Lower Turonian record of belemnite *Praeactinocamax* from NW Siberia and its palaeogeographic significance

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Specimens of the belemnitellid *Praeactinocamax* Naidin, 1964 are described from the Upper Cretaceous of NW Siberia (Taimyr Region, Lower Agapa River, Russia). The rostra determined as *Praeactinocamax* aff. *plenus* consist of an aragonitic anterior part and a calcitic posterior part with a sharp boundary in between. This boundary surface is referred to as the "alveolar fracture", and it is a typical morphological feature of early belemnitellids and not a result of diagenetic processes. The occurrence of *Praeactinocamax* in Arctic areas shows a wider palaeobiogeographical distribution of the genus in the Late Cenomanian–Early Turonian interval than previously known. This finding suggests that migration of the late Cenomanian–early Turonian fauna occurred across Turgai channel. The geographic position of these new records may also explain the occurrence of *Praeactinocamax* in the Turonian of the US Western Interior Seaway, the origin of which has been hitherto unclear.

Key words: Belemnitellidae, *Praeactinocamax*, palaeobiogeography, Cenomanian, Turonian, Upper Cretaceous, Northern Siberia, Russia.

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Introduction

Cenomanian–Turonian early belemnitellid *Praeactinocamax* Naidin, 1964 is well known from Central Asia, Russian Platform, Europe, Greenland, and Northern America (Christensen 1997b; Košťák 2004). During this time interval, the genus shows widest palaeogeographic distribution in its history. Since Coniacian, the distribution rapidly decreased and the genus became extinct in the early Santonian (Košťák and Wiese 2006). In August 1973, Dmitriy P. Naidin (Moscow State University, Russia) collected numerous molluscs from dark brownish-grey clay-ironstone concretions along the Lower Agapa River (Piasina River basin, Usť Yenisei Lowlands, Taimyr Region, NW Siberia, see Fig. 1) with preserved aragonitic mineralogy of the shells including nacreous layers. This exceptionally preserved fauna of late Cenomanian to early Turonian age included fragments of calcitic belemnitellid rostra with preserved aragonitic phragmocones. These rostra were previously assigned to the genus *Goniocamax* Naidin, 1964 (Naidin et al. 1978; Teys et al. 1978; Barskov et al. 1997; Dauphin et al. 2007), the generic assignment that is critically reviewed in this paper. The goal if this paper is to re-examine taxonomic status of these fossils based on the presence of the so-called "alveolar fracture" (Figs. 2, 3), and to discuss their palaebiogeographic significance.

Institutional abbreviation.—IGP, Institute of Geology and Palaeontology Faculty of Science, Charles University Prague, Czech Republic; MSU, Lomonosov Moscow State University, Russia.

Other abbreviations.—FAD, First Appearance Data; OAE, Oceanic Anoxic Event.

Geological setting

The collecting site is located ca. 120 km north of the town of Noril'sk, in river cliff exposures on the Agapa River (Fig. 1A). The observed facies development there suggests a gradual shift from continental to fully marine deposits at the Cenomanian–Turonian boundary. A subdivision into several lithostratigraphic units given by Zakharov et al. (1989; see also Fig. 1B) is briefly summarized here.

The base of the section (Bed I-thickness = 25 m) is formed by cross-bedded alluvial/ deltaic quarzitic sediments (sandstones) with wood fragments (lignite) forming lenses, coal intercalations, and amber (retinite) grains containing a few insects. These are overlain by horizontally-bedded sandstones, siltstones, and claystone with sideritic concretions, intercalated by lenses of clayey breccia (Bed II-thickness = 9.2 m). Bed III (12.5 m) consists of clayey siltstones with the first marine fauna (inoceramid and other bivalves, gastro-
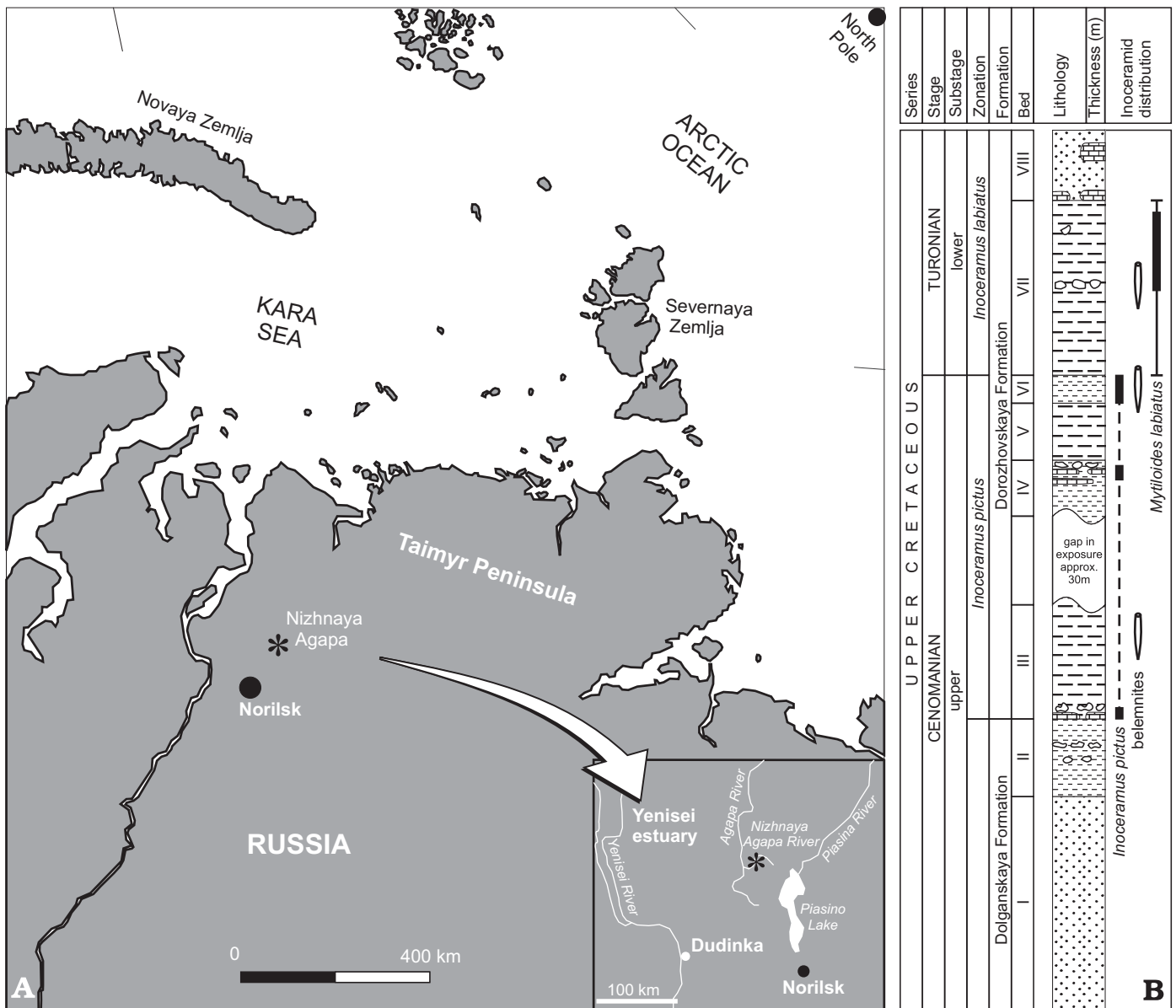
Fig. 1. **A**. The geographic position of the North Siberian Upper Cretaceous belemnite locality at the Agapa River (Taimyr Peninsula). **B**. Schematic sketch of the exposed section at the find locality. Belemnite levels are indicated, for more details see text.

pods and undetermined belemnites). Sideritic beds at the bottom of Bed III yielded *Inoceramus pictus* J. de C. Sowerby, 1829. In the higher parts of the bed, there are shell accumulations of lopatinid and ctenodontid bivalves, gastropods, and undetermined belemnite rostra fragments. Bed IV (5.5 m) consists of fine-grained greenish-grey to green (leptochlorite) sandstone. In the upper part, there are two separate horizons of calcareous sandstone. In the terminal part of this unit, a horizon with sideritic concretions yielded *Inoceramus pictus* and other fauna. Bed V (6.8 m) comprises an alternation of bioturbated siltstone and silty grey claystone with accumulations of small bivalves and gastropods. Bed VI (3.5 m) is represented by a greenish-grey leptochloritic siltstone with phosphatic nodules containing *I. pictus* and other unde-

termined bivalves, gastropods, ammonites (large *Placenticeras* and rarer *Borissiakoceras*), and belemnite fragments. Bed VII (20 m) is a dark grey, bituminous clayey siltstone. According to Zakharov et al. (1991), this bed represents the maximum transgressive level in North-western Siberia and it may be the local expression of the global OAE II (see Tsikos et al. 2004; with further references therein). In its middle part, a horizon of greenish grey siltstone with large (100–400 mm) clay-ironstone concretions occurs. These concretions yielded a very rich fauna consisting of *Mytiloides labiatus* (Schlotheim, 1813), *Inoceramus agapensis* Khomentovsky, 1992, *Mytiloides* cf. *hattini* Elder, 1991, *Borissiakoceras inconstans* Cobban and Cryc, 1961, *Praeactinocamax* aff. *plenus* (Blainville, 1825), small bivalves (*Cucullaea* sp.),

and gastropods with primary aragonite preserved. The succeeding Bed VIII is formed by light grey fine-grained sands with fossiliferous carbonate concretions at the base. Teys et al. (1978), Naidin et al. (1978), Efremova (1978), Barskov et al. (1997), and Mikhailova and Naidin (2002) reported the following additional ammonite fauna from the Lower Agapa sections: *Borissiakoceras inconstans* Cobban and Cryc, 1961; *B.* aff. *ashurkoffae* Cobban and Cryc, 1961; *B. orbiculatum* Stephenson, 1955; *Placenticeras* cf. *pseudoplacenta* Hyatt, 1903; *Placenticeras* sp.; *Proplacenticeras* sp.; *Scaphites subdelicatulus* Cobban and Gryc, 1961, *Scaphites* sp., the assemblage which proves an early Turonian age. However, Zakharov et al. (2003) reported large *Placenticeras* and—less frequent—*Borissiakoceras* already in the late Cenomanian (see above).

The exposures of the Lower Agapa River (Piasina River basin) were previously considered to be exclusively early Turonian in age (Naidin et al. 1978; Barskov et al. 1997). Based on the occurrence of *Inoceramus pictus*, Zakharov et al. (1989, 1991, 2003), Khomentovsky (1992), and Dhondt and Naidin (2004) extended the stratigraphic range of the Lower Agapa River section downward to include the upper Cenomanian. The exposures can be safely dated by the occurrence of *I. pictus* and *Mytiloides labiatus* as late Cenomanian to early Turonian. The precise position of the C/T boundary has not been established and cannot be determined from the literature data alone. Judging from the mode of preservation in clay-ironstone nodules, the *Praeactinocamax* remains described herein can be safely referred to Bed VII sensu Zakharov et al. (1989)—see Mikhailova and Naidin (2002), and they are, therefore, early Turonian in age.

Systematic palaeontology

Class Cephalopoda Cuvier, 1795

Order Belemnitida Zittel, 1895

Family Belemnitellidae, Pavlow, 1914

Genus *Praeactinocamax* Naidin, 1964

Type species: *Belemnites plenus* Blainville, 1827, Upper Cenomanian (Late Cretaceous), England (see Blainville 1825–27: 376, figs. 3, 11).

Emended diagnosis.—Medium-sized to large belemnitellids (guard up to 115 mm long) with allometric growth; adult specimens stouter and more lanceolate in ventral view than juvenile specimens; usually with short cone-shaped alveolar fracture, but some species with very shallow pseudoalveolus; ventral fissure absent; ventral furrow and ventral notch sometimes present; juvenile guards long and slender (needle-shaped); adult guards predominantly lanceolate in dorsoventral view and subcylindrical in lateral view. Dorsolateral compressions and furrows usually present; striation and vascular imprints in some species; granulation rare (modified from Blainville 1825–27; Christensen 1997a; Košťák 2004).
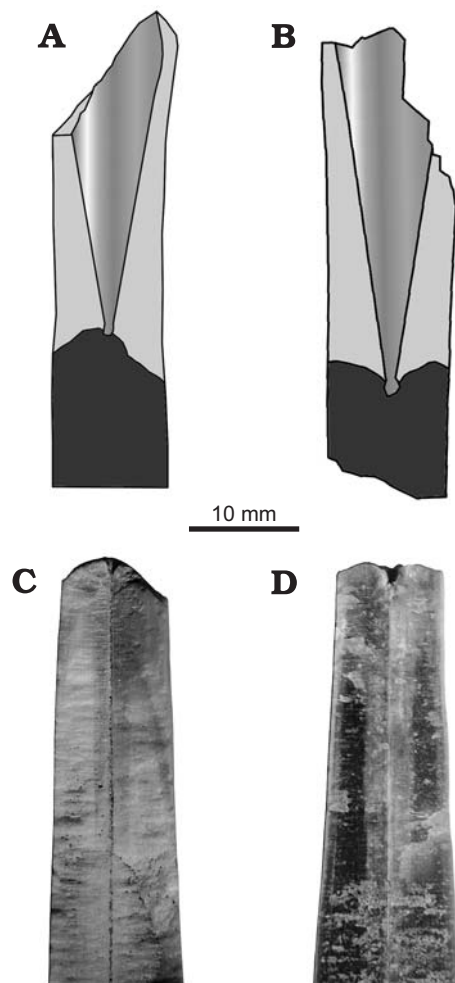

Fig. 2. Two morphotypes *Praeactinocamax* aff. *plenus*. Schematic sketches of morphotype A (**A**) in direct comparison with morphotype B (**B**) from Kazakhstan (Upper Cenomanian). Lateral sections of rostra showing alveolar end of morphotype A (**C**, specimen IGP KK8/15) and morphotype B (**D**, specimen IGP 170/11).

Praeactinocamax aff. *plenus* Blainville, 1825
Figs. 2, 3, 4A–I.

Material.—Three uniquely well preserved alveolar fractures with phragmocones and several belemnite fragments of *Praeactinocamax* aff. *plenus* (MSU 3025-3). They were collected together with undetermined gastropods, small bivalves (*Cucullaea* sp.), *Inoceramus agapensis* Khomentovsky, 1992 (upper Cenomanian–?lower Turonian) and *Mytiloides* cf. *hattini* (see Dhondt and Naidin 2004), suggesting an early Turonian age. Zakharov et al. (1989) showed also the First Appearance Data (FAD)—of *M. labiatus* in Bed VII (Fig. 1B).

Description.—The material studied represents two distinct morphologies: (i) *Morphotype* A (Figs. 2A, C, 3A, 4A–C, E, H) characterized by a low cone-shaped alveolar fracture, which shows in this respect the greatest similarities with those of *P. primus* (Arkhangelsky, 1912) and *P. plenus*, (ii) *Morphotype* B (Figs. 2B, 3B, 4D, G, I) characterized by a
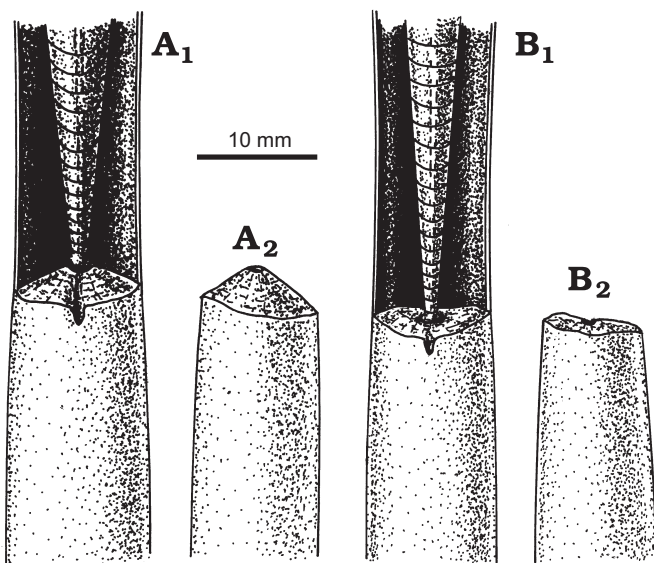
Fig. 3. The alveolar fracture (alveolar end) reconstruction of *Praeactinocamax* aff. *plenus* with the position of phragmocone. **A**. Morphotype A, specimen MSU 3025-3/1 with low cone-shaped fracture, in ventral (A_1) and lateral (A_2) views. **B**. Morphotype B, specimen MSU 3025-3/2 with a very shallow pseudoalveolus with a pit in the centre, in ventral (B_1) and lateral (B_2) views.

very shallow pseudoalveolus (not exceeding 1.5–2 mm). The calcitic rostrum is fragmentarily preserved (Fig. 4A). It is medium sized (not exceeding ca. 65–70 mm) and is ventrally markedly flattened. The flanks are slightly depressed and form a dorsolateral depression. No dorsolateral double furrows or vascular imprints have been recognized. The alveolar angle is ca. 21°. The diameter of the protoconch is about 1 mm. The calcitic posterior part of the rostrum terminates in a low cone-shaped alveolar fracture and/or an extremely shallow pseudoalveolus or depression with a pit in the centre (Figs. 2, 3). This part juts into a white, anterior part of the rostrum, which is usually not preserved. The boundary between the white and the dark calcitic parts is very sharp (Fig. 4), without any transitional zones albeit the laminar growth lamellae continue from the calcitic into the white anterior part part without any visible interruptions. A shallow pit in the centre of the alveolar fracture marks the position of the protoconch (Fig. 4C–E). The area between the walls of the aragonitic anterior part of the rostrum and the phragmocone is formed by aragonitic matter (Barskov et al. 1997; Dauphin et al. 2007). However, in the specimen figured on Fig. 4D, G, this space was more altered than the walls.

Discussion.—Of interest is the fact that the anterior parts of the rostra, including the phragmocone, are preserved. The preservation of the anterior parts of belemnite rostra is exceptionally rare and only few records of this can be found in the literature (Saemann 1861–1862; Schlüter 1876; Moberg 1885; Jeletzky 1948). The original composition of the anterior part, separated from the calcitic posterior part by the

so-called "alveolar fracture" (see Figs. 2, 3) was considered to have been primarily horny or formed by some another undetermined organic material without, or containing only a very low, calcium carbonate content (Saeman 1861–1862; Crick 1904), whereas the calcitic posterior part is generally regarded as being composed of low-Mg calcite. Naidin (1969) supposed that the alveolar fracture originated as a result of postmortal diagenetic processes, while Barskov et al. (1997) and Dauphin et al. (2007) suggested, also based on material from the Taimyr Region, that the original material of the anterior part of the rostrum was aragonite.

In our specimens, there is a very sharp and distinct boundary between the aragonitic anterior, and the calcitic posterior part of the rostrum (Fig. 4). This contact likewise marks the morphological feature known as the alveolar fracture. Judging from a wealth of literature data (Naidin 1964, 1969; Christensen 1974, 1997a; Košťák and Pavliš 1997) and our own studies based on thousands of specimens (MK) of *Praeactinocamax primus*, *P. plenus*, and related species from Tadzhikistan in the east to England in the west in several different sediments (i.e., sandstone, marl, claystone, limestone etc.) with totally different diagenetic, histories, the shape of the alveolar fracture shows great morphological stability. In the case of *P. primus*, virtually no differences in this feature have been observed, while *P. plenus* shows slight differences in alveolar fracture morphology (see also morphometric analysis in Christensen 1997a: 67). The observed stability of the alveolar fracture morphology cannot be explained by diagenetic processes. Instead, the clear demarcation line between the calcitic and aragonitic part of the endoskeleton is suggestive of complex biomineralization process, which must have been genetically controlled. As can be seen from younger representatives of *Praeactinocamax*, the progressive calcification of the anterior part of the rostrum and the resultant progressive deepening of the pseoudoalveolus are important features in the evolution of this genus (Košťák 2004) as well as other Late Cretaceous belemnite lineages i.e., *Goniocamax–Belemnitella* (see Ernst 1964; Christensen and Schulz 1997; Christensen 1995, 1997a, 2000). The morphology of the alveolar fracture can thus be considered a reliable taxonomic feature of the Belemnitellidae. A conical alveolar fracture as described above is exclusively known from the genera *Actinocamax* Miller, 1823 and *Praeactinocamax*.

All species of *Actinocamax* are characterized by a high-conical alveolar fracture and only slight differences are observable between the species. The mean value of the length of the rostra is between 30–35 mm and it usually does not exceed 55 mm (Christensen and Schulz 1997). The earliest species of this genus (*A. verus antefragilis* Naidin, 1964) occurred in the early Turonian and the genus became extinct about the Early/Late Campanian boundary (Christensen 1997a). No high-conical alveolar fracture (as the one of the most important taxonomic feature) is present in the material studied and hence these specimens can be safely excluded from *Actinocamax*. The size of the guard remains supports
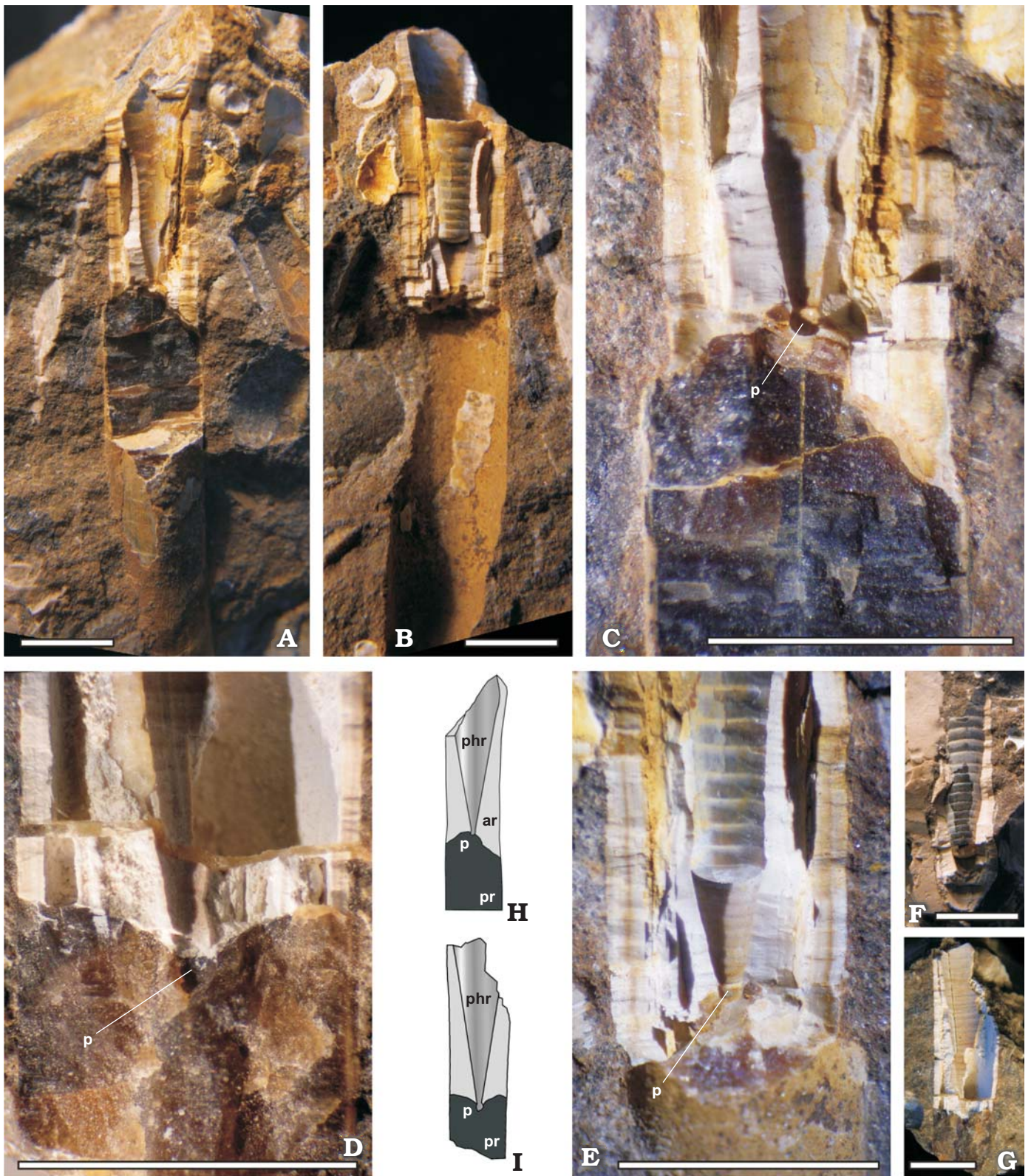
Fig. 4. Belemnitellid *Praeactinocamax* aff. *plenus* Blainville, 1827; Cenomanian–Turonian boundary interval. Lower Agapa River, Northern Siberia (Russia). **A–C**, **H**, **E**. Morphotype A. Specimen MSU 3025-3/1 with low cone-shaped fracture, calcitic posterior rostrum (dark grey), aragonitic anterior part of the rostrum (light yellow) with phragmocone, lateral view. **D**, **I**, **G**. Morphotype B. Specimen MSU 3025-3/2 with a very shallow pseudoalveolus with a pit in the centre, calcitic posterior rostrum (dark grey), aragonitic anterior part of the rostrum (light yellow) with phragmocone; dorso-ventral view. **F**. Phragmocone MSU 3025-3/3 surrounded by aragonitic matter of the aragonitic anterior part of the rostrum (light). The calcitic posterior part is not preserved. Scale bars 10 mm. Abbreviations: phr, phragmocone; p, protoconch; ar, aragonitic anterior part of the rostrum; pr, calcitic posterior rostrum.

this idea. The guard diameter at protoconch area is about 10 mm in specimens studied, while in *Actinocamax* it is less than 1–2 mm (both, the top of high conical alveolar fracture and protoconch area are identical in any species of this genus). The maximum lateral diameter in *Actinocamax* rarely exceeds 5 mm (in few Coniacian and Santonian species) whereas lateral diameter of the studied Siberian specimens under question is two times larger.

Praeactinocamax is characterized by medium-sized guards not exceeding 115 mm in length (Christensen 1997a). The alveolar fracture is usually low cone-shaped, however, a relative deep (up to 6 mm) pseudoalveolus can be developed in some species (Naidin 1964; Košťák 2004). The depth of pseudoalveolus and the shape of the alveolar fracture are definitely not a result from preservation, and own data from material from various facies (i.e., sandstones, marlstones, limestones etc.) clearly show a morphological stability of this feature in all *Praeactinocamax* species (Naidin 1964; Košťák 2004). In *Praeactinocamax*, a trend towards a deepening of the pseudoalveolus can be observed. However, the morphologic lineage [*P. primus*; early to middle Cenomanian—*P. plenus*; late Cenomanian—*P. planus* (Makhlin, 1965); late Turonian—*P. cobbani* (Christensen, 1993); middle Coniacian–*P. groenlandicus* (Birkelund, 1956); early Santonian] kept a stable morphology of the alveolar fracture. The development of the pseudoalveolus is based on the deepening of the central pit and the calcification of its margin. A first slight deepening occurs in the late Cenomanian *P. plenus* (Christensen 1990, 1997a; Košťák and Pavliš 1997) and it is well developed in *P. triangulus* Naidin, 1964 (early Turonian), a possible derivative of *P. plenus* (Naidin 1964; Christensen 1974; Košťák 2004; Košťák et al. 2004). Within this context, our material can be attributed to *Praeactinocamax*.

This feature has been reported from several *P. plenus* populations (see Christensen 1974; Košťák and Pavliš 1997; Christensen 1997a) that have been partly referred to *P. triangulus*, a species formerly regarded as a subspecies of *P. plenus* (Naidin 1964; Košťák 2004). A very shallow to deeper pseudoalveolus (2–5 mm) is also known in the early Turonian species *P. sozhensis* (Makhlin, 1973), *P. contractus* (Naidin, 1964), and *P.* sp. 1 sensu Košťák (2004). However, due to the extremely limited material available from the section under discussion more precise taxonomic comments at species level are not possible, but we safely can re-assign the material to *Praeactinocamax* (*P.* aff. *plenus*).

Naidin et al. (1978), Teys et al. (1978), Barskov et al. (1997), and Dauphin et al. (2007) identified the belemnites from the Lower Agapa River section as *Goniocamax*. This generic assignment cannot be followed here due to the unequivocal *Praeactinocamax* character of the alveolar end in these belemnites. *Goniocamax* is characterized by the so-called "bottom of ventral fissure", a line connecting the pseudoalveolus wall (near the protoconch area) with the ventral rostrum surface at the ventral notch (Christensen and Schulz 1997). Christensen and Schulz (1997) established the stratigraphic range of *Goniocamax* to be from the base of the Coniacian through lower Santonian. Košťák (2005) described the late Turonian species *G. christenseni* from Central Russia. The origin of *Goniocamax* is currently under examination by one of the authors (MK): no forms related to *Goniocamax* appeared until the late middle Turonian *Inoceramus lamarcki* Zone (Košťák et al. 2004; Košťák 2005).

Dauphin et al. (2007), based on material from the same section, showed that the anterior white part consists of aragonite. They introduced a hypothesis concerning the original mineralogy of the entire rostrum. Microstructural and geochemical composition studies showed that the aragonite in all the shells from the Bed VII nodules (including the belemnites) had been affected to a greater or lesser extent by diagenetic alteration. The coexistence of both calcitic and aragonitic components in the same rostrum favoured their hypothesis that the primary mineralogy of the entire rostrum was aragonite rather than low Mg-calcite), and that the originally aragonitic posterior part of the rostrum had become secondarily calcitized in the course of diagenesis. Dauphin et al. (2007: text-fig. 1) showed an irregular and diffuse boundary between the calcitic—in their view diagenetically altered—posterior and the primary aragonitic anterior part of the rostrum. In fact, this may well be an expression of a geochemical/diagenetic boundary and we agree that there is geochemical evidence for diagenetic alteration. However, on both morphological and geochemical grounds, we do not agree with their final conclusion concerning the primary mineralogy of the posterior part of the rostrum, which we consider to have been composed of low-Mg calcite. Further evidence that this part of the rostrum of *Praeactinocamax* was primarily composed of low-Mg calcite rather than aragonite derives from combined cathodoluminescence, geochemical and microstructural investigations of well preserved posterior rostra of *P. plenus* composed of low Mg-calcite from Upper Cenomanian chalks of southern England (see Voigt et al. 2003: fig. 2). Those authors demonstrated that the parts of the rostra composed of completely fresh (i.e., unaltered) calcite were non-luminescent, while any diagenetically altered parts showed reddish-orange luminescence due to the early diagenetic incorporation of Mn in the calcite lattice (Machel et al. 1991). The good preservation of the unaltered calcite was supported not only by the low concentrations of Mn and Fe, and high concentrations of Sr, but also by carbon stable isotope data.

Stratigraphic and geographic range.—Early Turonian of NW Siberia.

Discussion

Whilst lower and upper Upper Cretaceous belemnite palaeobiogeography is well recorded in the literature (Christensen 1997b), the knowledge on the worldwide distribution of
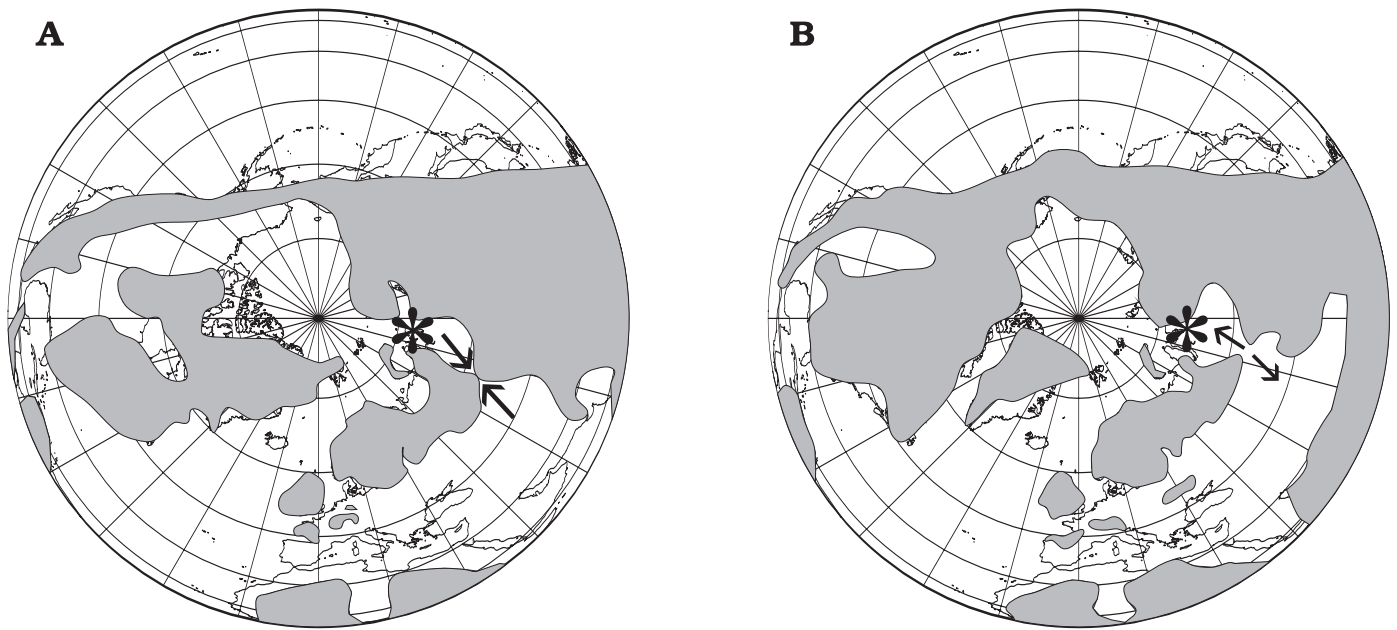
Fig. 5. Palaeogeographic map of the Northern hemisphere (North pole projection). **A**. Turonian. **B**. Maastrichtian. Asterisked is locality Lower Agapa River under this study; arrows indicate the position of Turgai Channel; grey are lands, white are seas and oceans.

Cenomanian to Turonian belemnites and their palaeobiogeography is poor due to rare and stratigraphically/geographically patchy occurrences. In addition, taxonomic uncertainties (see below) also hindered the development of refined distribution and migration maps. The value of the records described here in results from the fact that it is the first record of *Praeactinocamax* from the Russian Arctic region of northern Siberia. Its occurrence there provides new palaeobiogeographic data, and it raises the possibility of a marine connection between the study area and the Russian Platform (Fig. 5A).

Praeactinocamax primus, the first representatives of the Late Cretaceous Belemnitellidae, appeared for the first time in the early but not earliest Cenomanian *Mantelliceras mantelli* Ammonite Zone in the Central Russian Subprovince (Christensen 1997) and continued into the Middle Cenomanian *Acanthoceras rhotomagense* Ammonite Zone (Naidin 1964; Košťák 2004). From there, it spread towards the west (Europe), but migration occurred mainly as short-term incursion events resulting from regression (connected shallow seas) and the initial transgression (Mitchell 2005; Wilmsen et al. 2007). Apart from the Russian Platform and the Russian Arctic area, there are Turonian records of *Praeactinocamax* from Europe (Christensen 1982; Košťák 1996; Košťák et al. 2004) and the US Western Interior Seaway (Christensen 1997b; Košťák 2004; see comments below).

The occurrence of *Praeactinocamax* in northern Siberia is enigmatic. The radiation centre of belemnitellid evolution is conventionally considered to have been located on the Russian Platform (see above), but no evidence of Cenomanian to Santonian marine connection with the Arctic region has been proven so far by palaeobiogeographic similarities. Only during Maastrichtian times was the Turgai Channel opened (Fig. 5B), connecting both areas and enabling faunal migration (Zakharov et al. 2002). The occurrence of late Cenomanian (still indetermined belemnite rostra) to early Turonian representatives of *Praeactinocamax* both on the Russian Platform and in the Russian Arctic region, however, clearly demonstrates the existence of a previously unknown fully marine seaway between them. The possibility of such a seaway was questioned earlier by Zakharov et al. (2002), who mentioned a possible connection located in the northern Ural region based on similar inoceramid faunas from the upper Cenomanian to lower Campanian in the Russian Platform, Northwest Europe and the Arctic area.

The presence of early belemnitellids in the Cenomanian and Lower Turonian of Northern Siberia not only fills a gap in knowledge but also helps in understanding the occurrence of *Praeactinocamax* in the US Western Interior Seaway (Jeletzky 1950, 1961) and the possible dispersal routes of this genus during Turonian times. Christensen (1982, 1997a, b) derived the origin of the North American *Praeactinocamax* from a North European Turonian *Praeactinocamax* stem via north-eastern Greenland. Later, Košťák and Wiese (2002), Košťák (2004, 2005), and Košťák et al. (2004) showed that North and Central European records are younger than those in the Western Interior Seaway. The latter authors (Košťák and Wiese 2002; Košťák 2004) therefore suggested an origin of the North American *Praeactinocamax* stem from the middle Cenomanian *P.* cf. *primus* and early Turonian *Praeactinocamax* cf. *manitobensis* (Whiteaves, 1889) de-

scribed by Seibertz and Spaeth (1995) from NE Mexico. However, a taxonomic and stratigraphic re-assessment of this material has shown that these records actually represent specimens of *Neohibolites*. The material comes from so-called "Cuesta del Cura Formation", the age of which is commonly given as upper Albian to upper Cenomanian (see Stinnesbeck 1991, 1993 for ammonite data), and this is in accordance with the re-assessment of the figured specimens as *Neohibolites* (Košťák and Wiese 2006), which are well known from the Cuesta del Cura Formation in Mexico together with *Mesohibolites* (see Seibertz 1987; Seibertz and Spaeth 2005). As a consequence, the North American middle Turonian belemnitellids must have been of different origin. In the light of the new records from North Siberia it appears possible that the WIS belemnitellids immigrated into the Western Interior Seaway via the North Pole area, from where they spread via Greenland to Europe (see discussion in Košťák and Wiese 2002; Košťák et al. 2004; Košťák and Wiese 2006). This interpretation is supported by the marked morphological similarity between the alveolar fractures in the *Praeactinocamax* described here and those of the *P. manitobensis/walkei/sternbergi* group of the Western Interior Seaway, Canada, and Greenland (Jeletzky 1961; Christensen 1982; Christensen and Hoch 1983).

Conclusions

- Exceptionally well preserved belemnite rostra from the northern Siberia previously attributed to *Goniocamax* sp. are herein attributed to *Praeactinocamax* aff. *plenus* based on morphology of the alveolar fracture.
- The alveolar fracture of the Belemnitellidae shows morphological stability within the *Praeactinocamax* and *Actinocamax* (Naidin 1964; Christensen 1997b; Košťák 2004). The typical alveolar low cone-shaped alveolar fracture marks the boundary between the aragonite anterior part (which normally is not preserved due to early diagenetic dissolution) and the calcite posterior part. As this contact exhibits stable morphology in thousands of specimens seen so far, the variable biomineralization aragonite versus calcite must be strictly genetically controlled. Our interpretation contrasts with that of Dauphin et al. (2007) who, based on geochemical data, suggested a primary aragonite mineralogy for the entire rostrum.
- The occurrence of *Praeactinocamax* in the Arctic region during late Cenomanian–Turonian times suggests the existence of a connecting seaway between the Russian Arctic and the North European Province or East European Province (for more detail see Košťák 2004; Košťák et al. 2004). However, the migration patterns and marine connections are still uncertain. The Arctic representatives of *Praeactinocamax* are potentially the ancestors of the belemnitellids that occurred in the middle Turonian of Northern America (i.e., North American Province).

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