

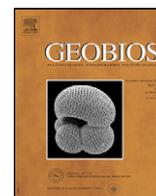


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Original article

On the Turonian origin of the *Goniocamax-Belemnitella* stock (Cephalopoda, Coleoidea)[☆]

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ABSTRACT

A new subgenus within the genus *Goniocamax*, *Progoniocamax* nov. subgen., is described. It includes the Late Turonian–Early Coniacian species “*Actinocamax*” *surenensis* Naidin and *Actinocamax intermedius* Arkhangelsky. The new subgenus represents a transition between the genera *Praeactinocamax* and *Goniocamax*. It occurs in the Central Russian Subprovince. From a geographical point of view, it indicates the origin of the *Goniocamax-Belemnitella* stock to be situated in the Russian Platform (Central Russian Subprovince, East European Province) during the Late Turonian. The origin of the Upper Cretaceous belemnitellid *Goniocamax* Naidin, and consequently the *Belemnitella*-stock, is explained herein by the deepening of the pseudoalveolus and the gradual calcification of the anterior part of the rostrum. The occurrence of the so-called “bottom [base] of ventral fissure”, a major morphological feature known in the later belemnitellids (*Goniocamax*, *Goniotoothis*, *Belemnitella*), the enlarging of the ventral fissure, and the calcification of its surrounding area, enabled a gradualistic increase of the rostra within the *Progoniocamax-Goniocamax-Belemnitella* evolutionary lineage.

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1. Introduction

The Upper Cretaceous belemnitellid *Goniocamax* Naidin, 1964 played an important role in the origin of *Goniotoothis* Bayle, 1878 and *Belemnitella* d'Orbigny, 1840. Christensen and Schulz (1997: p. 20) suggested that the earliest species of these genera, i.e. *Goniotoothis praewestfalica* Ernst and Schulz, 1974 (middle Coniacian–early Santonian) and *Belemnitella schmidi* Christensen and Schulz, 1997 (early Santonian) may have been derived from *Goniocamax lundgreni* (Stolley, 1897) (early Coniacian–early Santonian; Fig. 1(F)) by allopatric speciation.

While the evolution of *Goniotoothis* and *Belemnitella* has been described in great details (Jeletzky, 1955; Ernst, 1964; Naidin, 1964; Christensen, 1995, 1997a, 2000; Christensen and Schulz, 1997), the origin of *Goniocamax* was considered to be unclear. Nevertheless, it was suggested to lie in some species of *Praeactinocamax* Naidin, 1964 in the Central Russian Subprovince (CRS) (Christensen, 1988, 1997a, 1997b; Christensen and Schulz, 1997; Košťák, 2004, 2005; Košťák et al., 2004). Naidin (1964) placed the origin of *Goniocamax* in the Late Turonian *Goniocamax medwedicus* Naidin, 1964. Later, Christensen (1997a: p. 66–67) placed this species in *Praeactinocamax*. Košťák (2004) confirmed this opinion, and assumed *P. medwedicus* to be a descendant of

the Early to Middle Turonian *Praeactinocamax triangulus* Naidin, 1964 (Fig. 1(H)).

Christensen (1997a: p. 67) mentioned several species of *Praeactinocamax* as possible transitional forms between *Praeactinocamax* and *Goniocamax*. However, this model is not followed herein. For instance, *Praeactinocamax aralensis* (Arkhangelsky, 1912) and *P. mujnakensis* (Naidin, 1964) are Late Coniacian species (while the earliest *Goniocamax* occurred in the latest Turonian – see below). They do show strong affinities to the genus *Goniocamax* (Košťák and Wiese, 2006: p. 137). The Late Turonian *Praeactinocamax coronatus* (Makhlin, 1965) is an unambiguous but very rare endemic belemnite with well-developed calcitic pseudoalveolar walls, including the ventral part (the pseudoalveolus represents a more or less conical space between the phragmocone and a well calcificated rostrum; originally, it has been formed by aragonite, which was altered during the diagenesis; Košťák and Wiese, 2008). The Late Turonian *Praeactinocamax medwedicus* (Naidin, 1964) possesses a larger, markedly stouter rostrum. Consequently, it is not a likely ancestral candidate for *Goniocamax*. Moreover, this species is extremely rare, and to date only two specimens are known.

Naidin (1964) assigned both Middle/Upper Turonian *Praeactinocamax matesovae* (Naidin, 1964) and *P. medwedicus* to the genus *Goniocamax*, that is, the oldest more “primitive” part of the *Goniocamax* lineage (Naidin, 1964: pp. 177–178). However, their alveolar parts with a well-developed calcitic pseudoalveolus, but apparently without the development of a “bottom [base] of ventral fissure” (BVF; Fig. 2), points to the genus *Praeactinocamax*. The

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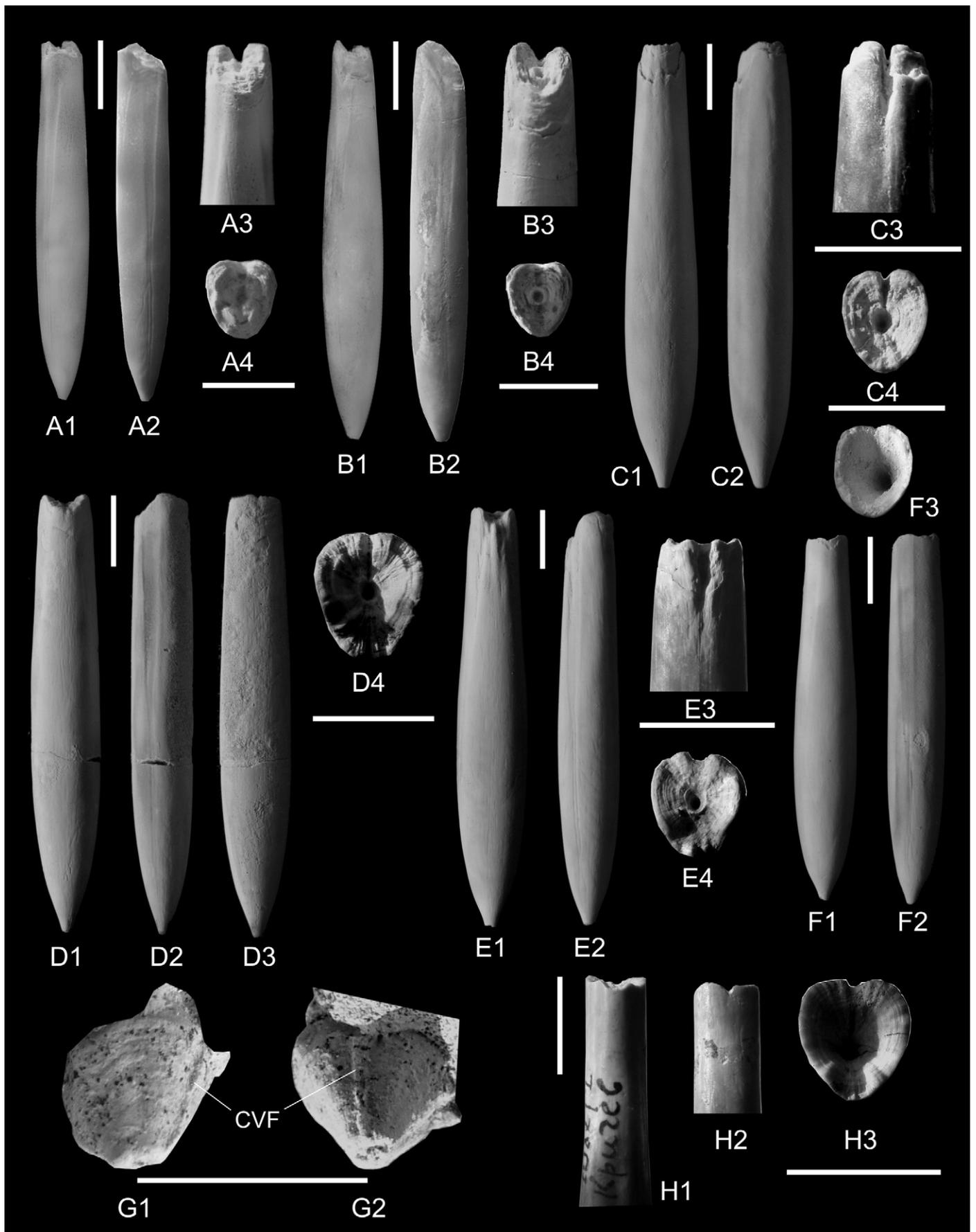


Fig. 1. A. *Goniocamax* (*Progoniocamax*) *surensis* (Naidin, 1964). A1, dorsal view; A2, lateral view; A3, anterior part (dorsal view); A4, pseudoalveolus. Paratype. Specimen No. 87/19–1077/13, Gayshin (Sozh River), S from Slavgorod, Mogilev District, Republic of Belarus. Late Turonian/Early Coniacian. B. *Goniocamax* (*Progoniocamax*) *surensis* (Naidin,

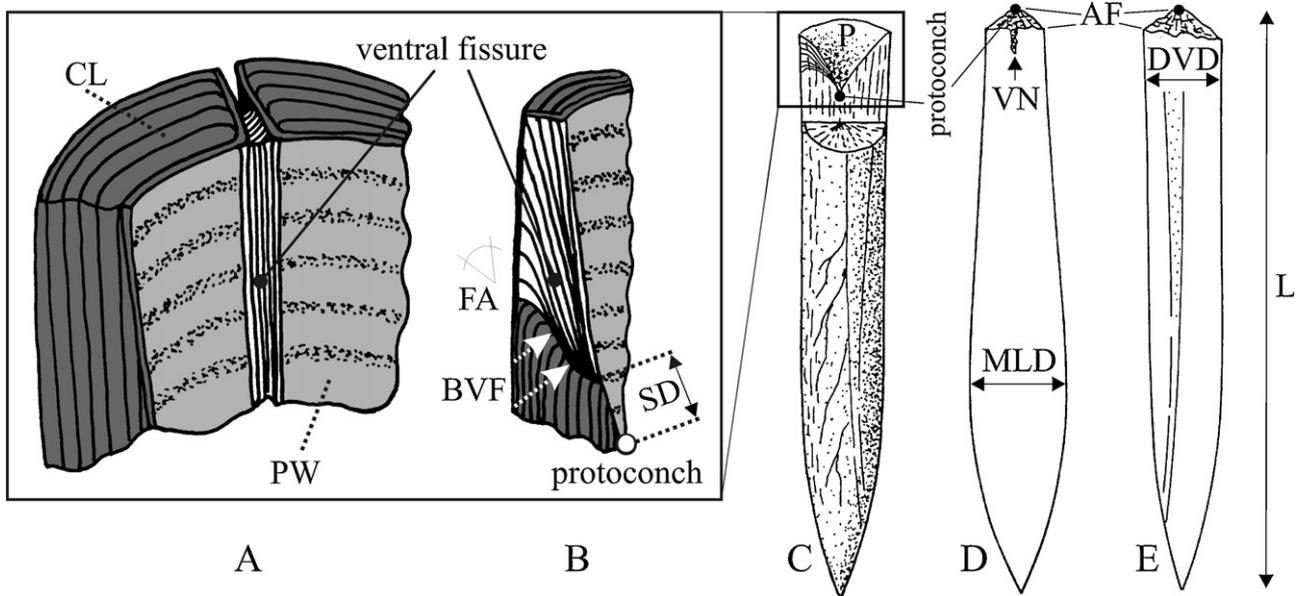


Fig. 2. A, B. Schematic sketch of the rostrum anterior part bearing the ventral fissure. A. View from the inner pseudoalveolus part. B. Longitudinal section of the ventral fissure. CL, calcitic layers; PW, pseudoalveolus wall; BVF, bottom [base] of ventral fissure; FA, fissure angle (angle between the BVF and the pseudoalveolus wall); SD, Schatzky distance (distance between the protoconch and the BVF). Modified after Naidin, 1969. C. *Goniocamax* rostrum: lateral view. P, pseudoalveolus. D. *Praeactinocamax* rostrum: ventral view. E. *Praeactinocamax* rostrum: lateral view. L, length of the rostrum; MLD, maximum lateral diameter; DVD, dorso-ventral diameter; AF, alveolar fracture; VN, ventral notch. Modified after Košťák (2004).

morphological similarity in the shape of the rostrum to *Goniocamax* is basically a matter of convergency.

Another rare species, the Middle/Upper Turonian “*Actinocamax*” *surensis* Naidin, 1964, typically possesses morphological features indicative for both *Praeactinocamax* and *Goniocamax*. This species was included into *Goniocamax* by Košťák (2004: pp. 64–65). According to Košťák (2005: pp. 117–118, fig. 5), both *Goniocamax christenseni* Košťák, 2005 and *G. ex gr. lundgreni* evolved either from *G. intermedius* (Arkhangelsky, 1912) or *Goniocamax surensis* (Naidin, 1964) on the basis of marked similarity of the shape and size of the rostrum. Thus, it appears as being an ancestor taxon for *Goniocamax*. In first instance, these species were placed in *Praeactinocamax* by Christensen and Schulz (1997) based on the absence of the BVF. However, Košťák (2004, 2005) and Košťák et al. (2004) retained them in *Goniocamax* due to their specific morphology and ontogeny.

Herein, *G. intermedius* and *G. surensis* are included into the new subgenus *Progoniocamax* within the genus *Goniocamax*. A well preserved internal mould of the pseudoalveolus of *G. (Pr.) intermedius* (Fig. 1(G1, 2)) has been recorded by the author in the Volga River Region of Central Russia; it clearly shows the presence of a ventral fissure. The aim of this paper is to characterise the evolutionary relationship between the *Belemnitella* stock, including *Goniocamax*, and the genus *Praeactinocamax* from which this stock originated, most likely in the Russian Platform (Central

Russian Subprovince, East European Province *sensu* Košťák et al., 2004: p. 524) during the Late Turonian.

Abbreviations: CRS: Central Russian Subprovince; EEP: East European Province (for the palaeobiogeography see Košťák, 2004; Košťák et al., 2004; Košťák and Wiese, 2006). L: length; MLD: maximum lateral diameter; DVD: dorso-ventral diameter; BVF: bottom [base] of ventral fissure [*sensu* Naidin, 1952; “Fissurboden” *sensu* Ernst, 1964: fig. 3a]; FA: fissure angle (angle between the BVF and the pseudoalveolus wall); SD: Schatzky distance (distance between the protoconch and the BVF).

2. Systematics

Class CEPHALOPODA Cuvier, 1795
 Subclass COLEOIDEA Bather, 1888
 Order BELEMNITIDA Zittel, 1895
 Family BELEMNITELLIDAE Pavlow, 1914
Type genus: *Belemnitella* d’Orbigny, 1840.
Diagnosis: see Christensen (1997a: p. 64).

Goniocamax Naidin, 1964
Type species: *Goniocamax lundgreni* (Stolley, 1897).
Diagnosis: see Christensen and Schulz (1997).

Progoniocamax nov. subgen.
 Figs. 1(A–E, G), 3(C)

1964). B1, dorsal view; B2, lateral view; B3, anterior part (dorsal view); B4, pseudoalveolus. Holotype. Specimen No. 86/19–380, Belovodje (Sura River), Ulyanovsk District, Volga River Region, Russian Federation. Late Turonian. C. *Goniocamax (Progoniocamax) intermedius* (Arkhangelsky, 1912). C1, dorsal view; C2, lateral view; C3, anterior part (ventral view); C4, pseudoalveolus. Specimen No. 250, Novaya Derevnya, Tambov District, Kyrsanovsk Region, Russian Federation. Middle/Late Turonian. D. *Goniocamax (Progoniocamax) intermedius* (Arkhangelsky, 1912). D1, dorsal view; D2, lateral view; D3, ventral view; D4, pseudoalveolus. Specimen No. 8016b, Pudovkino, S from Saratov, Saratov District, Volga River, Russian Federation. Late Turonian. E. *Goniocamax (Progoniocamax) intermedius* (Arkhangelsky, 1912). E1, dorsal view; E2, lateral view; E3, anterior part (ventral view); E4, pseudoalveolus. Specimen No. 5545/16, Kamenka (Sozh River), Kritchev (Krychaw) Town, Mogilev District, Republic of Belarus. Middle/Late Turonian. F. *Goniocamax (Goniocamax) lundgreni* (Stolley, 1897). F1, dorsal view; F2, lateral view; F3, pseudoalveolus. Specimen No. 1079/2, Gayshin (Sozh River), S from Slavgorod, Mogilev District, Republic of Belarus. Early/Middle Coniacian. G. *Goniocamax (Progoniocamax) intermedius* (Arkhangelsky, 1912), pseudoalveolus internal mould. G1, lateral view; G2, ventral view; CVF, cast of the ventral fissure. Specimen No. S1999/p, Svyataya Gora, Surskoe Town (Sura River), Ulyanovsk District, Volga River Region, Russian Federation. Late Turonian. H. *Praeactinocamax triangulus* Naidin, 1964. H1, dorsal view; H2, ventral view with slightly indicated ventral fissure; H3, pseudoalveolus. Specimen No. 1082/2, Kritchev (Krychaw), Sozh River, Mogilev District, Republic of Belarus. Early Turonian. A, B: Collections of the Moscow State University, Moscow; C–H: Collections of the Institute of Geology and Palaeontology, Faculty of Science, Charles University, Prague. A, B, C1–2, D1–3, E1–2, F1–2 are coated with ammonium chloride. Scale bars: 1 cm.

Derivatio nominis: being ancestral (hence *pro*) to *Goniocamax*.

Type species: *Actinocamax intermedius* Arkhangelsky, 1912 (p. 582, pl. IX, fig. 30).

Species included: *Goniocamax* (*Progoniocamax*) *intermedius* (Arkhangelsky, 1912) (Fig. 1(C–E, G)), *Goniocamax* (*Progoniocamax*) *surensis* (Naidin, 1964) (Fig. 1(A, B)).

Stratigraphical distribution: Late Middle Turonian (*Inoceramus lamarcki* Zone)–early Coniacian (?*Cremnoceras rotundatus* Zone).

Geographical distribution: central Russian Subprovince (see Košťák, 2004; Košťák et al., 2004). *G. (Pr.) intermedius* occurs in the Saratov, Ulyanovsk, Tambov and Volgograd districts (Russian Federation), while *G. (Pr.) surensis* occurs in the Ulyanovsk and Volgograd districts (Russian Federation) and in the Mogilevsk district (Republic of Belarus).

Diagnosis: medium-sized rostrum (L 52–75 mm, average 65 mm), lanceolate in dorso-ventral view and slightly lanceolate to subcylindrical in lateral view. Ventral side markedly flattened. Cross-section oval to triangular. Alveolar end poorly calcified, especially at the dorsal and ventral margins. Ventral fissure usually poorly calcified, with a typical V-shaped mark in dorso-ventral view. Distance from the protoconch to the margin of the pseudoalveolus shorter in dorsal side. Average depth of the pseudoalveolus 4–6 mm. Ventral fissure often not preserved due to poor calcification of this area. Dorso-lateral compression distinctive and double lateral lines fully developed. Striations and vascular imprints well developed in most specimens; granulation not observed.

Differential diagnosis: *Progoniocamax* is a transitional form between *Praeactinocamax* and *Goniocamax*. Pseudoalveolus relatively deep; ventral and especially dorsal walls still poorly calcified, in contrast to *Goniocamax*. Isometric growth relationship between length and maximal lateral diameter of the rostrum, like in *Praeactinocamax*, but allometric growth relationship between the length of the rostrum and the dorso-ventral diameter of the protoconch. Overall shape and major outer-morphological features of the rostrum almost identical to the stratigraphically younger *G. ex gr. lundgreni* and *G. christenseni*; main difference relates to the poorly calcified walls of the pseudoalveolus in *Progoniocamax*, and especially in the ventral fissure-area.

Remarks: The uniquely preserved internal mould of the pseudoalveolus of *G. (Pr.) intermedius* shows the presence of a well-developed and relative long ventral fissure (Fig. 1(G)), which makes up a part of the non-calcified and/or poorly calcified anterior part of the guard.

3. Morphology and evolutionary trends in the Turonian belemnitellids

The alveolar fracture (conical structure with a very sharp and distinct boundary between calcitic and aragonitic part of the rostrum; Fig. 3(A, B); Košťák and Wiese, 2008) is a very important taxonomical feature in belemnitellids; in *Actinocamax* Miller, 1823 and *Praeactinocamax*, the alveolar fracture is conical-shaped; in *Actinocamax*, it is even highly conical, while in *Praeactinocamax*, it is less conical but with the onset of a pseudoalveolus. In some species of *Praeactinocamax* and in part in *Progoniocamax*, often a short fraction of the ventral fissure is preserved. In phylogenetically more advanced belemnitellids (*Goniocamax*, *Goniot euthis*, *Belemnelloamax* (Naidin, 1964), *Belemnitella*, and *Belemnella* (Nowak, 1913)), the ventral fissure is characterized by narrowing of the calcitic layers towards the margin, by higher density of growth lines, and by the disruption of the continuity of the calcitic layers at the ventral fissure (Fig. 2). The internal parts of the walls of the ventral fissure are built up by very thin calcitic layers. The

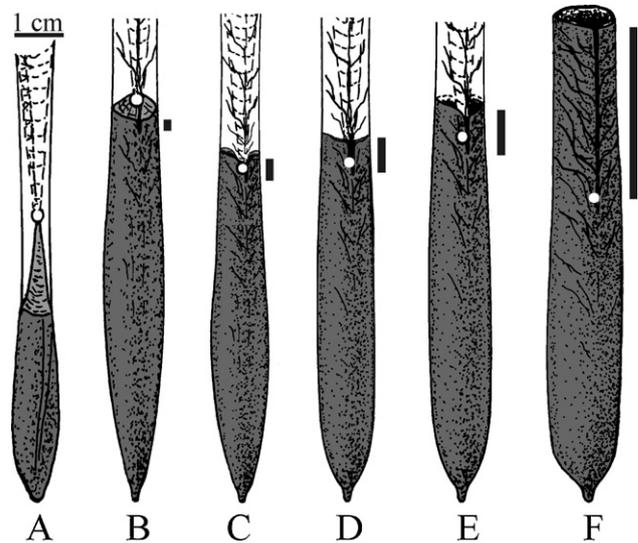


Fig. 3. The progressive calcification of the rostrum in genera: **A.** *Actinocamax* with highly conical alveolar fracture (lateral view). **B.** *Praeactinocamax*. **C.** *Goniocamax* (*Progoniocamax*). **D.** *Goniocamax* (*Goniocamax*). **E.** *Goniot euthis*. **F.** *Belemnitella* (B–F ventral views). Light grey, alveolar fracture; dark grey, well-calcified rostrum; white dot, position of the protoconch; black lines, length of the ventral fissure. White parts of the rostra (A–E) with phragmocone and vascular imprints indicated; aragonitic anterior part (usually not preserved).

distinct boundary between the calcitic layers of the ventral fissure and those of the guard itself, is called the “bottom [base] of ventral fissure”, cf. Naidin, 1952: fig. 12; Naidin, 1964: fig. 2; Naidin, 1969: fig. 24). A third kind of calcitic layer fills in the open space in the ventral fissure. It can occasionally be observed in some well-preserved guards (recorded mainly in genera *Belemnitella* and *Belemnella*), but it is not clear, if it is present in all belemnitellids.

It is generally accepted, however without any relevant evidence, that the morphology of this part of the body of the belemnite (i.e., ventral fissure vicinity) was connected with some unidentified organ or fins (Ernst, 1964, fig. 21; Stevens, 1965: fig. 18, pp. 50–53). As the imprints of soft parts on the guard are virtually unknown in belemnitellids, this theory could eventually be supported by circumstantial evidence only; for instance the higher density of vascular imprints, which apparently indicates an enhanced blood circulation. In this respect, the calcification of the ventral fissure-area played an important role in the re-inforcement, and subsequently the protection of this part of the animal.

In *Actinocamax*, we can observe a quite conservative morphology during phylogeny. All species are characterized by a high conical alveolar fracture and only little differentiation is noted between the species. The length of the rostra does not exceed 55 mm (Christensen and Schulz, 1997; Košťák and Wiese, 2008: p. 672), except in the Early Campanian *Actinocamax laevigatus* (Arkhangelsky, 1912), which is significantly larger. The growth of the rostrum is isometric. The ventral fissure, pseudoalveolus and consequently the BVF are absent. Granulation may be present in some specimens (Naidin, 1964; Christensen and Schulz, 1997: p. 22). The earliest species of this genus (*A. verus antefragilis* Naidin, 1964) occurred in the Early Turonian and the genus became extinct in the Lower/Upper Campanian boundary interval (Christensen, 1997a: fig. 1). The ancestor of *Actinocamax* is unknown but is generally believed to be related to some Early Cenomanian belemnopseid.

Praeactinocamax is characterized by medium-sized rostra, not exceeding 115 mm (Christensen, 1997a). The alveolar fracture is usually a low cone-shaped type, however a relative deep (up to 6 mm) pseudoalveolus can be present in some species (Naidin, 1964; Košťák, 2004). A very short ventral fissure can be present.

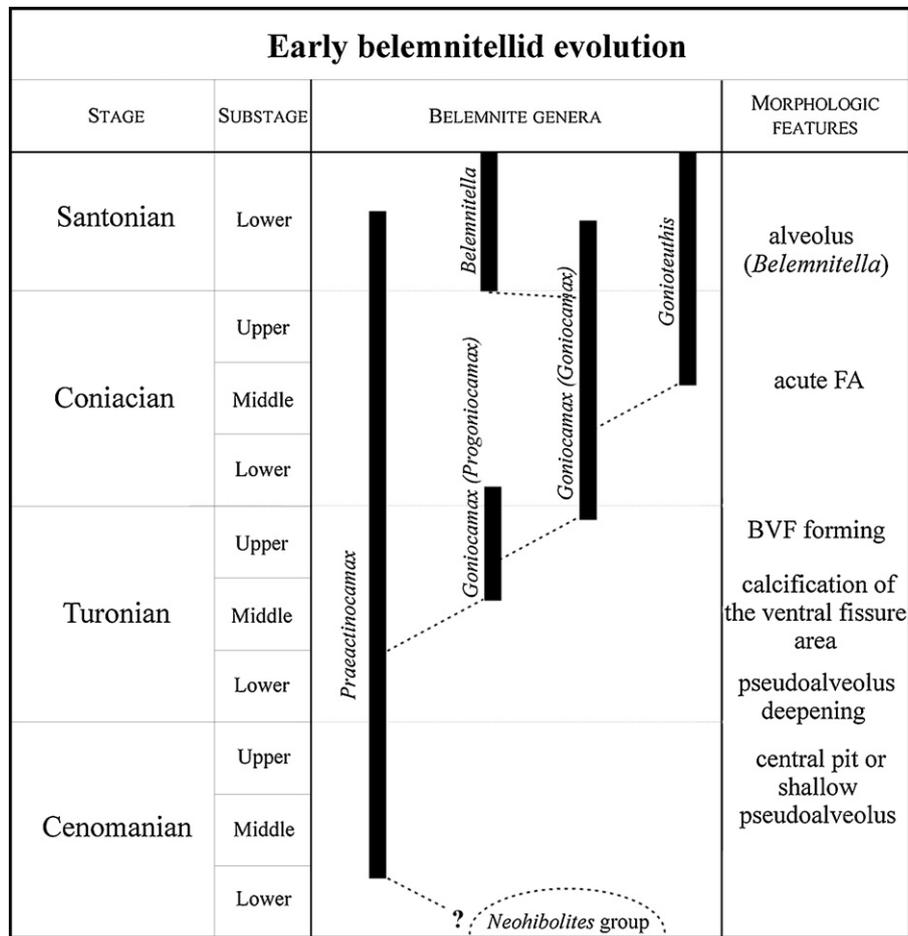


Fig. 4. Phylogeny of the *Praeactinocamax*-*Belemnitella* lineage in relation to occurrence of major morphological features.

The growth of the rostrum (L/MLD) is allometric, however not in all growth stages in different species (see Košťák, 2004: p. 56). Adult specimens are generally stouter than juvenile specimens (Košťák and Pavliš, 1997). In this genus, a trend towards deepening of the pseudoalveolus is observable. Recently, the pseudoalveolus deepening has been described by Košťák and Wiese (2011) in extremely rare Turonian specimens of *P. aff. strelhensis* (Fritsch and Schlönbach, 1872) from the locality Úpohlavý (Bohemian Cretaceous Basin).

In *Goniocamax (Progoniocamax)*, the pseudoalveolus is already relatively deep (4–6 mm). However, only a part of the ventral fissure is occasionally preserved. The evolutionary lineage is represented by two species so far. The late Middle Turonian *G. (Pr.) intermedius* and the Late Turonian–Early Coniacian *G. (Pr.) surensis*. *Progoniocamax* may be evolved from the Early to Middle Turonian species *Praeactinocamax triangulus*, based on the following reasoning:

- the cross-section of the adoral end and the general alveolar characteristics highly correspond;
- the gradual calcification in both the lateral and the ventral alveolar part in juvenile *P. triangulus* specimens (the particular V-shaped notch; Košťák, 2004: pl. 4, fig. 3);
- the growth and partly the shape of adult *G. (Pr.) intermedius* is similar to juvenile/adolescent specimens of *P. triangulus* (up to 61 mm, i.e. ~75% of the total length of the adult rostrum; the growth is isometric with respect to L/MLD). The average length in adult *G. (Pr.) intermedius* specimens is 65 mm. Juvenile rostra of both species are almost identical (Košťák, 2004: pl. 4, figs. 2–4; Naidin, 1964: pl. 8, fig. 2b);

- *P. triangulus* is a quite common and widespread species on the Russian Platform; it ranges from the Early to Middle Turonian (~2.5 My). Therefore, it might be a good candidate as a precursor.

The origin of both taxa (*P. triangulus* and *G. (Pr.) intermedius*) lies in the same area (EEP, CRS) and these taxa probably overlap for a short time in the Middle Turonian. However, precise stratigraphical data do lack at the moment. Moreover, as they occurred in the same geographical area, and probably coexisted for a short time, the *G. (Pr.) intermedius* based on derivation from *P. triangulus* probably could not be explained by allopatric speciation. However, some morphological and ontogenetic similarities between juvenile to subadult specimens of *P. triangulus* and adult specimens of *G. (Pr.) intermedius*, a neotenuous origin of *Progoniocamax* is likely. It could also explain the decrease in the length of the rostrum (Fig. 3) in the earliest species of the lineage *Progoniocamax*-*Goniocamax*-*Belemnitella*. During later phylogeny, the size of the rostrum increased and gradual calcification of the adoral part continued (Ernst, 1964; Christensen, 1995, 1997a, 2000; Christensen and Schulz, 1997).

Goniocamax (Goniocamax) is characterized by small to medium-sized rostra (60–80 mm) and the presence of a BVF. In general, the BVF is straight or slightly curved. The average depth of the pseudoalveolus is 5–6 mm. The angle between the BVF and the FA is 30–50°. The Schatzky distance is small (2–4 mm). Christensen (1997a) reported an allometric relationship in L/DVD, however in L/MLD, this genus shows isometric growth. Probably, *Goniocamax (Goniocamax)* evolved from *Goniocamax (Progoniocamax)* in the Late Turonian. However, Košťák (2005: p. 97, fig. 5) advocated the existence of a common ancestor of both taxa already in the late

Middle Turonian, because the earliest species of *Goniocamax* (*Goniocamax*) (i.e., *G. christenseni*) already have a well-calcified pseudoalveolus and quite an acute FA (28°). Therefore it is most probable that both *G. christenseni* and *G. ex gr. lundgreni* had a common ancestor in the *intermedius/surensis*-group.

4. Discussion

The phylogeny of *Praeactinocamax* is well documented, especially in the EEP (Naidin, 1964; Christensen, 1997b; Christensen and Schulz, 1997; Košťák, 2004, 2005; Košťák et al., 2004). The oldest representative of this genus, *P. primus* (Arkhangelsky, 1912), first occurred in the late Early Cenomanian; its descendant *P. plenus* (de Blainville and Ducrotay, 1825) disappeared in the Late Cenomanian (however, Košťák and Wiese (2008) reported *P. aff. plenus* from the earliest Early Turonian of NW Siberia). They are characterized by a calcitic short, cone-shaped alveolar fracture, with a very shallow central pit (Košťák and Wiese, 2008). These authors assumed that this shallow pit, surrounding the protoconch, represented the origin of the pseudoalveolus. This process, in which the pseudoalveolus progressively calcified, apparently first occurred in the (?) late Middle Cenomanian and continued through the Turonian, culminating in the Late Turonian into an unusual, endemic species (*P. coronatus*) showing maximum depth of the pseudoalveolus in this genus.

In *Goniocamax* (*Progoniocamax*), the calcification process evolved slightly differently. It initiated at the ventro-lateral part of the wall of the pseudoalveolus and continued into the ventral sides, to the ventral fissure vicinity. The time-gap that existed between a phase of poor calcification of this area and the secondary gradual calcification is supposed herein to be the beginning of the BVF forming. The original matter was later substituted by calcitic layers, but was most probably originally aragonitic (Barskov et al., 1997; Dauphin et al., 2007; Košťák and Wiese, 2008). The size and the shape of the *G. (P.) intermedius* and *G. (P.) surensis* rostra already fully correspond to those in the earliest species of *Goniocamax* (*Goniocamax*).

In *Goniocamax* (*Goniocamax*), the BVF occurs for the first time in the Late Turonian species *G. christenseni*. However, in some specimens of the older *Goniocamax* populations, i.e. the Early/Middle Coniacian *G. ex gr. lundgreni*, an “atavistic” expression was observed. Apparently, they do seem to lack the BVF (Naidin, 1964; Ernst, 1964; Košťák, 2004). In *G. christenseni*, this “atavistic” phenomenon has not been observed yet, probably because of the rarity of the species, as only four specimens are known so far. This “atavistic” phenomenon additionally could support the idea of an evolutionary derivation from *Praeactinocamax* ancestors, in which there is no BVF present, neither in shallow nor in deeper, both well calcified pseudoalveoluses.

5. Conclusions

Morphological changes in the studied taxa are explained by the gradual calcification of the anterior (adoral) part of the rostrum and the deepening of the pseudoalveolus (Fig. 3). Species in *Progoniocamax* are considered to be the direct ancestors of the *Goniocamax-Belemnitella* stock (Fig. 4). Species of *Progoniocamax* subgen. nov. are most probably derived from the Early to Middle Turonian species *P. triangulus*.

The origin of the earliest representatives of the *Belemnitella* stock, i.e. the genus *Goniocamax*, has been explained by gradual calcification of the pseudoalveolus in a species derived from the genus *Praeactinocamax*. However, a relatively long ventral fissure connecting the pseudoalveolus and the external part of the rostrum existed already in *G. (P.) intermedius*. This morphological

feature is known thanks to the uniquely preserved internal mould of a pseudoalveolus of *G. (P.) intermedius* described and figured in this paper.

Progoniocamax nov. subgen., represents the transition between *Praeactinocamax* and *Goniocamax*. This evolution likely occurred in the Central Russian Subprovince. Consequently, the radiation within the belemnitellids initiated on the Russian Platform during the Cenomanian–Coniacian. The *Goniocamax-Belemnitella* stock originated during the Late Turonian as a descendant of the *G. (P.) intermedius/surensis*-group. The Late Cretaceous belemnite family Belemnitellidae is confirmed to be monophyletic, except for *Actinocamax*, which origin still remains enigmatic.

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