents in the Indo-Western Pacific (Buckeridge 1996), albeit they are currently believed to have evolved in nearshore environments (Gale et al. 2015a, 2015b), which was also confirmed by the discovery of the earliest known chionelasmatid *Archaeochionelasmus nekvasilovae* from the Upper Cenomanian sediments of a nearshore/shallow water facies at Předboj near Prague (**paper VIII**). Analogously, Cretaceous calanticids inhabited intertidal environments (Gale and Sørensen 2015b, Gale 2016, **papers III, IV**) and Buckeridge (1983) supposed that the group became increasingly more restricted to relatively deep-water settings during the Neogene. The majority of extant representatives typically inhabit deep water (depths between 340 to >3,000 m), although *Calantica spinosa* from New Zealand was found attached to rocks and algal holdfasts in the lower intertidal.

As mentioned above, barnacles are not distributed uniformly, but they are rather zoned (Foster and Buckeridge 1987). Many papers have focused on influences to dispersion of recent barnacle larvae along coastal margins (*e.g.* Pineda and López 2002, Pfeiffer-Herbert et al. 2007) as well as on biostratigraphic zonations based on fossil barnacle assemblages (Collins and Mellen 1973, Zullo 1982). Although we may detect similar zonal stratification in the BCB, where sessile barnacle *Archaeochionelasmus*, and pedunculate cirripedes *Myolepas* and *Capitulum* were better adapted to wave-exposed rocky shores in comparison to other scalpelliformes, species are still sparse in the fossil record and to be useful as palaeoecology indicators, they need to be more abundant in the sediment. Their paucity is caused, among others, by erosive rather than depositional character of the wave-energetic littoral environment and intertidal zones, where barnacles have been most dense (Foster and Buckeridge 1987).

c) Palaeogeography distribution and migratory patterns of studied species were discussed in **papers I–IX**. Frequent migrations of marine animals during the Upper Cretaceous were possible due to the proximity of the continents to one another and the open communication among the basins during the Upper Cenomanian/Lower Turonian transgression (*e.g.* Fraaye 1996a, Feldmann and Schweitzer 2006, Vega et al. 2010). Moreover, the Bohemian Cretaceous Basin formed a narrow Seaway connecting the North Sea Basin and the Tethys Ocean, and thus the faunas of Bohemia were influenced to a varying extent both from the Boreal and Tethys through time as documented by Košťák et al. (2004), Wiese et al. (2004), Vodrážka et al. (2009) or Čech (2011). It also reflected the composition of crustacean fauna which continuously migrated through the BCB during the Upper Cretaceous. Clawed lobster *Enoploclytia*, one of the most common decapod genus in the BCB which were simultaneously very abundant in the Upper Cretaceous sediments within the whole Europe, had a worldwide distribution (**paper VII**). Many decapod genera, despite its wide geographical range during the Cretaceous, retain sporadic regarding the number of the specimens (*Ctenocheles, Ferroranina*). Whereas the Upper Cretaceous ctenochelids are known by only three species (from Madagascar, the Netherlands, and the Czech Republic), since the Cenozoic, the genus has been widely reported from all over the world, and today, its generic distribution covers the marine part of the world except for eastern Pacific (Sakai 1999a, 1999b, 2005, 2011 in **paper II**). This paucity in the fossil record is caused by taphonomical bias of ghost shrimps. Analogously, *Ferroranina* is known by three species from the Upper Cretaceous of Mexico, Texas, India and the Czech Republic. The genus could follow two different directions to Europe during the Upper Cretaceous; either eastward through the North Atlantic from Mexico or Texas, whence *F. dichrous* was described in the Upper Cenomanian sediments or westward via Tethys based on the occurrence of *F. tamilnadu* from the Middle Cenomanian of India (**paper IX**). Regarding decapod crustaceans from the BCB, both these migration ways were possible, as illustrated by the transatlantic migration of brachyuran genus *Graptocarcinus* known from the Barremian to the Upper Maastrichtian strata of Texas, Mexico, England, Spain, the Czech Republic, Italy, France and The Netherlands (Fraaye 1996b, Jagt et al. 2010, Hyžný and Kroh 2015, **paper IV**) as well as by the migratory pathway via Tethys used by lobster genus *Paraclythia* which fossil record is restricted to the Turonian-Maastrichtian strata of Germany and the Czech Republic in central Europe, and the Campanian sediments of northern Iran where *Paraclythia* was able to spread through the shallow epicontinental sea (McCobb and Hairapetian 2009).

Future study is necessary to understand fully the questions regarding crustacean fauna from the BCB. We cannot afford to rest on our laurels because only gathering a large number of new material and its correct interpretation can add more data about the true diversity of cirripedes and decapod crustaceans during the Mesozoic Era.

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Paper I

Kočová Veselská, M., Kočí, T., Buckeridge, J. 2013. A systematic revision of species *Stramentum* (*Stramentum*) *pulchellum* Sowerby, 1843 (Cirripedia, Thoracica, Stramentidae) from the Bohemian Cretaceous Basin (Czech Republic). *Acta Musei Nationalis Pragae, Series B (Historia Naturalis) 69(3-4)*, 151–158.

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A SYSTEMATIC REVISION OF *STRAMENTUM* (*STRAMENTUM*) *PULCHELLUM* (G.B. SOWERBY JR., 1843) (CIRRIPEDIA, THORACICA, STRAMENTIDAE) FROM THE BOHEMIAN CRETACEOUS BASIN, THE CZECH REPUBLIC

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Abstract. We review the single species within the genus *Stramentum* Logan, 1897, *Stramentum* (*Stramentum*) *pulchellum*, from the Lower to Upper Turonian strata in the Bohemian Cretaceous Basin (BCB). Only seven specimens are known to date; one is housed at Krupka Museum (Teplice), the others are held in the palaeontological collections of the National Museum in Prague. These specimens were first described in 1887 by Fritsch and Kafka, but have not received attention since. Despite the fact that stramentids are rare within the BCB, all individuals available are articulated and very well preserved and, without exception, belong to *S.* (*S.*) *pulchellum*. The Krupka Museum specimen differs in the shape of both the scuta and the upper latera, but this is interpreted as a result of slight disarticulation. Varying numbers of peduncular scales amongst individuals are indicative of several age groups and small, juvenile stramentids occur as external moulds in one lot at the National Museum. Most Czech stramentids have been found attached to shells of the ammonite genera *Lewesiceras* and *Collignoniceras*.

■ Cirripedia, *Stramentum*, Late Cretaceous, Lower to Upper Turonian, Bohemian Cretaceous Basin

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Introduction

Cirripede assemblages from the Bohemian Cretaceous Basin (BCB) comprise representatives of six families, Zeugmatolepadidae Newman, 2004, Calanticidae Zevina, 1978, Scalpellidae Pilsbry, 1907, Stramentidae Withers, 1920, Brachylepadidae Woodward, 1901 and Verrucidae Darwin, 1854. Dissociated capitular plates of cirripedes are relatively common in this area (see Kafka 1885; Fritsch and Kafka 1887; Kočí and Kočová Veselská 2012). In contrast, articulated specimens of the genus *Stramentum*, all collected near the end of the nineteenth century and now housed in Czech museums, are rare. All of them are well preserved and probably were epizoic on ammonite shells. The first scientists to study *Stramentum* from the BCB were Frič (1878, 1880), Kafka (1885), and Fritsch and Kafka (1887), who assigned the material to *Loricula pulchella* Sowerby, 1843 and distinguished two morphotypes, var. *gigas* Frič, 1878 and var. *minor* Frič, 1878. These authors also compiled lists of all cirripede taxa then known from the BCB, with indications of their stratigraphic and geographic provenance (Fritsch and Kafka 1887). All specimens except one are deposited in the palaeontological collections of the National Museum (Prague); a single individual is housed at Krupka Museum in northern Bohemia. Later, Withers (1920, 1935) revised the family Stramentidae Withers, 1920, distinguishing three genera: *Stramentum*, *Loriculina* Dames, 1885 and *Squama* Logan, 1897. Withers (*loc. cit.*) also mentioned stramentids from the BCB, including a single scutum of *Loriculina laevissima* (Zittel, 1885) from the out-quarried and now overgrown locality of 'Na Vinici', northeast of Kolín, an outcrop some 237 meters above sea level. Unfortunately, he did not describe or illustrate this scutum; the original (NHM 31672) forms part of the collections of the Natural History Museum, Department of Palaeontology (London). Consequently, it is uncertain whether this scutum really belongs to *Loriculina*. Frič (1878) and Fritsch and Kafka (1887) neither recorded nor described any dissociated plates of *Loriculina*. Recent authors (Jagt and Collins 1989; Hauschke 1994; Hauschke et al. 2011; Ifrim et al. 2011; Schöllmann and Hauschke 2012), have also referred to stramentids from the BCB, but have not discussed these in any detail. *Stramentum* from the area was mentioned briefly by Kočová Veselská and Kočí (2012).

Stratigraphic and geographic setting

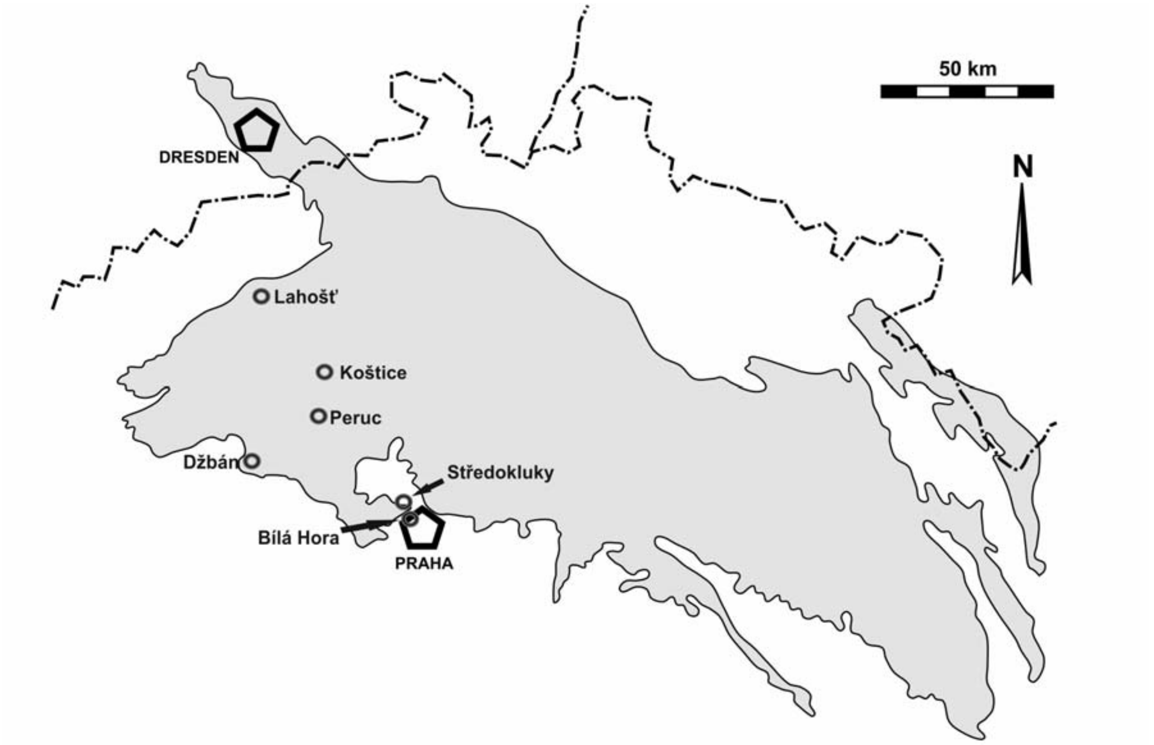
The exact provenance of *Stramentum* in the BCB is problematic, because all material known to date comprises old museum collections. In addition, some of the localities that yielded stramentids have long been excavated, eroded or are inaccessible. In all, eight specimens of *Stramentum* are available from six localities within the area (see text-fig. 1). Five of these originate from the Lower-Middle Turonian (Bílá Hora Formation, *Mytiloides labiatus/Mytiloides hercynicus* Zone) at Bílá Hora in Prague (now overgrown quarries), Středokluky (now overgrown outcrops), Peruc vicinity near Louny (one of several overgrown quarries) and probably an old disused quarry in the Džbán Plateau (Hředle vicinity near Rakovník; see below). Three others are from the Upper Turonian (Teplice Formation, *Mytiloides labiatoidiformis*/*striatoconcentricus*-*Cremnoceramus erectus* Zone) at Koštice and Lahošť. All localities are situated in the western part of the basin and the strata exposed mainly reflect shallow-water marine (hemipelagic) settings.

Although it is not known precisely from what lithologic horizons stramentids originate, it is very likely that they were epizoic on shells of the ammonites *Collignoniceras woollgari* and *Lewesiceras peramplum*. The former ammonite species helps date stramentids because its first appearance datum (FAD) is at the Lower-Middle Turonian boundary. *Lewesiceras peramplum* may occur first in the uppermost Cenomanian, as based on putative records from the Dölzschen Formation in Saxony, eastern Germany (Wilmsen and Nagm 2013). Otherwise, this species is common in the Lower to lower Upper Turonian of Germany, the Czech Republic, Poland, France, Tunisia and Morocco (see Wright and Kennedy 1981).

The Bílá Hora Formation consists mainly of shallow-water marine marlstones. Glauconite occurs in horizons at both the base and in the upper part of the formation. Typical of most rocks of this unit is the high admixture of sponge spicules; spongilites are commonly present. In the western and northern ranges of the BCB, the formation is developed as quartzose sandstones. Along the southern margin of the basin, a surf facies, consisting of conglomerates and biomicritic and biosparitic limestones, is developed. Across most of the BCB, strata assigned to this formation show coarsening-up cycles (for summary see Čech et al. 1980).

The locality of Bílá Hora was Frič's standard section, where "marlite" (calcareous marlstone) was quarried. From here, Frič (1878, 1880) described inoceramids (*Mytiloides labiatus*, *M. hercynicus*), ammonites (*Mammites nodosoides*, *Collignoniceras woollgari*), echinoids (*Epiaster michelini*), decapod crustaceans (*Enoploclytia leachi*, *Glyphea bohemica*, *Paraclytia nephropica*, species of *Hoploparia* and *Thalassinoides* burrows) and other biotic groups.

Frič's (1878) original sample of *Stramentum*, which comprises juveniles only, was collected from the Lower-Middle Turonian sediments of an old overgrown quarry in the Džbán Plateau (its precise geographical position is unknown). These juveniles are preserved as external moulds on a shell of the ammonite *Collignoniceras woollgari* Mantell, 1822. Unfortunately, the original specimen and its label have been replaced by other juveniles, in the same state of preservation, but from an unknown locality. However the nature of the matrix suggests that these have come from similar horizons; in all probability, they were recovered from the same locality as the misplaced (lost) original. Strata at the Džbán Plateau comprise mainly silty, sandy marlstones, spongilitic



Text-fig. 1. Simplified map of the Bohemian Cretaceous Basin (grey) showing the occurrence of *Stramentum* (*Stramentum*) *pulchellum* (G. B. Sowerby jr., 1843).

sandstones and siltstones with spongilite cavities (15– 20 cm in diameter) with an abundant molluscan fauna containing bivalves e.g. *Mytiloides labiatus* (Schlotheim) and ammonites, e.g. *Mammites nodosoides* (Schlotheim). A diverse assemblage, dominated by *Protocallianassa bohemica* (Fritsch), occurs in the upper part of the spongilitic sandstone (Váně 1999; Svoboda 2003).

The lower part of the Teplice Formation is characterized by shallow-water, marine biomicritic limestones. Calcareous claystones to marlstones, with limestone intercalations occur higher in the sequence. This formation differs from both underlying and overlying units in comprising fewer psammitic sediments. At the base of Teplice Formation, a 'coprolite layer' is developed, with a high glauconite content, phosphatic nodules, casts of shells and coprolites (Čech et al. 1980). Macrofossils from this unit include mainly inoceramids (*Inoceramus costellatus*, *I. cuvieri*), ammonites (*Lewesiceras peramplum*, *Scaphites geinitzii*, *Helicoceras reussianum*, *Baculites undulatus*), gastropods (*Natica*, *Pleurotomaria*, *Turbo*), non-inoceramid bivalves (*Isocardia cretacea*, *Cardium bipartitum*, *Nucula semilunaris*, *Syncyclonema nilsoni, Spondylus spinosus*) and other groups.

Two stramentids are known from the Teplice Formation at Koštice (GPS co-ordinates: 50°23'59.680"N, 13°57'47. 190"E) and Lahošť (GPS co-ordinates: 50°37'52.999"N, 13°45'50.894"E) in the northwest of the basin. At Koštice exposures are mainly of clayey limestones and calcareous marlstones; at present this locality is covered by scree and is much overgrown. Koštice is the site of Frič's sample locality and is now referred to as the Teplice Formation. Accumulations of comminuted mollusc and ostracod shells, vertebrate bones and large benthic foraminifera known as 'Koštice plates' occur at the base of this formation. Below this and close to the surface of the River Ohře, a coprolite bed occurs. Above the 'Koštice plates' horizon, is a compact horizon of clayey limestones also known as 'Hundorf limestone' with ammonites (*Lewesiceras peramplum*) or their body chambers (Váně 1999). From these, Frič (1889a, 1889b) described a specimen of *Stramentum* (*S.*) *pulchellum*.

Outcrops at Lahošť near Teplice expose very compact quartzites at the base with glauconitic sandstones above. The upper part has clayey and calcareous marlstones, which yield most of the fauna, and probably is the source of a single individual of *Stramentum*.

Methods

All stramentids known from the BCB were examined. Ammonium chloride sublimate was used, hoping to achieve a higher contrast when photographing the specimens from the collections of the National Museum in Prague (NM). However, with the exception of NM O3449, the results were not satisfactory. Photographs of NM O3448 and NM O3449 were taken using the microphotography setting Olympus DP70 and photographs of additional material deposited in NM (O3445 – O3447 and O7132) were taken using the microphotography setting Keyence VHX-2000. Specimen PA 1476 was photographed by museum curator Miroslav Radoň from Krupka Museum where material is deposited. Plates were made using Corel Graphic Suite X4.

Systematic palaeontology

In terminology and taxonomy, we follow Fritsch and Kafka (1887), Logan (1897), Withers (1920, 1935), Hattin (1977), Stevenson (1979), Collins (1986), Breton and Boiné (1993), Hauschke (1994), Hauschke et al. (2011) and Wittler (1996).

Subclass **Cirripedia Burmeister, 1834**

Superorder **Thoracica Darwin, 1854**

Order **Scalpelliformes Buckeridge et Newman, 2006**

Family **Stramentidae Withers, 1920**

Genus and subgenus ***Stramentum*** **Logan, 1897**

Type species. *Pollicipes haworthi* Williston, 1897; Late Santonian of Kansas.

***Stramentum* (*Stramentum*) *pulchellum* (G.B. Sowerby jr., 1843)**

Pl. 1, figs 1–9

1843 *Loricula pulchella*; G. B. Sowerby jr., p. 260.
1851 *Loricula pulchella*; Darwin, p. 81.
1878 *Loricula gigas* Fr.; Frič, p. 147.
1880 *Loricula gigas* Fr.; Frič, p. 137.
1885 *Loricula gigas* Frič; Kafka, p. 21, pl. 3, fig. 5.
1886 *Loricula gigas* Frič.; Kafka, p. 573.
1887 *Loricula pulchella*, Sow.; Fritsch and Kafka, p. 1 (including var. *minor* and var. *gigas*).
1889a *Loricula pulchella*, Sow. var. *gigas*, Fr.; Frič, p. 96.
1889b *Loricula pulchella*, Sow. var. *gigas*, Fr; Frič, p. 90.
1920 *Stramentum pulchellum*, G. B. Sowerby, jun., sp.; Withers, p. 70.
1935 *Stramentum pulchellum* (G. B. Sowerby, jun.); Withers, p. 316.
1977 *Stramentum pulchellum* (Sowerby); Hattin, p. 812.
1986 *S. pulchellum* (G. B. Sowerby jr); Collins, p. 130.
1989 *Stramentum pulchellum* (Sowerby); Oekentorp, p. 134, pl. 1, fig. 1; pl. 2, figs. 3– 4; pl. 4, figs. 1, 4.
1993 *Stramentum pulchellum* (G.B. Sowerby jun., 1843); Breton and Boiné, p. 20.
1994 *Stramentum* (*Stramentum*) *pulchellum* (Sowerby); Hauschke, p. 15, pls. 1– 5.
1996 *Stramentum (S.) pulchellum* (Sowerby 1843); Wittler, p. 94.
2011 *Stramentum* (*Stramentum*) *pulchellum* (Sowerby, 1843); Ifrim et al., p. 527.
2011 *Stramentum* (*Stramentum*) *pulchellum* (Sowerby); Hauschke et al., p. 202, figs. 3– 5.
2012 *Stramentum* (*Stramentum*) *pulchellum* (Sowerby); Schöllmann and Hauschke, p. 64, fig. 5; taf. 1, figs. 1– 7.

Holotype. A specimen from the Turonian (Upper Chalk) at Rochester, England; described and illustrated by G. B. Sowerby jr. (1843); in the collections of the Natural History Museum (London), registration number NHM 59150.

Material. A total of eight specimens; NM O3445 – O3449, NM O4255 and NM O7132 in the palaeontological collections of the National Museum (Prague) and PA 1476 at Krupka Museum. With the exception of NM O3448, NM O7132 and PA 1476, these represent Fritsch's (1877) and Fritsch and Kafka's (1887) originals. NM O3445 – O3447, NM O3449, NM O4255 and NM O7132 were recorded as epizoans on shells of *Lewesiceras* or *Collignoniceras*. The original substrate of NM O3448 and PA 1476 is uncertain. All ontogenetic stages, from juvenile to adult, are presented and all individuals are (semi-) articulated.

Distribution. Cenomanian of England, France and northwest Germany; Turonian of northern Ireland, England, northwest Germany and the Czech Republic; Coniacian of Mexico; ?lower Campanian of northern Germany (Jagt 2013). For summaries of geographical and stratigraphical distribution, reference is made to Hauschke (1994), Nomura et al. (2009), Ifrim et al. (2011), Hauschke et al. (2011) and Schöllmann and Hauschke (2012). Specimens from the BCB originate from the Lower-Upper Turonian, as follows: Lower to Middle Turonian (Bílá Hora, Prague: NM O3446, NM O3447; Středokluky: NM O3449; Peruc vicinity NM O7132; Džbán: NM O3448, see below), Upper Turonian (Koštice: NM O3445, with negative imprint NM O4255; Lahošť: PA 1476).

Diagnosis. Tergum triangular with growth lines sharply upturned (near occludent margin); scutum triangular with umbo removed from apex by between one quarter to one third the length of the plate; ventro-apical (occludent) margin straight or gently convex; carinolatus with growth lines sharply upturned along tergal margin; upper latus triangular; peduncular plates arranged in eight vertical imbricating rows: six broad rows aligned beneath and of about the same width as the carinolatera, upper latera and scuta; two narrower rows aligned beneath the carina and rostrum; rostrum is not preserved.

Description. All specimens conform broadly to the species; PA 1476 differs slightly in scutal and upper lateral outline. Individuals expose external surfaces of capitular and peduncular plates, representing either left-hand (NM O3445, NM O3446) or right-hand sides (NM O3447 – O3449, NM O7132, PA 1476). NM O4255 represents an internal mould of NM O3445. Rostrum not preserved (it may seem that a rostral fragment is preserved in NM O7132, but a small piece placed on the connection of the occludent and basal margin is only a broken part of a scutum).

Capitulum about one third length of peduncle. Scutum subtriangular with convex occludent margin, growth-lines sub-parallel to basal margin, then sharply upcurving to parallel upper lateral margin; scutal umbo removed from apex by about one quarter to a third the length of occludent margin. Upper latus almost isosceles-triangular in outline, length comparable to scutum; growth-lines parallel to basal margin. Tergum broadly triangular with acute occludent-upper lateral angle, carinolateral margin straight to slightly convex, apex acute and level with that of carinolatus; growth-lines parallel upper lateral margin, but upturn sharply to run sub-parallel to occludent margin; basal angle of tergum extends to just above the capitulum-peduncle boundary. Carinolatus obliquely triangular with growth lines parallel to a straight or gently convex basal margin. Carina narrow and long triangular slightly convex with length comparable to carinolatus.

Peduncle. Heavily calcified, joining capitulum obliquely and sloping gradually towards rostral side, widest at one third of length (measured from base of capitulum) narrowing towards base and capitulum, with size of single plates decreasing. Arranged with three broad vertical rows aligned with paired scuta, upper latera and carinolatera and two narrower, unpaired outer rows (rostral and carinal). All plates with fine growth lines parallel to plate outline; plates of scutal, upper lateral and carinolateral columns of similar size, becoming narrower, towards both capitulum and the base. Shape of scutal and carinolateral columns broadly sub-trapezoidal, straight or gently convex on rostral and carinal sides, plates of upper lateral column broadly sub-hexangular with convex upper margin and concave lower margin (more markedly than in adjacent columns), plates narrower just below capitulum and with near-straight upper margins; width about four times height. Carinal plates almost quadrangular, slightly higher than wide and slightly less than four times width of corresponding plates in adjacent column. Plates of rostral column rather subtrapezoidal; of similar size to carinal row, but broader in width; towards base, plates become narrower and scutal margin straightens. Outer plates overlap neighboring inner plates; row of plates corresponding to upper latus overlapped from both sides. Within each row, overlapping occurs from base to top. Basal plates of peduncle not preserved.

Lot NM O3445 contains two specimens, the upper one preserving only scutum, upper latus and a deformed tergum; occludent margin in both capitula straight, peduncle is almost complete, lacking solely lower part of carinal column, lower specimen lacks rostrum, carina and lower half of peduncle, uppermost plates of carinolateral and scutal columns are sub-hexangular as in upper lateral column; plates of rostral column have convex upper margins and heavier growth lines.

NM O3446 has a fragmentary part of the right-hand side scutum exposed; tergum longer than carinolatus and carina and tergum exceeding both; plates in rostral column about twice width of those in carinal column; peduncle almost complete, lacking only lowest part of each column.

NM O3447 lacks rostrum, carina and apex of a rounded and deformed tergum, occludent margin straight; three main columns of peduncle complete, rostral column and most of carinal column not preserved.

Lot NM O3448 represents some juvenile individuals as external moulds; very small juveniles have about 6-8 plates in peduncular columns, most of them preserved only as fragments of capitulum or peduncle; a single specimen almost complete, capitulum without carina and rostrum and peduncle with three main columns (scutal, upper lateral, carinolateral) corresponding to description above; occludent margin of capitulum straight.

NM O3449 capitulum incomplete (rostrum, scutum and rostral and scutal column of peduncle lost); scutal margin of upper latus broken; remaining part of occludent margin straight, only upper lateral, carinolateral and carinal columns preserved, all lacking lower parts; size and shape of two main columns similar, upper plates narrowest; towards base, plates of carinolateral column rather broadly subtrapezoidal as in other specimens, lower plates of carinal column with spurs on both sides and with convex upper and lower margins (rhomboidal outline), connection of upper lateral and carinolateral columns disarticulated; slight deformation displaced upper lateral margin towards carinolateral row.

Lot PA 1476 comprises two specimens, the upper (smaller and younger) lacking rostrum, tergum and upper parts of scutum and upper latus; peduncle almost complete, lacking only lower part; rostral column disarticulated; the lower specimen (larger and more mature) lacking only rostrum and apex of tergum; specimen retaining part of second scutum from left-hand side as in NM O3446; scutum and upper latus slightly deformed, scutum with strongly convex upper lateral margin (*vs* straight in other specimens) and outline less rounded-triangular and upper latus with concave scutal margin. This results from slight disarticulation of some peduncular plates (N. Hauschke, pers. comm., 2012). Occludent margin convex (because of lack of uppermost part of tergum and almost rounded scutum), upper lateral and rostral columns nearly complete, only few plates of carinal column and upper half of carinolateral and scutal columns present; upper and lower margins of scutal and carinolateral plates almost straight, towards base, plates of rostral column rhomboidal (with spur on both sides) rather than subtrapezoidal.

Remarks. All material, collected near the end of the nineteenth century, is articulated or semi-articulated (e.g., PA 1476) and well preserved. NM O3445 (and counterpart NM O4255), NM O3446, NM O3447, NM O3449 and NM O7132 were found as epizoans of body chambers of ammonite shells. We are not certain about the original substrate of NM O3448 and PA 1476. NM O3448, which represents external moulds of juvenile individuals and was recorded by Fritsch and Kafka (1887) as an epizoan of *Collignoniceras woollgari*. As noted, the original has been replaced with other juveniles in a similar state of preservation. Fritsch's original stems from the Lower-Middle Turonian calcareous marlstones from a defunct quarry in the Džbán Plateau; he differentiated three growth stages – on the basis of the number of peduncular plates; all individuals have four capitular plates preserved: scutum, upper latus, tergum and carinolatus. NM O3448 also comprises juveniles, but unfortunately, information on either the substrate or provenance area is lacking, but we assume them to have come from Džbán as well. One of the juveniles is nearly complete, having four capitular plates and 6-8 plates in each peduncular column. Others also have four capitular plates, but due to their fragmentary preservation it is impossible to distinguish growth stages. It cannot be determined whether specimens in lot NM O3448 were attached or not, but in view of the good state of preservation, it is most likely that these juveniles were also attached to some shell. A similar case is PA 1476, which also comprises two well-preserved stramentids, although it is not clear what were originally attached to. Only small pieces of matrix survive with these collections.

Fritsch and Kafka (1887) described two varieties of *Stramentum pulchellum* from the BCB, namely *minor* and *gigas*, on the basis of differences in peduncular plates and overall body size. Var. *gigas* was recorded to have pointed plates in the carinal column (reflecting rapid growth of the body), with plates of the carinolateral and scutal columns broadly subtrapezoidal and produced into a spur on the upper lateral sides, and plates of the upper lateral column equally developed on the upper lateral and scutal sides and all plates of the three main columns have rounded margins. However, these features are typical of all Czech stramentids. Individuals of var. *gigas* are also larger, reflecting older age and these have a greater number of peduncular plates. Fritsch's var. *minor* comprised six specimens of 15 to 20 mm in size, all from the Lower-Middle Turonian; unfortunately, only three of these survive (NM O3446, NM O3447 and NM O3449). NM O3446 was described as an epizoan of the body chamber of a juvenile *Lewesiceras peramplum*; it is the largest and best preserved of individuals of var. *minor.* The substrate of NM O3447 was *Collignoniceras woollgari*, while the deformed NM O3449 was fixed on *L. peramplum*. All individuals are from the Lower-Middle Turonian. NM O3445 comprises two stramentids, originally described by Fritsch and Kafka (1887) as var. *gigas*, as epizoans on the body chamber of a large *L. peramplum*. PA 1476 is of the Upper Turonian age. In short, any preferred orientation and position of attached stramentids cannot be recognised, contrary to other Cretaceous stramentids described by Breton and Boiné (1993), Hauschke (1994), Wittler (1996), Hauschke et al. (2011), Ifrim et al. (2011) and Schöllmann and Hauschke (2012).

Finally, it should be stressed that the figures and animal restorations (drawings) presented in works by Fritsch (notably in Fritsch and Kafka 1887) often do not fully correspond with the original specimens (pers. obs. MKV, TK) as in many cases his reconstructions are idealised. This is especially true for stramentids NM O3446 (figured in Fritsch and Kafka 1887: pl. 1, fig. 2) or NM O3449 (figured in Fritsch and Kafka 1887: pl. 1, fig. 4). Thus, caution must be taken when dealing with Frič's taxa on the basis of published figures only.

Palaeoecology and taphonomy

Stalked barnacles, a highly successful group of crustaceans, most often occur in the fossil record as dissociated plates of capitulum and peduncle, because soon after death plates tend to disarticulate and become scattered, similar to modern lepadids and scalpellids (Hauschke et al. 2011). The Cretaceous genus *Stramentum* provides some notable exceptions, because under certain conditions, individual plates of heavily calcified stramentids have remained articulated during fossilisation. Unfortunately, finds of articulated stramentids are rather rare and their occurrence appears to be restricted to three exceptional circumstances: when their cypris larvae attached directly to a substrate (e. g. ammonite shells); when cirripedes were embedded in black shales; or when cirripedes were rapidly buried. Examples of completely articulated stramentids, often in groups, on shells of ammonites or inoceramid bivalves, are commoner than finds from anoxic settings exemplified by black shales. Attachment was by the uncalcified basal part of the peduncle. In the majority of cases, attachment occured on live ammonites, and a few generations are occasionally represented (Ifrim et al. 2011). Stramentids appear to have preferred rather smooth planispiral ammonite morphotypes with widely spaced, shallow ribs, such as members of the genera *Collignoniceras*

Breistroffer, 1947 and *Lewesiceras* Spath, 1939. However, there is a single case of attachment to heteromorph ammonites of the genus *Sciponoceras* Hyatt, 1894 from northwest Germany (Hauschke et al. 2011). Schöllmann and Hauschke (2012: table 1) presented a highly detailed picture of palaeoecological and palaeogeographical relationships and of preservational and taphonomical implications of *Stramentum*.

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Explanations of the plate

PLATE 1

***Stramentum* (*Stramentum*) *pulchellum* (G. B. Sowerby jr., 1843)**

1, 2. NM O3446 from the Lower-Middle Turonian, Bílá Hora (Prague); nearly complete specimen and detail of capitulum, respectively. Frič's original (figured in Fritsch and Kafka 1887: pl. 1, fig. 2). Explanation of names of capitular plates: c = carina, cl = carinolatus, t = tergum, ul = upper latus, sc = scutum. Scale bars 2 mm.

3. NM O3447 from the Lower-Middle Turonian, Bílá Hora (Prague). Frič's original (figured in Fritsch and Kafka 1887: pl. 1, fig. 3). Scale bar 2 mm.

4, 5. NM O3449 from the Lower-Middle Turonian, Středokluky; fragmentary specimen and detail of capitulum, respectively. Frič's original (figured in Fritsch and Kafka 1887: pl. 1, fig. 4). Scale bars 2 mm.

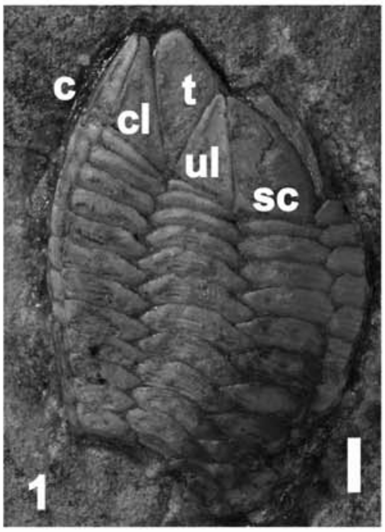
6. NM O7132 from the Lower-Middle Turonian, Peruc vicinity (one of several overgrown outcrops), collected by Mr. Daneš. Scale bar 2 mm.

7. NM O3445 from the Upper Turonian, Koštice. Frič's original (figured in Fritsch and Kafka 1887: pl. 1, fig. 1). Scale bar 1 cm.

8. PA 1476 from the Upper Turonian, Lahošť, which is deposited in Krupka Museum (North Bohemia). Scale bar 1 cm.

9. NM O3448, external mould of juvenile specimens from the Lower-Middle Turonian, old overgrown quarry in the Džbán Plateau. Scale bar 5 mm.

PLATE 1



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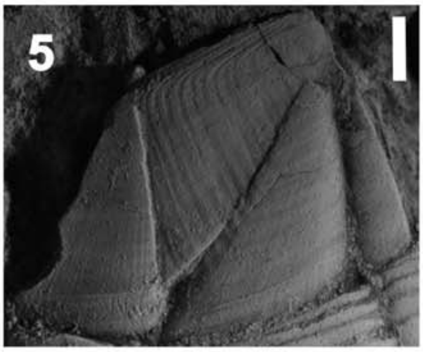

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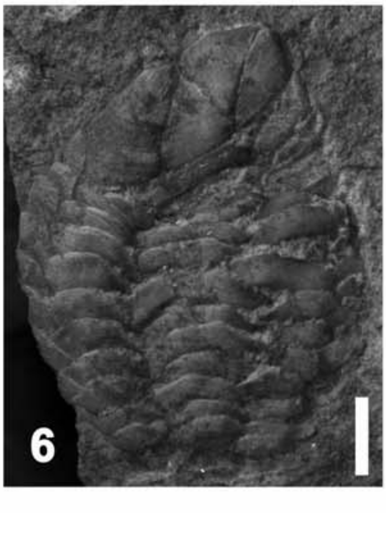

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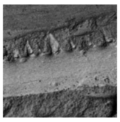
Paper II

Hyžný, M., Kočová Veselská, M., Dvořák, P. 2014. On the occurrence of *Ctenocheles* (Decapoda: Axiidea: Ctenochelidae) in the Bohemian Cretaceous Basin including a description of a new species. *Bulletin of Geosciences 89*, 245–256.

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

MATÚŠ HYŽNÝ, MARTINA KOČOVÁ VESELSKÁ & PAVEL DVOŘÁK



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.*

HYŽNÝ, M., KOČOVÁ VESELSKÁ, M. & DVOŘÁK, P. 2014. On the occurrence of *Ctenocheles* (Decapoda, Axiidea, Ctenochelidae) in the Bohemian Cretaceous Basin. *Bulletin of Geosciences 89(2)*, 245–256 (6 figures, 1 table). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received February 21, 2013; accepted in revised form February 3, 2014; published online xxxx xx, 2014; issued xxxxx xx, 2014.

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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.

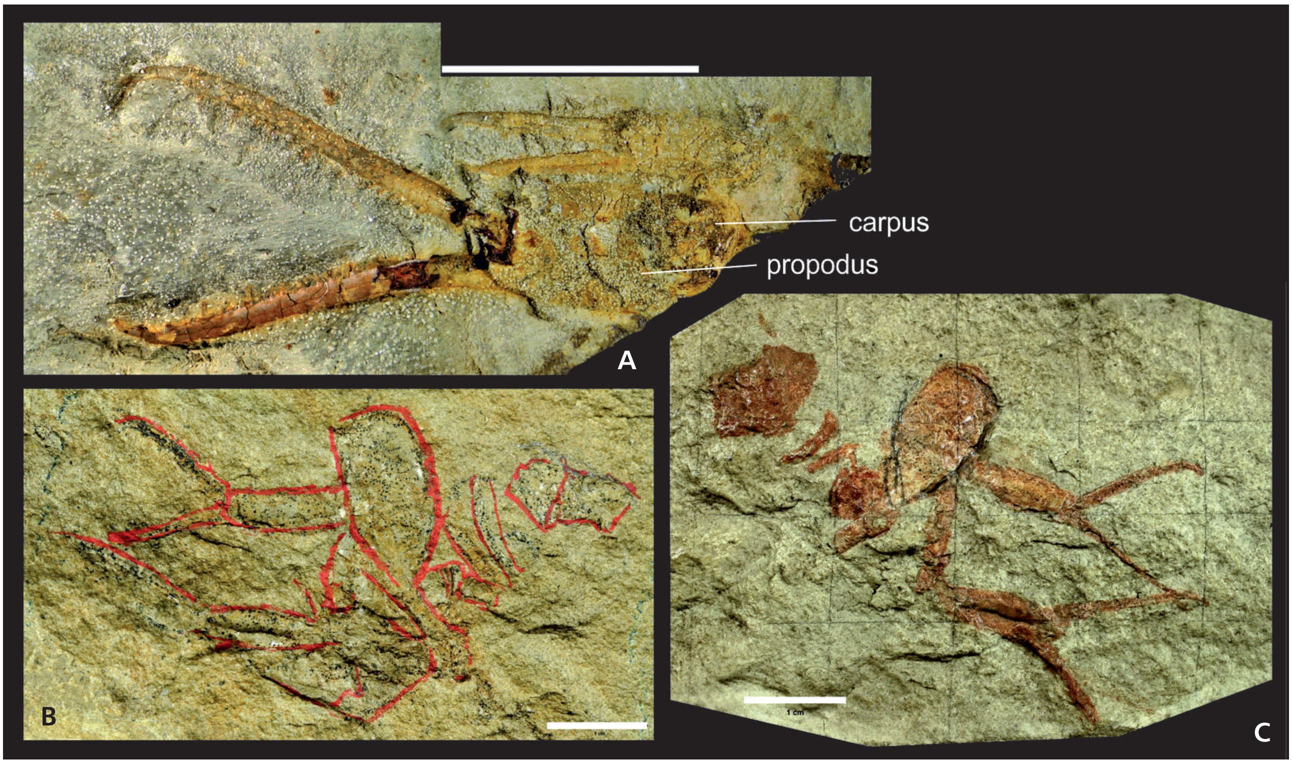


Figure 1. A – the holotype of *Ctenocheles fritschi* sp. nov. (NM O3456) originally described as one of the specimens of *Stenocheles parvulus* Fritsch *in* Fritsch & Kafka, 1887 (figured in Fritsch & Kafka 1887, pl. 3, fig. 4). • B, C – lectotype of *S. parvulus* (NM O3455, NM O6862), part and counterpart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

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

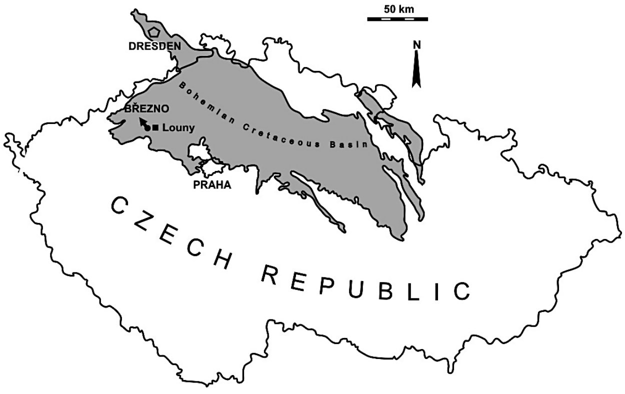


Figure 3. Location of the Březno locality within the Bohemian Cretaceous Basin.

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 Sphaeosiderite 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

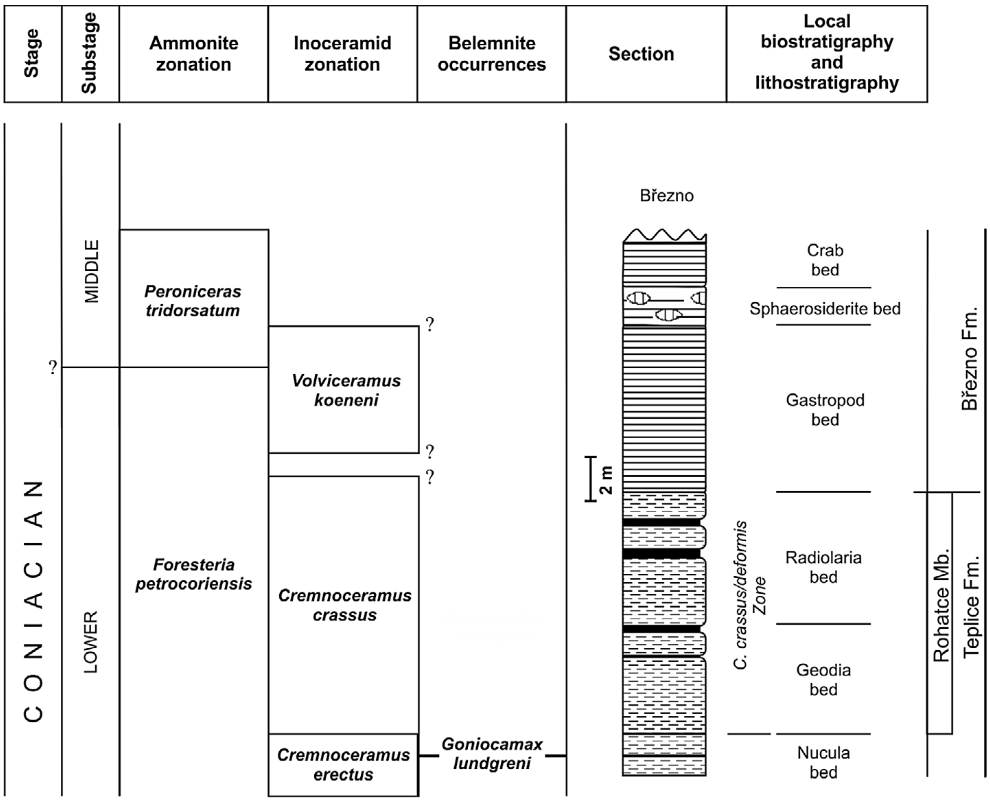


Figure 4. Bio- and lithostratigraphical correlation of the section at Březno. *Ctenocheles fritschi* sp. nov. is found in the Gastropod and Crab beds of the Březno Formation.

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

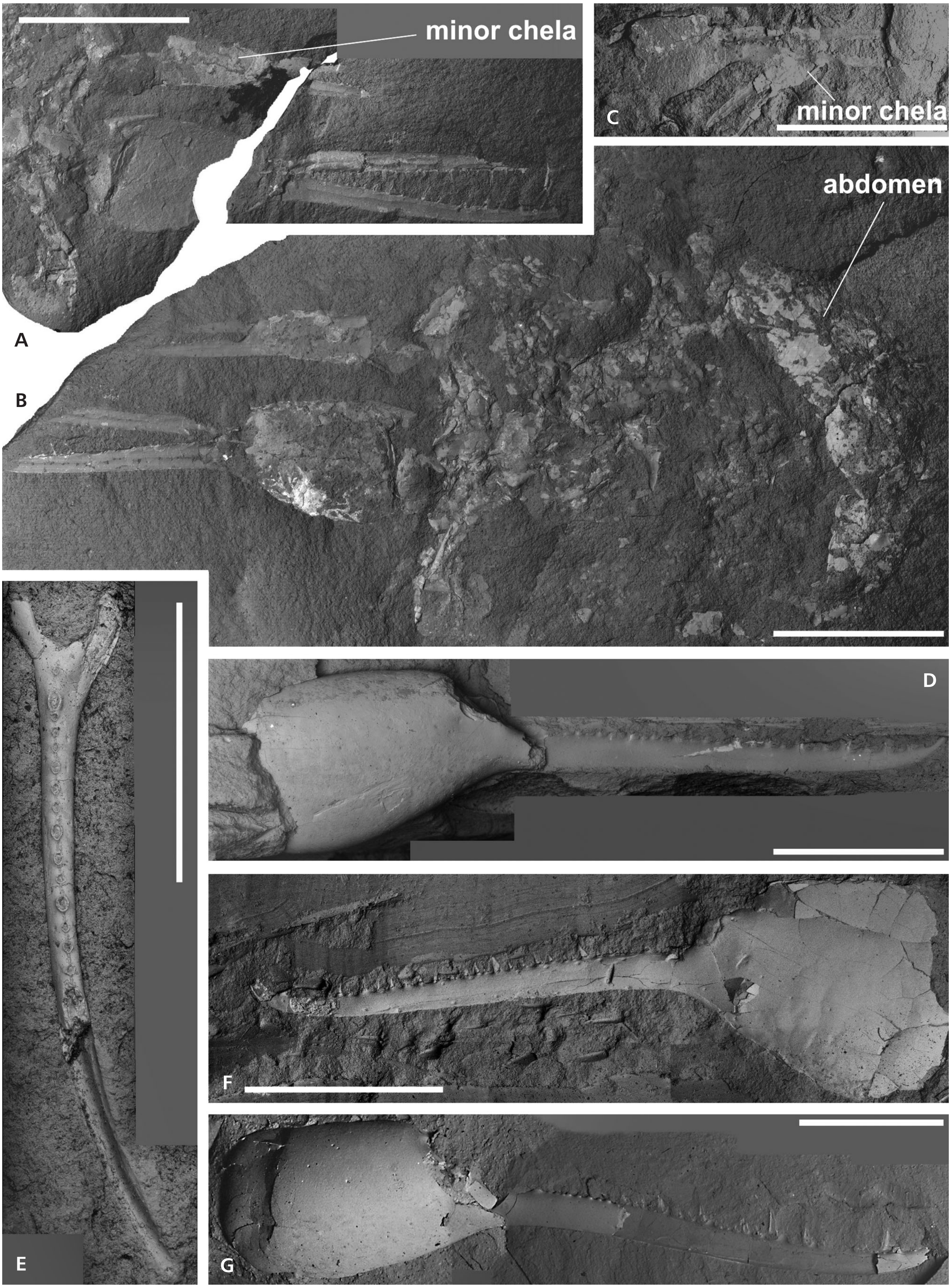
partim 1887 *Stenocheles parvulus*; Fritsch & Kafka, p. 40.
partim 1887 *Stenocheles gracilis* (nomen nudum) – Fritsch & Kafka, pl. 3, fig. 4 (non fig. 3).
?1893 *Stenocheles gracilis* (nomen nudum). – Fritsch, p. 106.
?1894 *Stenocheles gracilis* (nomen nudum). – Fritsch, p. 103.
partim 1929 *Ischnodactylus 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. All specimens are to scale. Scale bar equals 5 mm.


minor chela
C
minor chela
abdomen
A
B
D
E
F
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-

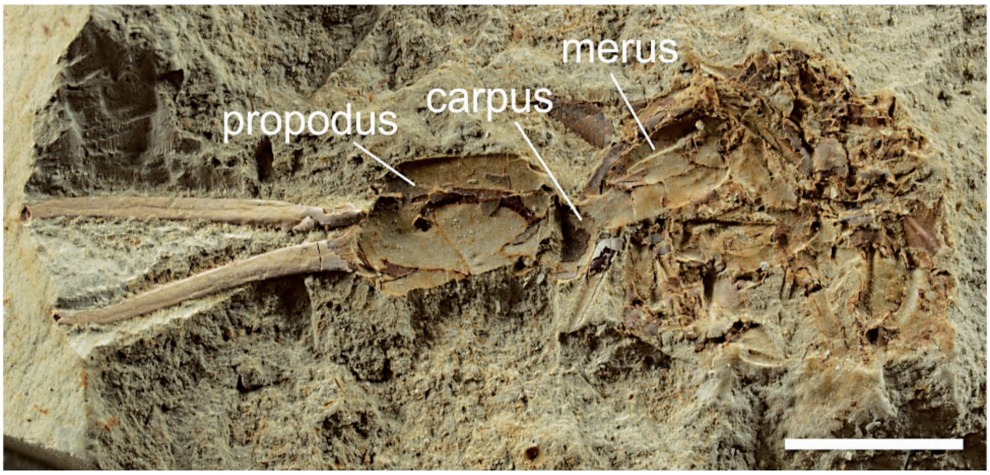


Figure 6. *Ctenocheles fritschi* sp. nov., nearly complete specimen NM O7121 from the Crab Bed of Březno.

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 photo-documentation 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 the best preserved fossil material of the genus reported to date.

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Paper III

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BARNACLES (CRUSTACEA, CIRRIPEDIA, THORACICA) FROM THE BOHEMIAN CRETACEOUS BASIN DESCRIBED BY FRITSCH AND KAFKA (1887), WITH THE EXCLUSION OF THE FAMILY STRAMENTIDAE

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Abstract. The original types of seven cirripede taxa recorded between 1885 and 1887 by J. Kafka and A. Fritsch et J. Kafka are redescribed and reillustrated. These stalked (scalpellomorph) and sessile (brachylepadomorph) species include '*Scillaelepas*' *conica* (REUSS, 1844), *Titanolepas tuberculata* (DARWIN, 1851), *Cretiscalpellum glabrum* (ROEMER, 1841), *Cretiscalpellum striatum* (DARWIN, 1851), *Arcoscalpellum angustatum* (GEINITZ, 1843), *Arcoscalpellum maximum* (J. DE C. SOWERBY, 1829) and *Brachylepas fallax* (DARWIN, 1851). Information on the palaeoecology and taphonomy of these cirripedes in the Bohemian Cretaceous Basin (the Czech Republic) has been added.

■ Scalpellomorpha, Brachylepadomorpha, Cretaceous, taxonomy

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Introduction

The first cirripedes to be recorded from the Bohemian Cretaceous Basin (BCB) in the Czech Republic are those recorded by Reuss (1844, 1845–1846, 1864), all were from the Ohře area of the basin. Later, both Kafka (1885) and Fritsch and Kafka (1887) provided detailed accounts of cirripedes from the same area, referring also to work by Darwin (1851, 1854), Reuss (1864) and Geinitz (1843, 1845, 1875a,b). A few decades later, Withers (1935) presented a modern revision of all Cretaceous cirripedes from Europe and elsewhere; he also studied and, in part, illustrated material recorded by authors such as A. Frič (Fritsch), J. Perner and J. Šulc. Withers (1935) examined material from the following Czech localities: Kaňk, Kamajka, Na Vinici, Kučlín u Bíliny, Koštice, Duchcov, Bílá Hora, Holice, Lhota Úhřetická and Choceň, recording eleven species of cirripede, inclusive of two stramentids, *viz*. (in original nomenclature): *Zeugmatolepas cretae* (STEENSTRUP, 1837), *Calantica* (*Scillaelepas*) *conica* (REUSS, 1844), *Calantica* (*Titanolepas*) *tuberculata* (DARWIN, 1851), *Cretiscalpellum glabrum* (ROEMER, 1841), *Cretiscalpellum striatum* (DARWIN, 1851), *Scalpellum* (*Arcoscalpellum*) *angustatum* (GEINITZ, 1850), *Scalpellum* (*Arcoscalpellum*) *maximum* (J. de C. SOWERBY, 1829), *Loriculina laevissima* (VON ZITTEL, 1884), *Stramentum pulchellum* (G. B. SOWERBY, jun., 1843), *Proverruca vinculum* WITHERS, 1914 and *Brachylepas fallax* (DARWIN, 1851). Of these, *Z. cretae* is housed in the collections of the Natural History Museum (Department of Palaeontology, London); *P. vinculum* was in the J. Šulc Collection, but has been lost. The most recent papers on dissociated cirripede valves from the BCB are those by Kočí and Kočová Veselská (2012, 2013) and Kočová Veselská *et al*. (in prep.).

Here we revise and reillustrate material first recorded by Kafka (1885) and Fritsch and Kafka (1887), and add notes on the palaeoecology and taphonomy of cirripedes from the BCB. Table 1 lists all cirripede taxa described by those authors, their status and their current names.

Interestingly, most illustrations of cirripedes provided by Kafka (1885) and Fritsch and Kafka (1887) are the same, the majority being idealised (e.g., *Brachylepas fallax*). Fortunately, figures of some species, such as *Cretiscalpellum striatum* and *Arcoscalpellum maximum*, match actual specimens.

Systematic palaeontology

With a few exceptions,the taxonomic assignments below mostly follow Withers (1935), Newman *et al*. (1969), Babinot *et al*. (1979), Buckeridge (1983), Viaud *et al*. (1983), Zullo and Sohl (1985), Jagt and Collins (1989, 1999), Collins and Jagt (1999) and Carriol and Collins (2000, 2002).

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Table 1. Cirripede taxa recorded by Fritsch and Kafka (1887), indicating page numbers and illustrations; current names are shown in bold.

Pollicipes conicus Reuss (p. 11, fig. 21)	**‘*Scillaelepas*’ *conica* (Reuss)**
Scalpellum tuberculatum Darwin (p.6, fig. 9)	***Titanolepas tuberculata* (Darwin)**
Scalpellum nitens Kafka (p. 7, fig. 11)	***Cretiscalpellum glabrum* (Roemer)**
Pollicipes glaber Roemer (p. 8, fig. 13)	***Cretiscalpellum glabrum* (Roemer)**
Pollicipes bronnii Roemer (p. 9, fig. 14)	***Cretiscalpellum glabrum* (Roemer)**
Pollicipes cuspidatus Kafka (p. 11, fig. 18)	***Cretiscalpellum glabrum* (Roemer)**
Pollicipes unguis Sowerby (p. 12)	***Cretiscalpellum glabrum* (Roemer)**
Pollicipes costatus Kafka (p. 9, fig. 15)	***Cretiscalpellum striatum* (Darwin)**
Pollicipes košticensis Kafka (p. 11, fig. 19)	***Cretiscalpellum striatum* (Darwin)**
Pollicipes striatus Darwin (p. 9, fig. 16)	***Cretiscalpellum striatum* (Darwin)**
Scalpellum quadratum Darwin (p. 5, fig. 3)	***Arcoscalpellum angustatum* (Geinitz)**
Scalpellum quadricarinatum Reuss (p. 5, fig. 4)	***Arcoscalpellum angustatum* (Geinitz)**
Scalpellum kamajkense Kafka (p. 5, fig. 5)	***Arcoscalpellum angustatum* (Geinitz)**
Scalpellum fossula Darwin (p. 5, fig. 6)	***Arcoscalpellum angustatum* (Geinitz)**.
Scalpellum maximum (Sowerby) (p. 6, fig. 7)	***Arcoscalpellum angustatum* (Geinitz)**
Scalpellum angustum Dixon (p. 6, fig. 8)	***Arcoscalpellum angustatum* (Geinitz)**
Scalpellum crassum Kafka (p. 7, fig. 10)	***Arcoscalpellum angustatum* (Geinitz)**
Pollicipes elongatus Steenstrup (p. 11, fig. 20)	***Arcoscalpellum angustatum* (Geinitz)**
Scalpellum maximum var. *bohemica* Kafka (p. 6)	***A. maximum* (J. de C. Sowerby)**
Scalpellum maximum J. de C. Sowerby (p. 6, fig. 7)	***A. maximum* (J. de C. Sowerby)**
Pollicipes fallax Darwin (p. 10, fig. 17)	***Brachylepas fallax* (Darwin)**

Subclass: **Cirripedia Burmeister, 1834**

Superorder: **Thoracica Darwin, 1854**

Order: **Scalpelliformes Buckeridge et Newman, 2006**

Family: **Calanticidae Zevina, 1978**

Genus: ***Scillaelepas* Seguenza, 1876 (*s. lat.*)**

‘*Scillaelepas*’ *conica* (Reuss, 1844)

Pl. 1, figs 1–9

*1844 *Pollicipes conicus* Reuss, p. 216.
1887 *Pollicipes conicus* Reuss: Fritsch and Kafka, p. 11, fig. 21.
1889 *Pollicipes conicus* Reuss: Fritsch, p. 95, text-fig. 119.
1911 *Pollicipes conicus* Reuss: Frič, p. 69.
1935 *Calantica* (*Scillaelepas*) *conica* (Reuss): Withers, p. 120, pl. 8, figs. 1–7 (with synonymy).

Material. Studied specimens from the locality of Kaňk, sold by Fritsch in 1897, and deposited in the collections of the Natural History Museum (London) comprise five scuta (NHM In. 16739-40, In. 16742-45, one carina (NHM In. 16746), one rostrum (NHM In. 16747) and four terga (NHM In. 16753-56). In addition, we also examined all material which is deposited in NHM (London) which consists of a total of 84 plates sold by Fritsch (coll. numbers are mentioned by Withers (1935, pp. 120–122)). Unfortunately, the collections of the National Museum (Prague) do not contain any material from Fritsch and Kafka‘s (1887) original collection.

Description. For a full description, please refer to Withers (1935, pp. 120–122).

Remarks. In his account of the ‘Teplitzer Schichten’ (= current Teplice Formation), Fritsch (1889) used Reuss’s type specimen (1844, p. 216) from Sauerbrunnberg bei Bilina (= Kyselka u Bíliny). Fritsch and Kafka (1887) recorded the present species from the ‘Priesener Schichten’ (= current Březno Formation) from the locality of Luschitz, while Frič (1911) merely noted a single occurrence from Cenomanian strata (current Korycany Member) at Bílina and Kyselka u Bíliny, but did not provide an illustration. From the locality Kaňk – Na Vrších more than 500 articulated capitular plates were recently obtained from fieldwork during 2014 (T. K. and M. K. V.) and the new material pertaining to this species has recently been studied (Kočí, Kočová Veselská, Buckeridge, Jagt, Collins, Gale *in prep*.). It is probable that this new material represents a new genus (Gale, personal communication) and species based on the study of the holotype (T. K. and M. K. V., August 2014) which is deposited in NHMW in Vienna.

Occurrence (BCB). Upper Cenomanian (Kaňk); upper Turonian (Kyselka u Bílliny, Lužice; Březno Formation).

Overall range. Upper Cenomanian to ? Upper Turonian (or ? Coniacian; Březno Formation).

Genus: ***Titanolepas* Withers, 1913**

Titanolepas tuberculata (Darwin, 1851)

Pl. 2, fig. 1

*1851 *Scalpellum tuberculatum* Darwin, p. 43, pl. 1, fig. 10.
1887 *Scalpellum tuberculatum* Darwin: Fritsch and Kafka, p. 6, fig. 9.
1935 *Calantica* (*Titanolepas*) *tuberculata* (Darwin); Withers, p. 130, pl. 11, figs. 1–10; pl. 12, figs. 1–3.

Material. A single, rather poorly preserved tergum from Kamajka (National Museum, NM O3407), Kafka's original (1885, p. 14, pl. 1, fig. 7; see also Fritsch and Kafka, 1887, p. 6, fig. 9).

Description. Tergum diamond shaped, elongated; apicobasal ridge almost straight, prominent, thickening towards acute basal angle; conspicuous ornamentation, longitudinal ridges crossed by transverse ridges, creating short, blunt spines.

Remarks. *Titanolepas tuberculata* can be differentiated from the younger *T. subtuberculata* (Withers, 1935) by its straight apicobasal ridge, the latter having a sigmoidally curved apicobasal ridge on the tergum. In addition, the coarse, close-set ridges are fewer and finer. *Titanolepas martini* (Withers, 1926), from the Late Cretaceous Niobrara Group, has a subrhomboidal tergum and lacks the blunt spines on the valve surface.

Occurrence (BCB). Kamajka. Withers (1935) also listed this species from the upper Turonian of Na Vinici, northeast of Kolín, a locality now defunct, on the basis of the J. Šulc Collection held at the Natural History Museum (London). This lot comprises six carinae, five scuta, six terga and two lower latera. The remainder of this collection was lost during the turmoil of the Second World War. Unfortunately, the original locality is lost so we cannot determine whether a nearshore or pelagic facies was once exposed; the age has recently been documented as Middle Turonian (Zelenka *et al*. 2011).

Overall range. Cenomanian to Upper Turonian.

Genus: ***Cretiscalpellum*** **Withers, 1922**

Cretiscalpellum glabrum **(Roemer, 1841)**

Pl. 2, fig. 2

*1841 *Pollicipes glaber* Roemer, p. 104, pl. 16, fig. 11a-c.
1887 *Scalpellum nitens* Kafka.: Fritsch and Kafka, p. 7, fig. 11a, b.
1887 *Pollicipes glaber* Roemer: Fritsch and Kafka, p. 8, fig. 13.
1887 *Pollicipes Bronnii* Roemer: Fritsch and Kafka, p. 9, fig. 14a-c.
1887 *Pollicipes fallax* Darwin: Fritsch and Kafka, p. 10, fig. 17 (*partim*).
1887 *Pollicipes cuspidatus* Kafka: Fritsch and Kafka, p. 11, fig. 18.
1887 *Pollicipes unguis* Sowerby: Fritsch and Kafka, p. 12.
1889 *Pollicipes glaber* Roemer: Fritsch, p. 95, fig. 117.
1887 *Pollicipes bronni* Roemer: Fritsch, p. 95, fig. 118.
1893 *Pollicipes glaber* Roemer: Fritsch, p. 109.
1897 *Pollicipes glaber* Roemer: Fritsch, p. 70.
1935 *Cretiscalpellum glabrum* (F. A. Roemer): Withers, p. 161, pl. 15, figs. 8–17; pl. 16, figs. 1–10; pl. 17, figs. 1–21; pl. 18, figs. 1–5.

Material. The original carina collected by Fritsch and Kafka (1887, fig. 13), from Koštice, NM O4375 (no. 6532) in the collections of the National Museum (Prague); it measures 14.6 mm in length and 6.3 mm in basal width. *Pollicipes* sp./*Scalpellum* Frič A.,- carina and two fragments of a left tergum from Měcholupy railway station - this material was collected by Antonín Frič in 1901, unpublished data., and deposited in collection of NM, without an inventary number.

Description. Carina with broken apex, lacking parietes and intraparietes; median ridge distinct; lateral margins slightly rounded inwards; surface of carina apparently smooth, but at higher magnification distinct sharp lines parallel to basal margin become visible.

Remarks. The present species bears the closest resemblance to *C. striatum*, the carina of which has a stronger apicobasal ridge than other longitudinal lines and strongly developed transverse lines. The carina of *C. bronni* (Roemer, 1841), from the Cenomanian of Germany and northwest France, has no transverse lines and the apicobasal keel is less prominent, while that of *C. unguis* (J. de C. Sowerby, 1829), from the Albian of England and France, is wider, has slightly rounded parietes and the most strongly developed transverse lines within the genus *Cretiscalpellum*. The early Campanian *C. obtusum* Jagt et Collins, 1999 has a trapezoidal scutum that is more convex than that of *C. glabrum*.

Occurrence (BCB). Upper Cenomanian (Velim, Přemyšlany [Přemyšlení is now part of the hamlet of Zdiby near Prague), Černovičky; Lower Turonian (Velim, Kamajka, Turkaňk, Karlov, Odolena Voda, Běstvina u Ronova nad Doubravou, Chrtníky); Middle Turonian (Semice, Bousov, Všetaty, Mikulovice near Pardubice); Upper Turonian (Koštice, Úpohlavy, Čížkovice, Želenice near Bílina, Kostomlaty, Radim u Luže, Teplice, Kystrá, Měcholupy); Upper Turonian – Lower Coniacian (Lužice, Lány na Důlku near Pardubice, Úhřetická Lhota); Lower – Middle Coniacian (Litomyšl).

Overall range. Upper Albian – Upper Maastrichtian.

Cretiscalpellum striatum **(Darwin, 1851)**

Pl. 2, fig. 3

*1851 *Pollicipes striatus* Darwin, p. 70, pl. 4, fig. 5a-c.
1887 *Pollicipes costatus* Kafka: Fritsch and Kafka, p. 9, fig. 15.
1887 *Pollicipes striatus* Darwin: Fritsch and Kafka, p. 9, fig. 16.
1887 *Pollicipes košticensis* Kafka: Fritsch and Kafka, p. 11, fig. 19.
1889 *Pollicipes košticensis* Kafka: Fritsch, p. 95, fig. 116.
1935 *Cretiscalpellum striatum* (Darwin): Withers, p. 183, pl. 20, figs. 1–5, 15-21; pls. 21, 22.

Material. NM O4027 (no. 6531), the original tergum described by Kafka (1889, pl. 2, fig. 4).

Description. Tergum elongated, irregularly rhomboidal; apical umbo acute; apicobasal ridge distinct and sharply rounded; occludent margin straight; scutal margin forming angle of 50 degrees with occludent margin; longitudinal lines on carinal part of tergum clear and distinct; scutal margin formed by apicoscutal groove, ending at scutal margin, 2 mm from occludent margin; distinct transverse lines parallel to scutal margin; inner part smooth and with distinct growth lines of carinal fold near carinal margin.

Remarks. The present species has a more elongated tergum than *C. glabrum*. The main distinguishing features are the sharp longitudinal and transverse lines; these are absent in *C. glabrum*. *Cretiscalpellum paucistriatum* (Woodward, 1901) has an elongated tergum, which is much less clearly longitudinally striated (almost smooth in some cases) and with a peculiar transverse convexity, while *C. naidini* Alekseev, 2009 has a strongly convex tergum with a very thick axial portion and a wide occludent rib. The carina of *C. sharapovi* Alekseev, 2009 has a thick-set apical part which is covered by narrow ribs which are curved into the outer side.

Occurrence (BCB). Lower Turonian (Velim, Karlov [recorded by Žítt and Nekvasilová, 1989, p. 86, as *Pollicipes costatus* Kafka], Běstvina u Ronova nad Doubravou [recorded by Žítt and Nekvasilová, 1994, p. 26, as *Pollicipes costatus* Kafka]; Upper Turonian (Koštice).

Overall range. Lower Cenomanian – Upper Maastrichtian.

Family: **Scalpellidae Pilsbry, 1916**

Subfamily: **Arcoscalpellinae Zevina, 1978**

Genus: ***Arcoscalpellum* Hoek, 1907**

***Arcoscalpellum angustatum* (Geinitz, 1843)**

Pl. 2, fig. 4

*1843 *Pollicipes angustatus* Geinitz, p. 7, pl. 4, fig. 10.
1885 *Scalpellum quadratum* Darwin: Kafka, pl. 1, fig. 1d.
1887 *Scalpellum quadratum*, Darwin: Fritsch and Kafka, p. 5, fig. 3a-d.
1887 *Scalpellum quadricarinatum* Reuss: Fritsch and Kafka, p. 5, fig. 4a-c.
1887 *Scalpellum kamajkense* Kafka: Fritsch and Kafka, p. 5, fig. 5a, b.
1887 *Scalpellum fossula* Darwin: Fritsch and Kafka, p. 5, fig. 6a, b.
1887 *Scalpellum maximum* Sowerby sp.: Fritsch and Kafka, p. 6, fig. 7c (*non* 7a, b).
1887 *Scalpellum angustum* Dixon sp.: Fritsch and Kafka, p. 6, fig. 8a-d.
1887 *Scalpellum crassum* Kafka: Fritsch and Kafka, p. 7, fig. 10.
1887 *Pollicipes elongatus* Steenstrup: Fritsch and Kafka, p. 11, fig. 20a, b.
1889 *Scalpellum angustatum* Dixon: Fritsch, pp. 95, 96, fig. 120.
1893 *Scalpellum quadratum* Darwin: Fritsch, pp. 108, 109, fig. 142.
1935 *Scalpellum* (*Arcoscalpellum*) *angustatum* (Geinitz): Withers, p. 215, pl. 25, figs. 2–20; pl. 26, fig. 1.

Material. A single left scutum only (NM O 4021) survives from Fritsch and Kafka's (1887) original collection; it measures 7.7 mm in length and 4 mm in basal width.

Description. Scutum trapezoidal, elongated; cross section slightly convex; length about twice the width; occludent margin straight or slightly curved and basal margin at right angles; edge of occludent margin bending inwards; basal margin slightly concave to straight; lateral margin extending to about two-thirds of scutal height and tergal margin to one third of scutal height; apicobasal margin distinct and rounded; towards lateral and tergal margins, area of scutum slightly sloping; lateral margin convex; tergolateral angle distinct.

Remarks. The present species resembles *A. fossula* (Darwin, 1851), but differs from it in the scutal construction (see also Collins in Viaud *et al*. 1983). *Arcoscalpellum lineatum* (Darwin, 1851), from the Upper Albian to ?Lower Santonian of England, France and Germany, differs in having longitudinal lines on the carinal tectum, narrower terga and wider scuta. The scutum of *A. maximum* (J. de C. Sowerby, 1829) (see below) has a less pronounced apicobasal ridge and generally shows finer transverse and longitudinal ornamentation.

Occurrence (BCB). Upper Cenomanian (Předboj, Černovičky [recorded by Žítt *et al*., 1999, p. 112, as *Scalpellum* sp.); Lower Turonian (Velim, Kamajka, Turkaňk, Kněžívka [recorded by Žítt *et al*., 1999, as *Scalpellum crassum*], Odolena Voda [recorded by Hradecká *et al*., 1994, p. 19, as *Scalpellum crassum*], Chrtníky [recorded by Žítt *et al*., 2006, unit 7, 8f as Scalpellid gen. et sp. indet.], Běstvina u Ronova nad Doubravou [recorded as *Scalpellum* sp. by Žítt and Nekvasilová, 1994, p. 26]; Middle Turonian (Všetaty); Upper Turonian (Úpohlavy, Novosedlice, Stradouň); Upper Turonian – Lower Coniacian (Lány na Důlku near Pardubice).

Overall range. Albian – Lower Santonian.

***Arcoscalpellum maximum* (J. de C. Sowerby, 1829)**

Pl. 2, figs. 5–7

1829 *Pollicipes maximus* J. de C. Sowerby, p. 222, pl. 606, figs. 4, 6 (*non* figs. 3, 5).
1885 *Scalpellum maximum* (Sowerby): Kafka, p. 12, pl. 1, fig. Aa-c (*non* fig. 5B, C).
1886 *Scalpellum maximum*, var. *bohemica* Kafka: Kafka, p. 564, pl. 1, fig. A (*non* fig. B, C).
1887 *Scalpellum maximum*, var. *bohemica* Kafka: Fritsch and Kafka, p. 6, fig. 7a (*non* fig. 7b, c).
1893 *Scalpellum maximum* (Sowerby): Fritsch, p. 109, text-fig. 141 (incl. var. *bohemica*).
1935 *Scalpellum* (*Arcoscalpellum*) *maximum* (Sowerby): Withers, p. 239, pl. 29, figs. 2-10; pl. 30, figs. 1–12; pl. 31, figs. 1–19.

Material. The lectotype carina of var. *bohemicum,* NM O4022, is from Holice. Another specimen from Kunětická Hora was collected by Jan Jiljí Jahn (see Fritsch and Kafka, 1887, p. 6).

Description. Carina with moderately to strongly convex tectum and moderately transversely arched, subcarinated and with prominent distinct narrow ridge on both sides; ridges separate tectum from parietes; parietes narrow, equalling about half tectal width, inclined outwards and sligthly concave; intraparietes slightly wider than the entire side of the valve side, set slightly inwards; intraparietes divided from parietes by strong distinctly rounded ridge; tectum length ranging from five to three times its width and moderately bowed inwards; wall very thin and widening gradually from apex; depth of valve approximately half width of tectum; basal margin acutely angular and inner margin almost straight.

Remarks. It is interesting to note that all illustrations in the papers listed above (synonymy) are the same and all repeat the incorrect identification, as outlined by Withers (1935, p. 243). *Arcoscalpellum angustatum* (see above) develops only very fine apicobasal lines on the tectum and the carina is of smaller size.

Occurrence (BCB). Holice.

Overall range. Lower Santonian – Upper Maastrichtian.

Order: **Sessilia Lamarck, 1818**

Suborder: **Brachylepadomorpha Withers, 1923**

Genus: ***Brachylepas* Woodward, 1901**

***Brachylepas fallax* (Darwin, 1851)**

Pl. 3, figs. 1a–m, 2a–g; Pl. 4, figs. 1–8

1851 *Pollicipes fallax* Darwin, p. 75, pl. 4, fig. 8a, b.
1885 *Pollicipes fallax* Darwin: Kafka, p. 19, pl. 3, figs. 2r (*non* fig. 2l), 3a, b (*non* fig. 3sl, l′).
1887 *Pollicipes fallax* Darwin: Fritsch and Kafka, p. 10, fig. 17 (*non* l′, sl).
1893 *Pollicipes fallax* Darwin: Fritsch, p. 309.
1935 *Brachylepas fallax* (Darwin): Withers, p. 367, pl. 48, figs. 1–24.

Material. Specimens from Uhřetická Lhota are as follows: a right scutum (NM O4023; the original from Fritsch and Kafka, 1887, fig. 17b (s), collected by J. J. Jahn), a rostrum (NM O4024; the original from Fritsch and Kafka, 1887, fig. 17r); a right scutum (NM O4025); a left scutum (NM O4026). Lot NM O4093 comprises a right tergum and four lower latera, the originals from Fritsch and Kafka, 1887, fig. 17. Lot NM-ČL6989 (nos 387, 388, 390) represents the originals from Fritsch and Kafka (1887, fig. 17t, t, c), while lot NM-ČL6990 (no. 879) comprises a scutum, a rostrum and a carina. Specimen NM-ČL6992 (Os 292), from Choceň (Sutiny), is also the original from Kafka (1885, pl. 3, 2 r).

Description. Carina semiconical, slightly bowed inwards, strongly convex transversely, yet not carinate; basal margin slightly concave; outer surface with a number of strong distinct flattened transverse ridges, regularly spaced; longitudinal ornamentation of very fine distinct longitudinal lines, preserved only in NM-ČL6989 (no. 390). The carina from Úhřetická Lhota measures 5.85 mm in length, while NM-ČL6989 (no. 390), which lacks the apex, measures 5 mm in length and 2.35 mm in basal width. NM-ČL6992 (Os 292), from Choceň (Sutiny), measures 5.6 mm in length and 2.6 mm in basal width. Rostrum semiconical, wider than carina, bowed inwards and strongly convex transversely; transverse ornamentation resembles that of the carina, but less pronounced. Distinct longitudinal apicobasal ridge developed. NM-ČL6990 measures *c.* 6 mm in length and *c.* 4.64 mm in basal width. Measurements (estimated because matrix partially covered) of NM O4024 are: length *c.* 4.5 mm and width *c.* 7 mm. Scutum elongated triangular in outline, moderately convex transversely. Rounded, strongly convex occludent margin with acuminate apex. Apex strongly bowed towards tergum. Tergo-lateral margin slightly concave, mainly in upper part, near apex. Edge of basilateral margin protruding sharply; basilateral angle 100° (NM O4025); basal margin almost straight. Rostral angle 130° (NM O4025). Apicobasal ridge significantly pronounced , broad and curved convexly. Broad apicobasal ridge in NM O4026 measuring 0.45 mm in width. Transverse ridges significantly pronounced, equally spaced and thickened at occludent margin, narrowing near upper part of tergal margin. Overall length of right scutum NM O4023 *c.* 5 mm, basal width 3.4 mm, that of another right scutum, NM O4025, *c.* 6.4 mm, basal width 5 mm. Left scutum (NM O4026) *c.* 5.9 mm, basal width 3.7 mm. Tergum (NM-ČL6989, no. 388) subrhomboidal in outline, moderately convex transversely with prominent broad apicobasal ridge, curved towards carino-lateral margin and concave towards occludent and scutal margin. Apex acuminate, slightly bowed inwards towards occludent margin. In upper third of valve a distinct sharp concave apico-scutal ridge, parallel to apicobasal ridge. Transverse ridges prominent and equally spaced, as in scutum. Longitudinal ornamentation consisting of very fine lines. Basal angle between lateral and scutal margin 70°. Carinal angle between lateral and carinal margin 60°. Overall length 5.95 mm.

Remarks. *Brachylepas* has carinae, rostra, scuta, terga and upper latera that closely resemble those of *Pycnolepas* Withers, 1914. In fact, Withers (1914) included *B. fallax* in *Pycnolepas*. However, the latter can be differentiated by the more prominent transverse and longitudinal ridges on the carina, rostrum and upper latus, with the exception of *B. naissanti* (Hébert, 1855), which has lower L/W ratios, a semicircular basal outline and thickened inner margine (Jagt, 2007). The scutum of *Pycnolepas* is more elongate and the apex more acute. *Brachylepas naissanti* has a wide semi-conical carina and rostrum with significantly raised longitudinal ribs. The terga and scuta of *B. naissanti* have less prominent transverse sculpture than *B. fallax*. The imbricating plates of the latter lack longitudinal ribs and differ from those of *B. naissanti* in being more rounded at the apex. The longitudinal ribs of the imbricating plates of *B. fallax* are developed as furrows. *Brachylepas guascoi* (Bosquet, 1857) has a wider carina with more prominent transverse ridges, a scutum with very pronounced transverse ridges and tergum with a straight apicobasal ridge nearer the scutal margin than in *B. fallax*. More details on the relationships between species of *Brachylepas* can be found in Jagt (2007). *Brachylepas nervosa* Alekseev, 2009, from the upper Lower Maastrichtian of Crimea (Ukraine) has a straighter carina and rostrum and the ridge on the scutum divides the valve into two unequal parts. Alekseev (2009, p. 34) considered some western European records of *B. fallax* to pertain to *B. nervosa*.

Occurrence (BCB). Upper Turonian – Lower Coniacian (Úhřetická Lhota, Choceň (Sutiny).

Overall range. Upper Turonian – uppermost Maastrichtian.

Palaeoecology and palaeogeography

Stalked cirripedes are relatively common faunal elements in nearshore/shallow-water facies in the BCB, but are rare constituents of hemipelagical deposits in the area. Species lived attached to substrates in high-energy settings, near the storm wave base, an environment similar to that of representatives of the recent genus *Pollicipes* which occur on wave-exposed rocky shores and which are mostly intertidal in distribution (Fernandes *et al*., 2010).

Bathymetric records of extant members of the genus *Arcoscalpellum*, as mentioned by Pilsbry (1907), range between 46 and 5.365 m. Weisbord (1977) indicated 1.555–3.028 m. Preservation of shallow water taxa is inhibited by a higher energy environment, thus completely preserved capitula of cirripedes are rare. In nearshore/shallow-water and hemipelagic facies in the BCB, ciripedes occur exclusively as disarticulated valves, the commonest being carinae, scuta, rostra and terga. Upper latera, carinal latera and rostral latera are rare. A single exception is *Brachylepas fallax* (see Pl. 3a; NM-ČL6990, no. 879) which comprises a number of plates that probably belonged to three separate individuals. These capitular plates were not displaced after decomposition of the capitula and covered by sediment immediately afterwards as was more usual. This kind of preservation is recorded here for the first time from the BCB. For specimens with strongly connected (articulated) capitular plates to be preserved more or less intact, tranquil environments, rapid burial and absence of subsequent scavenging/burrowing would be required. With the exception of the genus *Stramentum*, cirripedes from the BCB have never been found as articulated capitula, in contrast to occurrences in the Upper Cretaceous in northwest Europe, e.g., of *Arcoscalpellum unguis*, *A. fossula*, *A. maximum*, *Zeugmatolepas mockleri*, *Brachylepas naissanti* and others (see e.g., Withers, 1935).

‘*Scillaelepas*’ *conica*, *Titanolepas tuberculata*, *Cretiscalpellum striatum*, *Arcoscalpellum maximum* and *Brachylepas fallax* are comparatively rare in the BCB, while *C. glabrum* and *A. angustatum* are more abundant. All of these species occur widely across Europe.

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Explanation of the plates

PLATE 1

‘*Scillaelepas*’ *conica* (Reuss), Kaňk, collection of the Natural History Museum, London.
1a. Scutum (external part, NHM In. 16742); **1b.** Scutum (inner part, NHM In. 16742); **2a.** Scutum (external part, NHM In. 16743); **2b.** Scutum (inner part, NHM In. 16743); **3a.** Scutum (external part, NHM In. 16744); **3b.** Scutum (inner part, NHM In. 16744); **4a.** Scutum (external part, NHM In. 16745); **4b.** Scutum (inner part, NHM In. 16745); **5a.** Scutum (external part, NHM In. 16739); **5b.** Scutum (inner part, NHM In. 16740); **6.** Tergum (external part, NHM In. 16753); **7.** Tergum (external part, NHM In. 16754); **8a.** Carina (external part, NHM In. 16746); **8b.** Carina (inner part, NHM In. 16746); **9a.** Rostrum (inner part, NHM In. 16747); **9b.** Rostrum (external part, NHM In. 16747). All scale bars equal 1 mm. Photographs by H. Taylor (Natural History Museum, London).

PLATE 2

1. *Titanolepas tuberculata* (Darwin), Kamajka (NM O3407), partial tergum. Scale bar = 0.5 mm.
2. *Cretiscalpellum glabrum* (Roemer), Koštice (NM O4375, no. 6532), carina. Scale bar = 5 mm.
3. *Cretiscalpellum striatum* (Darwin), Koštice (NM O4027), tergum. Scale bar = 1 mm.
4. *Arcoscalpellum angustatum* (Geinitz), Lány na Důlku near Pardubice (collected by Jan J. Jahn; NM O4021), left scutum. Scale bar = 5 mm.
5–7. *Arcoscalpellum maximum* var. *bohemicum* Kafka, from Holice (NM O4022), carina. Scale bar = 1 mm.

(Figs 2–7 photographed by Jan Sklenář and Martina Aubrechtová, 2014; all others by the authors)

PLATE 3

1. *Brachylepas fallax* (Darwin), figured specimen from Fritsch and Kafka (1887, p. 10, fig. 17), Úhřetická Lhota (NM-ČL6990, no. 879). Scale bar = 5 mm.

a. Carina; **b.** Right tergum; **c.** Fragmentary right scutum; **d.** Left scutum; **e.** Fragmentary indeterminate valve; **f.** Left tergum (imprint); **g.** Right tergum (imprint); **h.** Right scutum; **ch.** ?Upper latus (imprint); **i.** Right tergum; **j.** Left scutum; **k.** Fragmentary ?rostrum; **l.** Fragmentary ?left tergum.

2. *Brachylepas fallax*, (Darwin), NM O4893. Scale bar = 1 mm.
a. Fragmentary right scutum; **b.** Fragmentary scutum; **c.** Rostrum; **d.** Right scutum; **e.** Indeterminate valve (imprint).

(Fig. A photographed by Jan Sklenář, 2013; Fig. B by the authors)

PLATE 4

Brachylepas fallax (Darwin), Úhřetická Lhota.
1. Right sputum, NM O4023;
2. Rostrum and left sputum, NM O4024;
3. Left sputum, NM O4025;
4. Right sputum, NM O4026;
5. Carina, NM-ČL6989, no. 390;
6. Left tergum with crushed apex, NM-ČL6989, no. 387;
7. Carina, NM-ČL6990, no. 879;
8. Right tergum, NM- ČL6989, no. 388.

All scale bars equal 1 mm.
(Photographs by Jan Sklenář and Martina Aubrechtová, 2014)

PLATE 1

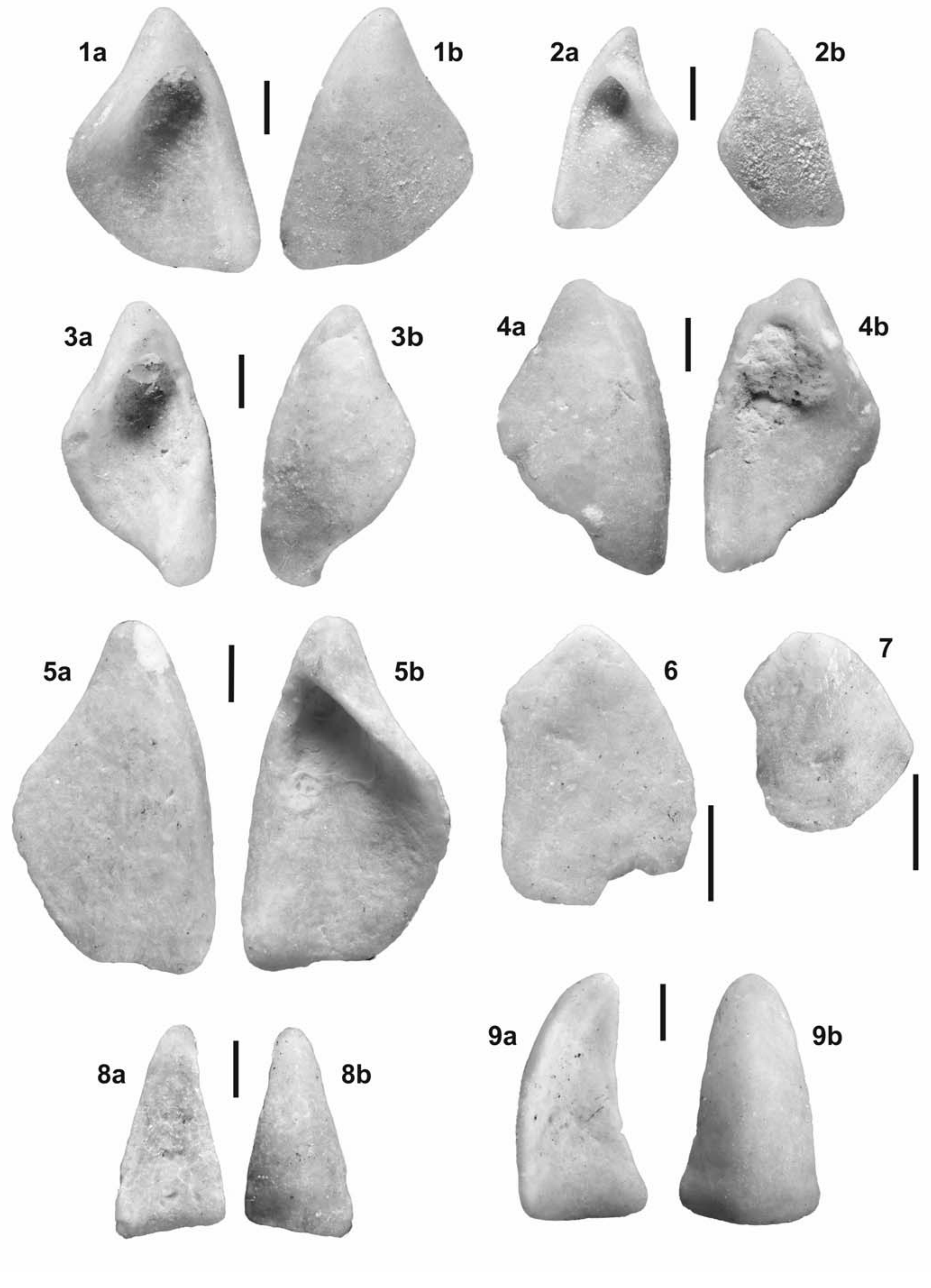

PLATE 2

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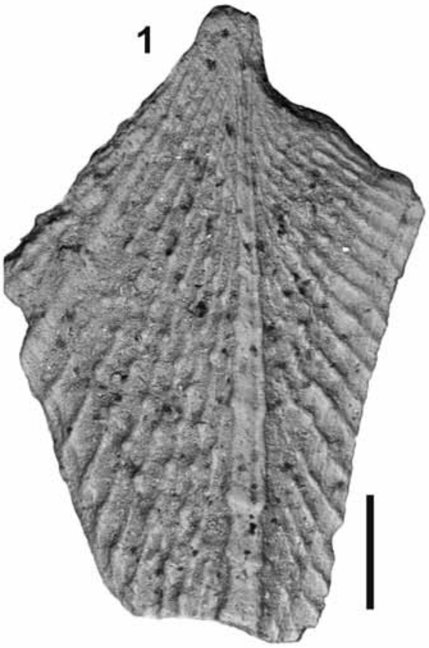

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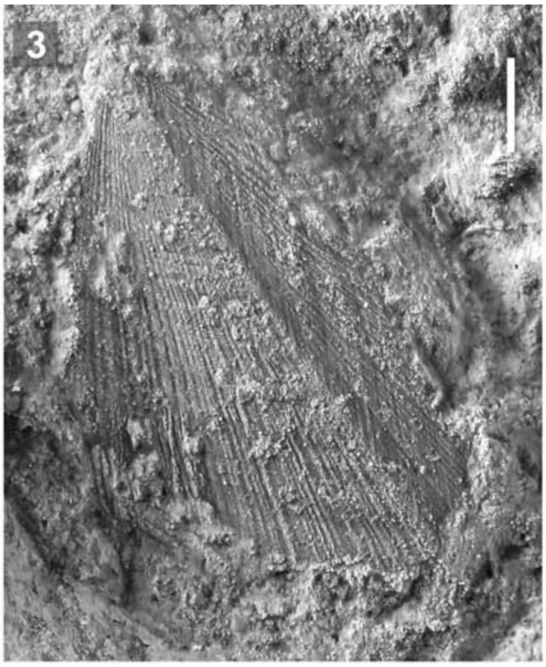

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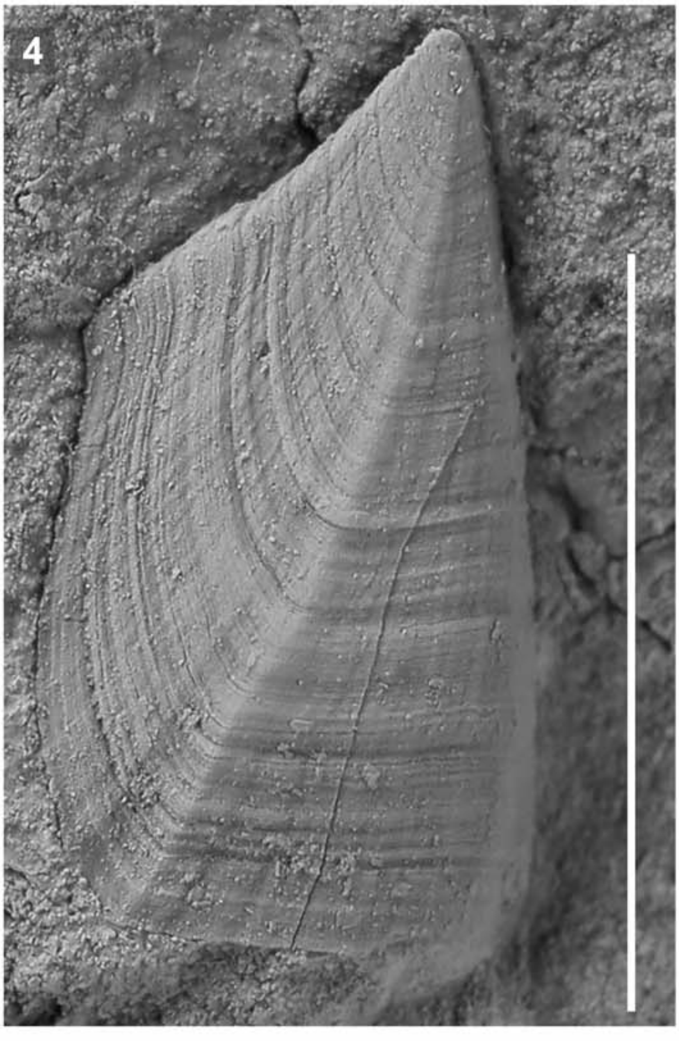

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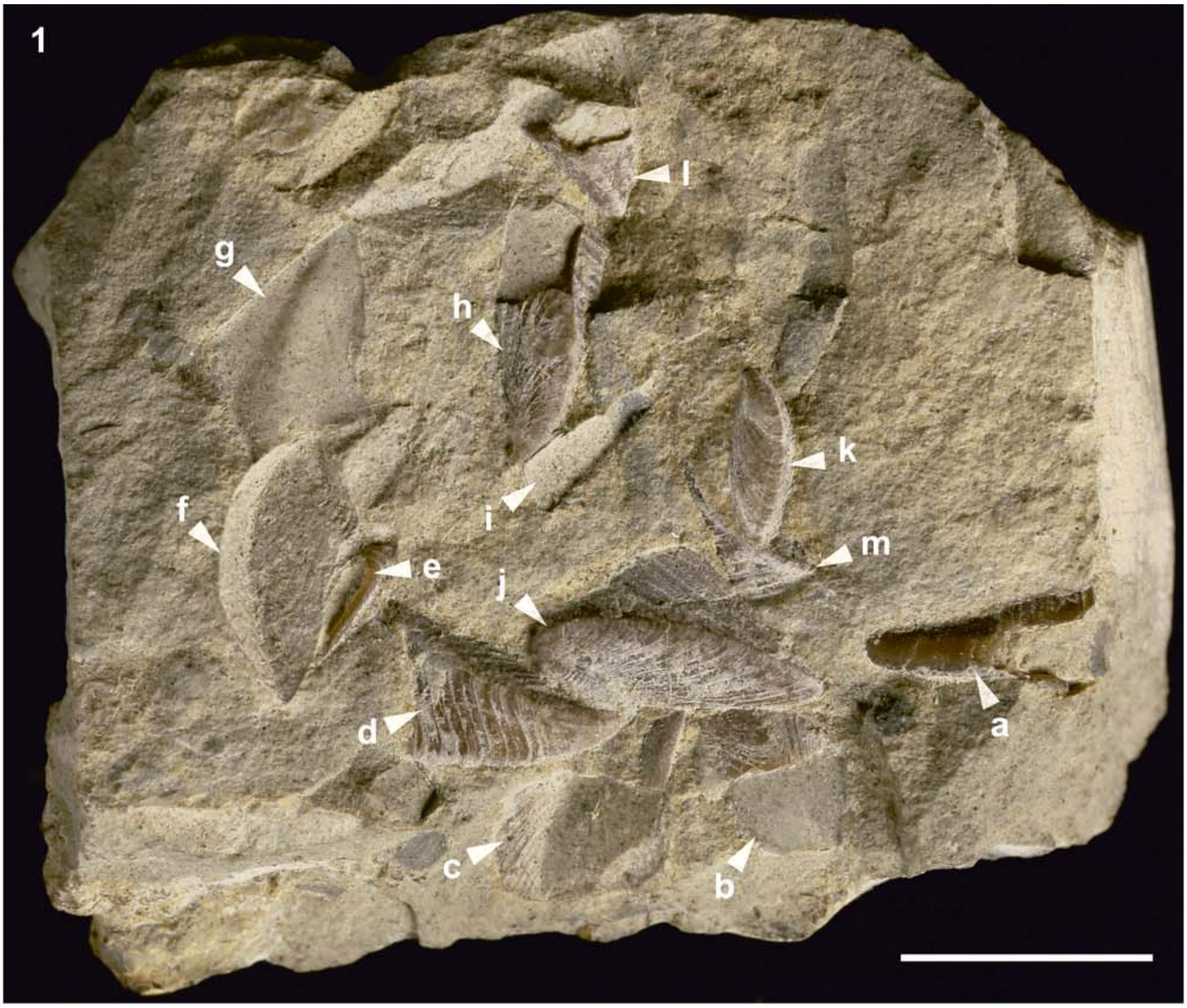

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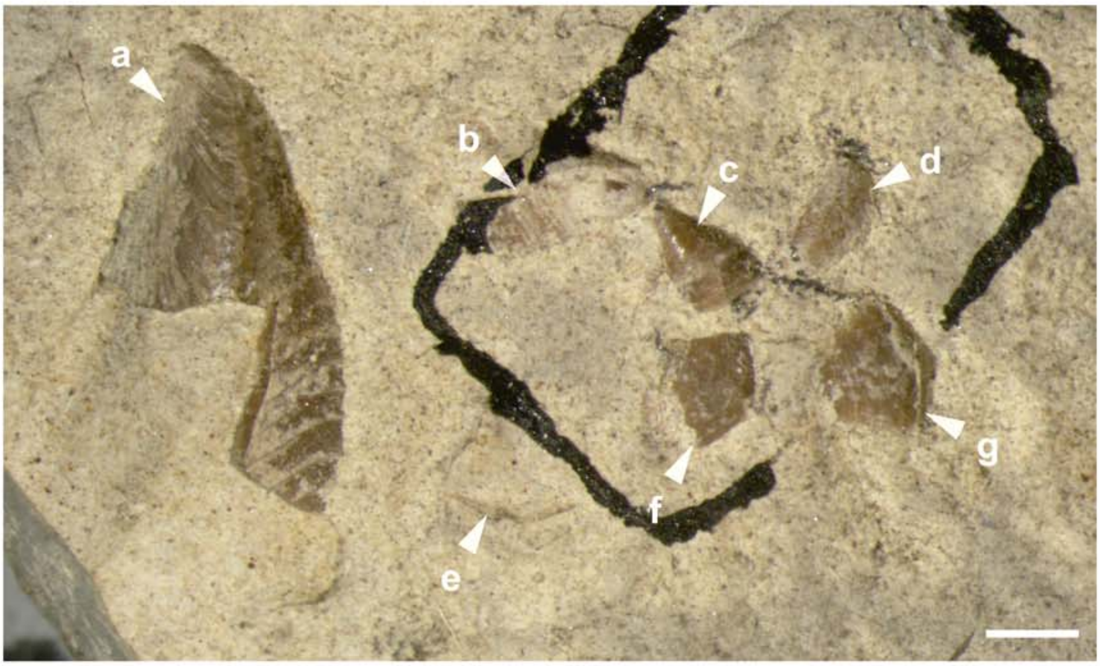

PLATE 4


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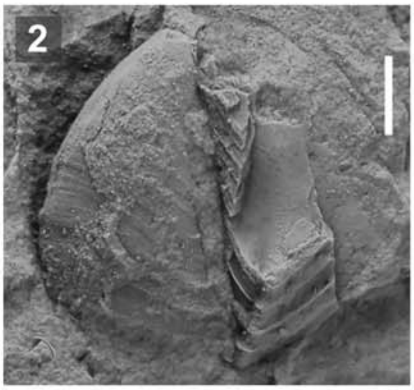
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Paper IV

Kočová Veselská, M., Kočí, T., Kubajko, M. 2014. Dynomenid crabs (Decapoda, Brachyura) and stalked barnacles (Cirripedia, Scalpelliformes) from upper Cenomanian-lower Turonian nearshore, shallow-water strata in the Bohemian Cretaceous Basin, Czech Republic. *Scripta Geologica 147*, 49–81.

Dynomenid crabs (Decapoda, Brachyura) and stalked barnacles (Cirripedia, Scalpelliformes) from upper Cenomanian-lower Turonian nearshore, shallow-water strata in the Bohemian Cretaceous Basin, Czech Republic

M. Kočová Veselská, T. Kočí & M. Kubajko

Kočová Veselská, M., Kočí, T. & Kubajko, M. Dynomenid crabs (Decapoda, Brachyura) and stalked barnacles (Cirripedia, Scalpelliformes) from upper Cenomanian-lower Turonian nearshore, shallow-water strata in the Bohemian Cretaceous Basin, Czech Republic. *In*: Fraaije, R.H.B., Hyžný, M., Jagt, J.W.M., Krobicki, M. & Van Bakel, B.W.M. (eds.), Proceedings of the 5th Symposium on Mesozoic and Cenozoic Decapod Crustaceans, Krakow, Poland, 2013: A tribute to Pál Mihály Müller. *Scripta Geologica*, **147**: 49-81, 3 figs., 2 tables, 6 pls. Leiden, October 2014.

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Key words – Dromioidea, Graptocarcininae, Thoracica, Upper Cretaceous, palaeoecology.

Crustacea (dynomenid crabs and cirripedes) from the upper Cenomanian-lower Turonian nearshore, shallow-water bioclastic limestones to marly siltstones found along the southern and eastern margins of the Bohemian Cretaceous Basin (BCB) are described. Crabs are rather rare in this area, and mostly restricted to fragmentary pereiopods, i.e., isolated claws or dactyli. In view of the confused taxonomy of isolated claws, their proper identity could not be determined; they were mostly referred to the necrocarcinid genus *Necrocarcinus* Bell, 1863. A recent re-examination of material deposited in the collections of the National Museum (Národní Muzeum, Prague), and of new finds, has revealed that all allegedly necrocarcinid pereiopods and nearly all carapaces from these shallow-water strata actually belong to the dynomenid *Graptocarcinus* Roemer, 1887 (carapaces) and the 'form genus' *Roemerus* Bishop, 1983 (isolated claws). Here we present a summary report of occurrence of these dynomenid genera in the BCB. Cirripedes are more abundant, yet all available material is in the form of disarticulated, isolated capitular plates, which is typical for almost all Mesozoic thoracicans. More than 400 capitular plates of stalked barnacles have been discovered in sieve residues during the last decade. A study of newly recovered specimens, together with a revision of material contained in museum collections, has resulted in the description of a new species of the genus *Zeugmatolepas* Withers, 1913 and confirmation of the occurrence of '*Scillaelepas*' *conica* (Reuss, 1844), *Titanolepas tuberculata* (Darwin, 1851), *Smilium*? *parvulum* (Withers, 1914), *Cretiscalpellum glabrum* (Roemer, 1841), *C. striatum* (Darwin, 1851) and *Arcoscalpellum angustatum* (Geinitz, 1843).

Contents

Introduction

Despite almost two centuries of palaeontological research in the Bohemian Cretaceous Basin (BCB), our knowledge of crabs from the nearshore/shallow-water deposits remains poor. The material studied herein was extensively recorded by Fritsch & Kafka (1887) and Frič (1911). Since then the systematics and taxonomy have changed significantly and much of the material from museum collections is in need of a modern revision (Veselská, 2009, 2011). Moreover, numerous new isolated crab claws and dactyli have been recovered during the last decade from nearshore, shallow-water facies of the BCB. Well-preserved carapaces and first pereiopods, often with major and minor chelae, of decapod crustaceans have been considered relatively well represented in the pelagic facies of the BCB; nearly one hundred specimens are known to date, including historical and newly collected ones. The fossil record of decapods from the nearshore deposits is rather scanty, and so far limited to fragments of brachyuran crabs. Unfortunately, crab carapaces are very rare and mostly poorly preserved, lacking associated chelipeds.

Brachyuran crabs. It is clear that conditions conducive to preservation of small crabs in nearshore, shallow-water deposits of the BCB were poor, which explains the paucity of carapaces in the area. Fritsch *in* Fritsch & Kafka (1887, p. 47, pl. 10, figs. 2, 10, 11, 13; p. 48, pl. 10, fig. 12, respectively) erected *Necrocarcinus avicularis* to accommodate isolated brachyuran chelipeds and (*Cancer*?) *modestus* [*sic*] for caparaces from nearshore deposits in the BCB. That author noted (Fritsch *in* Fritsch & Kafka, 1887, p. 49) that carapaces of the second taxon came from the same horizon and from the same locality as chelipeds of *N. avicularis*. Glaessner (1929) considered that remains of (*C*?). *modestus* were indeterminate. Later, Förster (1968) synonymised, albeit with a query, (*C*?). *modestus* with *Graptocarcinus integrimarginatus* Wright & Wright, 1950 (a junior synonym of *G. texanus* Roemer, 1887), a decision subscribed to by Wright & Collins (1972, p. 54), who provisionally synonymised (*C*?). *modestus* with *G. texanus.* Fraaye (1996) subsequently noted that morphologically (*C*?). *modestus* was very close to *G. muiri* (another junior synonym of *G. texanus*, see below). Schweitzer *et al.* (2010) assigned *N. avicularis* to *Necrocarcinus*, while (*C*?). *modestus* was erroneously listed under *Cancer*. Jagt *et al.* (2010) preferred to use parataxonomy for such cases and noted that isolated claws of *N. avicularis* would also be best assigned to the 'form genus' *Roemerus* Bishop, 1983, which was considered to be a dynomenid, since it co-occurred with carapaces. Subsequently, Veselská (2011) and Van Bakel *et al.* (2012) proposed that both the claws (Fritsch & Kafka, 1887, pl. 10, figs. 2, 10, 11) and the carapace fragment (Fritsch & Kafka, 1887, pl. 10, fig. 12) could belong to *Graptocarcinus*, but that the material was too fragmentary and dissociated to be certain.

In addition, a note on the inconsistency in Fritsch's usage of the name (*Cancer*?) *modestus* is called for. In the paper in which (*C*?). *modestus* is erected (Fritsch & Kafka, 1887, p. 49), the captions of the figures read *Necrocarcinus avicularis*. The same name is used also in a later paper (Frič, 1911), despite the fact that he had previously (1887, p. 49) considered the carapaces of (*C*?). *modestus* and chelipeds of *N. avicularis* not to represent the same taxon.

Cirripedes. The first studies dealing with cirripedes from the BCB are those by Reuss (1844, 1845-1846, 1864), followed by Kafka (1885), Fritsch & Kafka (1887), Frič (1911) and Withers (1935). The last-named listed eleven species, mentioning also the collections of A. Frič and J. Šulc. Moreover, numerous new finds of cirripede capitular plates (some 400 specimens) have been made during the last decade. During 2001-2013, the authors conducted several field campaigns at Velim, Kamajka and Chrtníky (situated along the southeast margin of the BCB), where more than 200 kg of residue were amassed and sieved (1 mm mesh width). Our analyses of newly recovered specimens, together with a re-examination of material from museum collections, have resulted in the description of a new species of *Zeugmatolepas* (Kočová Veselská *et al*., in press) and confirmation of the occurrence of the scalpelliform cirripedes *Cretiscalpellum glabrum*, *C. striatum*, *Arcoscalpellum angustatum*, *Zeugmatolepas cretae* (Steenstrup, 1837) and *Smilium*? *parvulum* in the nearshore, shallow-water deposits of the BCB (Kočí & Kočová Veselská, 2012a, b, 2013a, b). All material studied is preserved as disarticulated, isolated capitular plates, which is typical of almost all Mesozoic thoracicans. A preliminary

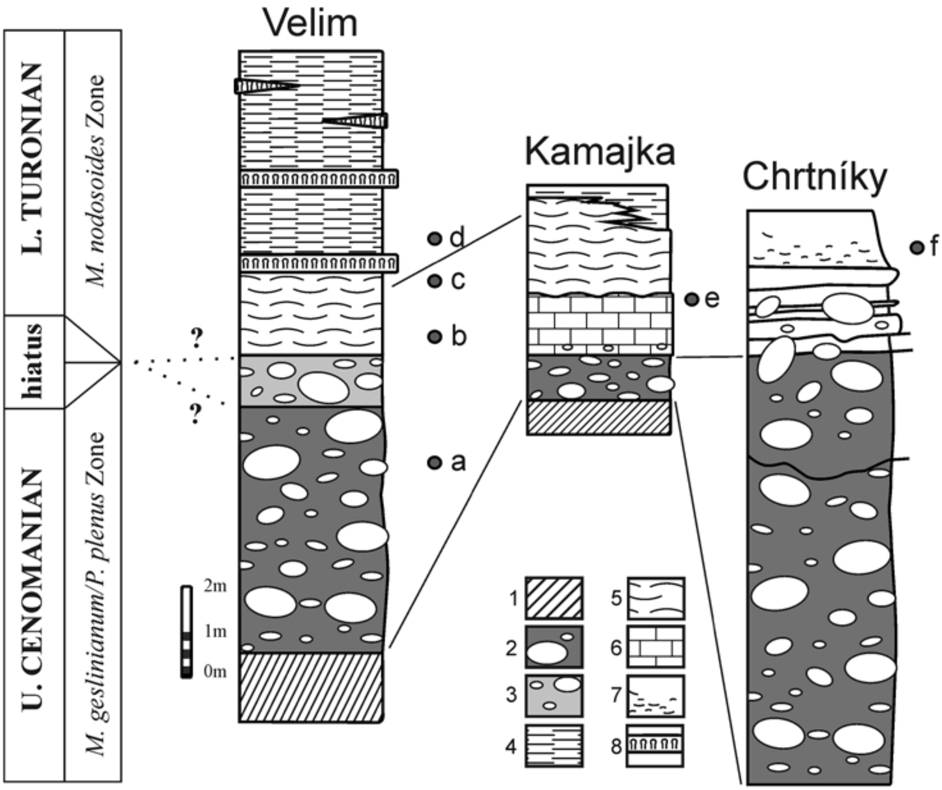

Fig. 1. Stratigraphic provenance of crabs and cirripedes. A. Velim, B. Kamajka, C. Chrtníky. Legend: 1 – crystalline basement; 2 – basal Cenomanian conglomerate; 3 – redeposited Turonian conglomerate; 4 – marly siltstone with intercalations of phosphatised horizon; 5 – organodetritic clayey limestone; 6 – organodetritic limestone with calcitiic-clayey matrix; 7 – clayey siltstone with abundant fauna; 8 – sponge ‘meadows’ (modified from Žítt *et al*., 2006; Košťák *et al*., 2010). Lower-case letters indicate the presence of crustacean taxa: a-d – isolated dactyli and cirripede plates; e – crab claws and carapaces; f – one crab claw and isolated dactyli.

study has revealed approximately 180 plates (mainly terga, scuta and carinae) of *C. glabrum* and *A. angustatum*. In contrast, merely a single carina of *S.*? *parvulum* and one scutum of *C. striatum* are known from the area (Kočí & Kočová Veselská, 2012a, b).

Geography and stratigraphy

The present material comes from nearshore, shallow-water deposits situated along the southern and eastern margin of the BCB, which are interpreted to have been laid down under high-energy conditions (Žítt *et al*., 1997a, b). Currently, these outcrops are overgrown and, in part, covered in scree (Žítt & Nekvasilová, 1994; Žítt *et al*., 1999). Newly recovered specimens come from Velim (GPS co-ordinates: 50°3′38.14″N, 15°7′46.34″E), Kamajka (GPS co-ordinates: 49°57′45.790″N, 15°22′19.163″E) and Chrtníky (GPS co-ordinates: 49°58′36.875″N, 15°36′25.421″E), which are situated approximately 60-100 km east of Prague in the vicinity of Kolín (Figs. 2, 3), where nearshore, shallow-water sediments are exposed in depressions of metamorphic rocks. Whereas strata containing cirripedes and brachyuran crabs at Kamajka and Chrtníky are exclusively of early Turonian age, crustaceans from Velim are from both upper Cenomanian and lower Turonian nearshore sediments. Unfortunately, the exact correlation between the localities is complicated by frequent non-sequences and redeposition of older faunas. The sedimentation was also influenced by palaeohydrodynamics, palaeogeography, clast distribution and character and abundance of detrital material (Žítt & Nekvasilová, 1989, 1994, 1996; Žítt, 1992; Hradecká *et al*., 1994; Žítt *et al*., 1999, 2006). Generally, the horizont yielding crabs and cirripedes is developed in characteristic facies. Lithologically, these consist of bioclastic limestones to marlstones and siltstones with sponges at Chrtníky, of organodetritic clay limestones at Kamajka and /or calcareous siltstones with abundant organodetritus at Velim and Kamajka. The rich fauna from Velim was studied and described in detail by Žítt *et al*. (1997a, b) and rich fossil communites from Chrtníky were examined by Žítt *et al*. (2006). The stratigraphic position of crabs and cirripedes is shown in Fig. 1.

Material and methods

All specimens (Fritsch's original material together with newly collected isolated chelipeds or dactyli and cirripede capitular plates) are deposited in the palaeontological collections at the National Museum (Prague) and at the Natural History Museum (London).

Between 2001 and 2013, the authors conducted field work at Velim, Chrtníky and Kamajka, during which an additional 200 kg of rubble were amassed and sieved (Fig. 1). These sessions have confirmed the occurrence of isolated dactyli and cirripede plates. Material is rich in sabellid and serpulid worms, bryozoans, bivalves and echinoderms (especially crinoids), but unfortunately none of these are key index taxa. Macrofaunal elements associated are listed in Table 1. An additional crustacean collection was deposited in the basement of the National Museum (NM); this was put at our disposal. During 2005 and 2010, a total weight of *c*. 40 kg of this residue was washed and screened through a 1 mm-sieve. This yielded 95 cirripede plates belonging to *Zeugmatolepas* n. sp. (Kočová Veselská *et al*., in press). Unfortunately, the original labels

Table 1. Macrofaunal composition of the original sieve residues stored at the National Museum (Prague); see text for explanations.

	rare	**common**
Octocorallia		
Moltkia foveolata (Reuss, 1846)	●	
Sabellid worms		
Glomerula serpentina (Goldfuss, 1831)		●
Serpulid worms		
Dorsoserpula gamigensis (Geinitz, 1875)	●	
Dorsoserpula wegneri (Jäger, 1983)	●	
Propomatoceros sp.		●
Neovermilia ex gr. *ampullacea* (J. de C. Sowerby, 1829)		●
Cementula? cf. *sphaerica* (Brünnich Nielsen, 1931)		●
?*Conorca* sp.	●	
Filogranula cincta (Goldfuss, 1831)	●	
Placostegus zbyslavus (Ziegler, 1984)	●	
Placostegus sp.	●	
Pyrgopolon cf. *tricostata* (Goldfuss, 1831)	●	
Pyrgopolon sp.	●	
Neomicrorbis crenatostriatus subrugosus (Münster *in* Goldfuss, 1831)	●	
Bryozoa		
Stomatopora sp.		●
Cyclostomata indet.		●
Cheilostomata indet.		●
Brachiopoda		
Terebratulina striatula (Mantell, 1822)	●	
Phaseolina phaseolina (Valenciennes *in* Lamarck, 1819)	●	
Gisilina? *rudolphi* (Geinitz, 1875)		●
Ancistrocrania sp.	●	
Bivalvia		
Amphidonte (A.) *reticulatum* (Reuss, 1846)	●	
Gryphaeostrea canaliculata (J. Sowerby, 1813)		●
Rastellum carinatum (Lamarck, 1819)		●
Rastellum diluvianum (Linnaeus, 1767)		●
Ostreidae gen. et sp. indet.		●
Spondylus sp.	●	
Neithea (*Neithella*) *notabilis* (Münster *in* Goldfuss, 1833)	●	
Neithea (*Neithea*) *aequicostata* (Lamarck, 1819)	●	
Isognomon lanceolatum (Geinitz, 1845)	●	
Gastropoda		
Neritopsis nodosa (Geinitz, 1840)	●	
Echinodermata - Crinoidea		
Isocrinus? cf. *cenomanensis* (d'Orbigny, 1850)		●
Echinodermata - Echinoidea		
Temnocidaris (*Stereocidaris*) *vesiculosa* (Goldfuss, 1829)	●	
Tylocidaris sorigneti (Desor, 1858)	●	
Salenia sp.	●	
Echinodermata - Asteroidea		
Metopaster sp.	●	
Vertebrata - Selachii		
Paranomotodon angustidens (Reuss, 1846)	●	
Scaphanorhynchus rhaphiodon (Agassiz, 1843)	●	

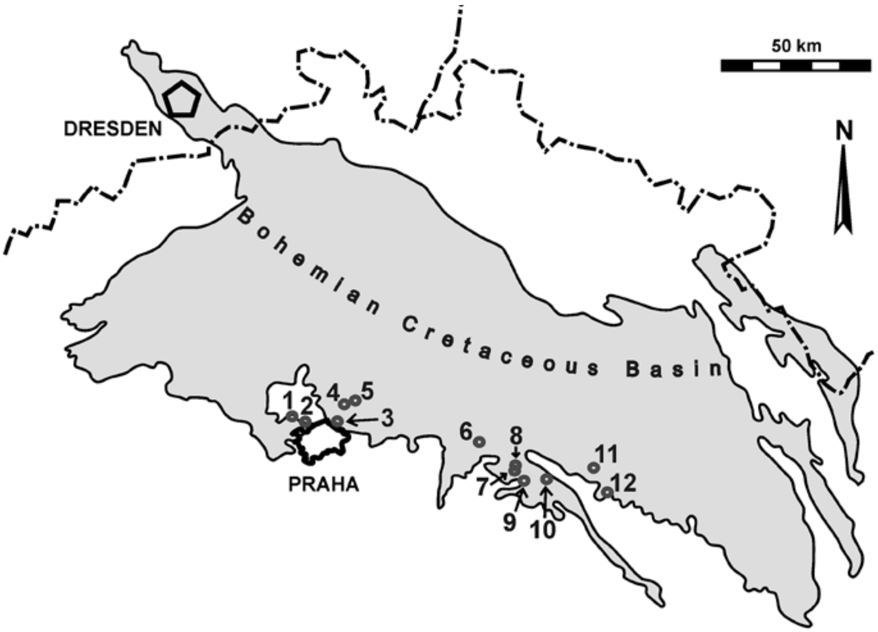

Fig. 2. Simplified map of the Bohemian Cretaceous Basin (BCB, Czech Republic), showing the occurrence (circles) of cirripedes in nearshore, shallow-water deposits, from west to east: 1 - Černovičky (upper Cenomanian), 2 - Kněžívka (lower Turonian), 3 - Odolena Voda (lower Turonian), 4 - Předboj (upper Cenomanian), 5 - Kojetice (upper Cenomanian), 6 - Velim (upper Cenomanian, lower Turonian), 7 - Kaňk (upper Cenomanian), 8 - Turkaňk (lower Turonian) 9 - Karlov (lower Turonian), 10 - Kamajka (lower Turonian), 11 - Chrtníky(lower Turonian) and 12 - Běstvina (lower Turonian).

were lost and the precise stratigraphical position of the material is uncertain. What we do know is that all material comes from an outcrop exposing upper Cenomanian and lower Turonian strata (Žítt *et al.*, 1997a, b). All material is preserved as disarticulated, isolated capitular plates. Some cirripede material and dactyli from now overgrown localities (i. e. Karlov, Běstvina, Černovičky, Předboj, Kněžívka; see Figs. 2, 3) are known only from Žítt & Nekvasilová (1989) and Hradecká *et al.* (1994). The presence of *Cretiscalpellum glabrum* and *Arcoscalpellum angustatum* was also mentioned by Košťák *et al.* (2010) in faunal lists for the localities of Kamajka, Turkaňk and Velim.

To achieve better contrast when photographing the specimens, standard procedure using ammonium chloride sublimate was initially adopted (excluding Frič's original NM O4014, which is very fragile). The results were, however, unsatisfactory, which is why different photographic documentation was used. Frič occasionally painted or varnished the specimens to enhance contrast of the fossil – as a result, many details are obscured by painting and proper re-examination is hampered. This is also true for grooves on the dorsal surface of (*Cancer*?) *modestus* (as here interpreted). Photographs of Frič's original crab material were taken under low-angle light, using a Canon EOS 550D digital camera. Photographs of other cirripede capitular plates were taken using scanning electron microscope (SEM) Hitachi S-3700N in low vacuum at the NM (Prague) and JEOL JSM-6380LV in low vacuum at the Institute of Geology and Palaeontology

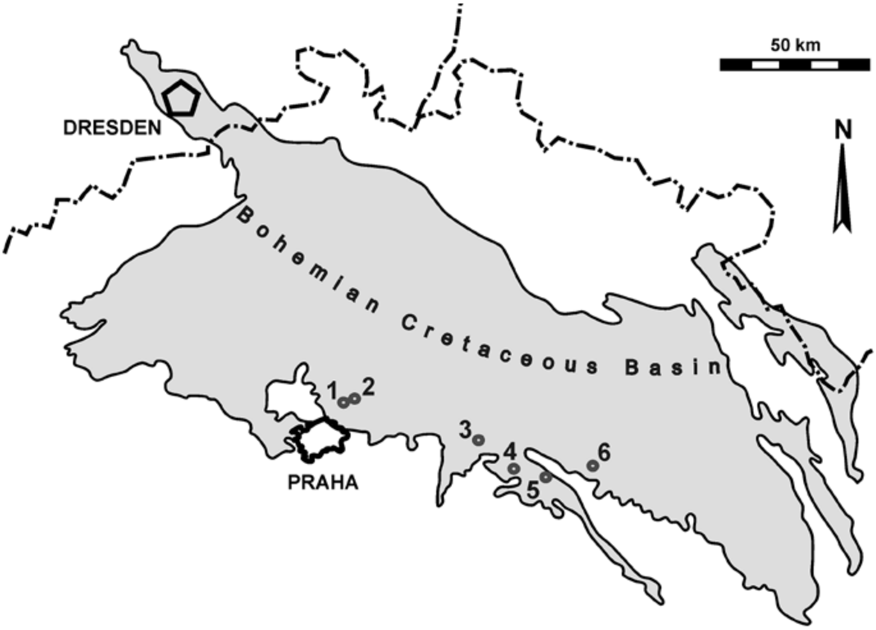

Fig. 3. Simplified map of the Bohemian Cretaceous Basin (BCB, Czech Republic), showing the occurrence (circles) of *Graptocarcinus texanus* Roemer, 1887 and *Roemerus avicularis* (Fritsch *in* Fritsch & Kafka, 1887) in nearshore, shallow-water deposits, from west to east: 1 - Odolena Voda (lower Turonian), 2 - Předboj (upper Cenomanian), 3 - Kojetice (upper Cenomanian), 4 - Velim (upper Cenomanian, lower Turonian), 5 - Kaňk (upper Cenomanian), 6 - Chrtníky (upper Cenomanian, lower Turonian).

(Charles University, Prague). When using SEM, the specimens were left uncoated, hence the use of low vacuum. 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 X4.

Systematic palaeontology

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Podotremata Guinot, 1977
Subsection Dynomeniformia Guinot, Tavares & Castro, 2013
Superfamily Dromioidea De Haan, 1833
Family Dynomenidae Ortmann, 1892
Subfamily Graptocarcininae Van Bakel, Guinot, Corral & Artal, 2012
Genus *Graptocarcinus* Roemer, 1887

Type species – *Graptocarcinus texanus* Roemer, 1887, by monotypy.

Species included – See Klompmaker (2013, p. 152).

Graptocarcinus texanus Roemer, 1887
Pl. 1, figs. 1-4.

1887 *Graptocarcinus texanus* Roemer, p. 173, text-fig.
1887 (*Cancer*?) *modestus* Fritsch *in* Fritsch & Kafka, p. 49, pl. 10, fig. 12.
1911 *Necrocarcinus avicularis* Fritsch; Frič, p. 71, fig. 300c.
?1972 *Graptocarcinus texanus* Roemer; Wright & Collins, p. 55 (with synonymy).
?1996 *Graptocarcinus muiri* Stenzel; Fraaye, p. 463.

Material – Three poorly preserved, partially crushed carapaces, lacking chelipeds or other appendages (NM O4015, NM O4016 and NM O7147) from the lower Turonian calcareous siltstones at Kamajka. NM O4015 and NM O4016 are the originals of Fritsch *in* Fritsch & Kafka (1887), and both are syntypes of (*Cancer*?) *modestus*. NM O4015 is designated lectotype herein.

Diagnosis – See Wright & Collins (1972, p. 54).

Description – Carapace transversely oval in outline, wider than long. Dorsal surface convex longitudinally and transversely, nearly flat in central part. Orbitofrontal margin narrow, broken, only right orbit preserved (NM O7147; Pl. 1, figs. 3, 4), small, rather shallow, with slightly upturned rim bordered by row of granules; left orbit and rostrum absent; anterolateral margins slightly convex, right one with preserved granulated flanged rim; posterolateral margins poorly preserved, straight, about the same length as anterolateral; posterior margin not preserved. Cervical groove distinct, well developed, broadly V-shaped, as wide as fronto-orbital margin, interrupted in median part; branchial grooves indistinct, shorter and weaker (preserved only in NM O4015), defined only in their anterior parts as converging grooves, parallel to cervical groove. Carapace surface damaged (mainly in NM O4016), uniformly ornamented with large, blunt granules, mostly with hollow tops and surrounded by numerous minute setal pits.

Remarks – (*Cancer*?) *modestus*, as originally described by Fritsch *in* Fritsch & Kafka (1887), is based only on three rather poorly preserved, fragmentary carapaces the morphology of which is typical of graptocarcinines. Unfortunately, Fritsch *in* Fritsch & Kafka (1887) did not state which one of the two originally described carapaces of (*C*?). *modestus* was the holotype, which means that both need to be considered syntypes. In view of the fact that in the original paper only specimen NM O4015 was illustrated (as pl. 10, fig. 12, under the name of *N. avicularis*), we designate this herein as lectotype of (*C*?). *modestus*.

There are few records of (*Cancer*?) *modestus* in the literature. Wright & Collins (1972, p. 55), who concluded that *G. muiri* was a junior synonym of *G. texanus*, already suspected (*C*?). *modestus* to be synonymous with *G. texanus*. However, subsequently Bishop (1986), Fraaye (1996) and Van Bakel *et al.* (2012) treated *G. muiri* and *G. texanus* as separate species on the basis of differences in carapace shape, tuberculation and variously developed raised margins covered with granules and tubercles. Fraaye (1996, p. 463) also noted that the incomplete carapace illustrated by Fritsch & Kafka (1887) as *Necrocarcinus avicularis* was probably close to *G. muiri*. Specimens of (*C*?). *modestus* are slightly broader and oval in outline rather than pentagonal and show coarser tuberculation.

These features indeed correspond to *G. muiri*. By contrast, (*C*?). *modestus* is very close to *G. texanus* in having developed raised rims covered with granules along the right anterolateral margins (left ones are not preserved) and a groove pattern with a broadly V-shaped cervical groove and a branchial groove in NM O4015. Its absence in other Czech specimens is most likely a function of the poor state of preservation. Finally, Klompmaker (2013, p. 154) considered *G. muiri* to be a junior synonym of *G. texanus*, and discussed all potential differences between these two species (i.e., carapace shape and size, length/width ratio, presence of a rostral protrusion and raised margins covered with granules and tubercles). A variety of features often overlap between these forms and none of the minor differences justifies specific separation.

Nomenclature – Wright & Collins (1972, p. 55) also noted a potential nomenclatorial problem regarding the priority of Fritsch's and Roemer's papers, both published in 1887. We have been unable to ascertain the exact dates. Thus, in the interests of stability and preservation of the long-established name *G. texanus* in its accustomed meaning (ICZN Article 23. 9), we opt for the specific name *texanus* to take precedence over *modestus*.

'Form genus' *Roemerus* Bishop, 1983

Type species – *Roemerus robustus* Bishop, 1983, by original designation.

Diagnosis – For a detailed diagnosis, reference is made to Jagt *et al*. (2010, p. 179).

Roemerus avicularis (Fritsch *in* Fritsch & Kafka, 1887)

Pl. 1, fig. 5 [in part], 7; Pl. 2, figs. 1-10.

*1887 *Necrocarcinus avicularis* Fritsch *in* Fritsch & Kafka, p. 47, pl. 10, figs. 2, 10, 11, 13 (manus only).
1911 *Necrocarcinus avicularis* Fritsch; Frič, p. 71, fig. 300a, b, d.

Types – Five claws (NM O4004, NM O4005, NM O4013, NM O4014 and NM O4018 [part]), the originals of Fritsch (*in* Fritsch & Kafka, 1887), all syntypes. NM O4004 is here designated lectotype. All material comes from the lower Turonian calcareous siltstones at Kamajka.

Material – In addition to the types (see above), numerous isolated dactyli (collective number P/5137c) from the upper Cenomanian at Předboj, Kojetice, Kaňk, Velim and from the lower Turonian at Velim and Chrtníky, plus one claw (NM O7148) from the lower Turonian at Kamajka are available.

Description – Manus subrectangular in outline; upper margin slightly rounded, depressed proximally; lower margin nearly straight, more or less in line with fixed finger; outer and inner surfaces convex longitudinally and transversely, passing rather sharply into broad upper surface; outer surface with short vertical groove close to dactyl articulation, subparallel to distal margin; broad furrow separating finely granular carpal artuculation from remainder of manus; propodus/carpus articulation with distinctive bulge. Surface uniformly covered by rows of large, blunt tubercles mostly with hollow tops, forming slightly curving horizontal lines; and by several smaller tubercles scattered among these lines; tubercles becoming progressively smaller towards fixed finger. Fingers short, stout; moderately curved, strongly downturned dactylus with shallow furrow parallel to arched upper margin and terminating halfway of dactylus length; fixed finger about one quarter of manus length, with one proximal large cusp on occlusal surface near base, deep depression occuring below cusp. Both fixed finger and dactylus covered with several rows of fine granular humps decreasing in size distally and continuing almost to tips.

Remarks – Fritsch *in* Fritsch & Kafka (1887) erected *Necrocarcinus avicularis* to accommodate isolated claws (NM O4004, O4005, O4013 and O4014) and a single carapace fragment, with an unassociated manus preserved on the same matrix slab, NM O4018 (Fritsch & Kafka, 1887, pl. 10, fig. 13) from Kamajka. Nevertheless, he did not state which specimen of *N. avicularis* was the holotype; thus, all are syntypes. In view of the fact that in the original paper specimen NM O4004 is illustrated first and also represents the best-preserved crab cheliped in the original collection, we here designate this lectotype.

Conditions conducive to the preservation of small crabs in nearshore deposits in the BCB were poor, which explains why carapaces in the area are very rare. Excluding three specimens of *Graptocarcinus texanus* (see above) and a carapace fragment (part of NM O4018), no other carapaces are known from the nearshore deposits in this area. In contrast, crab claws and dactyli are common in the nearshore, shallow-water strata in the BCB. However, such isolated decapod appendages are notoriously difficult to identify (Jagt *et al*., 2010). Isolated crab chelipeds and dactyli originally described as *N. avicularis* are covered with small tubercles and are rectangular in outline with a distinctive bulge on the propodus/carpus articulation which is typical of graptocarcinines (Jagt *et al*., 2010; Van Bakel *et al*., 2012). Although these chelipeds (NM O4004, O4005, O4013 and O4014, plus a fragment of O4018) come from the same horizon and the same locality, Kamajka, as specimens of *G. texanus*, they have not yet been found articulated with carapaces. Jagt *et al*. (2010) preferred to use parataxonomy for such cases and suggested using the 'form genus' *Roemerus* for isolated dynomenid chelae. In fact, records of carapaces preserving appendages are extremely sparse amongst graptocarcinines, and so far, such preservation is known only in specimens of *Graptocarcinus urbasaensis* Van Bakel, Guinot, Corral & Artal, 2012 from the Upper Cretaceous of northern Spain (Álava and Navarra). Other species of *Graptocarcinus* are only known from carapace material.

A recent re-examination of cheliped remains deposited in the National Museum at Prague has revealed that all alleged necrocarcinid claws or dactyli from nearshore strata in the BCB indeed correspond to the diagnosis of the dynomenid 'form genus' *Roemerus*, in size, ornament, development of fixed and moveable fingers and presence of ovate depressions in dactylus and fixed finger. Although still not found articulated with carapaces, these claws may be conspecific with the co-occurring, carapace-based species, *G. texanus*, at Kamajka.

A re-examination of specimens of *N. avicularis* has also shown that the carapace fragment and manus on the same matrix slab, NM O4018, represent two entirely different taxa. Whereas the manus represents the 'form genus' *Roemerus*, the carapace does not seem to have affinities with dynomenids, but rather is of a necrocarcinid nature. The carapace itself is very poorly preserved, representing merely a small fragment with oblique margin without raised rim; its surface is covered with sparse, large granules (no other structure is present) and no grooves are seen. Thus, the true identity of this carapace (Fritsch & Kafka, 1887, pl. 10, fig. 13) remains unresolved, at least for the time being.

Subclass Cirripedia Burmeister, 1834
Superorder Thoracica Darwin, 1854
Order Scalpelliformes Buckeridge & Newman, 2006
Family Zeugmatolepadidae Newman, 2004
Genus *Zeugmatolepas* Withers, 1913

Type species – *Zeugmatolepas mockleri* Withers, 1913, by original designation.

Zeugmatolepas n. sp. Kočová Veselská, Kočí & Collins, in press
Pl. 5, figs. 1-13.

Material – Two carinae (NM O7031 and NM O7032), 18 right scuta (NM O7033, NM O7034, NM O7045-7060) and 19 left scuta (NM O7035-O7037, NM O7044, NM O7062-O7077), five right terga (NM O7038, NM O7078-O7081) and nine left terga (NM O7039 [holotype], NM O7082-O7089), plus 27 rostra (NM O7040-O7043, NM O7090-O7112).

Description – Reference is made to Kočová Veselská *et al.* (in press).

Remarks – *Zeugmatolepas cretae* is distinguished by having an elongated apex and subcentral umbo in the scutum, a rhomboidal tergum; in addition, plates are generally smooth. For more details, reference is made to Kočová Veselská *et al.* (in press).

Occurrence (BCB) – ?Upper Cenomanian-lower Turonian (Velim, eastern part).

Stratigraphic range – ?Upper Cenomanian-lower Turonian.

Family Calanticidae Zevina, 1978
Genus *Cretiscalpellum* Withers, 1922

Type species – *Pollicipes unguis* J. de C. Sowerby, 1836, by original designation.

Cretiscalpellum glabrum (Roemer, 1841)
Pl. 6, figs. 1-7.

1935 *Cretiscalpellum glabrum* (Roemer); Withers, p. 161, pl. 15, figs. 8-17; pl. 16, figs. 1-20; pl. 17, figs. 1-21; pl. 18, figs. 1-5 (with additional synonymy).
1999 *Cretiscalpellum glabrum* (Roemer); Jagt & Collins, p. 102, figs. 2A, 6A-I.
2013a *Cretiscalpellum glabrum* (Roemer); Kočí & Kočová Veselská, p. 109, figs. 24, 25.
2013 *Cretiscalpellum glabrum* (Roemer); Jagt, p. 251, figs. 11, 12.

Material – 75 carinae, 45 scuta, four carinal latera, one rostral latus, 42 right terga, 47 left terga, 70 fragmentary terga (left and right), plus a single rostrum. All these specimens are deposited in the collections of the National Museum (Prague).

Description – Carina with obtuse apex, lacking parietes and intraparietes. Median ridge of carina distinct. Lateral margins of carina slightly rounded inwards. Carinal surface at first glance appearing smooth, but under microscope distinct sharp lines parallel to basal margin visible. Tergum of subrhomboidal shape. In first third, apicoscutal groove in form of narrow channel, parallel to occludent margin. Distinct median furrow from apex. Basal angle between scutal and carinal margins sharp. Surface with distinct grooves parallel to scutal margin, leading to grooves parallel to basal margin. Occludent margin of scutum straight and basal margin at right angles, tergal margin gradually turning into lateral margin. Surface with fine sharp grooves parallel to basal margin.Tergal lines and lateral surfaces at right angles. From apex two prominent folds, forming flat surface and dividing scutum into four parts. All lines sharp, straight, distinct and typically forming dense network of parallel grooves. Carinal latus square, diagonally divided into two parts, surface with very fine grooves. Rostrum very small, triangular, dorsally convex, one and half times wider than tall, with wide apicobasal ridge. Lateral margin almost straight, basal margin concave in median part under apicobasal ridge and laterobasal margin convex in places.

Remarks – The present species most closely resembles *C. striatum* (see below) which has a wider tergum with a more clearly protruding apicobasal ridge that extends to the laterobasal margin. The carina of *C. striatum* has an apicobasal ridge that is stronger than other longitudinal lines, and also has markedly developed transverse lines. In addition, it has a wider scutum with more distinct longitudinal lines. *Cretiscalpellum bronni* (Roemer, 1841) has a carina which lacks transverse lines and has a less prominent apicobasal ridge. The tergum has a more prominent apicobasal ridge and its shape is elongated rhomboidal. *Cretiscalpellum unguis* (J. de C. Sowerby, 1829) differs in having a wider carina with slightly rounded parietes and strongly developed transverse lines. The tergum of *C. unguis* is more elongated with a rounded carinal margin, while the scutum is wider in the basal part, the lateral part being narrow and curved inwards. The early Campanian *C. obtusum* Jagt & Collins, 1989 has a more convex, trapezoidal scutum in which the apicobasal ridge is broad, with distinct longitudinal and transverse lines.

Occurrence (BCB) – Upper Cenomanian at Velim and ?Černovičky; lower Turonian at Velim, Kamajka, Turkaňk, Karlov, Odolena Voda, Běstvina and Chrtníky.

Stratigraphic range – Upper Albian-upper Maastrichtian.

***Cretiscalpellum striatum* (Darwin, 1851)**

Pl. 6, fig. 8.

1935 *Cretiscalpellum striatum* (Darwin); Withers, p. 183, pl. 20, figs. 1-5, 15-21; pls. 21, 22 (with additional synonymy).
1989 *Cretiscalpellum striatum* (Darwin); Jagt & Collins, p. 189, fig. 4l, m.
1999 *Cretiscalpellum striatum* (Darwin); Collins & Jagt, p. 159, figs. 2C-E, 3A-G.
2000 *Cretiscalpellum striatum* (Darwin); Carriol & Collins, p. 142, pl. 1, fig. 5.
2002 *Cretiscalpellum striatum* (Darwin); Carriol & Collins, p. 5, pl. 1, fig. 5.
2013a *Cretiscalpellum striatum* (Darwin); Kočí & Kočová Veselská, p. 113, figs. 26, 27.
2013 *Cretiscalpellum striatum* (Darwin); Jagt, p. 250, figs. 8-10.

Material – A single left tergum (NM O7461) from the lower Turonian at Velim, in the collections of the National Museum (Prague).

Description – Tergum elongated and irregularly rhomboidal. Apical umbo sharp and slightly curved. Apicobasal ridge distinct and sharp. Occludent margin straight; scutal margin forming angle of 50° with occludent margin. Longitudinal lines on carinal part of tergum clear and distinct. Apicobasal groove near scutal margin, ending at scutal margin 2 mm from occludent margin. Distinct transverse lines parallel to scutal margin. Inner part smooth and with distinct growth lines of carinal fold near carinal margin.

Remarks – *Cretiscalpellum striatum* has a more elongated tergum than *C. glabrum*. The main distinguishing features are the sharp longitudinal and transverse lines in the former. The congener *C. paucistriatum* (Woodward, 1906) (see Jagt & Van Bakel, 2007) has an elongated tergum, which is much less clearly longitudinally striated to near-smooth and shows a peculiar transverse convexity. *Cretiscalpellum naidini* Alekseev, 2009, from eastern Mangyshlak (lower Campanian), has a markedly convex tergum with very thick axial part and a wide occludent rib. The carina of *C. sharapovi* Alekseev, 2009, also from eastern Mangyshlak (lower Campanian), has a thick apical part, covered by narrow ribs.

Occurrence (BCB) – Lower Turonian at Velim. *Cretiscalpellum striatum* was also mentioned from the lower Turonian at Velim and Karlov by Žítt & Nekvasilová (1989, p. 86, as *Pollicipes costatus* Kafka) and from coeval levels at Běstvina by Žítt & Nekvasilová (1994, p. 26 as *P. costatus* Kafka).

Stratigraphic range – Lower Cenomanian-upper Maastrichtian.

Genus *Scillaelepas* Seguenza, 1876

Type species – *Pollicipes carinatus* Philippi, 1836, by original designation.

'*Scillaelepas*' *conica* (Reuss, 1844)

Pl. 3, figs. 1-16.

Synonymy – See Withers (1935, p. 120).

Material – All material from Kaňk is deposited in the collections of the Natural History Museum (Department of Palaeontology, London); this comprises five scuta (NHM In. 16739-40, In. 16742-45), one carina (NHM In. 16746), one rostrum (NHM In. 16747) and four terga (NHM In. 16753-56).

Description – For a detailed account, reference is made to Withers (1935, pp. 120-122), who described material collected by A. Frič in 1897 and subsequently sold to the NHM London.

Remarks – Frič (1889a, b) referred to the type specimen of Reuss (1844, p. 216) from Kyselka near Bílina (Reuss's Sauerbrunnberges) in his account of the 'Teplitzer Schichten', while earlier Fritsch (*in* Fritsch & Kafka, 1887) had recorded this species from the Priesener Schichten (now Březno Formation) at Luschitz. Frič (1911), in his account of the upper Cenomanian (now Korycany Member), mentioned but a single occurrence, from Kyselka (Sauerbrunnberges), but did not present any illustration. More detailed remarks were made by Withers (1935, p. 121).

Occurrence (BCB) – Upper Cenomanian at Kaňk; and ?upper Turonian at Kyselka, ?lower Coniacian at Luschitz.

Stratigraphic range – Upper Cenomanian (-?lower Coniacian).

Genus *Titanolepas* Withers, 1913

Type species – *Scalpellum tuberculatum* Darwin, 1851, by original designation.

Titanolepas tuberculata (Darwin, 1851)

Pl. 4, fig. 1.

1935 *Calantica* (*Titanolepas*) *tuberculata* Darwin; Withers, p. 130, pl. 11, figs. 1-10; pl. 12, figs. 1-3 (with additional synonymy).

1983 *Calantica* (*Titanolepas*) *tuberculata* Darwin; Collins *in* Viaud *et al*., p. 330, pl. 3, figs. 3-5.

Material – A single poorly preserved tergum from Kamajka (NM O3407), plus a similarly preserved tergum (NM O7462) from Velim, both deposited in the collections of the National Museum (Prague).

Description – Tergum diamond shaped, elongated. Apicobasal ridge almost straight and very prominent. Apicobasal ridge thickening towards very acute basal angle. Surface more highly ornamented, longitudinal ribs crossing transverse ribs and creating short blunt spines.

Remarks – *Titanolepas tuberculata* is distinguished from *T. subtuberculata* Withers, 1935 in that the latter has a sigmoidally curved apicobasal ridge and the prominent, coarse, close-set lines on the tergum are finer and less numerous. Another species, *T. martini* (Withers, 1913), from the upper Senonian (Niobrara Group) of Kansas, is differentiated by a subcentral scutum.

Occurrence – Lower Turonian at Kamajka and at Velim. Withers (1935) also mentioned some capitular plates of *T. tuberculata* from the ?upper Turonian (*Holaster* [*Sternotaxis*] *planus* Zone) at Na Vinici near Kolín in the southern part of the BCB. Unfortunately, this locality is now completely overgrown; it cannot be determined if a nearshore or a pelagic facies was formerly exposed there. Collections of fossils from this locality made by the palaeontologist Dr J. Šulc included 30 carinae, 29 scuta, 34 terga and five lower latera of *T. tuberculata*, but unfortunately this material was lost during the Second World War, with the exception of six carinae, five scuta, six terga and two lower latera which he had donated to the British Museum (Natural History; now the Natural History Museum, London).

Stratigraphic range – Lower Turonian (?upper Turonian).

Genus *Smilium* Leach, 1825

Type species – *Scalpellum* sp. (*sensu* Darwin 1851).

Smilium? *parvulum* (Withers, 1914)

Pl. 4, figs. 2, 3.

1935 *Smilium* (?) *parvulum* (Withers); Withers, p. 141, pl. 12, figs. 9-15 (with additional synonymy).
2012b *Smilium* (?) *parvulum* (Withers); Kočí & Kočová Veselská, p. 39, fig. 1.
2013a *Smilium* (?) *parvulum* (Withers); Kočí & Kočová Veselská, p. 107, fig. 23.
2013b *Smilium* (?) *parvulum* (Withers); Kočí & Kočová Veselská, p. 149, text-fig. 3.

Material – A single minute carina (NM O7133), 4 mm in length and 1.4 mm in basal width, in the collections of the National Museum (Prague).

Description – Umbo below rounded apex, about one third from apex. Carina rounded in upper third of umbo, not developing longitudinal ridge on tectum. At two-thirds from basal edge, parietes developed; lateral sides with distinct transverse lines. Intraparietes form carinal elongation, rendering beak-like, tapered shape. Growth lines fine, yet distinct. Inner surface smooth, lacking growth lines.

Remarks – Reference is made to Withers (1935), Collins (1974) and Kočí & Kočová Veselská (2013a, b).

Occurrence (BCB) – Lower Turonian (possibly *Mytiloides labiatus* Zone) at Velim.

Stratigraphic range – Upper Albian-upper Turonian.

Family Scalpellidae Pilsbry, 1916
Subfamily Arcoscalpellinae Zevina, 1978
Genus *Arcoscalpellum* Hoek, 1907

Type species – *Arcoscalpellum velutinum* Hoek, 1907, by original designation.

Arcoscalpellum angustatum (Geinitz, 1843)

Pl. 4, figs. 4-9.

1935 *Arcoscalpellum angustatum* (Geinitz); Withers, p. 215, pl. 25, figs. 2-20; pl. 26, fig. 1 (with additional synonymy).
1983 *Arcoscalpellum angustatum* (Geinitz); Collins *in* Viaud *et al.*, p. 330, pl. 3, figs. 6, 7; pl. 4, figs. 1-3, 5.
2013a *Arcoscalpellum angustatum* (Geinitz); Kočí & Kočová Veselská, p. 116, figs. 28-36.

Material – Two carinal latera from Velim (eastern part); 27 carinae, one scutum, ten terga (one of them complete), 16 carinal latera, and three upper latera from Velim (western part). All material is deposited in the collections of the National Museum (Prague).

Description – Carina narrowly expanding to basal margin with sharp apex. Tectum almost flat. On both sides of tectum prominent straight edges. On tectal transverse lines, V-shaped. Fine longitudinal lines may occur, inclusive of distinct median line. Parietes narrow, concave and forming almost right angle with tectum. Intraparietes wider than parietes. Intraparietes separated from parietes by thick protruding, distinct ridges. Intraparietes convex in upper basal half. Surface with fine and distinct lines almost parallel to transverse lines of tectum. Carina light to dark brown in colour (?original colour); abraded material white. Carina of square cross section. Scutum trapezoidal, elongated. Cross section slightly convex, length about twice width. Occludent margin straight or slightly curved and basal margin at right angles. Edge of occludent margin bending inwards. Basal margin slightly concave to straight. Lateral margin extending to about two-thirds of scutal height and tergal margin in first third of scutal height. Apicobasal margin distinct and rounded. Towards lateral and tergal margins, area of scutum slightly sloping. Lateral margin convex. Tergolateral angle distinct. Inner surface with deep indentation for adductor muscle. Small indentation near occludent margin. Tergum subtriangular, flat, elongated, more than twice longer than wide. Occludent margin straight, with blunt scutal angle. Carinal margin almost straight. Apicobasal groove distinct. Surface with bold lines, V-shaped, inner surface smooth. Occludent and carinal margins bowed, indistinct protruding growth lines in inner part of tergum.

Carinal latus wide, triangular in shape with rounded, unequal sides. Apex of right carinal latus curved to left and left carinal latus curved to right. Carinal margin perpendicularly cut at right angles. Central rib extending from apex to basal margin distinct. Surface with grooves, parallel to basal margin. Upper latus triangular, equilateral. Basal scutal angle sharp and obliquely bevelled. Tergal basal angle obtuse. Apex apical, umbo subapical. Scutal margin slightly concave, tergal margin convex to almost straight. Convex basal margin thinned. Flat groove from apex along tergal margin, steep slopes in scutal part. Distinct edge near tergal and scutal margins. Between inner surface and edge, longitudinal strip ending at apex. Inner surface smooth and flat. Outer surface with growth lines parallel to basal margin.

Remarks – *Arcoscalpellum angustatum* is very close to *A. fossula* (Darwin, 1851), but is differentiated by carinal, tergal and scutal construction. The carina of *A. fossula* has more prominent ridges along the tectum and parietes are visible from above, the tergum differing by the presence of apicoscutal grooves and a more protruding apex. The scutum of *A. fossula* has a more clearly curved apex, the inner structure of near the tergal margin being closer to the apex, with deeper and longer depressions and the scutal margin closer to the apex being higher. Upper latera of *A. fossula* have undulate growth lines. *Arcoscalpellum lineatum* (Darwin, 1851) differs in showing longitudinal lines on the carinal tectum, plus narrower terga and wider scuta, while *A. maximum* (J. de C. Sowerby, 1829) is larger and the scutum has a weaker apicobasal ridge and generally finer transverse and longitudinal ornament. The carina of *A. maximum* has a well-developed apicobasal ridge.

The carinal latus of *A. angustatum* coincides with the original description by Kafka (1885) of a specimen from Kamajka. In shape, this resembles the carinal latus of *A. fossula*, which has a more curved apex, a wider median groove and better-developed lines that are parallel with the basal margin. The most strongly developed grooves parallel to the basal margin are found in the carinal latus of *A. gracile* (Bosquet, 1854), but this has a less pronounced central rib running from the apex to the basal margin.

Occurrence (BCB) – Upper Cenomanian and lower Turonian at Velim. Žítt *et al.* (1999, p. 112, as *Scalpellum* sp.) also mentioned the occurrence of *A. angustatum* in the upper Cenomanian at Předboj and Černovičky, as well as from the lower Turonian at Velim, Kamajka, Turkaňk and Kněžívka (Žítt *et al.*, 1999, p. 112, as *Scalpellum crassum* Kafka). Other records include Žítt & Nekvasilová (1994, p. 26, as *Scalpellum* sp.) from the lower Turonian at Běstvina, and Hradecká *et al.* (1994, p. 19, as *Scalpellum crassum* Kafka) from the lower Turonian at Odolena Voda.

Stratigraphic range – Albian-lower Santonian.

Palaeoecology and palaeogeography

Dynomenid crabs are assumed to have inhabited coral-rich carbonate (and siliciclastic) settings, with respect to modifications and adaptations of their claws. Their propodus/carpus and carpus/merus articulations have bulges, which leaves no openings between these articles when bent (Jagt *et al.*, 2010; Van Bakel *et al.*, 2012). This modification probably protected the claws when the crabs moved between coral or sponge colonies or during feeding, similar to extant dynomenids (see McLay, 1999, p. 428). Together with the possession of clumps of stiff setae at the inner and outer margins of fixed and moveable fingers which close the space between both fingers and thus help obtain food by sieving fine sediment, these modifications are characteristic of dynomenids (McLay, 1999; Jagt *et al.*, 2010). Dynomenids from the BCB are also known from coral- or sponge-rich localities. Their distribution, together with cirripedes, is shown in Fig. 1, while the coral-associated fauna from Kamajka, Velim and Chrtníky are tabulated in Table 2.

Table 2. Coral assemblages from nearshore deposits, associated with dynomenid crabs (data from Eliášová, 1989, 1997a, b), Žítt *et al.* (2006) and Košťák *et al.* (2010).

Species	**Kamajka**	**Velim**	**Chrtníky**
Anthophyllum cylindricum (Reuss)	+	+	+
Actinastrea cribellum (Počta)	-	+	-
Synhelia gibbosa (Goldfuss)	+	+	+
Colonicyathus geinitzi Bölsche	-	+	-
Leptophyllia sp.	-	+	-
Microphyllia maeadrinoides (Reuss)	-	+	-
Columellophora velimensis Eliášová	-	+	-
Onchotrochus hatifnatus Stolarski & Eliášová	-	+	-
Arctangia(?) sp.	-	+	-
Misistellidae gen. indet.	-	+	-
Trochosmilia sp.	-	+	+
Moltkia foveolata (Reuss)	+	+	+
Moltkia solidum Počta	+	+	-
corals gen. et sp. indet	+	+	+

Stalked cirripedes are relatively common faunal elements in nearshore/shallow-water facies within the BCB. Cirripedes lived attached to the substrate in high-energy settings, near wave action, i.e., in an environment similar to the one inhabited by the modern genus *Pollicipes* which occurs mostly intertidally on wave-exposed rocky shores (Fernandes *et al*., 2010). However, both *C. glabrum* and *A. angustatum* rather appear in hemipelagic facies in the BCB (see Kočí & Kočová Veselská, 2013a). The bathymetric records of extant members of the genus *Arcoscalpellum* is 46-5,365 m (Pilsbry, 1907) or 1,555-3,028 m (Weisbord, 1977).

Entire cirripede capitula are rare because such preservation requires a tranquil environment with rapid burial by fine sediment. In nearshore, shallow-water deposits from the BCB, cirripedes are found only as disarticulated plates. The commonest types are scuta, rostra and terga. The palaeo-association of cirripedes from Velim consists of *Zeugmatolepas* n. sp., *C. glabrum*, *A. angustatum*, *C. striatum* and *S.*? *parvulum*. Other faunal elements and palaeoenvironmental relationships were discussed by Žítt *et al.* (1997a, b) (see Tables 1, 2). *Zeugmatolepas* n. sp. has a wider wall of capitular plates in comparison to *C. glabrum*, *C. striatum* and *A. angustatum* and was better adapted to a high-energy setting.

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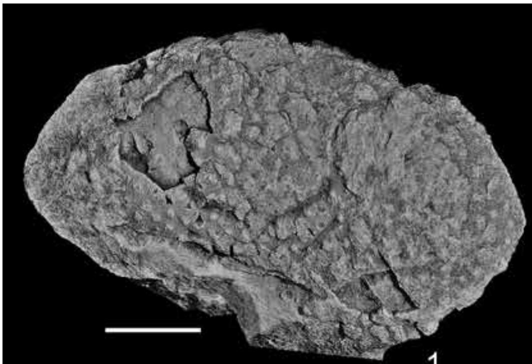
Plate 1

Dynomenid and ?necrocarcinid crabs from the Bohemian Cretaceous Basin. Scale bars equal 5 mm.

Figs. 1, 2. *Graptocarcinus texanus* Roemer, 1887 (NM O4015), lower Turonian, Kamajka; originally described as (*Cancer*?) *modestus* Fritsch *in* Fritsch & Kafka (1887, pl. 10, fig. 12), lectotype (here designated). Carapace in dorsal view and detail of right anterolateral margin bordered by a row of granules, respectively.

Figs. 3, 4. *Graptocarcinus texanus* Roemer, 1887 (NM O7147), lower Turonian, Kamajka. Carapace in dorsal view and detail of right anterolateral margin and orbits bordered by a row of granules, respectively.

Figs. 5-7. Fragmentary carapace of ?necrocarcinid, with associated yet unrelated manus (syntype) of *Roemerus avicularis* (Fritsch *in* Fritsch & Kafka, 1887), preserved on the same matrix slab (NM O4018), lower Turonian, Kamajka. Both carapace and manus were originally described as *Necrocarcinus avicularis* Fritsch *in* Fritsch & Kafka (1887, pl. 10, fig. 13).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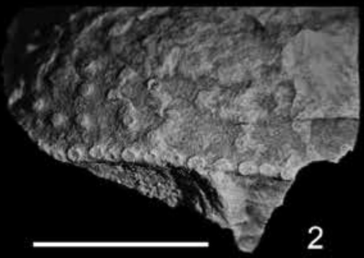
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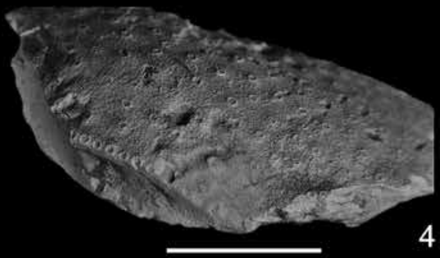
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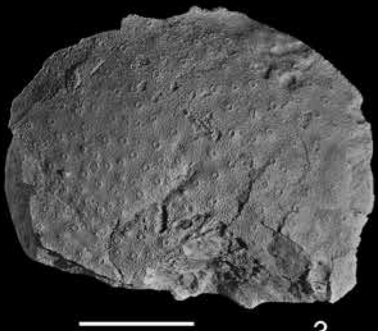
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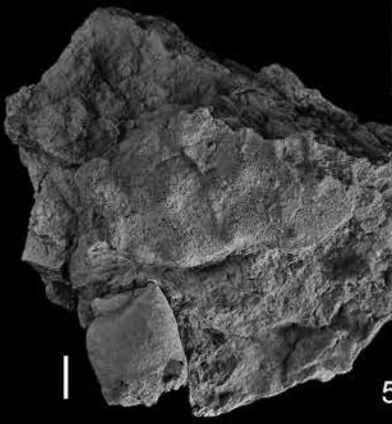
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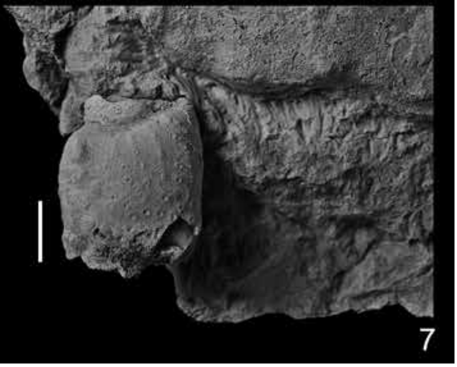
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Plate 2

Isolated claws and dactyli of *Roemerus avicularis* (Fritsch *in* Fritsch & Kafka, 1887). Scale bars equal 2 mm (Figs.1-4) and 5 mm (Figs. 5-8).

Figs. 1, 2. Isolated dactylus (collective number P/5137c), lower Turonian, Chrtníky (layer 7 according to Žítt *et al*., 2006).

Figs. 3, 4. Isolated dactylus (collective number P/5137c), lower Turonian, Velim (pocket Václav).

Fig. 5. Major cheliped lacking fixed and moveable fingers (NM O4014, syntype), lower Turonian, Kamajka; originally described as *Necrocarcinus avicularis* Fritsch *in* Fritsch & Kafka (1887, pl. 10, fig. 11).

Fig. 6. Left claw retaining both fixed and moveable fingers (NM O7148), lower Turonian, Kamajka.

Figs. 7, 8. Left manus (NM 04013, syntype), lower Turonian, Kamajka; originally described as *Necrocarcinus avicularis* Fritsch *in* Fritsch & Kafka (1887, pl. 10, fig. 10), in inner and outer views, respectively.

Fig. 9. Left claw retaining both fixed and moveable fingers (NM O4005, syntype), lower Turonian, Kamajka; originally described as *Necrocarcinus avicularis* Fritsch *in* Fritsch & Kafka, 1887.

Fig. 10. Left claw retaining both fixed and moveable fingers (NM O4004, lectotype, here designated), lower Turonian, Kamajka; originally described as *Necrocarcinus avicularis* Fritsch *in* Fritsch & Kafka (1887, pl. 10, fig. 2a-f).


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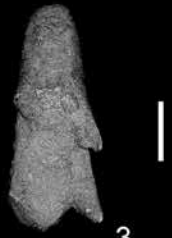
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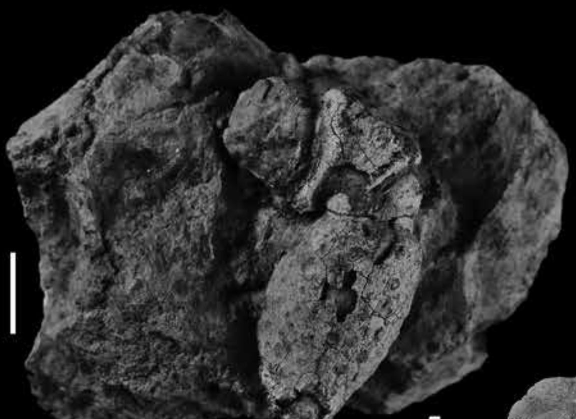
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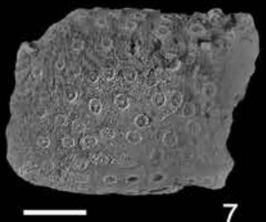
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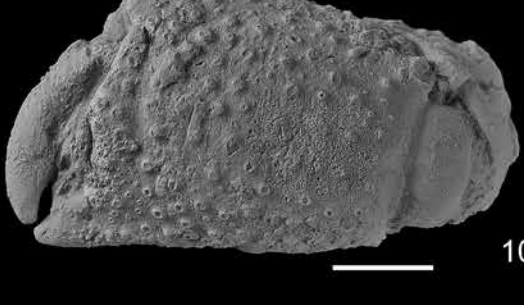
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Plate 3

`*Scillaelepas*' *conica* (Reuss, 1844), upper Cenomanian, Kaňk; all material housed in collections of the Natural History Museum (London). Scale bars equal 1 mm (Figs. 1, 2, 11-16) and 5 mm (Figs. 3-10). Photographed by H. Taylor (NHM, London) and with permission to publish.
Fig. 1. Scutum (NHM In. 16739); outer view.
Fig. 2. Scutum (NHM In. 16740); inner view.
Figs. 3, 4. Scutum (NHM In. 16742); inner and outer views, respectively.
Figs. 5, 6. Scutum (NHM In.16743); inner and outer views, respectively.
Figs. 7, 8. Scutum (NHM In. 16744); inner and outer views, respectively.
Figs. 9, 10. Scutum (NHM In. 16745); inner and outer views, respectively.
Fig. 11. Tergum (NHM In. 16753); outer view.
Fig. 12. Tergum (NHM In. 16754); outer view.
Figs. 13, 14. Carina (NHM In. 16746); outer and lateral views, respectively.
Figs. 15, 16. Carina (NHM In. 16747); lateral and outer views, respectively.

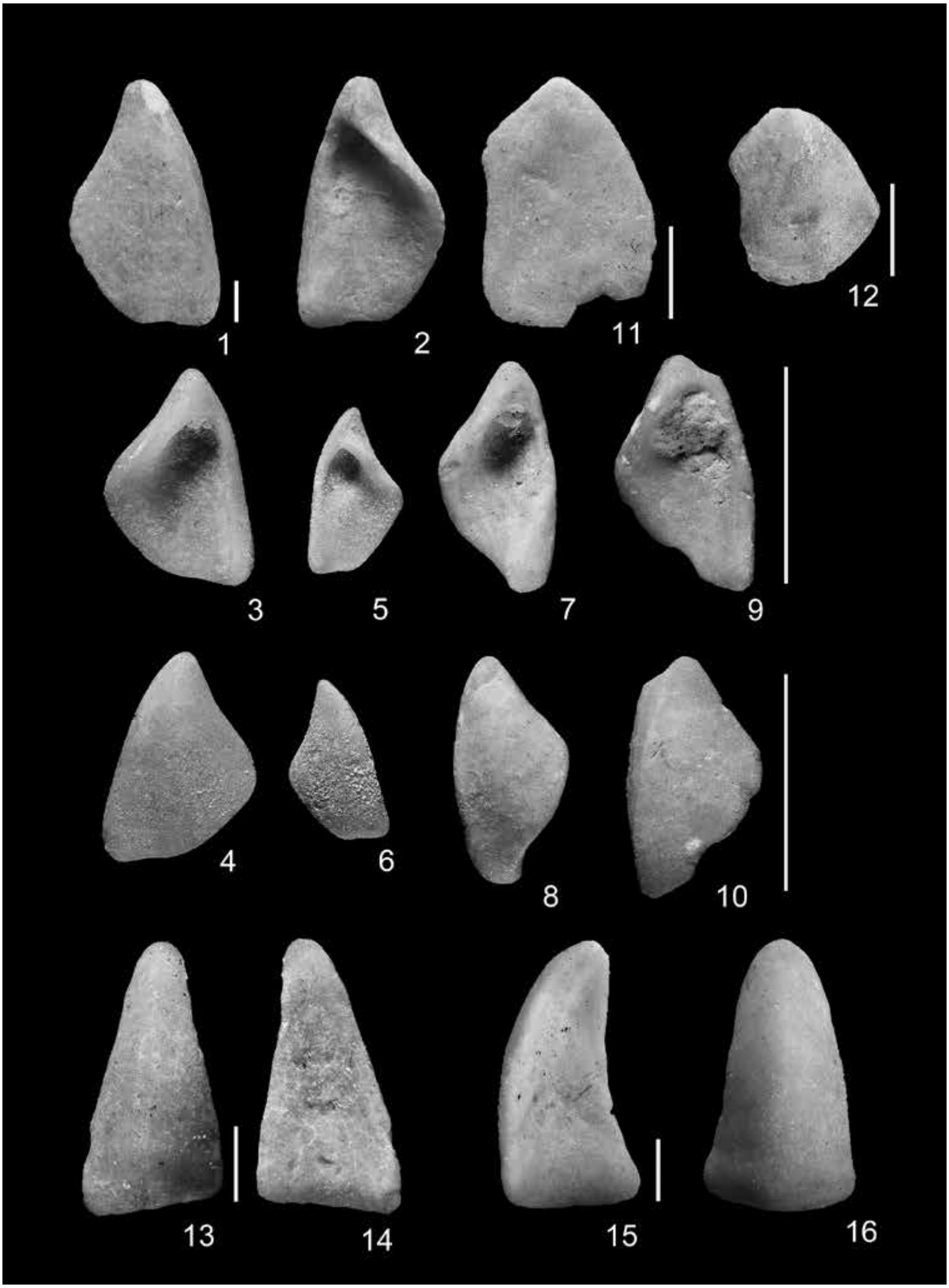
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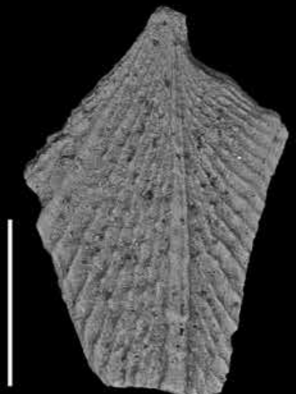
Plate 4

Titanolepas tuberculata (Darwin, 1851), upper Cenomanian, Kamajka. Scale bar equals 0.5 mm.
Fig. 1. Tergum (NM O3407), outer view.

Smilium? *parvulum* (Withers, 1913), lower Turonian, Velim. Scale bar equals 0.5 mm.
Figs. 2, 3. Carina; outer and lateral views, respectively.

Arcoscalpellum angustatum (Geinitz, 1843), lower Turonian, Velim (pocket Václav, western part of quarry). Scale bars equal 2 mm.
Fig. 4. Left carinal latus.
Fig. 5. Right carinal latus.
Fig. 6. Carina.
Fig. 7. Left scutum.
Fig. 8. Right tergum.
Fig. 9. Upper latus.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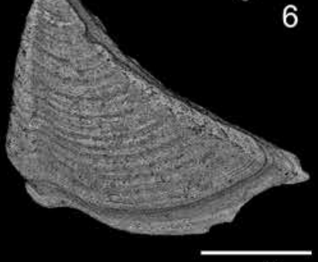
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Plate 5

Zeugmatolepas n. sp. (Kočová Veselská *et al.*, in press); ?upper Cenomanian-lower Turonian, Velim (eastern part). All scale bars equal 0.5 mm.
Figs. 1, 2. Right scutum (NM O7033); outer and inner views, respectively.
Figs. 3, 4. Left scutum (NMO7036); outer and inner views, respectively.
Figs. 5, 6. Right tergum (NM O7038); outer and inner views, respectively.
Figs. 7, 8. Left tergum (NM O7039, holotype); outer and inner views, respectively.
Figs. 9, 10. Rostrum (NM O7041); outer and inner views, respectively.
Figs. 11, 12, 13. Carina (NM O7032); outer, inner and lateral views, respectively.

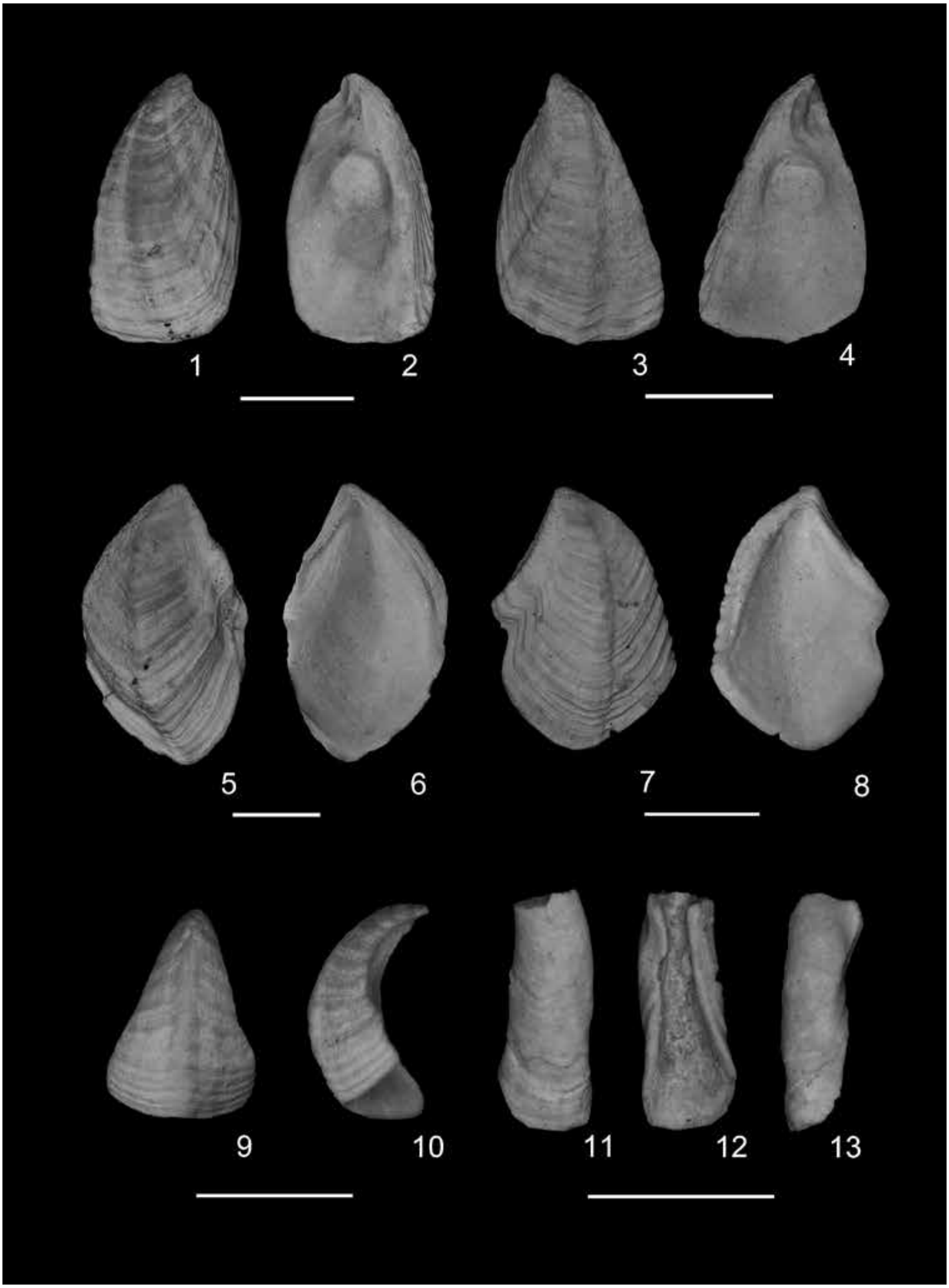
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Plate 6

Cretiscalpellum glabrum (Roemer, 1841), lower Turonian, Velim (pocket Václav, western part of quarry). Scale bars equal 2 mm (Figs. 1-5, 7) and 1 mm (Fig. 6). All in collections of National Museum (Prague).
Fig. 1. Carina.
Fig. 2. Left scutum.
Fig. 3. Right scutum.
Fig. 4. Right tergum.
Fig. 5. Left tergum.
Fig. 6. Rostrum.
Fig. 7. Carinal latus.

Cretiscalpellum striatum (Darwin, 1851), lower Turonian, Velim (pocket Václav, western part of quarry). Scale bar equals 4 mm.
Fig. 8. Left tergum.


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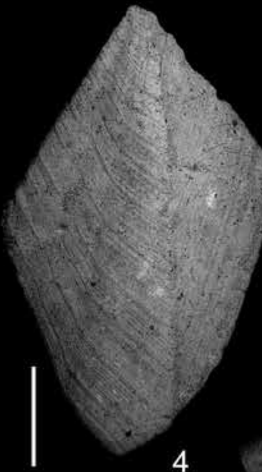
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Paper V

Kočová Veselská, M., Kočí, T., Collins, J.S.H., Gale, A.S. 2015. A new species of scalpelliform cirripede (Crustacea, Cirripedia) from the Upper Cenomanian–Lower Turonian shallow-water facies at Velim (Bohemian Cretaceous Basin) and its palaeoecological implications. *Neues Jahrbuch für Geologie und Paläontologie*-*Abhandlungen 278(2)*, 201–211.

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Article

A new species of scalpelliform cirripede (Crustacea, Cirripedia) from the Upper Cenomanian–Lower Turonian shallow-water facies at Velim (Bohemian Cretaceous Basin) and its palaeoecological implications

Martina Kočová Veselská, Tomáš Kočí, Joe S. H. Collins, and Andrew S. Gale

With 3 figures and 3 tables

Abstract: A new species of stalked cirripede *Capitulum sklenari* sp. nov. is described from shallow-water deposits of Late Cenomanian-Early Turonian age at Velim (near Kolín, Bohemian Cretaceous Basin, Czech Republic). *Capitulum sklenari* together with associated fauna at Velim are interpreted as reflecting shallow-water conditions at this locality within the Bohemian Basin during the Cretaceous. This is the stratigraphically earliest record of the living genus *Capitulum*. The palaeogeographical distribution of all Cretaceous species of pollicipedids is discussed.

Key words: *Capitulum sklenari*, Pollicipedidae, Cirripedia, Upper Cenomanian–Lower Turonian, near-shore facies, Czech Republic.

1. Introduction

Despite almost two centuries of palaeontological research within the Bohemian Cretaceous Basin (BCB), our knowledge of cirripedes from the near-shore, shallow and pelagic facies still remains poor. The first studies dealing with such fossils from the BCB are those by Reuss (1844, 1845-1846, 1864), Kafka (1885), Fritsch & Kafka (1887) and Fritsch (1911). Between 1930-1933, the palaeontologist Jaroslav Šulc (Institute of Geology and Palaeontology, Charles University) collected ten capitular plates (5 scuta, 5 terga) of *Zeugmatolepas cretae* (Steenstrup, 1837) from the Upper Turonian (*Holaster* [*Sternotaxis*] *planus* Zone) strata from the now completely overgrown locality of Na Vinici near Kolín in the southern part of the BCB (Withers 1935). Unfortunately, his collection has probably been lost, with the exception of one scutum and one tergum which he donated to the British Museum (Natural History; now The Natural History Museum), London (registration numbers: NHM 31673-4). Cirripedes from the BCB have subsequently been recorded in detail by Withers (1935), who listed eleven species, mentioning the collections of A. Fritsch and J. Šulc.

The aim of the present note is to describe and name cirripedes from two boxes of unsorted residue found stored in the basement of the National Museum (NM) at Prague and to record one newly recovered specimen from Velim.

2. Material and methods

The first of two boxes of residue was made available for study in 2005, the second one in 2010. Some 40 kilogrammes of residue were screen washed through a sieve of 1 mm mesh. This yielded 95 capitular plates of the new species *Capitulum sklenari*. Unfortunately, the original labels were lost and the precise stratigraphical provenance of the material

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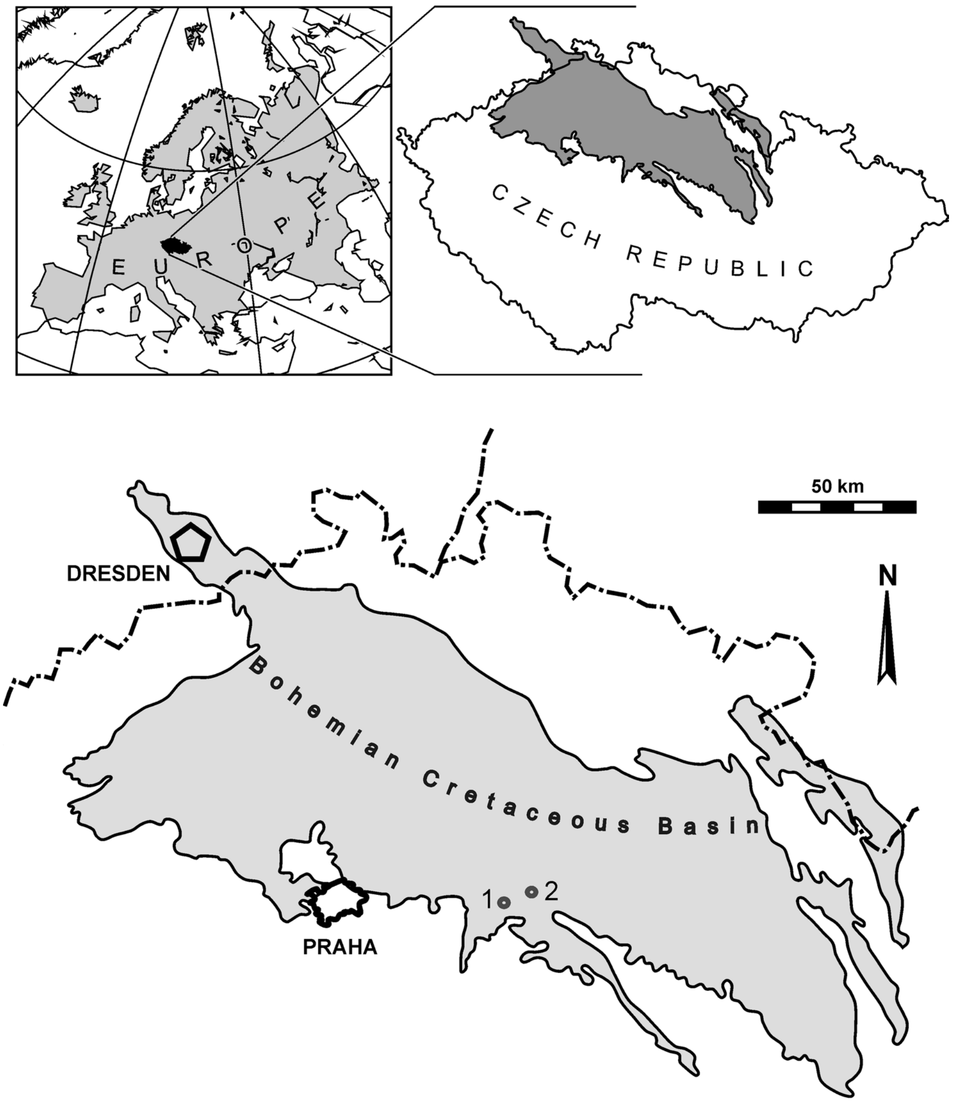

Fig. 1. Simplified map of the Bohemian Cretaceous Basin (BCB, Czech Republic), showing the localities of Velim (near-shore, shallow-water, with *Capitulum sklenari* sp. nov.) and Na Vinici, which yielded *Z. cretae* (Steenstrup, 1837).

remains uncertain. However, it is clear that all comes from a former quarry at Velim (GPS co-ordinates: 50°3'38.14" N, 15°7'46.34" E; compare Fig. 1) where the Upper Cenomanian–Lower Turonian near-shore sediments crop out in depressions of the metamorphic basement (Žítt et al. 1997). Both the associated fauna and the character of matrix preserved inside the plates have yielded more relevant stratigraphic data (see below).

Associated macrofaunal elements in the material processed from the original two boxes are listed in Table 1. Common are sabellid and serpulid worms, bryozoans, bivalves and echinoderms (especially crinoids), but unfortunately these taxa are not age-diagnostic. Between 2001 and 2011, two of us (TK and MKV) conducted fieldwork at this locality, during which an additional 60 kilogrammes of rubble from the western and eastern part of the quarry were amassed and sieved. Collections from the western part have yielded a single rostrum of early Turonian age, thus confirming the presence of *Capitulum* at this locality. All material available consists of disarticulated capitular plates, which is the typical state of preservation for almost all Late Mesozoic cirripedes. Photographs of these plates were taken using the microphotography system Olympus DP70 (at NM) and SEM in low vacuum (JEOL JSM-6380LV) at the Institute of Geology and Palaeontology (Charles University, Prague) and Hitachi S-3700 N SEM at the National Museum in Prague; Figs. 1-6 were made using Corel Graphic Suite X4 software.

Table 1. Summary of the macrofaunal composition of the original sieve residues stored at the National Museum (Prague).

	Rare	Common
Octocorallia		
Moltkia foveolata (Reuss, 1846)	●	
Sabellid worms		
Glomerula serpentina (Goldfuss, 1831)		●
Serpulid worms		
Dorsoserpula gamigensis (Geinitz, 1875)	●	
Dorsoserpula wegneri (Jäger, 1983)	●	
Propomatoceros sp.		●
Neovermilia ex gr. *ampullacea* (J. de C. Sowerby, 1829)		●
Cementula? cf. *sphaerica* (Brünnich Nielsen, 1831)		●
?*Conorca* sp.	●	
Filogranula cincta (Goldfuss, 1831)	●	
Placostegus zbyslavus (Ziegler, 1984)	●	
Placostegus sp.	●	
Pyrgopolon cf. *tricostata* (Goldfuss, 1831)	●	
Pyrgopolon sp.	●	
Neomicrorbis crenatostriatus subrugosus (Münster in Goldfuss, 1831)	●	
Bryozoa		
Stomatopora sp.		●
Cyclostomata indet.		●
Cheilostomata indet.		●
Brachiopoda		
Terebratulina striatula (Mantell, 1822)	●	
Phaseolina phaseolina (Valenciennes in Lamarck, 1819)	●	
Gisilina? *rudolphi* (Geinitz, 1875)		●
Ancistrocrania sp.	●	
Bivalvia		
Amphidonte (*A.*) *reticulatum* (Reuss, 1846)	●	
Gryphaeostrea canaliculata (J. Sowerby, 1813)		●
Rastellum carinatum (Lamarck, 1819)		●
Rastellum diluvianum (Linnaeus, 1767)		●
Ostreidae gen. et sp. indet.		●
Spondylus sp.	●	
Neithea (*Neithella*) *notabilis* (Münster in Goldfuss, 1833)	●	
Neithea (*Neithea*) *aequicostata* (Lamarck, 1819)	●	
Isognomon lanceolatum (Geinitz, 1845)	●	
Gastropoda		
Neritopsis nodosa (Geinitz, 1840)	●	
Echinodermata - Crinoidea		
Isocrinus? cf. *cenomanensis* (d'Orbigny, 1850)		●
Echinodermata - Echinoidea		
Temnocidaris (Stereocidaris) vesiculosa (Goldfuss, 1829)	●	
Tylocidaris sorigneti (Desor, 1858)	●	
Salenia sp.	●	
Echinodermata - Asteroidea		
Metopaster sp.	●	
Vertebrata - Selachii		
Paranomotodon angustidens (Reuss, 1846)	●	
Scaphanorhynchus rhaphiodon (Agassiz, 1843)	●	

3. Systematic palaeontology

Subclass Cirripedia Burmeister, 1834
Superorder Thoracica Darwin, 1854
Order Scalpelliformes Buckeridge & Newman, 2006
Family Pollicipedidae Leach, 1817

Diagnosis: Pedunculate thoracicans in possession of a stout peduncle armoured with numerous tiny scales; capitulum massively constructed, low, laterally compressed, sharply demarcated from peduncle; lateral plates numerous, including upper latus, carinolatus, rostrolatus, subrostrum, subcarina, and up to 10 smaller lateral plates, which decrease in size towards the peduncle.

Genus *Capitulum* Gray, 1825

Diagnosis: Pollicipedid with apical and acuminate umbo in scuta, rhomboidal terga with prominent apico-basal ridge, which may be contorted in some specimens, broadening towards scutal side, producing a shallow fold. Scutum possess distinct tergal notch, which is strong and triangular and in apical part is straight. Surface lined with coarse, concentric growth lines. The longitudinal sculpture is from short radiating ridges developed between transverse growth lines in all capitular plates. Carina possesses a narrow, rounded tectum; rostrum and subrostrum triangular with coarse concentric sharp growth lines.

Remarks: Affiliation to the genus *Capitulum* Gray, 1825 is confirmed by numerous similarities, including the sculpture of the capitular valves, comprising parallel, narrow growth ridges. The shape and detailed morphology of the apical interior of the scutum are also similar, in that both possess a deep tergal notch (see Gale & Sørensen 2014: 10, fig. 8B) which is straight towards the apex with comparison with tergal notch of genus *Pycnolepas* (see Gale & Sørensen, 2014: 10, fig. 8C). The claw-like form of the lower laterals, which are incurved, with acutely pointed apices provides another similarity. The carina and rostrum are V-shaped in cross section, and carry several strong longitudinal ridges.

Capitulum sklenari sp. nov.
Figs. 2A-K, 3A-X, Cs, Ps

2012 *Zeugmatolepas* sp. – Kočí & KočováVeselská, pp. 130-131, fig. 1A-K.
2013 *Zeugmatolepas* sp. – Kočí & Kočová Veselská, pp. 99-106, figs. 12-22.
2014 *Zeugmatolepas* n. sp. – Kočová et al., p. 59, pl. 5, figs. 1-13.

Etymology: The specific epithet honours Dr Jan Sklenář, curator at the National Museum, Prague.

Holotype: A left tergum, NM O7039 (see Fig. 2Ka, b).

Paratypes: One carina, NM O 7040;18 right scuta, NM O7033, NM O7034, NM O7045-O7060 and 19 left scuta, NM O7035-O7037, NM O7044 and NM O7062-O7077; 5 right terga, NM O7038, NM O7078-O7081 and 8 left terga, NM O7082-O7089; 26 rostra, NM O7041-O7043 and NM O7090-O7112.

Material: The species is represented by 95 capitular isolated valves (scuta, terga, rostra, carinae) of distinctive morphology. We originally identified this material as belonging to a new species of *Zeugmatolepas* sp. (Kočí & Kočová Veselská 2012, 2013) and Kočová Veselská et al. (2014) because the shapes of the scuta and terga are similar to those found in Zeugmatolepadidae. However, the material shows much closer affinities with material from the Campanian of southern Sweden, referred by Gale & Sørensen (2015) to *Capitulum caelatum* (Withers, 1935).

Type locality and horizon: Velim, Czech Republic; Upper Cenomanian–Lower Turonian (see below).

Distribution: The new species appears to be confined to the Upper Cenomanian–Lower Turonian boundary strata at Velim in the BCB. Unfortunately, the precise age of the samples remains uncertain. An Early Turonian date is hinted at by the near-identical faunal assemblage recorded from the same stratigraphical position (see Žítt et al. 1997; Košťák et al. 2010). However, according to Dr Jiří Žítt (pers. comm., 2013) the material is probably of Late Cenomanian age, in view of the occurrence of the crinoid *Isocrinus*? cf. *cenomanensis* (d'Orbigny, 1850) and absence of *Isocrinus*? aff. *lanceolatus* (Roemer, 1840) in the original sieved residue; both of these *Isocrinus* species invariably co-occur in sediments of Early Turonian age.

Diagnosis: A *Capitulum* with a narrowly rounded tectum in carina; apex and umbo of scutum apical, basal tergal margin moderately rounded; tergum elongate, broader than

Fig. 2. *Capitulum sklenari* sp. nov. **A** – Rostrum, NM O7042 (paratype): a – outer view, b – inner view. **B** – Rostrum, NM O7041 (paratype): a – outer view, b – lateral view. **C** – Right scutum, NM O7033 (paratype): a – outer view, b – inner view. **D** – Right scutum, NM O7034 (paratype) with deformed surface: a – outer view, b – inner view. **E** – Left scutum, NM O7036 (paratype): a – outer view, b – inner view. **F** – Left scutum, NM O7037 (paratype), with roughened surface: a – outer view, b – inner view. **G** – Carina, NM O7040 (paratype): a – outer view, b – inner view, c – latero-inner view. **H** – Right tergum, NM O7038 (paratype): a – outer view, b – inner view. **I** – Left tergum, NM O7039 (holotype): a – outer view, b – inner view. All scale bars equal 500 μm.

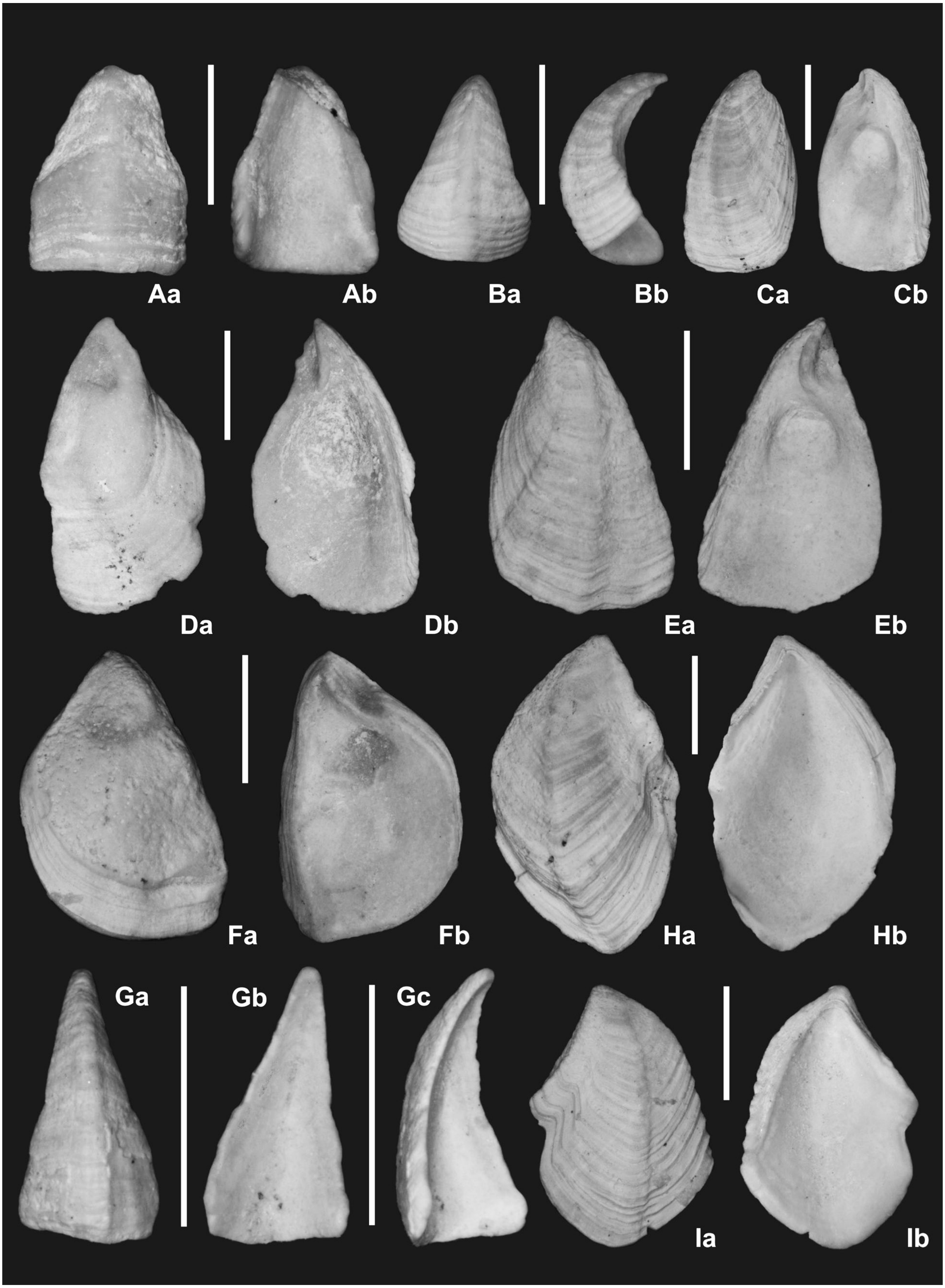

Fig. 2.

long; upper and lower carinal margins forming an obtuse angle; rostrum triangular, narrow with acute apex, prominent apicobasal ridge and distinct V-shaped growth lines on inner surface.

Description: Carina (Figs. 2G, Fig. 3L, M). Isosceles – triangular in outline, with acute apex and prominent apicobasal ridge; basilateral angles gently rounded to near-straight basal margin. Coarse growth lines extending parallel to basal margin. Laterally plate near-straight to slightly convex, but less than in rostrum. Inner surface broadly concave with slightly thickened apical margins. Fine V – shaped growth lines extending to mid-plate length. Additional evidence is that the internal boundary between the lined upper part and the smooth lower part (where the membrane attaches) is lower in the rostrum and slightly higher in the carina.

Rostrum (Fig. 2A, B, I, 3I-O). Isosceles–triangular in outline, with acute apex and prominent apicobasal ridge; basilateral angles gently rounded to near-straight basal margin. Coarse growth lines extending parallel to basal margin. Laterally, plate nearly straight to slightly convex. Inner surface broadly concave with slightly thickened apical margins. Fine V- shaped growth lines extending to mid-plate length.

Scutum (Figs. 2C-F, 3A-D, Cs) is subtriangular to subquadrate in outline; the umbo is apical and acuminate. Short tergal margin, moderately curved or straight, forming an angle of 70–90° with lateral margin. Lateral margin smoothly rounded. Two or three indistinct apico-basal ridges extending towards lateral angle. Another, similar ridge extending to basal midline. Apex rounded with margins bowed inwards. Distinct, coarse concentric ridges forming surface ornament. On inner surface, a ridge, divided by a narrow groove, separating narrow depression extending along tergal margin from deep adductor muscle pit; occludent side of pit thickened and marked by coarse growth lines.

Tergum (Figs. 2J, K, 3P-S, Ps) subrhomboidal in outline, moderately convex transversely. Apex directed slightly towards scutum. Short, convex occludent margin bounded by prominent fold producing distinct cleft before rounded scutal margin. Carinal margin boldly curved in upper third, becoming straight towards base, forming an angle with basal margin. Prominent apico-basal ridge, which may be contorted in some specimens, broadening towards scutal side, producing a shallow fold. Surface lined with coarse, concentric growth lines. And only in SEM are visible distinct very short longitudinal ridges (see Fig. 3Ps). This fine radiating structure of the surface are developed in all plates. On inner surface, carinal and occludent margins inturned and marked by growth lines, becoming finer towards the apex.

Measurements: Measurements of disarticulated capitular plates of *Capitulum sklenari* sp. nov. are listed in Tables 2 and 3.

Table 2. Measurements (in mm) of rostra, carinae and terga of *Capitulum sklenari* sp. nov.

Carinal plates	**Length**	**Width**	**Carinal plates**	**Length**	**Width**
rostrum			**rostrum**		
O 7041	4.2	2.1	O 7109	4.8	3.6
O 7042	4.4	3.2	O 7110	broken	4
O 7043	5.7	3.7	O 7111	2.9	2.4
O 7090	6.6	3	O 7112	4.4	3.4
O 7091	5.6	2.4	**carina**		
O 7092	6.2	3.4	O 7040	4.9	3.7
O 7093	5	2.3	**right tergum**		
O 7094	4.2	2.6	O 7038	10.3	6
O 7095	4.1	2.5	O 7078	9.6	6.8
O 7096	3.6	1.6	O 7079	7.3	4.8
O 7097	4.6	2.7	O 7080	6.4	4.7
O 7098	4	2.2	O 7081	5.3	4
O 7099	3.8	2.2	**left tergum**		
O 7100	4.1	2.3	O 7039	7.5	5.2
O 7101	3.7	2.4	O 7082	9.5	5.5
O 7102	4.6	3.2	O 7083	7.5	5.7
O 7103	broken	2.7	O 7084	7.4	5.5
O 7104	5.6	2.9	O 7085	7.3	4.6
O 7105	5.3	3	O 7086	7	4.4
O 7106	4	2.4	O 7087	6	3.9
O 7107	5.4	4.2	O 7088	6.8	4.4
O 7108	5.4	4	O 7089	5.7	4.3

Fig. 3. *Capitulum sklenari* sp. nov. **A** – Left scutum, NM O7036 (paratype) – outer view. Scale bar is 3 mm. **B** – Left scutum, NM O7036 (paratype) – inner view. Scale bar is 3 mm. **C** – Left scutum, NM O7037 (paratype), with roughened surface – outer view. Scale bar is 3 mm; Cs: The detail view of roughened surface of the left scutum NM O7037 (paratype). Scale bar is 500µm. **D** – Left scutum NM O7037 (paratype), with roughened surface – inner view. **E** – Right scutum, NM O7034 (paratype) with deformed surface – outer view. Scale bar is 3 mm. **F** – Right scutum, NM O7034 (paratype) with deformed surface – inner view. Scale bar is 3 mm. **G** – Right scutum, NM O7033 (paratype) – outer view. Scale bar is 3 mm. **H** – Right scutum, NM O7033 (paratype) – inner view. Scale bar is 3 mm. **I-K** – Rostrum, NM O7041 (paratype); I: outer view, scale bar is 2 mm; J: inner view, scale bar is 2 mm. K: latero-inner view, scale bar is 3 mm. **L-M** – Carina, NM O7040 (paratype); L: inner view, scale bar is 1 mm; M: outer view, scale bar is 1 mm. **N-O** – Rostrum, NM O7042 (paratype); N: outer view, scale bar is 3 mm; O: inner view, scale bar is 2 mm. **P-Q** – Left tergum, NM O7039 (holotype); P: outer view, scale bar is 3 mm; Q: inner view, scale bar is 3 mm; Ps: left tergum, detail of transversal fine ridges between growth ridges on the surface, which is visible only in SEM. Scale bar is 500 µm. **R-S** – Right tergum, NM O7038 (paratype); R: outer view, scale bar is 3 mm; S: inner view, scale bar is 3 mm.

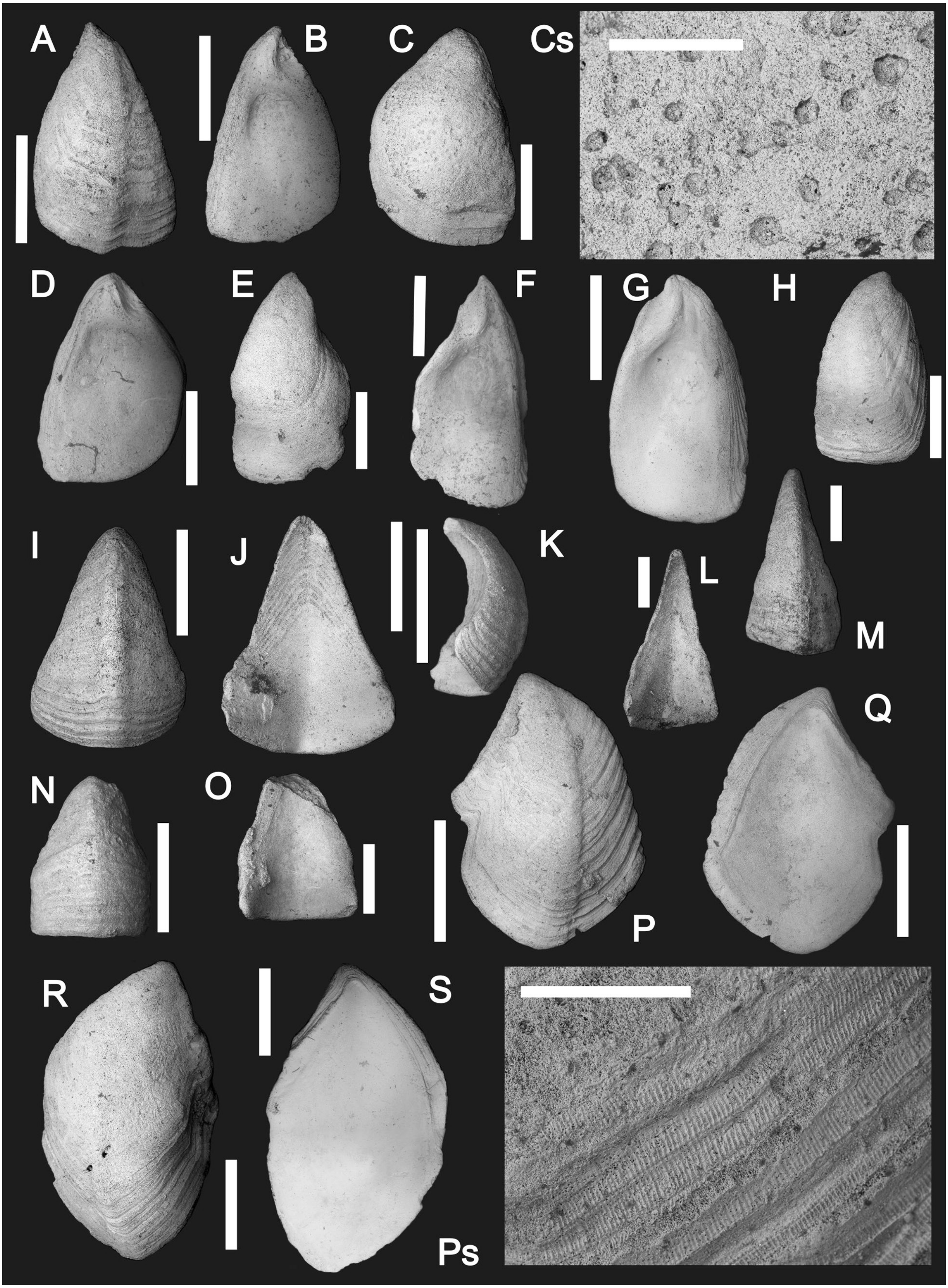

Fig. 3.

Table 3. Measurements (in mm) of scuta of *Capitulum sklenari* sp. nov.

Carinal plates	Length	Width	Carinal plates	Length	Width
right scutum			**left scutum**		
O 7033	7.5	4.2	O 7035	6.8	3.7
O 7034	8.9	4.6	O 7036	7	4
O 7045	5.5	3.2	O 7037	7	4.8
O 7046	5.9	4	O 7044	3.7	2
O 7047	5.5	3.4	O 7062	7	4
O 7048	7.2	4	O 7063	7	4.2
O 7049	6.6	3.8	O 7064	6.3	4.2
O 7050	6.7	4	O 7065	7.9	5
O 7051	6.2	3.2	O 7066	6.2	3.6
O 7052	5.8	3.3	O 7067	4.9	2.8
O 7053	7	4.3	O 7068	6.6	4.9
O 7054	6	3.9	O 7069	6.2	4
O 7055	6.4	3.6	O 7070	5.2	3.2
O 7056	6.8	4.4	O 7071	7	3.7
O 7057	5.9	3.9	O 7072	4.5	2.7
O 7058	7.3	4.4	O 7073	5.2	2.8
O 7059	5.6	2.9	O 7074	6.2	3.6
O 7060	8	5	O 7075	4.6	2.8

Remarks: The genus *Capitulum* is well known from the extant species *C. mitella*, which lives attached to rocks in the intertidal zone of the Indo-west Pacific region (Chan et al. 2010). *Capitulum sklenari* represents the first occurrence of the genus in the Bohemian Cretaceous. The Late Cretaceous species *Capitulum caleatum* (Withers, 1935) from the Campanian of Ivö Klack in Sweden (Gale & Sørensen 2015) possesses very similar terga, but can be distinguished by the shape of the scuta. Similarities include the form of the scutal auricles and tergal notches of the terga, and scuta, and the outlines of the terga, and the range of variation in the form of the terga (compare Gale & Sørensen 2015, fig. 12H, T with Fig. 3P, R herein). The scuta of *Capitulum sklenari* differ from those of *C. caelatum* in the presence of a depressed region adjacent to the occludent margin (compare Gale & Sørensen 2015, fig. 12G with Fig. 3A herein) and the slightly straighter occludent margin. The rostra and carinae of *C. sklenari* have a more pronounced central ridge and more acuminate apices than *C. caelatum*. *Capitulum sklenari* sp. nov. is the oldest known species of the genus *Capitulum*. The tergum of *Pachyscalpellum cramptoni* Buckeridge, 1991, from littoral Santonian-Campanian sediments of Hawkes Bay, New Zealand (Buckeridge 1991, fig. 2a) is very similar in morphology to both *Capitulum sklenari* and *C. caelatum;* the strongly incurved tergum has a prominent, narrow scutal auricle, and a broad, raised apicobasal ridge. We suspect that *P. cramptoni* should also be referred to the genus *Capitulum*. However, according to J. S. Buckeridge (personal communication, 20 July, 2015) this comparison is not valid, because material of *P. cramptoni* is very distinct, and shows a peculiar but consistent growth habit of the tergum. Furthermore, the interior of the scutum is unknown, and the exterior of the scutum differs significantly from that of *C. sklenari* and *C. caelatum*.

4. Palaeoecology

The robust capitular plates of *Capitulum sklenari* are suggestive of high-energy environments. Yet, in comparison with extant species of *Capitulum mitella* (Linnaeus, 1758) and *Pollicipes polymerus* (Sowerby, 1883), which are adapted to wave-exposed rocky shores and are mostly intertidal in distribution (Fernandes et al. 2010), *Capitulum sklenari* from the BCB appears to possess less well armoured with somewhat thinner capitular plates. Anderson (1984) observed that scalpellomorphs (stalked barnacles) penetrated littoral settings only sporadically, whereas balanomorphs (sessile barnacles) became extraordinarily diverse, being evolutionarily better adapted to such environments. Intertidal thoracicans are either cryptic (e.g., *Ibla*) or strongly plated and functionally convergent with balanomorphs (Pollicipedidae, Calanticidae). Therefore, we assume that *Capitulum sklenari* might have preferred sheltered habitats on submarine rocky elevations, located in the southern part of the BCB, i.e. the vicinity of Kolín.

In near-shore and shallow-water facies within the BCB, cirripedes are mostly found as disarticulated capitular plates (scuta, rostra and terga). At the western end of Velim quarry cirripede plates have proved abundant: 1202 capitular valves of *Cretiscalpellum glabrum* (Roemer, 1841), 12 capitular plates of *Cretiscalpellum striatum* (Darwin, 1851), 141 capitular plates of *Arcoscalpellum angustatum* (Geinitz, 1843), 94 capitular valves of *Titanolepas tuberculatum* (Darwin, 1851), two carinae of *Smilium*? *parvulum* (Withers, 1914) and a single rostrum of *Capitulum sklenari* sp. nov. by Kočová Veselská et al. (2014), Kočí & Kočová Veselská (2014) and unpublished data of recovered collection, which was collected by Dr Olga Nekvasilová (all material is deposited in NM Prague). In contrast, merely one scutum and two carinolaterals of *A. angustatum* are known from the eastern part of the quarry (Kočí & Kočová Veselská 2012). For other associated faunal elements and palaeoenvironmental relationships, reference is made to Žítt & Nekvasilová (1996) and Žítt et al. (1997). Macrofaunal taxa associated with specimens of *Capitulum sklenari* sp. nov. in the original sieved residues are listed in Table 1. Unfortunately, it is not known from which part of the quarry these samples originate.

The similar mixed fauna is present at Ivö Klack (Early Campanian, Sweden) Gale & Sørensen (2015). The material represents intertidal to offshore habitats – i.e. up to 30 m depth, mixed together and deposited between the boulders. The genus *Capitulum* has occupied a similar habitat, encrusting rocky substrata in the intertidal or sublitoral zone, since at least the Cenomanian.

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Paper VI

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Article

A new barnacle, *Myolepas reussi* (Cirripedia, Scalpelliformes), from a near-shore, shallow-water facies in the Bohemian Cretaceous Basin, Czech Republic

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With 8 figures and 1 table

Abstract: Cirripede remains from upper Cenomanian to lower Turonian strata at Kaňk-Na Vrších (Kolín area, Bohemian Cretaceous Basin, Czech Republic) are described; a new scalpelliform species, *Myolepas reussi*, is proposed. A palaeoecological analysis of the Na Vrších fauna shows that intertidal-subtidal conditions prevailed at the site during the early Late Cretaceous.

Key words: Thoracica, rocky coast facies, upper Cenomanian, palaeogeography, palaeoecology, borings.

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1. Introduction

Cirripedes are a common component of mesofaunal assemblages from Upper Cretaceous near-shore, shallow-water deposits in the Bohemian Cretaceous Basin (BCB) of the Czech Republic (see e.g., Fritsch & Kafka 1887; Frič 1911; Kočová Veselská et al. 2014), as well as elsewhere in Europe and even further afield (Withers 1935; Carlsson 1953; Alekseev 1974, 1979, 1982, 2004, 2009; Babinot et al. 1979; Buckeridge 1983; Viaud et al. 1983; Jagt & Collins 1989, 1999; Carriol & Collins 2000, 2002; Alekseev et al. 2008; Gale & Sørensen 2015). The locality Kaňk-Na Vrších is an important, classic site for highly diverse, fossil-rich, near-shore facies near the Cenomanian–Turonian boundary in the BCB. The most detailed descriptions of cirripedes from the BCB can be found in monographs by Kafka (1885) and Fritsch & Kafka (1887), who cited earlier publications that included basic data on BCB cirripedes, principally papers by Reuss (1844, 1845-1846, 1864).

The first modern revision, description and account of fossil ciripedes from the Cretaceous of the world is that of Withers (1935). In this monograph the list of cirripede taxa from the BCB is significantly expanded. Withers's material, predominantly from the Kolín area (localities: Na Vinici, Kamajka near Chotusice), was supplied by Dr Jaroslav Šulc and supplemented by an earlier collection of 84 capitular plates of '*Scillaelepas*' *conica* collected by Dr Anton Frič and sold to the (then) British Museum of Natural History (now The Natural History Museum, London), on October 23, 1897. More recent work on cirripedes from BCB includes that by Kočí & Kočová Veselská (2012a, b, 2013a-c, 2014), Kočí et al. (2014) and Kočová Veselská et al. (2014a, b, 2015). However, apart from Kočí et al. (2014) and Kočová Veselská et al. (2014), who mentioned and illustrated old museum material of '*Scillaelepas*' *conica* held at the Natural History Museum (London), in none of these recent papers have cirripede remains from Kaňk-Na Vrších been discussed. During recent fieldwork (2014-2015) by two of us (TK, MKV), some 1,300 capitular plates have been recovered and these, along with the holotype of *Pollicipes conicus* Reuss, 1844, have been studied for the present paper.

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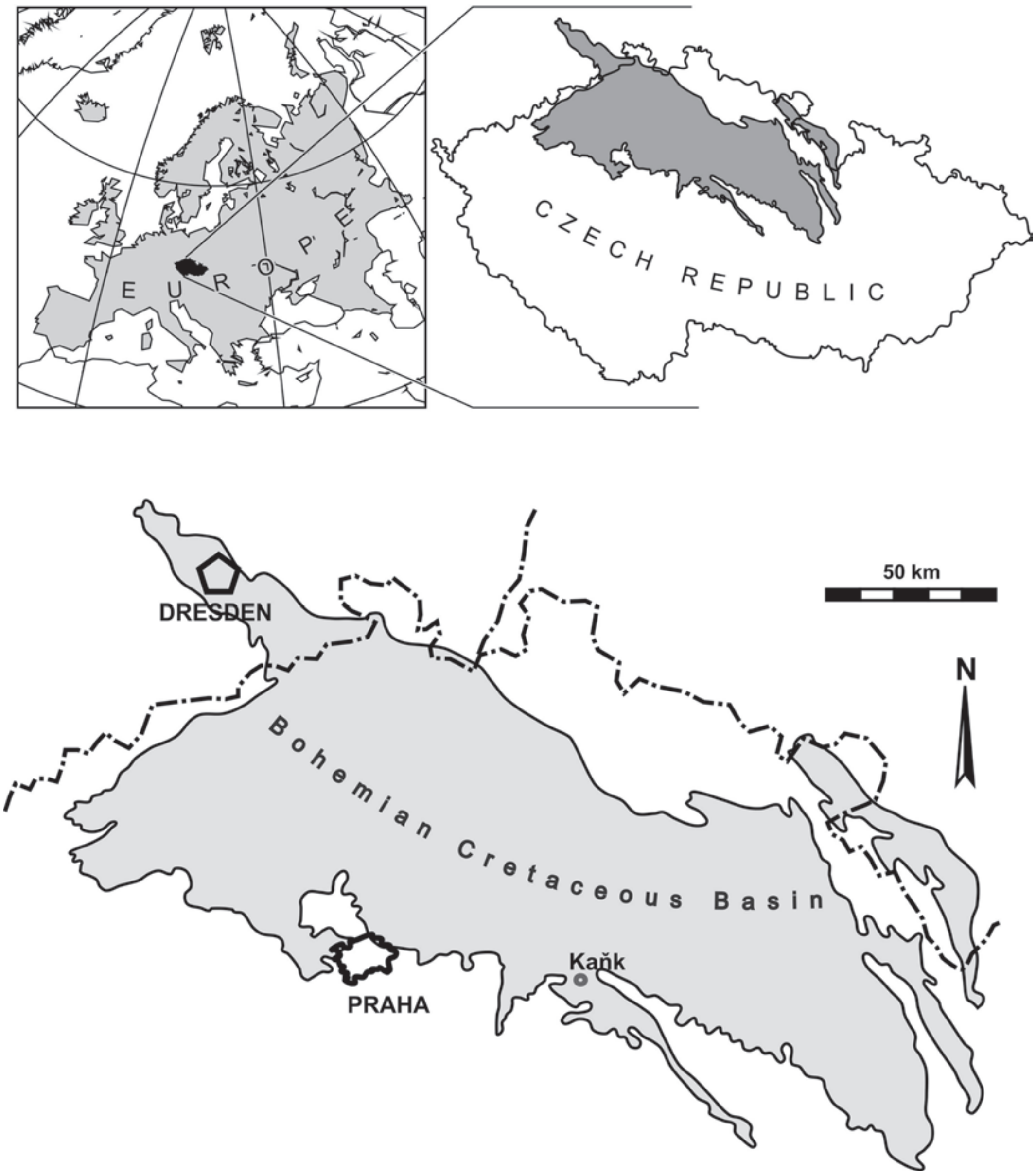

Fig. 1. Location of the Bohemian Cretaceous Basin (BCB) within the Czech Republic. 1 – Kaňk-Na Vrších.

2. Geological and geographical setting

The ‘Na Vrších’, or Kaňk State Nature Reserve, is an abandoned quarry where gneiss was once mined (Figs. 1-2). During the early Late Cretaceous the gneiss was exposed as coastal cliffs, providing a substrate for shallow-water benthos (Počta 1892; Gregory 1906; Frič 1911; Lang 1916; Kühn 1924; Withers 1935; Prantl 1940; Zázvorka 1952; Čech & Soukup 1955; Nekvasilová 1964, 1973; Pajaud 1970; Hercogová 1974; Štemproková-Jírová 1976; Němec 1978; Žítt 1986; Pokorný 1989; Eliášová 1997; Štorc 1997, 2004; Sviták 2005; Hradecká & Švábenická 2007; Taylor & Zágoršek 2011, and Kočí 2012). The resultant shallow-water facies has been divided into two parts: a basal, coarse-grained gneiss conglomerate with a bioclastic

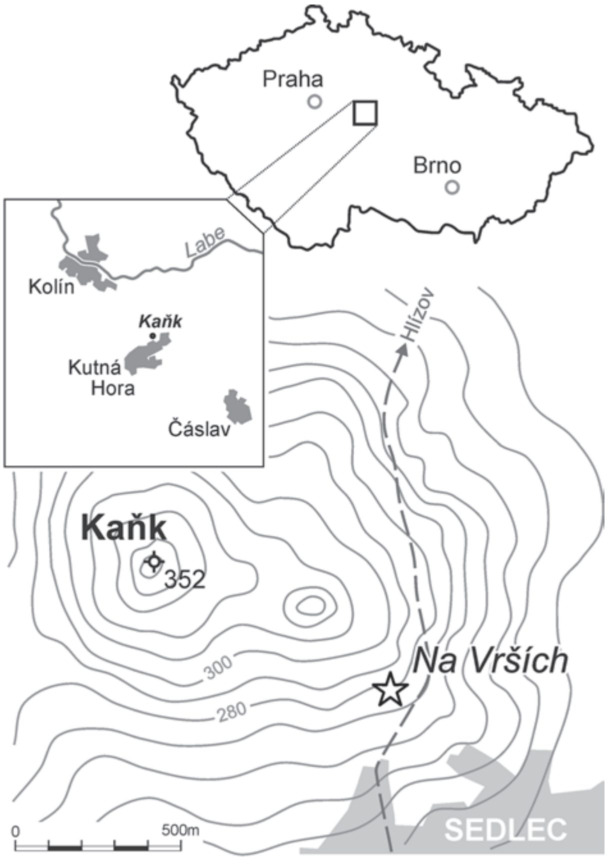

Fig. 2. Location of Kaňk Hill; the locality Na Vrších is close to the village of Sedlec.

limestone matrix (1 metre in thickness), which grades into an upper, 1.8 metre thick, white bioclastic limestone. This shallow-water facies is unconformably overlain (with a clear erosional surface) by calcareous claystones of 1 metre thickness (Žítt 1992). The presence of the foraminifer *Pseudotextulariella cretosa* (Cushman, 1932) in the matrix of the conglomerate and the lower part of the bioclastic limestone dates the sequence as late Cenomanian (Korycany Formation). However, Hradecká & Švábenická (2007) demonstrated, on the basis of calcareous nannofossils, that this was a mixed unit, of late Cenomanian to early Turonian age, extending to the base of the lower Turonian Bílá Hora Formation. The overlying calcareous claystones (sensu stricto) belong to the Bílá Hora Formation. For a more detailed review of the lithology, reference is made to Žítt (1992) and Vodrážka et al. (2013). A simplified stratigraphy, showing the distribution of cirripedes, is illustrated in Figure 3.

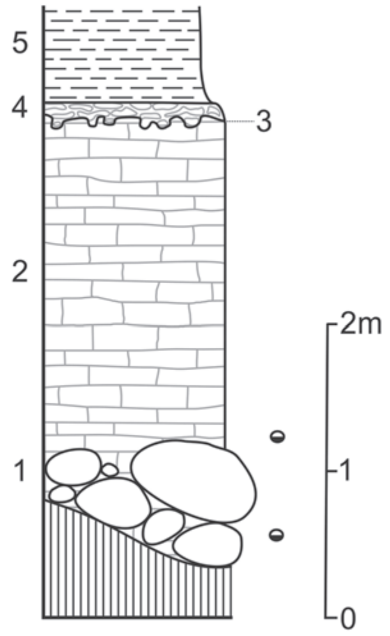

Fig. 3. Simplified stratigraphic section at the Kaňk Quarry; black/white circles denote cirripede-bearing horizons (see text for details).

3. Material and methods

Twenty field trips were conducted to Kaňk-Na Vrších (2014-2015), during which approximately 700 kg of upper Cenomanian–lower Turonian sediment from the basal conglomerate layer, containing cirripedes, was collected for analysis. A further 70 kg of lower Turonian material was amassed from the top of the right (east) part of the outcrop, but this did not contain any cirripede remains. The material obtained was washed and sieved on a mesh width of 1 mm, yielding in excess of 1,300 capitular plates. Selected capitular plates were cleaned using hydrogen peroxide (*c.* 3-5%) and photographed using a Canon EOS 550D and SEM in low vacuum (JEOL JSM-6380LV) at the Institute of Geology and Palaeontology (Charles University, Prague). Corel Draw 4 was used to prepare the plates. All new material is housed in the collections of the National Museum (Narodní Muzeum) at Prague under registration numbers NM-O7633 to O7648.

Further comparative material from Kaňk is held in the collections of the Natural History Museum (Department of Palaeontology, London); this comprises three scuta (NHM In. 16739-16741), 52 scuta (NHM In. 16742-16745), 1 carina (NHM In. 16746), two rostra (NHM In. 16747-16748) and four terga (NHM In. 16753-16756). Specimens illustrated by Kočová Veselská et al. (2014) and Kočí et al. (2014) include five scuta (NHM In. 16739-16740, 16742-16745), one carina (NHM In. 16746), one rostrum (NHM In. 16747) and four terga (NHM In. 16753-16756). We have examined and compared two species, '*Scillaelepas*' *dorsata*

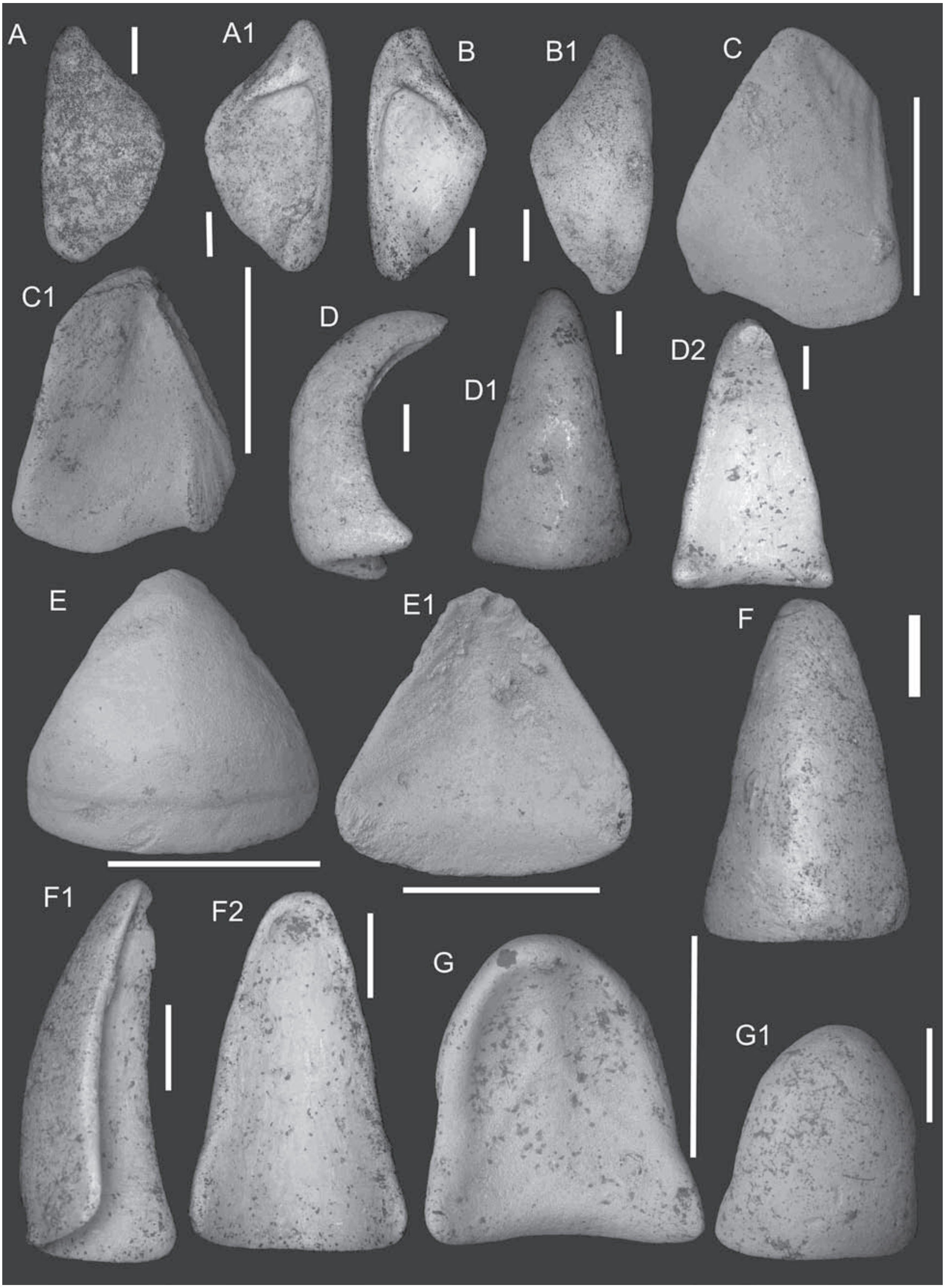

Fig. 4.

(Steenstrup, 1839) (NHM In. 16606-16616) from the middle Danian 'bryozoan chalk' at Faxe, eastern Denmark, and *Myolepas scanica* (Withers, 1935) (NHM In. 29420, 29422, 29424, 29425, 29426). We have also studied the holotype of *Pollicipes conicus* at the Naturhistorisches Museum in Wien (Vienna, Austria; NHMW 1877/0025/0087 – note: the original paper label states 1877 XXV. 87).

4. Systematic palaeontology

Classification follows Withers (1928, 1935, 1953), Foster (1978), Buckeridge (1983), Buckeridge & Newman (2006) and Gale & Sørensen (2015).

Subclass Cirripedia Burmeister, 1834
Superorder Thoracica Darwin, 1854
Order Scalpelliformes Buckeridge & Newman, 2006
Family Calanticidae Zevina, 1978
Genus *Myolepas* Gale in Gale & Sørensen, 2015

Type species: *Calantica* (*Scillaelepas*) *scanica* Withers, 1935; upper lower Campanian, southern Sweden.

Diagnosis [emended]: Capitulum with primary whorl comprising carina, rostrum, paired scuta and terga, plus a lower whorl with paired medial latera, carinolatera and rostrolatera? All plates thick; tergum and scutum articulated by means of tergal auricle and furrow and corresponding upper scutal notch on the scutum, in the plane of the valves, and corresponding blade-like process on the tergum; both scutum and tergum possess grooved and toothed insertion sites for large depressor muscles on scuto-basal and tergo-basal margins, respectively, set on processes which extend from basal margins of valves; scutum with apicobasal groove adjacent to occludent margin; carinae and rostra bear a thickened median internal ridge. Lateral plates triangular, interior with growth lines on lateral margins meeting centrally. Peduncular scales with large, flattened external surface.

Remarks: Originally, the present material was excluded from *Myolepas* on account of the presence of lateral plates. Gale in Gale & Sørensen (2015) specifically noted that these were absent in his new genus, *Myolepas*. Thus, on the basis of the latera, this taxon could comfortably be placed within either *Calantica* or *Scillaelepas*; however, the tergum is very unusual and conforms closely to that of *Myolepas*. This left three options: the first being to emend the diagnosis for *Myolepas*, the effect of which would be to move that genus from close to the Eolepadinae (see Gale & Sørensen 2015: 214) to firmly within the Calanticidae, the second to propose another genus, the third to consider that the material from Kaňk comprised more than one species.

The morphological consistency of the plates (e.g., thickness, ornament, probable reconstruction) is considered sufficient to retain all these plates as a single species. We consider a further genus, although an easy option, would likely to lead to future synonymies, and on this basis chose to revise *Myolepas*. The reconstruction of *Myolepas* provided by Gale & Sørensen (2015: 217, fig. 5C) is far from elegant, and permits insertion of latera without overly compromising an acceptable reconstruction. Further, when Gale in Gale & Sørensen (2015) proposed *Myolepas*, it was part of a remarkably abundant and diverse cirripede fauna from a very localised site at Ivö Klack (southern Sweden); they erected 28 different species from this one location, using more than 3,000 plates, none of which were articulated.

Fig. 4. A, A1 – Right scutum (NM-O7633), in outer and inner views, respectively; **B, B1**– left scutum (NM-O7634), in inner and outer views, respectively. Scale bars equal 1 mm; **C, C1** – left tergum (NM-O7635), in outer and inner views, respectively. Scale bars equal 2 mm; **D, D1, D2** – rostrum (NM-O7636), in lateral, outer and inner views, respectively. Scale bars equal 500 μm; **E, E1** – medial latus (NM-O7637), in outer and inner views, respectively. Scale bars equal 2 mm; **F, F1, F2** – carina (NM-O7638), in outer, lateral and inner views, respectively. Scale bars equal 500 μm; **G, G1** – subcarina (NM-O7639), in inner and outer views, respectively. Scale bar equals 2 mm and 1 mm, respectively.

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Fig. 5. A, **A1** – carinal latus (NM-O7640), in outer and inner views, respectively. Scale bars equal 2 mm; **B**, **B1** – right scutum (NM-O7641), in outer and inner views, respectively. Scale bars equal 5 mm; **C**, **C1**, **C2** – medial latus (NM-O7637), in outer, inner and ventral views, respectively. Scale bars equals 2 mm (C) and 3 mm (C1, C2); **D**, **D1** – ?medial latus (NM-O7642), in outer and inner views, respectively. Scale bars equal 4 mm. Note: white arrows point to growth lines and black arrows indicate inverted V-shaped growth lines on inner surfaces.

Fig. 6. A, **A1**, **A2** – right scutum (NM-O7643), with *Oichnus* isp., in outer and inner views, respectively. Scale bars equal 1 mm; detail of borehole. Scale bar equals 200 μm; **B**, **B1** – drill near tergal margin of scutum (NM-O7644), and detail of the same. Scale bars equal 1 mm; **B2** – same specimen with microborings (white rectangle in B). Scale bar equals 2 mm; **C**, **C1** – carinal latus (NM-O7645) with detail of *Oichnus paraboloides* Bromley, 1981. Scale bar equals 400 μm; outer view of specimen. Scale bar equals 2 mm; **D**, **D1** – carinal latus (NM-O7646); the two white arrows indicate microborings not illustrated here in detail. Scale bar equals 2 mm; detailed view of white rectangle in D. Scale bar equals 500 μm; **E**, **E1** – drill hole in medial latus (NM-O7647). Scale bar equals 2 mm, and detail of the same. Scale bar equals 300 μm; **F** – right scutum (NM-O7648), with *Oichnus* isp., white arrow pointing at unknown borings. Scale bar equals 2 mm.

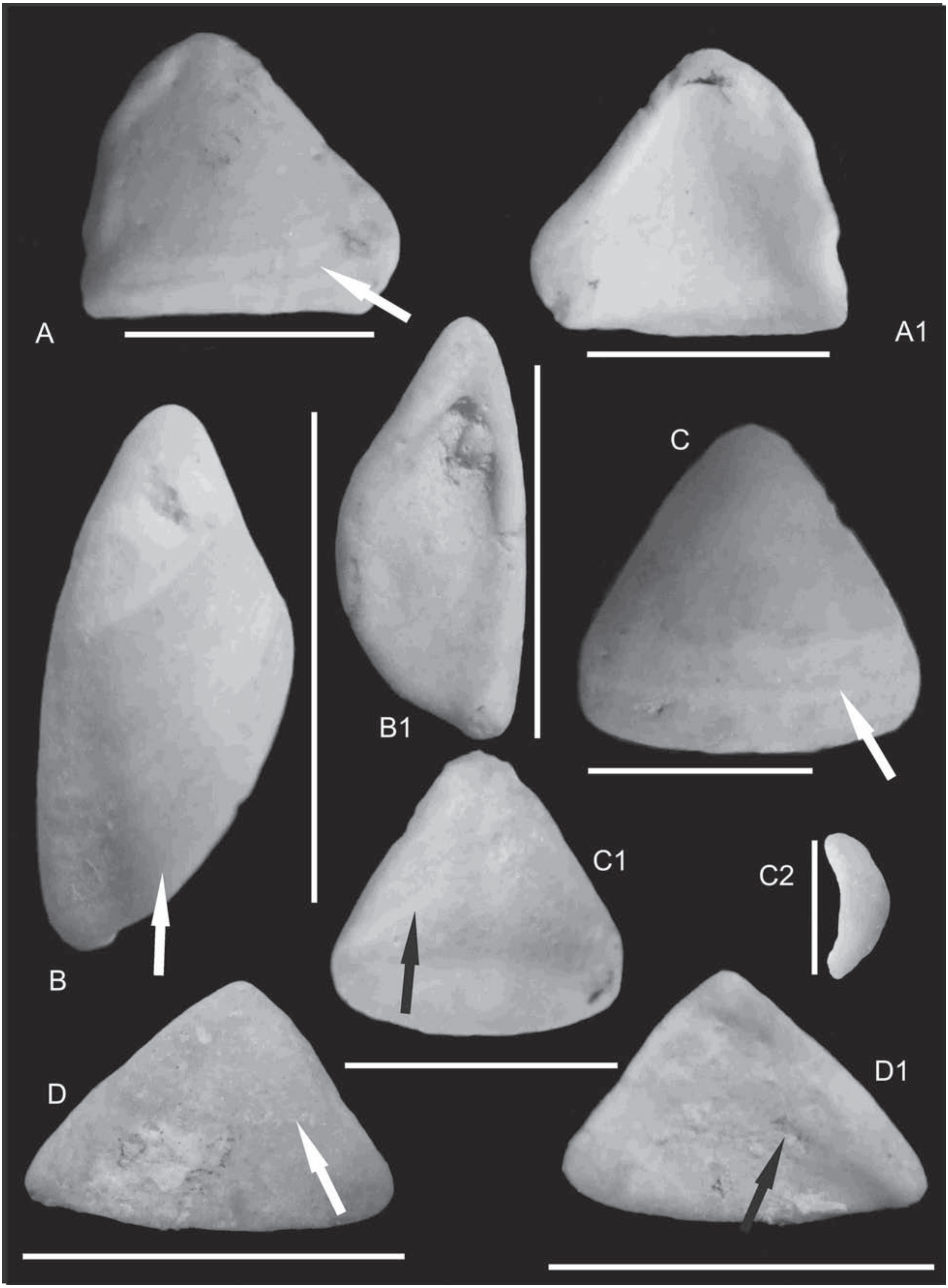

Fig. 5.

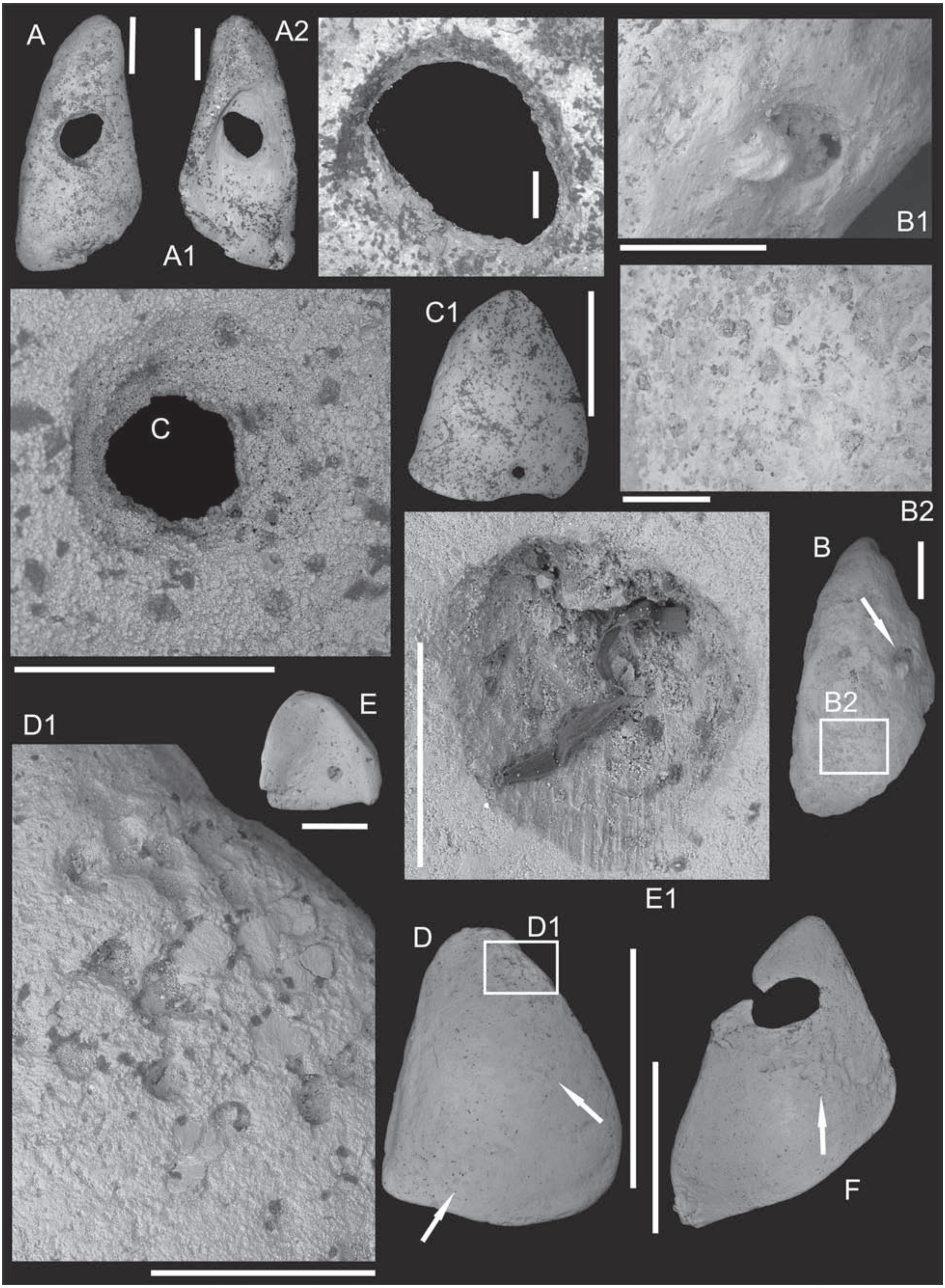

Fig. 6.

Myolepas reussi sp. nov.
Figs. 4A-G, 5A-D, 6A-F

non 1844 *Pollicipes conicus* Reuss, p. 216.
1935 *Calantica* (*Scillaelepas*) *conica* (Reuss). – Withers, pp. 120-122, pl. 8, figs. 1-7.
2014 „*Scillaelepas*“ *conica* (Reuss). – Kočová Veselská et al., pp. 61-62, pl. 3, figs. 1-16.
2014 „*Scillaelepas*“ *conica* (Reuss). – Kočí et al., p. 224, pl. 1, figs. 1-9.

Etymology: Named after August Emanuel Rudolph von Reuss (1811-1873), an Austrian geologist and palaeontologist, born at Bílina (Bohemia). The results of his research were published in ‘Geognostische Skizzen aus Böhmen’ (Reuss 1840-1844) and ‘Die Versteinerungen der Böhmischen Kreideformation’ (Reuss 1845-1846). In 1849, he became professor of mineralogy at the University of Prague, where he established a fine mineralogical collection and became the first lecturer on geology in Bohemia. In 1863 he was appointed professor of mineralogy at the University of Vienna. He studied Cretaceous faunas from Gosau, notably cirripedes, corals, and bryozoans. In addition, he described foraminifera of various geological formations and countries.

Types: The holotype, selected from new material, is a carina (NM-O7638); paratypes comprise specimens from Fritsch’s original material from Kaňk, purchased by the Natural History Museum London, namely: six scuta (NHM In. 16739, 16740, 16742–16745), two terga (NHM In. 16753, 16754), one carina (NHM In. 16746) and one rostrum (NHM In. 16747), as well as five right scuta (NM-O7633, NM-O7641, NM-O7643, NM-07644, NM-O7648), one left scutum (NM-O7634), one left tergum (NM-O7635), one rostrum (NM-O7636), three medial latera (NM-O7637, NM-O7642, NM-O7647), three carinal latera (NM-O7640, NM-O7645, NM-7646) and one subcarina (NM-O7639,) all collected from Kaňk in 2014 and 2015.

Additional new material: More than 1,300 capitular plates including scuta, carinae, subcarinae, rostra, subrostra, terga and lateral plates (carinal and medial latera).

Type locality and horizon: Upper Cenomanian and upper Cenomanian/lower Turonian boundary interval at Kaňk-Na Vrších (Kolín area, Bohemian Cretaceous Basin, Czech Republic).

Diagnosis: *Myolepas* with capitular plates possessing apical umbones and with weak to moderate, well-spaced transverse growth ridges; carina gently arcuate, lacking distinct parietes; scuta elongated triangular with length of basal margin approximating that of tergal margin; tergum subrhomboidal, with a narrow band of apical growth lines in interior; rostrum strongly incurved with distinct apical umbo; medial latus triangular, internally with well-formed lateral growth ridges meeting centrally; subcarina isoscelene triangular.

Remarks: The holotype of *Pollicipes conicus* is a carina. Although very poorly preserved, it does show a weak apico-basal ridge in the upper part and is indistinguishable from that of *Cretiscalpellum glabrum* (Roemer, 1841). The carinae of the new material and of Fritsch’s original (in Withers, 1935) does not possess an apico-basal ridge, nor do any of the carinae from Kaňk that had previously been ascribed to ‘*Scillaelepas*’ *conica*. It is clear that Reuss’ holotype belongs to *Cretiscalpellum glabrum* and as a result, *Pollicipes conicus* Reuss, 1844 becomes unavailable (see Article 49, ICZN, 2012): ‘Use of a species-group name wrongly applied through misidentification’).

Description: Carina conical to semi-cylindrical, thick; no apico-basal ridge; exterior with poorly developed growth lines; basal margin very slightly concave; lateral margins straight to very slightly concave; parietes absent; interior without growth lines in apical region, not thickened apically; apex sharply rounded. Subcarina resembling carina, but shorter. Scutum thick, obtusely triangular, length varying from one-third to more than one and a half times width; basi-tergal angle broadly rounded; tergal margin slightly concave to concave, basal margin broadly convex; occludent margin convex, with sharply rounded ridge extending along length of this margin; plate abruptly bent inwards almost at right angles to outer surface to form steep-sided occludent margin, extending to produce tooth-like process at rostral angle; exterior with weak transverse growth lines crossed by indistinct, rounded longitudinal ridge extending from apex to basal margin; interior with small narrow groove extending down from apex, adductor muscle pit deep, inner tergal edge rounded with very weakly developed articular furrow. Tergum subrhomboidal, slightly convex transversely; surface smooth with very fine transverse growth lines; centrally with weak, wide flat apico-basal ridge extending towards scutal margin; internally weakly concave, occludent, apical and upper carinal margins thickened, marked by distinct growth lines; basally, occludent edge developing a fold which extends beyond basal margin as tooth; scutal angle arcuate and protuberant. Rostrum conical to semi-cylindrical, thick, apex recurved, externally with fine transverse growth lines. Subrostrum resembling rostrum, but shorter. Medial latera equilaterally triangular, externally with weak transverse growth lines; internally with lateral margins marked by flattened border with subparallel growth lines meeting centrally. Carino-latera obliquely triangular, externally with fine transverse growth lines; with small rounded protrusion at basi-rostral angle; weak longitudinal apicobasal ridge extending close to carinal margin.

Remarks and relationships: Fritsch (1889) referred to the type specimen of Reuss (1844: 216) from Kyselka near Bílina (= Reuss’s ‘Sauerbrunnberg bei Bílina’) in his account of the ‘Teplitzer Schichten’, while earlier Fritsch & Kafka (1887) had recorded this species from the Priesener Schichten (now Březno Formation) at Luschitz. In his account of the upper Cenomanian (now Korycany Member), Frič (1911) mentioned but a single occurrence, from Bílina and Kyselka (‘Sauerbrunnberg’), but did not provide an illustration. More detailed remarks were made by Withers (1935: 121). The relationships of the material mentioned by Fritsch (1889), Fritsch & Kafka (1897) and Frič (1911) is uncertain but most probably it should all be assigned to the calanticid

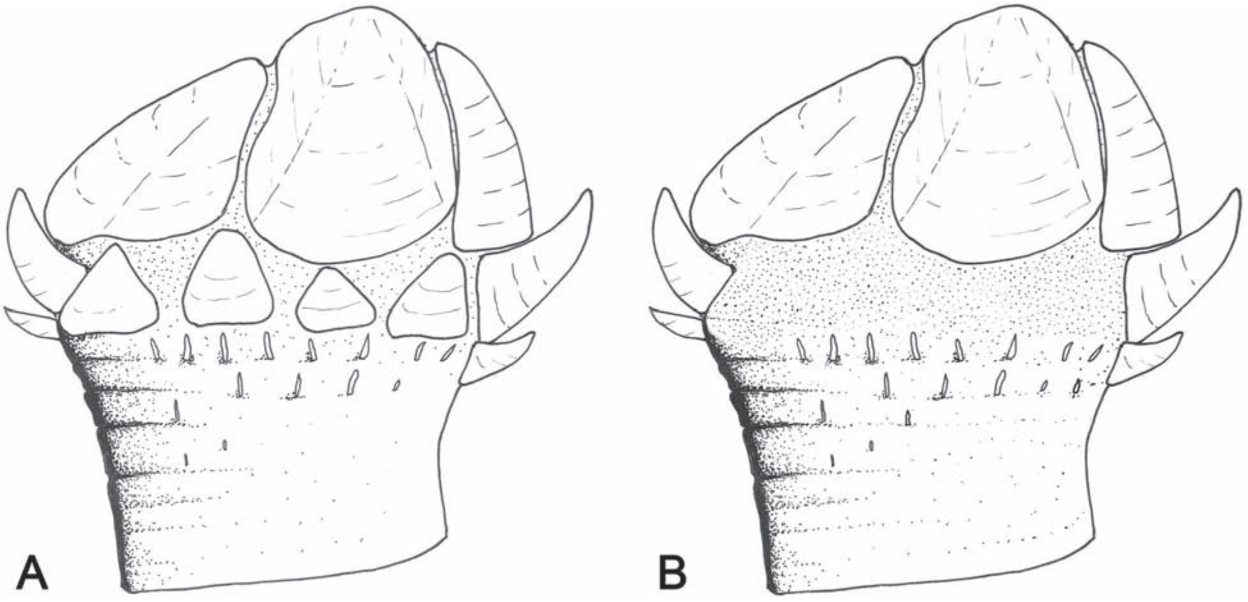

Fig. 7. *Myolepas reussi* sp. nov. **A** – Interpretative reconstruction of the capitulum with latera, subcarina and subrostrum. (orig. by JB). **B** – Interpretative reconstruction without lateral plates (orig. by JB and TK).

Cretiscalpellum glabrum. The lateral plates of *Myolepas reussi* sp. nov. are distinguished from those of '*Scillaelepas*' *dorsata* by their smooth external surfaces. The tergum of the new species can be differentiated from that of '*S.*' *dorsata* by the less distinct apico-basal ridge, while the scuta of the former lack the two apicobasal ridges of the latter. *Myolepas reussi* sp. nov. may also be distinguished by scutal and tergal outlines. *Myolepas reussi* sp. nov. may be distinguished from *M. scanica* by scuta that are more elongated and possess a less well-developed internal muscle scar.

Note: An anonymous reviewer interpreted the latera as rolled calcite shell fragments, and as such concluded that *Myolepas* should still have no lateral plates. Nonetheless, we contend that all of the plates that we have identified as latera conform to the expected pattern, and thus represent a secondary whorl of lower capitular plates. We note that this is at variance to the reconstruction in Gale & Sørensen (2015: 217, fig. 5C), where latera are absent, and in light of this, we have included two possible reconstructions, first with latera (Fig. 7A) and second without them (Fig. 7B). The reviewer also suggested that there could be more than one taxon in the collection. However, the latera are morphologically consistent with the scuta and terga – all of which show varying degrees of abrasion. When there are no articulated specimens available, there are likely to be alternative reconstructions. In this case, utilizing parsimony, we conclude that latera are present and that there is insufficient evidence for more than one species; as such, *Myolepas reussi* sp. nov. possessed a secondary whorl of lower plates in the capitulum and the reconstruction provided in Fig 7A is the most likely.

5. Palaeoecology

The palaeoecology of extinct cirripedes has been, at least in part, discussed in numerous papers dealing with cirripede taxonomy (e.g., Gale & Sørensen 2014, 2015; Buckeridge 1975, 1983; Foster & Buckeridge 1987; Kočová Veselská et al. 2015). This new calanticid possessed a relatively heavily armoured capitulum, an adaptation to withstand the effects of a high-energy setting, although it may also have inhabited the micro-environment between larger boulders, where currents would be less turbulent (see associated fauna; Table 1). We believe that *Myolepas reussi* sp. nov. inhabited a high-energy intertidal environment similar to that of extant members of *Pollicipes* and *Capitulum.* The high abundance, but low diversity, of scalpelliforms at this locality – only one taxon – is similar to that of living intertidal calanticids such as *Calantica spinosa* (Quoy & Gaimard, 1834) (Fig. 8).

During the Neogene calanticids became increasingly more restricted to relatively deep-water settings (Buckeridge 1983, 1984). Extant representatives include the genera *Calantica* Gray, 1825 and *Scillaelepas* Seguenza, 1876, which typically inhabit deep water, although, *Calantica spinosa* (Quoy & Gaimard, 1834) from New Zealand, is found attached to rocks and algal holdfasts in the lower intertidal (Foster 1979).

Table 1. Associated fauna at Kaňk-Na Vrších, based on personal observations and data supplied by Perner (1892), Počta (1892), Gregory (1906), Frič (1911), Lang (1916), Kühn (1924), Withers (1935), Prantl (1940), Cushman (1944), Zázvorka (1952, 1954), Čech & Soukup (1955), Nekvasilová (1964, 1973), Pajaud (1970), Hercogová (1974, 1988), Štemproková-Jírová (1976, personal communication March 2016), Němec (1978), Žítt (1986), Pokorný (1989), Eliášová (1997), Štorc (1997, 2004), Sviták (2005), Hradecká & Švábenická (2007), Taylor & Zágoršek (2011), and Kočí (2012). Only the most typical taxa are listed.

	Rare	Common
Foraminifera		
Lenticulina rotulata (Lamarck, 1804)		●
Bdelloidina cribrosa (Reuss, 1846)	●	
Octocorallia		
Moltkia foveolata (Reuss, 1846)		●
Sabellid worms		
Glomerula serpentina (Goldfuss, 1831)		●
Serpulid worms		
Neovermilia ex gr. *ampullacea* (J. de C. Sowerby, 1829)		●
Pyrgopolon cf. *tricostata* (Goldfuss, 1831)		●
Pyrgopolon sp.		●
Bryozoa		
Stomatopora sp.		●
Reptomultelea acupunctata (Novák, 1877)		●
Biforicula biseriata (Počta, 1892)		●
Idmonea plana Počta, 1892		●
Membranipora sp.		●
Brachiopoda		
Phaseolina phaseolina (Valenciennes *in* Lamarck, 1819)	●	
Cyclothyris zahalkai Nekvasilová, 1973	●	
Ancistrocrania sp.	●	
Bivalvia		
Amphidonte (*Ceratostreon*?) *sigmoideum* (Reuss, 1845)		●
Amphidonte (*C.*) *reticulatum* (Reuss, 1846)		●
Gryphaeostrea canaliculata (J. Sowerby, 1813)		●
Rastellum carinatum (Lamarck, 1819)		●
Rastellum diluvianum (Linnaeus, 1767)		●
Lyropecten (? *Aequipecten*) *ternatus* (Münster, 1833)		●
Ctenoides tecta (Goldfuss, 1836)		●
Spondylus sp.		●
Isognomon lanceolatum (Geinitz, 1845)		●
Gastropoda		
Pleurotomaria geinitzi (d'Orbigny, 1850)		●
Neritopsis sp	●	
Turritella sp.	●	
Cephalopoda		
Nautilorhynchus simplex (Fritsch, 1872)	●	
Echinodermata - Crinoidea		
Isocrinus? cf. *cenomanensis* (d'Orbigny, 1850)		●
Glenotremites discoidalis (Gislén, 1925)	●	
Echinodermata - Echinoidea		
Temnocidaris (Stereocidaris) vesiculosa (Goldfuss, 1829)	●	
Pyrina desmoulinsii (d'Archiac 1847)		●
Tylocidaris sorigneti (Desor, 1858)		●
Echinodermata - Asteroidea		
Metopaster sp.		●
Vertebrata - Selachii		
Paranomotodon angustidens (Reuss, 1846)	●	
Scaphanorhynchus rhaphiodon (Agassiz, 1843)	●	

Fig. 8. *Calantica spinosa* (Quoy & Gaimard, 1843) *in situ*. The greatest concentration of these barnacles is along fissures and other sheltered zones within the limestone substrate. Exposed at low tide on Lighthouse Rock, Castlepoint, New Zealand 40.899S, 176.231E. (photographed by JB on January 18th, 2016). A similar habit is envisaged for *Myolepas reussi* sp. nov. (scale = 23.25 mm diameter).

The latter genus is known from depths between 340 to >3,000 m (Newman 1980).

The occurrence of but a single calanticid taxon at this locality may also reflect the phylogenetic position of *M. reussi* sp. nov., in comparison with cirripede distribution in other shallow-water, Late Cretaceous examples, such as Velim (six taxa), Kamajka (four) and Chrtníky (two). Although sedimentological arguments put forward by Eliáš & Zelenka (2002) suggest deeper waters for the locality Kaňk-Na Vrších, the presence of shallow-water corals (*Dimorphastrea* sp., *Meandrastraea pseudomeandrina*, *Calamophylliopsis* sp., *Proaplophyllia*? sp.) would seem indicative of a depth range of 0-50 m (Eliášová 1997). This conforms broadly to what was recorded by Houša (1991), who noted that the basal conglomerates, which formed at depths of 5 metres, provided the only depositional pockets that were sufficiently deep to provide shelter for fossils to accumulate in. The basal conglomerates pass relatively rapidly into biodetritic limestones, which form the next sedimentary infills of so-called pockets – facies of biodetritic limestones. In many shallower pockets or in certain parts of these, basal limestone predominates because the areal extent of sedimentation of biodetritic limestone was greater than that of the basal conglomerate. Houša (1991) deduced that biodetritic limestones would have been deposited at depths of 5-15 m. The overlying layers are calcareous claystones, which Houša (1991) referred to as a ‘small oyster facies’ dominated by *Amphidonte* (*Ceratostreon*) *reticulatum* (Reuss, 1846) and *A.* (*C.*?) *sigmoideum* (Reuss, 1845), for which he interpreted a depositional depth of 5-30 m. The abundance of these oysters suggests that on the bottom in the vicinity still enough solid substrates, such as boulders, remains of valves and other organisms were available, to which these oysters attached. This zone was still within wave action which also precluded deposition of finer material and excluded organisms that required a quiet environment. This observation contrasts with Sviták (2005), who suggested a deeper environment on the basis of the presence of the benthic foraminifera *Gavelinella berthelini* (Keller, 1935) and *Marsonella oxycona* Reuss, 1860.

6. Traces of predation

Evidence of predation and *in vivo* damage by boring organisms is also found in the Kaňk-Na Vršĭch assemblage. Examples of the ichnogenus *Oichnus* Bromley, 1981 are found in three right scuta (Fig. 6A-F). Some of these drill holes (Fig. 6A, A1, A2, F) are elliptical in outline, while a typical example of *O. paraboloides* in a tergum, with a near-circular, bevelled outline is shown in Fig. 6C. Two non-penetrative pits in a right scutum (Fig. 6B, E) are identified as *Oichnus* isp. Another specimen (Fig. 6E) shows a non-penetrative borehole that originated on the inner surface; it probably is the result of unsuccessful drilling of isolated capitular plates already dispersed on the sea floor after the death of the cirripede. Although holes and non-penetrative pits of the ichnogenus *Oichnus* may be ascribed to a range of organisms (Zonneveld & Gingras 2014; Wisshak et al. 2015), it is most likely that the borings in our examples were made by carnivorous gastropods such as naticids and muricids. These have been recorded from the locality studied.

In general, evidence of *in vivo* predation in cirripedes is rare. Recent records include a right scutum and a carina of *Cretiscalpellum glabrum* from ‘pocket Václav’ at Velim (section VII of Žítt et al. 1997; lower Turonian), late Maastrichtian verrucids from the Netherlands (Gale 2014) and from various species of late early Campanian age in southern Sweden (Gale & Sørensen 2014, 2015). For more examples and a detailed discussion, reference is made to Klompmaker et al. (2015).

The Kaňk-Na Vršĭch material also reveals evidence of abundant microborings produced by algae, clionid sponges or hydroids. Such borings are present in median latera (Fig. 6B2, D1) in particular, which may be indicative of *in vivo* interaction, as *Myolepas reussi* sp. nov. was presumbly heavily encrusted with soft-bodied organisms, and only the apical parts of capitular plates protruding. Another type of microboring is seen in a scutum (Fig. 6F); its affinity is unknown.

7. Conclusions

Myolepas reussi sp. nov. from the upper Cenomanian at Kaňk-Na Vršĭch was originally described as *Pollicipes conicus* Reuss, 1844 (= *Cretiscalpellum glabrum*) and later, by Withers (1935), as *Calantica* (*Scillaelepas*) *conica*. It had a heavily armoured capitulum to withstand high-energy conditions and to deter drilling predators; records of *Oichnus*-type drill holes and microborings demonstrate that the species was not always successful in fending off predators.

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Paper VII

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Review of the Late Cretaceous erymid lobsters (Crustacea: Decapoda) from the Western Tethys

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ABSTRACT

The Erymidae Van Straelen, 1925 had a worldwide distribution during the Jurassic and the Cretaceous. Twenty-seven species among four genera were reported in the Late Cretaceous, but confusions in diagnoses have led to wrong generic identifications of many erymid species. In the light of recent clarifications of the diagnoses of erymid genera, the Late Cretaceous species are here reviewed. We recognize thirteen of them including three European species which benefit of new descriptions: *Palaeastacus sussexiensis* (Mantell, 1824), *Enoploclytia leachi* (Mantell, 1822) and *Enoploclytia seitzi* Glaessner, 1932. Furthermore, a comparison of the Late Cretaceous erymid fauna with that from the Early Cretaceous emphasizes some changes. A decrease in diversity on genus and species level is noted with the absence of *Eryma* Meyer, 1840 in the Late Cretaceous and the predominance of *Enoploclytia* M'Coy, 1849 (including almost half of the species). Despite the scarcity of the fossil record, our palaeobiogeographic interpretations led us to propose hypotheses about the provenance of North American populations in the end of Early Cretaceous and in Late Cretaceous: (1) their supposed absence since the Callovian (Jurassic) is due to collecting and/or reporting bias or (2) they were the result of migrations of European populations. Moreover, the report of a chela assigned to *Stenodactylina* cf. *armata* (Secrétan, 1964) in France confirms the existence of migration routes between European and Malagasy faunas during the Late Cretaceous.

1. Introduction

Erymid lobsters are typical Mesozoic decapod crustaceans reported from Europe (*e.g.*, Mantell 1833; Bell 1850, 1863; Oppel 1861, 1862; Lahusen 1894; Van Straelen 1925; Beurlen 1928; Glaessner 1931; Reuss 1854; Bachmayer 1959; Förster and Rieber 1982; Garassino 1996; Jagt and Fraaije 2002; Garassino and Krobicki 2002; Bravi et al. 2014), in the Middle East (Roger, 1946; Förster and Seyed-Emani 1982; Garassino 1994; Charbonnier et al. 2017), in Africa (Beurlen 1933; Joleaud and Hsu 1935; Secrétan 1964, 1984; Charbonnier et al. 2012), in America (Rathbun 1923, 1926; Stenzel 1945; Feldmann and McPherson 1980; Aguirre-Urreta and Ramos 1981; Aguirre-Urreta 1982, 1989; Schweitzer and Feldmann 2001; Feldmann and Titus 2006; Feldmann and Haggart 2007; Vega et al. 2013; J. Luque, pers. com.), in Japan (Karasawa et al. 2008; Kato et al. 2010), in Australia (Woodward 1877; Etheridge 1914; Woods 1957), and in Antarctica (Taylor 1979; Aguirre-Urreta 1989). Despite this worldwide distribution, the fossil record of erymid lobsters remains sparse and fragmentary partially due to the low fossilization potential of decapod crustaceans (scavenging, decortication, disarticulation, carapace fragmentation), and bias related to collection and reporting (Plotnick 1986; Bishop 1986; Plotnick et al. 1988; Tshudy et al. 1989; Müller et al. 2000; Stempien 2005; Mutel et al. 2008; Krause et al. 2011; Hyžný and Klompmaker 2015; Klompmaker et al. 2017). Currently, twenty-seven species are known in the Late Cretaceous. However, until recently, the diagnoses of erymid genera, mainly based on carapace groove pattern and morphology of the chelae of

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the first chelipeds (Van Straelen 1925; Förster 1966; Glaessner 1969), remained confused. Some recent studies tried to clarify the concepts of erymid genera and proposed new diagnoses (Hyžný et al. 2015; Devillez et al. 2016). Thus, considering these revisions, the present contribution aims to give a new look on Late Cretaceous erymid fauna with a focus on European taxa, which benefit of new descriptions, and to compare with Early Cretaceous erymid fauna.

2. Material and methods

The studied material includes 272 specimens from the Cretaceous (Table 1). They were mostly studied using a CETI Belgium MEDO binocular microscope. Most of them consist of isolated carapaces and first chelipeds. Almost all European specimens examined in this work are assigned to *Enoploclytia leachi* (Mantell, 1822) or *Palaeastacus sussexiensis* (Mantell, 1824). These species are represented by numerous fossils in the Late Cretaceous chalk formations from southeast United Kingdom and only *E. leachi* is abundantly present in the Bohemian Cretaceous Basin (Czech Republic). In both areas, the fossils are relatively undeformed and few specimens are preserved with some anatomical parts which are uncommonly preserved (pleon, antennulae, antennae, third maxillipeds).

2.1. Institutional abbreviations

BAS	British Antarctic Survey, Cambridge (United Kingdom).
BGR	Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin (Germany).
BM	Booth Museum of Natural History, Brighton (United Kingdom).
MNHN	Muséum national d'Histoire naturelle, Paris (France).
MUZ	Museo de Múzquiz, Coahuila (Mexico).
NHMUK	Natural History Museum, London (United Kingdom).
NM	Národní Muzeum, Prague (Czech Republic).
STI	Steinmann Institut für Geologie, Mineralogie und Paläontologie, Bonn (Germany).
SM	Sedgwick Museum of Earth Sciences, Cambridge (United Kingdom).
NPL	Non-Vertebrate Paleontology Laboratory, Jackson School of Geosciences, University of Texas, Austin (United States).
USNM	United States National Museum of Natural History, Smithsonian Institution, Washington, D.C. (United States).

2.2. Anatomical abbreviations

a1	Antennulae.
a2	Antennae.
CL	Carapace length (excluding rostrum).
CH	Carapace height.
Mxp3	Third maxilliped.
ω	Attachment site of mandibular muscle.
χ	Attachment site of adductor testis muscle.
P1–P5	Pereiopods 1–5.
s1–s6	Pleonal somites 1–6.

3. Systematic Palaeontology

MALACOSTRACA Latreille, 1802

DECAPODA Latreille, 1802

ERYMIDA *sensu* Schram and Dixon, 2004

Superfamily ERYMOIDEA Van Straelen, 1925

Family ERYMIDAE Van Straelen, 1925

INCLUDED GENERA. — *Enoploclytia* M'Coy, 1849; *Eryma* Meyer, 1840; *Palaeastacus* Bell, 1850; *Pustulina* Quenstedt, 1857; *Stenodactylina* Beurlen, 1928; *Tethysastacus* Devillez et al., 2016.

PRELIMINARY REMARKS. — Currently, the phylogenetic position of Erymidae is debated. Indeed, many authors have included this family within the Astacidea Latreille, 1802 (Van Straelen 1925; Glaessner 1969; Aguirre-Urreta 1989; Schweigert et al. 2000; Garassino and Krobicki 2002; Crônier and Courville 2004; Garassino and Schweigert 2006; Feldmann and Titus 2006; Schweigert 2013; Charbonnier et al. 2013) while recent contributions recognized this family to belong to Glypheidea Zittel, 1885 (De Grave et al. 2009; Schweitzer et al. 2010; Wahle et al. 2012; Karasawa et al. 2013; Feldmann et al. 2015). However, results of phylogenetic analysis by Charbonnier et al. (2015) suggest to remove Erymidae from Glypheidea. So, following Hyžný et al. (2015), we consider the systematic position of the Erymidae as uncertain. Then, according to Schram and Dixon (2004), we include the Erymidae in the separate clade Erymida, without listing taxonomic rank beyond superfamily.

Genus *Eryma* Meyer, 1840

TYPE SPECIES. — *Macrourites modestiformis* Schlotheim, 1822, by subsequent designation of Glaessner (1929).

DIAGNOSIS. — An emended diagnosis was proposed by Devillez et al. (2016: 518) and does not need to be repeated here.

REMARKS. — Among the numerous species of *Eryma* listed by Schweitzer et al. (2010), four are known in the Late Cretaceous. Three of them are from the United States: *Eryma americanum* Rathbun, 1923,*Eryma flectum* Rathbun, 1926, and *Eryma stantoni* Rathbun, 1935. These species are based on fragments of P1 chelae and carapaces and, after careful examination of figures presented by Rathbun (1923, 1926, 1935), we follow Förster (1966: 125) and Devillez et al. (2016: 520) who consider that *E. americanum*, *E. flectum* and *E. stantoni* do not belong to Erymidae. The last listed species is *Eryma cretaceum* Roger, 1946 from the Cenomanian of Lebanon. Based on the carapace groove pattern and the morphology of the P1 chelae, Charbonnier et al. (2017) transfered this species to *Pustulina* Quenstedt, 1857. We concur with this transfer.

In conclusion, to our current knowledge, there is no representative of *Eryma* in the Late Cretaceous and the last occurrence of this genus is *Eryma vocontii* Devillez et al., 2016 from the Albian (Early Cretaceous) of southeast France.

Genus *Stenodactylina* Beurlen, 1928

TYPE SPECIES. — *Stenodactylina liasina* Beurlen, 1928, by monotypy.

DIAGNOSIS. — An emended diagnosis was proposed by Devillez et al. (2016: 522) and does not need to be repeated here.

REMARKS.— *Stenodactylina* includes thirteen species mostly from the Jurassic (Devillez et al. 2016). Only two species are reported from the Late Cretaceous: *Stenodactylina triglypta* (Stenzel, 1945) (Coniacian, Texas, United States) and *S. armata* (Secrétan, 1964) (Campanian, Madagascar). These species are known from only a few fossils. *Stenodactylina armata* is known from four incomplete P1 chelae initially assigned to *Enoploclytia* M'Coy, 1849 (Secrétan 1964; Förster 1966; Schweitzer et al. 2010; Charbonnier et al. 2012). These P1 chelae exhibit a strong, rectangular propodus, slightly compressed dorso-ventrally, with a slight concavity of the outer margin at the basis of the index and with a strongly inflated dactylar bulge (Fig. 1A, B). As pointed out by Devillez et al. (2016), these characteristics fit the general morphology of the P1 chelae of

Table 1
List of the examined material of Cretaceous erymid lobsters.

Taxa	Examined material	Anatomy	Ages	Localities
Eryma Meyer, 1840				
Eryma vocontii n. sp.	holotype MNHN.F.A57457, paratype MNHN.F.A57458.	carapace, P1 chela	Albian	France
Enoploclytia M'Coy, 1849				
Enoploclytia collignoni Secrétan, 1964	—holotype MNHN.F.R03925, 43 paratypes. —16 additional specimens MNHN.F.A33041, A33058, A33079, A33137, A33162, A33164, A33167, A33178, A33186, A33187, A33193, A33229, A33332, A33362, A33469, A33472.	carapaces, P1 chelae, pleons	Campanian	Madagascar
Enoploclytia leachi (Mantell, 1822)	—lectotype NHMUK 5636, 2 paralectotypes NHMUK 5623, In.61020. —86 additional specimens NHMUK 5600, 5606, 5609, 5610, 5611, 5615, 5616, 5634, 34404, 59825, I.193, I.1977, I.1980, I.2190, In.27682; BM 007759, 007760, 007762, 007763, 007764, 007765, 007766, 016987, 016989; MNHN.F.A60030, A66890, A66894, B16580, B16612, R03372; NM O1261, O3500, O4002, O4042, O4043, O4062, O4063,O4915, O6084, O6085, O6086, O7123, O7124, O7125, MV 1-MV 11, MV 17-MV 24, MV 26-MV 31, MV 39-MV 45, MV 53-MV 56, MV 62-MV 68.	carapaces, P1 chelae, pleons	Cenomanian – Campanian	United Kingdom France, Czech Republic, United Kingdom
	—holotype STIPB-Schlüter-124 of *E. granulicauda* Schlüter, 1879.	carapace, P1 chela, pleon	Campanian	Germany
Enoploclytia seitzi Glaessner, 1932	lectotype BGR X 00266, 1 paralectotype BGR X 00267.	carapaces	Albian	Germany
	1 additionnal specimen NHMUK 5918.	carapace, P1 chela, pleon	Cenomanian	United Kingdom
Enoploclytia tumimanus Rathbun, 1935	holotype USNM PAL 73799, 8 paratypes USNM PAL 336023A, 336023 B, 336023 C, 336023 D, 336023 E, 336023 F, 336023 G, 336023 H.	carapaces, P1 chelae	Maastrichtian	United States
Enoploclytia tepeyacensis Vega et al., 2013	holotype MUZ-824, 1 paratype MUZ-825.	carapaces	Campanian	Mexico
Palaeastacus Bell, 1850				
Palaeastacus kimzeyi Rathbun, 1935	holotype USNM PAL 73797, 2 paratypes USNM PAL 335146, 73841.	carapace, P1 chelae	Campanian	United States
Palaeastacus sussexiensis (Mantell, 1824)	—lectotype NHMUK 5601, 13 paralectotypes NHMUK 5024, 5584, 5586, 5589, 5600, 5602, 5608, 5613, 5618, 5624, 5626, 5629, 10760. —37 additional specimens NHMUK In.27682, In.36768, I.62, I.2190, I.2628, 5685, 35124, 44343, 024318, 026316, 46782, 59668, 59824, 59824; BAS KG.103.134; BM 002548, 002549, 007751, 007752, 007753, 007754, 007755, 007758, 008632, 008633, 008635, 008636, 008637, 008659, 016988, 024317, 024318, 026316; MNHN.F.A58710, A66893, B14182, B17969.	carapaces, P1 chelae, pleons	Cenomanian – Turonian	United Kingdom
	3 syntypes SM B8884, B8885, B8886 of *Enoploclytia brevimana* M'Coy, 1849.	P1 chelae	Cenomanian	United Kingdom
	8 syntypes SM B8892, B8893, B8894, B8895, B8896, B8897, B8898, B8899 of *Enoploclytia imagei* M'Coy, 1849.	carapace, P1 pereiopods	Cenomanian	United Kingdom
	— lectotype NHMUK 41938, 2 paralectotypes NHMUK 39377, 39380 of *Hoploparia scabra* Bell, 1863. —4 additional specimens NHMUK In.27684, In.61022, In.27685, In. 27686 of *Hoploparia scabra* Bell, 1863.	carapaces and P1 pereiopods	Albian	United Kingdom
	—lectotype BM 007750, paralectotype NHMUK I.1916, of *Palaeastacus dixoni* Bell, 1850. —1 additionnal specimen BM 007757 of *Palaeastacus dixoni* Bell, 1850.	carapaces, P1 chelae, pleon	Cenomanian	United Kingdom
	2 syntypes SM B22448, B22449 of *Phlyctisoma granulatum* Bell, 1863.	carapaces	Albian	United Kingdom
Pustulina Quenstedt, 1857				
Pustulina cretacea (Roger, 1946)	2 syntypes MNHN.F.B18903, MNHN.F.B18904. —11 additional specimens MNHN.F.A30680, A30681, A30682, A30683, A30684, A30685, A30686, A30687, A38526, A38527, A38528.	carapaces, P1 chelae, pleons	Cenomanian	Lebanon
Pustulina trisulcata (Schweitzer and Feldmann, 2001) nov. comb.	holotype USNM 512150.	carapace, pleon	Cenomanian	United States
Stenodactylina Beurlen, 1928				
Stenodactylina armata (Secrétan, 1964)	—holotype MNHN.F.R03913, 3 paratypes MNHN.F.A33209, A33464, R03912. —additionnal specimen MNHN.F.A33331.	P1 chelae	Campanian	Madagascar
Stenodactylina cf. *armata* (Secrétan, 1964)	MNHN.F.A66891.	P1 perieiopod	Santonian	France
Stenodactylina triglypta (Stenzel, 1945)	lectotype NPL TMM-BEG 21127; 2 paralectotypes NPL TMM-BEG 21124, 21125.	carapaces, P1 chela	Coniacian	United States
Non erymid species				
Eryma americanum Rathbun, 1923	holotype USNM PAL 31899, 2 paratypes USNM PAL 31900, 31901.	carapaces, P1 chela	Late Cretaceous	United States
Eryma flectum Rathbun, 1926	holotype USNM PAL 73115.	P1 chela	Maastrichtian	United States
Eryma stantoni Rathbun, 1935	holotype USNM PAL 73790.	P1 chela	Maastrichtian	United States
Enoploclytia sculpta Rathbun, 1926	holotype USNM PAL 73119.	P1 pereiopod, pleon	Maastrichtian	United States
Palaeastacus selmaensis Rathbun, 1935	holotype USNM PAL 73848.	Unidentifiable fragment	Late Cretaceous	United States

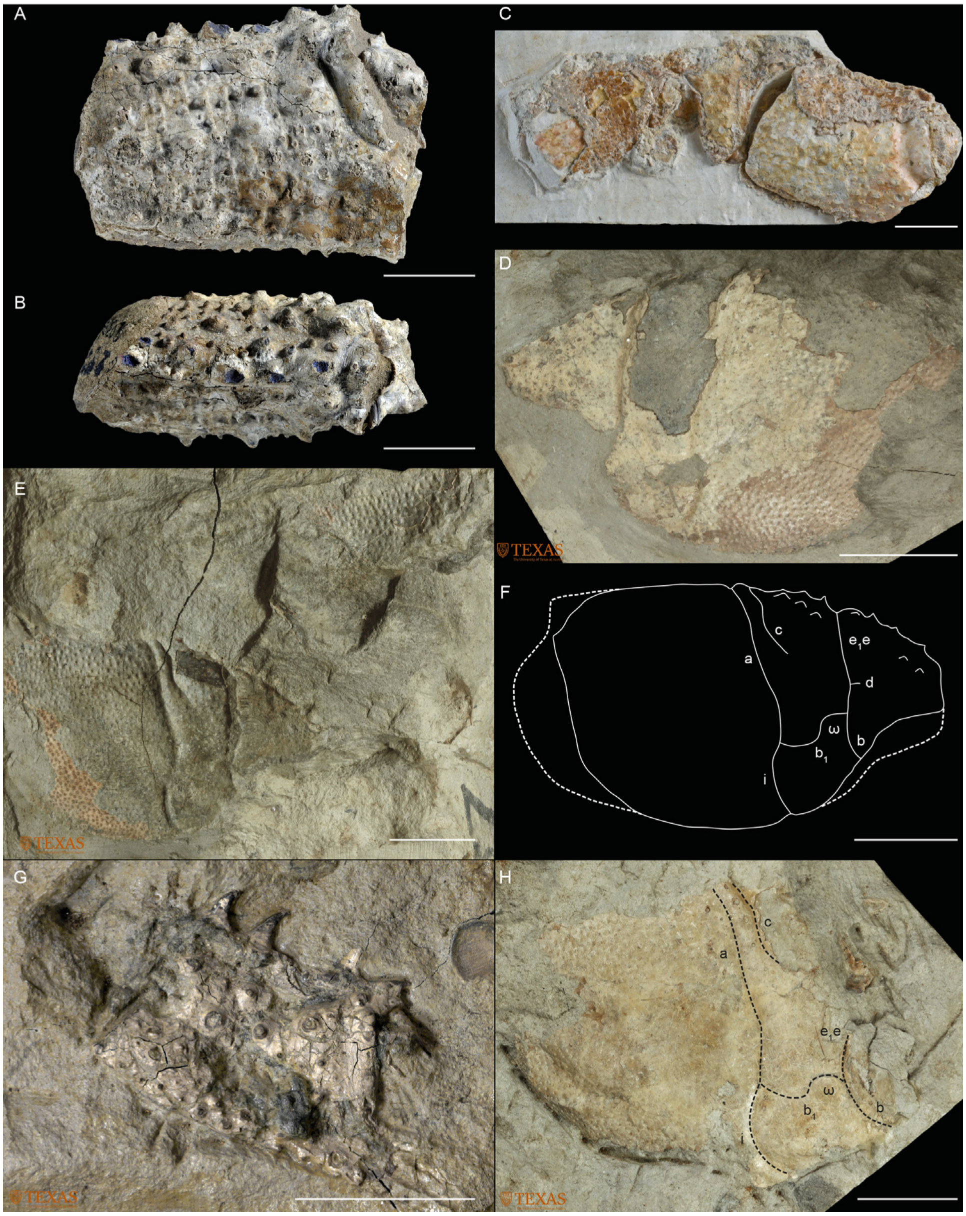

Fig. 1. Late Cretaceous specimens of *Stenodactylina* Beurlen, 1928. A, B, holotype MNHN.F.R03913 of *Stenodactylina armata* (Secrétan, 1964) from the Campanian of Belo-sur-Tsiribihina, Madagascar: right P1 chela in dorsal view (A), and inner view (B); C, specimen MNHN.F.A66891 of *Stenodactylina* cf. *armata* from the Santonian of Cognac, France, dorsal view of right P1; D–H, *Stenodactylina triglypta* (Stenzel, 1945) from the Coniacian of Savoy, USA: lectotype TMM-BEG 21127 (D–F) showing part and counter part of carapace, and line drawing; paralectotype TMM-BEG 21124 (G) showing incomplete P1 chela; paralectotype TMM-BEG 21125 (H) showing fragment of right side of carapace with superimposed line drawing of grooves. Scale bars: 20 mm. Abbreviations: a: branchiocardiac groove; b: antennal groove; b_1: hepatic groove; c: postcervical groove; d: gastro-orbital groove; e_1e: cervical groove; i: inferior groove; ω: attachment site of mandibular muscle. Preparation: Y. Despres (C). Photographs: C. Lemzaouda (A, B), P. Loubry (C), Non-vertebrate Paleontology Laboratory, Jackson School of Geosciences, The University of Texas at Austin (D, E, G, H). Line drawing: J. Devillez.

the representatives of *Stenodactylina* and justify the assignation of the species to this genus. A fragment of P1 cheliped exhibiting a morphology very similar (propodus shape, dactylar bulge, finger bases, surface ornamentation) to that of *S. armata* (Fig. 1C) was found in Santonian deposits of Cognac (France). So, we identified this specimen as *S.* cf. *armata*, which supposes possible palaeogeographic link between the Western and the Southern Tethys.

Stenodactylina triglypta is known from two fragments of carapaces, designated by Stenzel (1945) as "syntype 1" (Fig. 1H) and "syntype 2" (Fig. 1D–F), and a fragment of a P1 chela, designated as "syntype 3" (Fig. 1G). They were initially assigned to *Enoploclytia* but the review of Devillez et al. (2016) demonstrated that the carapace groove pattern is characteristic of *Stenodactylina*: it does not show a junction between postcervical and branchiocardiac grooves, the postcervical groove is interrupted in hepatic region and the branchiocardiac groove is joined to the posterior extremity of the hepatic groove (Fig. 1F).

Since the publication of Stenzel (1945), no lectotype has been designated. Considering the quality of preservation of the carapace which allows the observation of almost all the carapace grooves, we select herein the specimen TMM-BED 21127, stored in the NPL collections, as lectotype for *S. triglypta* ("syntype 2"; Fig. 1C–E). The two paralectotypes are NPL TMM-BEG 21124 ("syntype 1"; Fig. 1H) and 21125 ("syntype 3"; Fig. 1G).

Genus *Palaeastacus* Bell, 1850

TYPE SPECIES. — *Astacus sussexiensis* Mantell, 1824, by subsequent designation of Glaessner (1929).

DIAGNOSIS. — An emended diagnosis was proposed by Devillez et al. (2016: 525) and does not need to be repeated here.

REMARKS. — Among the numerous species of *Palaeastacus* listed by Schweitzer et al. (2010), eight are known from the Late Cretaceous. The type species *Palaeastacus sussexiensis* (Mantell, 1824) (Fig. 2A–F) is redescribed and discussed below. One listed species, *Palaeastacus plauensis* Geinitz, 1875 (Cenomanian, Germany), was previously included into the synonymy of *P. sussexiensis* based upon the shape and ornamentation of the P1 propodus and fingers (Förster 1966; Devillez et al. 2016). Two other species are from Europe: (1) *Palaeastacus macrodactylus* Bell, 1850 (Late Cretaceous chalk, United Kingdom) and (2) *P. cenomaniensis* Hée, 1924 (Cenomanian, France). Carefull examination of the figure presented by Bell (1850: pl. 38, fig. 6) shows that *Palaeastacus macrodactylus* exhibits P1 chelae with long slender fingers typical of *Enoploclytia* (see discussion under *Enoploclytia leachi* for more details). *Palaeastacus cenomaniensis* is known from isolated fragments of P1 chelae lost since World War II (Förster 1966). After the description and figures presented by Hée (1924), the propodus has a square shape with a strongly tuberculate upper side, an almost smooth lower side and thin fingers. P1 chelae of *Palaeastacus* representatives have usually a rectangular or trapezoidal propodus, strongly ornamented on both sides, and wide fingers. Therefore, we do not consider *P. cenomaniensis* to be a representative of *Palaeastacus*. Moreover, the particular shape and

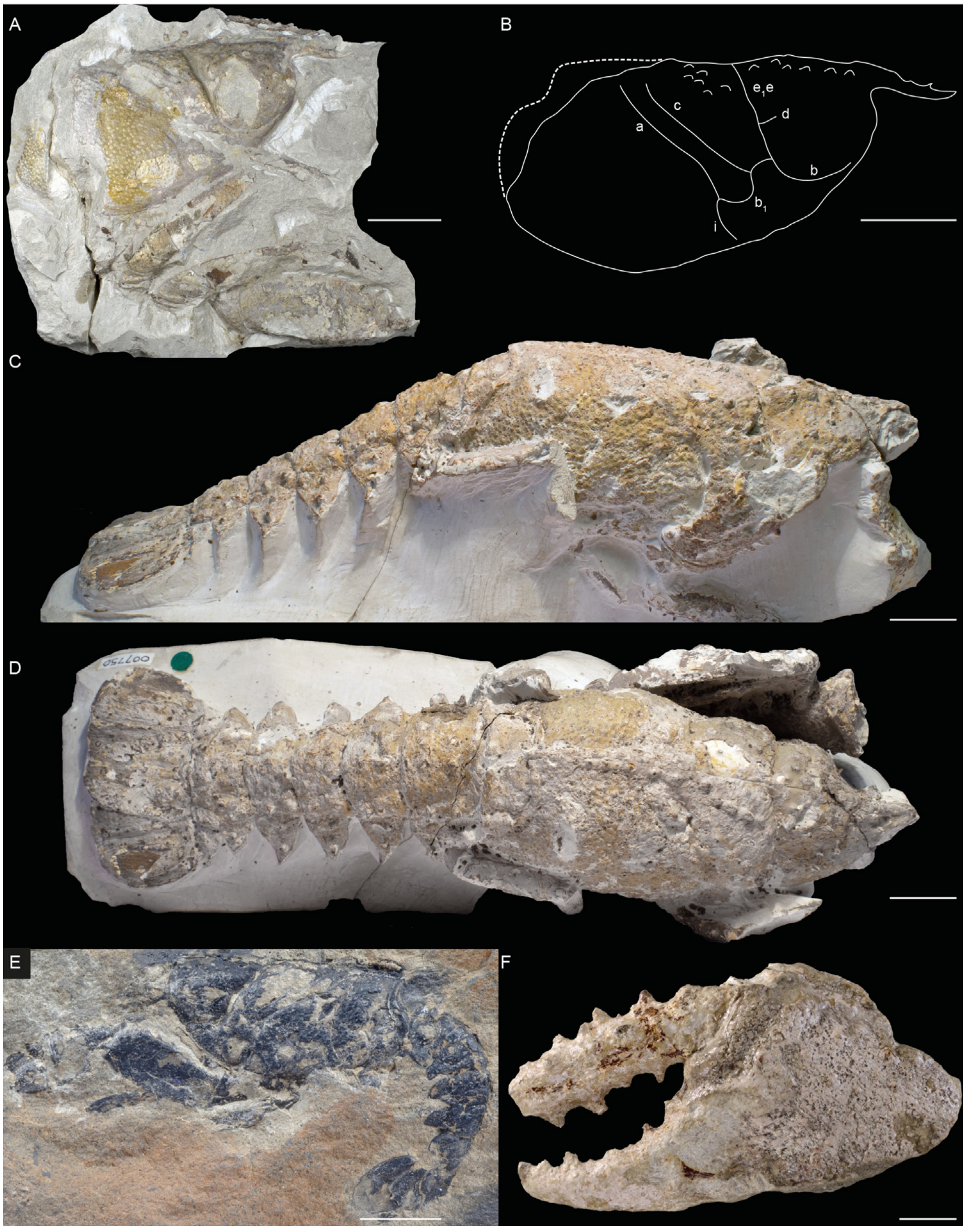

Fig. 2. *Palaeastacus sussexiensis* (Mantell, 1824). A, B, lectotype NHMUK 5601 (Mantell coll.) from the Cenomanian of Sussex, United Kingdom: right side of carapace with parts of pereiopods (A) and line drawing of carapace (B); C, D, lectotype BM 007750 (Willet coll.) of *Palaeastacus dixoni* Bell, 1850 from the Cenomanian of Glynde, United Kingdom: subcomplete specimen in right lateral view (C) and dorsal view (D); E, specimen BAS KG.103.134 from the Aptian of Alexander Island, Antarctica, left lateral view; F, specimen MNHN.F.A58710 from the Turonian of Saint Florentin, France, dorsal view of left P1 chela. Scale bars: 10 mm. Abbreviations: a: branchiocardiac groove; b: antennal groove; b_1: hepatic groove; c: postcervical groove; d: gastro-orbital groove; e_1e: cervical groove; i: inferior groove. Preparation: Y. Despres (F). Photographs: J. Devillez (A, C, D), H. Blagbrough (E), L. Cazes (F). Line drawing: J. Devillez.

ornamentation of the propodus leads us to follow Förster's opinion by removing this species from the Erymidae.

The four remaining species were found in North America. *Palaeastacus kimzeyi* Rathbun, 1935 (Campanian, Texas, United States; Fig. 3A–C) is known from incomplete P1 chelae and a fragment of carapace exhibiting the main characteristics of the genus: postcervical groove joined to median inflexion of the hepatic groove, sub-rectangular P1 propodus, slightly compressed dorso-ventrally and wide fingers. Careful examination of the holotype of *Palaeastacus trisulcatus* Schweitzer and Feldmann, 2001 (Cenomanian, California, United States; Fig. 3D, E) reveals an interruption of the branchiocardiac groove in the branchial region, and the presence of a cardiac groove rising from the postcervical groove and joined to the dorsal margin. This groove pattern is

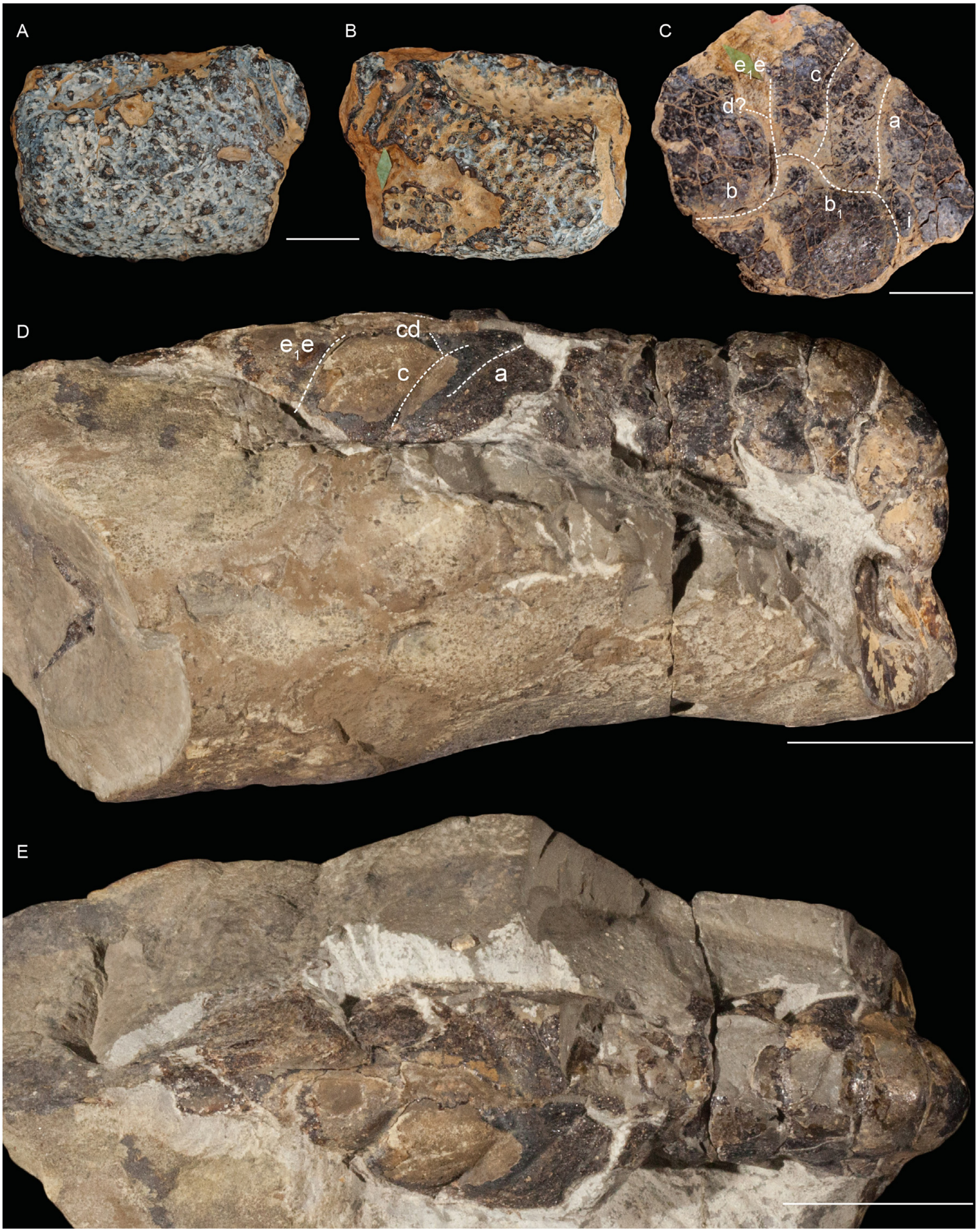

Fig. 3. *Palaeastacus kimzeyi* Rathbun, 1935 from the Campanian of Farmersville, United States (A–C) and *Pustulina trisulcata* (Schweitzer and Feldmann, 2001) n. comb. from the Cenomanian of Sites, United States (D, E). A, B, holotype USNM PAL 73797: P1 propodus, dorsal surface (A) and ventral surface (B); C, paratype USNM PAL 73841: fragment of carapace, left lateral view with superimposed line drawing of grooves; D, E, holotype USNM PAL 512150, subcomplete specimen, left side of carapace and pleon with superimposed line drawing of grooves (D) and dorsal view (E). Scale bars: 10 mm. Abbreviations: a: branchiocardiac groove; b: antennal groove; b$_1$: hepatic groove; c: postcervical groove; cd: cardiac groove; d: gastro-orbital groove; e$_1$e: cervical groove; i: inferior groove. Photographs: L. O'Reilly. Line drawings: J. Devillez.

characteristic of *Pustulina* Quenstedt, 1857. Hence, we proposed the new combination *Pustulina trisulcata* (Schweitzer and Feldmann, 2001). As pointed out by Förster (1966), *Palaeastacus selmaensis* Rathbun, 1935 (Maastrichtian, Alabama, United States) is known from unrecognizable fragments, so we consider these fragments to be Incertae sedis. The last species, *Palaeastacus ornatus* Whiteaves, 1886 (Campanian, Canada) exhibits a groove pattern and longitudinal, tuberculate carinae along branchial and gastric regions, and dorsal margin, and there is no intercalated plate (Feldmann and McPherson 1980: pl. 2, fig. 1). These characteristics are typical of the Nephropidae Dana, 1852. So, we concur with Mertin (1941) and Feldmann and McPherson (1980) who considered this species to be a representative of *Palaeonephrops* Mertin, 1941.

In conclusion, only two species of *Palaeastacus* are herein recognized in the Late Cretaceous: *P. sussexiensis* and *P. kimzeyi*.

Palaeastacus sussexiensis (Mantell, 1824)

(Fig. 2A–F)

Astacus sussexiensis Mantell, 1824: 11, pl. 29, fig. 15; 1833: 124, 373, 379, fig. 2; 1844: 238, fig. 4. — Quenstedt 1852: 269; 1885: 411, fig. 129.

Enoploclytia imagei M'Coy, 1849: 331; 1854: 136. — Reuss 1854: 3. — Woodward 1877: 9. — Glaessner 1929: 146. — Schweitzer et al. 2010: 22.

Enoploclytia brevimana M'Coy, 1849: 332; 1854: 137. — Reuss 1854: 3. — Bronn 1851–1852: 352. — Woodward 1877: 9. — Schweitzer et al. 2010: 22.

Palaeastacus dixoni Bell, 1850: 344, 345, pl. 38, fig. 1–5. — Geinitz 1875: 292. — Schlüter 1879: 602. — Schweitzer et al. 2010: 25.

Hoploparia scabra Bell, 1863: 28, pl. 7, fig. 3–7. — Glaessner 1929: 221.

Phlyctisoma granulatum Bell, 1863: 36, pl. 11, fig. 9-10. — Glaessner 1929: 314. — Monaco and Garassino 2000: 297.

Palaeastacus plauensis Geinitz, 1875: 291, pl. 64, fig. 9.

Astacus leachii (pars.) — Mantell 1822: 223, pl. 30, fig. 3.

Glyphea sussexiensis — Roemer 1841: 105.

Enoploclytia sussexiensis — Morris 1854: 108. — Willet 1871: 42–43. — Woodward 1877: 10. — Woodward 1878: 377, pl. 38, fig. 1–4. — Schlüter 1879: 602. — Glaessner 1932: 578 — Van Straelen 1936: 12.

Palaeastacus sussexiensis — Glaessner 1929: 200. — Rathbun 1935: 23. — Förster 1966: 133, fig. 24, pl. 17, fig. 6. — Morris 1980: 13. — Aguirre-Urreta and Ramos 1981: 609, fig. 4c. — Morris 1987: 196, pl. 42, fig. 4–5. — Aguirre-Uretta 1989: 510, fig. 8-10. — Wittler 1998: 18, fig. 5. — Garassino and Schweigert 2006: 11. — Schweitzer et al. 2010: 26. — Karasawa et al. 2013: 79, 102. — Devillez et al. 2016: 526, fig. 6, fig. 7A–E.

Palaeastacus ? *plauensis* — Glaessner 1929: 290.

Enoploclytia dixoni — Woods 1930: 83, pl. 23, fig. 9–12, pl. 24, fig. 1–3. — Van Straelen 1936: 11.

Enoploclytia (Palaeastacus) sussexiensis — Mertin 1941: 161, fig. 4a.

Enoploclytia (Palaeastacus) imagei — Roberts 1962: 164.

Palaeastacus scaber — Förster 1966: 132, fig. 26, pl. 17, fig. 7–9. — Morris 1980: 13. — Schweitzer and Feldmann 2001: 174. — Garassino and Schweigert 2006: 11. — Schweitzer et al. 2010: 25. — Karasawa et al. 2013: 102.

Palaeastacus cf. *sussexiensis* — Taylor 1979: 30, fig. 10e, pl. 4 fig. d–f.

Palaeastacus ? *plavensis* — Schweitzer et al. 2010: 25.

Pustulina granulata — Schweitzer et al. 2010: 26.

Pustulina scabra — Schweitzer et al. 2010: 26.

TYPE MATERIAL. — Lectotype NHMUK 5601 (Fig. 2A, B), designated by Devillez et al. (2016); 13 paralectotypes NHMUK 5024, 5584, 5586, 5589, 5600, 5602, 5608, 5613, 5618, 5624, 5626, 5629, 10760.

TYPE LOCALITY. — Sussex, United Kingdom (precise type locality not indicated on the original labels).

TYPE AGE. — Cenomanian, Late Cretaceous.

DESCRIPTION. — *Carapace*. Subcylindrical carapace (lectotype: CL = 82 mm, CH = 41 mm); long spiny rostrum; fusiform andtuberculate intercalated plate; ridge on dorsal margin of branchial region; deep cervical groove, joined to dorsal margin and to antennal groove; deep antennal groove; short gastro-orbital groove originating as a slight median inflexion of cervical groove; postcervical and branchiocardiac grooves subparallel; dorsally deep, sinuous postcervical groove, shallowing ventrally, not joined to dorsal margin, joined to hepatic groove; narrow branchiocardiac groove, strongly inclined, shallower than postcervical groove, not joined to dorsal margin, joined to hepatic groove; concavo-convex, narrow hepatic groove, joined to cervical groove; inflated ω area; flat χ area; deep inferior groove, joined to hepatic groove.

Ornamentation of carapace. Carapace densely covered by rounded tubercles in branchial region and widely spaced coarse tubercles in cardiac, hepatic and cephalic regions; row of coarse tubercles parallel to dorsal margin in cardiac and branchial regions; two oblique rows of coarse tubercles in cardiac region; row of tubercles parallel to the intercalated plate in gastric region.

Pleon and uropods. Pleonal somites with terga ornamented by four pairs of strong spines and by rounded, coarse tubercles on the remaining surface (Fig. 2C, D); subtriangular pleura, with pointed ventral margin, ornamented with two strong spines; telson with rounded extremity; telson with longitudinal median ridge flanked by two wide lateral ridges interrupted at telson mid-length; telson covered by coarse rounded tubercles; uropods as long as telson, covered by tubercles; uropodal endopod with longitudinal carina; uropodal exopod with diaeresis.

Thoracic appendages. Mxp3 with the inferior side of the first two segments adorned with numerous small spines, the inferior distal extremities of the third segment is adorned by a strong spine; chelate P1; short, trapezoidal, slightly globose P1 propodus, with two divergent rows of spines on ventral and dorsal surfaces; inner margin with strong spines; wide fingers, slightly longer than propodus; occlusal margins with short, spaced teeth; index wider than dactylus; dactylus adorned with spines; spiny P1 carpus and merus (after Devillez et al. 2016: 526).

DISTRIBUTION. — *Palaeastacus sussexiensis* is a well-known species represented by numerous fossils, mainly from the Late Cretaceous chalk formations of southeast United Kingdom. It has also a wide stratigraphic range associated to a wide geographic distribution. Indeed, *P. sussexiensis* occurs in (1) the Aptian of Alexander Island (Antarctica; Fig. 2E; Taylor 1979) and Patagonia (Argentina; Aguirre-Urreta 1989), (2) the Albian of England (Bell, 1863; Woods, 1930; Förster 1966), (3) the Cenomanian of England (Fig. 2A, C and D; Bell 1850; Förster 1966; Morris 1987), Germany (Mertin 1941) and France (Van Straelen 1936; Förster 1966), and (4) the Turonian of England (Mantell 1822, 1833, 1844; Morris 1987), Germany (Wittler 1998) and France (Fig. 2F).

Palaeastacus kimzeyi Rathbun, 1935

(Fig. 3A–C)

Palaeastacus kimzeyi Rathbun, 1935: 23, pl. 2, figs. 15–21. — Förster 1966: 135. — Förster and Rieber 1982: 777. — Schweitzer and Feldmann 2001: 174, 176. — Garassino and Schweigert 2006: 11. — Schweitzer et al. 2010: 25.

Enoploclytia kimzeyi — Stenzel 1945: 414. — Secrétan 1964: 94, 95. — Taylor 1979: 25. — Feldmann 1981: Table 1.

TYPE MATERIAL. — Holotype USNM PAL 73797 (Fig. 3A, B); 1 paratype USNM PAL 73841, and 9 paratypes USNM PAL 335146.

TYPE LOCALITY. — Farmersville, Texas, United States.

TYPE AGE. — Campanian, Late Cretaceous.

DESCRIPTION. — *Carapace*. Deep cervical groove, joined to antennal groove; deep antennal groove; short gastro-orbital groove; postcervical and branchiocardiac grooves subparallel; slightly curved postcervical groove, joined to hepatic groove; slightly curved branchiocardiac groove, joined to hepatic groove; concavo-convex hepatic groove, joined to cervical groove; inflated ω area; flat χ area; inferior groove joined to hepatic groove; carapace covered by small rounded tubercles, presence of coarse tubercles in cephalic and hepatic regions.

Thoracic appendages. Chelate P1; subrectangular, slightly globose P1 propodus, covered by rounded tubercles; both sides of P1 propodus with longitudinal depression parallel to the inner margin; strongly compressed inner margin; inflated, narrow dactylar bulge; wide fingers, covered by tubercles.

DISCUSSION. — Comparisons between *P. kimzeyi* and *P. sussexiensis* are only possible at level of the P1 propodus because the carapace of the first species is too fragmentary. The P1 propodus of *P. sussexiensis* shows no longitudinal depression along the inner margin on both sides. Besides, there are rows of tubercles on the dorsal and ventral surfaces of the P1 propodus (no row in *P. kimzeyi*).

Genus *Enoploclytia* M'Coy, 1849

(Fig. 4A, B)

TYPE SPECIES. — *Astacus leachii* Mantell, 1822, by original designation.

EMENDED DIAGNOSIS. — An emended diagnosis was proposed by Devillez et al. (2016: 530). We add that the P1 merus exhibits strong, prominent distal process at outer side of the ventral extremity (Figs. 5A, B, 6C, 7C).

REMARKS. — Among the numerous species of *Enoploclytia* listed by Schweitzer et al. (2010), twelve are known from the Late Cretaceous. Half of these species were found in Western Europe: *Enoploclytia brevimana* M'Coy, 1849 (Cenomanian, United Kingdom), *Enoploclytia granulicauda* Schlüter, 1879 (Campanian, Germany), *Enoploclytia imagei* M'Coy, 1849 (Cenomanian, United Kingdom), *Enoploclytia leachi* (Mantell, 1822) (Cenomanian to Campanian, Western and Central Europe), *Enoploclytia paucispina* Schlüter, 1868 (Santonian, Germany) and *Enoploclytia seitzi* Glaessner, 1932 (Albian, Germany; Cenomanian, United Kingdom). *Enoploclytia leachi* and *E. seitzi* are described and discussed below and *E. granulicauda* is herein considered as a synonym of *E. leachi* based on its carapace groove pattern and ornamentation (see discussion about *E. leachi*). *Enoploclytia brevimana* and *E. imagei* exhibit morphological characters (carapace groove pattern, ornamentation, P1 chelae) typical of *Palaeastacus* and, according to Förster (1966) and Devillez et al. (2016), these species are considered to be synonyms with *P. sussexiensis*. *Enoploclytia paucispina* is known from a finely tuberculate fragment of carapace and from a P1 chela exhibiting a compressed propodus and wide, curved fingers armed with small, flattened teeth. Given that *Enoploclytia* has a globose P1 propodus bearing slender, straight fingers armed with long sharp teeth, we follow Mertin (1941) and Förster (1966) and do not consider *E. paucispina* to be an erymid lobster but a representative of *Oncopareia* Bosquet, 1854.

Two species are reported from the Campanian of Madagascar. *Enoploclytia collignoni* Secrétan, 1964 exhibits the typical carapace groove pattern and P1 chelae of the genus: postcervical and branchiocardiac grooves not joined; sinuous postcervical groove, joined to hepatic groove; reduced branchiocardiac groove; globose P1 propodus; slender and straight P1 fingers. *Enoploclytia armata* Secrétan, 1964 is known from some P1 chelae exhibiting the typical characteristics of *Stenodactylina* (see remarks about *Stenodactylina*). Thus, we follow Devillez et al. (2016), and we consider this species to be a representative of *Stenodactylina*.

The four remaining species were found in North America. *Enoploclytia sculpta* Rathbun, 1926 (Maastrichtian, Tennessee, United States) is known from a specimen showing a part of the pleon and a poorly preserved P1. The terga lack of relief and are densely covered by small pits (Rathbun 1926: pl. 76, fig. 3). Representatives of *Enoploclytia* usually have a pleon with longitudinal bulges on the pleural basis and a coarse, wide-spaced ornamentation. Thus, following Stenzel (1945) and Förster (1966), we conclude that this species is not a representative of *Enoploclytia* and probably not an erymid lobster. *Enoploclytia triglypta* Stenzel, 1945 (Coniacian, Texas, United States) exhibits a groove pattern diagnostic for *Stenodactylina* as discussed by Devillez et al. (2016) (see remarks about *Stenodactylina*). *Enoploclytia tumimana* Rathbun, 1935 (Maastrichtian, Alabama, United States) is known from several fragments of carapace and P1 (including fragments of merus, propodus and fingers). Careful examination of high resolution pictures of the holotype USNM PAL 73799 (Rathbun 1935: pl. 1, figs 10–11) leads us to confirm the typical characteristics of *Enoploclytia*: well-marked gastro-orbital groove; postcervical and branchiocardiac grooves not joined; reduced branchiocardiac groove; subrectangular, globose P1 propodus; straight, slender fingers. *Enoploclytia minor* (Woodward, 1900) (Maastrichtian, Canada) is known from a poorly preserved specimen showing the carapace and at least the P1-P3 (Feldmann and McPherson 1980: pl. 1, figs. 1-2). The carapace groove pattern is not recognizable but the globose P1 propodus, bearing long slender fingers, allows us to maintain this species into the genus.

Since the publication of the systematic list of Schweitzer et al. (2010), *Enoploclytia tepeyacensis* Vega et al., 2013 was described from Mexican Campanian deposits. This species is known from two carapaces exhibiting a groove pattern typical of *Enoploclytia* (well-marked gastro-orbital groove; postcervical and branchiocardiac grooves not joined; sinuous postcervical groove; reduced branchiocardiac groove). Some unidentified fragments attributed to *Enoploclytia* have also been reported from Campanian rocks of Seymour Island (Antarctica; Feldmann 1984) and of the Delaware and the New Jersey (USA; Roberts, 1962).

In conclusion, with six species (*E. collignoni*, *E. leachi*, *E. minor*, *E. seitzi*, *E. tepeyacensis* and *E. tumimanus*), the genus *Enoploclytia*, has reached higher diversity during the Late Cretaceous (supposedly absent before the Cretaceous and four species known in the Early Cretaceous: *E. augustobonae* Devillez et al., 2016, *E. gigantea* Devillez et al., 2016, *E. seitzi*, *E. wintoni* Stenzel, 1945).

Enoploclytia leachi (Mantell, 1822)

(Figs. 4C–J, 5, 6)

Astacus leachi Mantell, 1822: 221, pl. 29, fig. 1, 2, 5, pl. 30, figs. 1–2 (non 3), pl. 31, figs. 1–4; 1824: 11, pl. 29, fig. 15; 1833: 122, fig. 1. — Geinitz 1839: 14, pl. 7, fig. 4, 39, pl. 9, fig. 1. — Mantell 1844: 536, pl.

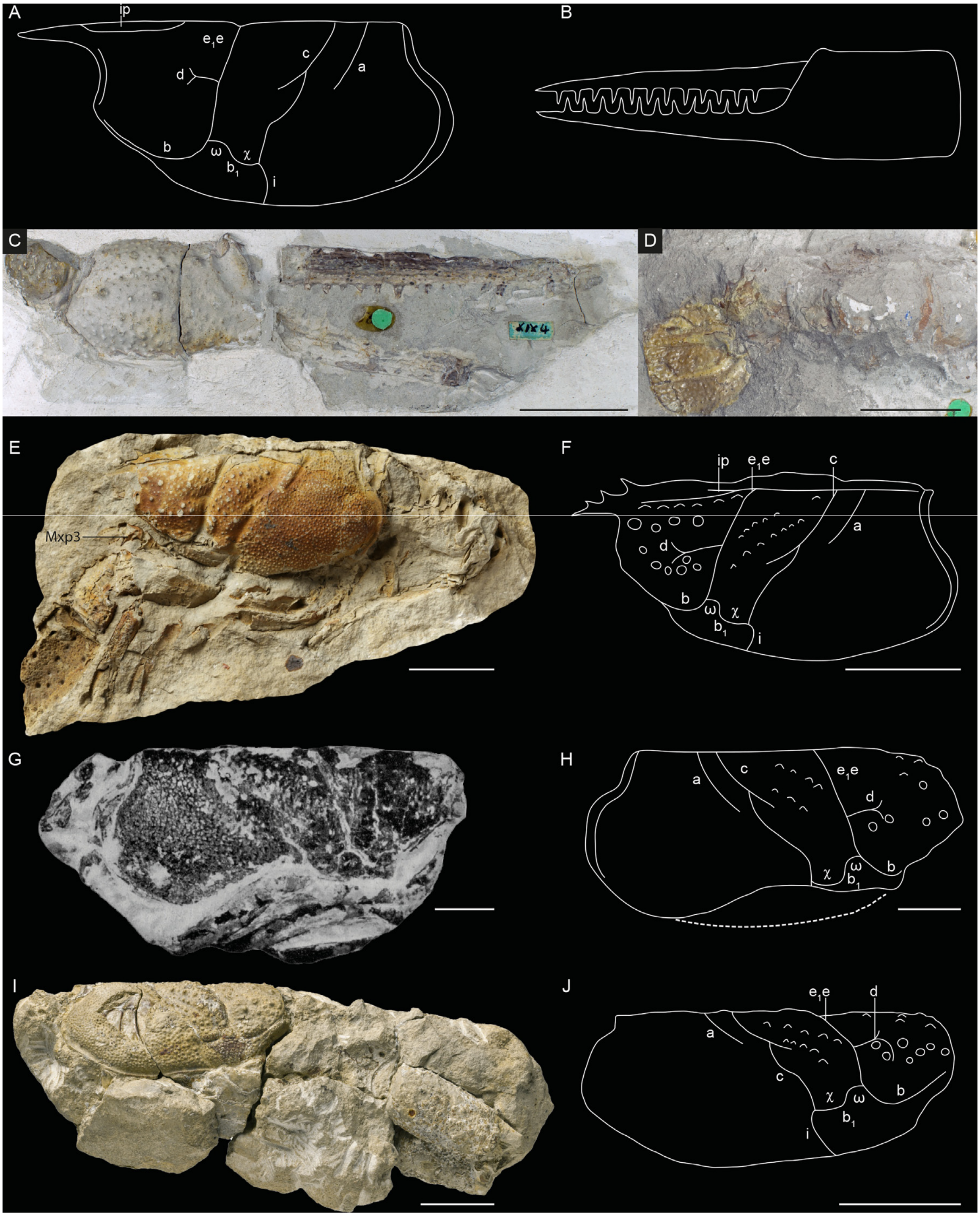

Fig. 4. Historical specimens of *Enoploclytia leachi* (Mantell, 1822). A, line drawing of carapace groove pattern characteristic of *Enoploclytia* M'Coy, 1849; B, line drawing of P1 chela characteristic of *Enoploclytia*; C, lectotype NHMUK 5636 (Mantell coll.) from the Turonian of Sussex, United Kingdom, left P1 chela; D, paralectotype NHMUK In.61020 from the Late Cretaceous of Sussex, United Kingdom, fragment of pleon; E, F, specimen NM O7125 (figured by Reuss 1854: pl. 1, fig. 2) from the Turonian of Prague, Czech Republic: general view showing the third maxilliped (E) and line drawing of carapace (F); G, H, syntype of *Enoploclytia heterodon* Schlüter, 1862 from the Santonian of Dülmen, Germany: original figure of Mertin (1941: pl. 5, fig. 1) (G) and line drawing of carapace (H); I, J, holotype STIPB-Schlüter-124 of *Enoploclytia granulicauda* Schlüter, 1879 from the Campanian of Coesfeld, Germany: general view (I) and line drawing of the carapace (J). Scale bars: 20 mm. Abbreviations: a: branchiocardiac groove; b: antennal groove; b_1: hepatic groove; c: postcervical groove; d: gastro-orbital groove; e_1e: cervical groove; i: inferior groove; ip: intercalated plate; Mxp3: third maxilliped; ω: attachment site of mandibular muscle; χ: attachment site of adductor testis muscle. Photographs: J. Devillez (C, D), M. Kocová Veselská (E), G. Oleschinski (I). Line drawings: J. Devillez.

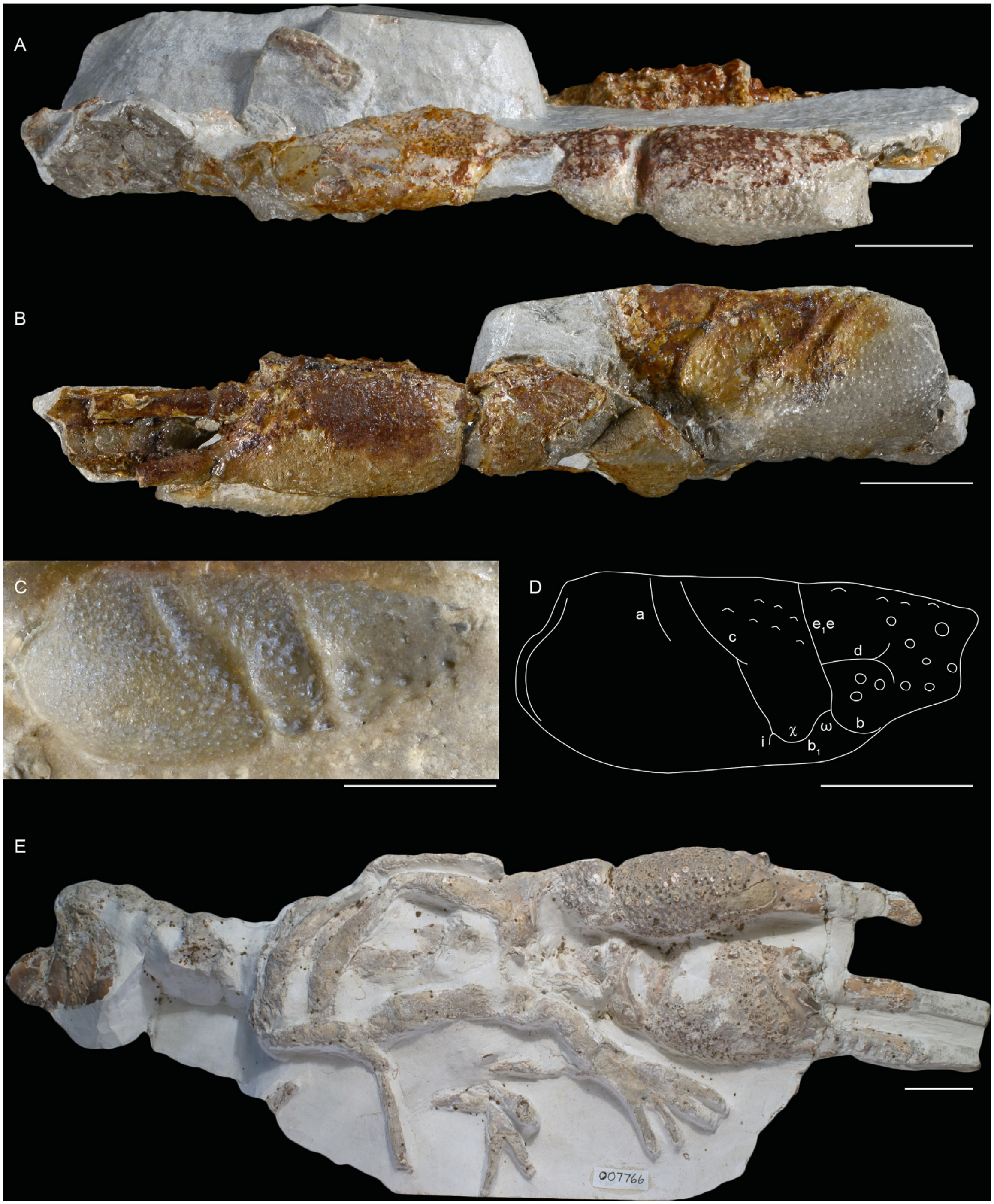

Fig. 5. New specimens of *Enoploclytia leachi* (Mantell, 1822). A, B, specimen MNHN.F.B16580 from the Cenomanian of La Ferté-Bernard, France: right lateral view showing the merus with prominent distal process (A) and left lateral view (B); C, D, specimen MNHN.F.A66890 (Pezy coll.) from the Cenomanian of Villers-sur-Mer, France: general view (C) and line drawing of carapace (D); E, specimen BM 007766 from the Late Cretaceous of Brighton, United Kingdom. Scale bars: 20 mm. Abbreviations: a: branchiocardiac groove; b: antennal groove; b_1: hepatic groove; c: postcervical groove; d: gastro-orbital groove; e_1e: cervical groove; i: inferior groove; ω: attachment site of mandibular muscle; χ: attachment site of adductor testis muscle. Preparation: Y. Despres (A, B). Photographs: P. Loubry (A–C), J. Devillez (E). Line drawing: J. Devillez.

116, figs. 1–3. — Quenstedt 1852: 269, pl. 20, fig. 11; 1867: 321, pl. 25, fig. 11; 1885: 411, pl. 32, fig. 11. — Etheridge, 1914: 272, pl. 24, fig. 2.

Palaeastacus dixoni Bell, 1850 (pars.): 344, pl. 38, fig. 5.

Palaeastacus macrodactylus Bell, 1850: 345, pl. 38, fig. 6.

Enoploclytia heterodon Schlüter, 1862: 724, pl. 11, figs. 2–4; 1879: 600. — Glaessner 1929: 146. — Secrétan 1964: 87.

Enoploclytia granulicauda Schlüter, 1879: 599, pl. 14, fig. 1–4. nov. syn. — Glaessner 1929: 146. — Van Straelen 1936: 11. — Förster 1966: 150, pl. 19, fig. 6. — Taylor 1979: 25, 29. — Jagt and Fraaije 2002: 92. — Schweitzer et al. 2010: 22.

Glyphea leachi — Roemer 1841: 105. — Schlüter 1862: 703.

Klytia leachi — Reuss 1845: 14, 103, pl. 6, figs. 1–6, pl. 42, fig. 3. — Geinitz 1849: 96. — Bronn 1852: 352. — Gümbel 1868: 752, 762. — Gosselet 1881: 267.

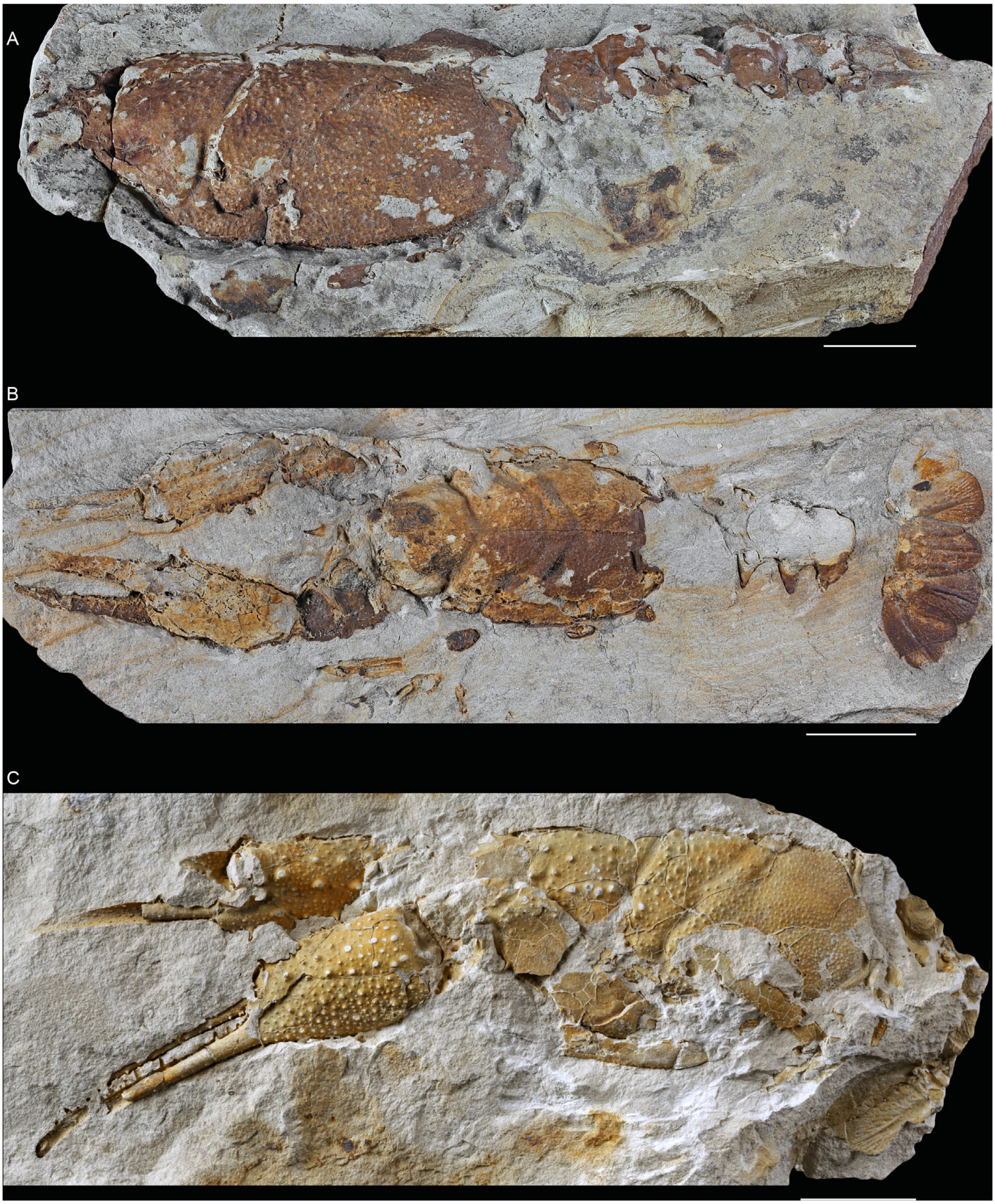

Fig. 6. *Enoploclytia leachi* (Mantell, 1822) from the Turonian of Bílá Hora, Czech Republic. A, specimen NM O4062 (figured by Reuss 1854: pl. 2, fig. 4), carapace and pleon, left lateral view; B, specimen NM O4042 (listed by Fritsch and Kafka 1887), subcomplete specimen, dorsal view; C, specimen NM O7123, subcomplete specimen, left lateral view. Scale bars: 20 mm. Photographs: M. Kocová Veselská.

Clytia leachi — Bronn 1849: 578. — Reuss 1854: 1, pl. 1–5.

Enoploclytia leachi — M'Coy 1849: 331; 1854: 136. — Morris 1854: 108. — Schlüter 1862Schlüter 1862: 725. — Schlüter and von der Marck 1868: 295. — Willet 1871: 43. — Geinitz 1875: 292. — Woodward 1877: 10; 1878: 378, pl. 38, figs. 5-6. — Schlüter 1879: 602. — Zittel 1885: 694. — Fritsch and Kafka 1887: 27, figs. 48–52. — Fritsch 1877: 145; 1889: 91; 1893: 107. — Leonhard 1897: 63. — Wanderer 1908: 23. — Rathbun 1926: 188. — Glaessner 1929: 146. — Woods 1930: 85, pl. 24, fig. 4, pl. 25, fig. 1. — Glaessner 1932: 577. — Joleaud and Hsu 1935: 100. — Rathbun 1935: 19. — Van Straelen 1936: 11. — Secrétan 1964: 87. — Förster 1966: 148, pl. 19, figs. 4–5, 7–8 (non 3). — Taylor 1979: 24. — Morris 1980: 6; 1987: 196, pl. 42, fig. 3. — Aguirre-Urreta 1989: 516. — Wittler 1998: 17, figs. 3-4, 6. — Jagt and Fraaije 2002: 91, pl. 1, figs. a–c. — Vega et al. 2007: 1434. — Veselská 2010: 174, fig. 3. — Schweitzer et al. 2010: 22. — Karasawa et al. 2013: Table 1.

Hoploparia sp. — Hallez 1869: 297, figs. 1–4.

Xanthopsis leachi — Gosselet 1883: pl. 22, fig. 3.

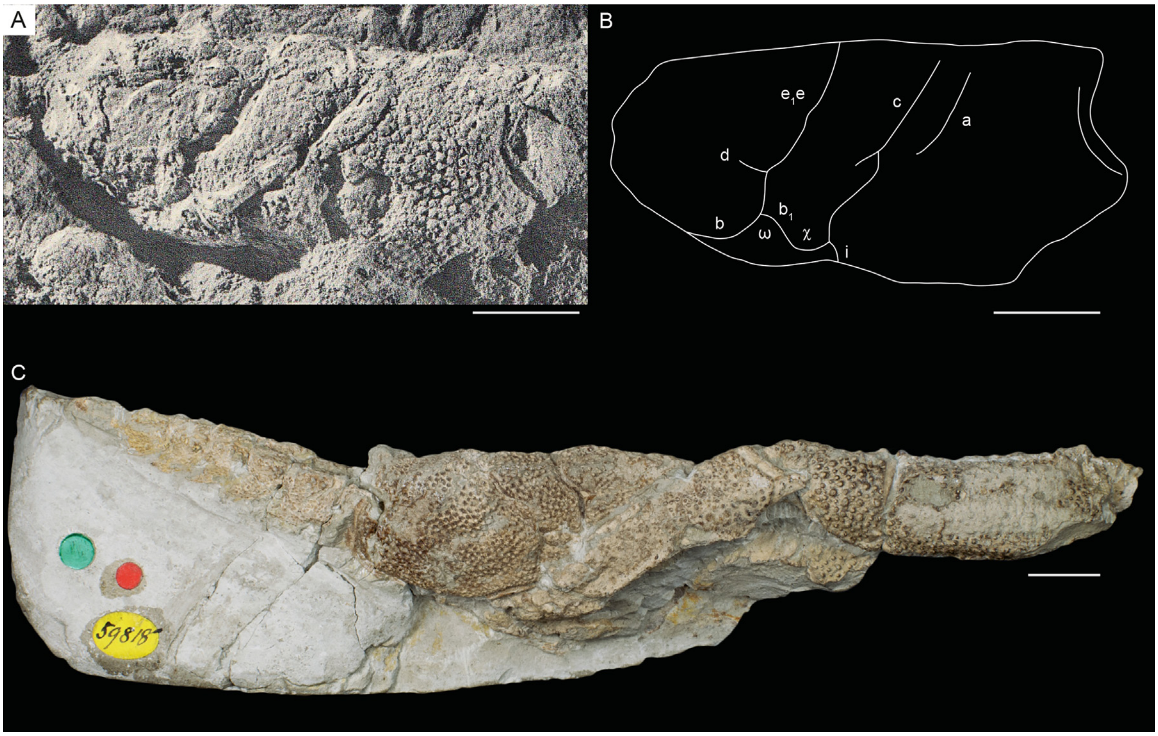

Fig. 7. *Enoploclytia seitzi* Glaessner, 1932. A, B, holotype BGR X 00266 (not found) from the Albian of Wettensen, Germany: original figure of Förster (1966: pl. 19, fig. 1) (A) and line drawing of carapace (B); C, specimen NHMUK 5918 (initially named as *Enoploclytia scabrosa* by Woodward 1873 — nomen nudum) from the Cenomanian of Dover, United Kingdom: right lateral view showing the prominent distal process of the P1 merus. Scale bars: 10 mm. Abbreviations: a: branchiocardiac groove; b: antennal groove; b_1: hepatic groove; c: postcervical groove; d: gastro-orbital groove; e_1e: cervical groove; i: inferior groove; ω: attachment site of mandibular muscle; χ: attachment site of adductor testis muscle. Photographs and line drawing: J. Devillez.

Enoploclytia (*Enoploclytia*) *leachi* var. *granulicauda* — Mertin 1941: 20, 242, figs. 5f–h, pl. 1, fig. 8.

Enoploclytia (*Enoploclytia*) *leachi* — Mertin 1941: 162, 242, figs. 4c, 5a–e, pl. 1, figs. 1, 5–7 (non 2–4, 8).

TYPE MATERIAL. — Lectotype NHMUK 5636 (Mantell coll.) (Fig. 4C), designated by Förster (1966); two paralectotypes NHMUK 5623, In.61020 (Fig. 4D).

TYPE LOCALITY. — Sussex, United Kingdom (precise type locality not indicated on the original labels).

TYPE AGE. — Turonian, Late Cretaceous.

DESCRIPTION. — *Carapace*. Subcylindrical carapace; spiny rostrum; fusiform and tuberculate intercalated plate; deep, wide cervical groove, joined to dorsal margin and to antennal groove; deep antennal groove; long gastro-orbital groove originating as a median inflexion of cervical groove, with two short and divergent branches, delimiting two gastro-orbital lobes (flat upper lobe, slightly inflated lower lobe); postcervical and branchiocardiac grooves subparallel; deep, sinuous postcervical groove, joined to dorsal margin and to hepatic groove, with ventral extension at carapace mid-height, deepening towards its junction to hepatic groove; narrow, deep branchiocardiac groove, joined to dorsal margin and not to postcervical groove, interrupted at almost carapace mid-height; concavo-convex hepatic groove, joined to cervical groove; inflated ω and χ areas; wide, deep inferior groove, joined to hepatic groove.

Ornamentation of carapace. Heterogeneous ornamentation; carapace entirely and densely covered by small tubercles; two oblique rows of coarse tubercles in cardiac region; row of coarse tubercles parallel to intercalated plate in gastric region; longitudinal row of coarse tubercles in gastric region; antennal row of coarse tubercles in antennal region preceded by an antennal spine.

Cephalic appendages. Strong a1 peduncle, with three segments, last segment (basipodite) articulated with two flagella, flagella composed of numerous short cylindrical articles; a2 with one long flagellum composed of numerous short cylindrical articles; stout scaphocerite.

Pleon and uropods. Somites with terga homogeneously ornamented by spaced tubercles; longitudinal bulge at the basis of the pleura; s2 with an elongated pleura, anteriorly subrectangular and posteriorly subtriangular; s3-s6 exhibiting subtriangular pleura, with sharply pointed ventral margins; telson with rounded extremity; telson with four longitudinal, sub-parallel carina; telson with a row of tubercles on each carina, a strong tubercles adorn the proximal part of the two central carina; uropods as long as telson; uropodal endopod with longitudinal carina and irregularly ornamented by fine tubercles; uropodal exopod with longitudinal carina and diaeresis.

Thoracic appendages. Mxp3 partially known (Fig. 4E), theinferior distal extremities of the segments are adorned by a strong spine; P1-P3 chelate; massive globose P1 propodus, densely covered by small tubercles and with spaced coarse tubercles organized in longitudinal rows on dorsal and ventral surfaces; inner margin with short conical spines; narrow, inflated dactylar bulge; long slender P1 fingers, straight in dorsal view, slightly curved downward, equal in length; occlusal margins armed with slender sharp teeth; subtriangular P1 carpus, densely covered by small tubercles and some coarse tubercles irregularly arranged; upper margin with short conical spines; P1 merus covered by small tubercles; strong, prominent distal process at extern side of the ventral extremity of P1 merus (Figs. 5A, 6C); short conical spines on the upper margin of P1 merus; P2–P3 with small chelae; P2–P5 surface almost smooth.

COMPARISONS. — The Late Cretaceous deposits of United Kingdom and Germany yielded several species of erymid lobsters which are here considered as junior synonyms of *Enoploclytia leachi*. An almost complete specimen of *E. leachi* was assigned to *Palaeastacus dixoni* by Bell (1850: pl. 38, fig. 5) although it exhibits main characteristics of the previous species: (1) wide cervical groove; (2) postcervical and branchiocardiac grooves not joined; (3) branchiocardiac groove interrupted near the carapace mid-height; (4) dense ornamentation made of small tubercles in branchial region; (5) two oblique rows of coarse tubercles in cardiac region; (6) s3-s6 with subtriangular pleura, exhibiting sharply pointed ventral margins and (7) P1 chelae with long, slender fingers, armed with teeth on their occlusal margins. Bell (1850: pl. 38, fig. 6) also described *Palaeastacus macrodactylus* based on a well-preserved pair of P1 chelae showing globose propodi, adorned with longitudinal rows of spiny tubercles on inner margins and on dorsal and ventral surfaces, the fingers are long and slender and have numerous teeth on their occlusal margins. Identical characteristics are known on the P1 chelae of *E. leachi*. Thus, we follow Förster (1966) and the synonymy between *P. macrodactylus* and *E. leachi* is maintained here.

Later, Schlüter (1862) described two species from Westphalia (Germany). The material of *Enoploclytia heterodon* Schlüter, 1862 (Coniacian), a carapace and a P1 chela, is lost since World War II (Förster 1966) but the carapace has been figured by Mertin (1941: pl. 1, fig. 5; Fig. 4G, H). It exhibits the typical groove pattern and the same ornamentation as in *E. leachi* (postcervical groove not joined to branchiocardiac groove; branchiocardiac groove interrupted near the carapace mid-height; carapace densely covered by tubercles; coarse tubercles arranged in rows in cephalic and cardiac regions; P1 chela with subrectangular propodus bearing long, slender fingers, numerous teeth on occlusal margins). Hence, according to Mertin (1941) and Förster (1966), these similarities justify the placement of *E. heterodon* into the synonymy of *E. leachi*. *Enoploclytia granulicauda* Schlüter, 1879 (Campanian) is based on a specimen showing an almost complete carapace, P1 chelae partially preserved and a part of the pleon (s1 and s2; Fig. 4I, J). This fossil clearly exhibits the typical groove pattern and ornamentation of *E. leachi*: postcervical groove not joined to branchiocardiac groove; branchiocardiac groove interrupted near the carapace mid-height; carapace densely covered by small tubercles; coarse tubercles arranged in rows in cephalic and cardiac regions; P1 chela with subrectangular propodus; propodus covered with numerous small tubercles and coarse tubercles arranged in longitudinal rows; slender fingers. In conclusion, we consider *E. granulicauda* as a junior synomym of *E. leachi*.

Enoploclytia leachi is distinct from the five other Late Cretaceous species by its particular ornamentation: numerous fine tubercles and rows of coarse ones in cephalic and cardiac regions. Indeed, *Enoploclytia collignoni* and *E. seitzi* have a dense, coarse ornamentation made of tubercles and depressions, which gives a scabrous aspect to their respective carapaces (Charbonnier et al. 2012: fig. 7A-B; Fig. 7). *Enoploclytia tumimana* exhibits a heterogeneous carapace ornamentation made of coarse tubercles and numerous small pits; *Enoploclytia tepeyacensis* has coarser tubercles than *E. leachi* in branchial region; *Enoploclytia minor* has a P1 propodus covered by coarse tubercles (small tubercles and longitudinal rows of coarse ones in *E. leachi*). Furthermore, some other characteristics support the distinction between *E. leachi* and the other Late Cretaceous species: *E. collignoni* has a strongly prominent χ area (less inflated in *E. leachi*); the dorsal part of the postcervical groove of *E. tepeyacensis* is strongly inclined and almost horizontal at the level of the gastro-orbital groove (postcervical groove far less inclined in *E. leachi*); *E. seitzi* has a shallow and narrow branchiocardiac groove, a strongly elongated P1 propodus in comparison to its height (P1 propodus not so long in comparison to its height in *E. leachi*).

DISTRIBUTION. — *Enoploclytia leachi* is known from numerous fossils found in Western and Central Europe from the Cenomanian to the Campanian, especially in the Bohemian Cretaceous Basin of the Czech Republic. Indeed, *E. leachi* occurs (1) in the Cenomanian — Santonian of France (Fig. 5A–D; Hallez 1869; Van Straelen 1936; Förster 1966), (2) in the Turonian — Campanian of United Kingdom (Figs. 4C, D, 5E; Mantell 1822, 1824, 1833, 1844; M'Coy 1849, 1854; Woodward 1878; Woods 1930; Förster 1966; Morris 1987), (3) in the Campanian of Belgium (Jagt and Fraaije 2002), (4) in the Cenomanian — Campanian of Germany (Fig. 4G, I; Schlüter 1862, 1879; Wanderer 1908; Förster 1966; Wittler 1998) and (5) in the Turonian — Coniacian of the Czech Republic (Figs. 4E, 6; Geinitz 1839; Reuss 1845, 1854; Fritsch and Kafka 1887; Förster 1966, Veselská 2010). *E. leachi* belongs to the most common fossil lobsters found within the whole Bohemian Cretaceous Basin. Carefull examination of specimens from the Prague palaeontological collections led us to identify some fossils figured in Reuss's monography (1854): NM O7125 (Fig. 4E) corresponds to his pl.1, fig. 2, NM O4062 (Fig. 6A) corresponds to his pl.2, Fig. 4 and NM O4063 corresponds to his pl.4, fig. 10. Moreover, the specimen NM O4042 (Fig. 6B), one of the most complete and best-preserved from the Czech Republic, corresponds to the specimen 61 listed by Fritsch and Kafka (1887). This specimen was used as a model for their reconstruction of *E. leachi* on their figs 48-49. All the specimens figured here come from the lower-middle Turonian of Bílá Hora (Weissenberg) in Prague. This locality was Fritsch's standard section from where many fossils were described, like inoceramids, ammonites, echinoids, decapod crustaceans and vertebrates (Fritsch 1872, 1878; Fritsch and Kafka 1887).

Enoploclytia seitzi Glaessner, 1932

(Fig. 7A–C)

Enoploclytia scabrosa Woodward, 1873: 524. — Woodward 1877: 10 — Glaessner 1929: 148. (nomina nuda).

Enoploclytia seitzi Glaessner, 1932: 578, fig. 1. — Secrétan 1964: 94. — Förster 1966: 147, pl. 19, fig. 1-2. — Taylor 1979: 25. — Morris 1980: 6. — Schweitzer et al. 2010: 22.

TYPE MATERIAL. — Lectotype BGR X 00266 designated by Förster (1966) (not recovered; Fig. 7A, B); 1 paralectotype BGR X 00267.

TYPE LOCALITY. — Wettensen, Lower Saxony, Germany.

TYPE AGE. — Albian, Early Cretaceous.

DESCRIPTION. — *Carapace*. Subcylindrical carapace (holotype: CL = 37 mm, CH = 16 mm); rostrum and intercalated plate not preserved; deep, sinuous cervical groove, joined to dorsal margin and to antennal groove; deep antennal groove; deep gastro-orbital groove originating as median inflexion of cervical groove; deep postcervical groove, strongly inclined, weakly sinuous, joined to dorsal margin and to hepatic groove, with a short ventral extension at carapace mid-height; narrow branchiocardiac groove, joined to dorsal margin and not to postcervical groove, extending near the carapace mi-height; concavo-convex hepatic groove, joined to cervical groove; inflated ω and χ areas; wide, deep inferior groove, joined to hepatic groove; carapace with scabrous surface, densely covered by coarse tubercles separated by strong depressions.

Pleon and uropods. Somites poorly preserved; terga ornamented by rounded tubercles and deep, irregular depressions; subtriangular pleura, with pointed ventral margin, directed backward, ornamented by deep depressions; telson and uropods not preserved

Thoracic appendages. Chelate P1; elongated, rectangular, globose P1 propodus, densely covered by coarse tubercles; inflated dactylar bulge; index and dactylus not preserved; elongated P1 carpus, densely covered by coarse tubercles; P1 mersus densely covered by coarse tubercles; strong, prominent distal process at extern side of the ventral extremity of P1 merus (Fig. 7C).

DISCUSSION. — Woodward (1873) named *Enoploclytia scabrosa* based on a specimen found in the Cenomanian chalk of Dover (United Kingdom). However, he did not described nor figured this specimen, so this is a *nomen nudum* clearly identified by Glaessner (1929). Later, Glaessner (1932) described *Enoploclytia seitzi* based on specimens from the Albian of Westphalia (Germany). After carefull examination and following Förster (1966), we identify the specimen NHMUK 59818, mentioned by Woodward (1873) (see Fig. 7C), as a specimen of *E. seitzi* based on (1) the strong inclination of the postcervical groove, (2) the shallow depth and narrow width of the branchiocardiac groove and (3) the dense ornamentation made of tubercles separated by depressions which give a scabrous aspect to the carapace. *Enoploclytia seitzi* is distinct from *E. collignoni* by its slightly prominent χ bulge (strongly prominent in *E. collignoni*), its homogeneous ornamentation made of tubercles separated by depressions all over the carapace (heterogeneous in *E. collignoni*: wide depressions in branchial regions and coarse tubercles and depressions in cephalic, cardiac and hepatic regions) and its strongly elongated P1 propodus (shorter in *E. collignoni*).

Enoploclytia seitzi exhibits a groove pattern and an ornamentation different from *E. tepeyacensis*: (1) the cervical groove is more sinuous, (2) the postcervical groove is dorsally less inclined and less sinuous, (3) the branchiocardiac groove is narrower and shallower, (4) the ornamentation is homogeneous and made of tubercles separated by depressions.

Enoploclytia seitzi differs from *E. tumimana* by a higher sinuosityof the cervical groove, a homogeneous ornamentation with wider depressions and a more elongated P1 propodus. The poorly preserved *Enoploclytia minor* reduces the comparison to the P1 propodus: elongated and covered by tubercles and depressions in *E. seitzi* while it is shorter and covered by coarse tubercles in *E. minor*.

Genus *Pustulina* Quenstedt, 1857

TYPE SPECIES. — *Pustulina suevica* Quenstedt, 1857, by monotypy.

DIAGNOSIS. — An emended diagnosis was proposed by Devillez et al. (2016: 531) and does not need to be repeated here.

REMARKS. — Among the species of *Pustulina* listed by Schweitzer et al. (2010), only *Pustulina dawsoni* (Woodward, 1900) is known from the Late Campanian — Early Maastrichtian formations of Hornby Island (Canada).

Two other species have been recently assigned to *Pustulina*: Charbonnier et al. (2017) transferred *Eryma cretaceum* to *Pustulina* (see remarks about *Eryma*) and we also add *Palaeastacus trisulcatus* to the genus based on its typical groove pattern showing a cardiac groove (see remarks under *Palaeastacus*; Fig. 3D, E).

4. Comparison between Early and Late Cretaceous erymid faunas

4.1. Palaeobiodiversity

The modifications in erymid lobsters diversity during the Cretaceous are difficult to analyze mainly due to the scarcity of the fossil record and sampling bias. After the review of the Early Cretaceous erymids (Devillez et al., 2016) and the present work on the Late Cretaceous taxa, 32 erymid species are now known from the Cretaceous deposits around the world (Table 2, Fig. 8A).

The Early Cretaceous erymid fauna is composed of 21 species distributed in six genera (*Eryma*, *Enoploclytia*, *Palaeastacus*, *Pustulina*, *Stenodactylina*, *Tethysastacus*) and appears to be more diversified than that of the Late Cretaceous (13 species distributed in *Enoploclytia*, *Palaeastacus*, *Pustulina*, and *Stenodactylina*). *Eryma* and *Tethysastacus* are not present in the Late Cretaceous. This decrease of the number of species confirm the Cretaceous decline of erymid lobsters suggested by Schweitzer and Feldmann (2014).

With six species of *Palaeastacus*, five of *Enoploclytia* and *Pustulina*, four of *Eryma*, and one of *Stenodactylina* and *Tethysastacus*, there is no domination of one erymid genus during the Early Cretaceous. However, with six species, *Enoploclytia* clearly dominates the erymid diversity in the Late Cretaceous.

4.2. Palaeobiogeography

Erymids were widespread in Early Cretaceous as the reports of their fossil occurences from Europe, America, Australia, Antarctica, Madagascar and Japan document (Fig. 8B). Most of Early Cretaceous species are present in Western Europe (13 species; Devillez et al., 2016). For the Late Cretaceous, the erymid occurences are almost exclusively concentrated in the Northern Hemisphere (Fig. 8C). The only known Late Cretaceous erymid fauna of the Southern Hemisphere was found in the Campanian deposits of Madagascar (Secrétan, 1964; Charbonnier et al., 2012). Secrétan (1964) recognized the affinities of the Malagasy fauna with those of Europe, North America and Australia. This led her to suggest the presence of migration routes between Madagascar and other continents. The presence in France of a P1 chela attributed to *Stenodactylina* cf. *armata* (see remarks about *Stenodactylina*; Fig. 1C) confirms the existence of faunal exchanges between Europe and Madagascar.

During the Mesozoic, the presence of erymid lobsters seems to have been discontinuous in North America. Three occurences are reported in the Middle and Late Jurassic: *Eryma foersteri* Feldmann 1979 (Callovian), *Eryma jungostrix* Feldmann and Titus, 2006 (Oxfordian) and *Stenodactylina walkerae* (Feldmann and Haggart, 2007) (middle Bajocian — early Callovian) and then no erymid is known between the Oxfordian and the Albian. At the end of the Early Cretaceous and in the Late Cretaceous, most of North American species (*Enoploclytia gigantea* Devillez et al., 2016, *E. tumimana*, *E. wintoni*, *Palaeastacus kimzeyi*, *P. walkeri* (Whitfield, 1883), *Stenodactylina triglypta*) occurred in the north of the Gulf of Mexico, which included the flooded part of the south of the United States (Texas, Louisiana, Mississippi, Alabama, Georgia, Florida). The gap in the erymid record between the Oxfordian and the Albian could be explained by (1) a collecting and/or reporting bias or by (2) the real absence of erymid lobsters in North America. In the second case, the settlement of a new erymid fauna in the north part of the Gulf of Mexico could be the result of migration of populations from the other area. Eurasia and South America were the closest continents at the end of the Early Cretaceous, but only the Eurasiatic fauna included species of *Enoploclytia*, *Palaeastacus* and *Stenodactylina* during the Early Cretaceous (there was only some species of *Palaeastacus* at the extreme south of South America). Moreover, there were no connection between North America and South America at the end of the Early Cretaceous, while the northern part of the Atlantic Ocean was not completely opened (Scotese, 2014a). Thus, a migration of Eurasiatic erymid populations to the west, through the northern part of the Atlantic, and then to the south, along the east coast of North America until they reached the Gulf of Mexico, was certainly possible.

We notice that no fossils of erymid lobsters are reported from the deposits of the Western Interior Seaway (WIS). This epicontinental sea has started to flood the North America in the Aptian and linked the Boreal Ocean with the Atlantic Ocean during almost all the Late Cretaceous (Gill and Cobban 1966, 1973; Molenaar and Rice 1988; Eicher and Diner 1989; Scotese 2014a,b). The absence of erymid lobsters in the WIS, while five species are present at its south-eastern extremity (Texas), is probably due to

Table 2
List and occurrences of the Early and Late Cretaceous erymid species.

	Ages	Occurrences
Late Cretaceous		
Europe		
Enoploclytia leachi (Mantell, 1822)	Cenomanian to Campanian	France, United Kingdom, Germany, Belgium, Czech Republic
Enoploclytia seitzi Glaessner, 1932	Albian to Cenomanian	United Kingdom, Germany
Palaeastacus sussexiensis (Mantell, 1824)	Aptian to Turonian	France, United Kingdom, Germany, Antarctic
Stenodactylina cf. *armata* (Secrétan, 1964)	Santonian	France
North America		
Enoploclytia minor Woodward, 1900	Maastrichtian	Canada
Enoploclytia tepeyacensis Vega et al., 2013	Campanian	Mexico
Enoploclytia tumimana Rathbun, 1935	Maastrichtian	USA
Palaeastacus kimzeyi Rathbun, 1935	Campanian	USA
Pustulina dawsoni (Woodward, 1900)	Campanian to Maastrichtian	Canada
Pustulina trisulcata (Schweitzer and Feldmann, 2001) nov. comb.	Cenomanian	USA
Stenodactylina triglypta (Stenzel, 1945)	Coniacian	USA
Other regions		
Enoploclytia collignoni Secrétan, 1964	Campanian	Madagascar
Pustulina cretacea (Roger, 1946)	Cenomanian	Lebanon
Stenodactylina armata (Secrétan, 1964)	Campanian	Madagascar
Early Cretaceous		
Europe		
Eryma glaessneri Van Straelen, 1936	Hauterivian	France
Eryma sulcatum Harbort, 1905	Hauterivian	United Kingdom, Germany
Eryma sulcatum Harbort, 1905	Albian	France
Eryma vocontii Devillez et al., 2016	Barremian	France
Enoploclytia seitzi Glaessner, 1932	Albian to Cenomanian	United Kingdom, Germany
Palaeastacus loryi (Van Straelen, 1923)	Valanginian	France
Palaeastacus sussexiensis (Mantell, 1824)	Aptian to Turonian	France, United Kingdom, Germany, Antarctic
Palaeastacus sussexiensis (Mantell, 1824)	Hauterivian	France
Pustulina colossea Devillez et al., 2016	Berriasian	France
Pustulina tuberculata (Bell, 1863)	Albian	United Kingdom
Pustulina tuberculata (Bell, 1863)	Berriasian	France
Pustulina victori Devillez et al., 2016	Berriasian	France
Tethysastacus tithonius (Van Straelen, 1936)	Valanginian	France
North America		
Enoploclytia gigantea Devillez et al., 2016	Albian	USA
Palaeastacus walkeri (Whitfield, 1883)	Albian	USA
Other regions		
Eryma nippon Karasawa et al., 1936	Barremian	Japan
Palaeastacus foersteri Taylor, 1979	Barremian	Antarctic
Palaeastacus terraereginae (Etheridge, 1914)	Barremian	Antarctic, Argentina, Australia
Palaeastacus tenuidigitatus (Woods, 1957)	Aptian	Australia
Pustulina spinulata Secrétan, 1964	Valanginian to Hauterivian	Madagascar

collecting and/or reporting biases. Indeed, the connection between the Gulf of Mexico and the WIS remained relatively stable during the Late Cretaceous (Sageman and Arthur 1994; Robinson Roberts and Kirschbaum 1995; Scotese 2014b), so no geographic barrier could have prevent the settlement of an erymid fauna in the WIS. The last three North American species (*Enoploclytia minor*, *Pustulina dawsoni*, *P. trisulcata*) occurred along the west coast of United States and Canada, in the Pacific Ocean (Fig. 8C).

5. Conclusions

The present review of the Late Cretaceous erymid lobsters includes 13 species with a worldwide distribution. Four genera are represented: *Enoploclytia*, with six species (*E. collignoni*, *E. leachi*, *E. minor*, *E. seitzi*, *E. tepeyacensis*, *E. tumimana*), *Palaeastacus*, with two species (*P. kimzeyi*, *P. sussexiensis*), *Pustulina* with three species (*P. cretacea*, *P. dawsoni*, *P. trisulcata* nov. comb.), *Stenodactylina* with two species (*S. armata*, *S. triglypta*).

We emphasize a change in the composition of erymid fauna between Early and Late Cretaceous. To our knowledge, there is a fewer number of species in the Late Cretaceous. Almost half of them are assigned to *Enoploclytia* while no genus clearly included more species than others in the Early Cretaceous. Moreover, *Eryma*, well-represented during the Jurassic and the Early Cretaceous, is absent in the Late Cretaceous. This decrease in erymid diversity suggests a progressive decline of these lobsters, previously suggested by Schweitzer and Feldmann (2014).

The scarcity and the discontinuity of the record of the Erymidae is a limit for the palaeobiogeographic interpretations. This difficulty prevent us to know if the presence of an erymid fauna in North America was continuous between the Late Jurassic and the Early Cretaceous or if the Cretaceous populations result of migrations from the other continent. In this case, the area of origin could have been Europe because of its connections, the geographic proximity and affinities of its erymid fauna (all the Cretaceous North American genera are represented in Western Europe in the first half of the Early Cretaceous). Moreover, we have noted that almost all the erymids known during the Late Cretaceous are reported from the northern hemisphere. The only erymids of the southern hemisphere were found in Madagascar and the report of a P1 chela of *S.* cf. *armata* in France confirms the existence of migration between Europe and Madagascar as suggested by Secrétan (1964). This asymmetric

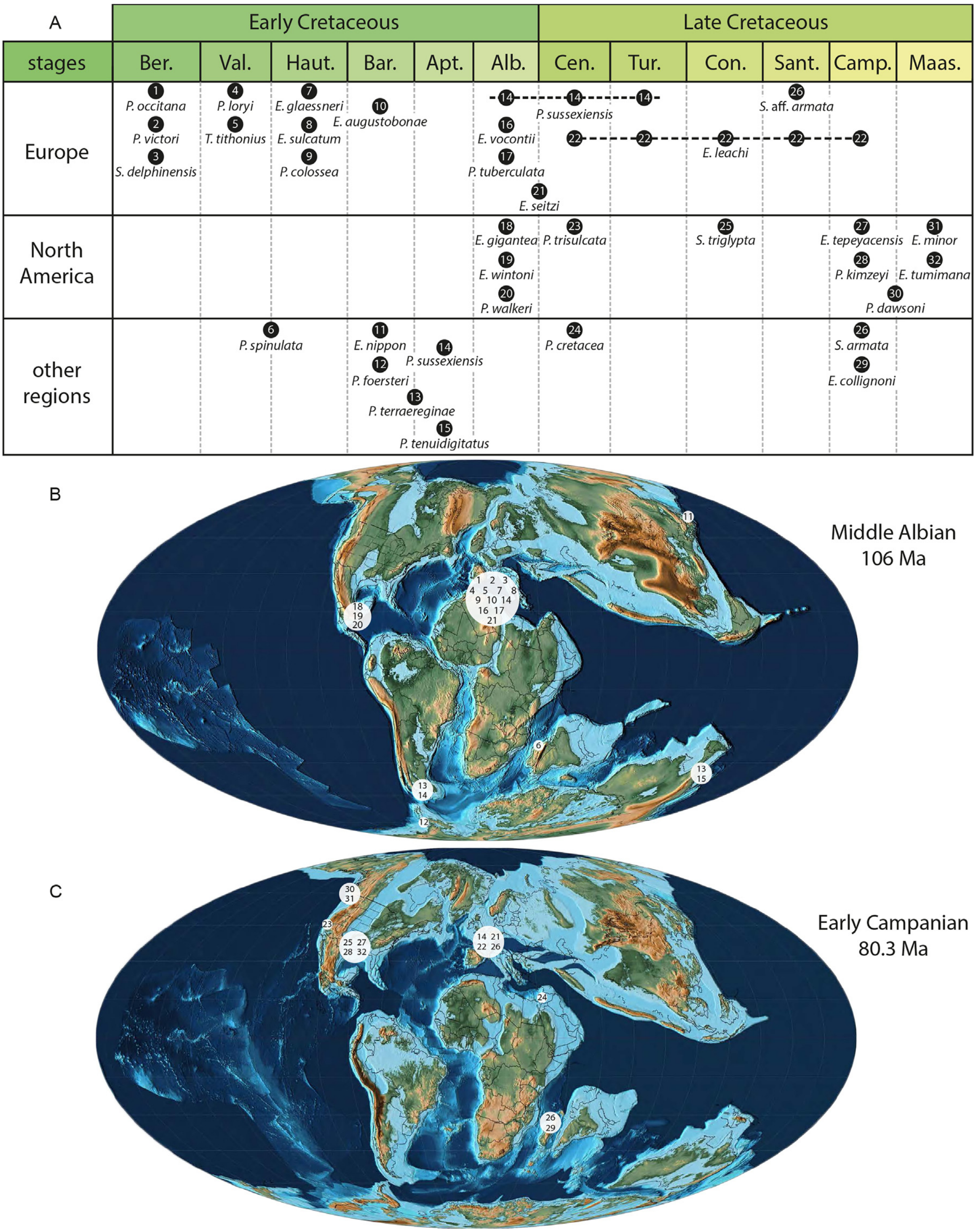

Fig. 8. Stratigraphic (A) and geographic distribution (B, C) of the erymid lobsters during the Cretaceous. Palaeogeographic maps of the Middle Albian (B) and Early Campanian (C) from R. C. Scotese (2014a, 2014b).

repartition between the two hemispheres is probably due to collecting and/or report biases. So, only new reports, especially in the southern hemisphere, could allow us to identify the migration channels of the erymid lobsters during the Cretaceous and the geographic origins of the different faunas.

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Paper VIII

Kočí, T., Kočová Veselská, M., Newman, W.A., Buckeridge, J.S., Sklenář, J. 2017. *Archaeochionelasmus nekvasilovae* gen. et sp. nov. (Cirripedia, Balanomorpha, Chionelasmatoidea) from the Bohemian Cretaceous Basin (Czech Republic): the first bona fide Cretaceous neobalanoform. *Zootaxa 4294(2)*, 181-196.

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Archaeochionelasmus nekvasilovae gen. et sp. nov. (Cirripedia, Balanomorpha, Chionelasmatoidea) from the Bohemian Cretaceous Basin (Czech Republic): the first *bona fide* Cretaceous neobalanoform

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Abstract

This paper records a new sessile cirripede from a nearshore, shallow-water facies at Předboj near Prague, Czech Republic. The new taxon, *Archaeochionelasmus nekvasilovae* **gen. et sp. nov.**, is the earliest known neobalanoform barnacle, and while it may have been an obligate commensal of a cephalopod or marine reptile, that it was a shore barnacle cannot be ruled out. (**Zoobank registration**: urn:lsid:zoobank.org:pub:177CC951-CEC1-425C-B693-46ADB83BD5D9)

Key words: Cirripedia, Balanoformes infraord. nov., Neobalanoformes comb. nov. (pro Neobalanomorpha), phylogeny, upper Cenomanian, Předboj, Bohemian Cretaceous Basin.

Introduction

Until now, only one sessile cirripede, the brachylepadomorph *Brachylepas fallax* (Darwin, 1851) has been recorded from the Bohemian Cretaceous Basin (BCB) (see Withers 1935: 368). The material was collected by Josef Kafka from a location near Úhřetická Lhota and Choceň (Fritsch & Kafka 1887: 10; Kočí *et al.* 2014). The first supposed balanomorph cirripede from the BCB was described by Kafka (1885: 22–23) and Fritsch & Kafka (1887). However, Withers (1935) believed that this specimen, under the name of *Balanula* (sic) *cretacea*, was a brachiopod. Kafka's specimen has apparently been lost and so as Withers (1935: 393) noted, no more can be said about it.

It needs to be observed that we, like Gale & Sørensen (2014; 2015) and a few contemporaries before them, follow Woodward (1901) and Withers (1912a, b) regarding the origin and evolution of the balanomorphs, in having a brachylepadomorph, unknown to Darwin (1854), intervening between them and their pedunculate ancestor. However, taken at face value, molecular genetics places the only living brachylepadomorph and its pedunculate ancestral stock well apart from the line leading to the balanomorphs (compare Herrera *et al*. 2015). But when the unsupported nodes are collapsed in their figure 2, this is by no means compelling. Therefore, we endorse a brachylepadomorph origin, not only because it better fits the palaeontological, ontogenetical and morphological data than does a direct pedunculate origin, but because the transition to the chionelasmatids, which the phylogenetics place at the stem neobalanoforms, is virtually seamless, as will be discussed and illustrated herein.

The fossil record of Mesozoic balanomorph barnacles has long been contentious. Withers (1935: 390) considered there to be but a single Cretaceous species, *Catophragmus* (*Pachydiadema*) *cretacea* from the upper 'Senonian' (= upper lower Campanian). Buckeridge (1996a: 262) re-examined Withers' material and concluded that rather than a balanomorph, it was more likely a brachylepadid or a heavily armoured scalpellid. More recently,

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Gale & Sørensen (2014; 2015), working on material from the *Belemnellocamax mammillatus* beds at Ivö Klack in southern Sweden, have proposed a new phylogeny of early balanomorphs. Their extensive collection included numerous isolated plates of *P. cretacea*. They reassembled some parts and concluded, as did Withers (1935), that it was an early balanomorph. However, upon re-examination and as can be seen from Gale & Sørensen's (2014, Figs 2 G2–3, 4 B) reconstruction, the arrangement of its lateral plates compares more favourably with a scillaelepadine (confer, Innocenti *et al.* 2015) than with an 8-plated balanomorph. To complicate matters, the way the latera overlap with each other differs between their figures 20 and 22, as well as the aforementioned figures 2G2–3 and 4B.

Furthermore, the laterals themselves as well as the carina and rostrum not only have almost parallel rather the sloping margins (Gale & Sørensen 2014, fig. 20E–H, K, W), most have and all are illustrated as having a straight internal median ridge (see their fig. 4B) that projects into the body chamber in their reconstruction, where it would interfere with the suspension of the operculum within the sheath. As noted by Withers (1935: 389), such median ridges form abutments against which the adjacent plates bear. Thus arranged, the several whorls in *Pachydiadema* would form a more or less cylindrical body chamber, more in keeping with a heavy scalpellomorphan peduncle and capitulum than a balanomorphan wall. As a curious coincidence in this regard, it is instructive to note that Gale and Sørensen (2014: 24) suggested that Withers (1953) may have confused parts of his *Scillaelepas ifoensis* with *P. cretacea*, both reconstructed from isolated plates from the same lithostratigraphic unit. Distinguishing between presumed similar forms reconstructed from isolated parts without regard for ontogenetic stages and natural variation can be misleading, as it apparently was here. So, pending further study it is proposed that *Pachydiadema* be returned *incertae sedis* to the calanticine-like scalpellomorphs in which l^1 has been incorporated into effectively an operculum. The peduncle is built in whorls of eight plates whereby "RM-i-M" of Gale & Sørensen (2014: fig. 7 H) is rl^1-l^2- cl^1.

It follows that if the nomenclature of the wall of the Late Cretaceous balanoforms reconstructed in Gale & Sørensen (2014) is converted to the currently recognized nomenclature of neobalanoforms, which is based on ontogeny as well as morphology and evolution, the new form to be described herein from the Upper Cretaceous, being 6-plated, fits into the phylogeny astonishingly well. We can be as certain as one can be that our new form is a neobalanoform, since the specimen consists of a carina (C) articulated with a complete carinolateratus (CL) and rostrolaterus (RL), which would be complete if the rostrum (R) were added, for an inferred six-plated configuration of R-RL-CL^1-C. With or without all or part of the rostrum (R), the complete parietal wall is readily reconstructed by placing a mirror image of the laterals of the animal's right side into the vacant space on the opposite side and, adding the rostrum to the open end (Fig. 3).

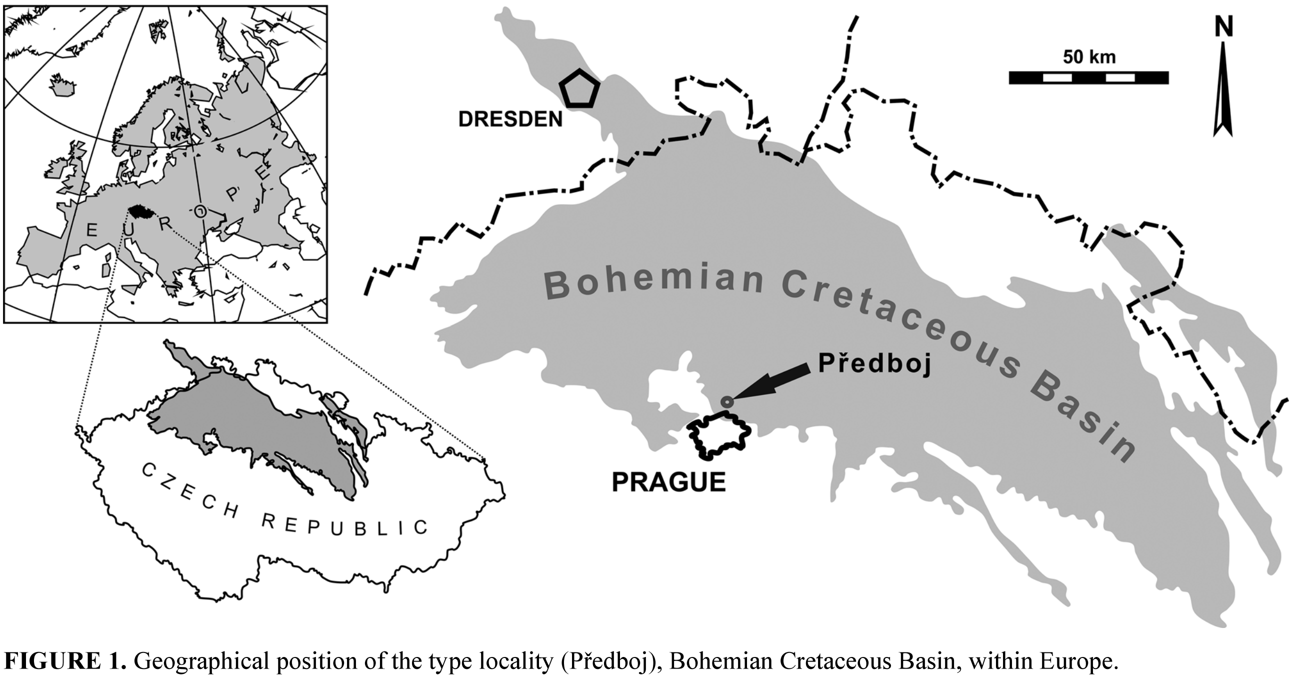


FIGURE 1. Geographical position of the type locality (Předboj), Bohemian Cretaceous Basin, within Europe.

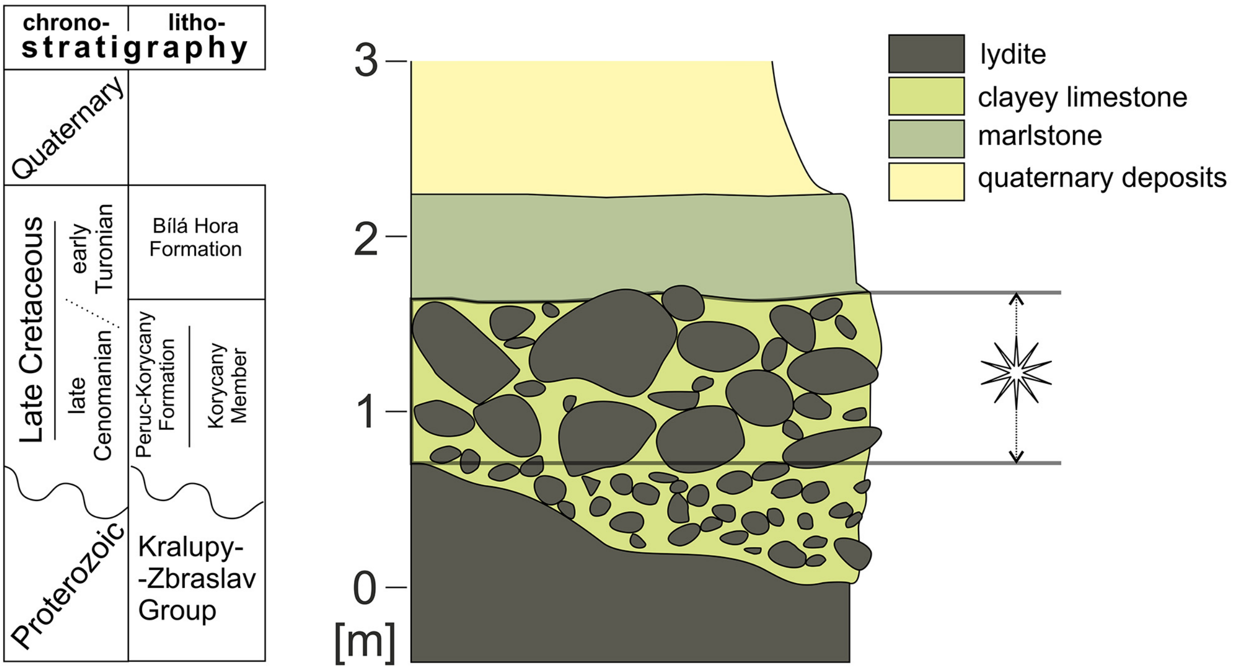


FIGURE 2. Stratigraphical section at Předboj, modified from Žítt *et al.* (1999). Asterisk marks the original source bed of *A. nekvasilovae* specimen. i.e. Stratigraphical section at Předboj, modified from Žítt *et al.* (1999). Asterisk marks the original source bed of *A. nekvasilovae* specimen.

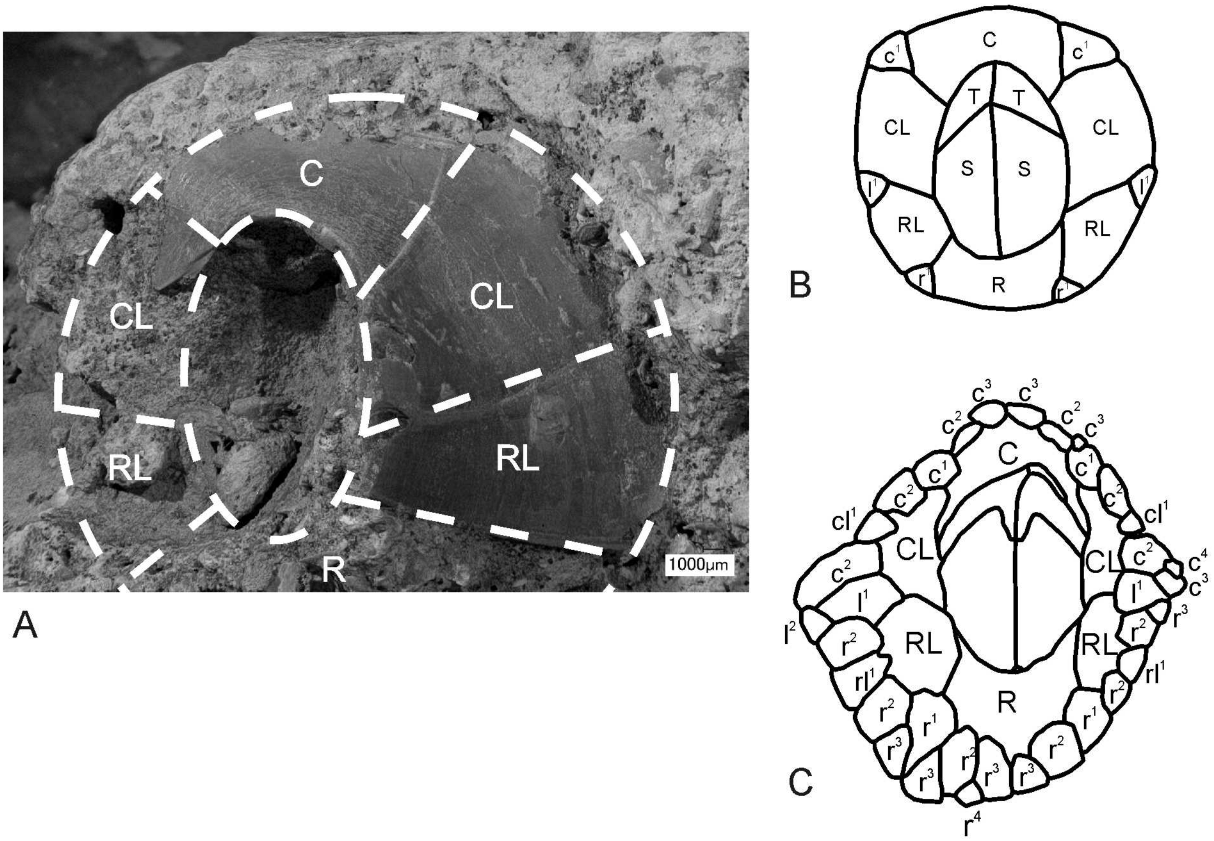
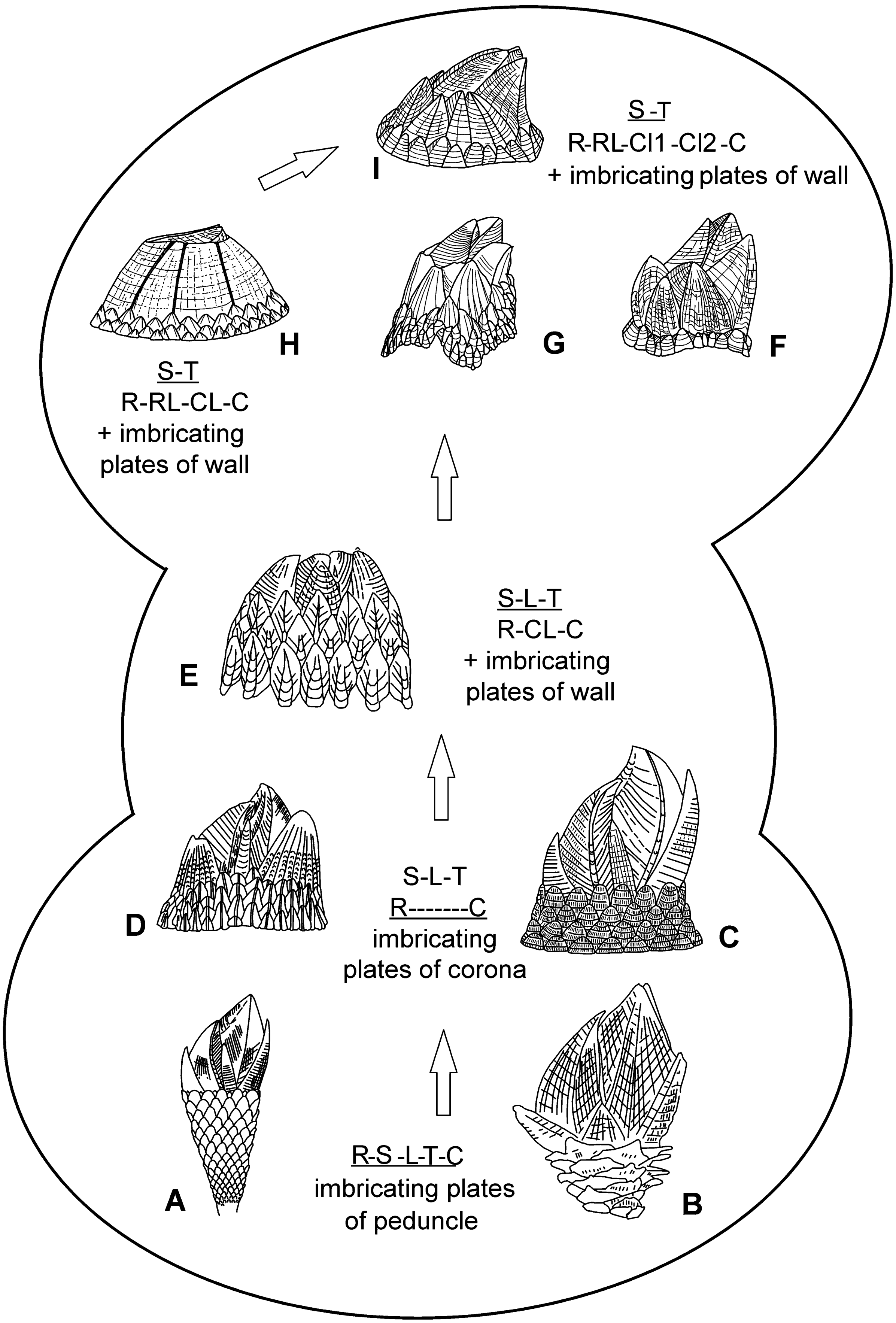


FIGURE 3. Comparison of (A) the reconstructed wall of *Archaeochionelasmus nekvasilovae* **gen. et sp. nov.** with (B) an illustration of a juvenile of *Chionelasmus ohtai* having the first whorl of basal imbricating plates (from a line drawing by D.S. Jones, with permission *in litt.* 2016), and (C) an adult of *Chionelasmus ohtai*; CL overlaps the ala of C, as is indicated on left side, whereas CL abuts rather than overlaps R (Yamaguchi & Newman 1990, fig. 8B), their articulation being strengthened and protected by the addition of the RL applied over the abutment of CL and R, dividing SRL into more or less equal halves.


I
S -T
R-RL-Cl1 -Cl2 -C
+ imbricating plates of wall
H
G
F
S-T
R-RL-CL-C
+ imbricating
plates of wall
E
S-L-T
R-CL-C
+ imbricating
plates of wall
D
S-L-T
R-------C
imbricating
plates of corona
C
A
R-S -L-T-C
imbricating plates
of peduncle
B

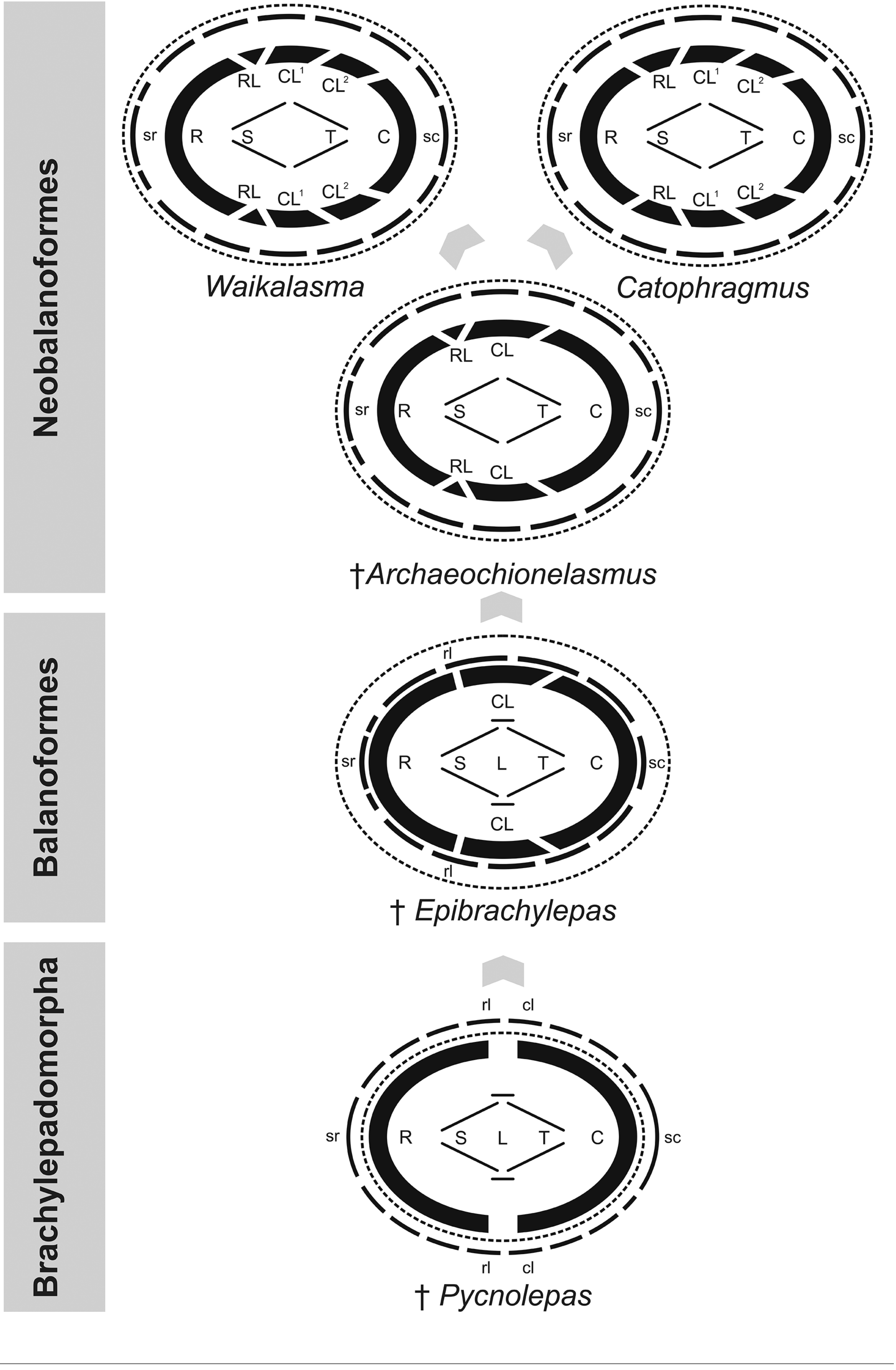
A comparison of the ground plan of the new form with the diagnoses of the walls of the living neobalanoforms reveals it is the same as the most primitive known living balanomorphan, the Chionelasmatidae, previously known from the Lower Eocene as well as presently at bathyal-abyssal depths, including hydrothermal vents of the Indo-Western Pacific.

Had this new 6-plated form been represented by numerous disarticulated plates rather than an articulated fragment, it could have been reconstructed as an 8-plated form (R-RL-CL^1-CL^2-C) since the two lateral plates, CL^1-CL^2, are almost indistinguishable, especially in primitive forms (compare *Waikalasma*; Ross & Newman 2001, fig. 4). Therefore, it was indeed fortunate that the articulated plates in the present form were RL-CL-C, for if the three plates had been R-RL-CL or CL-C-CL, there would have been no way of telling whether it were 6- or 8-plated.

Stratigraphical and geographical setting. The single specimen of this new species came from a quarry that once existed near Předboj, a village situated north of Prague on the so-called Unhošť-Tursko High (see Fig. 1). The quarry, known for its fossils since the 1920s (Prantl 1929; Zázvorka 1939), was located east of the road to the village of Horňátky. The exact location of the specimen was a narrow fissure called “Pavel” (i.e. “Paul”), with co-ordinates 50°14'9"N, 14°28'23"E.

The quarry walls exposed sections through a number of depressions and fissures in the Upper Proterozoic lydite (flinty shale, kieselschiefer) basement. These were carved out by Cenomanian sea abrasion in shapes displaced by prevailing tectonics in WSW-ENE, WNW-ESE and N-S directions. The depressions, characterized by abraded, often almost smooth lydite surfaces, were infilled with lydite conglomerates with a matrix comprised of yellowish clayey limestone (Korycany Member; see Fig. 2). Whereas the basal conglomerates are well sorted, the subsequently deposited clasts are reported to be rather coarse and unsorted, with a matrix comprising a yellowish, clayey limestone rich in fossils (Žítt *et al.* 1999). On the basis of this matrix, we conclude that this upper level was most probably the source of the type specimen. Upwards, the conglomerates are replaced by marls of the Bílá Hora Formation, deposited during the early Turonian relative sea level rise. Nevertheless, analogous to many other “rocky-coast” localities of the Bohemian Cretaceous Basin (BCB; e.g. Žítt *et al.* 1997, 1999, 2015), the Cenomanian/lower Turonian boundary is situated below the marl layer, within the conglomerates. Its exact position

FIGURE 4. Evolution of symmetrical sessile cirripedes from a pedunculate stock. The capitulum and basal imbricating whorls (IPs) of the peduncle of neolepadines (**A, B**) gave rise to the wall and part of the operculum of the sessile barnacles, the former initially comprising the rostrum and carina (R and C), the latter the latera (L) as well as the scuta and terga (S, T). The peduncular IPs formed a corona standing as many as four whorls high, as seen in brachylepadomorphs (**D**, **C**). The step to the balanoforms (second arrow), the (**E**) level of organization, includes reversing the direction IPs were added from down to up relative to and a consequence of the now basal equatorum, and the filling of the gap between R and C with CL from the cl site (compare plan views, Fig. 5). A 4-plated primary wall, like that seen here (**E**), is recapitulated in the ontogeny of higher forms beginning with the chionelasmatids (**F**–**H**; compare Ross & Newman 1996)) included loss of the opercular L and the addition of RL from the rl site on the skeletogenous equatorum, followed by the proximal IPs becoming dedicated to the wall proper (above third arrow). The final step, giving rise to the 8-plated wall, involved replication of CL, as seen in the ontogeny of neobalanoforms and first appearing in waikalasmatids (**I** via fourth arrow). Like the four-plated level and the replication of CL, a functional vestige of the peduncle is also seen in the ontogeny of higher neobalanomorphs (compare Newman 2013).
A—*Pedupycnolepas* Gale, 2015. Type species *Pycnolepas articulata* Collins, 1980, fossil having a limited stratigraphical range: Bluff Formation, ?lower Aptian, Early Cretaceous, Alexander Island, Antarctica. **B**—*Ashinkailepas* Yamaguchi, Newman & Hashimoto, 2004. Type species *Ashinkailepas seephiophila* Yamaguchi, Newman & Hashimoto, 2004, Recent, from hydrothermal seeps, depth 1,173 metres, off Hatsushima Island, Japan. **C**—*Pycnolepas* Withers, 1914. Type species *Pollicipes rigidus* J. de C. Sowerby, 1836, fossil species, Albian, Gault, Early Cretaceous, England. Stratigraphical range: Albian to Middle Miocene (Helvetian). **D**—*Brachylepas* Woodward, 1901. Type species *Brachylepas naissanti* (Hébert, 1855), fossil species, upper Campanian of Norwich, Norfolk, England. Stratigraphical range: Turonian to Maastrichtian, Late Cretaceous. **E**—*Epibrachylepas* Gale, *in* Gale & Sørensen, 2015. Type species *Epibrachylepas newmani* Gale, *in* Gale & Sørensen, 2015, fossil species, Late Cretaceous, upper lower Campanian, Ivö Klack, southern Sweden. Stratigraphical range: upper lower Campanian to Maastrichtian. **F**—*Archaeochionelasmus* **gen. et sp. nov.** Type species *Archaeochionelasmus nekvasilovae* sp. nov., fossil species, upper Cenomanian, Předboj, Czech Republic. **G**—*Eochionelasmus* Yamaguchi, 1990. Type species *Eochionelasmus ohtai* Yamaguchi & Newman, 1990, Recent species from abyssal hydrotermal vents, depth 1,990 metres, North Fiji Basin, southwest Pacific. **H**—*Chionelasmus* Pilsbry, 1911. Type species *Chionelasmus darwini* (Pilsbry, 1911), fossil and Recent species, 500 m, Indo-West Pacific. Stratigraphical range: Upper Eocene to Recent. **I**—*Waikalasma* Buckeridge, 1983. Type species *Waikalasma juneae* Buckeridge, 1983 (extinct), Lower Miocene (Otaian–Altonian), New Zealand. Stratigraphical range: Early Miocene to Recent.


Neobalanoformes
RL
CL¹
CL²
sr
R
S
T
C
sc
RL
CL¹
CL²
Waikalasma
RL
CL¹
CL²
sr
R
S
T
C
sc
RL
CL¹
CL²
Catophragmus
RL
CL
sr
R
S
T
C
sc
RL
CL
†Archaeochionelasmus
Balanoformes
rl
CL
sr
R
S
L
T
C
sc
CL
rl
† Epibrachylepas
Brachylepadomorpha
rl
cl
sr
R
S
L
T
C
sc
rl
cl
† Pycnolepas

as well as the original position of the specimen described here remains unknown, and even an early Turonian date cannot be excluded for the fossil. The locality is no longer accessible as it was filled with waste during 1960s and subsequently covered with soil.

Material and methods

The remarkable specimen described herein was collected by Dr Olga Nekvasilová in 1963 and labelled "Pavel pocket", Předboj. Its significance remained unknown until it was noticed by one of the authors (J.S.) in the old collection material transferred in 2013 from the Czech Academy of Sciences to the National Museum. The specimen was studied and photographed using an Olympus SZX-12 stereomicroscope with a DP70 camera, and a Kayence VHX-2000 3D microscope (both at National Museum, Prague).

Systematic palaeontology

Class Thecostraca Gruvel, 1905

Subclass Cirripedia Burmeister, 1834

Superorder Thoracica Darwin, 1854

Order Balanomorpha Pilsbry, 1916 (= Sessilia Lamarck, 1818 *sensu* Buckeridge & Newman, 2006)

Infraorder Balanoformes Kočí, Buckeridge & Newman nov.

The new infraorder is proposed herein to accommodate the so-called basal balanomorphs *Parabrachylepas* and *Epibrachylepas* (but not *Pachydiadema*, as discussed above) of Gale (*in* Gale & Sørensen 2014; compare Figs 2E1–3, F1–3, respectively).

FIGURE 5. Evolution of wall of sessile barnacles by reduction, multiplication and reorganization of the plates:
†*Pycnolepas*, Brachylepadomorpha—Comprised of a capitulum of paired latera, scuta and terga suspended by the arthrodial membrane within a wall consisting of the rostrum and carina (R-S-L-T-C), while the imbricating plates inherited from peduncule of its neolepadine ancestor (outermost heavy dashed oval) form a corona standing as many as four whorls high (heavy dashed oval in which by hindcasting consist of the incipient subrostrum, rostrolatera, carinal latera and subcarina can be identified; that is sr, rl, cl & sc, respectively). This and subsequent whorls, like those of the peduncle, develop sequentially downward from the equatorum (lightly dashed oval), whereby the basalmost are the oldest. It is likely more than coincidental that, like the corona of brachylepadomorphs, the corona of *Eochionelasmus* and *Chionelasmus* is also composed of four whorls (Newman, 1987, figs 4B, 5A; Yamaguchi & Newman, 1997, fig. 2A, B), whereas the pattern breaks down into an indeterminant number of whorls after the third in *Pollicipes* (Newman, 1987, fig. 5B). Thus, while the corona of the new form is only indicated by some traces, like that of *Epibrachylepas* it may have stood four whorls high (it ranges from two to five in the reconstruction, Fig. 6).
†*Epibrachylepas*, Balanoformes—Distinguished from the brachylepadomorph level of organization largely by the inferred reversal in the direction the whorls of IPs were added by the equatorum, from downward to upward, during phylogeny and recapitulated in the ontogeny of living coronate balanomorphs, whereby the basalmost are the youngest rather than the oldest. The carino-latera were added to form the 4-plated stage (R-CL-C) with a 6-plated operculum (S-L-T). That the additional pair of wall plates is the CLs was observed ontogenetically in *Chionelasma* (compare Yamaguchi & Newman, 1990, fig. 8).
†*Archaeochionelasmus* **gen. nov.**, Neobalanoformes—Wall comprised of 6 plates, the RLs having been added by the skeletogenous tissue in the rl region of the equatorum as they have been observed to do in the ontogeny in *Eochionelasmus* (Yamaguchi & Newman, 1990, & D.S. Jones *in litt.* 2016); L of the operculum, sometimes vestigial in brachylepadomorphs and neobalanoforms, is lost here on up.
Waikalasma, Neobalanoformes—wall comprised of 8 plates by replication of CL^1 forming CL^2, as observed in the ontogeny of some Neobalanoformes (see e.g., Costlow & Bookhout, 1956). It will be noted that, as in chionelasmatids, RL does not enter the sheath, whereas it enters the sheath in *Catophragmus* on up. Whether or not RL enters the sheath in the new form could not be fully resolved to our mutual satisfaction in the material at hand.

Diagnosis. Extinct balanomorphs (*Parabrachylepas* and *Epibrachylepas*) differing from the largely extinct brachylepadomorphs in having a primary wall of four plates (compare Gale & Sørensen, 2014, Fig. 4B and C, respectively) in which lateral plates dubbed marginal (M) and rostro-marginal (RM) = CL^1 and RL in contemporary nomenclature. Operculum including a pair of latera (L); principal imbricating whorl of eight plates (r^1-rl^1-l^1-cl^1-c^1) standing four or fewer whorls high, as in brachylepadomorphs and their asymmetrical derivatives, the neoverrucids. Equatorum basal, as in all balanomorphs (see text and Fig. 5).

Infraorder Neobalanoformes Gale, 2014, new comb.

To accommodate Neobalanomorpha (Gale *in* Gale & Sørensen 2014)

Diagnosis. Symmetrical sessile barnacles differing from †Balanoformes nov. in having a primary wall consisting of a rostrum (R) and carina (C) and two or three pairs of lateral plates: the carinolatera (CL^1) and rostrolatera (RL) as in the chionelasmatids, and a second pair of carinolatera (CL^2) added by replication during early ontogeny of eight-plated forms; various reductions following in higher forms (compare Ross & Newman 1996). Operculum of four plates: paired terga and scuta. When present in lower forms, imbricating plates (IPs) are added at the basal margin, or equatorum, adjacent to the substratum, in whorls ranging from numerous (*Eochionelasmus* and the catophragmids) to as few as four or less as in *Waikalasma* (Buckeridge 1996: Fig. 4b) and likely in the new form, or the four effectively integrated into a single whorl as in *Chionelasmus* (Newman 1987, Fig. 4).

Superfamily Chionelasmatoidea Buckeridge, 1983 (Upper Cretaceous–Recent)

Diagnosis. Neobalanoformes having a primary wall of six plates (R-RL-CL^1-C) plus few to numerous whorls of IPs (Jones 2000).

Family Chionelasmatidae Buckeridge, 1983 (Upper Cretaceous–Recent)

Archaeochionelasmus Kočí, Buckeridge & Newman gen. nov.

Pl. 1, figs A–F; Pl. 2, figs A–H; Text-figs 3, 6

Diagnosis. Low conical neobalanoform with a six-plated wall comprised of a carina (C) and a rostrum (R) plus paired carinolatera (CL^1) and rostrolatera (RL) and at least one whorl of basal imbricating plates (IPs); pseudo-radii present on overlapping margins of RL and CL^1; alae unexposed, rostrolatera perhaps included in the sheath; no trace of a calcareous basis.

Etymology. *Archaeo* (Greek *arkhaio-*) = early, or before *Chionelasmus.*

Stratum typicum. Upper Cenomanian, Korycany Member, Bohemian Cretaceous Basin.

†*Archaeochionelasmus nekvasilovae* Kočí, Newman & Buckeridge, sp. nov.

Text-fig. 6; Pls. 1, 2

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Diagnosis. As for the genus.

Etymology. Named in honour of Dr Olga Nekvasilová (*1928), a prominent palaeontologist who contributed greatly to the knowledge of Mesozoic brachiopods as well as the Late Cretaceous hard-substrate communities. Dr Nekvasilová discovered this specimen in 1963.

Holotype. NM-O7615, collections of the National Museum, Prague.

Material. Three articulated parietal plates—carina, left carinal latus and left rostral latus. The form of the rostrum is readily reconstructed, but the nature of the operculum and IPs is unknown.

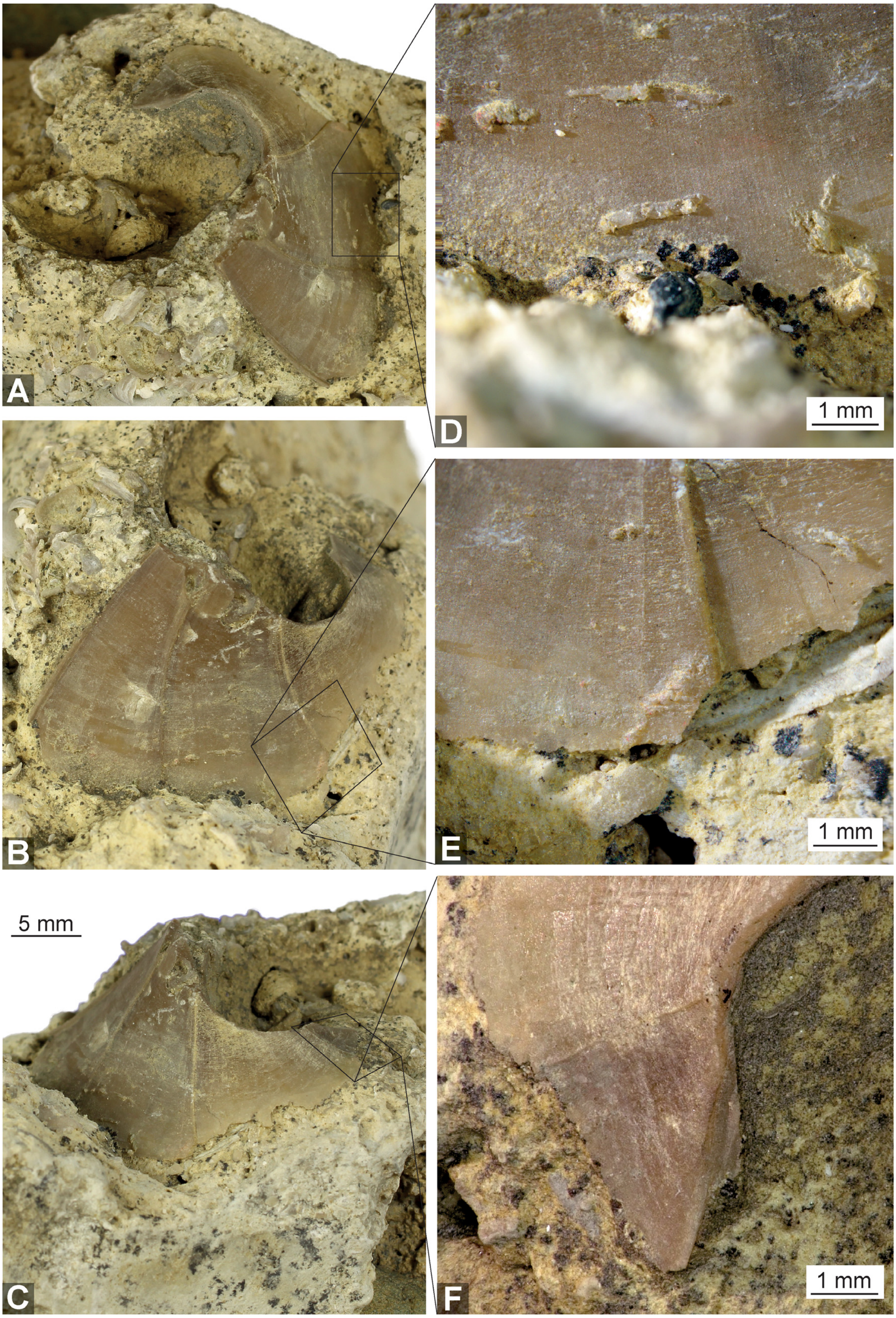

PLATE 1. A–C General views of the specimen. Rostrolatera (RL) is oriented down and to the left in A and B; rightmost in **C** is carina**. D** Detail of base of carinolatera (CL) with possible traces of original imbricating plates. Note the rough surface observable at CL base to left (see this feature also in Pl. 2G). **E** Detailed view of junction of CL and C plates at their basalmost portion. **F** Detailed view of ala of C. A–C are identical in scale, A–C digital macrophotography, D–E optical microphotography, F 3D microscope image.

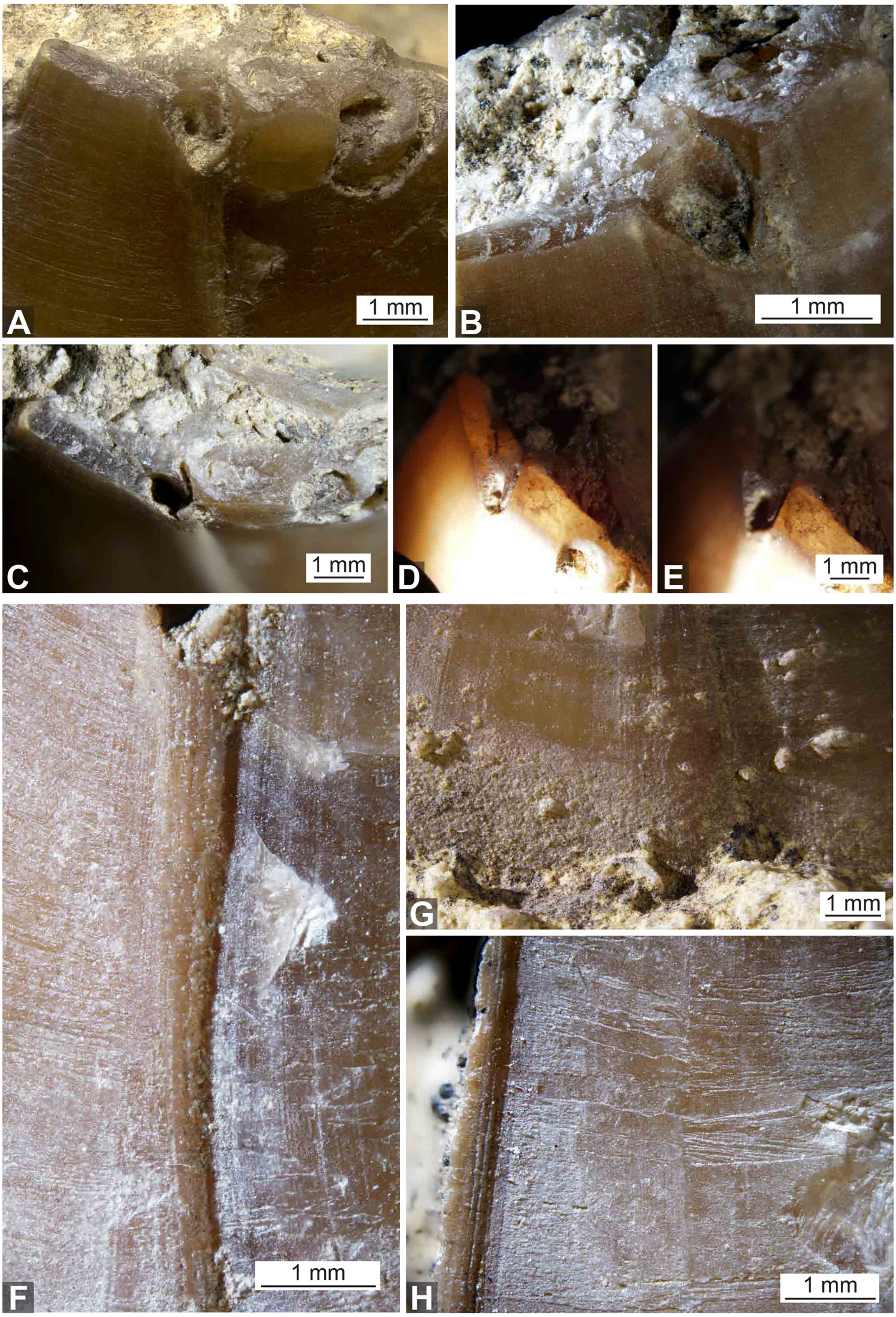

PLATE 2. A–E detailed views of rostrolatera (left)/carinolatera (right) junction**. A–B** Top-lateral views, **C** Top view**. D–E** Details in similar view using refracted light. Although these plates show partial recrystallization, some internal features are still observable in refracted light**. F** Detail of RL/CL junction showing overlapping margin of RL**. G** Detail of the RL/CL junction at their basal portions with rough surface. **H** Detail showing left radius of the RL plate. Compare delicate ornamentation of the plate surface with F. D–E are identical in scale. A is a 3D microscope image, B–H optical microphotography.

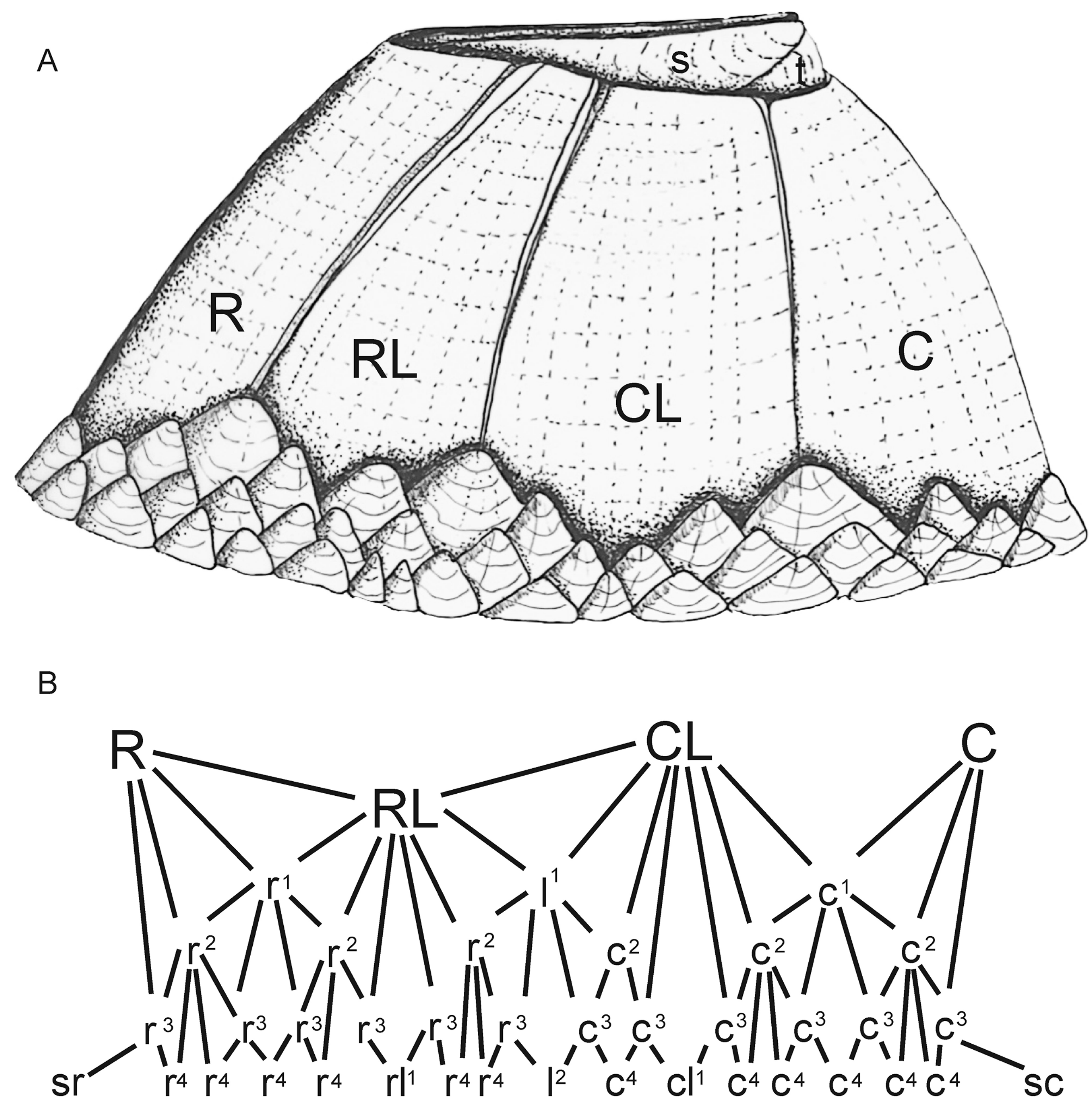

FIGURE 6. Reconstruction of †*Archaeochionelasmus nekvasilovae* Kočí, Newman & Buckeridge, **gen. et sp. nov. A.** Wall based on the fossil, operculum low in accordance with the low profile and tight sutures of the wall that suggest it may have been an epibiont of large marine reptiles or cephalopods. The presence of imbricating plates is based on ribbons of sediment adhering to the base of the wall plates. Their arrangement is patterned after that found in B, the generalized form as typified by *Eochionelasmus ohtai* Yamaguchi & Newman, 1990. which is the basis for their arrangement in higher forms; cf. *Waikalasma boucheti* Buckeridge, 1996 and *Catophragmus* in Ross & Newman (2001). Parietal plates R, RL, CL and C (rostrum, rostrolatus, carinolatus & carina respectively) and opercular s and t (scutum and tergum respectively), with the relative positions of the paired and unpaired plates making up the imbricating whorls identified accordingly.

Description. Shell smooth, medium-low conical, comprising six compartmental plates—C, CL[1], RL, R (rostrum reconstructed). Pseudo-radii narrow, running sub-parallel to the articular margins, slightly overlapping the edges of the parietes along both margins of the RL and the carinal margin of the CL[1] (Fig. 3, 6, 7), separated from them by a well-formed longitudinal groove; wider nearer summit, with width increasing by accretion of the fine transverse and longitudinal ridges; the transverse growth lines are not upturned (as in true radii that develop later in balanomorph evolution). Note that these pseudo-radii are not precursors of the true radii, which developed later in the Palaeogene. The longitudinal ridges represent successive growth increments, with new ridges and grooves gradually added at the base; RL and CL[1] rhomboid, with summits parallel to the base; C semi-conic. RL—narrow: 16 mm basal length: 9.9 mm, length in upper portion 2.4 mm; CL[1]—high 9–5 mm, length in basis 13 mm, length in upper portion 7.7 mm.

Although no complete whorls of IPs are retained, the basal margin of the parietal plates (where not eroded or damaged) and the exposed ala (Pl.1, Fig. F) have variously arranged indentations indicating where tissue within extended out underneath the basal IPs and the wall. The delicate, sinuous, lateral calcareous ridges occurring near the base of the compartments (Pl. 1, Fig. D) are interpreted as sites that entrapped fine calcareous sediment along the zone where the imbrications abutted the compartments. There are also some fragments of shell near the base that could be the remains of IPs that survived the preparation of the specimen (Pl. 1, Fig. E).

Mode of life and palaeoecology. A reconstruction of *Archaeochionelasmus* nov. gen. (Fig. 6) shows a moderately low profile similar to that of the "turtle barnacle" *Emersonius* Ross & Newman, 1967 recorded in the Eocene of Florida (USA), *Protochelonibia* from the Lower Miocene of the Central Paratethys (Austria) (Harzhauser *et al.* 2011), extant *Chelonibia* (Zardus *et al.* 2013), *Platylepas* and *Stomatolepas* (Southward 2008). The form of *Archaeochionelasmus* nov. gen. is consistent with that required for attachment to living substrates such as an ammonite or turtle, both of which are recorded in the BCB (Ekrt *et al.*, 2001; Kear *et al.*, 2014). Although direct evidence is lacking, we suggest that *Archaeochionelasmus* nov. gen. may have lived as an obligate commensal with ammonites and/or marine reptiles. Notwithstanding this, it is quite possible that it lived on hard, inorganic substrates in the littoral zone. However, further indirect support for commensal life is the absence of any other neobalanomorph plates, conspecific or otherwise, at this locality. Although negative evidence, it suggests there were no other barnacles present, compared to, for example, the variety of forms known to have lived on hard substrates along the rocky coast at Ivö Klack (southern Sweden) during the Campanian (Withers 1935; Gale & Sørensen 2015).

Discussion

Archaeochionelasmus **gen. nov.** has the 6-plated configuration of the most primitive known living balanomorphs such as *Eochionelasmus* Yamaguchi & Newman, 1990: a wall consisting of the rostrum (R), paired rostro-laterals (RL), paired carino-laterals (CL) and a carina (C), plus numerous whorls of IPs. This could be expressed as R-RL-CL-C+IPs if the presence of IPs could be fully confirmed. IPs are likely in *Archaeochionelasmus* **gen. nov.**, not just because they are found in the primitive balanomorphans of the superfamily Chionelasmatoidea and the Catophragmidae, but because their presence can be inferred by proxy, i.e., by the lineations of fine sediment that adhere near the base of the fossil that apparently accumulated between the imbrications and the compartment, by large, low elevations in wall plates that likely aligned with the larger of the IPs, and by the thin, variously scalloped basal margin of the wall under which skeletogenous tissue of the equatorum[1] that produced them stayed in contacted with them (Fig. 5, dashed line).

Transverse-sections produced by breakage of the compartments show interlaminate figures (see Pl. 1, Fig. F), comparable but not identical to those of some lower balanomorphs such as *Hesperibalanus hesperius* or *Semibalanus balanoides* (e.g. Cornwall 1956, text-fig. 3a, b, and Davadie, 1963; Pl. 52, 5, respectively). The compartmental configuration seen in chionelasmatids, such as *Archaeochionelasmus* **gen. nov.** was evidently derived from the brachylepadomorph wall of R-C+IPs (Newman 1987, fig. 11; Newman & Hessler 1989; Newman & Yamaguchi 1995) by production of a pair of CLs at the site of the skeletogenous tissue on the equatorum. An intermediate configuration, R-CL-C+IPs, between the two is reconstructed in *Parabrachylepas* and *Epibrachylepas* from the upper lower Campanian at Ivö Klack by Gale & Sørensen (2015, Fig. 20 A–C & D–F). However, given that L went with the operculum in the evolution of the sessile barnacles, Gale & Sørensen (2014, especially Figs. 4 A–C) apparently did not understand the evidence presented by Yamaguchi & Newman (1990)

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[1] The skeletogenous band (dashed line in Fig. 5) at the capitulo-peduncular junction of scalpellomorph barnacles first discussed by Darwin (1852) is herein named the *equatorum* because it is the same band of tissue in all the thoracicans and their close allies discussed herein.

demonstrating that, as noted above, CL was the first lateral plate to be added in the ontogeny of chionelasmatoids, or that it was followed by RL, thus completing the chionelasmatoid primary wall. Instead, they considered current homologies of lateral plates in balanomorphs are incorrect, whereby the first pair of lateral plates was dubbed M (marginal) rather than CL. Further, they proposed that the balanomorph primary wall evolved *de novo*, apparently by modification of peduncular scales. However, they offer no reason why their M plate is not a CL, which it clearly is, as its manner of overlap is consistent with that in all extant balanomorphs. In balanomorphs phylogenetically above chionelasmatoids, it gives rise to CL^2 by replication, as first fully confirmed by Costlow & Bookhout (1956) and applied evolutionarily by Yamaguchi & Newman (1990).

Once the RLs were produced by skeletogenous activity at the rl site on the equatorum, the addition of whorls of IPs switched from downwards, as in brachylepadomorphs, neoverrucids (Yamaguchi & Newman 1990; Newman & Yamaguchi 1995), to upwardly from around the now basal equatorum, whereby they remained in contact with the substratum. Thus, the first-formed whorl of IPs remains with the primary wall when the second is formed, and so on until the definitive number of whorls is reached. These two processes are recapitulated in the ontogeny of *Neoverruca* on the one hand and chionelasmatoids on the other (Newman 1989; Yamaguchi & Newman 1990; D.S. Jones *in litt.* 2016).

This primitive and basal six-plated configuration (R-RL-CL-C+IPs) first seen in balanoforms and perfected in chionelasmatoids (Fig. 3B, C), provided the way to an eight-plated wall (R-RL-CL^1-CL^2-C+IPs) configuration by the acquisition of the second pair of carino-latera (CL^2) by replication of the CL^1s, a process that exists in the ontogeny of higher balanomorphs (Costlow & Bookhout 1956; Yamaguchi & Newman 1990), which are dubbed the neobalanoforms herein. This 8-plated configuration plus IPs is developed in the chionelasmatoid genus *Waikalasma* Buckeridge, 1983 (Buckeridge & Newman 1992) and in *Catophragmus* s.l. (Darwin 1854; Newman 1987; Buckeridge 1996b; Ross & Newman 2001). Importantly, while the RLs were added from the equatorum to the wall before the replication of the CLs, it was thought they did not become fully integrated; that is, they were not incorporated into the sheath until the *Catophragmus* level of organization was achieved. Curiously, it appears they were at least partially integrated into the sheath in the new form.

Evolutionarily, the primary wall plates did not gain full contact with the substratum until the whorls of IPs were eliminated. This was because the living tissue maintaining them extended under the wall. A notable feature of *Archaeochionelasmus* **gen. nov.** is that the wall plates (C-CL-RL and probably R) were partially, rather than fully, in contact with substrate.

Conclusions

Archaeochionelasmus nekvasilovae **gen. et sp. nov.** is the earliest representative of the Chionelasmatidae Buckeridge, 1983 as well as of the Neobalanoformes. The family has been considered pivotal to our understanding of the origin of balanomorphs (Newman 1987; Yamaguchi & Newman 1990), for while the sessile barnacles first appear in the Mesozoic, until now the earliest confirmed neobalanoform with IPs was *Chionelasma* from the Eocene (Buckeridge 1983). Thus, the finding of a new chionelasmatid from the Upper Cretaceous (upper Cenomanian) is exciting news indeed since genetics (Herrera *et al.* 2015), as well as comparative morphology and the fossil record, suggested something like it should have existed at this time.

This new chionelasmatid is specialized compared to the extant forms which are refugial in bathy-abassyal and hydrothermal habitats–albeit they are currently believed to have originally evolved in near-shore environments (Buckeridge 1996a, b), as were the Late Cretaceous forms described by Gale & Sørensen (2014; 2015). It is suggested here, because of its specializations relative to these shallow-water forms, that the new form may have lived as an obligate commensal on marine reptiles and/or ammonites rather than along the shore.

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Plate IX

Kočová Veselská, M., Van Bakel, B., Kočí, T. (submitted). The palaeocorystid crab *Ferroranina fritschi* (Glaessner, 1929) from the lower-middle Coniacian of the Bohemian Cretaceous Basin (Czech Republic), the first record of *Ferroranina* for Europe. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*.

The palaeocorystid crab *Ferroranina fritschi* (GLAESSNER, 1929) from the lower-middle Coniacian of the Bohemian Cretaceous Basin (Czech Republic), the first record of *Ferroranina* for Europe

Martina Kočová Veselská, Barry van Bakel and Tomáš Kočí

Abstract

The re-examination of palaeocorystid crab *Palaeocorystes*? sp. from the lower-middle Coniacian of Březno locality, later redescribed as *Notopocorystes fritschi* by GLAESSNER (1929a), is provided. A new detailed study of the single, well-preserved dorsal carapace of the specimen with conspicuous cuticular morphology (fungiform nodes, distinct trilobate post-frontal terrace, medially defined cervical groove with V-shaped medial portion) confirm the assignation of the specimen to *Ferroranina* VAN BAKEL, GUINOT, ARTAL, FRAAIJE & JAGT, 2012, rather than to any other palaeocorystid genus. Previous record of the genus has been known by three species from the late Cretaceous of India, Madagascar, Mexico and Texas. The Czech specimen constitutes the fourth known member of the genus and simultaneously the first fossil record of *Ferroranina* for Europe and thus extends the previously known geographic distribution of the genus during the Cretaceous period. The potential migration routes of the genus to the Bohemian Cretaceous Basin are also discussed.

Key words: Raninidae, palaeobiogeography, upper Createceous, Březno Formation

Introduction

During the late Cretaceous the area of present day Bohemian Cretaceous Basin (BCB) formed a narrow Seaway connecting the North Sea Basin and the Tethys Ocean and thus represents a gateway between the Tethys and the Boreal realm, and together with Brannau-Regensburg Basin (Danubian Cretaceous Group) in Bavaria, formed a peri-Tethyan shelf zone during the Late Cretaceous (ČECH 2011). A Tethyan Circumblobal Current which connected the polar regions with the tropics allowed the mixture of waters and a low-latitude communication between all of the major ocean basins (HAY 2011, LUQUE et al. 2012).

The faunas of Bohemia are influenced to a varying extent both from the Boreal and Tethys through time (more in WIESE et al. 2004, VODRÁŽKA et al. 2009). This is evidenced by the occurrences of the warm-water fauna like rudist, colonial hexacorals or thick-shelves bivalves as well as several incursions of typical Boreal belemnites in the BCB (KOŠŤÁK et al. 2004, ČECH 2011). The same migration trend can be observed in the upper Cretaceous decapod crustaceans found in the BCB where specimens with worldwide distribution like *Enoploclytia* M'COY, 1849, *Hoploparia* M'COY, 1849 or *Ctenocheles* KISHINOUYE, 1926 were abundantly presented.

The primary purpose of this paper is to re-examine the FRITSCH's original of palaeocorystid crab *Palaeocorystes*? sp. from the lower-middle Coniacian of Březno locality, later redescribed as *Notopocorystes fritschi* by GLAESSNER (1929a) and subsequently as *Notopocorystes* (*Cretacoranina*) *fritschi* by MERTIN (1941). Depending on new data of Palaeocorystoidea (VAN BAKEL et al. 2012), authors provided new detailed study of the specimen and reassigned it to *Ferroranina* VAN BAKEL, GUINOT, ARTAL, FRAAIJE & JAGT, 2012 in this paper. The genus has been known from the late Cretaceous of India, Madagascar, Mexico and Texas so far. The Czech specimen thus represents the first fossil record of

Ferroranina for Europe and extends the previously known geographic distribution of the genus during the Cretaceous period.

Geological and stratigraphical setting

The studied locality Březno is situated on the NNE slope of Březno Hill, on the right bank of the Ohře River in the vicinity of Louny (Czech Republic); GPS: 50° 21' 23.864" N, 13° 44' 16.919" E (Fig.1). In the outcrop calcareous claystones and siltsones of the Teplice and Březno formations are exposed (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 collapsed and covered with debris.

FIG. 1 NEAR HERE

The first description of the outcrop was made by FRITSCH (1893) who distinguished altogether six lithological members (called "beds") from the bottom to the top: Nucula Bed, Geodia Bed, Radiolaria Bed, Gastropod Bed, Sphaerosiderite Bed and Crab Bed (Fig.2). The decapod crustaceans assemblage herein has been documented since REUSS (1845-1846), FRITSCH (1867, 1893, 1894) and FRITSCH & KAFKA (1887) provided description and illustration of abundant fauna from the upper part of the outcrop represented by lower-middle Coniacian Gastropod, Sphaerosiderite and Crab beds, in which well-preserved specimens are said to be abundant. By contrast, no crustaceans are known from the lower part of the outcrop yet. The summary of decapod fauna known from Březno was recently provided by VESELSKÁ (2009) and KLOMPMAKER (2013: appendix B). Lately, FRITSCH's original of *Stenocheles parvulus* from this area was recognized by HYŽNÝ et al. (2014) as a member of *Ctenocheles* which represents one of the oldest records and simultaneously one of the best preserved fossil material of the genus reported to date.

FIG. 2 NEAR HERE

Gastropod, Sphaerosiderite and Crab beds are characterized by calcareous claystones and can be assigned to the lower–middle Coniacian (upper part of the *Cremnoceramus crassus* and *Inoceramus kleini* zones). These beds are very rich in fossil remains. Ammonites are very abundant (for details see FRIČ 1893); stratigraphically significant taxa are represented by *Foresteria* (*Harleites*) *petrocoriensis* (COQUAND, 1859) and *Peroniceras tridorsatum* (SCHLÜTER, 1867). For Sphaerosiderite Bed almost complete lack of glauconite is typical, whereas the sphaerosiderite concretions are common; they have gray core enveloped by red or yellow (oxidized) surface and attain a diameter up to 60 cm. Yellowish-grey and orange coloured sediments of Crab Bed contain more carbonates (about 25%) than lower beds (POKORNÝ et al. 1983). Calcareous nannofossils and foraminifers are more abundant in these beds than in underlying beds (FRIČ 1893, ČECH & ŠVÁBENICKÁ 1992, ČECH et al. 1996, LEES 2008). The first occurrence of calcareous nannoplankton taxon *Micula staurophora* (GARDET, 1955) is known from the Gastropod Bed (*I. kleini* Inoceramid Zone), corresponding to the base of UC10 Zone (for details see ČECH & ŠVÁBENICKÁ 1992, LEES 2008). Yellowish-grey and orange coloured sediments of Crab Bed contain more carbonates (about 25%) than lower beds (POKORNÝ et al. 1983).

According to FRITSCH (1893, 1894) and FRITSCH & KAFKA (1887), fossil decapod remains are more abundant in claystones of the Crab Bed than in the Gastropod Bed. However, it does not have to be so. Many specimens, including *Ferroranina fritschi*, originally described from the Crab Bed were assignated by III carved in the matrix slab (means the 3rd layer of the outcrop from the bottom to the top, the lowermost Nucula Bed was marked as 0) and collectors thus signed finds from the Gastropod Bed, not from the Crab Bed. Currently, it is not able to determined from which of these two beds fossils originated because of the same character of sediment. So, the precise chronostratigraphic information of the sole specimen of *F. fritschi* is still needed, although a lower-middle Coniacian age of Březno Formation has been suggested for the species.

Material and methods

The decapod crustacean material is compacted in very fine-grained calcareous claystones, allowing preservation even of poorly calcified exoskeleton parts. Whereas lobsters and axiidean shrimps are often nearly complete with pleons and pereiopods; fossil crabs, except for *Polycnemidium* (REUSS, 1845) with unassociated chelae, are preserved only as dorsal parts of carapace lacking chelipeds or other appendages. It is also true for the sole specimen of *Ferroranina fritschi*. In spite of numerous visits to the locality during last five years, no other fossil representative of the studied species have been found.

Because of clayey character of sediment, it can not be use the standard procedure of ammonium chloride sublimate to achieve better contrast before photographing. Thus, photographs were taken using scanning electron microscope (SEM) Hitachi S-3700N in low vacuum at the National Museum in Prague. When using SEM, the specimen were left uncoated, hence the use of low vacuum. Series of photograps were assembled into final image using the computer freeware Microsoft Image Composite Editor 1.4.4.

The carapace terminology follows that of VAN BAKEL et al. (2012). Specimen was measured under the microphotography setting Olympus DP70. Measurements are given in millimetres (mm).

Systematic paleontology

Order Decapoda LATREILLE, 1802

Section Podotremata GUINOT, 1977

Subsection Raninoidia DE HAAN, 1839

Superfamily Palaeocorystoidea LŐRENTHEY *in* LŐRENTHEY & BEURLEN, 1929

Family Palaeocorystidae LŐRENTHEY *in* LŐRENTHEY & BEURLEN, 1929

Genus *Ferroranina* VAN BAKEL, GUINOT, ARTAL, FRAAIJE & JAGT, 2012

Type species. *Notopocorystes dichrous* STENZEL, 1945, by original designation.

Species included. *Ferroranina australis* (SECRETAN, 1964) [as *Notopocorystes*], *F. dichrous* (STENZEL, 1945) [as *Notopocorystes*], *F. fritschi* (GLAESSNER, 1929a) [as *Notopocorystes*], *F. tamilnadu* VAN BAKEL, GUINOT, ARTAL, FRAAIJE & JAGT, 2012.

Diagnosis. For a detailed diagnosis, reference is made to Van Bakel et al. (2012, p. 29)

Ferroranina fritschi (GLAESSNER, 1929)

(Figure 3)

1893 *Palaeocorystes*? sp. – FRITSCH, p. 105, fig. 133

1894 *Palaeocorystes*? sp. – FRITSCH, p. 101, fig. 133

1929a *Notopocorystes fritschi* GLAESSNER, p. 155, taf. 10. fig. 5

1929b *Notopocorystes fritschi* GLAESSNER, p. 276

1941 *Notopocorystes* (*Cretacoranina*) *fritschi* (GLAESSNER) – MERTIN, p. 239

1989 *Notopocorystes* (*Cretacoranina*) *fritschi* (GLAESSNER) – BERLUNG & FELDMANN, p. 72

1998 *Cretacoranina fritschi* (GLAESSNER) – TUCKER, p. 334, Table 4

2009 *Cretacoranina fritschi* (GLAESSNER) – WAUGH et al., p. 20, Table 1; p. 21, Table 2

2012 *Cretacoranina fritschi* (GLAESSNER) – VAN BAKEL et al., 19; p. 201, Appendix

2013 *Cretacoranina fritschi* (GLAESSNER) – KLOMPMAKER, Appendix A

2014 *Cretacoranina fritschi* (GLAESSNER) – KARASAWA et al., p. 24

2014 *Cretacoranina fritschi* (GLAESSNER) – HYŽNÝ et al., 248

Material. Single well-preserved dorsal carapace with cuticle, lacking chelipeds or other appendages from the lower-middle Coniacian at Březno. The specimen is FRITSCH's original (1893, 1894) deposited in the palaeontological collections at the National Museum in Prague, Czech Republic (NM O4296).

Diagnosis. Carapace of small size, elongated, subhexagonal in outline, widest at the third anterolateral spine, situated approximately one-third of total carapace length from front, dorsal surface convex in transverse cross section, weakly convex from front to posterior margin; front produced; axial carina absent, orbitofrontal margin wide; supraorbital margin with 2 fissures; anterolateral margin convex, with 4 short broad-based spines directed anteriorly, including epibranchial teeth; posterolateral margin nearly straight, narrowly rimmed; short, strongly concave posterior margin; dorsal surface with conspicuous division of anterior carapace portion along jagged line comprising 4 narrowly rounded lobes on each side; small tubercles on hepatic region; carapace regions poorly defined; cardiac grooves short, curved; carapace ornamentation typical for palaeocorystids with upright and fungiform nodes; upright nodes of variable sizes and density developed along carapace margins (outside the jagged line), density raises posteriorly (from about 40 nodes per mm^2 in frontal region to more than 70 nodes per mm^2 at the level of the third lobe); remaining dorsal surface (closed by jagged line) covered by dense mosaic of fungiform nodes, fungiform structure along the jagged line typically mosaic with closely packed, flat sided nodes; fungiform nodes in gastric and cardiac regions less densely spaced, not in contact with each others, circular in outline.

FIG. 3 NEAR HERE

Description. Carapace small (total length, from tip of rostrum to posterior margin, 10,3 mm), elongated; greatest width (7 mm) anterior of mid-line at level of epibranchial teeth (about one third of carapace length), weakly convex longitudinally, moderately so transversely; axial carina absent; front produced, rostrum extends well beyond orbits, with one pair of spines forming bifid termination and 2 strongly reduced well ornamented subdistal spines, longer than wide, with thin central spiny ridge extended to carapace, curved grooves between subdistal spines and central ridge smooth; fronto-orbital margin wide (7 mm including outer orbital spine), thin, convex; supraorbital margin with 3 elements, separated with 2 open fissures, outer fissure only partially preserved, inner widest anteriorly, slightly constricted posteriorly; element adjoining rostrum with short broad-based anterolaterally directed blunt spine at inner fissure, reaching the base of rostrum; second element wide, subquadrate (inner margin weakly convex, outer strongly convex, sigmoid), downturned, with pair of comparable spines (inner directed anteriorly, outer anterolaterally); third element slighlty broader than second, rectangular, with one most prominent broad-based spine at outer margin directed anteriorly; features of orbits and suborbital margins not observable; lateral margins downturned, anterolateral margin convex, with 4 short spines, which bases direct laterally and tips strongly turned anteriorly, including smaller epibranchial teeth; posterolateral margin nearly straight, narrowly rimmed, tapering to short, strongly concave posterior margin (just less than one third maximum width; 2,1 mm), almost smooth (only left and right side narrowly rimmed); dorsal surface with conspicuous division of anterior carapace portion along jagged line, delineating a lower-lying anterior portion, extending from root of rostrum to close to epibranchial tooth and then continues along posterolateral and posterior margin; jagged line comprising 4 narrowly rounded lobes on each side, first three lobes directed anteriorly, posteriormost strongly turns laterally, 4 pointed recesses, first three directed posteriorly, the outermost laterally (caused by the concavity of outer margin of the fourth lobe); anteriorly carapace with larger, well-spaced upright nodes of variable sizes; node tops are often abraded and broken with a central dark spot; posteriorly, starting with the third lobe, nodes more abundant along jagged line (in high density of about 70 per mm^2), apper in chains and not strictly upwards with direction follows the shape of lobes; hepatic region with small prominent tubercle; remaining dorsal surface (closed by jagged line) covered by fungiform nodes, fungiform structure along the jagged line dense mosaic with closely packed, flat sided nodes (each node in contact with a neighboring one); fungiform nodes in gastric and cardiac regions less densely spaced, not in contact with each others, circular in outline and often abraded leaving only laminated depressions with raised rims and central dark spots; carapace regions poorly defined; cervical groove only partially visible, V shaped; cardiac region narrow, bounded by short, curved branchiocardic grooves, more distinct than cervical groove. No sternal elements or chelae are preserved.

Occurrence. The occurrence of *Ferroranina fritschi* is so far limited to lower–middle Coniacian of the Březno Formation at the locality Březno, Czech Republic.

Remarks. The first report of Palaeocorystidae from the Bohemian Cretaceous Basin was reffered by FRITSCH (1893, 1894 in Czech) who shortly described and illustrated the new palaeocorystid crab [questionably named as *Palaeocorystes*? sp.] from the late Cretaceous of Březno locality. Later, GLAESSNER (1929a) revised the genus *Notopocorystes* MCCOY 1849 and named the new species *Notopocorystes fritschi* for the unique specimen from Březno. He also redrew the specimen, because animal restoration in paper by FRITSCH (1893: fig. 133, 1894: fig. 133) did not fully correspond with the original specimen, reconstruction was idealized and some features missing (i.e. cervical groove). Nevertheless, GLAESSNER's line drawing (1929a, taf. 10. fig. 5) is also inaccurate, because of lacking distinct trilobate post-frontal terrace preserved on the original material.

In 1941 MERTIN subdivided the genus *Notopocorystes* into three subspecies-*Notopocorystes, Cretacoranina* and *Eucorystes,* based upon surface ornamentation and aspect of the carapace groove patterns, and simultaneously included the Czech species *Notopocorystes fritschi* in the subgenus *Cretacoranina* [as *Notopocorystes* (*Cretacoranina*) *fritschi*]. Subsequently, GLAESSNER (1969) agreed with MERTIN and considered *Cretacoranina* to be a subgenus of *Notopocorystes*. Also both WRIGHT & COLLINS (1972) and COLLINS (1996) argued that the differences in ornamentation and other features (such character of frontal area) among *Notopocorystes*, *Eucorystes* and *Cretacoranina* were gradational and that they inclined to adopt *Cretacoranina* as subgenus within *Notopocorystes*. TUCKER (1998) elevated these three subgerenera to generic level distinguishable upon the basis of ornamentation and character of dorsal carapace (number and character of frontal and lateral spines, presence of longitudinal carina and depressed frontal area and the smoothness of the carapace). Recently, VAN BAKEL et al. (2012) stated that the generic definition of *Cretacoranina* is too wide and erected new genera *Joeranina* and *Ferroranina* on the basis of dorsal carapace and sternal features (VAN BAKEL et al. 2012, table 4) and subdivided *Cretacoranina* sensu lato into *Cretacoranina* emend., *Joeranina* and *Ferroranina*.

Depending on these new data of Palaeocorystoidea, raninid specimen from Březno is revised herein. Although some features of the specimen indeed correspond to *Cretacoranina* (typical fungiform nodes on dorsal carapace or absence of medial carina) these characters are however typical for both *Cretacoranina* and *Ferroranina*. Nevertheless, several other characters support assignment of the present species to *Ferroranina*, rather than to *Cretacoranina* or any other palaeocorystid genus: frontal furrows on rostrum that slightly extended onto carapace, presence of distinct trilobate post-frontal terrace and medially defined cervical groove with V-shaped medial portion (see VAN BAKEL et al. 2012). All these carapace details clearly point to an identification of the material as a member of *Ferroranina*.

Ferroranina fritschi with its 10,3 mm in length and 7 mm in width is smaller-sized than other *Ferroranina* species; *F. dichrous* and *F. australis* are approximately three times wider and longer (more than 30 mm in length and 20 mm in width) and *F. tamilnadu* is even almost six times longer (59 mm excluding rostrum, see more in VAN BAKEL et al. 2012) than the studied specimen. In addition to its small size, *F. fritschi* differs clearly from others in having broader and less prominent elements of orbitofrontal margin (fissures are shorter), longer spine on the third, outer element of orbitofrontal margin, different course of jagged line on carapace, more concave posterolateral margin and in absence of medial carina.

Morphologically closest to *F. fritschi* is *F. australis*. Both have rounded orbitofrontal margin, comparatively lenght and same number of anterolateral spines, but that of *F. fritschi* directed more anteriorly. *F. australis* is more elongated (width at level of epibranchial teeth c. 78 % length excluding rostrum in *F. australis* compared to c. 82 % in *F. fritschi*) with two small pits just behind the furrows of the rostrum (not seen in *F. fritschi*) and has less distinct recesses between lobes of jagged line.

F. fritschi has a similar rostrum structure in common with *F. dichrous*, but that of *F. fritschi* has more prominent and rather anteriorly directed rostral spines. There are also differences in number and character of anterolateral spines. *F. dichrous* has developed a pair of small epibranchial spines which are not seen in *F. fritschi* and possesses more laterally directed anterolateral spines. Moreover *F. fritschi* differs from *F. dichrous* in having flatter and more elongated carapace.

Ferroranina tamilnadu differs from *F. fritschi* in number of anterolateral spines (*F. fritschi* lacks small epibranchial spines) and in narrower orbitofrontal margin. Both these species have similar shape of carapace and lack two small pits just behind the grooves of the rostrum. However, it can not be compare structures of rostrum, because that of the sole specimen of *F. tamilnadu* is broken off.

Finally, BERGLUND & FELDMANN (1989) claimed the close relative of *Notopocorystes* (*Cretacoaranina*) *fritschi* (here revised as *Ferroranina fritschi*) may have been *Rogueus orri* BERLUNG & FELDMANN, 1989. The comparison with *Rogueus orri* concentrated on „the strong similarity in morphology of the anterior margins and configuration of the sternal plastron“. VAN BAKEL et al. (2012) argued that the ventral characters of *Cretacoranina fritschi* (here *F. fritschi*) have never been described, nor illustrated. It is true, because only a single dorsal carapace of *F. fritschi* is available, no additional material with preserved ventral parts or appendages does exist. Moreover, the carapace of *F. fritschi* is typical for Palaeocorystidae (see above), that of *R. orri* for Lyreididae.

Discussion. The main interest of the present specimen lies in the fact that it constitutes one of the best-preserved fossil material of *Ferroranina*, and the sole known individual of the genus from Europe to date. The spatial and temporal range of the genus would be marked by the *F. dichrous* from the upper Cenomanian of Texas and Mexico and *F. tamilnadu* from the middle Cenomanian of India, and its last appearance of *F. australis* from the Campanian of Madagascar which appears to be the youngest known fossil member of the genus (VAN BAKEL et al. 2012). Thus the occurrence of *F. fritschi* in Coniacian rocks of the BCB extends the geographic range and Cretaceous occurence of the genus. However, despite its wide geographical range during Cretaceous, the number of species retain sporadic.

The presence of *F. fritschi* in the lower-middle Coniancian claystones of the BCB suggest that the genus may follow two different directions to Europe during the late Cretaceous; either eastward through the North Atlantic from Mexico or Texas, where *F. dichrous* was described in the upper Cenomanian sediments, or westward via the Tethys based on the occurence of *F. tamilnadu* from middle Cenomanian of India. Regarding decapod crustaceans from the BCB both these migration ways have been already described, e.g. transatlantic migration of brachyuran genus *Graptocarcinus* ROEMER, 1887 known from the Barremian to the late Maastrichtian strata of Texas, Mexico, England, Spain, the Czech Republic, Italy, France and the Netherlands (FRAAYE 1996b, JAGT et al. 2010, KOČOVÁ VESELSKÁ et al. 2014, HYŽNÝ & KROH 2015) as well as a migratory pathway via Tethys represented by lobster genus *Paraclythia* FRITSCH, 1877 which fossil record is restricted to the Turonian-Maastrichtian strata of Germany and the Czech Republic in central Europe and the Campanian sediments of northern Iran, where *Paraclytia* was able to spread through the shallow epicontinental sea (McCobb & Hairapetian 2009). Both migration routes were possible due to the proximity of the continents to one another during the late Cretaceous and the open communication among the basins during the late Cenomanian/early Turonian transgression (Fraaije 1996a, Schweitzer 2001, Feldmann & Schweitzer 2006, Fraaije et al. 2008, Vega et al. 2010).

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Captions

Fig. 1 Geographical position of studied locality Březno within the Bohemian Cretaceous Basin.

Fig. 2 Simplified stratigraphic section at Březno outcrop. 1 – dark calcareous claystones with thin intercalations of calcareous siltstones of the Teplice Formation, these sediments are accessible only when the water level is low, 2 – glauconitic calcareous clayey siltstones of the Rohatce Member (the Teplice Formation), 3 – calcareous claystones of the Březno Formation, 4 – calcareous claystones with abundant sphaerosiderite concretions.

Fig. 3 *Ferroranina fritschi* (GLAESSNER, 1929) from the lower-middle Coniacian of Březno. Fritsch's original NM O4296, deposited in the National Museum, Prague. A – dorsal view of carapace, B – detail of the groove pattern, C – detail of abraded fungiform nodes, leaving only circular laminated depressions with raised rims and central dark spots, D – orbitofrontal margin. Scale bars: A-B, D = 1 mm, C = 0,1 mm.

Fig. 1

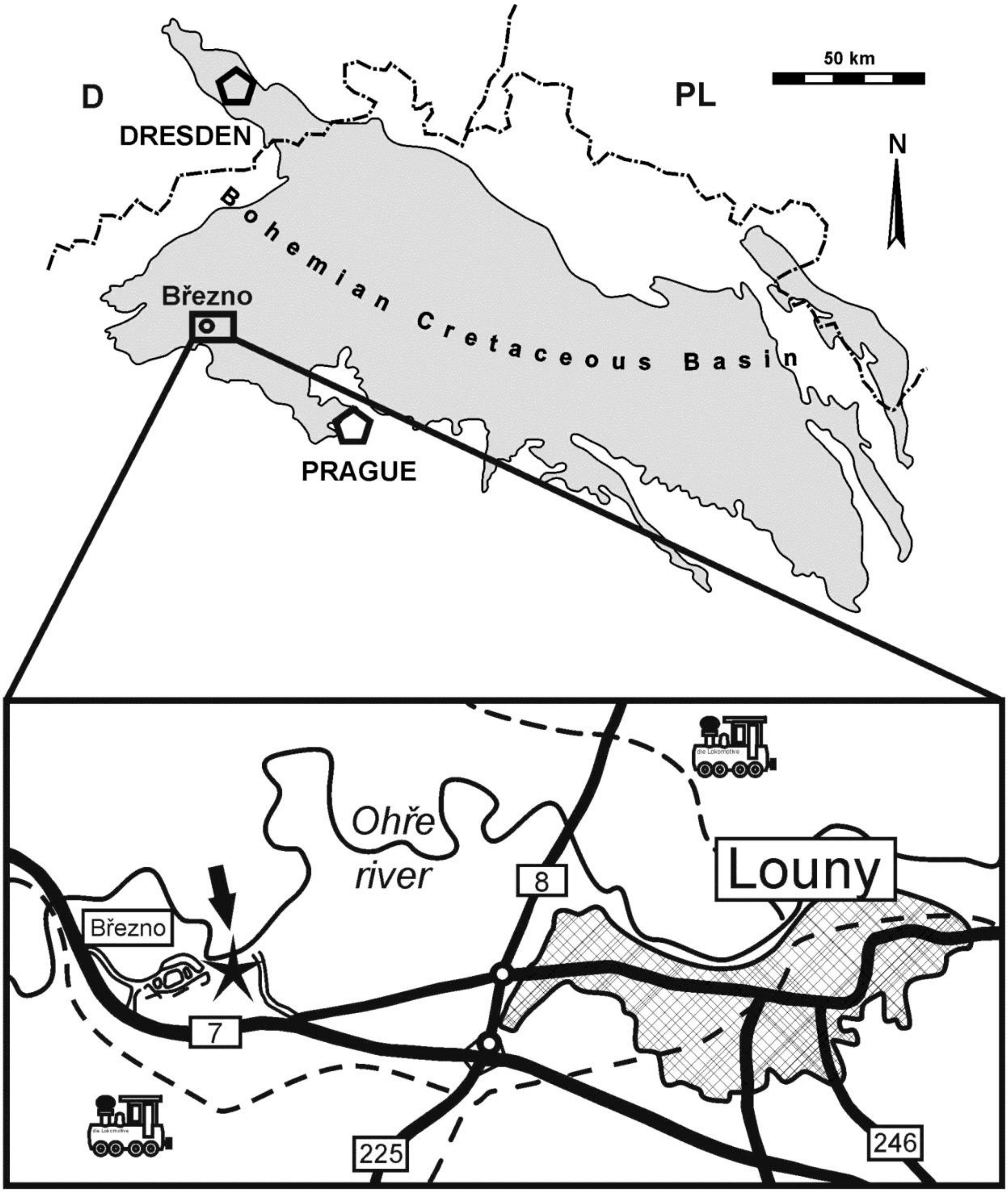
D
PL
DRESDEN
50 km
N
Bohemian Cretaceous Basin
Březno
PRAGUE
Ohře river
Louny
Březno
8
7
225
246
die Lokomotive
die Lokomotive

Fig. 2

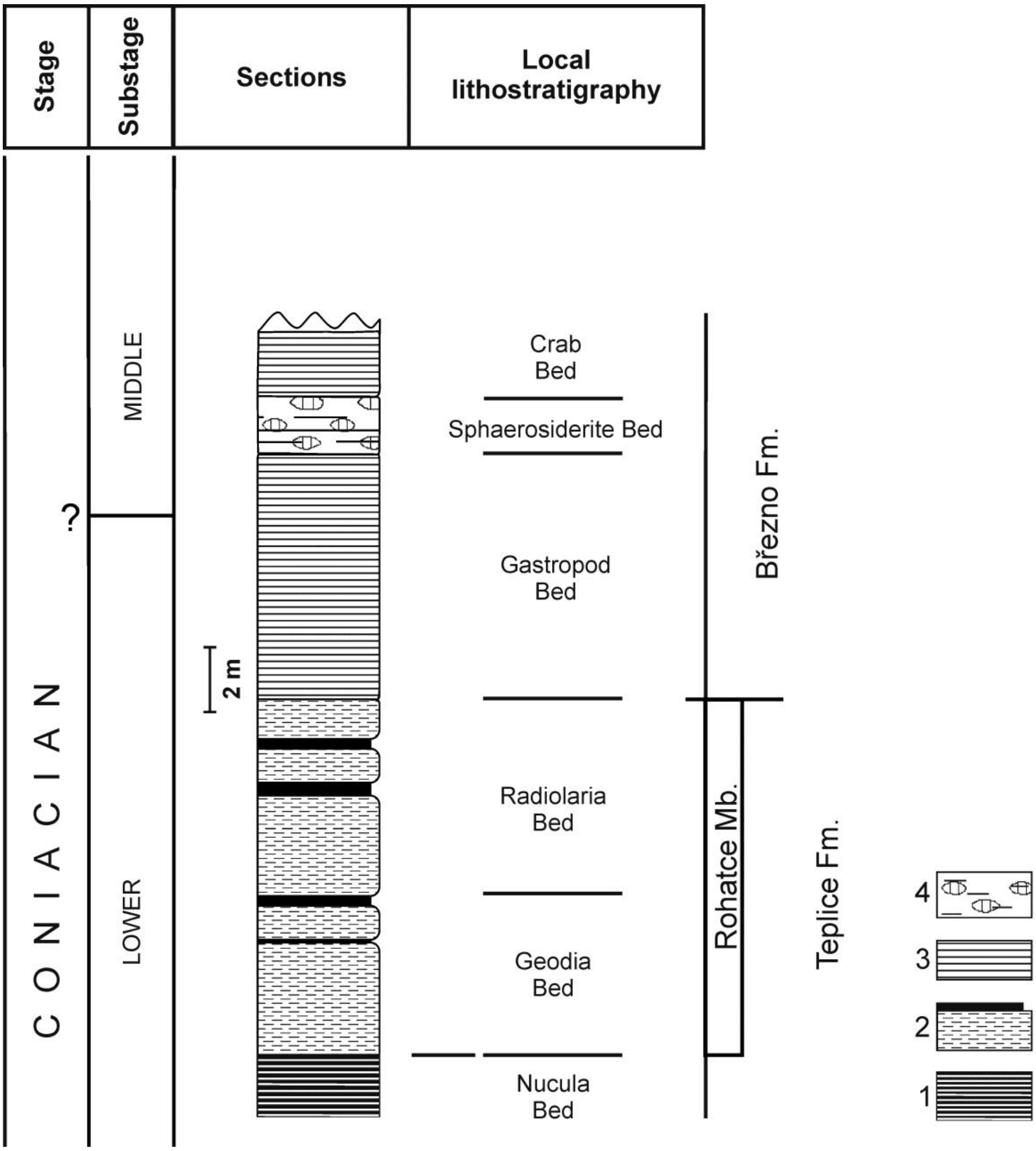
Stage
Substage
Sections
Local lithostratigraphy
CONIACIAN
MIDDLE
?
LOWER
2 m
Crab Bed
Sphaerosiderite Bed
Gastropod Bed
Radiolaria Bed
Geodia Bed
Nucula Bed
Březno Fm.
Rohatce Mb.
Teplice Fm.
4
3
2
1

Fig. 3