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Belemnites of the Bohemian Cretaceous Basin in a global context

MARTIN KOŠŤÁK[1], STANISLAV ČECH[2], BORIS EKRT[3], MARTIN MAZUCH[1],
FRANK WIESE[4], SILKE VOIGT[5], CHRISTOPHER J. WOOD[6]

[1]*Institute of Geology and Palaeontology, Charles University, Albertov 6, Prague 2, 128 43, Czech Republic,*
E-mail: kostak@natur.cuni.cz, mmazuch@centrum.cz
[2]*Czech Geological Survey, Klárov 3, 118 21, Czech Republic, E-mail: cech@cgu.cz*
[3]*National Museum, Václavské náměstí 68, Prague 1, 115 79, Czech Republic, E-mail: ekrtb@nm.cz*
[4]*Fachrichtung Paläontologie, FU Berlin, Malteserstr. 74-100, D-12249 Berlin, Germany, E-mail: frwiese@snafu.de*
[5] *Geological Institute, University of Cologne, Zülpicher Str. 49a, D-50764 Cologne, Germany, E-mail: silke.voigt@uni-koeln.de*
[6]*31 Periton Lane, Minehead, Somerset, TA24 8AQ, UK, chrisjwood@btopenworld.com*

ABSTRACT:

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Belemnites occur infrequently from the Upper Cenomanian through the Middle/Upper Coniacian in the Bohemian Cretaceous. Four species of the family Belemnitellidae PAVLOW, 1914 have been described so far. A typical boreal faunal incursion, represented by belemnites, happened five to six times in the Bohemian Cretaceous Basin (BCB). *Praeactinocamax plenus* immigrated during the Late Cenomanian *Metoicoceras geslinianum* ammonite Zone (*plenus* Event); there were two short-term incursions of *P. bohemicus* in the Late Turonian (*Subprionocyclus neptuni* to *Prionocyclus germari* ammonite zones) and an incursion of *Goniocamax lundgreni* in the late Early Coniacian (below and intra-*Cremnoceramus crassus* inoceramid Zone). A single belemnite fragment was recorded from the "Chlomek Beds"; Middle to Upper Coniacian. Bohemian Cretaceous belemnite systematics, palaeobiogeography (including palaeobiogeographic maps reconstructed), palaeoecology (including the relationship to other coleoid groups – i. e. teuthids) and stratigraphy are discussed.

Key words: Belemnites, Upper Cretaceous, Palaeobiogeography, Palaeoecology, Stratigraphy, Bohemian Cretaceous Basin.

INTRODUCTION

Upper Cretaceous belemnites are very rare in the Mid-European basins. They occur infrequently from the Cenomanian through the Upper Coniacian (FRIČ 1889, 1893, 1897, 1911; KLEIN 1966, KOŠŤÁK 1996, PETRASCHECK 1934, SVOBODA 1985, 1998, ZÁZVORKA 1929, 1930, 1965). During this interval, five to six short-term belemnite incursions can be seen in the Bohemian Cretaceous Basin (BCB), which will be described here in the context of their relationship to the global Upper Cretaceous belemnite assemblage.

Upper Cretaceous belemnites of the family Belemnitellidae PAVLOW 1914 were studied in detail by many authors in the nineteenth century (for example MILLER 1823; BLAINVILLE 1825-27; SCHLÜTER 1876; BAYLE 1879; STOLLEY 1897) and their modern taxonomy was established by ARKHANGELSKY (1912), PAVLOW (1914) and STOLLEY (1916) (see CHRISTENSEN 1970-2002 for bibliographic details). In the last decades, JELETZKY

(1946, 1950, 1961 and 1972 unpublished), Kongiel (1962), Ernst (1964a, 1968), Birkelund (1956, 1957) and especially Naidin (1952, 1964, 1969, 1978) contributed to the systematic description of this belemnite group. At the species level, Nikitin (1958), Makhlin (1965, 1973), Glazunova (1972), Ali-Zade (1972), Marcinowski (1972), Marcinowski & *al.* (1996), Seibertz & Spaeth (1995), Cobban (1991), Košťák (1996, in prep.), and Košťák & Pavliš (1997) presented modern taxonomic overviews, and especially Christensen (papers from 1970 – 2002) established the basis of contemporary belemnitellid nomenclature with a review of all taxa known so far.

In the BCB, research on belemnitellids started with Frič (in Fritsch & Schloenbach 1872), who described and figured a single specimen of *Belemnites lanceolatus* Sowerby [= Cenomanian *Praeactinocamax plenus* (Blainville)] and two significantly different specimens of

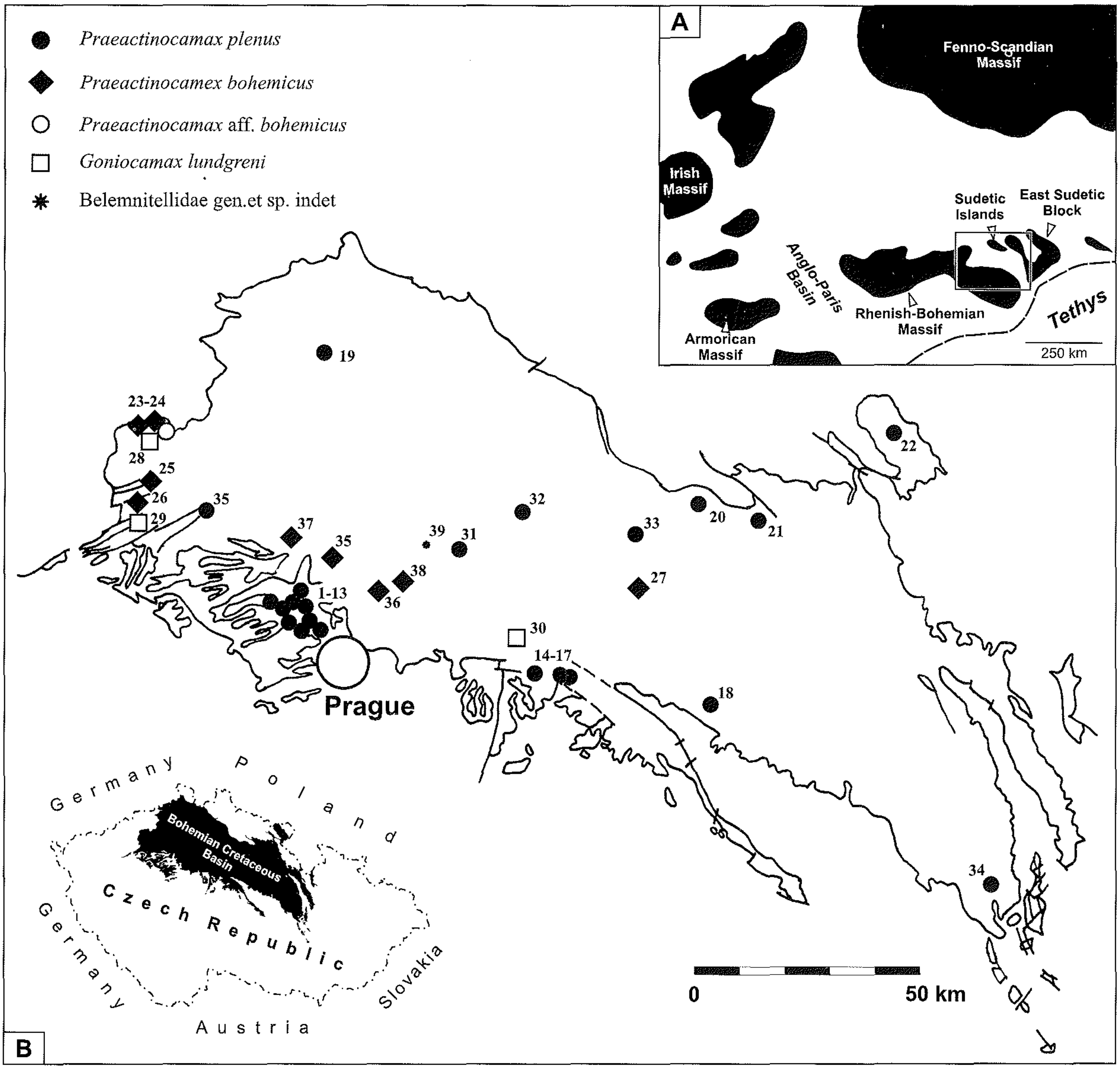

Fig. 1. **A.** Late Cretaceous (Cenomanian) palaeogeographic situation in Europe (black – lands; white - seas; modified after Diedrich 2001). **B.** Geographic position of belemnite localities in the Bohemian Cretaceous Basin: 1-22) *P. plenus*: 1-13) Kralupy n. Vltavou area: Kojetice, Neratovice, Kostelec n. Labem, Nelahozeves, Hled'sebe, Zlončice, Zibohlavy, Velká Ves, Otvovice, Kozomín, Odolená voda, Korycany, Úžice. 14-17) Kolín area: Plaňany, Kutná Hora, Nová Ves. 18) Reškovice. 19) Srnčí Ves. 20) Lázně Bělohrad (reworked guards). 21) Mezilečí. 22) Vápenka in the Police Basin (Intrasudetic Basin); 23-27) *P. bohemicus* and *P.* aff. *bohemicus*: 23) Lahošť. 24) Hudcov. 25) Úpohlavy. 26) Lenešice. 27) Lány na Důlku. 35) Slapy nad Bechlínem. 36) Hostín. 37) Nučničky. 38) Vtelno; 28-30) *G. lundgreni*: 28) Radovesice. 29) Březno. 30) Vrbice. 31-33) Borehole *P. plenus* records: 31) Kbl-2 Kbel (reworked guards). 32) KN-5 Sobčice (reworked guards). 33) DB-1 Dolní Bousov (including also boreholes MJ-3 Doubravice a KN-6 Polní Chrčice). 34) *P. plenus* Lower Turonian reworked guards – Březinka; 39) Belemnitellidae gen. et sp. indet. – Chlomek u Vinařic

Belemnites strehlensis FRIČ, one from Saxony and one from the BCB. The specimen from the BCB was redescribed by STOLLEY (1916), who distinguished it from the *B. strehlensis* from Saxony and made it the holotype of the new species *Actinocamax* [=*Praeactinocamax*] *bohemicus*. *P. strehlensis* has so far only been recorded from Saxony and is known only from FRIČ's drawing (FRITSCH & SCHLÖNBACH 1872, pl. 16, figs 10-12), as the original seems to be lost. Several specimens of *P. bohemicus* have been recorded from the Upper Turonian of the BCB (SOUKUP 1949, KOŠŤÁK 1996, KOŠŤÁK & WIESE 2002, WIESE & *al.* 2004). This species is known especially from NW Bohemia, but SOUKUP (1949) reported it additionally from eastern Bohemia (near the town of Pardubice). Critical reviews of this species were published by CHRISTENSEN (1982) and KOŠŤÁK (1996). KOŠŤÁK (1996) also described a related taxon, *P.* aff. *bohemicus*.

Cenomanian occurrences of *Praeactinocamax plenus* from the BCB were revised by ZÁZVORKA (1929, 1930, 1965), who considered it to be exclusively an Early Turonian taxon (see below). A complete revision of *P. plenus* from the BCB was given by KOŠŤÁK & PAVLIŠ (1997).

The occurrence of *Goniocamax lundgreni* (STOLLEY) in the Lower Coniacian of the BCB was recorded by KOŠŤÁK (1996).

SYSTEMATIC PALAEONTOLOGY

Class Cephalopoda CUVIER, 1795
Subclass Coleoidea BATHER, 1881
Order Belemnitida ZITTEL, 1895
Suborder Belemnopseina JELETZKY, 1965
Family Belemnitellidae PAVLOW, 1914

Genus *Praeactinocamax* NAIDIN, 1964

TYPE SPECIES: *Belemnites plenus* BLAINVILLE, 1825-1827, p. 376, pl. 11, fig. 3.

DIAGNOSIS: Guards of medium to large size (65-115 mm), predominantly lanceolate in dorsoventral view. Maximum lateral diameter situated mostly in one half of guard. Ventral side markedly flattened. Alveolar fracture low conical with central shallow pit. Cross-section of pseudoalveolus oval to triangular. Ventral furrow sometimes developed. Dorsolateral depressions and furrows usually fully developed. Striation usually present. Vascular imprints can be significant, granulation rarely present.

DISCUSSION: CHRISTENSEN & SCHULZ (1997) raised the subgenus *Praeactinocamax* NAIDIN, 1964 to generic rank.

OCCURRENCE: Cenomanian to the Lower Santonian; Europe – North European Region (Province) – Central European Subprovince and Baltoscania; East European Province – Russian Platform, Transcaspian area; western Siberia, Russian Arctic region; Tethyan Realm (SE France), Mediterranean Region (Turkmenistan, Tadzhikistan – Afghanistan borders); North American Province – North America, Greenland, Mexico.

Praeactinocamax plenus (BLAINVILLE, 1825)
(Pl. 1, Figs B-E)

REMARKS: For comprehensive synonymy see BÜLOW-TRÜMMER (1920), NAIDIN (1964) and CHRISTENSEN (1974).

SHORT DESCRIPTION: Guards are 55-92 mm long, the final shape of the guard is the result of dimensional changes during ontogeny. Juvenile specimens are slightly lanceolate in dorsoventral view and subcylindrical in lateral view. Adolescent specimens are slightly lanceolate to lanceolate in dorsoventral view and slightly lanceolate to subcylindrical in lateral view. The maximum lateral diameter is located between one half and one third of the length of the guard from the apex. Guards are ventrally flattened. The alveolar fracture is low-conical, with a shallow central pit. The cross-section is oval to slightly triangular at the alveolar fracture area, with concentric and radial structures present. The surface of the guard is smooth, with dorsolateral depressions and double furrows developed. Striation occurs in some specimens. The apex is central, with an angle between 30° to 40°. A ventral furrow can occur; a mucro is developed in some stouter specimens.

AFFINITIES AND REMARKS: *P. plenus* is considered to be a descendant of *P. primus* (ARKHANGELSKY, 1912). Juvenile specimens of *P. plenus* are almost identical to *P. primus*. Adult populations of *P. plenus* differ from *P. primus* in their statistically significantly larger sizes and thicker guards.

P. sozhensis (MAKHLIN, 1973) from the Late Cenomanian – Early Turonian, C/T boundary interval of the Central Russian Subprovince is similar to *P. plenus* in its size and, to some extent, in the shape of the guard. However, it differs from the latter in the absence of ventral flattening and in the more elongated growth during ontogeny. In addition, the anterior part is only poorly calcified and striations occur. The Lower Turonian *P. triangulus* (NAIDIN, 1964) is somewhat similar to *P. plenus* and was considered as a subspecies of *P. plenus* (*P. plenus triangulus* NAIDIN, 1964) (NAIDIN 1964, CHRISTENSEN 1974). However, it differs from *P. plenus* in its different ontogeny, its different guard shape and especially in its relatively deep, up to 6 mm, triangular pseudoalveolus, the latter being missing in *P. plenus* (see also NAIDIN 1964, KOŠŤÁK & PAVLIŠ 1997). It is therefore considered to be an independent species.

P. contractus (NAIDIN, 1964) show some morphological overlap with stout specimens of *P. plenus*, but differs from *P. plenus* in having a shorter and stouter guard and a poorly calcified anterior part. *P. contractus* has no pseudoalveolus in contrast to *P. triangulus* and *P.* sp. 1 (KOŠŤÁK, in prep.), guards of *P. contractus* are stouter and more massive. It slightly resembles *P. sozhensis* in the character of its alveolar fracture, but it differs in the shape and the size of the guard. NAIDIN (1964) described *P. contractus* as a subspecies of *P. plenus* (*P. plenus contractus*) on the base of a single complete specimen from the lower Turonian of the Cherkassy region, Ukraine. CHRISTENSEN (1974) synonymized this subspecies with *P. plenus* and did not mention it in his later papers; however, his biometrical analysis did not support this interpretation.

KOŠŤÁK (in KOŠŤÁK & PAVLIŠ 1997) reopened this question and pointed to the need for a revision of *P. plenus* and its possible subspecies (*P. plenus triangulus*, *P. plenus contractus*, *P. plenus crassus* NAIDIN). This revision was carried out in 1998-2002 by one of the authors (KOŠŤÁK), during which time nine additional specimens of *P. contractus* were discovered in the D. P. NAIDIN collection from the Central Russian Subprovince. The material shows the morphological stability of *P. contractus* and the well defined, constant differences from *P. plenus*. *P. contractus* is therefore considered to represent an independent species. In addition, both forms are stratigraphically well separated: *P. plenus* occurs in the Upper Cenomanian, while *P. contractus* is an exclusively Lower Turonian taxon. *P. plenus crassus* has recently been synonymized with other species (KOŠŤÁK, in prep.)

Middle to Upper Turonian specimens of *P. planus* (MAKHLIN 1965) from the East European palaeobiogeographical Province (EEP – see NAIDIN & KOŠŤÁK 2000; KOŠŤÁK & WIESE 2002; KOŠŤÁK in prep.) greatly resemble *P. plenus*. *P. planus* is considered to be a descendant of *P. plenus* (KOŠŤÁK, in prep). In the absence of transitional taxa in the Late Cenomanian through late Middle Turonian interval, there is no evidence of a continous *P. plenus* - *P. planus* evolutionary lineage; however, the morphological similarities between these two stratigraphically separate species are striking. *P. planus* is an endemic species surviving only in the East European Province (Central Russian Subprovince) (see section on palaeobiogeography of this paper).

A few similar species of *Praeactinocamax* have been found in the Turonian of the North American palaeobiogeographical Province (NAP – see JELETZKY 1946-1972, COBBAN 1991, CHRISTENSEN 1997). Their origin is unknown but certain morphological similarities, especially in the alveolar part of the guard, suggest that they could have been derived from the *primus/plenus* group.

OCCURRENCE: Outside Europe *Praeactinocamax plenus* occurs 1.5 metres above the local base of the Upper Cenomanian of the Mangyshlak peninsula, northwest Kazakhstan, (Koksyrtau-Aksyrtau section, bed 24 of MARCINOWSKI & *al.* 1996); it is absent from the overlying bed 25 and the terminal Cenomanian *Neocardioceras juddii* Zone (bed 26). Reported Lower Turonian occurrences of *P. plenus* from Russian and adjacent areas (NAIDIN 1964) have been reassessed and can be referred to other belemnitellid species (KOŠŤÁK 2003a; in prep). Unpublished records from the Central Asian Province (S Turkmenistan, Tadzhikistan – Afghanistan borders) are imprecisely assigned to the Upper Cenomanian.

According to CHRISTENSEN (1992), the stratigraphic range of *P. plenus* in NW Europe falls in the upper part of the *Metoicoceras geslinianum* ammonite Zone. In the Anglo-Paris Basin, *P. plenus* occurs in beds 4-6 of the Plenus Marls, being particularly common in bed 4, with a single unique record from Bed 8 (GALE & CHRISTENSEN 1996, fig. 4). Oxygen stable isotope data ($\delta^{18}O$) from Folkestone indicate a significant fall in temperature at this level, which GALE & CHRISTENSEN (1996) termed the Plenus Cold Event.

The Plenus Cold Event was also reported from the Tethyan Realm, from Les Lattes in the Alpes de Haute-Provence, SE France (GALE & CHRISTENSEN 1996). Here, towards the eastern margin of the Vocontian Basin, a bed of glauconitic sandy silt within a succession of silty marls with calcareous concretions contained numerous guards of *P. plenus* and a diverse calcitic and aragonitic fauna that enabled correlation with Bed 4 of the the Plenus Marls in the marly chalk facies of the Anglo-Paris Basin (GALE & CHRISTENSEN 1996, fig. 3). It is noteworthy that all growth stages of *P. plenus* were represented, indicating that it was a breeding population.

The Plenus Cold Event has also been recorded from the Bohemian Cretaceous Basin (KOŠŤÁK & PAVLIŠ 1997). The event is represented here by the occurrence of elements of the faunal assemblage of the so-called "North Boreal Group" (JEFFERIES 1962) such as *Entolium orbiculare* (SOWERBY), *Aequipecten arlesiensis* WOODS and the serpulid *Hamulus* sp., in association with *Praeactinocamax plenus*. The well-documented increase in $\delta^{13}C$ values in the Late Cenomanian (ULIČNÝ & *al.* 1993) is also clearly marked in the BCB. Cenomanian carbon stable isotope and sequence stratigraphy for localities in the western and south central part of the BCB were presented in detail by ULIČNÝ & *al.* (1993); unfortunately, stratigraphically reliable records of *P. plenus* from the localities studied by them are lacking, except for one poorly preserved and probably reworked specimen from Velim-Nová Ves in the the Kolín area E of Prague (Text-fig. 1) (ÎÍTT 1997, pers. comm.).

SVOBODA (1989) established a lithostratigraphic framework for the Upper Cenomanian between the Kralupy n.Vltavou area (localities 1-13 in Text-fig. 1) and the Slaný area (about 20 km NW of Prague), comprising units A–F, in ascending order. The index ammonite *Metoicoceras geslinianum* occurs in unit D, E and F. However, due to an existing palaeorelief, these units are not developed throughout the area. Unit D is missing from the area between Kralupy n. Vltavou and Korycany. *Praeactinocamax plenus* is recorded exclusively from unit F, together with a bivalve assemblage: "*Chlamys nilssoni* (SOWERBY), *Tellina semicostata* (ROEMER), *Neithea notabilis* (MÜNSTER), *Amphidonte obliquata* (PULTENEY) and *Uchauxia chelloneixi* (BARROIS & GUERNE)" (SVOBODA 1998).

The serpulid *Hepteris (Hamulus) septemsulcata* (ROEMER) occurs together with *P. plenus* at the same level (unit F) as the index ammonite *Metoicoceras geslinianum* (e.g. at Odolená Voda and Kozomín in the Kralupy n.Vltavou area: SVOBODA 1985; KOŠŤÁK & PAVLIŠ 1997; SVOBODA 1998; Text-fig. 2). The marls containing this assemblage have a thickness of about 15-20 cm. This stratigraphical level in the Kralupy n.Vltavou area is characterized by the greatest abundance of indigenous *P. plenus*. Abundant, albeit reworked, guards are typical of nearshore localities in the Kralupy n.Vltavou vicinity (depositional settings over highs), the Kolín area east of Prague, and in eastern Bohemia (notably locality 34).

In the Kolín area (localities 14-17 in Text-fig 1), *P. plenus* occurs typically in nearshore facies. In the Plaňany working quarry, redeposited specimens are found in glauconitic organodetritic limestones with *Lopha diluviana* (LINNE) and indigenous specimens occur in the calcareous claystones (SVOBODA 1985b). The latter overlie coral-bearing limestones with *Inoceramus pictus* and *Schloenbachia varians trituberculata* (SOUKUP 1971).

The horizon with *P. plenus in situ* in unit F can be considered as the stratigraphical equivalent of Bed 4 of the Plenus Marls in the Anglo-Paris Basin. The establishment of a *Praeactinocamax plenus* Zone in the BCB may be possible in the near future, when the sections in question have been macrofaunally re-sampled in order to establish a precise biostratigraphic framework.

Siltstones in the BCB yielding *P. plenus* have previously been regarded as Early Turonian in age (*Actinocamax plenus* Subzone of the *Inoceramus labiatus* Zone), but this was based on a misidentification of the inoceramid fauna by ZÁZVORKA (1930) and DVOŘÁK (in TÁSLER & *al.* 1979), even though PETRASCHECK (1903) had already given a correct Cenomanian age.

In basinal siltstones of the central part of the BCB (boreholes 31-33 in Text-fig. 1), *P. plenus* occurs in association with *Inoceramus pictus* SOWERBY (KLEIN 1966) and *I. bohemicus* LEONHARDT (SVOBODA 1989). This association of *P. plenus* and *I. bohemicus* is also reported from the northwestern continuation of the BCB in Saxony (e.g. TRÖGER 1969, VOIGT & TRÖGER 1996). In the Dolní Bousov DB-1 borehole (locality 33 in Text-fig. 1) guards of *P. plenus* were found just above the disappearance of the planktonic foraminifer *Rotalipora cushmani*, and below a Turonian regional erosion surface (HRADECKÁ in ULIČNÝ & *al.* 1993; PRAŽÁK 1989). In the Cenomanian spiculitic opoka facies of the Intrasudetic basin in the NE part of the BCB (locality 22 in Text-fig. 1), *P. plenus* co-occurs with *I. pictus*, *I. bannewitzensis* TRÖGER and *I. bohemicus*; *Mytiloides hattini* ELDER (formerly reported as *Inoceramus labiatus* by DVOŘÁK in TÁSLER 1979) appears somewhat higher in the succession. However, in the tectonically active and uplifted source areas (West Sudetic Island in the N and the Îdárské vrchy high in the SE), the belemnites are found in a thin glauconitic bed with phosphatic nodules and abundant *Chondrites*, here just above the Turonian regional erosion surface (Text-fig. 2). In this bed, guards of *P. plenus* are commonly broken and co-occur with Early Turonian *Mytiloides kossmati* (HEINZ) and *M. goppelnensis* (BADILLET & SORNAY). The glauconitic bed is overlain by hemipelagic limestones and marlstones belonging to the *Mammites nodosoides* ammonite Zone and the *Helvetoglobotruncana helvetica* planktonic foraminifer Zone. Thus, erosion, reworking and stratigraphic condensation took place during regression and subsequent transgression, affecting the uppermost part of the *Metoicoceras geslinianum* to *Pseudaspidoceras flexuosum* ammonite zones in the BCB.

GEOGRAPHIC DISTRIBUTION: The geographic distribution of *P. plenus* (Text-fig. 6) is shifted towards the south compared to that of its ancestor *P. primus* (Text-fig. 5). It forms a narrower and more protracted belt, extending ca. 1000 km towards the east (Tadzhikistan – Afghanistan borders; NAIDIN, pers. comm.). The southernmost part of this belt also includes the northernmost parts of the Tethyan Realm, ranging from SE France, *via* the mid-European marginal shelf settings around the Bohemian Massif (Bavaria, Saxony, Bohemian Cretaceous Basin) and the Crimea (Ukraine) into regions of the Central Asian Province (S Turkmenistan, Tadzhikistan – Afghanistan borders) that were influenced by Tethyan water masses. The relationship to Bavarian occurrence is interesting. DACQUE (1939), DORN (1958) and SVOBODA (1985a) inferred a Cenomanian and Turonian marine connection between

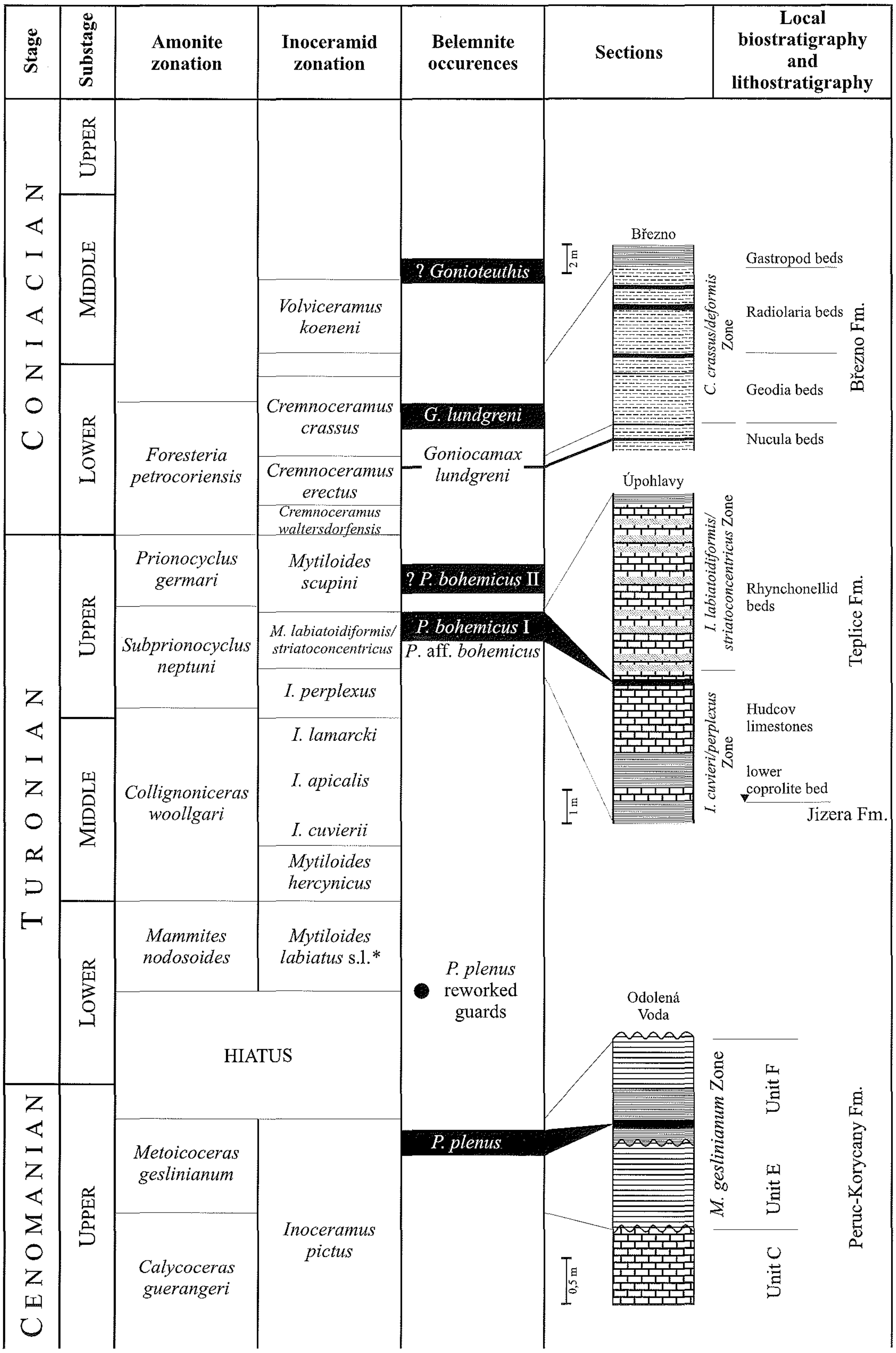

Fig. 2. Belemnite stratigraphic distribution in the Bohemian Cretaceous Basin: *P. plenus* Odolená Voda section after SVOBODA (1998); *P. bohemicus*, *P.* aff. *bohemicus* Úpohlavy section after WIESE & *al.* (2004); *G. lundgreni* Březno section after ČECH & *al.* (1996). * For the detailed *M. labiatus* s. l. Zone see WALASZCZYK & COBBAN (2000b)

the BCB and the so-called "Regensburge Kreide". According to them, *P. plenus*, a typical boreal species, immigrated here from the BCB. However, in the light of the discovery of a North Tethyan breeding population at Les Lattes in southern France (GALE & CHRISTENSEN 1996), the *P. plenus* incursion into Bavaria could equally well have happened by a southward incursion from the Anglo-Paris Basin. From Europe, northern occurrences are recorded from England, NW Germany, Poland and ?southern Scandinavia.

In the BCB, *P. plenus* inhabited preferentially near-shore settings, but rare occurrences from more distal basin parts are recorded from boreholes [Text-fig. 1, localities 31-33] (PRAŽÁK 1989).

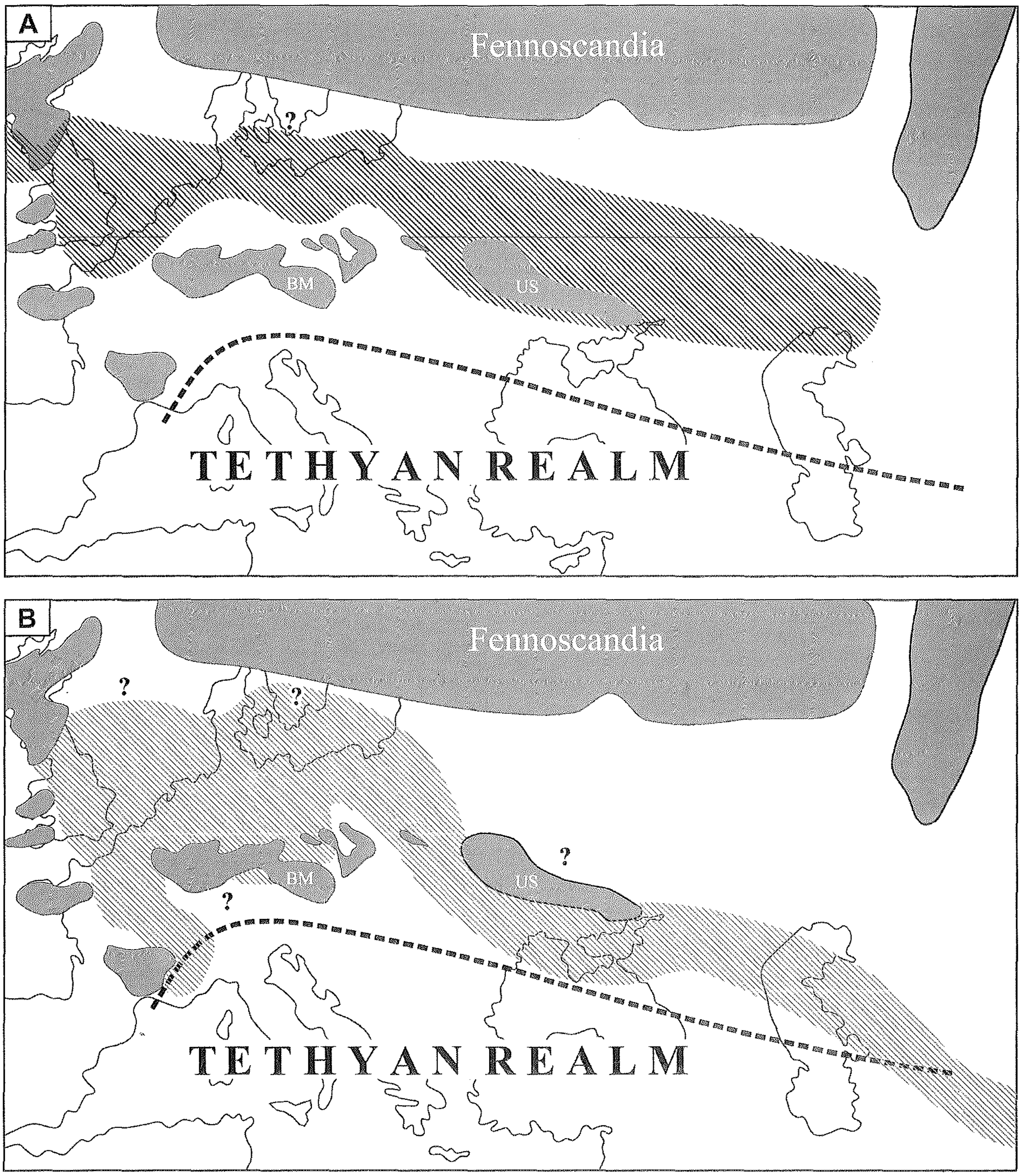

Fig. 3. **A**. Palaeobiogeographic distribution of *P. primus* (Middle Cenomanian) and **B**. *P. plenus* (Upper Cenomanian). Gray – lands, white – seas, hatch – belemnite distribution. BM – Bohemian massif, US – Ukrainian shield. (Palaeogeographic maps are modified after DIEDRICH 2001)

Praeactinocamax bohemicus (Stolley, 1916)
(Pl. 1, Fig. F)

TYPE: *Belemnites strehlensis* Fritsch & Schloenbach, 1872, pl. 16, fig. 17. It is stored in the National Museum Prague under the registration number O3217.

REMARKS: For a comprehensive synonymy see Christensen (1982) and Košťák (1996).

SHORT DESCRIPTION: The guards are of medium size, usually not exceeding 80 mm in length. The shape of the guard is cylindrical to subcylindrical in dorsoventral view and highly conical in lateral view.

	Guard characteristics	***P. bohemicus***	***P. ex gr. manitobensis***	***P. coronatus***
shape	large guards (80-110mm lenght)	-	+	-
	medium guards (65-80mm lenght)	+	+	+
	small guards (less than 65mm lenght)	-	-	-
	cigar shape in dorsoventral view	-	-	-
	lanceolate in dorzoventral view	-	-	-
	slightly lanceolate in dorzoventral view	+	+	-
	subcylindrical in dorzoventral view	+	+	+
	conical in dorzoventral view	-	-	-
	cigar shape in lateral view	-	-	-
	lanceolate in lateral view	-	-	-
	slightly lanceolate in lateral view	-	-	-
	subcylindrical in lateral view	+	+	-
	conical in lateral view	+	-	+
flattening	laterally flattened	-	-	-
	dorsally flattened	-	-	-
	ventrally flattened	+	-	+
alveolar fracture	high conical alveolar fracture	-	-	-
	low conical alveolar fracture	+	+	-
pseudoalveolus	shallow pseudoalveolus (less than 3mm)	+	+	-
	deep pseudoalveolus (more than 3mm)	-	-	+
cross section	oval cross section of alveolar fracture	-	-	+
	oval to triangular cross section of alveolar fracture	+	+	-
	triangular cross section of alveolar fracture	+	+	-
	circular cross section of alveolar fracture	-	-	-
conellae	conellae	-	-	-
BVF	bottom of ventral fissure	-	-	-
surface	dorsolateral furrows	-	+	+
	dorsolateral depressions	+	+	-
	granulation of the whole guard	+	+	-
	granulation of a part of the guard	+	+	-
	striation of the whole guard	-	-	-
	striation of a part of the guard	+	-	-
	vascular imprints frequent	-	-	-
	vascular imprints rare	-	-	-
mucro	mucro	-	-	-
furrows	ventral furrow	+	+	+

Fig. 4. Morphological similarities and differences between *P. manitobensis* (NAP – Middle Turonian), *P. bohemicus* (NEP – Upper Turonian) and *P. coronatus* (EEP – Middle/Upper Turonian)

AFFINITIES AND REMARKS: Morphologically, *P. bohemicus* shows the closest affinities to the North American group of *Praeactinocamax manitobensis/walkeri/sternbergi* (see JELETZKY 1950, 1961) with respect to the shape of the guard, the alveolar fracture and the cross-section at the alveolar end (see also CHRISTENSEN 1997 for discussion). *P. bohemicus* also slightly resembles the Greenland taxon, *P.* cf. *manitobensis* (CHRISTENSEN & HOCH 1983), so it could have been derived from the stock of the North American belemnite Province (also including Greenland). However, *P.* cf. *manitobensis* is a larger species.

There is no morphological similarity whatsoever with contemporaneous belemnite faunas from the Russian Platform (NAIDIN 1964). It must, therefore, be concluded that the origin of *P. bohemicus* cannot be located on the Russian Platform, which demands some comments on the spread of the taxon in time and space. Only a single Russian Turonian species, *P. coronatus* (MAKHLIN 1965), slightly resembles both *P. bohemicus* and *P.* aff. *bohemicus* (KOŠŤÁK 1996) in having a similar shape and size of the guard. However, the alveolar end differs significantly in the presence of a deep and well developed pseudoalveolus. The phylogeny of this taxon is unclear and it represents a very rare and endemic species of the CRS.

Morphological details on *P. bohemicus* and the differences from *P. manitobensis* (WHITEAVES, 1889) and *P. coronatus* are shown in Text-fig. 7.

P. bohemicus closely resembles *P. paderbornensis* (SCHLÜTER, 1894), known from a single incomplete specimen from the Lower Coniacian of the eastern part of the Münster Basin (CHRISTENSEN 1982, 1997a, b). These similarities relate particularly to the character of the alveolar fracture. The main difference is in the larger size of the guard: large specimens of *P. bohemicus* are not known.

OCCURRENCE: The holotype of *P. bohemicus* comes from Koštice, Czech Republic, and is of late *Subprionocyclus neptuni* ammonite zonal age. Time-equivalent occurrences from Saxony, Germany are several specimens from the Strehlen Limestone and one specimen from the correlative Limestone of Weinböhla, also of *neptuni* zonal age. Both limestones are stratigraphic equivalents of the upper part of the *Hyphantoceras* Event, an event that yielded a single fragment of *Praeactinocamax*? in Westphalia (METZDORF 1992).

In the BCB, five specimens of *P. bohemicus* are recorded from the limestones of Hudcov (Hundorf) and Lahošť (Loosch) and one specimen of *P.* aff. *bohemicus* is recorded from Hudcov (KOŠŤÁK 1996). All of these records are from the *neptuni* Zone. The lower part of the terminal Turonian *Prionocyclus germari* Zone of Lenešice near Louny has yielded one fragment of *P. bohemicus* and a pyritized alveolus (FRITSCH 1893). Another single find comes from the *germari* Zone of Lány na Důlku near Pardubice in East Bohemia (SOUKUP 1949). It is therefore probable that incursions of *P. bohemicus* into mid European basins took place at least twice during the Late Turonian, first in the *neptuni* Zone and then in the *germari* Zone. A specimen of *P. bohemicus* was collected recently *in situ* in the Úpohlavy working quarry (NW Bohemia), from the uppermost part of Xba sensu ZAHÁLKA (1900) (= Bed 4 – WIESE & *al.* 2004; in part of the *Hyphantoceras* Sequence *sensu* WIESE & *al.* (2004) (*S. neptuni* Zone) and thus within a transgressive setting. The specimen (WIESE & *al.* 2004, p. 333, fig. 4b) consists of the anterior third of the guard with a very well preserved alveolar part which is identical to that of the holotype. The granulation and fine striation on the surface of the guard are also identical to those of the holotype.

SOUKUP (1949) also reported finds from East Bohemia (Lány na Důlku near Pardubice (locality 27 in Text-fig. 1). According to SOUKUP (1949), "*P. strehlensis*" (= *P. bohemicus*) occurs together with the brachiopods *Terebratula semiglobosa* SOWERBY and *Crania ignabergensis* RETZIUS, the echinoids *Micraster cortestudinarium* (GOLDFUSS) and *Cardiaster planus* (MANTELL) [=*Plesiocorys plana* (MANTELL)]. Additional records of *P. bohemicus* are reported from Slapy nad Bechlínem and Hostín (localities 35 and 36 in Text-fig. 1) (SOUKUP 1949). There are also records from Nučničky near Lovosice (locality 37 in Text-fig. 1) and Bechlín near Lovosice (locality 35 in Text-fig. 1; ZAHÁLKA 1895) and Vtelno near Mělník (locality 38 in Text-fig. 1).

In the context of inoceramid stratigraphy, *P. bohemicus* is recorded from the higher Upper Turonian *Inoceramus perplexus* Zone (sensu WALASZCZYK & COBBAN 2000a) [*Inoceramus costellatus* s.l. Zone of ERNST & *al.* 1983], or assemblage zone 19 of TRÖGER (1987), in the lower part of the Teplice Formation (Hundorfer Schichten) in the BCB and in the "Strehlener Kalk" in Saxony. Rare occurrences of *P. bohemicus* also occur in slightly higher Upper Turonian sediments (basal *Mytiloides scupini* Zone) in the localities Lány na Důlku (locality 27)(E Bohemia) and Lenešice (locality 26) (W. Bohemia).

From Särdal (S Sweden), *P. bohemicus* was recorded together with the Late Turonian ammonite *Lewesiceras mantelli woodi* and a *Pseudopuzosia* sp. (BIRKELUND 1973, CHRISTENSEN 1982). This is the only other record of *P. bohemicus* outside the BCB and Germany apart from a juvenile belemnitellid referred to *P. bohemicus* from the early Middle Coniacian *Volviceramus koeneni* inoceramid Zone of Little Weighton (Yorkshire), in eastern England (CHRISTENSEN 1982). This juvenile guard has not been studied in this investigation but, to judge from the published illustrations, it could belong either to *Praeactinocamax* or to *Goniocamax*. The Middle Coniacian horizon of this specimen makes reference to *P. bohemicus* extremely unlikely in view of the fact that this species appears to be restricted to the Late Turonian *Subprionocyclus neptuni* and *Prionocyclus germari* zones

As already discussed by KOSTAK & WIESE (2002), the main occurrence of *P. bohemicus* can be shown to be stratigraphically limited to the uppermost *neptuni* Zone, linked to a transgressive pulse in Bohemia, Saxony and parts of NW Germany. This period fell into the later part of a significant Late Turonian cooling phase, characterized by a reorganization of faunal provinces and palaeoceanographic settings (VOIGT & WIESE 2000). In this context, the co-occurrence of cooling and transgression points to an immigration event resulting from a southward shift of cooler waters during transgression. The distribution in time of *P. bohemicus* and closely allied taxa suggests a migration from the US Western Interior *via* Greenland and Scandinavia into the the Central European shelf seas. The relationship to the Siberian occurrences published by BARSKOV & *al.* (1997) as *Goniocamax* must be investigated further.

Praeactinocamax aff. *bohemicus* (STOLLEY, 1916)
(Pl. 1, Fig. F)

1996. *Praeactinocamax* aff. *bohemicus*; KOŠŤÁK, p. 100-101, pl. 1, fig. 4.

SHORT DESCRIPTION: The guard is slightly lanceolate in dorsoventral view and highly conical in lateral view. The alveolar end cross section is oval, with a shallow pit in the centre. The ventral furrow is fully developed. Dorsolateral double furrow-like depressions are not visible. The surface of the guard is smooth and a mucro is not developed.

AFFINITIES AND REMARKS: *P.* aff. *bohemicus* shows the closest similarities to *P. bohemicus*. It differs in having a more lanceolate shape of the guard and in an oval cross-section of the anterior end. Due to the different cross section in the middle part of the guard and its more lanceolate shape, this taxon is referred here to *P.* aff. *bohemicus*. For affinities to other belemnitellid species see above (*P. bohemicus*).

OCCURRENCE: *P.* aff. *bohemicus* is recorded from the limestones of Hudcov (locality 24 in Text-fig. 1) and Lahošť (locality 23) in the BCB (the exact horizons are not known). These limestones are stratigraphic equivalents of the sections quarried today and exposed in the Úpohlavy working quarry (locality 23) (Xba of ZAHALKA 1900; uppermost Bed 4 of WIESE & *al.* 2004) [*Subprionocyclus neptuni* ammonite Zone, *Mytiloides labiatoidiformis/striatoconcentricus* inoceramid Zone]

Genus *Goniocamax* NAIDIN, 1964

TYPE SPECIES: *Actinocamax lundgreni* STOLLEY, 1897, p. 285, pl. 3, figs 16-20.

DIAGNOSIS: Guards from 50-60 to 80-95 mm long, lanceolate in dorsoventral view and in lateral view. Ventral side markedly flattened. Pseudoalveolus relatively deep – 1/5 to 1/7 of total length of guard. Cross-section triangularly oval to oval. Schatzky distance (SD) greater than 2 - 4 mm; angle between bottom of ventral fissure (BVF) and wall of pseudoalveolus (α_2) 30°-50°; alveolar angle (α_1 less than 30°. Dorsolateral depressions and double furrows fully developed. Striation usually present and well marked. Vascular imprints apparent.

DISCUSSION: CHRISTENSEN & SCHULZ (1997) raised the subgenus *Goniocamax* NAIDIN, 1964, of *Gonioteuthis* BAYLE, 1879, to the rank of a genus and gave its range as from the base of the Coniacian into the Lower Santonian. The two Turonian taxa from the Russian Platform, *G. intermedius* (ARKHANGELSKY) and *G. surensis* (NAIDIN), were excluded by them from *Goniocamax* due to the absence of a bottom of ventral fissure, and included in *Praeactinocamax* NAIDIN (CHRISTENSEN & SCHULZ 1997). However, the absence of this morphological character could be the result of very poor calcification of the adoral part. KOŠŤÁK (in prep.) recommended that the "primitive" taxa, *G. intermedius* and *G. surensis*, be included in *Goniocamax* because of the marked morphological similarities with *G. lundgreni* (overall shape and size of the guard, similar character of anterior end), albeit both taxa exhibited some transitional features that might merit separation at subgeneric level. The earliest record of "modern" *Goniocamax* is *G.* sp., which represents most probably a new species (KOŠŤÁK in prep.), described on the basis of four complete guards from Upper Turonian and basal Coniacian deposits of the Volga River Region. However, the total stratigraphic range of *Goniocamax*, including the "primitive" taxa, *G. intermedius* and *G. surensis*, extends down into the late Middle Turonian.

OCCURRENCE: East Europe: Russia – Volga River region (Ulyanovsk district, Kuybyshev district, Mordovska AR, Azovsk Sea region), western Siberia (Jenisey River), Kazakhstan – Ural-Emba district, Aral Lake, Mangyshlak peninsula), Belarussia (Mogilevsk district, Gomel district), NW Europe: Germany, Baltoscandia – Denmark (Bornholm), Central Europe – Czech Republic, Arctic area: ?Russia – Taymyr peninsula.

Goniocamax lundgreni (STOLLEY, 1897)
(Pl. 1, fig. A)

REMARKS: For a comprehensive synonymy see Košťák (1996).

SHORT DESCRIPTION: The guard is lanceolate in dorsoventral view and highly conical in lateral view. In ranges in length between 55 and 85 mm and is usually markedly flattened ventrally and slightly flattened dorsally. However, this area can also be slightly concave. The depth of the pseudoalveolus is less than 1/7 of the total length of the guard. The cross-section of the pseudoalve-

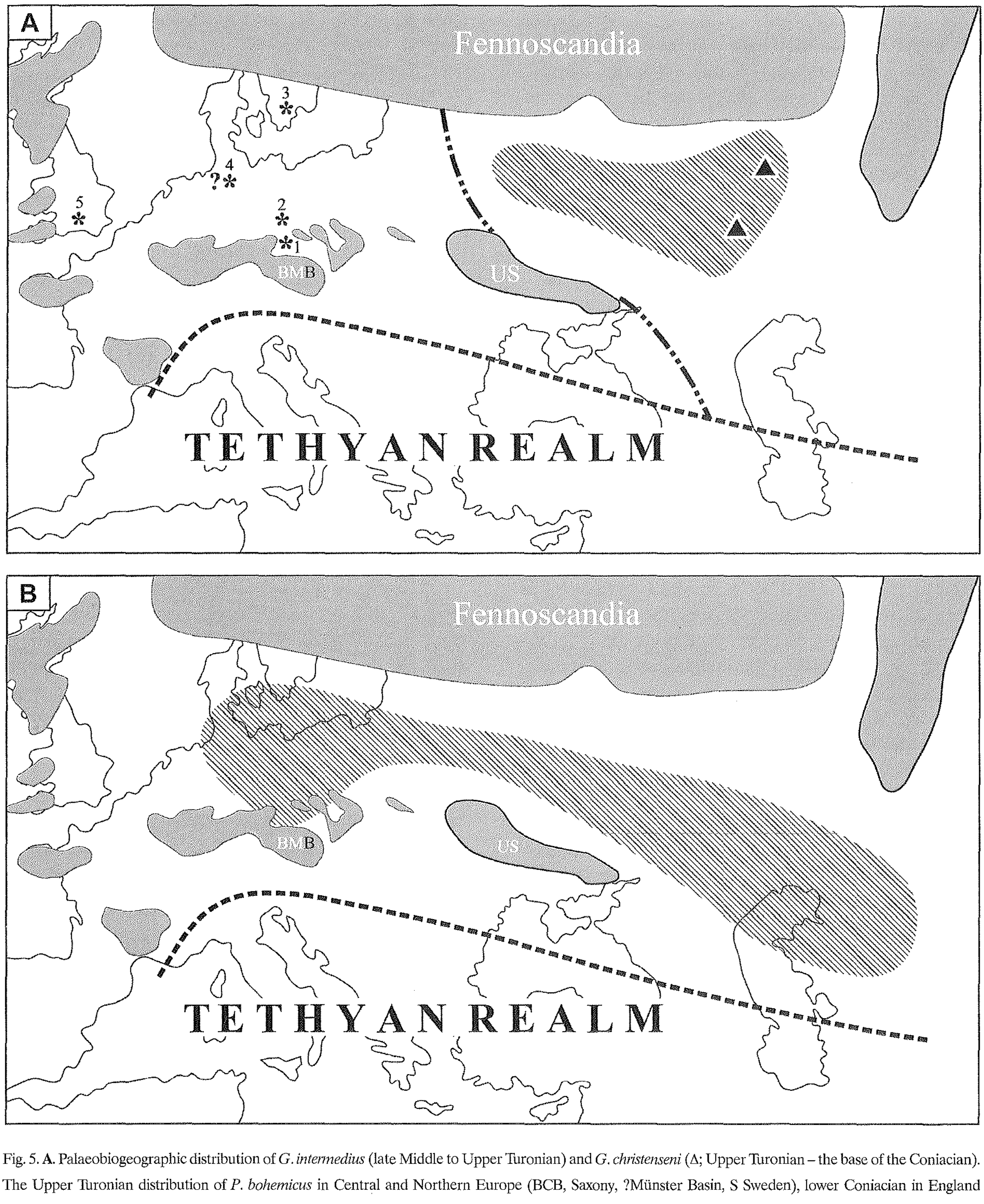

Fig. 5. **A.** Palaeobiogeographic distribution of *G. intermedius* (late Middle to Upper Turonian) and *G. christenseni* (Δ; Upper Turonian – the base of the Coniacian). The Upper Turonian distribution of *P. bohemicus* in Central and Northern Europe (BCB, Saxony, ?Münster Basin, S Sweden), lower Coniacian in England (Yorkshire). **B.** Palaeobiogeographic distribution of *G. lundgreni* s. l. (including all subspecies). The Lower Coniacian – the base of the Santonian (see Text). Gray – lands, white – seas, hatch – belemnite distribution. BM – Bohemian massif, US – Ukrainian shield. (Palaeogeographic maps are modified after Diedrich 2001)

olus at the alveolar end is pointed oval to subtriangular. Dorsolateral longitudinal depressions and double furrows are well developed. Prominent vascular imprints are apparent in the apical part. Longitudinal striation is visible, especially in the apical part of the dorsal side. A mucro is present.

AFFINITIES AND REMARKS: *G. lundgreni* resembles *Praeactinocamax matesovae* (NAIDIN, 1964) and, especially, *G. surensis* (NAIDIN, 1964) and *G. intermedius* (ARKHANGELSKY, 1912) in having a similar shape of the guard. *G. lundgreni* is almost identical to *G. intermedius* in all characters, with the exception of the alveolar end which is poorly calcified in *G. intermedius*.

CHRISTENSEN (1982) described a single specimen of *G. essenensis* from the Coniacian of the Münsterland Cretaceous Basin. It is almost identical to specimens of *G. lundgreni* from N Europe and from the BCB. CHRISTENSEN & SCHULZ (1997) and CHRISTENSEN (1997b) admitted the possibility that this species might be affiliated to *G. lundgreni*. However, because of the great similarity in both morphology and stratigraphical range of the two taxa, and the absence of additional material, it is recommended here that *G. essenensis* be synonymized provisionally with *G. lundgreni*.

OCCURRENCE: Due to some taxonomic uncertainties, (see above), we follow the stratigraphical interpretations given by CHRISTENSEN (1997a, b) and CHRISTENSEN & SCHULZ (1997), who stated that the total stratigraphical range of *G. lundgreni* in Northern Europe was from the base of the Coniacian to the middle Lower Santonian. The stratigraphical range of this species in the East European Subprovince is open to question. NAIDIN (1964) recorded four subspecies of *G. lundgreni*: *G. lundgreni lundgreni* (STOLLEY), *G. lundgreni excavata* (SINZOW), *G. lundgreni postexcavata* NAIDIN and *G. lundgreni uilicicus* (KOLTYPIN) from Coniacian – Early Santonian deposits of Belarus, Russia and Kazakhstan. These subspecies are very similar to each other and they could all be placed in synonymy. NAIDIN (1964) reported the first finds from the middle Coniacian (together with *Inoceramus involutus*), however some finds (i. e. *G. surensis*, see discussion above) suggest that the evolutionary lineage going to *lundgreni* began in the latest Middle Turonian.

G. lundgreni is reported to be an occasional immigrant into the BCB (KOŠŤÁK 1996; CHRISTENSEN 1997). However, only three specimens are known from the BCB, all from the Lower Coniacian. A complete specimen comes from Radovesice near Bílina (locality 28 in Text-fig 1), from pale marls containing a rich inoceramid fauna indicating the *Cremnoceramus crassus/deformis* inoceramid Zone (*sensu* WALASZCZYK & WOOD 1999). A determinable fragment has been recorded from Březno near Louny (locality 29 in Text-fig. 1), from the so-called "*Nucula* beds" (see also FRIČ 1894; ČECH & *al.* 1996) together with *C. waltersdorfensis* (ANDERT) and *C. erectus* (MEEK). Only a few metres above, *Cremnoceramus deformis crassus* was recorded (ČECH & ŠVÁBENICKÁ 1992; ČECH & *al.* 1996). The third find came from the Rohatce Member (Lower Coniacian) from the village of Vrbice near Poděbrady (locality 30 in Text-fig. 1).

A single indeterminate "*Actinocamax*" fragment is known from the Lower Coniacian of the Vienenburg Anticline, Lower Saxony, NW Germany (details in MORTIMORE & *al.* 1998). However, those authors' tentative determination of this fragment as *Praeactinocamax paderbornensis*? on purely stratigraphical grounds is open to question. The most important part of the guard, the anterior end, is not preserved. The Late Turonian through the Lower Coniacian is characterized by an extremely low diversity and abundance of *Actinocamax* (*Praeactinocamax*) in Central, West and Northwest Europe. The marked dorsal and ventral flattening exhibited by this guard fragment is seen in neither *P. bohemicus* (Upper Turonian-?lower Middle Coniacian) nor *P.* aff. *bohemicus* (Upper Turonian), and it is unknown in the problematic species *P. strehlensis* (?Upper Turonian) and *P. paderbornensis* (Lower Coniacian) Only the endemic species, *P. medwedicicus* (NAIDIN) (extremely rare in the Central Russian Subprovince), shows a similar flattening of the guard. However, that species is characterized by having a stouter guard. It is much more likely that the fragment from Lower Saxony belongs to some species of *Goniocamax*. The character of the flattening is similar to that of *G. lundgreni* and the stratigraphic level (*Cremnoceramus crassus/deformis* Zone) would also fit with occurrences of this species in the BCB.

OCCURRENCE: *G. lundgreni* is well known from northern Europe (NW Germany, Bornholm), Belarus (River Sozh), Russia (Volga river area), Kazakhstan (Mangyshlak peninsula, Ural-Emba district, Aral lake vicinity)

Belemnitellidae gen. et sp. indet

1872. *Belemnites Merceyi* MAYER; FRITSCH & SCHLOENBACH, p. 17.
1876. *Belemnites Merceyi*; SCHLÜTER, p. 7.
1897. *Belemnites Merceyi* MAYER; FRITSCH, p. 35.

DISCUSSION AND OCCURRENCE: FRIČ (in FRITSCH & SCHLOENBACH 1872) reported the find of a belemnite guard fragment from the so-called "Chlomek Beds" of Chlomek near Vinařice (locality 39 in Text-fig. 1)

(Middle/Upper Coniacian) as *Belemnites Merceyi* MAYER. The fragment was insufficiently complete for systematic determination, but FRIČ mentioned a granulated guard surface, providing at least one taxonomically indicative feature possibly suggestive of a belemnitellid. Unfortunately, FRIČ's specimen seems to be lost, since it has not been been found in the collections of the National Museum, Prague, which holds most of the fossils recorded by him.

There are only a few belemnitellids known from the Middle Coniacian to the Lower Santonian (see CHRISTENSEN 1997a, b, for details of the stratigraphical ranges). Middle to Upper Coniacian *Praeactinocamax* are represented by the two East European endemic species, *P. aralensis* (ARKHANGELSKY) and *P. mujnakensis* (NAIDIN) (however, the assignment of these species to *Praeactinocamax* is still open to question), one doubtful juvenile specimen of *P. bohemicus* from the early Middle Coniacian of England (Yorkshire) and *P. cobbani* CHRISTENSEN from the NAP. In addition to the above, there are *Actinocamax verus* MILLER, *Goniocamax lundgreni* and *G. birkelundae* (CHRISTENSEN & SCHULZ) from Bornholm. Of all these taxa, only *P. bohemicus* and *A. verus* are recorded as possessing the granulated guard surface mentioned above, however, the granulation is not so well developed in the latter species.

It is also possible that the fragment belongs to *Gonioteuthis* BAYLE, a typical representative of the NEP. Granulation is known in *Gonioteuthis praewestfalica* ERNST & SCHULZ 1974 and *Gonioteuthis westfalica* (SCHLÜTER, 1874). In *G. praewestfalica*, granulated specimens constitute less than than 10% of the population, while granulation is found in 50% of the population in *G. westfalica* (CHRISTENSEN 1997a, CHRISTENSEN & SCHULZ 1997). The granulation becomes a very conspicuous character in younger species (CHRISTENSEN 1997a). *G. praewestfalica* is the oldest species in the *Gonioteuthis* lineage and its stratigraphic range was estimated to be from the upper Middle Coniacian to the lower Lower Santonian. *Gonioteuthis westfalica* is a late Early Santonian – early Middle Santonian species (see CHRISTENSEN 1997a) and thus is significantly younger than the fragment from Chlomek.

Two *Praeactinocamax* species [*P. groenlandicus* (BIRKELUND 1956), *P.* aff. *groenlandicus* (BIRKELUND 1956)] were described from the Lower Santonian of central West Greenland (BIRKELUND 1956). Both taxa are characterized by granulated guards. These taxa are typical NAP inhabitants, and their incursion into Mid-European basins through the NEP belemnite province is highly improbable. Their stratigraphic ranges are also different.

Whichever genus this fragment from the Chlomek Beds belongs to – *Actinocamax*, *Praeactinocamax*, *Goniocamax* or *Gonioteuthis* – it represents a fifth to sixth pulse (Mid to Late Coniacian) of a southward belemnitellid incursion into the Mid-European Basins in the Late Cenomanian – Late Coniacian interval.

CENOMANIAN – EARLY CONIACIAN BELEMNITELLID PALAEOBIOGEOGRAPHY

For Late Cretaceous belemnites, CHRISTENSEN (1975, 1976, 1988, 1990b, 1993b, 1997a, b) developed a concept of palaeobiogeographic units (Realms, Provinces and Subprovinces). A South "Temperate" Realm was distinguished on the distribution of the family Dimitobelidae WHITEHOUSE, while a North "Temperate" Realm (Boreal) was characterized by the Belemnitellidae PAVLOW, the latter consisting of the North European Province (including the Central European Subprovince) and the North American Province (North America, Greenland) (CHRISTENSEN 1976). Belemnitellids from the North American Province (NAP) are represented by ?*Actinocamax* MILLER, *Praeactinocamax* NAIDIN and *Belemnitella* D'ORBIGNY. The North European Province (NEP) is characterized by *Belemnocamax* CRICK, *Actinocamax* MILLER, *Praeactinocamax* NAIDIN, *Goniocamax* NAIDIN, *Gonioteuthis* BAYLE, *Belemnellocamax* NAIDIN, *Belemnella* NOWAK (including three subgenera), *Belemnitella* D'ORBIGNY (CHRISTENSEN 1997a) and very rare *Fusiteuthis* KONGIEL.

CHRISTENSEN (1997a) established a further subdivision of the NEP into three subprovinces: the Central European, Central Russian and Baltoscandian subprovinces. Geographically, the NEP spreads from Northern Ireland in the west to the Ural Mountains area (across England, France, the Netherlands, Denmark, southern Sweden, Belgium, Germany, Poland, Lithuania, Belarus, Ukraine, Russia and Kazakhstan). The NEP partially overlaps in the south with the Tethyan biogeographic unit as recognized e.g. for bivalves (KAUFFMAN 1973). This is indicated by the southward extension of belemnitellid distribution into SE France (GALE & CHRISTENSEN 1996), the area W and S of Turkmenistan (NAIDIN 1964), the Tadzhikistan/Afghanistan border region, the Transcaspian area, western Siberia (Krasnoyarsk District – Makhlin MS, unpublished), and the Russian Arctic regions (Ob River estuary – NAIDIN, unpublished, Taymyr Region – NAIDIN & *al.* 1986; BARSKOV & *al.* 1997).

NAIDIN (1978) recommended the use of the term "European Palaeobiogeographic Region". Its northern parts include the central part of the Russian Platform, the Azov Sea area and SW Siberia. In the south, it includes the Carpathian areas, the Crimea, Caucasus, west middle Asia (Mangyshlak peninsula – NW Kazakhstan), Tuarkyr (W Turkmenistan) and the western Kopetdag (S Turkmenistan).

However, our data suggest that – based on the belemnitellid distribution – a redefinition of the eastern parts of the European Palaeobiogeographic Region (EPR) appears necessary for the latest Cenomanian to the Early Coniacian, as the eastern part of the EPR clearly shows an individual faunal character during that time. This area is named the East European Province herein (Text fig. 6b), and it is taken to also include the Central Russian Subprovince.

The European Palaeobiogegraphic Region (North European Province *sensu* CHRISTENSEN 1976)

This province includes the Central European Subprovince, Baltoscandia, the Central Russian Subprovince and the East European Province (persisting only during the latest Late Cenomanian to the beginning of the Coniacian – NAIDIN & KOŠŤÁK 2000).

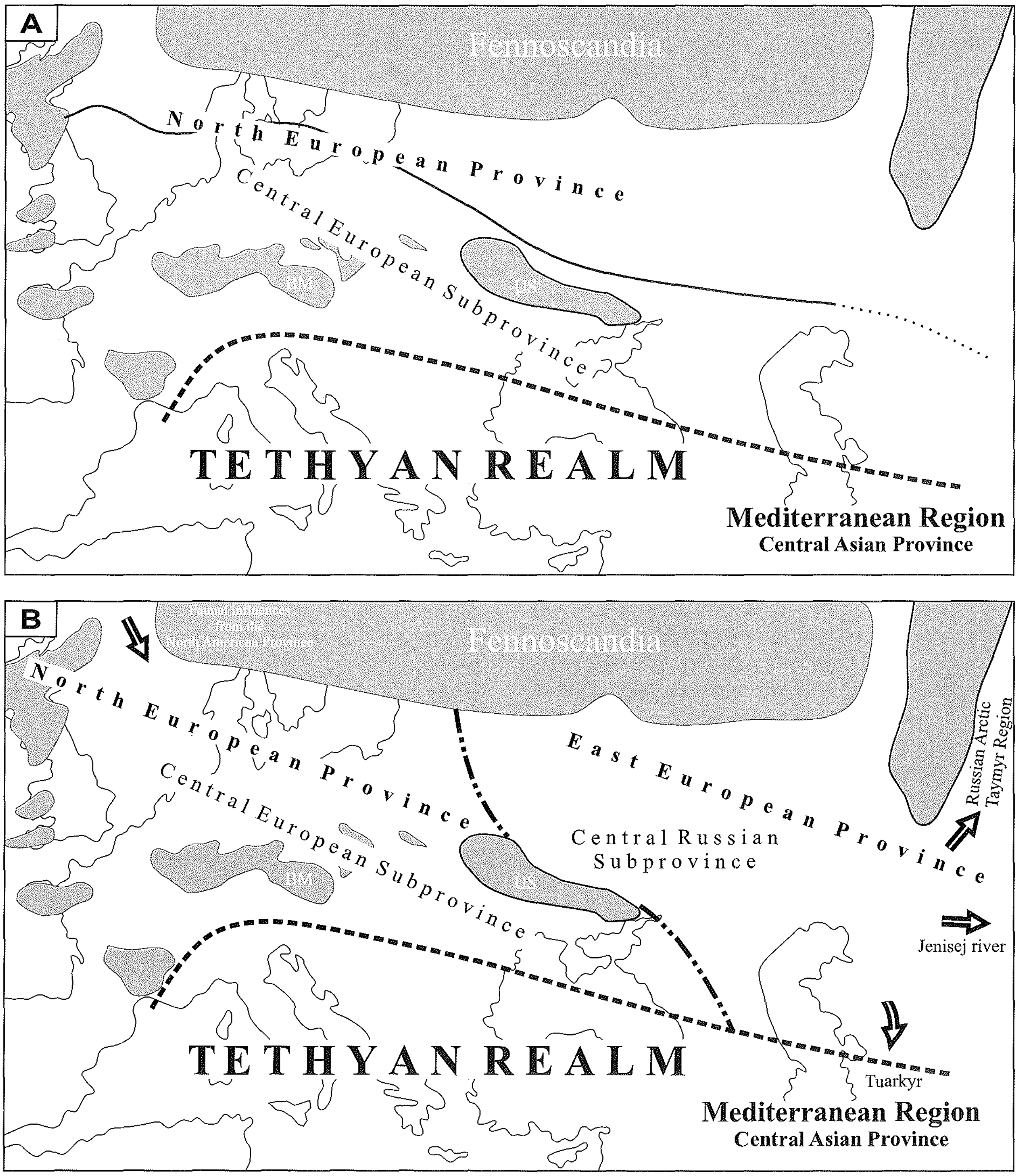

Fig. 6. **A.** The Cenomanian belemnitellid province distribution (after Christensen, 1976). **B.** The Turonian belemnitellid Province distribution.

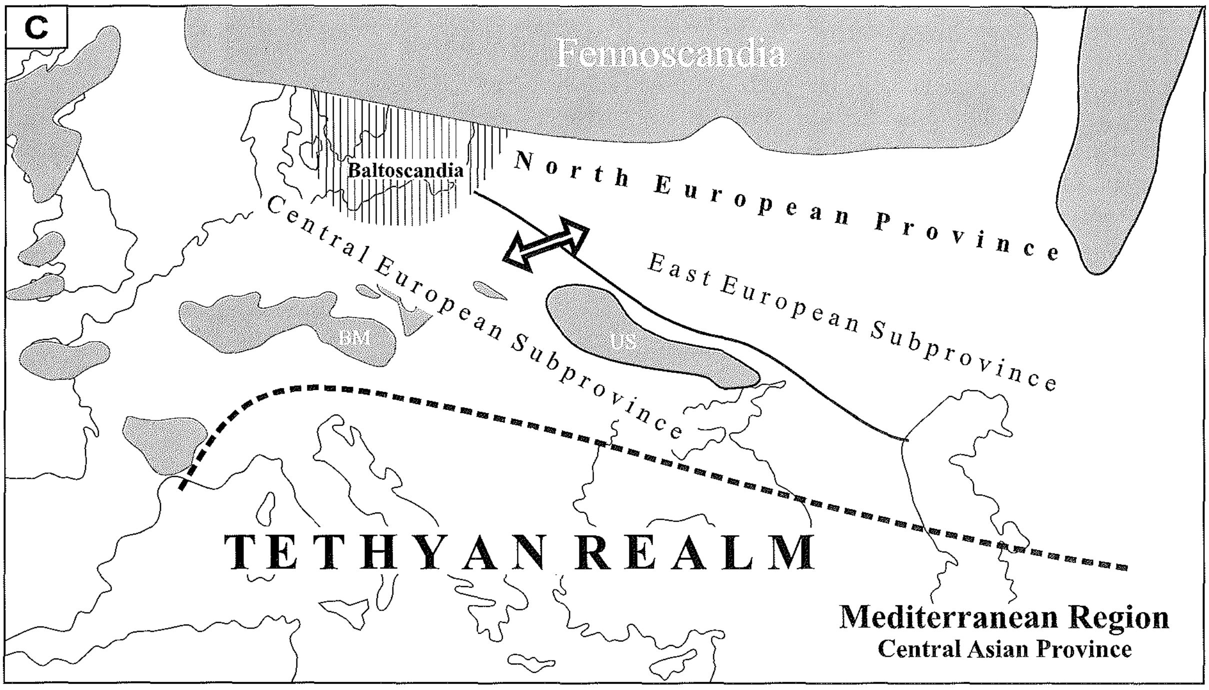

Fig. 6. C. The Coniacian belemnitellid province distribution (after CHRISTENSEN 1976 and 1997; NAIDIN & *al.* 1993). Gray – lands, white – seas, hatch – belemnite distribution. BM – Bohemian massif, US – Ukrainian shield. (Palaeogeographic maps are modified after DIEDRICH 2001)

The belemnitellids showed a cosmopolitan distribution from the mid- to the Late Cenomanian throughout the European Palaeobiogeographic Region (see Text-figs 3a, b; 6a). The first belemnitellid, *Praeactinocamax primus* (ARKHANGELSKY) is widespread from the north Caspian Sea area in the east to Northern Ireland in the west.

The low belemnitellid diversity in the Cenomanian-Turonian boundary interval may presumably be a result of the C/T boundary event. Only the highly endemic species, *P. sozhensis* (MAKHLIN), survived this time interval in the Central Russian Subprovince.

The eastern part of the European Palaeobiogeographic Region could be considered as an independent province (East European Province, EEP) with respect to the occurrence of 100% endemic taxa from the latest Cenomanian to the earliest Coniacian. This province existed for about 5 million years. The Central Russian Subprovince (CRS) is readily distinguishable from the Early Turonian to the earliest Coniacian. Communication with other areas was limited to the southeast (Transcaspian area), to western Siberia (Yenisey River), and to the north, to the Russian Arctic-Taymyr Region).

Praeactinocamax triangulus (NAIDIN) and *P. contractus* (NAIDIN) (see discussion above) are typical of the EEP in the Early Turonian. *P. triangulus* extends from Belarus in the west as far as Uzbekistan and western Turkmenistan in the southeast.

Goniocamax intermedius (ARKHANGELSKY) and *G.* sp. (KOŠŤÁK in prep.) are the late Middle Turonian (*G. intermedius*) through the earliest Coniacian (*G.* sp: late Turonian – earliest Coniacian) endemic taxa of the CRS.

The belemnitellids of the CRS (*Actinocamax, Praeactinocamax* and *Goniocamax* with 12 Turonian species) show high endemicity during the Turonian. They only rarely migrated into other regions. *Praeactinocamax matesovae* (NAIDIN) (or a similar species) occurs on the Mangyshlak peninsula (Caspian Sea, NW Kazakhstan). *Praeactinocamax* sp. is recently (KOŠŤÁK 2004a, in prep.) recorded from Tuarkyr (W Turkmenistan). Representatives of ?*Praeactinocamax* and *Goniocamax* were discovered in western Siberia (Jenisey River valley, Krasnoyarsk District – MAKHLIN, unpublished) and *Praeactinocamax* and ?*Goniocamax* are known from the Russian Arctic regions (Taymyr peninsula). Their occurrence probably proves the so-called North migration route (NAIDIN 1978; SAKS & NAL'NYAEVA 1975) across the Arctic circumpolar zones. This migration pathway connected the EEP with the North American Province during Turonian times (KOŠŤÁK & WIESE 2002).

The Central European Subprovince (CES) was completely isolated from the EEP during the whole Turonian (see Text fig. 6b) and no westward belemnite migrations from the EEP were documented. It is obvious that Late Turonian belemnites from the CES show significant similarities to Middle Turonian belemnites from the North American Province (including North America and Greenland.

The EEP and NEP ceased to exist at the beginning of the Coniacian (*G. lundgreni*, *?A. verus* ssp. – CHRISTENSEN & SCHULZ 1997) and fused into a single North European Province (= North European Region) (Text fig. 6c). Unhindered belemnite migration continued during the Coniacian, Santonian, Campanian and Maastrichtian: *Goniocamax, Gonioteuthis*, *Belemnitella*, *Belemnella* and the very rare *Fusiteuthis* had a geographically widespread occurrence.

The *Praeactinocamax plenus* occurrence in the BCB is an expression of the important Late Cenomanian belemnite event, the *plenus* event. It is recorded from the Tadzhikistan-Afghanistan borders in the east to England in the north-west. The origin of this belemnite can be located in NW Kazakhstan (NAIDIN 1964, MARCINOWSKI & *al.* 1996). The *plenus* incursion into the Central European basins, NW Europe and northern Tethys is isochronous (upper *Metoicoceras geslinianum* Zone; CHRISTENSEN & *al.* 1992, GALE & CHRISTENSEN 1996, KOŠŤÁK & PAVLIŠ 1997, SVOBODA 1998, see above).

The progressive spread of *Praeactinocamax* during the Turonian is interesting in a palaeogeographic context. Taxa morphologically very similar to *P. manitobensis* occur first during the Early Turonian in Mexico (SEIBERTZ & SPAETH 1995). Morphologically related forms such as *P. manitobensis*, *P. walkeri*, and *P. sternbergi* are recorded from the Middle Turonian of the North American Western Interior Seaway (WIS) (JELETZKY 1950), and one specimen was identified (JELETZKY 1950) as *P.* aff. *strehlensis,* a species which falls in the synonymy of *P. bohemicus* in this paper. Two specimens of *P.* aff. *manitobensis* have been described from Greenland, tentatively dated as Middle Turonian (CHRISTENSEN & HOCH 1983). From Särdal (S Sweden), *P. bohemicus* is recorded together with the Late Turonian ammonite *Lewesiceras mantelli woodi* (BIRKELUND 1973, CHRISTENSEN 1982). The numerous records from Germany and Czech Republic are all Late Turonian in age (see above, CHRISTENSEN 1982, KOŠŤÁK 1996).

Based on this stratigraphical and geographic distribution pattern, it seems reasonable to derive the European taxa from North America, indicating a NE-SW migration route from the WIS *via* arctic areas into the European shelf seas (KOŠŤÁK & WIESE 2002). This contradicts previous interpretations by JELETZKY (1950), BIRKELUND (1956) and CHRISTENSEN (1997), who all suggested an incursion of the *P. manitobensis/walkeri/sternbergi* group from Europe into the WIS. The idea of VOIGT & WIESE (2000), who suggested that the European *Praeactinocamax* came from the Russian Platform, is, therefore, also wrong: the North American/European representatives of *Praeactinocamax* show no relation to the belemnites of the Turonian of the East European belemnite province (NAIDIN 1964), which was characterized by endemic representatives of *Praeactinocamax*, subspecies of *Actinocamax* and by the first representatives of *Goniocamax.* No faunal exchange occurred during this time between Central, West and Northwest Europe and the Russian Platform, and the belemnite provinces were completely isolated from the Early Turonian to the Turonian/Coniacian boundary interval (NAIDIN & KOŠŤÁK 2000). The only migration trends observable within the Russian Platform were a southward migration to Turkmenistan and an eastward faunal shift to Siberia. BARSKOV & *al.* (1997) described microstructures of the *Goniocamax* rostrum from the Russian Arctic region (the Taymyr Region). However, this belemnitellid taxon from the Taymyr Region most probably belongs to *Praeactinocamax* (observation MK).

Goniocamax occurred for the first time in the late Middle to Late Turonian on the Russian Platform (*G. intermedius*, *G. surensis*, *G.* sp.) ZAKHAROV (2003, pers. comm.) also recorded rare Upper Turonian belemnitellids from the Taymyr Region, Piasina river). However, these belemnites still lack systematic treatment and their position within the Belemnitellidae and their palaeobiogeographic significance are still unclear. The strict faunistic barrier between the Russian Platform and the European shelf seas ceased to exist during Early Coniacian times as indicated by the successive westward spread of *Goniocamax lundgreni* and its rare incursion into the Central European basins. *G. lundgreni* is the first typical Early Coniacian species in the renascent NEP. It is possible that *G. lundgreni* occurred simultaneously (Early Coniacian) in both the CRS and NEP: *G. lundgreni* actually originated in the CRS and then migrated westward. However, the reported Early Coniacian age of the sediments with the earliest *G. lundgreni* on the Russian Platform requires to be re-investigated.

Middle/Late Coniacian belemnite incursions into Mid-European basins are virtually unknown. A single belemnite guard fragment was described by FRIČ (in FRITSCH & SCHLOENBACH 1872) from Middle-Upper Coniacian deposits ("Chlomek Beds") in the BCB but its systematic position within the Belemnitellidae remains unresolved (see above). The juvenile belemnite from the Middle Coniacian *koeneni* Zone in eastern England (CHRISTENSEN 1982) could also reflect a Middle Coniacian incursion of a taxon belonging to either *Praeactinocamax* or *Goniocamax.*

BELEMNITE PALAEOECOLOGY AND PALAEOBIOLOGY

The Upper Cretaceous Belemnitellidae PAVLOW constitute a very important nektonic group in the late Cretaceous shallow seas, which are restricted to the Northern Hemisphere.

Turonian belemnitellids are geographically and ethologically strongly related to settings close to ancient land massifs (NAIDIN 1969, CHRISTENSEN 1976). According to NAIDIN (1969, p. 271-272), Late Cretaceous belemnitellid distribution was controlled by shallower water conditions (with the depth not exceeding 100-200 m), and sea water temperatures ranging between 12.5-16.5°C (STEVENS 1965, NAIDIN 1969). This may have been the small ecological window within which belemnitellid evolution took place. VOIGT & *al.* (2001) established palaeotemperature on the basis of the oxygen stable isotopic composition of pelagic shark teeth, belemnites, brachiopods, inoceramids and oysters from Cenomanian-Turonian localities in Central and Western Europe. The palaeotemperatures calculated from the isotopic data from the shark teeth show a strong latitudinal palaeotemperature gradient, ranging from 10-19° C in Bohemia to 7-11° C in southern England ($\delta^{18}O_{phos}$ from 20.9 to 23.3‰ VSMOW; $\delta^{18}O_{w}$ = -1.0 ‰VSMOW for an ice-free world). Corresponding $\delta^{18}O_{calc}$ values of comparable belemnites are very similar (-0.63 to 0.66 ‰VPDB), representing temperatures between 9.5-14.5° C. Belemnites could have been a prey of sharks and they lived most of their lifetime in the same water mass. Both fossil groups were active swimmers and their oxygen isotopic composition should reflect a near-surface water signal (VOIGT & *al.* 2001).

Deeper water formed an additional barrier to belemnitellid distribution. The depths and high temperatures are the probable reasons for the absence of belemnitellids in the Tethyan Realm. The gradual Cenomanian transgression inundated large platform areas here, providing suitable conditions for belemnitellid evolution. However, the spread of deep oceanic areas prevented the migration of the belemnitellids, especially towards the south. The family Dimitobelidae WHITEAVES (derived from immigrants from the Northern Hemisphere) developed in the Southern Hemisphere as an independent belemnite fauna. Temperature, depth and physico-chemical factors of the sea-water, combined with ecological requirements caused their provinciality in the Late Cretaceous. Dependence on facies remains unproven (NAIDIN 1969, CHRISTENSEN 1976).

Generally, we can consider belemnites as inhabitants of shallower seas (nearshore areas) with mean temperature about 12°C. Higher abundance of guards (so called "battle fields") could be explained by an actualistic model in comparison with the ethology of Recent Coleoidea (common squid). Apparent mass mortality could have been the result of copulation (see also DOYLE & MAC DONALD 1993). Breeding sites were also visited by many predators (especially sharks), as suggested by the associated common shark teeth. The shark fauna is usually the only common fauna preserved together with belemnites in the EEP (author's observation).

EUSTASY AND BELEMNITELLID DIVERSITY FROM CENOMANIAN THROUGH TO EARLY CONIACIAN

During the Late Cretaceous, belemnitellids were common in the East European shallow seas of the EEP (see discussion above), where the Turonian was the period of maximum endemism and diversity. In the Upper Cenomanian through Lower Coniacian interval the most diversified belemnitellid fauna occurred in the Upper Turonian of the EEP, in the Middle Turonian of the North American Province (NAP), and in the Lower Coniacian of the North European Province (NEP). Revision of the systematics and stratigraphy of belemnitellids from the EEP enabled correlation between their occurrences and eustatic cycles in the EEP (see Text-fig. 7).

The low belemnitellid diversity was not triggered by the Cenomanian transgression (the reasons for the low diversity are not known). From the Turonian on, a relationship between belemnite diversity and trangression/regression pulses is observable in the EEP (KOŠŤÁK 2003a). There, belemnitellids were diversified in the Early Turonian and at the Early/Middle Turonian boundary interval. The Middle Turonian decrease in diversity in the EEP contrasts with a maximum diversity of belemnitellids in the NAP. There is a complete absence of belemnitellids in the Central European Subprovince of the NEP in the Lower and Middle Turonian. The most diverse belemnitellid fauna occurs in the Upper Turonian in the EEP. Rare species migrated into the NEP in the Late Turonian, probably from the NAP (see above).

SEXUAL DIMORPHISM?

Based on the analyses of ca. 100 guards (KOŠŤÁK & PAVLIŠ 1997), it appears that the *Praeactinocamax plenus* populations fall into two morphotypes (A and B; see KOŠŤÁK & PAVLIŠ 1997). The absence of the medium-sized class in the BCB could be explained by a higher fitness, that is to say a lower mortality of these specimens. Selection resulting from differential preservation of this size class can be excluded from consideration. However, this division into two morphotypes based on size could also represent sexual dimorphism. Sexual dimorphism in belemnites was described by some authors in the past, for example by DOYLE (1985) for the Jurassic belemnites. A. D'ORBIGNY (see ŠPINAR 1960, pp. 466-467) considered smaller guards as female and the larger as male. However, this interpretation is highly speculative. It is very difficult to define sexual dimorphism in belemnites, because in Recent cephalopods either males or females can be the larger gender.

The L/DAMLD and MLD/DAMLD parameter ratios seem to provide a key for the distinction of variability

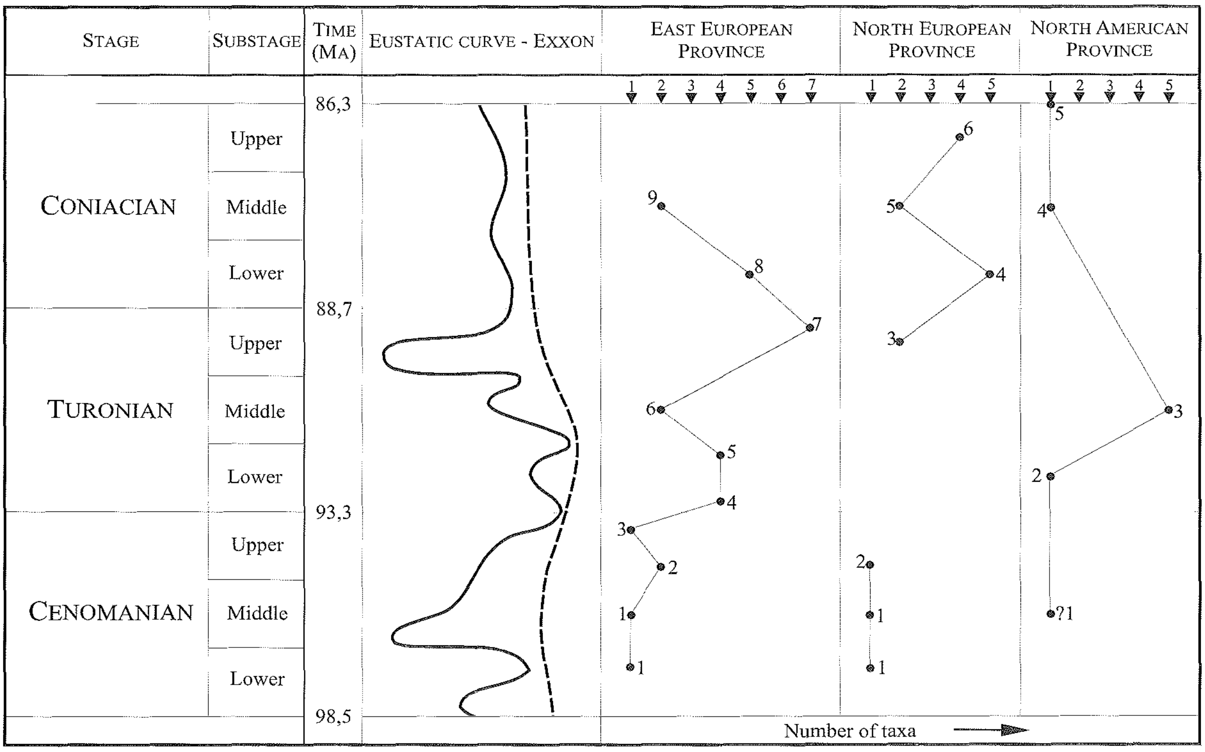

Fig. 7. Eustasy and belemnitellid diversity (Cenomanian – Coniacian): **2 1-7**) Number of taxa; •**1-9**) Species (see below). **East European Province: 1**. *Praeactinocamax primus*. **2**. *Praeactinocamax plenus*, ?*P. sozhensis*. **3**. *Praeactinocamax sozhensis*. **4**. *Praeactinocamax sozhensis*, *P. contractus*, *P. triangulus*, *Actinocamax verus antefragilis*. **5**.*Praeactinocamax triangulus*, *P. contractus*, *P.* sp. 1, *Actinocamax verus antefragilis*. **6**. *Actinocamax verus antefragilis*, *Praeactinocamax matesovae*. **7**. *Praeactinocamax planus*, *P. coronatus*, *P. medwedicicus*, *Goniocamax intermedius*, *G. surensis*, *G. christenseni*, *Actinocamax verus* ssp. **8**. *Goniocamax lundgreni*, *G. surensis*, *G.christenseni*, *Praeactinocamax* sp. 2, *Actinocamax verus* ssp. **9**. *Goniocamax lundgreni*, *Actinocamax verus* ssp. **North European Province: 1**. *Praeactinocamax primus*. **2**. *Praeactinocamax plenus*. **3**. *Praeactinocamax bohemicus*, *P.* aff. *bohemicus*. **4**. *Praeactinocamax bohemicus*, *P. paderbornensis*, *P. strehlensis*, *Goniocamax lundgreni*. **5**. *Goniocamax lundgreni*, *G. birkelundae*, *Actinocamax verus verus*, *Actinocamax verus subfragilis*, *Gonioteuthis praewestfalica*. **North American Province:** ?1. *Praeactinocamax primus*. **2**. *Praeactinocamax manitobensis*. **3**. *Praeactinocamax walkeri*, *P. sternbergi*, *P. manitobensis*, *P.* aff. *plenus*. *P.* aff. *groenlandicus*. **4**. *Praeactinocamax cobbani*. **5**. *Praeactinocamax groenlandicus* (lower Santonian) (after KOŠŤÁK 2003a)

within a population. Possible sexual dimorphism must be studied only in a large sample (more than 50 specimens from the same locality and stratigraphical level) in the context of growth parameters (e.g. isometric *versus* allometric growth).

BELEMNITES VS. TEUTHIDS

Upper Cretaceous teuthids are very rare in the Central European Subprovince. However, they occur in the Lower to Upper Turonian interval in the Bohemian Cretaceous Basin (KOŠTÁK 1999, 2002, 2003). Their occurrence and radiation were probably induced by large-scale palaeoclimatic and palaeoecologic changes in this area and also by reduction in the diversity of belemnites during this time interval. The Early and Middle Turonian were characterized by the lowest diversity of belemnites in the Central European Subprovince (CHRISTENSEN 1976). Belemnites became more diverse here in the Late Turonian but they are very rare (CHRISTENSEN 1982, KOŠŤÁK 1996). Coleoid diversity, stratigraphy and the relationship between belemnites and teuthoid occurrences in the Bohemian Cretaceous Basin are shown in Text fig. 8.

The radiation of teuthoids in the Bohemian Cretaceous Basin began at the end of the Early Turonian and the beginning of the Middle Turonian, and continued into the Late Turonian The occurrence and supposed radiation of teuthids during this time are not connected with their sedimentary preservation potential; they occur in different types of sediments – i. e. glauconitic sandstones, glauconitic marlstones and calcareous marlstones.

The presence of the Early to Middle Turonian teuthoid genera *Glyphiteuthis* REUSS and *Paraglyphiteuthis* KOŠŤÁK, as well as *Eoteuthoides* KOŠŤÁK, *Styloteuthis* FRITSCH and *Marekites* KOŠŤÁK, in the Middle to Upper Turonian boundary interval in the Bohemian Cretaceous Basin proves the existence of modern teuthid-like forms about 90 My ago. Teuthids with stylishly shaped gladii

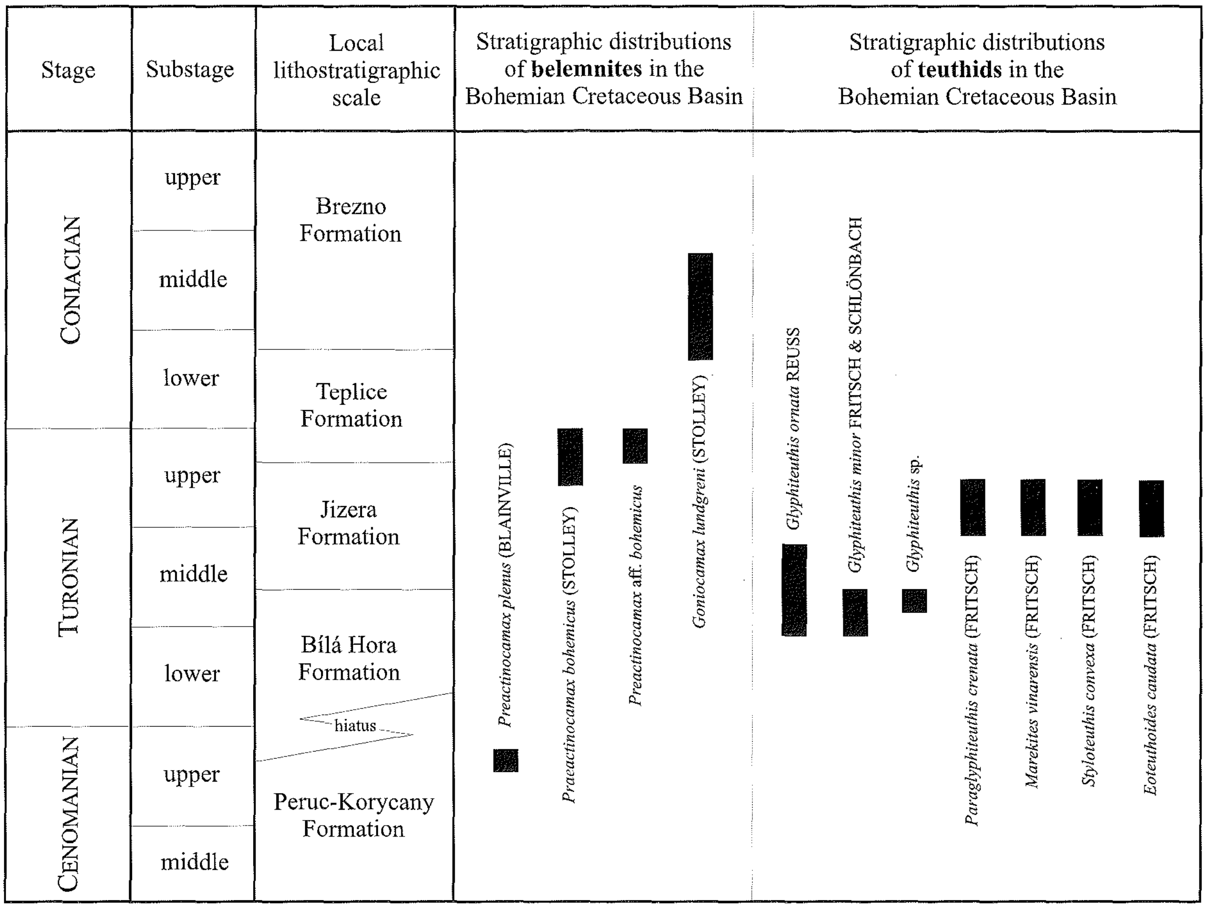

Fig. 8. Coleoid diversity, stratigraphy and the relation between the appearances of belemnites and teuthids in the Bohemian Cretaceous Basin (after KOŠŤÁK 2002, 2003b)

were in existence in the Middle to Late Turonian (KOŠŤÁK 2002, 2003b). It is clear that this radiation began sooner, before the belemnoid coleoids became extinct – in the Late Cretaceous, probably in areas with a virtual absence of belemnoid coleoids. The Bohemian Cretaceous Basin was one of these areas.

CONCLUSIONS

Having been an occasional Cenomanian through to Coniacian immigrants in the BCB, belemnites played an important role in mid European Cretaceous Basins. However, their mass occurrence here was recorded in *Praeactinocamax plenus* Zone only. A typical boreal faunal incursion, represented by belemnites, happened five to six times in the BCB.

1. An incursion of *P. plenus* from Central Asia in the east, through to England in the northwest, during the Late Cenomanian *Metoicoceras geslinianum* ammonite Zone (*plenus* Event)
2. One (two?) short-term incursions of *P. bohemicus* in the Late Turonian (*Subprionocyclus neptuni* to *Prionocyclus germari* ammonite zones).
3. A very short and poorly known incursion of *Goniocamax lundgreni* in the late Early Coniacian (below and intra-*Cremnoceramus deformis crassus* inoceramid Zone).
4. A single belemnite record from the Middle to Upper Coniacian "Chlomek Beds".

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PLATE 1

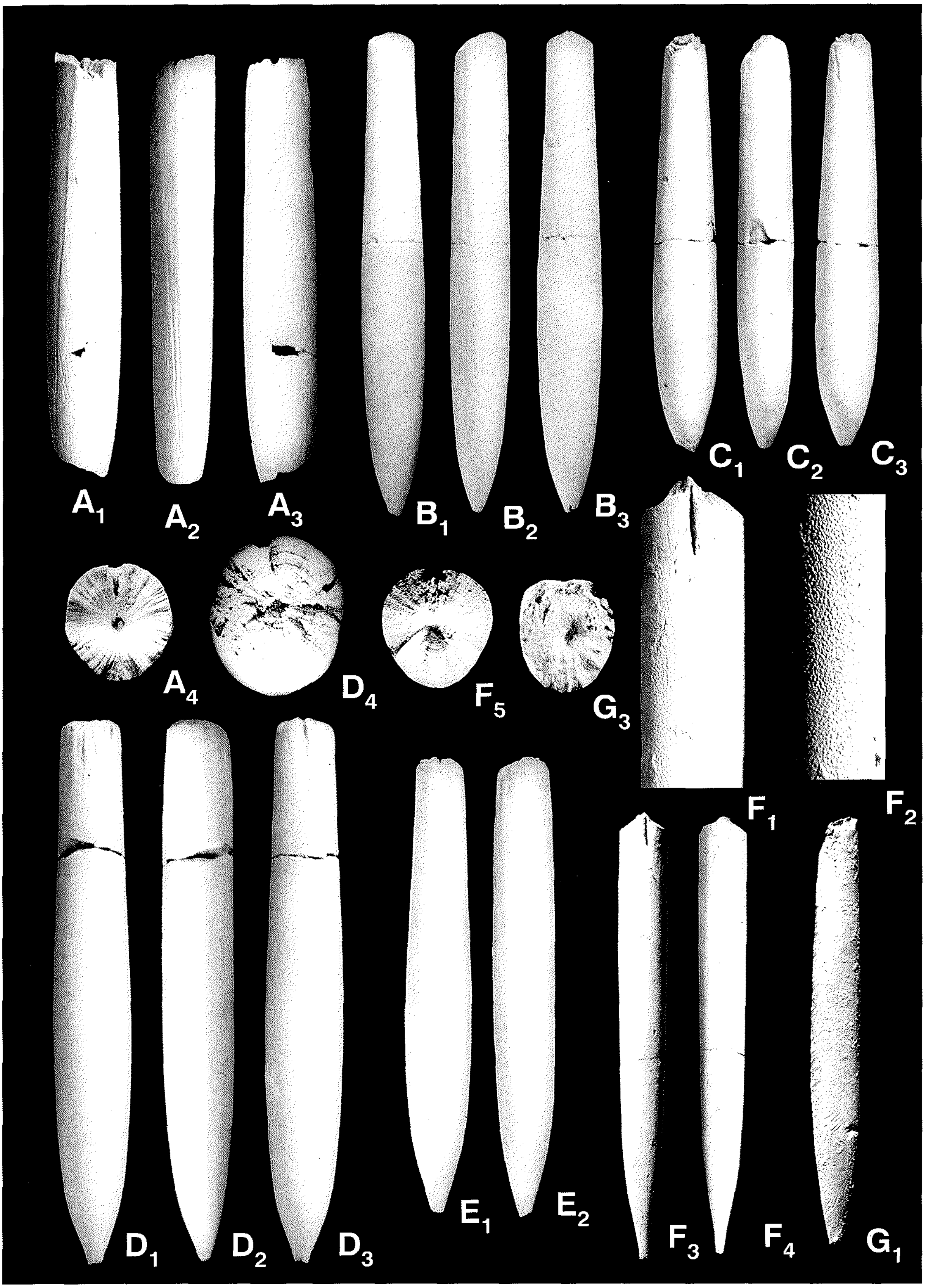
A – *Goniocamax lundgreni* (STOLLEY 1897), from the Bohemian Cretaceous Basin, Lower Coniacian, *Cremnoceramus crassus* Zone. Radovesice – dorsal (A_1), lateral (A_2), ventral (A_3) views, alveolar end (A_4)(×2). Private collection of Mr. Z. DVOŘÁK (Bílina Mines).

B-E – *Praeactinocamax plenus* (BLAINVILLE 1827), from the Bohemian Cretaceous Basin, Upper Cenomanian, *Metoicoceras geslinianum* Zone; B – National Museum Prague, O1268, Nová Ves - dorsal (B_1), lateral (B_2), ventral (B_3) views. C – National Museum Prague, O1509, Nelahozeves - dorsal (C_1), lateral (C_2), ventral (C_3) views. D – National Museum Prague, O1512, Neratovice - dorsal (D_1), lateral (D_2), ventral (D_3) views, alveolar end (D_4)(×2.2). E – National Museum Prague, O1449, Kostelec nad Labem – dorsal (E_1), lateral (E_2).

F – *Praeactinocamax bohemicus* (STOLLEY 1916), from the Bohemian Cretaceous Basin, Upper Turonian, *Subprionocyclus neptuni* Zone; National Museum Prague, O3217, Koštice – details of ventral fissure (F_1), details of granuled guard surface (F_2), ventral (F_3) and dorsal (F_4) views, alveolar end (F_5)(×2.2).

G – *Praeactinocamax* aff. *bohemicus*, from the Bohemian Cretaceous Basin, Upper Turonian, *Subprionocyclus neptuni* Zone; Regionální muzeum in Teplice, Pa.1 – ventral (G_1) view, alveolar end (G_2)(×2.2).

All belemnites are covered with ammonium chloride and are figured in nature size, unless otherwise indicated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