

Goniocamax christenseni n. sp. (Belemnitellidae, Belemnitida) – a new species from the Upper Cretaceous of Russia

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A new species of *Goniocamax* Naidin: *Goniocamax christenseni* n. sp. is described from the Upper Turonian and the lowermost Coniacian strata of the Volga river region in Russia. The new species occur together with 'primitive' species of *Goniocamax* i.e. *Goniocamax intermedius* (Arkhangelsky) and *G. surensis* (Naidin), which suggests that two parallel evolutionary lineages in *Goniocamax sensu* Naidin, 1964 were present and both of unknown origin. The origin of *G. lundgreni* (Stolley) can be explained by gradual calcification of the anterior part of the guard in the *intermedius/surensis* group. *G. christenseni* n. sp. has a well calcified pseudoalveolus and an acute angle at the bottom of the ventral fissure of the wall of the pseudoalveolus. Thus, *G. christenseni* n. sp. resembles the first representatives of *Belemnitella* D'Orbigny and is considered the likely ancestor of the *Belemnitella* group. Phylogeny and palaeobiogeography of the Late Turonian belemnitellids (genera *Praeactinocamax* Naidin and *Goniocamax* Naidin) are discussed.

Keywords: Belemnites, Upper Cretaceous, Russia, taxonomy, palaeobiogeography.

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Turonian and Early Coniacian belemnites of the East European Province (Košťák *et al.* 2004) were first studied in detail by Arkhangelsky (1912) followed by Naidin (1964, 1978, 1982), Makhlin (1965), Glazunova (1972), Christensen (1976, 1982, 1988, 1990, 1991, 1997a, 1997b), Christensen & Schulz (1997), Marciniowski *et al.* (1996), Košťák *et al.* (2004) and Košťák (2004). A modern biostratigraphic framework of the East European Province is given by Walaszczyk *et al.* (2004).

The belemnite fauna from East European Province of the entire Cenomanian through to the lowermost Coniacian is currently being investigated by the author. Amongst the material, a new species of *Goniocamax* was recognised on the basis of morphometric analysis. This new species named *Goniocamax christenseni* n. sp. is formally established and described in this paper. It is recorded from the collection of D.P. Naidin (Moscow State University), and an additional specimen was found during the summer of 1999 at an expedition to the Middle Volga river area (Surskoe town vicinity, Central Russia; Fig. 1).

Systematics

Types and all figured material are kept in the collections of the Institute of Geology and Palaeontology, Charles University, Prague.

Class Cephalopoda Cuvier, 1795
Subclass Coleoidea Bather, 1881
Order Belemnitida Zittel, 1895
Family Belemnitellidae Pavlow, 1914

Genus *Goniocamax* Naidin, 1964

Discussion. Christensen & Schulz (1997) raised the subgenus *Goniocamax* Naidin of *Goniotentis* Bayle to the rank of genus with the stratigraphical range extending from the base of the Coniacian into the Lower Santonian. The two Turonian taxa from the Russian Platform, *G. intermedius* and *G. surensis*, were excluded from *Goniocamax*, and included in *Praeactinocamax* Naidin due to the absence of a base to the ventral fissure (Christensen & Schulz 1997). How-



Fig. 1. Geographic position of localities with *Goniocamax christenseni* n. sp.

ever, the absence of this morphological character could be the result of very poor calcification of the anterior part.

Košťák (2004) allocated the 'primitive' taxa, *G. intermedius* and *G. surensis*, to *Goniocamax* even though the species exhibit transitional features that might justify a separation at the subgeneric level. This approach is followed here as the two species share important morphological characteristics – i.e. overall shape and size of the guard and similar character of the anterior end – with *G. lundgreni*.

Goniocamax christenseni n. sp.

Fig. 2A–J

2004 *Goniocamax* sp., Košťák *et al.*, pp. 520, 526

2004 *Goniocamax* sp. – Košťák, p. 77, figs 7–11, table 5.

Holotype. Fig. 2A–E

Etymology. In the honour of Walter Kegel Christensen, Danish cephalopod worker.

Type locality. Section in the western bank of the Volga river at Pudovkino village, Saratov district, Russia (Figs 1, 4).

Type horizon. The holotype comes from Bed 3 (phosphatic horizon containing the brachiopod *Concinthyris quidhamptonites*) in the section at the western bank of the Volga River at Pudovkino village; uppermost Turonian to base of Coniacian.

Material: Four complete or nearly complete specimens: the holotype No. 253/3 (Pudovkino, Saratov district), paratypes No. 249bg (Pudovkino, Saratov district) and No. S1999/7 (Surskoe, Ulyanovsk = Simbirsk district), and a juvenile specimen No. 249bg/10. One paratype originate from the Upper Turonian deposits – just above the LAD of *Inoceramus lamarcki* group, together with *G. intermedius*, and below the base of the Coniacian (Fig. 4), while the second paratype originates from the vicinity of Surskoe town, Central Russia (Fig. 1).

Diagnosis. Guards are about 70 mm long, slightly lanceolate in dorsoventral view and cylindrical in lateral view. Maximum lateral diameter (MLD) is situated in the proximal half of the guard. Depth of pseudoalveolus (D) is from 7 to 9 mm. Cross section of pseudoalveolus is oval. Schatzky distance (SD) 3.1 mm. Alveolar angle (AA) is 25°, angle between bottom of ventral fissure and the wall of pseudoalveolus (FA) is 28°. Riedel quotient (RQ) is 8.1. Dorsolateral depressions and double furrows are apparent. Striation and vascular imprints are present.

Description. The parameters given in the description are shown in Figure 3 and Table 1.

Guards are 63–73 mm long (adult specimens), lanceolate in dorsoventral view and cylindrical in lateral view. The maximum lateral diameter is attained

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Fig. 3. The position of measured diameters and terminology. PP – posterior part. AP – anterior part. L – length of the guard. LAP – length from apex to protoconch. MLD – maximal lateral diameter. LDAE – lateral diameter at alveolar end. DVDAE – dorsoventral diameter at alveolar end. DAMLD – distance from apex to maximal lateral diameter. MDVD – maximal dorsoventral diameter. DLD – dorsolateral depressions, D – depth of pseudoalveolus. D1 – distance from the BVF to the wall of pseudoalveolus. BVF – bottom of ventral fissure. C – conellae. $\alpha 1$ (AA) – alveolar angle, $\alpha 2$ (FA) – angle between pseudoalveolus wall and the bottom of ventral fissure. Quotient terminology: SD – Schatzky distance (distance from bottom of ventral fissure to protoconch). RQ – Riedel quotient (ratio of the length of the guard/pseudoalveolus depth). See also Table 1.

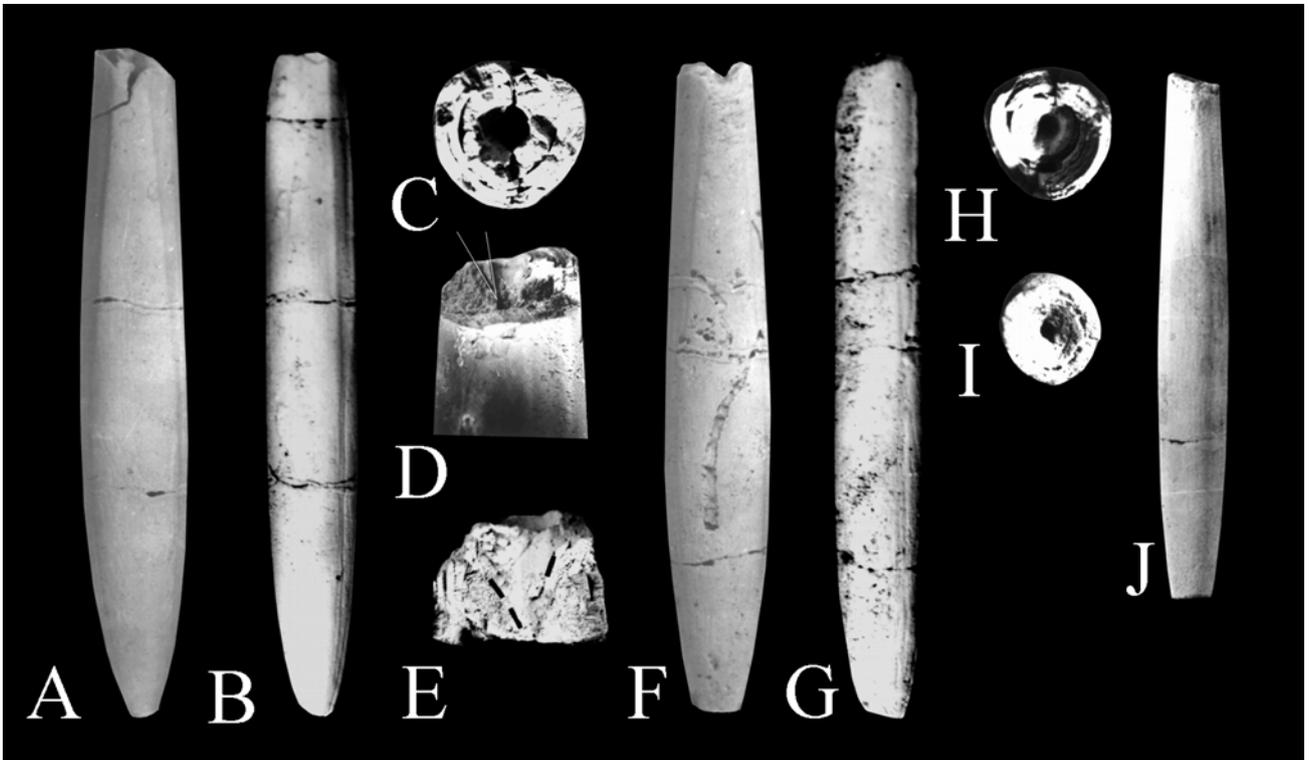


Fig. 2. A-E. *Goniocamax christenseni* n. sp. Specimen No. 253/3 - holotype, lowermost Coniacian - Pudovkino, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A - dorsal view. B - lateral view. C - anterior end. (x2). D - pseudoalveolus (x2). E - pseudoalveolus (x2) with conellae.
 F-H. *Goniocamax christenseni* n. sp. Specimen No. 249bg - paratype, upper Turonian - Pudovkino, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. F - Dorsal view. G - lateral view. H - anterior end. (x2).
 I-J. *Goniocamax christenseni* n. sp. Specimen No. 249bg/10, juvenile specimen, upper Turonian - Pudovkino, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. I - anterior end (x2). J - dorsal view.

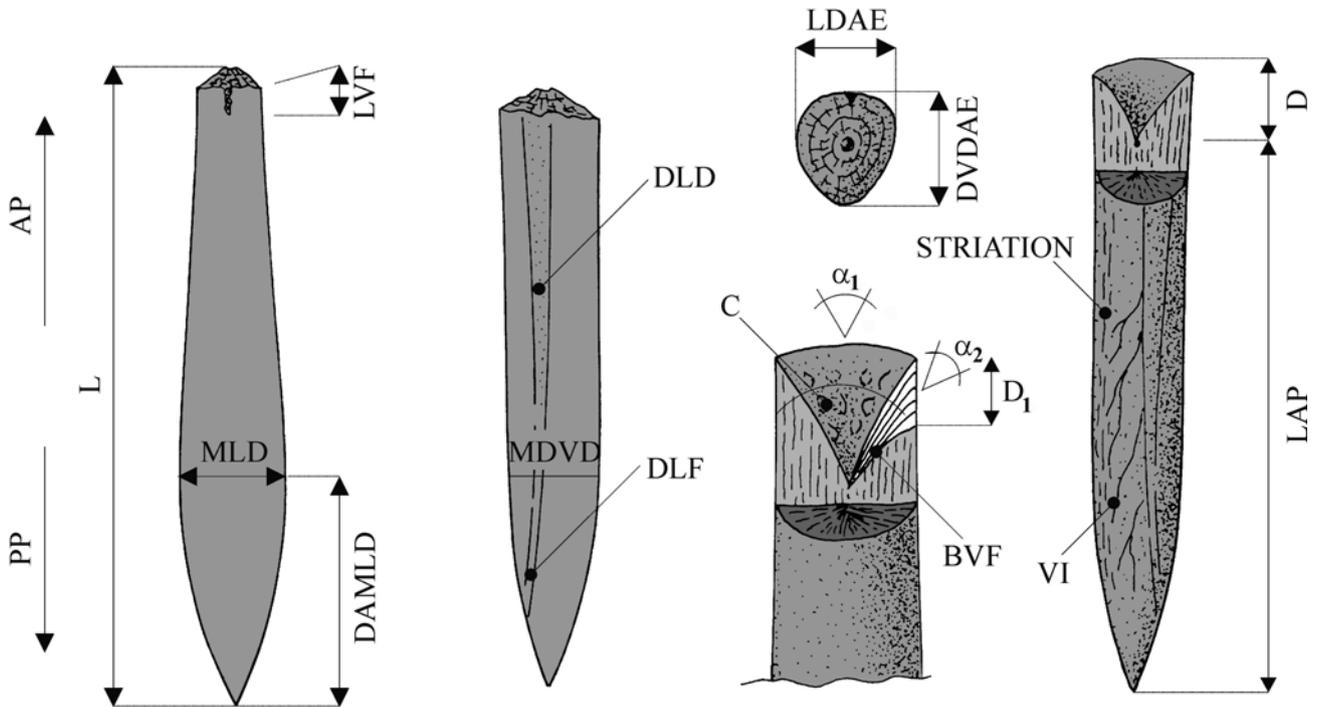


Table 1. Measured dimensions (mm)

No.	Specimen	L	MLD	DAMLD	LDAE	DVDAE	MDVD	D	Locality
1.	253/3	73	12	34	8.8	9.9	10.5	9	Pudovkino
2.	249bg	72*	11.4	34*	8.4	8.8	9.7	8.4	Pudovkino
3.	249bg10	58*	7.3	32*	5.7	5.9	6.5	4.4	Pudovkino
4.	S1999/7	63.2	10.4	26.6	7.8	8.2	9.2	7	Surskoe

L = Length of guard

MLD = Maximum lateral diameter

DAMLD = distance from apex to maximal lateral diameter.

LDAE = lateral diameter at alveolar end

DVDAE = dorsoventral diameter at alveolar end

MDVD = maximal dorsoventral diameter.

D = depth of pseudoaveolus

*estimated

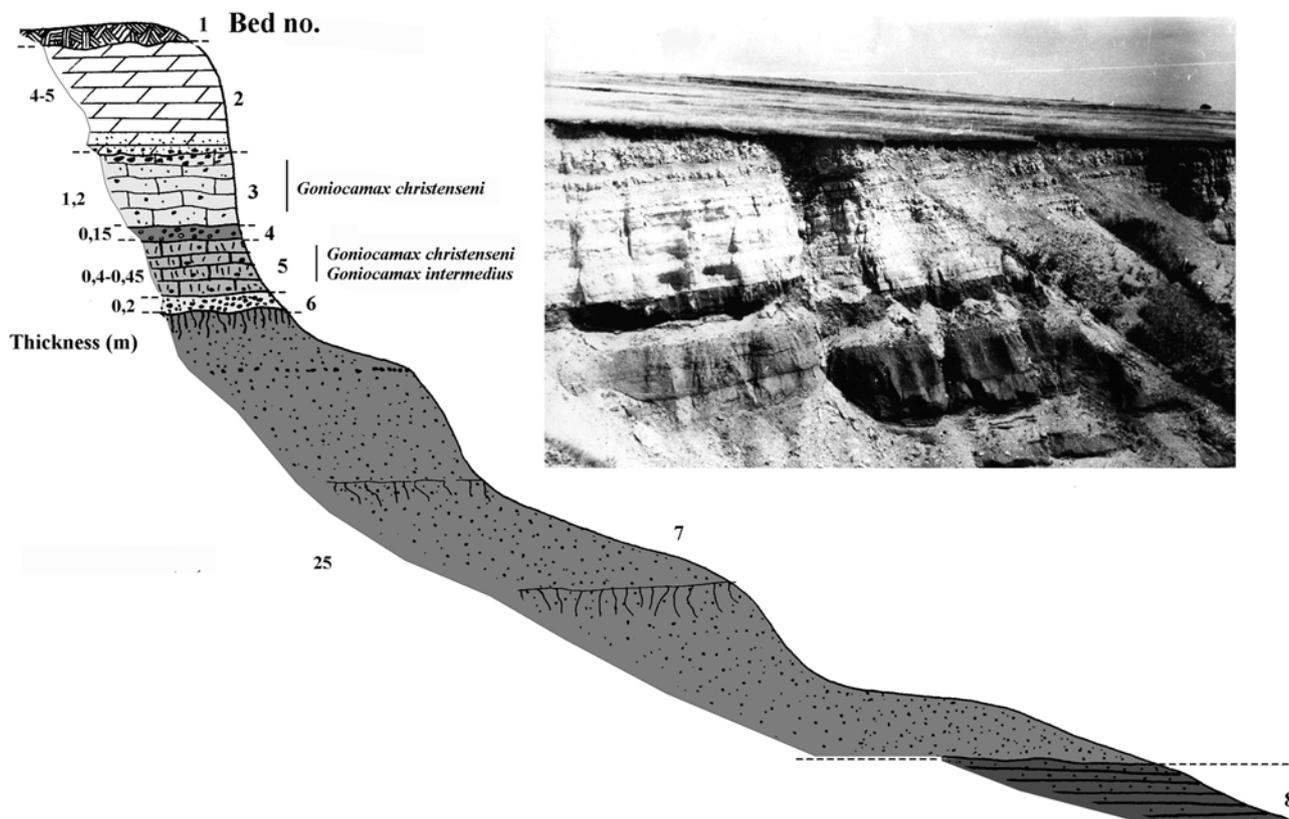


Fig. 4. The section of the type locality of Pudovkino (Russia, Saratov district).

1. Quarternary. 2. Lower Santonian – grey sandy marls, glauconitic at the base with phosphatic nodules, *Inoceramus cardissoides*, *Belemnitella propinqua propinqua*. 3. The uppermost Turonian through early Lower Coniacian, green to grey glauconitic chalk with phosphatic nodules, phosphatized sponges and inoceramids fragments. Holotype of *Goniocamax christenseni* n. sp. (No. 253/3) together with brachiopod *Concinnithyris quidhamtonites*. 4. Upper Turonian – beds with phosphatic nodules, *Goniocamax intermedius*. 5. ?middle – upper Turonian, sandy glauconitic chalk with phosphatic nodules, paratype of *Goniocamax christenseni* n. sp. (249bg) and *Goniocamax intermedius*. 6. ?lower – ?middle Turonian beds with phosphatic nodules, fish bones and shark teeth. 7. Cenomanian – dark grey sandstones with *Exogyra conica*, *Entolium orbiculare* and *Lingula krausei*. 8. Albian – grey claystones. The left numbers – (example 0.4–0.45) thickness in (m). (After Naidin, personal communication 2000).

at about one third of the length of the guard. Ventral and dorsal sides are markedly flattened, the ventral side is more flattened. Depth of the pseudoalveolus is 7–9 mm. The surface of the pseudoalveolus is covered by conellae in the holotype. The Schatzky distance (SD) is 3.1 mm. The alveolar angle is acute, up to 25°, and the angle between the bottom of ventral fissure and the wall of the pseudoalveolus (FA) is less than 30°. Cross section of the pseudoalveolus is oval.

Concentric layers are apparent in this area. Striation is marked on the whole surface of the guard. Dorsolateral compressions and double furrows are well developed. Vascular imprints are apparent especially near dorsolateral double furrows. They are more frequent on the dorsal side. Dorsolateral double furrows reach to the apex. The mucro is indicated but not fully developed in the specimens studied.

Remarks. *Goniocamax christenseni* differs from *G. intermedius* (Fig. 2A–J) by having a larger guard, marked flattening of the dorsal side and a deeper pseudoalveolus. Bottom of ventral fissure is missing in *G. intermedius* reflecting the original poor calcification of the ventral part of the pseudoalveolus in this species. Dorsal side of the guard is more flattened in *G. christenseni* (Fig. 2A) than in *G. lundgreni*. *G. christenseni* has a more acute pseudoalveolus than other common species of *Goniocamax*. In this respect *G. christenseni* shows more similarities to the first representatives of *Belemnitella* (*B. schmidi*, *B. propinqua*) than to *G. lundgreni*. *G. christenseni* n. sp. is the earliest ‘modern’ *Goniocamax* with strongly calcified adoral part.

Geographic distribution. The new species is only known from Russia, where it is recorded from the middle Volga River region, Pudovkino in the Saratov district, and Surskoe in the Ulyanovsk (= Simbirsk) district. *Stratigraphic range.* Upper Turonian – basal Coniacian. Upper Turonian (just above the *Inoceramus lamarcki* Zone – *Inoceramus costellatus* and *Mytiloides incertus* zones probably) to the base of the Coniacian (*Cremnoceramus rotundatus* Zone).

The earliest record of the ‘modern’ *Goniocamax* is *G. christenseni* n. sp. and is based on the four complete guards from Upper Turonian and basal Coniacian deposits of the Volga River region. However, the total stratigraphic range of genus *Goniocamax*, including the ‘primitive’ taxa, *G. intermedius* and *G. surensis*, extends down into the late Middle Turonian (Košťák *et al.* 2004).

Evolutionary history of *Goniocamax* and Turonian belemnite palaeobiogeography

The origin of *Goniocamax* is unknown (Christensen 1997; Christensen & Schulz 1997). Christensen (1988) proposed that the *Belemnitella* stock derived from *G. lundgreni*, which originated from species of *Praeactinocamax* in the Central Russian Subprovince. On the basis of the marked similarity in shape and size of the guard, *G. lundgreni* is here suggested to have evolved from the *G. intermedius*/*G. surensis* group. This group is considered to constitute a primitive clade within *Goniocamax* characterized by having poorly calcified dorsal and ventral pseudoalveolus wall areas (Košťák 2004). The species were placed within the genus *Praeactinocamax* by Christensen & Schulz (1997) on the basis of the absence of the bottom of the ventral fissure. Naidin (1964) described and figured typical specimens of *G. lundgreni* (1964, p. 132, fig. 27, p. 228) without the bottom of the ventral fissure. These specimens strongly resemble the paratype of *G. surensis* from the locality of Gayshin (Belarussia, Sozh River). These rare species were studied by the present author and are retained in *Goniocamax* with respect to their morphology and ontogeny. The bottom of the ventral fissure is probably missing owing to poor calcification of the pseudoalveolus during life. The origin of *G. lundgreni* can be explained by gradual calcification of the anterior part in the *intermedius/surensis* group. *G. christenseni* n. sp. occurs in the upper Turonian deposits of the Central Russian Subprovince (together with *G. intermedius*). It has a well calcified pseudoalveolus and a quite acute pseudoalveolus. This species resembles the first representatives of *Belemnitella* rather than the Coniacian *G. lundgreni* and can be considered an ancestor of the *Belemnitella* stock (Fig. 4). However, the origin of the *Belemnitella* group may be polyphyletic.

Several transitional forms existed between *Praeactinocamax* and *Goniocamax* during the Turonian: *P. matesovae* (Naidin), *P. coronatus* (Makhlin), and *P. sp.1* (Košťák 2004). Some representatives of *Praeactinocamax* resemble the first species of *Goniocamax*, especially by having a similar shape of the guard and by the depth of the pseudoalveolus. *P. matesovae* shows marked similarities to *Goniocamax* but its very shallow and well calcified pseudoalveolus is typical for *Praeactinocamax*. *P. coronatus* has a relatively deep (about 6 mm) pseudoalveolus (typical for *Goniocamax*), but its slender and subcylindrical to high conical guard somewhat resembles the middle Turonian species of *Praeactinocamax* from the North Amer-

Table 2. Late Turonian belemnitellids

North European Province, Central European Subprovince, Baltoscandia	East European Province, Central Russian Subprovince
– very rare and poorly diversified species of <i>Praeactinocamax</i> (including some affinities to the species from the North American Province)	– relative rare and richly diversified species of <i>Praeactinocamax</i> (having no affinities to species from the North European Province)
– no species of <i>Actinocamax</i>	– common subspecies of <i>Actinocamax verus</i>
– no species of <i>Goniocamax</i>	– more abundant and less diversified species of <i>Goniocamax</i>

ican Province - *P. manitobensis* (Whiteaves) and the rare upper Turonian belemnites from the Central European Subprovince and Baltoscandia - *P. bohemicus* (Stolley) and *P. aff. bohemicus* (Košťák 1996). *P. matesovae*, *P. coronatus*, and *P. sp.1* are very rare species of the Central Russian Subprovince (Table 2).

The Turonian belemnitellids of the Central Russian Subprovince (genera *Actinocamax*, *Praeactinocamax* and *Goniocamax* including 13 species; Košťák 2004) show a high endemism during the Turonian. They are not frequent and only rarely migrated to other regions. *Praeactinocamax matesovae* (or a very

similar species) occurs on the Mangyshlak Peninsula (Caspian Sea, NW Kazakhstan; figured as *A. strehlensis* in Marcinowski *et al.* 1996, table 15, fig. 3). *Praeactinocamax* sp. 2 is recorded recently from Tuarkyr (W. Turkestan; Košťák 2004). Late Turonian representatives of *?Praeactinocamax* and *Goniocamax* were discovered in western Siberia (Yenisei River valley, Krasnoyarsk District; Makhlin unpublished and *Praeactinocamax* and *?Goniocamax* are known from the lower (?middle) Turonian deposits of the Russian Arctic regions (Taimyr Region; Barskov *et al.* 1997; Naidin, personal communication 2000). Specimens from the

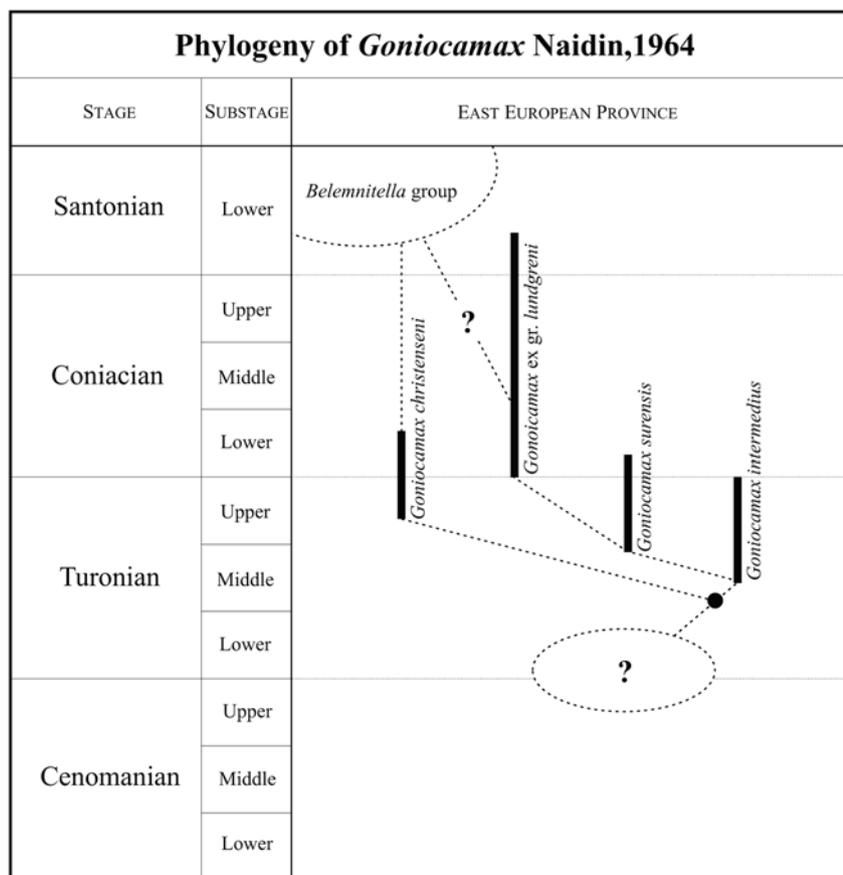


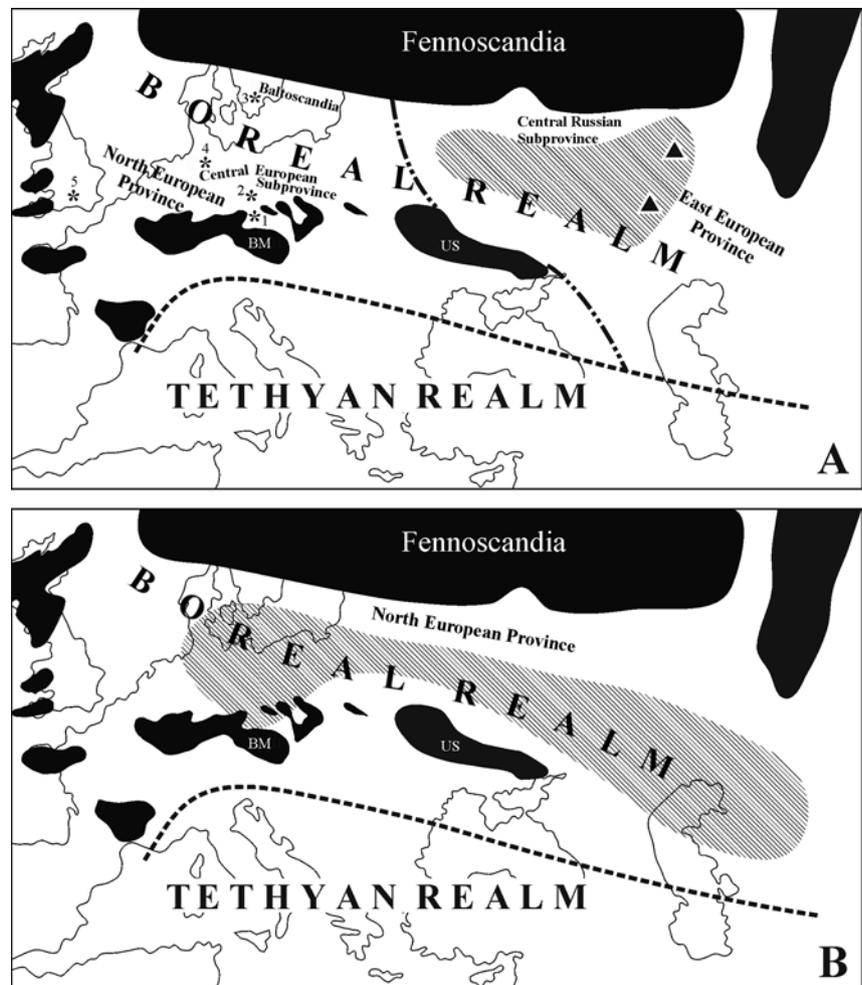
Fig. 5. Phylogeny of *Goniocamax* Naidin. Diagram shows two parallel evolutionary lineages in *Goniocamax* with a probable common ancestor (dot). *G. christensenii* n. sp. is supposed herein to be an older and lineal ancestor of the *Belemnitella* stock (see text).

Fig. 6. A. Palaeobiogeographic distribution of *G. intermedius* (hatch; late Middle to Upper Turonian) and *G. christenseni* (D; Upper Turonian – the base of the Coniacian).

* Indicates the distribution of *Praeactinocamax* in the Upper Turonian (*P. bohemicus* 1–3, *P. paderbornensis* 4, *P. ?bohemicus* 5) of Central and Northern Europe (1. Bohemian Cretaceous Basin, 2. Saxony, Germany, 3. S. Sweden, 4. Münster Basin), and the Lower Coniacian in England (5. Yorkshire).

B. Palaeobiogeographic distribution of *G. lundgreni* s.l. (hatch; including all subspecies) in the Lower Coniacian and basal Santonian.

Gray = land, white = sea. BM – Bohemian massif, US – Ukrainian shield. (after Košťák *et al.*, 2004).



Taimyr Region somewhat resemble the middle Turonian belemnitellids from the North American Province by having a similar shape of the guard (own observation). They have not been systematically evaluated yet. Their occurrence provides good evidence for the existence of the so-called ‘Northern migration route’ (Naidin 1978) across the Arctic circumpolar zones. This migration path could have connected the East European Province with the North American Province in the Turonian (Naidin & Košťák 2000; Košťák & Wiese 2002; Košťák *et al.* 2004; Košťák 2004).

The North European Province was completely isolated from the East European Province during the whole Turonian stage (Christensen 1997; Košťák *et al.* 2004; Table 2). The late Turonian belemnites from the North European Province show marked similarities to those from the North American Province (including North America and Greenland). The East European Province and the North European Province resumed connection in the earliest Coniacian, and fused into a single North European Province *sensu* Christensen (= North European Region *sensu* Naidin).

G. lundgreni is the first typical lower Coniacian species for this province.

Very rare representatives of *Praeactinocamax* immigrated to the Central European Subprovince and Baltoscandia (North European Province) probably from the North American Province in the late Turonian. Species of this genus show the highest diversity in the East European Province in the same time interval but have no known relationship to those in the North European Province. They are comparatively rare and endemic. The first representatives of *Goniocamax* (‘primitive’ – *G. intermedius*, *G. surensis* and ‘modern’ – *G. christenseni* n. sp.) are less diversified but more abundant (*G. intermedius*). The earliest record of the ‘modern’ *Goniocamax* is *G. christenseni* n. sp. is based on the four complete guards recorded from the Upper Turonian and basal Coniacian deposits of the Volga River region. However, the total stratigraphic range of genus *Goniocamax*, including the ‘primitive’ taxa, *G. intermedius* and *G. surensis*, extends down into the late Middle Turonian (Košťák *et al.* 2004). Palaeobiogeographically, *G. christenseni*

belongs to the Central Russian Subprovince of the East European Province (Košťák *et al.* 2004).

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