Cenomanian through the Lowermost Coniacian Belemnitellidae Pavlow (Belemnitida, Coleoidea) of the East European Province

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ABSTRACT: Seventeen Cenomanian through the lowermost Coniacian species of Belemnitellidae Pavlow from the East European Platform are redescribed, reviewed and re-evaluated. They belong to three genera – *Praeactinocamax* Naidin, *Actinocamax* Miller and *Goniocamax* Naidin. Three species (*Praeactinocamax* cf. *strehlensis*, *P.* sp. 1 and *P.* sp. 2) are retained in the open nomenclature with respect to shortage of material. *Goniocamax* sp. will be subsequently introduced as a new taxon in a separate paper. The unclear systematics of *Praeactinocamax plenus* Blainville and its related species is clarified. The Lower Turonian appearance of this species has not been confirmed. *Praeactinocamax triangulus* Naidin and *Praeactinocamax contractus* Naidin are raised to the rank of independent species. A poorly known *Praeactinocamax sozhensis* Makhlin is morphologically very similar to *Praeactinocamax plenus*; the differences between the two taxa are particularized. These species are statistically evaluated using also a new parameter – DAMLD/MLD quotient. The phylogeny is based on guard morphology and the known stratigraphic distribution. Palaeobiogeograhy of Cenomanian through Coniacian belemnitellids has been newly reconstructed. Maps showing their palaeobiogeographic distributions are figured. Belemnitellid habitats enabled to show the existence of Turonian biogeographic barriers. A new paleobiogeographic province (East European Province sensu Naidin et Košťák 2000) is particularized in more detail. Possible migration paths shows general trends of westward belemnite shift, a poorly known southward shift (to the Turkestan area), and a probable eastward and hypothetical northeastward migration via Turgay channel. The barrier between East European Province and Middle- and Northwest European areas in the Turonian was confirmed. Four belemnite biozones (*Praeactinocamax primus* Zone, *P. plenus* Zone, *P. triangulus* Zone and *Goniocamax intermedius* Zone) and belemnite events are established. Stratigraphic ranges are specified in the traditional three-substage division. The Upper Cretaceous belemnite occurrences in relation to generic eustatic curve are opened for discussion, however, the general trend observed shows a marked dependence between belemnitellid distribution and eustatic cycles. A possibility of sexual dimorphism in some Upper Cretaceous belemnitellids is highly probable. It is displayed especially in the larger set of *Praeactinocamax plenus* in which two different morphotypes are observed.

KEY WORDS: Upper Cretaceous Belemnites, Belemnitellidae, Systematics, Morphology, Phylogeny, Palaeobiogeography, Stratigraphy, Paleoecology, Cenomanian – Coniacian, East European Platform.

Introduction

This work is intended as a re-evaluation of the belemnite collection of Prof. D.P. Naidin. This collection was established by D.P. Naidin, M.I. Sokolov, Yu.I. Katz, O.V. Florova, N.P. Mikhailov, V.D. Ilyin, M.M. Pavlova and others during 1946–1996, and several tens of specimens were found during the summer 1999 expedition to the Volga River region. The collection contains several hundreds of specimens of Cenomanian through the lowermost Coniacian belemnitellids. This collection is valuable and deserves comparison with belemnitellids from western, northwestern and central Europe (revised by Christensen 1970–2000).

Belemnites of the eastern part of the European Palaeobiogeographic Region (EPR) were studied in detail by Arkhangelsky (1912), Pavlow (1914), Jeletzky (1948, 1949, 1955), Naidin (1952, 1956, 1959, 1964, 1969, 1978), Naidin and Reyment (1962), Nikitin (1958), Makhlin (1965, 1973), Glazunova (1972), Ali-Zade (1972) and Aliev and al. (1988) in the past, and were partly reviewed by Christensen (see 1974, 1990) more recently. East European belemnitellids are now virtually unstudied (except for separate records by Marcinowski et al. 1996). This study made use of previous older papers and monographs, original photos, and field diaries of Prof. Naidin, section drawings (Text-figs. 2–6), recently published stratigraphic and systematic revisions and personal communications.

Holotypes and paratypes housed in the collections of the Moscow State University were compared with the specimens studied. Author's field trips were concentrated to the important Volga region (Ulyanovsk = Simbirsk district) to clarify the stratigraphy and palaeobiogeography of the Turonian belemnitellids from Russia. Several specimens of the extremely rare *Praeactinocamax planus* (Makhlin) and *P. coronatus* (Makhlin) were found after more than 40 years.

The material studied comes from 38 localities of seven countries – Ukraine, Lithuania, Belarussia, Russia, Kazakhstan, Turkestan and Uzbekistan (see Text-fig. 1).

Belemnitellids are represented by three genera and 14 to 17 species. Three of these species are retained in the open nomenclature due to the lack of sufficient distinct material. *Goniocamax* sp. (Košťák in prep.) will be subsequently described as a new species.

The first stratigraphic sketch of the belemnite-bearing areas of the East European Platform was given by Arkhangelsky (1912). Precise stratigraphy of these areas was described and

■ **Text-fig. 1.** Geographic position of belemnitellid localities – species occurrence, basic geographic and stratigraphic characteristics, common fauna.

Belemnite localities are cited below in alphabetical order.

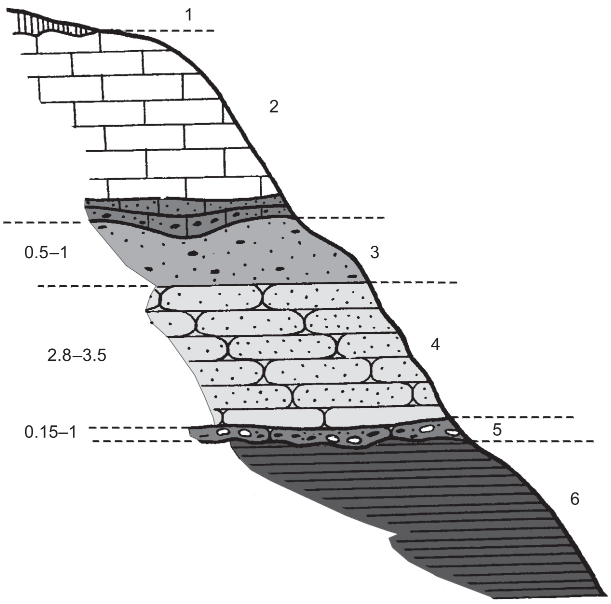
1. Ak-Kuly – *Praeactinocamax triangulus*; Turkistan, Tuarkyr; lower Turonian.
2. Ak-Kup – *Praeactinocamax* sp. 2. Turkistan, Tuarkyr; Turonian/Coniacian boundary interval; together with *Inoceramus schloenbachi*.
3. Aksyirtau – *Praeactinocamax plenus*; Kazakhstan (NW), Mangyshlak, Caspian sea, Aktau. *P. plenus* occure 1 m above the base of the upper Cenomanian together with *Inoceramus pictus bohemicus*.
4. Aktau – *Praeactinocamax plenus*; see Aksyirtau, Koksyirtau; upper Cenomanian.
5. Aktulagai – *Praeactinocamax primus*; Kazakhstan (NW), NW of the Caspin sea; middle Cenomanian.
6. Alexandrovka – *Praeactinocamax triangulus*; Russia, Penza District, Narovchat Region; lower Turonian.
7. Besh-Tyube – *Praeactinocamax triangulus*; Uzbekistan, Amu-Darya valley; upper middle Turonian; together with *Mammites nodosoides*, *Baculites romanovskii*, *Arkhangelskiceras* sp. (= *Watinoceras* sp.).
8. Betovo – *Praeactinocamax triangulus*, *P. sozhensis*; Russia, Bryansk District, Desna River, NW from Bryansk; middle/upper Cenomanian–lower/middle Turonian.
9. Boltaevka – *Praeactinocamax triangulus*, *P. planus*, *P. coronatus*, *Actinocamax verus*; Russia, Ulyanovsk (Simbirsk) District, 7 km S from Surskoe, Sura River; Albian, middle–upper Turonian.
10. Bryansk – *Praeactinocamax primus*, *P. triangulus*, *P. sozhensis*, *P. contractus*; Russia, Bryans District, Bryansk – cement quarry N from Bryansk; Cenomanian–lower Turonian.
11. Demorukoe – *Praeactinocamax triangulus*; Russia, Penza District, Penza; lower Turonian.
12. Donbas – *Praeactinocamax plenus*; Russia, 1. northern Donbas – lokality Zimogorje, upper Cenomanian limestones, 2. southern Donbas, Russia-Ukraine borders – lokality Beloyarovka, upper Cenomanian phosphatised marls.
13. Fokino – *Praeactinocamax primus*, *Praeactinocamax* aff. *triangulus*, *P. triangulus*, *P. sozhensis*, *G. intermedius*; Russia, Bryansk District, 20km N from Bryansk, middle/upper Cenomanian–Coniacian.

14. Gryaz – *Praeactinocamax triangulus*, *P. sozhensis*; Russia, Smolensk District, Khislavichi Region, Sozh River; Cenomanian–Turonian.
15. Kamenka – *Praeactinocamax triangulus*, *P. contractus*, *G. intermedius*; Belarussia, Mogilevsk District, 7 km from Kritchev, Sozh River; lower–upper Turonian.
16. Kanyev – *P. contractus*; Ukraine, Cherkassy District, southern from Kanyev town, Dnyepr River, locality Yarkiy Gnilovod; upper Cenomanian–lower Turonian.
17. Kelat – *Praeactinocamax plenus*; Turkistan, E from Ashkabad, eastern Kopetdag; upper Cenomanian.
18. Khoper – *Praeactinocamax triangulus*; Russia, Volgograd District, S from Uryupinsk town; lower Turonian.
19. Koksyirtau – *Praeactinocamax plenus*; see Aksyirtau; 3–4m above the base of the upper Cenomanian, together with *Oxytoma* sp.
20. Kolodec Kemal – *Praeactinocamax plenus*; Kazakhstan (NW), Mangyshlak peninsula; upper Cenomanian.
21. Kritchev – *Praeactinocamax triangulus*; Belarussia, Mogilevsk Dostrict, Kritchev Region, Sozh River, lower Turonian.
22. Kupol Troitskij – *Praeactinocamax primus*; Kazakhstan (NW), northern area of the Caspian sea; middle–upper Cenomanian..
23. Kyrsanovsk – *Goniocamax intermedius*; Russia, Tambov District, Kyrsanovsk Region; middle–upper Turonian.
24. Mangyshlak – *Praeactinocamax plenus*; see Aksyirtau, from several localities.
25. Medwedica – *Praeactinocamax triangulus*, *P. sozhensis*; Russsia, Volgograd District, Yegorovka; lower Turonian.
26. Nizhne Bezymianskiy – *Praeactinocamax primus*, *P. sozhensis*, *P. triangulus*; Russia, Volgograd District, S from Uryupinsk town, Khoper River; middle–upper Cenomanian–lower Turonian. Nizhne Soinskiy – see N. Bezymyanskiy.
27. Novaya Derevnya – *Goniocamax intermedius*; Russia, Tambov District, Kyrsanovsk Region; middle–upper Turonian, together with *Actinocamax verus fragilis*.
28. Ozarincy – *Praeactinocamax primus*; Ukraine, Vinitsa District, N from Mogilev Podolskiy, middle–upper Cenomanian. (also locality of J.A. Jeletzky).
29. Pady – *Praeactinocamax primus*; Russia, Saratov District, N from Balakovo town, Khoper River; middle–upper Cenomanian, together with *Oxytoma* sp.
30. Pudovkino – *Praeactinocamax triangulus*, *P. sozhensis*, *P. contractus*, *G. intermedius*, *G.* sp.; Russia, Saratov District, Volga River, S from Saratov; Albian–Santonian. Photo 2.
31. Shchigri – *Praeactinocamax triangulus*; Russia, Kursk District, E from Kursk; Cenomanian–Turonian.
32. Semiluky – *Praeactinocamax triangulus*; Russia, Voronezh District; lower Turonian.
33. Strypa – *Praeactinocamax plenus*; Ukraine, Ternopol District, Strypa River; upper Cenomanian.
34. Surskoe – *Praeactinocamax contractus*, *G. intermedius*, *G. surensis*, *G.* sp., *A. verus antefragilis*, *P.* sp. 1; Russia, Ulyanovsk (Simbirsk) District, Surskoe town – locality Promza River, Svyataya Gora; Albian, lower–upper Turonian.
35. Tcherpetovo – *Praeactinocamax primus*, *P. sozhensis*, *P. triangulus*; Russia, Bryansk District, N from Bryansk, Desna River; middle/upper Cenomanian -lower Turonian, together with *Cretirhynchia robusta*.
36. Tuarkyr – *Praeactinocamax triangulus*, *P.* sp. 1; Turkistan – see Ak-kup, Ak-kuly.
37. Valkininkai – *Praeactinocamax plenus*; Lithuania, SW from Viľnius; upper Cenomanian.
38. Vygonitchi – *Praeactinocamax primus*, *P. sozhensis*, *P. contractus*; Russia, Bryansk District, S from Bryansk; middle/upper Cenomanian–lower Turonian

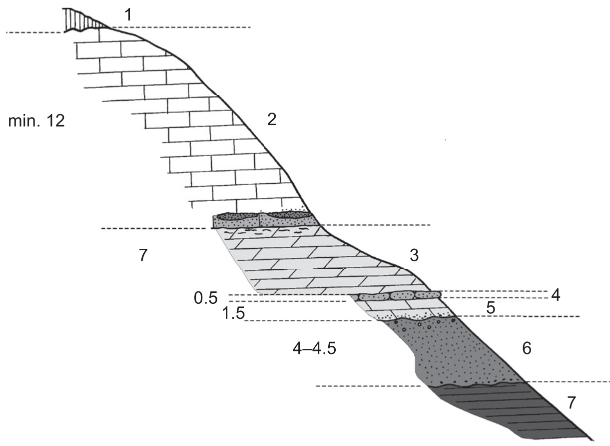
completed especially by Naidin (1952, 1956, 1959, 1964, 1978, 1982, 1985, 1987, 1995, 1996), Naidin and al. (1984, 1986, 1991, 1993), Naidin and Kopaevich (1988), Naidin and Volkov (1998). In the selected areas, the stratigraphy was studied in relation to belemnite occurrence by Nikitin (1958), Makhlin (1965, 1973), Glazunova (1972), Ali-Zade (1972), Aliev and al. (1988), Marcinowski and al. (1996). Russian traditional two-substage division (sensu Naidin – see above 1952–1996) was transformed into European “classic” three-substage division especially by Tröger (1981, 1987 – based on inoceramids) and Marcinowski and al. (1996 – ammonites and inoceramids). The three-substage division is followed in this paper, and the important work of Naidin and Kopaevich (1988) is used for comparison. Stratigraphy of the localities studied is discussed in more detail in the above mentioned publications. The compilation used herein is shown in Text–fig. 7.

Belemnites represented a dominant nektonic assemblage in the Late Cretaceous seas in the eastern parts of the European Palaeobiogeographic Region. Other nektonic animals are poorly preserved and infrequent, causing some problems with stratigraphic interpretations. However, ammonites together with belemnites (belemnitellids) have been recorded from a very few sections. Inoceramid stratigraphy also faces problems with unclear systematics (caused by intraspecific variability, the dependence on substrate etc.) and is used here where necessary. Brachiopods are cited in a few cases. Foraminiferal stratigraphy was completed in some sections in the Mangyshlak Peninsula (NW Kazakhstan – Marcinowski et al., 1996). The stratigraphy of index belemnite taxa – *Praeactinocamax primus* (Arkhangelsky), *P. plenus* (Blainville), *P. triangulus* Naidin, *Goniocamax intermedius* (Arkhangelsky) – was reviewed and is used here for biostratigraphic zonation in the eastern parts of the EPR. The index *G. lundgreni* (Stolley) will be evaluated later.

Belemnites (together with forams) seem to be the most suitable systematic group for biostratigraphic zonation in the East European Province (EEP), a palaeobiogeographic unit recently established by Naidin and Košták (2000) and in more detail in this paper. Belemnitellids are currently correlated with vertebrate fauna (fishes, sharks). They are used as index taxa because of their relative abundance, short and well-known stratigraphic ranges, clear



■ **Text-fig. 2.** Schematized section at the left band of Sura river – Surskoe, Svyataya gora, Ulyanovsk District. Beds 1–6: 1) Quarternary. 2) Upper Turonian. Yellow to white chalk with *Actinocamax verus* ssp. Glauconitic horizon at the base with *Actinocamax verus antefragilis* (No. Sav1999), *Goniocamax intermedius* and *G.* sp. (No. S1999/7). 3) Lower – middle Turonian. Dark green-grey calcareous sandstone, biturbated with phosphatic detritus. *P. triangulus* at the base. 4) Lower Turonian. Yellow-grey to green glauconitic, calcareous sandstones bioturbated. *Actinocamax verus antefragilis* and *Praeactinocamax triangulus*. 5) ?The base of the Turonian. Dark green-grey sandstones with gypsum and phosphatic nodules. 6) Albian. Dark grey to black claystones. After D. P. Naidin - unpublished. Left small numbers – thickness in (m).



■ **Text-fig. 3.** Schematized section of Surskoe, Promza river, Ulyanovsk District. Beds 1–7: 1) Quarternary. 2) Upper Turonian. Yellow to white chalk. Glauconitic sandstone lenses at the base with fragments of larger inoceramids. 3) Middle Turonian. Yellow-green marls, bioturbated (chalk infilling) at the top. *Inoceramus lamarcki*. 4) Middle Turonian. Yellow-green sandstone, dark grey quarzitic horizons and phosphatic nodules. 5) Middle Turonian. Light calcareous marls, glauconitic at the base, phosphatic nodules. Naidin (unpublished) reports on the find of *Goniocamax* cf. *matesovae*. 6) Lower Turonian. Grey-green glauconitic calcareous sandstones with phosphatick nodules and shark teeth at the base. *Praeactinocamax triangulus* and *Actinocamax verus antefragilis*. 7) Albian. Dark grey to black claystones. After D. P. Naidin - unpublished. Left small numbers – thickness in (m).

systematics, facies independence, good preservation potential and a wide geographic distribution. Four belemnite (belemnitellid) biozones are established in the Cenomanian through the lowermost Coniacian interval (see also Naidin 1964).

Systematic part

Short introduction into the terminology

The terminology applied herein follows the basic works on Upper Cretaceous belemnites – Naidin (1964, 1969); Ernst (1964); Stevens (1965); and Christensen (1974, 1975).

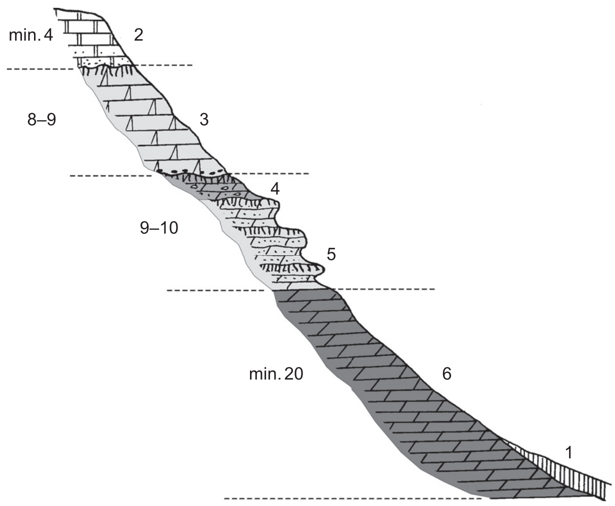
As no soft body parts are preserved for taxonomic distinction, belemnite taxonomy is mainly based on morphological and statistical characteristics of the belemnite guard. Fundamental morphological characteristics and related terminologies are explained in Text-figs. 8–9.

1) shape and size of the guard
2) structure of the alveolar end – i.e.. alveolar fracture, pseudoalveolus, ventral furrow, etc.
3) internal structures at alveolar end – i.e., the bottom of the ventral fissure etc.
4) ontogeny
5) correlation quotients (i.e., Riedel Quotient, Variability quotients: L/DAMLD – length vs. distance from the apex to the maximum lateral diameter, DAMLD/MLD – distance from the apex to the maximum lateral diameter vs. maximum lateral diameter; etc.)
6) external characteristics of the guard such as dorsolateral double furrows, striation, granulation etc.
7) structure of apex (i.e., the position of mucro etc.).

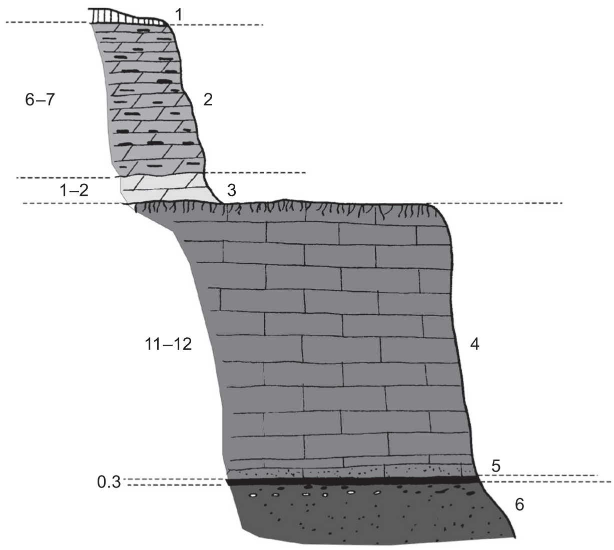
Sizes of the the guards were roughly subdivided into three classes: large guards – 80 to 110 mm; medium-sized guards 65 to 80 mm; and small-sized guards less than 65 mm.

The anterior part of the guard may end like in an alveolus or pseudoalveolus. Both features originated due to the poor level of calcification of this part. The alveolar fracture has a low conical shape, usually with a shallow pit in the centre. This pit is supposed to be a remain of the space surrounding the protoconch. The matrix between the phragmocone and the rest of the guard (rostrum) was primarily organic and/or slightly encrusted by aragonite (Barskov at al. 1997), and the surface of the alveolar fracture represents also the boundary between poorly calcified part (surrounding the phragmocone) and strongly calcified guard. This is of significance for systematics. The level of calcification varies among different species and is of some taxonomic relevance.

The pseudoalveolus is the second common type of alveolar structure. The phragmocone is surrounded by a very thin organic



■ **Text-fig. 4.** Schematized section of Tatarskie Gorenki – Belovodye, right band of Sura river, Ulyanovsk District. Beds 1–7: 1) Quarternary. 2) Upper early Campanian. Glauconitic chalk with *Belemnitella mucronata* and *Paractinocamax grossouvrei pseudotoucasi*. 3) Lower early Campanian. Green-grey marstones, glauconitic at the base. *Oxytoma tenuicostata*, *Inoceramus lobatus* and *Actinocamax laevigatus laevigatus*. 4) Middle to upper Coniacian. Yellow-green marls with dark-grey quarzitic nodules. 5) Middle Coniacian. Yellow-green sandstones with marl horizons. Silicified trace fossils. 6) Upper Turonian – lower Coniacian. Yellow-green marls with mica, bioturbated. *Inoceramus russiensis*, *I. sachsi*, *Goniocamax* ex gr. *lundgreni* and *Actinocamax verus subfragilis*. 7) Middle – upper Turonian. Light-grey marls with *Goniocamax surensis* („*Actinocamax*" *surensis* – holotype No. 380, Moscow State University) and *Inoceramus lamarcki*. After D.P. Naidin - unpublished. Left small numbers – thickness in (m).



■ **Text-fig. 5.** Schematized section of the Cement quarry in Fokino (20 km northern from Bryansk). Beds 1–6: 1) Quarternary. 2) Middle to upper Coniacian. Quarzitic marstones with quarzitic nodules and *Inoceramus subquadratus*. 3) Lower to middle Coniacian. Yellow bioturbated marls with *Inoceramus subquadratus* at the top. *Goniocamax intermedius* (7244b) at the base. 4) Lower to ?upper Turonian. White chlak, bioturbated with yellow quarzitic nodules. *Praeactinocamax triangulus* at the base. 5) The base of the Turonian. Glauconitic chalk (so called "surka" in Russia. 6) Middle to ?upper Cenomanian. Green midgrained glauconitic sandstones with phosphatic nodules. *Praeactinocamax primus* (No. 7240), *P.* aff. *triangulus*. Also *Entolium orbiculare*, *Chlamys aspera* and *Exogyra conica*. Phosphatic horizon i developed at the top of the bed. After D. P. Naidin – unpublished. Left small numbers – thickness in (m).

matter only and the walls of strongly calcified guard duplicate the phragmocone shape. The angle of pseudoalveolus is called "alveolar", however, no real alveolus is developed. Conotheca is neither present like phragmocone imprints – in this respect, it differs from the "classic" alveolus known, for example, from the Jurassic belemnites. The alveolar angle is of systematic significance.

In some belemnites, the so-called "bottom of ventral fissure" is developed, which is characteristic of the *Goniocamax* Naidin, *Gonioteuthis* Bayle, *Belemnitella* d'Orbigny and *Fusiteuthis* Kongiel. The fissure connects the protoconch area with the guard surface and is characterized by the different growth of prismatic calcite crystals building the guard (see also Ernst 1964).

The external structures developed on the guard surface originated from the vascular system (vascular imprints, striation) and fin attachment to the guard (dorsolateral depressions, dorsolateral double furrows). The granulation of the guard and its function have not been sufficiently explained yet, however, the granulation is not considered to be of significance for taxonomic classification.

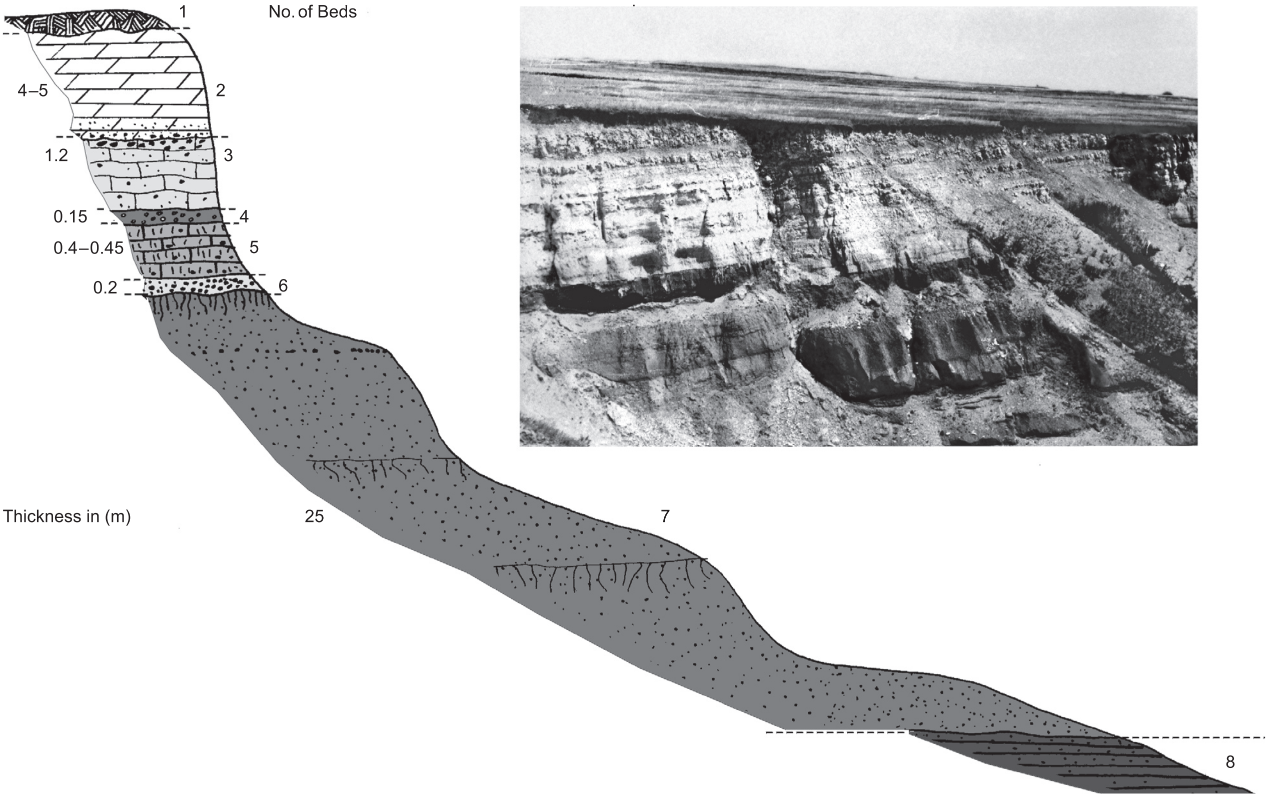
The position of the apex, which usually terminates in the mucro, may vary among the different species, however, its position in relation to the guard remains mostly constant.

Principles of morphometric analyses using correlation quotients were postulated in the papers of Reyment and Naidin (1962), Ernst (1964), Christensen (1974), Christensen and Schmid (1987), Christensen and Schulz (1997) and Košťák and Pavliš (1997), which are followed here.

Taxonomy

Class CEPHALOPODA Cuvier, 1795
Subclass COLEOIDEA Bather, 1881
Order BELEMNITIDA Zittel, 1895
Suborder BELEMNOPSEINA Jeletzky, 1965
Family BELEMNITELLIDAE Pavlow, 1914
Genus *Actinocamax* Miller, 1823
Type species: *Actinocamax verus* Miller, 1823, p. 63, Pl. 9:17.

Diagnosis: Guards are of small size – up to 55 mm in length, of variable shape – lanceolate to cylindrical. Alveolar fracture has a high conical shape. Ventral furrow is always missing, dorsolateral furrows are developed. Granulation sometimes present.
Discussion: Naidin (1964) divided the genus of *Actinocamax* Miller into three subgenera: *Actinocamax* Miller, 1823 (average



■ **Text-fig. 6.** Schematized section of the river band in Pudovkino, Saratov District. Beds 1–8: 1) Quarternary. 2) Lower Santonian. Grey, sandy marls, glauconitic at the base with phosphatic nodules. *Inoceramus cardissoides*, *Belemnitella propinqua propinqua*. 3) Upper Turonian – the base of the Coniacian. Green-grey sandy glauconitic chalk with phosphatic nodules, phosphatized Porifera a inocaramid fragments, *Goniocamax* sp. Brachiopoda – *Concinnithyris quidhamtonensis*. 4) Upper Turonian. Horizon with phosphatic nidules. *Goniocamax intermedius*. 5) ?Middle–upper Turonian. Sandy glauconitic chalk with phosphatic nodules. Bioturbated. *Goniocamax intermedius*, *Goniocamax* sp. 6) ?Lower–?middle Turonian. Horizon with phosphatic nodules, bones, teeth and scales of fishes and sharks. 7) Cenomanian. Dark grey bioturbated sandstones. *Exogyra conica*, *Entolium orbiculare* and *Lingula krausei*. 8) Albian. Grey sandy claystones. After D. P. Naidin – unpublished. Left small numbers – thickness in (m).

length of the guard 30–35 mm, stratigraphic range: Lower Turonian – Lower Campanian), *Praeactinocamax* Naidin, 1964 (average length of the guard from 65–85 mm to 90–102 mm, stratigraphic range: Lower Cenomanian – Lower Turonian) and *Paractinocamax* Naidin, 1964 (average length of the guard from 70–90 mm to 115 mm).
Stratigraphic range: Lower Turonian – Lower Campanian.
Geographic distribution: North European Region – Russian Platform (East European Province, Central Russian Subprovince), S and N of the Ural Mts. area, Crimea, NW Europe; ?North American Province – North America.

Actinocamax verus antefragilis Naisdin, 1964

Pl. I., figs. 1–3; Tab. 1

Holotype: *Actinocamax verus antefragilis* subsp. n; Naidin, 1964, p. 28, fig. 5–1. Housed in the paleontological collection of the Moscow State University (MSU – Moscow) as item No. 8023/3.

Synonymy:
1964 *Actinocamax verus antefragilis* Naidin, subsp. n.; Naidin, p. 28, fig. 5.1.
?1973 *Actinocamax* clavatiformis Makhlin, sp. nov; Makhlin, p. 87, Pl. 26, fig. 1, 4.
1973 *Actinocamax verus antefragilis* Naidin; Christensen, p. 134.
1976 *Actinocamax verus antefragilis* Naidin; Christensen, p. 118, fig. 2.
1997a *Actinocamax verus antefragilis* Naidin; Christensen, p. 469, fig. 4.
1997b *Actinocamax verus antefragilis* Naidin; Christensen, p. 66, fig. 2.
2003 *Actinocamax verus antefragilis* Naidin; Košťák, p. 65, fig. 1.

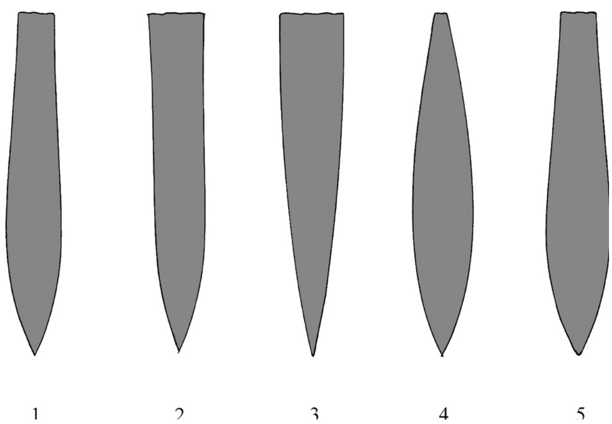
Material studied: One complete and three almost complete specimens housed in the collections of the Department of Geology and Palaeontology, Faculty of Science, Charles University, Prague as item Sav1999/1-4.

Stage	Substage	Cenomanian through lower Coniacian biostratigraphic zonation of eastern part of the European Palaeobiogeographical Region		
		Inoceramids and ammonites zonation (Compiled after Naidin et Kopaevich 1988 and Marcinowski et al 1996)		**Foraminiferal assemblages zonation** (After Naidin et Kopaevich 1988)
Coniacian	lower	Cremnoceramus crassus/C. deformis Cremnoceramus brogniarti Cremnoceramus rotundatus		**Gavelinella praeinfrasantonica,** G. kelleri, G. costulata, Cibicidoides praeeriksdalensis, Stensioeina gr. granulata, Reussella kelleri
Turonian	upper	Mytiloides incertus Inoceramus costellatus		**Atalophragmium nautiloides** Gavelinella gr. costulata, Globorotalites mishelinianus
Turonian	middle	Inoceramus lamarcki Inoceramus apicalis Mytiloides hercynicus		**Gavelinella moniliformis,** Spiroplectammina praelonga, Gaudryina variabilis, Globotruncana lapparenti
Turonian	lower	Mytiloides labiatus Mytiloides kossmati Mytiloides hattini	Mammites nodosoides Watinoceras amudariense	**Globorotalites hangensis**, Gyroidinanitida, Gavelinella vesca, Cibicidoides apprima
Cenomanian	upper	Neocardioceras judii		**Brotzenella berthelini**, Gavelinella vesca, Cibicidoides apprima
Cenomanian	upper	Inoceramus pictus bohemicus		
Cenomanian	upper	Eucalycoceras pentagonum		
Cenomanian	middle	Inoceramus crippsi: Acanthoceras jukesbrownei		
Cenomanian	middle	Inoceramus crippsi: Turrilites acutus Turrilites costatus	Acanthoceras rhotomagense	**Gavelinella cenomanica**, G. c. concava, G. baltica, Lingulogavelinella globosa, Cibicides polyrraphes polyrraphes, Thalmanninella appenninica
Cenomanian	lower	Inoceramus crippsi: Mantelliceras dixoni Mantelliceras mantelli		**Hoeglundina dorsoplana,** Gavelinella cenomanica, G. intermedia, Lingulogavelinella gr. globosa

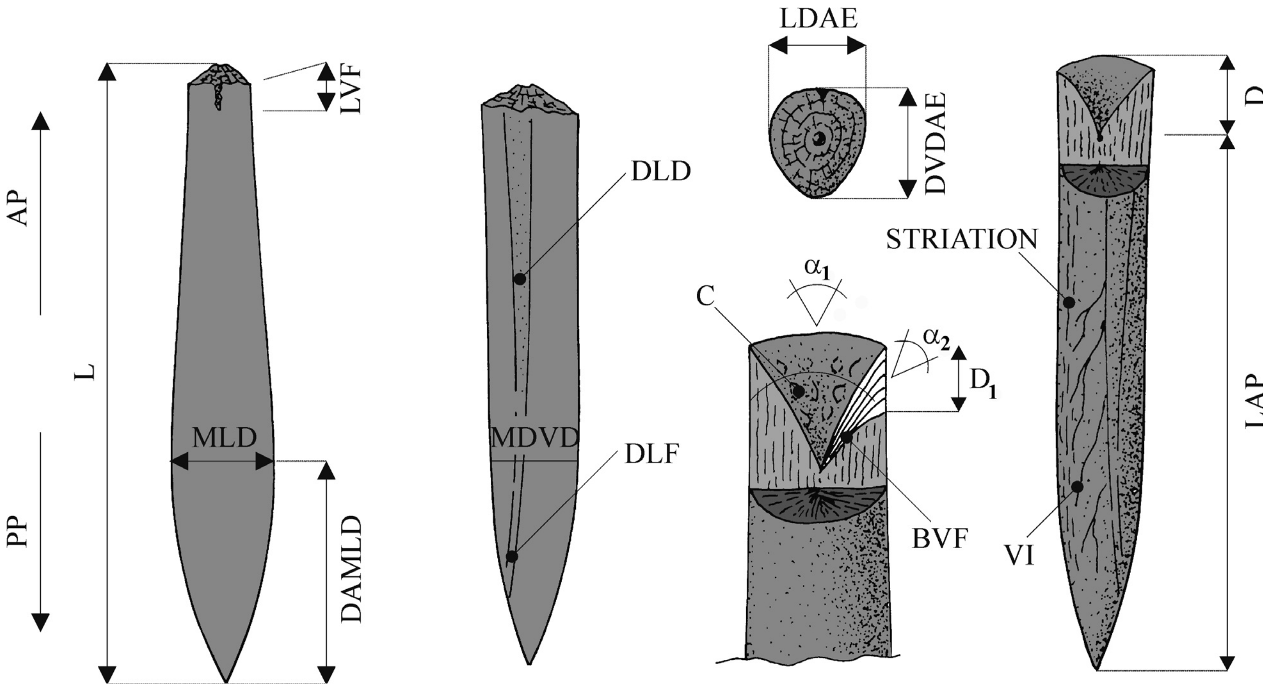
■ **Text-fig. 7.** Biostratigraphic zonation of the East European Region (after Naidin and Kopaevich, 1988; Marcinowski et al., 1996).

Short description: Guards are of small size: 20–30 mm, cigar-shaped in dorsoventral and lateral views. The maximum lateral diameter is situated at posterior third of the guard. Lateral sides slightly flattened. Apex is displaced towards the dorsal side. Alveolar fracture is highly conical and asymmetrical. Height of alveolar fracture forms one-half of the total length of the guard. Dorsolateral compressions are fully developed. Surface of the guard is smooth. Mucro is missing.

Affinities and remarks: *A. verus antefragilis* differs from *A. verus verus* Miller in having smaller guards, higher alveolar fracture, and different stratigraphic distribution. *A. verus fragilis* Naidin and *A. verus subfragilis* Arkhangelsky also possess lower alveolar fractures. However, the character of the alveolar fracture of *A. verus antefragilis* resembles *A. laevigatus* Arkhangelsky, but the lateral flattening of the guard is not so marked in *A. laevigatus*. *A. verus antefragilis* is the first representative of *Actinocamax* and also the ancestor of the *A. verus* ssp. group (Coniacian–Lower Campanian).



■ **Text-fig. 8.** The shape of the guard. 1. Slightly lanceolate. 2. Cylindrical. 3. Conical. 4. Cigar-shaped. 5. Lanceolate.



■ **Text-fig. 9.** The position of measured diameters and terminology. L – length of the guard. 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. D – depth of pseudoalveolus. BVF – bottom of ventral fissure. SD – Schatzky distance (distance from bottom of ventral fissure to protoconch). RQ – Riedel quotient (ratio of the lentgth of the guard/pseudoalveolus depth). α1 (AA) – alveolar angle, α2 (FA) – angle between pseudoalveolus wall and the bottom of ventrl fissure. Variability quotients – L/DAMLD, DAMLD/MLD.

Stratigraphic range: Lower Turonian (together with *P. triangulus*) – Middle/Upper Turonian (together with *P. planus* and *P. coronatus* – Boltaevka), ? Coniacian (Bornholm).
Geographic distribution: Russia – Ulyanovsk (Simbirsk) District, ? Denmark – Bornholm Island.

Genus *Praeactinocamax* Naidin, 1964
Type species: *Belemnites plenus* Blainville, 1825–1827, p. 376, Pl. 11 : 3.

Diagnosis: Guards are of a medium size: 65–115 mm, predominantly lanceolate in dorsoventral view. The maximum lateral diameter is situated mostly at one half of the guard. Ventral side is markedly flattened. Alveolar fracture has a low conical shape with a shallow pit in the centre. The pseudoalveolus is oval to triangular in cross section. Ventral furrow is sometimes developed. Dorsolateral compressions and furrows are usually fully developed. Striation is usually present. Vascular imprints may be significant. Granulation is present rarely.
Discussion: Christensen and Schulz (1997; ibid see discussion) raised the subgenus of *Praeactinocamax* Naidin, 1964 to generic rank and established its stratigraphic range at Cenomanian – Lower Santonian.
Geographic distribution: Europe – North European Region (Province) – Central European Subprovince and Baltoscandia; East European Province – Russian Platform, Transcaspian area; western Siberia, Russian Arctic region; Tethyan Realm (SE France), Mediterranean Region (Turkestan, Tadzhikistan/Afghanistan border); North American Province – North America, Greenland, Mexico.

Praeactinocamax primus (Arkhangelsky, 1912)

Pl. I, figs. 4–11; Pl. III, fig. 1; Tab. 2

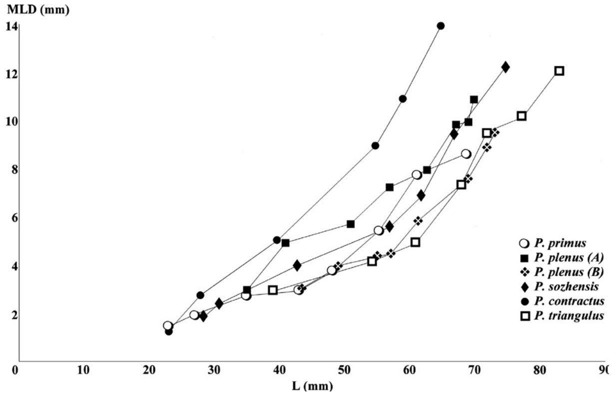
Lectotype: *Belemnites lanceolatus*; Sowerby, p. 208, Pl. 600, figs. 8–9.
Synonymy: see Christensen (1974, 1990)
Material studied: 75 specimens – 46 complete and 29 fragments with measured dimensions come from 11 localities; housed in the collections of the Department of Geology and Palaeontology, Faculty of Science, Charles University, Prague.
Short description: Guards are 38–92 mm long. The shape of the guard is connected with dimension 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 situated at one half to one third of posterior part of the guard. Guards are ventrally flattened. Alveolar fracture has a low conical shape, mostly with a shallow pit in the centre. Oval cross section with typical radial and concentric structure. Surface of the guard is smooth. Dorsolateral compressions and furrows are

well developed. Striation is sometimes present. Apex is acute (15–25°) and positioned centrally. Ventral furrow is slightly developed. Mucro is missing.
Ontogeny: The typical specimens of the following species similar to one another (*P. primus*, *P. plenus*, *P. triangulus*, *P. sozhensis* and *P. contractus* – see sections on their ontogeny below) were studied. These represent a medium-sized class. Longitudinal sections were made in the axial part in dorsoventral view. Marked and visible growth lines were numbered with Roman numerals to represent ontogenetic stages and measured. The most important sign of ontogeny were the observed iso- and allometric growth phases. The changes in the guard shape result from the iso- and allometric phases in different ontogenetic stages.
The typical specimen of *P. primus* (specimen No. 7240/5; L 69 mm, MLD 8.7 mm, DAMLD 22.8 mm) from the Fokino section was measured. The first visible guard ("embryonal rostrum"): L 23 mm, MLD 1.5 mm. Increase in the length and width of the guard is isometric until stage V (48.2 mm = 70 % of the total length of the guard including the first visible guard). Allometric increase in the length and width was recorded between stages V and VII (48.2–61.2 mm; this section represents 19 %). The following isometric phase (61.2–69 mm) finishes the growth. 81 % of the length result from isometric growth. Allometric growth is marked between stages V and VII and causes a transformation from the cigar shape (subcylindrical) to the lanceolate shape.
Affinities and remarks: *P. primus* is considered to be the phylogenetic ancestor of *P. plenus*. *P. primus* differs from *P. plenus* in having smaller and thinner guards. Christensen (1990) recommended the use of a sample containing about 10–20 specimens of medium size for distinguishing these species. *P.* aff. *triangulus* is derived here also from *P. primus* (longer specimens) on the basis of a similar shape of the guard. *P.* aff. *triangulus* has a shallow pseudoalveolus which is oval to slightly triangular in cross section. Naidin (1964, p. 176) reported *P. plenus* from the Upper Cenomanian sediments together with *Schloenbachia varians* Sowerby, *Acanthoceras rhotomagense* Defr., and Scaphites aequalis Sowerby. *Acanthoceras rhotomagense* is used as an index taxon in the lower Middle Cenomanian. The *Acanthoceras rhotomagense* Zone was established for the standard European zonation, and recently (Marcinowski et al. 1996) also for the eastern parts of the European Paleobiogeographic Region (Mangyshlak Peninsula, NW Kazakhstan). The guards studied here are referred to *P. primus* after this revision.
Stratigraphic range: *P. primus* first appears in the Lower Cenomanian in the eastern parts of the EPR – upper levels of the *Mantelliceras mantelli* Zone, at the beginning of the *Mantelliceras dixoni* Zone together with *Schloenbachia varians* Sowerby, and in the Middle Cenomanian *Acanthoceras rhotomagense* Zone. The occurrence of this species has not been proved in the Upper Cenomanian in the traditional West European three-substage division.
Geographic distribution: *P. primus* is widespread from the northern Caspian Sea area in the east to the Northern Ireland in the west. Geographic distribution of this species represents a belt about 1000 km wide and 4000 km long. NW Kazakhstan, Russia, Belarussia, Ukraine, ?southern Scandia, Germany, England, Northern Ireland.

Praeactinocamax plenus (Blainville, 1825)

Pl. I, figs. 12–15; Pl. II, figs. 1–6; Pl. III, fig. 2; Tab. 3

Holotype: *Belemnites plenus*; Blainville, 1825, p. 376; 1827, Pl. 11, fig. 3.
Synonymy: For the detailed synonymy see Bülow-Trümmer (1920), Naidin (1964), Christensen (1974), Košťák and Pavliš (1997).
Material studied: 80 specimens – 50 complete and 30 fragments with measured parameters from 9 localities. They are housed in the collections of the Institute of Geology and Palaeontology, Charles University, Prague.
Short description: Guards are 55–92 mm long. 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. Maximum lateral diameter is situated at one half to one third of the apical part of the guard. Guards are flattened ventrally. Alveolar fracture has a low-conical shape with a shallow pit in their centre. The cross section is oval to slightly triangular in the alveolar fracture area. Concentric and radial structures are apparent in this part. Surface of the guard is smooth with dorsolateral compressions and double furrows. Striation is apparent in some specimens. Apex is central. The angle of apex is from 30° to 40°. Ventral furrow is sometimes apparent. Mucro is developed in some stouter specimens.
Ontogeny: The two different morphotypes of *P. plenus* with the same number of growth lines were selected from the collection. Morphotype A (stouter and shorter guard) and morphotype B (thinner and longer guard).
Morphotype A: No. KK8/4 (L 70 mm, MLD 11 mm, DAMLD 27.3 mm) from the locality of Koksyirtau. The first visible guard is 35 mm long (MLD 3 mm). Allometric growth phase of length is visible between stages I and III (35–51 mm = 23 % of the total length of the guard) although the width increase remains isometric! The growth continues with isometric length increase and allometric width increase between stages III and V. Isometric length and width increase is apparent from stage V to stage VIII. Lanceolate shape of the guard is influenced mainly by allometric width increase between stages III and V.
Morphotype B: No. KK8/9 (L 72.8 mm, MLD 9.6 mm, DAMLD 34 mm) from the locality of Koksyirtau. The first visible guard is 43 mm long (MLD 3 mm). The length and width increase is isometric between stages I and V (43 mm–61.5 mm = 84.5 % of the total length of the guard). Allometric length and width increase is apparent only between stages V and VI (61.5 mm to 69 mm – this sector represents 10 % of total length of the guard). The almost isometric growth (L and W) continues from stage VI to stage VIII. The shape of the guard is slightly lanceolate as a result of only one allometric growth phase. 90 % of the total length of the guard resulted from isometric growth.
Affinities and remarks: *P. plenus* is considered to be a descendant of *P. primus*. Juvenile specimens of *P. plenus* are almost identical with *P. primus*. Species similar to *Praeactinocamax plenus* were statistically analysed. The Upper Cenomanian spe-



■ **Text-fig. 10.** Ontogeny comparisn of *P. primus*, *P. plenus* (morphotypes A and B), *P. sozhensis*, *P. contractus* and *P. triangulus*.

cies of *P. primus* and *P. sozhensis* were compared with *P. plenus* and the related Lower Turonian species of *P. sozhensis*, *P. triangulus* and *P. contractus* were compared, too.

Results of the descriptive statistical methods already used showed a considerable linear dependence between some variables. For example, for the correlation coefficient of parameter L/MLD – $R^2 = 0.8336$, this parameter is nearly directly proportional. Therefore, although several parameters were measured for the set, we must admit the fact that we can use only some of them to differentiate between individual varieties. This circumstance is due to the above mentioned close correlation between some parameters.

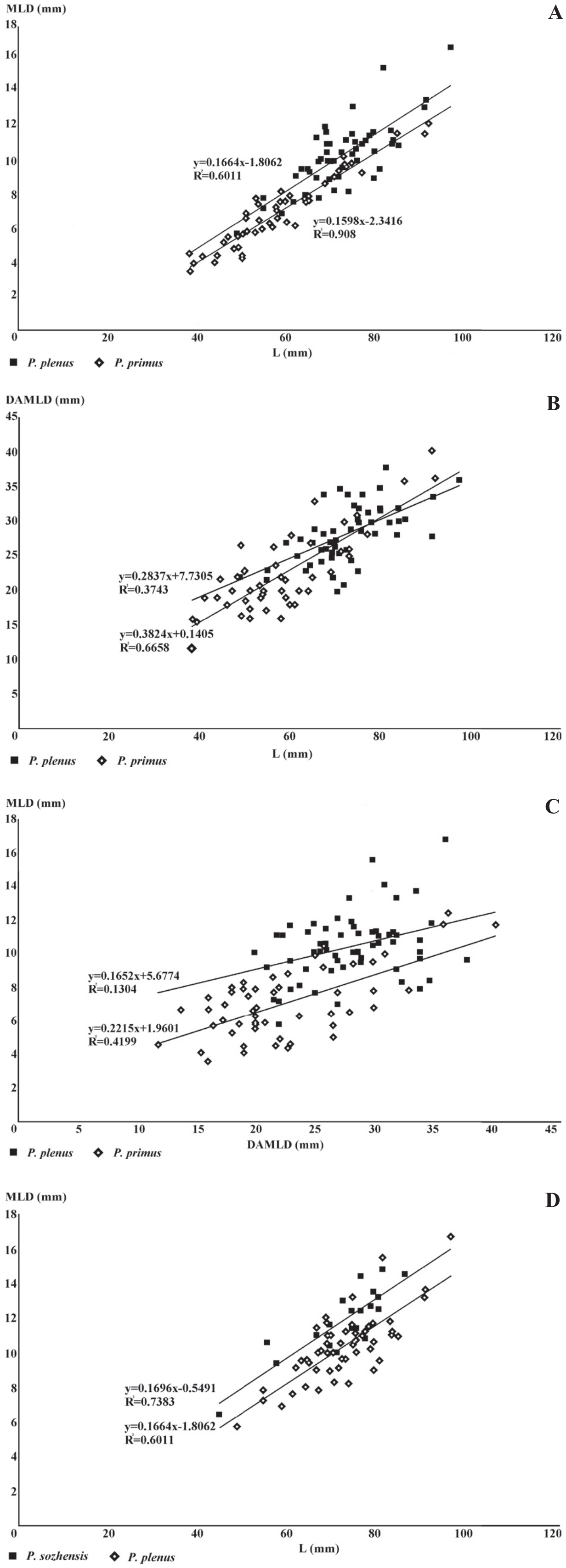
If linear dependence of parameter L/MLD is observed for the whole set, we can definitely expect only very subtle differences when comparing two similar species of belemnites on the basis of only these parameters (of course depending on the methods used, etc.). Parameters L and MLD are basically reduced to a single parameter. This has a rather significant impact on how we look at the behaviour of the set. However, since the guards of belemnites offer relatively few measurable parameters, we must accept this reality.

The above mentioned phenomenon – the very close linear dependence of most data – was found during the determination

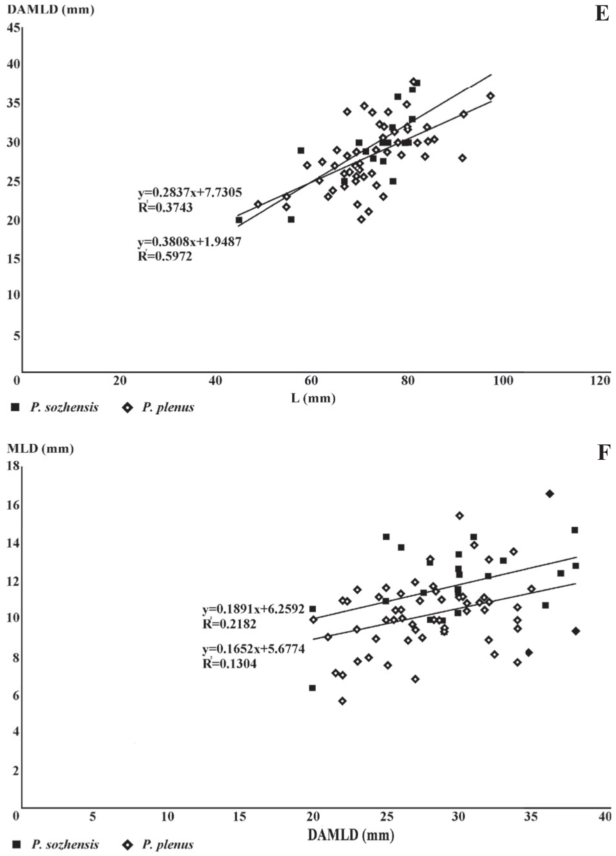
Growth stages	*primus*		*plenus* A		*plenus* B	
	length	width	length	width	length	width
I–II*	23–27*	1.5–2*	35–41*	3–5*	43–49*	3–4*
II–III	iso-	iso-	allo-	iso-	iso-	iso-
III–IV	iso-	iso-	iso-	allo-	iso-	iso-
IV–V	iso-	iso-	iso-	allo-	iso-	iso-
V–VI	allo-	allo-	iso-	iso-	allo-	allo-
VI–VII	allo-	allo-	iso-	iso-	iso-	iso-
VII–VIII	iso-	iso-	iso-	iso-	iso-	iso-

* I – II .... Length and width of the first visible guard and the second growth phase (in mm).

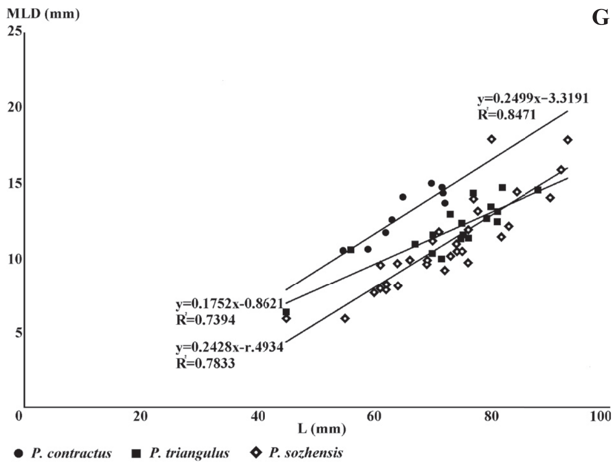
■ **Text-Tab. 1.** Table of iso- and allometric growth stages in *P. plenus* and *P. primus*



■ **Text-figs. 11 a–d.** Regression lines in *P. primus*/*P. plenus* (11a–c) and *P. plenus*/*P. sozhensis* (11 d–f).



■ **Text-figs. 11 e–f.** Regression lines in *P. primus*/*P. plenus* (11 a–c) and *P. plenus*/*P. sozhensis* (11 d–f).



■ **Text-fig. 11g.** Regression lines in *P. sozhensis*/*P. contractus*/*P. triangulus*.

of the mutual dependence of variables. This fact results in some problems when distinguishing between similar or related species of belemnites.

Variable DAMLD was found to have the greatest influence on total variability (Košťák and Pavliš 1997). This is well demonstrated in Text-fig. 11c, where the correlation coefficient DAMLD/MLD – R^2 is 0.1304 in *plenus*, 0.4199 in *primus* and 0.2182 in *sozhensis* (Text-figs. 11c and 11f). This implies the highest set variability in *P. plenus*, very high in *P. sozhensis* and lower in *P. primus*. We recommend to use the DAMLD parameter for the belemnite set and/or population variability. Generally, the low R^2 coefficient means a very low level of dependence but also a very high species variability. It is very difficult to determine when, for example, the L/DAMLD (Text-figs. 11b and 11e; regressions) divides the set into two parts. However, it is indisputable that this variable (DAMLD) clearly behaves differently from the other variables (for more details see Košťák and Pavliš 1997).

A few similar species of *Praeactinocamax* have been found in the Turonian of the North American paleobiogeographic Province (NAP); however, their origin is unknown. They could be derived from the *primus*/*plenus* group, as suggested by some morphological similarities, especially in the alveolar part. Middle to Upper Turonian species of *P. planus* from the East European paleobiogeographic Province (EEP) strongly resembles *P. plenus*. *P. planus* is considered to be a phylogenetic descendant of *P. plenus* in this paper. The *P. plenus* – *P. planus* evolutionary lineage is poorly documented, however, morphological similarities are marked. *P. planus* is an endemic species surviving only in the East European Province (Central Russian Subprovince).

Stratigraphic range: *P. plenus* occurs in the Upper Cenomanian – one metre above its base (Mangyshlak Peninsula, northwestern Kazakhstan) – together with *Inoceramus pictus bohemicus* Leonhardt and does not continue to the *Neocardioceras juddii* Zone on Mangyshlak (Marcinowski et al. 1996). Its stratigraphic range is almost identical with the ammonite *Metoicoceras geslinianum* Zone across the whole biogeographic area. Lower Turonian occurrences of this species described by Naidin (1964) are revised in this paper: guards coming from Lower Turonian deposits were revised by the present author and attributed to other belemnitellid species (see below).

Geographic distribution: The geographic distribution of *P. plenus* lies further south than that of *P. primus*, and is more narrow and protracted, about 1000 km towards the east (to the Tadzhikistan/Afghanistan border). *P. plenus* comes from the northern parts of the Tethyan Realm (SE France), Crimea (Ukraine), the Mediterranean Region of the Central Asian Province (S Turkestan, Tadzhikistan/Afghanistan border), central European basins (Bavaria, Saxony, Bohemian Cretaceous Basin). Occurrences further north have been reported from England, NW Germany, Poland and ?southern Scandia.

Praeactinocamax cf. *strehlensis*

Pl. VI, fig. 5; Tab. 4

Material studied: Specimen of *P.* cf. *strehlensis* No. 170/7 from the Koksyirtau locality (NW Kazakhstan, Mangyshlak Peninsula) kept in the collections of the Institute of Geology and Palaeontology, Charles University, Prague.
Short description: The guard is 67 mm long, lanceolate in dorsoventral and lateral views. The maximum lateral diameter is situated at 1/3–1/4 of posterior part of the guard. The ventral side is very slightly flattened. The alveolar fracture is oval to

triangular, with a shallow pit in its centre. Radial and concentric structures are apparent. A marked ventral notch (6 mm) is present. Dorsolateral compressions slightly developed, dorsolateral double furrows fully missing. The mucro is weakly developed. The apex is situated centrally.
Affinities and remarks: This specimen resembles *P. strehlensis* (Fritsch and Schlönbach, 1872) in the character of alveolar part – especially its ventral part with a marked notch. The specimen of *P. strehlensis* figured by Fritsch and Schlönbach, 1872 on p. 19, Pl. 16, figs. 10–12 has no dorsolateral double furrows developed, unlike the herein studied specimen No. 170/7. However, the cross sections of alveolar part are almost identical. The only difference is the position of the maximum lateral diameter. In specimen No. 170/7 this point is located more towards the apex. The holotype of *P. strehlensis* (the only adult specimen known) is probably lost. It comes from the vicinity of Strehlen near Dresden (Christensen 1982, Košťák 1996). Sediments exposed in this area belong stratigraphically to the uppermost Turonian through lower Coniacian ("Teplitzer Schichten" sensu Frič 1879). However, the late Cenomanian sediments are also exposed in this area. Several specimens of *P. bohemicus* Stolley from Germany (State Museum of Dresden – 6 specimens) and in the Czech Republic (Regional Museum of Teplice – 5 specimens, National Museum Prague – the holotype and two fragments) were formerly referred to *P. strehlensis* (see Christensen 1982, Košťák 1996). No typical specimen of *P. strehlensis* is preserved. It cannot be excluded that the only adult specimen of *P. strehlensis* represents an unusual (or slightly pathological) specimen of *P. plenus* in which the stratigraphical level was incorrectly determined. It is possible that *P.* cf. *strehlensis* from Koksyirtau represents an unusual or slightly pathological specimen of *P. plenus* (see below).
Stratigraphic and geographic distribution: Unusual specimen of *P.* cf. *strehlensis* (No. 170/7) comes from the same stratigraphic level as usual specimens of *P. plenus* – *Metoicoceras geslinianum* Zone, *Inoceramus pictus bohemicus* Zone, Mangyshlak Peninsula, NW Kazakhstan.

Praeactinocamax triangulus Naidin, 1964

Pl. IV, figs. 1–10; Tab. 5

Holotype: *Actinocamax* (*Praeactinocamax*) *plenus triangulus*; Naidin subsp. n., 1964, p. 48–49, Pl. 1, fig. 5–7. Housed in the paleontological collection of the MSU (Moscow) as item No. 1083/3.

Synonymy:
1964 *Actinocamax* (*Praeactinocamax*) *plenus triangulus* Naidin, subsp. n.; Naidin, p. 48–49, Pl. 1, fig. 5–7.
1964 *Actinocamax* (*Praeactinocamax*) *plenus crassus* Naidin, subsp. n.; Naidin, p. 46–48, Pl. 3, fig. 1, 2.
1973 *Actinocamax plenus triangulus* Naidin; Christensen, p. 136.
1974 *Actinocamax plenus* Naidin; Christensen, p. 12, 15, 21, 23.
1988 *Actinocamax plenus triangulus* Naidin; Christensen, p. 7.
1990 *Actinocamax plenus triangulus* Naidin; Christensen, p. 375, 376.
1991 *Actinocamax plenus triangulus* Naidin; Christensen, p. 699.
1997a *Praeactinocamax plenus triangulus* Naidin; Christensen, p. 459.
1997b *Praeactinocamax plenus triangulus* Naidin; Christensen, p. 80.
1997 *Praeactinocamax plenus triangulus* Naidin; Košťák and Pavliš, p. 1, 6–7, 9.
2000 *Praeactinocamax plenus triangulus* Naidin; Naidin and Košťák, p. 100.
2003 *Praeactinocamax triangulus* Naidin; Košťák, p. 65, fig. 1.

Material studied: 45 specimens – 34 almost complete, from 18 locations. They are kept in the collections of the Institute of Geology and Palaeontology, Charles University, Prague.

Holotype of *P. triangulus* No. 1083/3, paratypes 56/1, 8023/1, 6/2, 1745/2 a 8023/3; holotype of *P. plenus crassus* Naidin, 1964 – No. 5305/4 and paratypes 5305/13 and 5305/2 are kept in the collections of Lomonosov State University, Moscow.
Short description: Guards are lanceolate in dorsoventral view and slightly lanceolate to subcylindrical in lateral view. They are of a medium size of 45–93 mm. Isometric growth in juvenile to young adult specimens, allometric in very old specimens. Pseudoalveolus is strongly calcified and has a typical triangular cross section. The depth of the pseudoalveolus exceeds 5–6 mm. Concentric and radial layers are visible. The ventral notch is usually present. Dorsolateral compressions and double furrows are fully developed, striation is usually missing. The mucro is rare. The apex is displaced towards the dorsal side.
Ontogeny: A typical adult specimen of *P. triangulus* (specimen No. 1082/1; L 83 mm, MLD 12.2 mm, DAMLD 33 mm; locality of Kritchev) was investigated. The first visible guard is poorly preserved and was not measured. So, the growth phases are not numbered; nevertheless, the isometric growth of length and width is apparent until 61 mm (73.5 %). Allometric growth can be considered at 61 mm to 72 mm (13 %) but it is not so marked. The isometric growth phase continues until 83 mm. Some big and massive undetermined guards (or fragments) come from deposits containing *P. triangulus* guards. A complete specimen with a diagnostic mark – pseudoalveolus – is, however, still missing. If these guards belong to *P. triangulus* it means that the allometric growth appears in the latest stages in very old specimens.
Affinities and remarks: *P. plenus crassus* Naidin, 1964 – No. 5305/4 and paratypes 5305/13 and 5305/2 are referred to *P. triangulus* here on the basis of a markedly similar character of the alveolar end, especially their triangular pseudoalveolus. Although the biometry showed differences between the holotype, one paratype (5305/13) of *P. plenus crassus* and common specimens of *P. triangulus*, some of the old specimens of *P. triangulus* resemble *P. plenus crassus* in having a similar shape and partly a similar size of the guard. I consider the holotype and paratypes of *P. plenus crassus* as very old specimens of *P. triangulus* with extreme dimensions. The paratype of *P. plenus crassus* (No. 5305/2) is identical with larger specimens of *P. triangulus*. All specimens of *P. plenus crassus* come from the same locality as many specimens of *P. triangulus* and from the same stratigraphic level.

P. aff. *triangulus* from the middle Cenomanian resembles *P. triangulus* in having a similar guard shape. It differs from *P. triangu-*

lus in its deeper pseudoalveolus and the cross section, which is more triangular in *P.* aff. *triangulus*. *P. triangulus* is slightly similar to *P. plenus*. It was considered to be an independent subspecies of *P. plenus* (*P. plenus triangulus* Naidin 1964) in the past (Naidin 1964, Christensen 1974). Naidin (1964), Christensen (1974) and Košťák and Pavliš (1997) discussed the differences between the two taxa. *P. triangulus* is distinguished from *P. plenus* by its different ontogeny, its different guard shape and especially by its relatively deep (max. 6 mm) triangular pseudoalveolus, which is missing in *P. plenus*. The ontogeny (Naidin 1964, p. 49.) of *P. triangulus* is very similar to that of *P. primus*, which is a phylogenetic ancestor of *P. plenus*. *P. sozhensis* differs from *P. triangulus* in the shape of the guard and alveolar fracture (a poorly calcified alveolar fracture is present in *P. sozhensis*). *P. medwedicicus* shows marked relationship to *P. triangulus* with respect to similar pseudoalveolus, alveolar fracture and guards shape resemblance to very old specimens of *P. triangulus*. More intensive growth of the guard width is typical for senile specimens of *P. triangulus*. *P. medwedicicus* probably represents a phylogenetic ancestor derived from *P. triangulus*. *P.* sp. 1 differs from *P. triangulus* in the shape of the guard and the distinct cross section of its pseudoalveolus. *P. contractus* occurs together with *P. triangulus* and is different in all morphological aspects.

I consider *P. triangulus* to be an independent species for the following reasons:

1) morphology: slightly different shape of the guard, different structure of adoral part, well calcified and relatively deep triangular pseudoalveolus,
2) different ontogeny,
3) different stratigraphic range. This species represents also an index lower Turonian belemnite taxon for the East European Province (Naidin 1964).

Stratigraphic range: *P. triangulus* occurs in the western parts of the EEP (Belarussia, W Russia) just above the base of the lower Turonian. Acme zone of this species is identical with the inoceramid Mytiloides labiatus Zone and ammonite *Mammites nodosoides* Zone. The following common fauna was reported by Naidin (1964, Naidin 1996–2000, pers. comm.): ammonites *Placenticeras kharesmense* Lah., *Watinoceras amudariense* (Arkhangelsky) and *Borissjakoceras* sp., *brachiopods Concinnithiris protobesa* Sahni, *C. rowei* Sahni, *Cretirhynchia robusta* (Tate) and *Orbirhynchia* cf. *cuvieri* (d'Orbigny). *Triangulus* event can be introduced for the late lower Turonian – wide geographic distribution (Belarussia in the west to Turkestan in the southeast) and high abundance of specimens.

Geographic distribution: Eastern Belarussia, central and western Russia, Turkestan – Ak kup (eastern coast of the Caspian Sea), Uzbekistan – Amu-Darya River valley (Besh Tyube).

Praeactinocamax aff. *triangulus*

Pl. VI, fig. 1; Tab. 6.

Synonymy:

2003 *Praeactinocamax* aff. *triangulus*; Košťák, p. 65, fig. 1.

Material studied: Two specimens, one complete (No. 7240/2), from the locality of Fokino – Russia, Bryansk district); kept in the collection of the Institute of Geology and Palaeontology, Faculty of Science, Charles University, Prague.

Short description: The guard is 80 mm long, slightly lanceolate in dorsoventral view and subcylindrical in lateral view. The maximum lateral diameter is situated at 1/3 of the posterior part of the guard. Pseudoalveolus triangular in cross section, reaching almost 4 mm in depth. Dorsolateral compressions are developed as double furrows, which continue towards the apex. The ventral furrow is present. Striation marked in the apical part of the dorsal side only. The apex is broken at the site of the expected mucro.

Affinities and remarks: *P.* aff. *triangulus* resembles *P. triangulus* in having a similar shape and size of the guard, and especially in the character of its pseudoalveolus. The triangular cross section of the pseudoalveolus in *P. triangulus* is more marked, while no triangular pseudoalveolus is developed in *P. plenus*. *P.* aff. *triangulus* is similar to *P. primus* in the shape of the guard but differs in the size of the guard and the presence of a pseudoalveolus. *P. sozhensis* differs from *P.* aff. *triangulus* in the shape of the guard and a poorly calcified anterior part with no pseudoalveolus developed.

Stratigraphic and geographic distribution: Middle Cenomanian, Russia – Bryansk district, 20 km N of Bryansk, locality of Fokino.

Praeactinocamax sozhensis (Makhlin, 1973)

Pl. II, figs. 7–11; Pl. III, fig. 3, 7–9; Tab. 7

Holotype: *Actinocamax sozhensis* Makhlin, sp. nov; Makhlin, 1973, p. 90, text fig. 20 a–v, Pl. 26, fig. 3 a–g. Stored in the Museum of the "Vsesoyuznyi neftyannyi nauchno-issledovatelskii geologorazvedochnyi institut" – VNIGRI (St. Peterburg) as item No. 726/5.

Synonymy:

1964 *Actinocamax* (*Praeactinocamax*) *plenus* subsp.; Naidin, Pl. 1, fig. 8 b, k.
?1972 *Actinocamax plenus* (Blainville); Glazunova, tab XLI, fig. 1.
1973 *Actinocamax sozhensis* Makhlin, sp. nov; Makhlin, p. 90, text fig. 20 a–v, Pl. 26, fig. 3 a–g.
2000 *Praeactinocamax sozhensis* Makhlin; Naidin and Košťák, p. 100.
2003 *Praeactinocamax sozhensis* Makhlin; Košťák, p. 65, fig. 1.

Material studied: 30 specimens, 20 complete, come from 9 localities; they are kept in the collection of the Institute of Geology and Palaeontology, Faculty of Science, Charles University, Prague.

Short description: Guards are 47–87 mm long, markedly lanceolate in dorsoventral view and slightly lanceolate to subcylindrical in lateral view. The maximum lateral diameter is situated at the posterior third of the guard. The ventral side is flattened. The alveolar part is poorly calcified originally. The cross section is oval with a shallow pit in the centre or with a larger dissolved hole. Dorsolateral compressions and double furrows are fully developed. Striation is marked and dense. The mucro is missing. The apex is situated centrally.

Ontogeny: The typical adult specimen of *P. sozhensis* (No. 7247/1; L 75 mm, MLD 12.4 mm, DAMLD 30 mm; the locality of Vygonitchi) was studied. Isometric growth in length and width is stable during the whole ontogeny. Lanceolate shape of adult guard is almost identical with the shape of juvenile guard. Lanceolate shape shows no changes during the whole ontogeny – in all ontogenetic phases.
Affinities and remarks: *P. sozhensis* is similar to *P. plenus* in its size and partly in the shape of its guard. It differs from the latter in the absence of flattening of the ventral side and in a slightly different shape (more intensive length growth in *P. sozhensis* during ontogeny), poorly calcified anterior parts and a marked flattening. Striation is present in all specimens of *P. sozhensis* studied. *P. contractus* has a different shape and size of the guard. The character of the anterior end of the guard (alveolar fracture) somewhat resembles the representatives of *Actinocamax* Miller but the size of the guard is twice as long in *P. sozhensis*. Naidin (1964, Pl. 1, fig. 8 b, k) figured a specimen of *P. plenus* subsp. from the locality of Gryaz (the locus typicus of *P. sozhensis*). This specimen has a strongly dissolved alveolar part, which forms a high conus typical for *A. verus* Miller. This specimen is classified here as *P. sozhensis* on the basis of some morphological similarities such as the shape and size of the guard, marked striation, and poor calcification of alveolar fracture. *P. sozhensis* has never been found together with *P. plenus*. Its geographic distribution was lying further north from that of *P. plenus*. Makhlin (1973) described *P. sozhensis* from clayey siltstones of the uppermost Cenomanian in the Sozh River valley, Smolensk district. Some specimens studied come from the lower Turonian (together with *P. triangulus*).
Stratigraphic range: Uppermost Cenomanian to lower Turonian (together with *P. triangulus* – Betovo, Bryansk, Fokino, Pudovkino, Medwedica).
Geographic distribution: Russia – Bryansk, Volgograd, Saratov and Smolensk districts.

Praeactinocamax contractus Naidin, 1964

Pl. III, figs. 4, 10–13; Tab. 8

Holotype: *Actinocamax* (*Praeactinocamax*) *plenus contractus* Naidin, subsp. n.; Naidin, 1964, p. 46–47, Pl. 3, fig. 3. Kept in the paleontological collection of the MSU (Moscow) as item No. 6277/4.

Synonymy:
?1946 *Actinocamax* (sp.) aff. *plenus* Blv. (?=Act. lanceolatus Fritsch & Schlönbach non Sowerby); Jeletzky, p. 101, fig. 4.
1964 *Actinocamax* (*Praeactinocamax*) *plenus contractus* Naidin, subsp. n.; Naidin, p. 46-47, Pl. 3, fig. 3.
1972 *Actinocamax plenus* (Blainville); Glazunova, Pl. XLI, fig. 2–3.
1974 *Actinocamax plenus contractus* Naidin; Christensen, p. 12, 14, 21, 23.
1997 *Praeactinocamax plenus contractus* Naidin; Košťák and Pavliš, p. 6, 9.
2000 *Praeactinocamax plenus contractus* Naidin; Naidin and Košták, p. 100.
2003 *Praeactinocamax contractus* Naidin; Košťák, p. 65, fig. 1.

Material studied: 10 specimens from 6 localities, 9 complete specimens including the holotype No. 6277/4 (Lomonosov State University, Moscow) kept in the collection of the Institute of Geology and Palaeontology, Faculty of Science, Charles University, Prague.
Short description: Shorter (55–72 mm), stout and massive guards are lanceolate in dorsoventral view and slightly lanceolate to cylindrical in lateral view. The maximum lateral diameter is situated at the posterior third of the guard. The alveolar part is poorly calcified and often dissolved, oval to slightly triangular in cross section. A shallow pit in the centre is apparent in a few specimens. Dorsolateral compressions and double furrows are well developed; shallow vascular imprints are rare.
Ontogeny: A typical specimen of *P. contractus* (specimen No. 97–6; L 65 mm, MLD 14 mm, DAMLD 26 mm; the locality of Vygonitchi) was studied. The first visible guard is 23 mm long. Isometric growth continues until reaching 28 mm (43 % of total length of the guard). Allometric length and width growth follows from stages III–IV . The growth in the length decelerates from stage IV onwards (55 mm); on the other hand, the growth in the width stays invariable. The relatively stout and massive guard is the result of this type of ontogeny.
Affinities and remarks: *P. contractus* is similar to stouter specimens of *P. plenus*. It differs from *P. plenus* in having shorter and stouter guards and in having a poorly calcified anterior part. Unlike *P. triangulus* and *P.* sp. 1, *P. contractus* has no pseudoalveolus developed; guards of *P. contractus* are stouter and more massive. *P. contractus* somewhat resembles *P. sozhensis* in the character of its alveolar fracture but differs from the latter in the shape and size of the guard. Naidin (1964) described *P. contractus* as a subspecies of *P. plenus* (*P. plenus contractus*) on the basis of one complete specimen from the lower Turonian of the Cherkassy region. Christensen (1974) synonymized this subspecies with *P. plenus*; however, his biometrical analysis does not confirm this opinion, and this subspecies is not mentioned in his later papers. Košťák (in Košťák and Pavliš, 1997) opened this question again and recommended a new revision of the *plenus* subspecies: *P. plenus triangulus*, *P. plenus contractus* and *P. plenus crassus*. This revision was made in 1998 by the author, and nine other specimens of *P. contractus* were discovered in D. P. Naidin's collection. Based on a larger set of almost identical specimens, I consider *P. contractus* to be an independent species: it shows marked morphological differences from common *P. plenus* and also different stratigraphic distribution (lower Turonian).
Stratigraphic range: Lower Turonian, together with *P. triangulus* (Bryansk, Kamenka, Pudovkino).
Geographic distribution: Russia – Bryansk district (Bryansk), Saratov district (Saratov), Ulyanovsk district (Surskoe), Belarussia – Mogilev district (Sozh River), Ukraine – Tcherkassy district (Kanyev).

Praeactinocamax planus (Makhlin, 1965)

Pl. IV, figs. 11–15; Tab. 9

Holotype: *Gonioteuthis* (*Goniocamax*) *planus* Makhlin, sp. nov.; Makhlin, 1965, p. 29–32, text fig. 2 a–v, Pl. IV., fig. 3. Housed in the Museum of the "VNIGRI" (St. Peterburg) as item No. 726/1.

Synonymy:
1965 *Gonioteuthis* (*Goniocamax*) *planus* Makhlin, sp. nov.; Makhlin, p. 29–32, text fig. 2 a–v, Pl. IV., fig. 3–5.
1975 *Actinocamax planus* (Makhlin); Christensen, p. 27.
1976 *Actinocamax planus* (Makhlin); Christensen, p. 117.
1978 *Gonioteuthis* (*Goniocamax*) *planus* Makhlin; Naidin, p. 61.
1982 *Actinocamax planus* (Makhlin); Christensen, p. 63, 77–78.
1988 *Actinocamax planus* (Makhlin); Christensen, p. 10.
1993 *Actinocamax planus* (Makhlin); Christensen, p.441–442.
1997a *Praeactinocamax planus* (Makhlin); Christensen, p. 468.
1997b *Praeactinocamax planus* (Makhlin); Christensen, p. 66.
2003 *Praeactinocamax planus* (Makhlin); Košťák, p. 65, fig. 1.

Material studied: 9 specimens, 3 complete and 3 with measurable parameters come from the locality of Boltaevka (Ulyanovsk District); kept in the collections of the Department of Geology and Palaeontology, Faculty of Science, Charles University, Prague.
Short description: Guards are of a medium size (50–80 mm), markedly lanceolate in dorsoventral view and slightly lanceolate to subcylindrical in lateral view. The ventral side is markedly flattened. The maximum lateral diameter is situated at the posterior third of the guard. The alveolar fracture has a low conical to flat shape with a shallow pit in the centre. The cross-section is oval. Radial ribs and concentric layers are apparent. Dorsolateral compressions and double furrows are fully developed. Shallow vascular imprints are marked near double furrows. Striation is well visible. The length of the ventral notch does not exceed 5 mm. The mucro is fully developed in adult specimens only.
Affinities and remarks: *P. planus* strongly resembles Cenomanian *P. plenus*, especially in the shape and size of the guard and in having a similar alveolar fracture. Its cross section is slightly different. Guards of *P. planus* are more flattened ventrally. Middle Turonian *P.* aff. *plenus* differs from *P. planus* in its insignificant ventral flattening and its narrower anterior part. *P. planus* is considered here to be a descendant of the phyletic lineage of *primus*/*plenus* with respect to marked morphological similarities. Makhlin (1965) described this species from the locality of Kadyshevo (Sura River) from fine-grained calcareous sandstones together with *Inoceramus lamarcki* Park., which proves the late middle Turonian age. This species was re-discovered in 1999 in the same area in the overlying light upper Turonian marls at the locality of Boltaevka.
Stratigraphic range: Late middle Turonian (together with *I. lamarcki*) to upper Turonian [overlying light marls with *A. verus* ssp. – above the *I. lamarcki* Zone (Boltaevka)].
Geographic distribution: Russia – Ulyanovsk district, Sura River (Kadyshevo, Boltaevka).

Praeactinocamax coronatus (Makhlin, 1965)

Pl. IV, fig. 16

Holotype: *Gonioteuthis* (*Goniocamax*) *coronatus* Makhlin, sp. nov.; Makhlin, 1965, p. 26–29, text fig. 1 a–v, Pl. IV, fig. 1. Housed in the Museum of the "VNIGRI" (St. Peterburg) as item No. 726/5.

Synonymy:
1965 *Gonioteuthis* (*Goniocamax) coronatus* Makhlin, sp. nov.; Makhlin, p. 26–29, text fig. 1 a–v, Pl. IV, fig. 1–2.
1975 *Actinocamax coronatus* (Makhlin); Christensen, p. 27.
1976 *Actinocamax coronatus* (Makhlin); Christensen, p. 117.
1978 *Goniocamax coronatus* Makhlin; Naidin, p. 61.
1982 *Actinocamax coronatus* (Makhlin); Christensen, p. 63, 77–78.
1988 *Actinocamax coronatus* (Makhlin); Christensen, p. 10.
1993 *Actinocamax coronatus* (Makhlin); Christensen, p.441–442.
1997a *Praeactinocamax coronatus* (Makhlin); Christensen, p. 468.
l997b *Praeactinocamax coronatus* (Makhlin); Christensen, p. 66.
2003 *Praeactinocamax coronatus* (Makhlin); Košťák, p. 65, fig. 1.

Material studied: Anterior end with typical pseudoalveolus from the locality of Boltaevka (Ulyanovsk district, Sura River). Specimen No. Bco1999/7 (LDAE 8.4* mm, DVDAE 7.5 mm, D 6.2 mm) housed in the collections of the Department of Geology and Palaeontology, Faculty of Science, Charles University, Prague.
Short description: Guards of this species are slender and of a medium size – 80 mm long, subcylindrical in dorsoventral view and cylindrical to conical in lateral view. The maximum lateral diameter is situated at the posterior third of the guard. The ventral side is slightly flattened. The pseudoalveolus is relatively deep (6 mm), oval in cross section. Walls of pseudoalveolus with a typical crown-shaped margin. Concentric layers are apparent, radial ribs are poorly developed. Dorsolateral compressions are fully developed, dorsolateral double furrows are poorly developed. The ventral notch is short (not exceeding 4 mm). The apex is displaced towards the dorsal side.
Affinities and remarks: *P. coronatus* is similar to some rare upper Turonian belemnites – *P. bohemicus* (Stolley) and *P.* aff. *bohemicus* from the Central European Subprovince and Baltoscandia – and middle Turonian species of the North American Province – *P. manitobensis* (Whiteaves) – in having a similar shape and size of the guard. It, however, differs from the above species in its deeper and marked pseudoalveolus. *G. intermedius* differs from *P. coronatus* in the size and shape of the guard, in the cross section and poor calcification of its pseudoalveolus. *P. coronatus* differs from *P.* sp. 2 in the shape of the guard, the depth of pseudoalveolus, its cross-section and in the shape of pseudoalveolus margin. The relationship of *P. coronatus* to other species of *Praeactinocamax* from the EEP is not clear. *P. coronatus* is a highly endemic species of the Central Russian Subprovince (CRS). Makhlin (1965) reported *P. coronatus* from the locality of Kadyshevo, Sura River, from calcareous fine-grained sandstones together with inoceramids *I. lamarcki* Parkinson, which proves the upper middle Turonian in age. This species was re-discovered in the overlying upper Turonian light marls at the locality of Boltaevka in the same area in 1999.
Stratigraphic range: Upper middle Turonian (with *I. lamarcki*) to upper Turonian [the overlying light sandy marls with *A. verus* ssp. – above the *Inoceramus lamarcki* Zone (Boltaevka)].
Geographic distribution: Russia – Ulyanovsk district, Sura River (Kadyshevo, Boltaevka).

Praeactinocamax matesovae (Naidin, 1964)

Pl. VI, fig. 6, Tab. 10

Holotype: *Gonioteuthis* (*Goniocamax*) *matesovae* Naidin. sp. n.; Naidin, 1964, p. 109–110, Pl. 3, fig. 4. Kept in the paleontological collection of the MSU (Moscow) as item No. 5555.

Synonymy:
1964 *Gonioteuthis* (*Goniocamax*) *matesovae* Naidin. sp. n.; Naidin, p. 109–110, Pl. 3, fig. 4.
1975 *Actinocamax matesovae* (Naidin); Christensen, p. 27.
1976 *Actinocamax matesovae* (Naidin); Christensen, p. 117.
1982 *Actinocamax matesovae* (Naidin); Christensen, p. 63, 77–78.
1988 *Actinocamax matesovae* (Naidin); Christensen, p. 10.
1993 *Actinocamax matesovae* (Naidin); Christensen, p. 441.
1996 *Actinocamax strehlensis* (Fritsch et Schlönbach); Marcinowski and al., p. 43, Pl. 15, fig. 3 a–c.
1997a *Praeactinocamax matesovae* (Naidin); Christensen, p. 468.
1997b *Praeactinocamax matesovae* (Naidin); Christensen, p. 66–67.
2000 *Praeactinocamax matesovae* (Naidin); Naidin and Košťák, p. 100.
2003 *Praeactinocamax matesovae* (Naidin); Košťák, p. 65. fig. 1.

Material studied: Holotype No. 5555, kept in the collections of Lomonosov State University, Moscow. Specimen No. Spm1999/10 kept in the collections of the Department of Geology and Palaeontology, Faculty of Science, Charles University, Prague.
Short description: Guard is lanceolate in dorsoventral view and almost cylindrical in lateral view. The maximum lateral diameter is situated at the posterior third of the guard. The shallow pseudoalveolus (D = 1/11 of total length of the guard) is well calcified, oval in cross section. Concentric layers and radial ribs are apparent. Shallow and scarce vascular imprints reach out from dorsolateral double furrows. Striation is developed. The ventral notch is not apparent in the holotype. The mucro is well developed.
Affinities and remarks: In the shape of its guard *P. matesovae* resembles the earliest species of *Goniocamax* – *G. intermedius*, *G. surensis* and later *G. lundgreni*. It differs from these in having a shallower and well calcified pseodoalveolus. *G. lundgreni* differs in a different cross section of the pseudoalveolus. *P. matesovae* has a different size and shape of the guard compared to other species of *Praeactinocamax*. In the character of its pseudoalveolus, it somewhat resembles *P. triangulus* but differs in a different shape of the cross section. Naidin (1964) ranked this species together with *P. medwedicidus* to "primitive *Goniocamax*". However, its alveolar part is more similar to the early Turonian species of *Praeactinocamax*. The markedly similar shape of the guard with *Goniocamax* could be the result of convergence. Marcinowski and al. (1996, Pl. 15, fig. 3 a–c) figured a guard from the lower Coniacian deposits of the Mangyshlak Peninsula (NW Kazakhstan) as *Actinocamax* (= *Praeactinocamax*) *strehlensis* (Fritsch and Schlönbach). This specimen does not belong to *P. strehlensis*. The only figured adult specimen of *P. strehlensis* (Fritsch and Schlönbach 1972) shows no dorsolateral compressions and double furrows. The character of its alveolar part is also different. Marcinowski's *A. strehlensis* is fully identical with *P. matesovae* in the size and shape of the guard. However, the specimen from Mangyshlak has a much better developed ventral notch than *P. matesovae*. This systematic feature is not considered to be significant, however, specimens having as well as not having the notch are known in some species. Naidin (1964) also reported two other findings from the Volga River region.
Stratigraphic range: According to Naidin (1964), the stratigraphic range of *P. matesovae* is late middle Turonian to upper Turonian. With respect to the find of Marcinowski (Marcinowski et al. 1996), the stratigraphic range is revised here for middle/upper Turonian to lower Coniacian.
Geographic distribution: Russia – Saratov district (Volsk), Ulyanovsk district (Surskoe), NW Kazakhstan (Mangyshlak Peninsula).

Praeactinocamax medwedicicus (Naidin, 1964)

Tab. 11, not figured, see Naidin, 1964

Holotype: *Gonioteuthis* (*Goniocamax*) *medwedicicus* Naidin. sp. n.; Naidin, 1964, p. 109–110, Pl. 3, fig. 4. Housed in the paleontological collection of the MSU (Moscow) as item No. 5305/10.

Synonymy:
1964 *Gonioteuthis* (*Goniocamax*) *medwedicicus* Naidin. sp. n.; Naidin, p. 109–110, Pl. 3, fig. 4.
1975 *Actinocamax medwedicicus* (Naidin); Christensen, p. 27.
1976 *Actinocamax medwedicicus* (Naidin); Christensen, p. 117.
1982 *Actinocamax medwedicicus* (Naidin); Christensen, p. 63, 77–78.
1988 *Actinocamax medwedicicus* (Naidin); Christensen, p. 10.
1993 *Actinocamax medwedicicus* (Naidin); Christensen, p. 441.
1996 *Actinocamax medwedicicus* (Naidin); Košťák, p. 102.
1997a *Praeactinocamax medwedicicus* (Naidin); Christensen, p. 468.
1997b *Praeactinocamax medwedicicus* (Naidin); Christensen, p. 66–67.
2003 *Praeactinocamax medwedicicus* (Naidin); Košťák, p. 65, fig. 1.

Material studied: Holotype No. 5305/10 kept in the collections of Lomonosov State University, Moscow.
Short description: The guard is 75 mm long, cylindrical to very slightly lanceolate in dorsoventral view and cylindrical in lateral views. The maximum lateral diameter is situated at one half of the guard. The pseudoalveolus is 4 mm in depth, oval to triangular in cross section. Concentric layers are better visible than radial ribs. The rest of the ventral notch is visible. Dorsolateral compressions and double furrows are present. The mucro was not observed. Vascular imprints are missing.
Affinities and remarks: *P. medwedicicus* resembles very old specimens of *P. triangulus* especially in the similar character of pseudoalveolus. The shape of the guard is very different in young adult specimens and slightly different in old specimens of *P. triangulus* – the maximum lateral diameter is shifted towards the apex in *P. triangulus* (so, the shape of the guard is lanceolate). *P. mateso-*

vae and *P.* sp. 1 differ from *P. medwedicicus* in having smaller guards, different shapes and cross sections of the pseudoalveolus. Cenomanian *P. plenus* has a marked lanceolate guard shape and does not form this type of pseudoalveolus. *P. medwedicicus* differs from the first species of *Goniocamax* in its larger and more massive guards and in the character of its pseudoalveolus. *P. medwedicicus* is extremely rare and is a highly endemic species of the EEP (Central Russian Subprvince – CRP respectively). Its origin can be derived (based on alveolar part similarities) from *P. triangulus* (see Part III Phylogeny).
Stratigraphic range: Middle/upper Turonian to upper Turonian.
Geographic distribution: Russia – Volgograd district, Medwedica River.

Praeactinocamax sp. 1

Pl. VI, fig. 3; Tab. 12

Synonymy:
2003 *Praeactinocamax* sp. 1; Košťák, p. 65, fig. 1.

Material studied: One complete adult specimen No. 6302/1a; well-preserved alveolar part and juvenile specimen come from the same locality of Surskoe, Ulyanovsk district and the same stratigraphic level. Kept in the collection of the Institute of Geology and Palaeontology, Faculty of Science, Charles University, Prague.
Short description: Juvenile guard is 52 mm long, adult 69 mm long, very slightly lanceolate to subcylindrical in dorsoventral view and cylindrical in lateral view. The maximum lateral diameter is situated almost at one half of the guard. The ventral side is flattened, dorsal side is convex. Pseudoalveolus is relatively deep (6 mm), oval to triangular in cross section. Only concentric layers are apparent in the pseudoalveolus. A narrow margin of pseudoalveolus is poorly calcified. The ventral notch is missing. Dorsolateral compressions are fully developed, dorsolateral double furrows are missing. Poor and fine striation is apparent. The apex is situated centrally. The mucro is not present.
Affinities and remarks: *P.* sp. 1 markedly differs from all known Cenomanian through Turonian belemnitellid species in having a different shape of the guard and character of the pseudoalveolus. In the pseudoalveolus cross section *P.* sp. 1 slightly resembles *P. triangulus*. However, *P. triangulus* does not have a poorly calcified narrow margin of anterior end. The shape of the guard is markedly different. This species is retained in the open nomenclature with respect to shortage of material studied.
Stratigraphic range: The specimens were found in the lower Turonian deposits, according to the remarks of Yu. I. Katz (written notes attached to the specimens) together with brachiopods *Orbirhychia* cf. *mantelliana* and *Concinnithiris* cf. *rowei*.
Geographic distribution: Russia – Ulyanovsk district, Surskoe, Svyataya gora.

Praeactinocamax sp. 2

Pl. VI, fig. 4; Tab. 13

Synonymy:
2003 *Praeactinocamax* sp. 2; Košťák, p. 65, fig. 1.

Material studied: One complete specimen No. 672/62 comes from the locality of Ak-Kup, Tuarkyr (W Turkestan); housed in the collection of the Institute of Geology and Palaeontology, Faculty of Science, Charles University, Prague.
Short description: The guard is 70 mm long, lanceolate in dorsoventral view and cylindrical to subcylindrical in lateral view. The maximum lateral diameter is reached at the posterior third of the guard. Ventral and dorsal sides are markedly flattened (especially in posterior part of the guard). Pseudoalveolus is strongly calcified, irregularly oval to triangular in cross section. The depth of the pseudoalveolus is 4 mm. Concentric layers and radial ribs are apparent near the dorsal side. Ventral notch is marked (LVF 4 mm). Dorsolateral compressions are well developed. They markedly taper the dorsal side of the guard. Dorsolateral double furrows are not marked. Striation is poorly developed. Vascular imprints are missing. The apex is displaced towards the dorsal side, the most apical part is broken off.
Affinities and remarks: *P.* sp. 2 is similar to *P. strehlensis* in dorsoventral view. It differs in its marked ventral and dorsal flattening and in a different cross section of the pseudoalveolus. *P. triangulus* has a different character of the pseudoalveolus. In its pseudoalveolus, *P.* sp. 2 remotely resembles *P. coronatus* – the shape of the guard, the cross section and the depth of the pseudoalveolus are different. The specimen figured as "A. *strehlensis*" by Marcinowski and al. (1996) has no fully developed dorsolateral double furrows. Marcinowski's specimen (the base of the Coniacian) is referred to as *P. matesovae* here. This species is retained in the open nomenclature with respect to the shortage of material studied (only one complete specimen). However, marked morphological differences from all known species are apparent.
Stratigraphic range: The single specimen comes from the Turonian/Coniacian boundary interval, together with *Inoceramus schloenbachi*.
Geographic distribution: W Turkestan, Tuarkyr – east of the Caspian Sea, locality of Ak-Kup.

Genus *Goniocamax* Naidin, 1964
Type species: *Actinocamax lundgreni* Stolley, 1897, p. 285, Pl. 3: 16–20.

Diagnosis: Guards are 50–60 to 80–95 mm long, lanceolate in dorsoventral view and subcylindrical in lateral view. The ventral side is markedly flattened. The pseudoalveolus is relatively deep, 1/5 to 1/7 of total length of the guard, subtriangular to oval in cross section. The Schatzky distance (SD) is 2–4 mm, the angle between the bottom of the ventral fissure (BVF) and the wall of the pseudoalveolus (α_2) is 30°–50°, the alveolar angle (α_1) is less than 30°. Dorsolateral compressions and double furrows are fully developed. Striation is usually present and marked. Vascular imprints are apparent.
Discussion: Christensen and Schulz (1998) raised subgenus *Goniocamax* Naidin, 1964 to the rank of genus and established its stratigraphic range at the base of the Coniacian to lower Santonian. *G. intermedius* Arkhangelsky and *G. surensis* (Naidin) were not included in *Goniocamax* (these are supposed to be the species of *Praeactinocamax* Naidin – see Christensen and Schulz, 1998) with respect to the absence of the bottom of ven-

tral fissure. This morphological feature is not preserved primarily (see below). I recommend to include *G. intermedius* and *G. surensis* in *Goniocamax* with respect to their marked morphological similarities with *G. lundgreni* – the shape and size of the guard, and a similar character of the anterior end. *G.* sp. is described on the basis of four complete guards from the late Turonian – basal Coniacian deposits in the Volga River Region. It is *G.* sp. rather than *G. lundgreni* that resembles the first species of *Belemnitella*. In this paper, the stratigraphic range of *Goniocamax* is upper Turonian to lower Santonian.
Geographic distribution: East European Province – Russia – Volga River region (Ulyanovsk district, Kuybyshev district, Mordovska AR, Azovsk Sea region), western Siberia (Yenisei River), NW Kazakhstan – Ural-Emba district, Mangyshlak Peninsula), Belarussia (Mogilevsk district, Gomel district), Ukraine (Azovsk Sea region), North European Province – NW Germany, England, Baltoscandia – Denmark (Bornholm), Central European Subprovince – Czech Republic, ?Russia – Taimyr Region.

Goniocamax intermedius (Arkhangelsky, 1912)

Pl. V, figs. 1–6; Tab. 14

Holotype: *Actinocamax intermedius* Arkhangelsky; Arkhangelsky, 1912, p. 528, Pl. 9, fig. 30.

Synonymy:
1912 *Actinocamax intermedius* Arkhangelsky; Arkhangelsky, p. 528, Pl. 9, fig. 30-31, Pl. 10, fig. 6, 16–18.
1964 *Gonioteuthis* (*Goniocamax*) *intermedius* (Arkhangelsky); Naidin, p. 110-115, Pl. 8, fig. 1–3.
?1964 *Gonioteuthis* (*Goniocamax*) *intermedius* (Arkhangelsky); Naidin, Pl. 8, fig. 4, 5.
1965 *Gonioteuthis* (*Goniocamax*) *intermedius* (Arkhangelsky); Makhlin, p. 29, 30.
1975 *Actinocamax intermedius* Arkhangelsky; Christensen, p. 27.
1976 *Actinocamax intermedius* Arkhangelsky; Christensen, p. 117.
1982 *Actinocamax intermedius* Arkhangelsky; Christensen, p. 63, 68, 70, 71, 75–78.
1988 *Actinocamax intermedius* Arkhangelsky; Christensen, p. 8.
1993 *Actinocamax intermedius* Arkhangelsky; Christensen, p. 437.
1997a *Praeactinocamax intermedius* (Arkhangelsky); Christensen, p. 468.
1997b *Praeactinocamax intermedius* (Arkhangelsky); Christensen, p. 66.
2003 *Goniocamax intermedius* (Arkhangelsky); Košťák, p. 65, fig. 1.

Material studied: 17 guards, 12 complete, come from 7 locations. Housed in the collection of the Institute of Geology and Palaeontology, Faculty of Science, Charles University, Prague.
Short description: Guards are of medium size (average length 65 mm), lanceolate in dorsoventral view and slightly lanceolate to subcylindrical in lateral view. The ventral side is markedly flattened. The cross section is oval to triangular. The alveolar end is poorly calcified especially on dorsal and ventral margins. This unsettled part forms a typical V shape in dorsoventral view. The distance from protoconch to pseudoalveolus margin is smaller on dorsal side. The depth of the pseudoalveolus is 5 mm. The ventral notch is not preserved due to poor calcification of this place. A rest of the ventral notch is sometimes present. Dorsolateral compressions and furrows are fully developed. Striation is typical. Vascular imprints are well developed in some specimens.
Affinities and remarks: *G. intermedius* resembles *P. matesovae*, and especially *G. surensis* and *G. lundgreni*, by having a very similar shape of the guard. *G. lundgreni* is almost identical with *G. intermedius* in all characteristics with the exception of the alveolar end. This is poorly calcified in *G. intermedius*. A stronger calcification was recorded in specimen No. 8016b/1 (depth of pseudoalveolus 3.7 mm, shallow pit in the centre). *G. lundgreni* may be a descendant of *G. intermedius*. *G.* sp. n. sp. differs from *G. intermedius* in having larger guards, more convex dorsal side and a deeper pseudoalveolus. *G. intermedius* probably represents a parallel evolutionary lineage going to *G. lundgreni*. The determination of *G. intermedius* is possible in complete and well-preserved specimens only. Sinzov (1915), Jeletzky (1949b, 1950, 1961) and Naidin (1956) supposed that *G. intermedius* represents several similar species (see Naidin 1964, p. 112). Some lower Coniacian specimens of *G. lundgreni* and Cenomanian specimens of *P. plenus* were attributed to *G. intermedius* in the past (see Naidin, 1964). However, *G. intermedius* may include unknown species, too.
Stratigraphic range: Middle/upper Turonian to the base of the Coniacian.
Geographic distribution: Russia – Saratov district, Ulyanovsk district and Volgograd district.

Goniocamax surensis (Naidin, 1964)

Tab. 15, not figured, see Naidin, 1964

Holotype: "*Actinocamax*" *surensis* Naidin, sp. n.; Naidin, 1964, p. 78-80, Pl. 3, fig. 6. Housed in the paleontological collection of the MSU (Moscow) as item No. 380.

Synonymy:
1964 "*Actinocamax*" *surensis* Naidin, sp. n.; Naidin, p. 78–80, Pl. 3, fig. 6.
2003 *Goniocamax surensis* (Naidin); Košťák, p. 65, fig. 1.

Material studied: Holotype No. 380 (Lomonosov State University, Moscow) from the locality of Belovodye (Ulyanovsk district), paratype No. 1077/13 from the locality of Gayshin (Mogilevsk district). They are housed in the Lomonosov State University, Moscow.
Short description: Guards are of a medium size (50–60 mm long), slightly lanceolate in dorsoventral view. The maximum lateral diameter lies at 1/3 of posterior part of the guard. The ventral side is slightly flattened. The depth of the pseudoalveo-

lus does not exceed 3–4 mm. The cross section is oval to triangular. Concentric layers and radial ribs are apparent on walls of the pseudoalveolus. An unsettled V-shaped fracture is present at place of the ventral notch. Striation is apparent especially on the ventral side. Shallow vascular imprints are apparent near the dorsolateral furrows. The mucro is well developed.
Affinities and remarks: *G. surensis* is very close to *G. intermedius* and *G. lundgreni* in the size and shape of the guard. In the structure of its alveolar end it is almost identical with *G. intermedius*. I retain this poorly known species as an independent taxon for the time being but include this one to the genus *Goniocamax* (like *G. intermedius*) (cf. Naidin, 1964). Only two slightly different specimens are known. They may represent two species, too – *G. intermedius* (holotype No. 380) and *G. lundgreni* (paratype No. 1077/13). The paratype (1077/13) is almost identical with specimens of *G. lundgreni* from the same locality (Gayshin – Sozh River). However, I had the possibility to study only two specimens of *G. lundgreni* from this locality. *G. surensis* slightly differs from *G. lundgreni* in the structure of its alveolar part – the bottom of the ventral fissure (BVF) is not developed. Nevertheless, Naidin (1964) described and figured typical specimens of *G. lundgreni* with no BVF developed (p. 132, fig. 27 – 1079/13; p. 228 –1079/1, 1075/23). *G. intermedius* lacks BVF also due to poor primary calcification and poor preservation of this part of the pseudoalveolus. The holotype of *G. surensis* (No. 380) differs from *G. intermedius* in the position of the maximum lateral diameter, which is at one half in the holotype No. 380. The character of alveolar end is almost the same. It is possible that *G. surensis* represents a transition to *G. lundgreni*.
Stratigraphic range: Middle/upper Turonian (holotype No. 380) to basal Coniacian (paratype No. 1077/13) (cf. *G. intermedius* and *G. lundgreni*).
Geographic distribution: Russia – Ulyanovsk district, Belovodye – south of Surskoe, Belarussia – Mogilevsk district, Sozh River – Gayshin.

Goniocamax sp.

Pl. V, figs. 7–12; Tab. 16

Material studied: Four complete or nearly complete specimens No. 253/3 (Pudovkino, Saratov district), No. 249 bg (Pudovkino, Sarartov district) and No. S1999/7 (Surskoe, Ulyanovsk = Simbirsk district) and juvenile specimen No. 249bg/10. All specimens are kept in the collections of the Institute of Geology and Palaeontology, Charles University, Prague.
* The diagnosis, diferential diagnosis, locus typicus, stratum typicum and derivatio nominis of the new species will be given in separate paper by Košťák (in prep.)
Description: Guards are 63–73 mm long, lanceolate in dorsoventral view and cylindrical in lateral view. The maximum lateral diameter lies at one half of the length of the guard. Ventral and dorsal sides are markedly flattened, the ventral side is more flattened. The depth of pseudoalveolus is 7–9 mm. The surface of the pseudoalveolus is covered by conellae in the holotype. The Schatzky distance (SD) is 3 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 °. The cross section of 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.
Geographic distribution: Russia – Volga River region, Saratov district – Pudovkino, Ulyanovsk (=Simbirsk) district – Surskoe (Central Russian Subprovince).
Stratigraphic range: Upper Turonian (just above the *Inoceramus lamarcki* Zone – *Inoceramus costellatus* and *Mytiloides incertus* zones probably) to the base of the Coniacian (*Cremnoceramus rotundatus* Zone).

Phylogeny

The origin of Belemnitellidae Pavlow, 1914 has not been exactly explained to date. Jeletzky (1946) derived their origin from the Aptian Belemmnopseidae – probably from *Neohibolites ewaldi* (Strombeck) or N. clava Stolley on the basis of a similar alveolar part structure. Doyle (1987a, 1988a, 1992) supposed that belemnitellids are derived from some northern (boreal) endemics. Naidin and Alekseev (1975) supposed the origin of the first belemnitellid species – *Praeactinocamax primus* (Arkhangelsky) – from *Neohibolites repentinus* Naidin and Alekseev (early middle Cenomanian) with respect to the similar shape of the guard and the structure of the alveolar part. This opinion is incorrect – *P. primus* occurs in the same time interval and/or sooner than *N. repentinus*. Christensen (1997a) admitted a polyphyletic origin of the Belemnitellidae. *P. primus* and *N. repentinus* have probably a common ancestor in the *Neohibolites* group. The ancestor of other early belemnitellid *Actinocamax verus* Miller comes also from *Neohibolites* rather than from *Praeactinocamax* (Christensen 1997a). So, the origin of Belemnitellidae can be interpreted as monophyletic.

Praeactinocamax primus (Arkhangelsky) is the earliest representative of Belemnitellidae Pavlow, 1914. It occurs in the lower Cenomanian – at upper levels of the *Mantelliceras mantelli* Zone – and continues to lower parts of the *Mantelliceras dixoni* Zone in NW Europe. Naidin (1964) reported its stratigraphic range also from the lower Cenomanian, but in the sense of his two-substage division. The occurrence of *P. primus* was recorded in the upper lower Cenomanian together with *Schloenbachia varians* (Sowerby). Naidin (1964) also stated the occurrence of *P. primus* in the upper Cenomanian (Naidin's boundary between the lower and upper Cenomanian passes inside the *Acanthoceras rhotomagense* Zone – near the boundary between the *Turrilites costatus* Zone and *T. acutus* Zone).

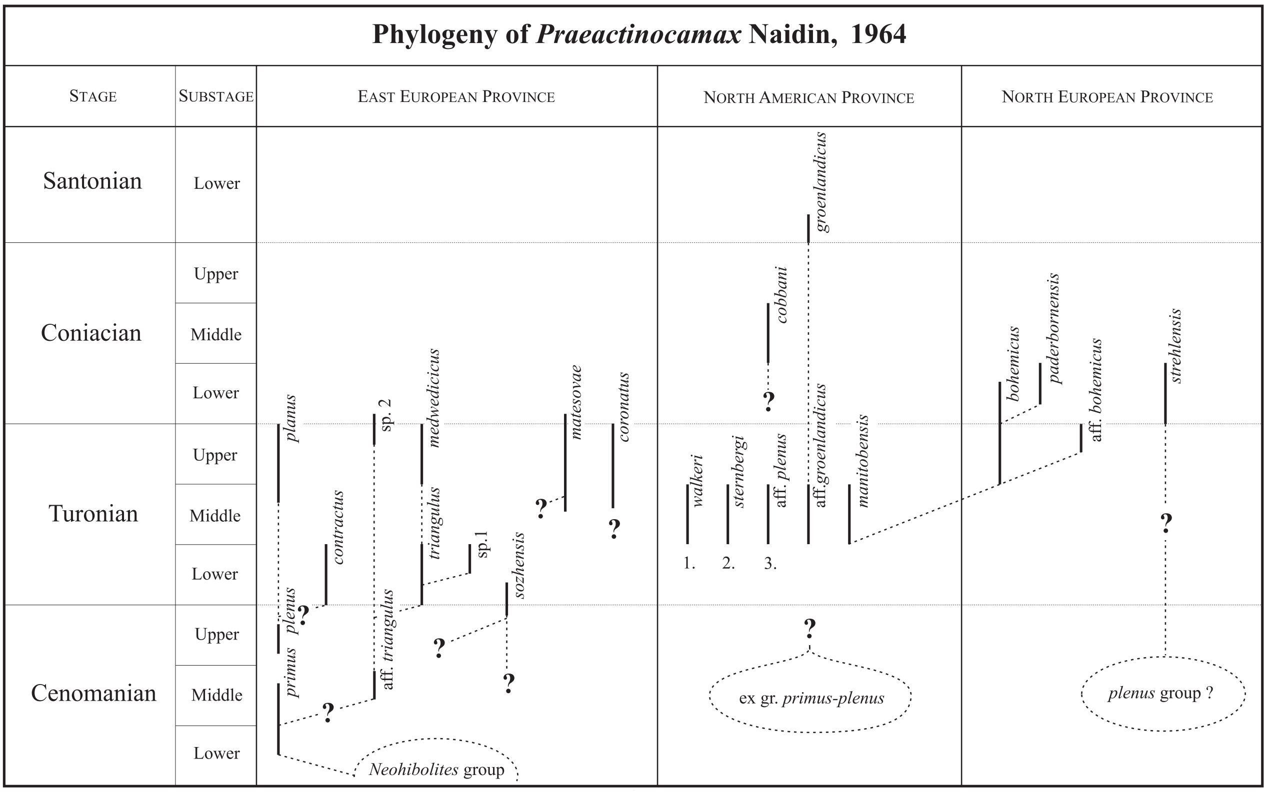
Praeactinocamax plenus (Blainville) is considered to be a direct phylogenetic descendant of *P. primus*. Christensen (1974, 1990 a) perfectly analysed the differences between these two species and confirmed a direct evolutionary lineage. *P. plenus* occurred in the upper Cenomanian 1m above its base (Mangyshlak Peninsula – Naidin 1964, Marcinowski and al. 1996) together with

Inoceramus pictus bohemicus Leonhardt. Stratigraphic range of *P. plenus* seems to be almost identical with the *Metoicoceras geslinianum* Zone in the whole area of its distribution. Evidence for this opinion is now lacking only from the easternmost parts of the *plenus* distribution area – the Tadzhikistan/Afghanistan border.

The rare and endemic lower Turonian species of *Praeactinocamax contractus* Naidin is widespread in the Central Russian Subprovince (CRS). In spite of the opinion of Christensen (1974), I consider *Praeactinocamax contractus* an independent species especially with respect to its specific morphology: shorter and stout massive guards and poorly calcified alveolar fracture. *P. contractus* is considered here to be a descendant of the *primus*/*plenus* evolutionary lineage – derived and specialized species, respectively. This species is known from the Volga River region and eastern Belarussia. Geographic distribution of *P. contractus* is one of the northernmost among the Belemnitellidae in the CRS.

The late Turonian *Praeactinocamax planus* (Makhlin) has probably its origin also in the *primus*/*plenus* evolutionary lineage. The morphology of *P. plenus* and *P. planus* is conservative and did not change during the Turonian (see Part II Systematics). Middle Turonian species of North American Province (NAP) – *P. manitobensis* (Whiteaves), *P. sternbergi* (Jeletzky), *P. walkeri* (Jeletzky), *P.* aff. *groenlandicus* a *P.* aff. *plenus* – are close to one another by having a similar alveolar fracture and partly also the shape of the guard. They are typical inhabitants of the NAP (including North America and Greenland). *Praeactinocamax* phylogeny is poorly recorded here. *Praeactinocamax cobbani* (Christensen) is known from the middle Coniacian and *P. groenlandicus* (Birkelund) from the lower Santonian. *P. groenlandicus* is the last representative of *Praeactinocamax*. Middle Turonian *Praeactinocamax* group in the NAP may be derived from *primus*/*plenus* ancestors, too. Their evolution passed independently in the North European Province (NEP) and in the East European Province (EEP). This group represents a typical parallel model of belemnitellid evolution. Species of the NEP – *P. bohemicus* (Stolley), *P.* aff. *bohemicus* and *P. paderbornensis* (Schlüter) –probably have their evolutionary roots in this group. *P. bohemicus*, *P.* aff. *bohemicus* a *P. paderbornensis* are extremely rare in Europe: they were described from the Upper Turonian through the lower Coniacian deposits of the Central European Subprovince (CES) and Baltoscandia. They may prove a connection between the NAP and NEP in the Turonian. On the other hand, the EEP was completely isolated from the NEP during the whole Turonian stage.

Praeactinocamax triangulus Naidin is raised to the rank of independent species here (see Part II Systematics). This species is derived from *P. primus* and/or especially from *P.* aff. *triangulus* rather than from *P. plenus*, as suggested by the guard shape and partly by ontogeny (not so marked allometric growth as in *P. plenus* – morphotype A). However, the *P. plenus* morphotype B shows almost isometric growth similar to *P. triangulus*. The single complete specimen of *P.* aff. *triangulus* known has a similar triangular shallower pseudoalveolus. Hypothetical evolutionary lineage is going to *P. triangulus* and can be possibly defined as follows: a common ancestor of *P. primus* (middle Cenomanian) and *P.* aff. *triangulus* (middle Cenomanian) – ? – *P. triangulus* (lower Turonian). During this evolution, a gradual calcification of alveolar part continued, a deeper pseudoalveolus formed, and the guard size increased. A similar calcification trend was described



■ **Text-fig. 12.** Phylogeny of *Praeactinocamax* Naidin, 1964.

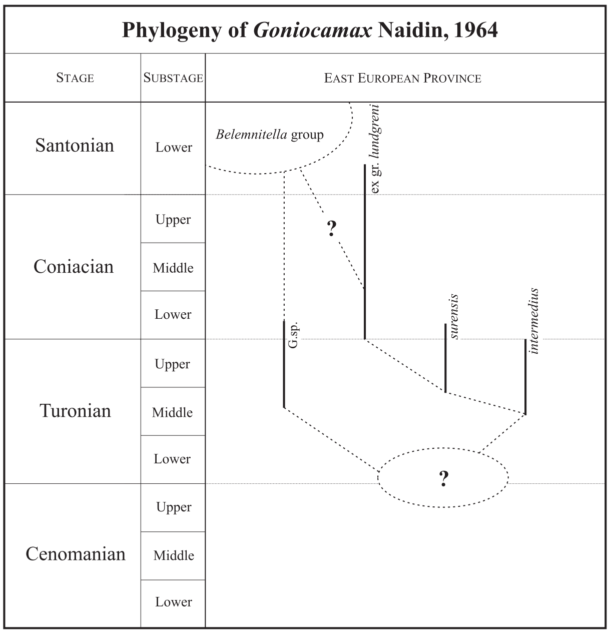
by Ernst (1964), Schulz (1974) and Christensen (1997) in *Gonioteuthis* Bayle, 1879.

The origin of *Praeactinocamax sozhensis* (Makhlin 1973) with poorly calcified alveolar fracture is not clear. This species probably represents a lineage parallel to *P. plenus* or convergence. Some morphological similarities like the shape and size of the guard could prove this opinion.

The origin of *Goniocamax* Naidin is unknown (Christensen 1997, Christensen and Schulz 1997). Christensen (1988) supposed that the *Belemnitella* stock is derived from *G. lundgreni* which originated from some species of *Praeactinocamax* in the Central Russian Subprovince. The origin of *G. lundgreni* is derived here from the *G. intermedius*/*G. surensis* group on the basis of the marked similarity in the shape and size of the guard. *G. intermedius* and *G. surensis* are supposed to be primitive species of *Goniocamax* in this paper. They are characterized by having poorly calcified dorsal and ventral pseudoalveolus wall areas. These species were placed into the genus *Praeactinocamax* by Christensen and Schulz (1997) on the basis of the absence of the bottom of ventral fissure (BVF). Naidin (1964) described and figured typical specimens of *G. lundgreni* (1964, p. 132, fig. 27 – No. 1079/13; p. 228 – Nos. 1079/1, 1075/23) with no BVF developed. These specimens strongly resemble the paratype of *G. surensis* (No. 1077/13) 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. Bottom of the ventral fissure is probably missing secondarily – ventral and dorsal parts of the pseudoalveolus were probably poorly calcified during the belemnite life. The origin of *G. lundgreni* can be explained by gradual calcification of the anterior part in the *intermedius*/*surensis* group. *G.* sp. occurs in the upper Turonian deposits of the Central Russian Subprovince (together with *G. intermedius*). It has well calcified pseudoalveolus and quite acute FA. This species resembles the first representatives of *Belemnitella* rather than the Coniacian *G. lundgreni*. This species can be considered an older ancestor of the *Belemnitella* group. On the other hand, the origin of *Belemnitella* may be polyphyletic.

Several "transitive forms" existed between *Praeactinocamax* and *Goniocamax* during the early through late Turonian: *P. matesovae* (Naidin), *P. coronatus* (Makhlin), and *P.* sp. 1. I suppose their morphology to be the result of convergence with *Goniocamax*. 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. The origin of *P. matesovae*, *P. coronatus*, and *P.* sp. 1 is not clear. *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 guards somewhat resemble the middle Turonian species of *Praeactinocamax* from the North American Province (*P. manitobensis*) and the rare upper Turonian belemnites from the Central European Subprovince and Baltoscandia (*P. bohemicus*, *P.* aff. *bohemicus*). *P. matesovae*, *P. coronatus*, and *P.* sp. 1 are very rare species of the Central Russian Subprovince. They show a high endemicity and diversity in this region.

The Turonian belemnitellids of the Central Russian Subprovince (genera *Actinocamax*, *Praeactinocamax* and *Goniocamax* including 13 species) show a high endemicity during the Turonian. They are not too frequent and only rarely migrate to other regions. *Praeactinocamax matesovae* (or a very similar species) occurs on the Mangyshlak Peninsula (Caspian Sea, NW Kazakhstan; Marcinowski and al. 1996 – figured as A. *strehlensis*, Pl. 15, fig. 3). *Praeactinocamax* sp. was recorded from Tuarkyr (W Turkestan) recently. 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– Naidin and al. 1986, Barskov and al. 1997, Naidin unpublished). Specimens from the Taimyr Region somewhat resemble the middle Turonian belemnitellids from the NAP by having a similar shape of the guard (author's observation). They have not been systematically evaluated yet. Their occurrence probably proves the so-called "North migration way" (Naidin 1978) across the Arctic circumpolar zones. This migration path could have connected the East European Province (EEP) with the North American Province in the Turonian.



■ **Text-fig. 13.** Phylogeny of *Goniocamax* Naidin, 1964.

The Central European Subprovince (CES) was completely isolated from the EEP during the whole Turonian stage. It is obvious that the late Turonian belemnites from the CES show marked similarities to those from the North American Province (including North America and Greenland). The EEP and the North European Province resumed connection in the earliest Coniacian again and fused into one North European Province sensu Christensen (= North European Region sensu Naidin). *Goniocamax lundgreni* (Stolley) is the first typical lower Coniacian species for this province (region).

Very rare representatives of *Praeactinocamax* immigrated to the CES and Baltoscandia (NEP) 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

North European Province, Central European Subprovince, Baltoscandia	East European Province, Central Russian Subprovince
very rare and poorly diversified species of *Praeactinocamax* (with some affinities to species from the North American Province)	relatively rare and richly diversified species of *Praeactinocamax* (with no affinities to species from the North European Province)
no species of *Actinocamax*	high abundance of *Actinocamax*, low diversity
no species of *Goniocamax*	more frequent and less diversified species of *Goniocamax*

■ **Text-tab. 2.** Late Turonian belemnitellids

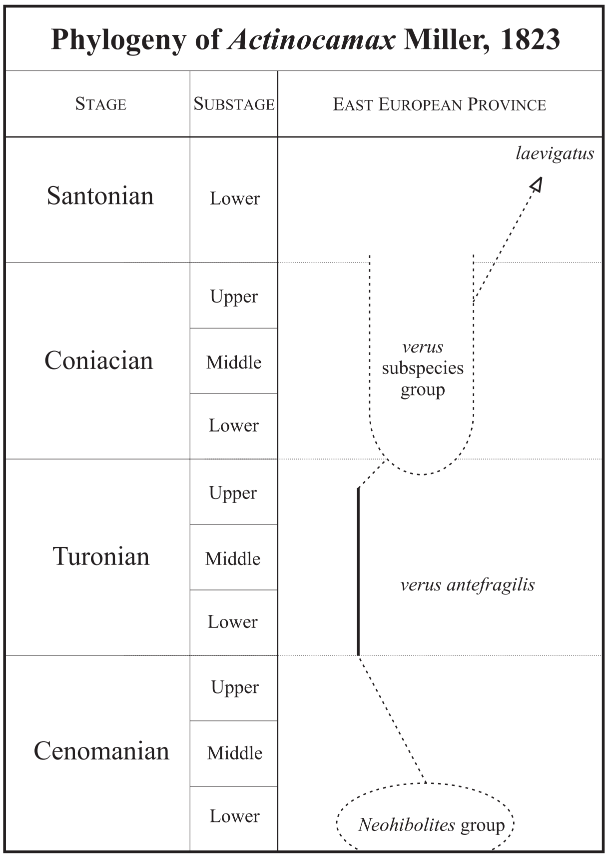
interval but have no known relationship to those in the NEP. They are relatively rare and endemic. The first representatives of *Goniocamax* ("primitive" – *G. intermedius*, *G. surensis* and "modern" – *G.* sp.) are less diversified but more frequent (*G. intermedius*).

A. verus antefragilis Naidin, 1964 is the earliest species of *Actinocamax* Miller, 1823. It occurs at the base of the Turonian in the EEP. The origin of this species is usually derived from *Neohibolites* (Naidin and Reyment 1962, Naidin 1964, Christensen 1993, 1997, Christensen and Schulz 1998). Christensen and Schulz (1998) proved isometric growth in *Actinocamax* and did not suppose the origin of *Actinocamax* from Cenomanian representatives of *Praeactinocamax* – *P. primus*/*P. plenus*. The subspecies of *A. verus fragilis* Arkhangelsky, *A. verus subfragilis* Naidin, *A. verus verus* Miller are derived from *A. verus antefragilis*.

Their radiation passed in the Turonian/Coniacian boundary interval in the EEP. These subspecies need new a revision with the use of large material from the Russian Platform. Their evaluation is not a part of this monograph.

Stratigraphy

Establishment of an exact belemnite stratigraphy is quite difficult in the East European Province. The almost complete absence of ammonites is typical for the Late Cretaceous eastern European epicontinental seas: if present, they are usually poorly preserved (see Naidin and Košťák, 1998). The exceptions are the southern to southeastern areas of the EEP (Mangyshlak Peninsula – NW Kazakhstan, Tuarkyr – Turkestan, Besh-Tyube – Uzbekistan). However, belemnites are rarer here than in the Central Russian Subprovince. We must use an inoceramid stratigraphy in the CRS for the biostratigraphic correlation. Foraminifera were obtained from some localities only (for example, Naidin and Kopaevich, 1988). The two-substage division used by Russian authors brings also some complications with exact stratigraphic interpretations. It was necessary to match the Russian two-substage division with the traditional West European three-substage division. Basic works for this compilation were those of Naidin and Kopaevich (1988) and Marcinowski and al. (1996).



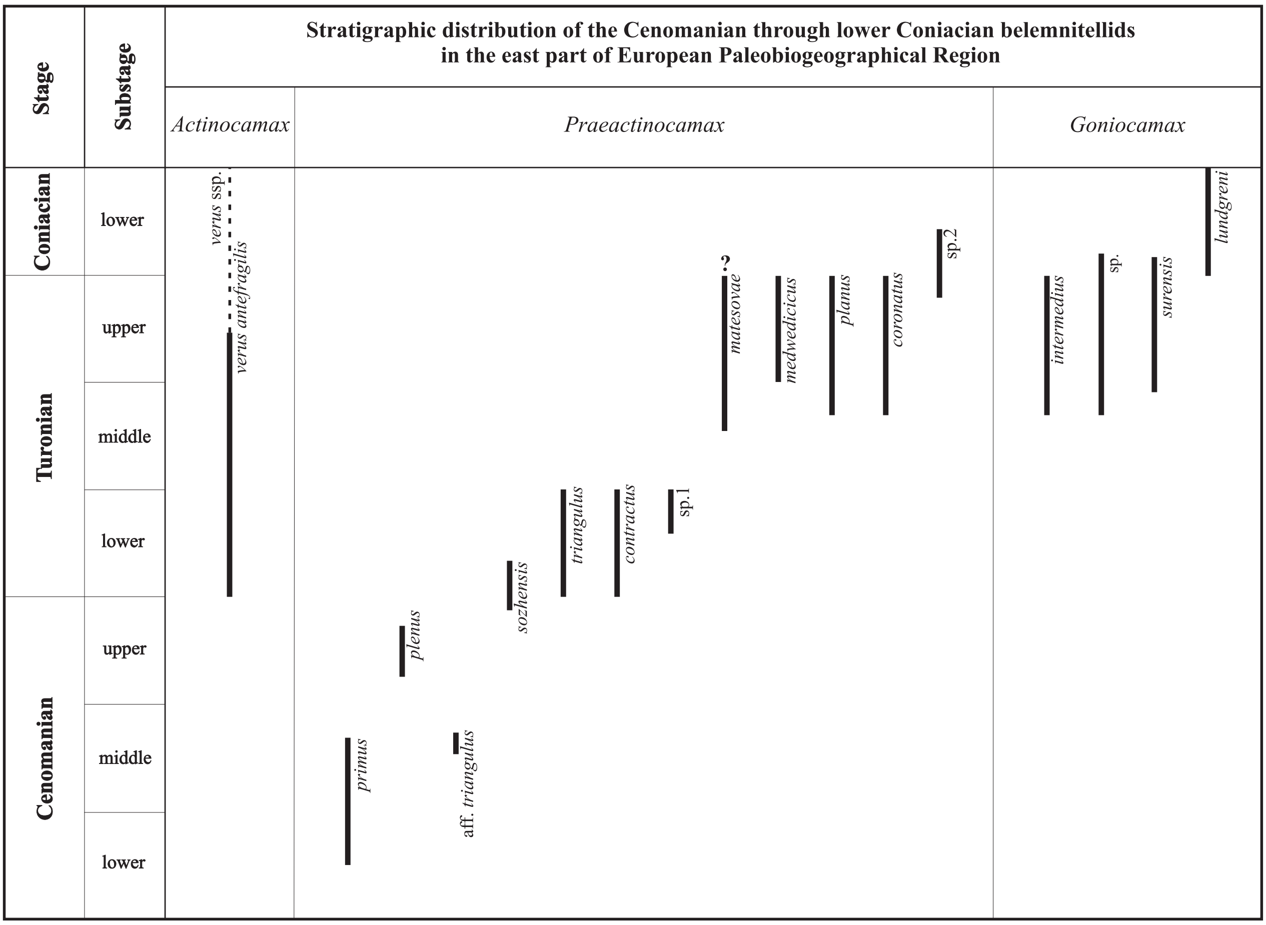
■ **Text-fig. 14.** Phylogeny of *Actinocamax* Miller, 1823.

Stratigraphic ranges of Cenomanian through the lowermost Coniacian belemnitellid taxa in the East European Province

Actinocamax verus appeared in the early Turonian together with *P. triangulus*, and continued through the middle to late Turonian together with *P. planus*, *P. coronatus* and *G. intermedius* – the *Inoceramus lamarcki* Zone.

P. primus occurred in the early Cenomanian – upper level of the *Mantelliceras mantelli* Zone and lower level of the *Mantelliceras dixoni* Zone, with *Schloenbachia varians* Sowerby and in the middle Cenomanian – the *Acanthoceras rhotomagense* Zone. Its occurrence in the upper Cenomanian sensu the three-substage division was not confirmed.

P. plenus is limited to the middle part of the upper Cenomanian (*Metoicoceras geslinianum* Zone) in the central and western Europe (Marcinowski 1972, Christensen and al. 1992, Gale and Christensen 1996, Košťák and Pavliš 1997). It occurs 1 m above the base of the upper Cenomanian (Mangyshlak Peninsula, Marcinowski and al. 1996), where it does not ranges into the *Neocardioceras juddii* Zone on Mangyshlak. The occurrence of *P. plenus* is probably identical with the *Metoicoceras geslinianum* range zone in its the whole paleobiogeographic distribution area. Lower Turonian occurrences (see Naidin 1964) were not confirmed, and lower Turonian belemnites formerly referred to *P. plenus* belong to other species (this paper).



■ **Text-fig. 15.** Stratigraphic ranges of belemnitellid species. Cenomanian through the lowermost Coniacian.

Makhlin (1973) described *P. sozhensis* from the upper Cenomanian sediments. The guards studied in this paper (prof. Naidin's collection) come from the lower Turonian deposits, too (with *P. triangulus* – Betovo, Bryansk, Fokino, Pudovkino, Medwedica).

P. triangulus appears just above the base of the Turonian in the western regions of the EEP in Belarussia and W Russia. The acme zone of this species is identical with the inoceramid *Mytiloides labiatus* Zone and ammonite *Mammites nodosoides* Zone. The following taxa were recorded with *P. triangulus*: – ammonites *Placenticeras kharesmense* Lah. and *Watinoceras amudariense* (Arkhangelsky), and brachiopods *Concinnithiris protobesa* Sahni, C. rowei Sahni, *Cretirhynchia robusta* (Tate) and *Orbirhynchia* cf. *cuvieri* (d'Orbigny) (see Naidin 1964).

P. contractus occurs in the lower Turonian together with *P. triangulus* (Bryansk, Kamenka, Pudovkino).

P. planus and *P. coronatus* appear together probably from the upper middle Turonian with *I. lamarcki* (*Inoceramus lamarcki* Zone) to the upper Turonian (the overlying light marls with *A. verus* ssp. at Boltaevka).

Naidin (1964) reported the stratigraphic range of *P. matesovae* and *P. medwedicicus* upper middle to upper Turonian. The specimen figured by Marcinowski et al. (1996) is referred to *P. matesovae* in this paper. It comes from the base of the Coniacian.

G. intermedius and *G. surensis* have similar stratigraphic ranges: middle/upper Turonian (*I. lamarcki* Zone) through the lowermost Coniacian, and *G.* sp. is the late Turonian to the lowermost Coniacian species.

Marked abundance and frequency of index belemnitellid species guards inside their range zones combined with their wide geographic distribution can be understood as belemnite events. High abundance of *P. primus* – the *primus* event was recorded north of the Caspian Sea (NW Kazakhstan) (lower part of the *Acanthoceras rhotomagense* Zone). This event approximately corresponds to those in NW Europe.

Stratigraphic range of *P. plenus* is very short and corresponds to the *Metoicoceras geslinianum* Zone in central and NW Europe and the *Inoceramus pictus bohemicus* Zone on the Mangyshlak Peninsula (between the *Acanthoceras jukesbrownei* Zone and *Neocardioceras juddii* Zone) – see Marcinowski and al. (1996). This range and the wide geographic distribution have the character of a separate event – the *plenus* event.

P. triangulus is used here as the lower Turonian index taxon (see also Naidin 1964). Maximum geographic distribution (from Belarussia in the west to Uzbekistan and Turkestan in the southeast) and high abundance of guards were recorded in the late lower Turonian (Mytiloides labiatus Zone and *Mammites nodosoides* Zone) – the *triangulus* event.

G. intermedius is used here as an index taxon for the middle/upper Turonian to the base of the Coniacian for the CRP and must be intensively studied in the future. The occurrence of

Stage	Substage	Inoceramids and ammonites zonation (Compiled after Naidin et Kopaevich, 1988 and Marcinowski et al, 1996)	**Belemnites zonation** (this paper)	**Foraminiferal assemblages zonation** (After Naidin et Kopaevich, 1988)
		Cenomanian through lower Coniacian biostratigraphic zonation of eastern part of the European Palaeobiogeographical Region		
Coniacian	lower	*Cremnoceramus crassus/C. deformis* *Cremnoceramus brogniarti* *Cremnoceramus rotundatus*	*Goniocamax lundgreni*	***Gavelinella praeinfrasantonica,*** *G. kelleri, G. costulata, Cibicidoides praeeriksdalensis, Stensioeina* gr. *granulata, Reussella kelleri*
Turonian	upper	*Mytiloides incertus* *Inoceramus costellatus*	*Goniocamax intermedius* (CRS)	***Atalophragmium nautiloides,*** *Gavelinella* gr. *costulata, Globorotalites mishelinianus*
Turonian	middle	*Inoceramus lamarcki* *Inoceramus apicalis* *Mytiloides hercynicus*	*Goniocamax intermedius* (CRS)	***Gavelinella moniliformis,*** *Spiroplectammina praelonga, Gaudryina variabilis, Globotruncana*
Turonian	lower	*Mytiloides labiatus* *Mytiloides kossmati* *Watinoceras amudariense/M. hattini* *Mammites nodosoides*	*Praeactinocamax triangulus*	***Globorotalites hangensis,*** *Gyroidinanitida, Gavelinella vesca, Cibicidoides apprima* *Hedbergella holzli, H. portsdownensis, H. brittonensis*
Cenomanian	upper	*Neocardioceras judii*		***Brotzenella berthelini,*** *Gavelinella vesca, Cibicidoides apprima*
Cenomanian	upper	*Inoceramus pictus bohemicus*	*Praeactinocamax plenus*	***Brotzenella berthelini,*** *Gavelinella vesca, Cibicidoides apprima*
Cenomanian	upper	*Eucalycoceras pentagonum*		
Cenomanian	middle	*Inoceramus crippsi* – *Acanthoceras jukesbrownei*		
Cenomanian	middle	*Inoceramus crippsi* – *Turrilites acutus* / *Acanthoceras rhotomagense*		
Cenomanian	middle	*Inoceramus crippsi* – *Turrilites costatus* / *Acanthoceras rhotomagense*	*Praeactinocamax primus*	***Gavelinella cenomanica,*** *G. c. concava, G. baltica, Lingulogavelinella globosa, Cibicides polyrraphes polyrraphes, Thalmanninella appenninica*
Cenomanian	lower	*Inoceramus crippsi* – *Mantelliceras dixoni* *Mantelliceras mantelli*	*Praeactinocamax primus*	***Hoeglundina dorsoplana,*** *Gavelinella cenomanica, G. intermedia, Lingulogavelinella* gr. *globosa*

■ **Text-fig. 16.** Belemnitellid biozones in the Cenomanian through the lower Coniacian interval.

G. lundgreni is marked in the late lower Coniacian of the European Palaeobiogegraphic region.

G. lundgreni rarely penetrated also to the central European basins (Cremnoceramus *crassus* Zone, Košťák, 1996). The appearance of this species finished the existence of the independent EEP. The belemnite fauna became cosmopolitan again. The easternmost occurrence of *G. lundgreni* was recorded from the Azovsk Sea area (Naidin, 1964), a problematical find comes from the lower Coniacian of the Mangyshlak Peninsula (*Actinocamax* cf. *lundgreni*, Marcinowski and al. 1996). The *lundgreni* event can be established for the late lower Coniacian later – after a revision of the material from eastern Europe.

Palaeobiogeography

Kauffman (1973) established a quantitative scheme for the Cretaceous biogeographic units defined on the basis of bivalve genera and subgenera distribution. Christensen (1975, 1976, 1988, 1990b, 1993b, 1997a,b) recognized realms, provinces and subprovinces on the basis of the Late Cretaceous belemnite distribution. South "Temperate" Realm is characterized by the family Dimitobellidae Whitehouse and North "Temperate" Realm (Boreal), by Belemnitellidae Pavlow in the Late Cretaceous.

Christensen (1976) divided the North "Temperate" Realm (=Boreal) into the North European Province (including Central European Subprovince) and North American Province (North America, Greenland) based on belemnite (belemnitellid) distribution. Belemnitellids of the North American Province (NAP) are characterized 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) and *Belemnitella* d´Orbigny (Christensen, 1997a). Christensen (1997a) established three subprovinces within the NEP in the Late Cretaceous: Central European,

Belemnites zones and events – primus, plenus and lundgreni events for the whole EPR; triangulus event is established for the EEPP.

Coniacian	lower	Goniocamax lundgreni	● lundgreni event
Turonian	upper	Goniocamax intermedius	
	middle		
	lower	Praeactinocamax triangulus	● triangulus event
Cenomanian	upper	Praeactinocamax plenus	● plenus event
	middle		
	lower	Praeactinocamax primus	● primus event

■ **Text-fig. 17.** Belemnitellid events in the Cenomanian through the lower Coniacian interval.

Central Russian and Baltoscandia. The NEP is widespread from the Northern Ireland in the west to the Ural Mountains (across England, France, the Netherlands, Denmark, southern Sweden, Belgium, Germany, Poland, Lithuania, Belarussia, Ukraine, Russia and Kazakhstan). Two belemnitellid genera (*Praeactinocamax* and *Goniocamax*) were recently recorded from the Bohemian Cretaceous Basin (Košťák 1996).

Belemnitellids migrated also into northern areas of the Tethyan Realm (SE France – Gale and Christensen, 1996), Mediterranean Region (W and S of Turkestan, Tadzhikistan/Afghanistan border), Transcaspian area, western Siberia (Krasnoyarsk district – Makhlin, unpublished), and Russian Arctic regions (Ob River estuary – Naidin, unpublished, Taimyr Region – Naidin et al. 1986, Barskov et al. 1997).

Naidin (1978) recommended to use the term European Palaeobiogeographic Region. The northern part of this region includes central part of the Russian Platform, Azovsk Sea area, SW Siberia. The southern part includes Carpathian areas, Crimea, Caucasus Mts., western Central Asia (Mangyshlak Peninsula in NW Kazakhstan), Tuarkyr (W Turkestan), and western Kopetdag (S Turkestan).

It is necessary to redefine paleobiogeographic units in the eastern parts of the European Palaeobiogeographic Region (EPR) during the latest Cenomanian through the earliest Coniacian on the basis of a review of the geographic distribution of belemnitellids. Eastern part of the EPR shows the character of an independent province (East European Province) during this interval. The Central Russian Subprovince should be included within the East European Province. It fused with the NEP during the early to late Cenomanian and from the earliest Coniacian to the Maastrichtian.

⇒ North European Province (sensu Christensen, 1976)
 ⇒ Central European Subprovince
 ⇒ Baltoscandia
⇒ East European Province (latest upper Cenomanian –base of the Coniacian – Naidin & Košťák, 2000; this paper)
 ⇒ Central Russian Subprovince

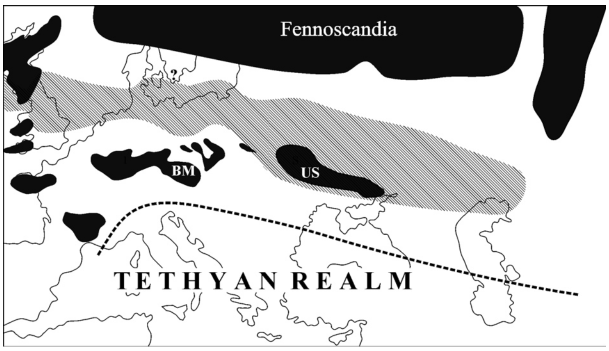
■ **Text-Tab. 3.** European Palaeobiogegraphic Region

Belemnitellids show a cosmopolitan distribution in middle to late Cenomanian in the whole European Palaeobiogeographic Region (= NEP sensu Christensen, 1976) (see Text-fig. 26). *Praeactinocamax primus* (Arkh.) is widespread from the northern Caspian Sea area in the east to Northern Ireland in the west. Geographic distribution of this species represents a belt 4000 km long and about 1000 km wide.

Geographic distribution of *P. plenus* (Blainv.), which is considered to be a phylogenetic descendant of *P. primus*, extends more than 1000 km to the east (to the Afghanistan/Tadzhikistan border) and also to the south (Tethyan Realm), central European basins, Crimea and southern Turkestan.

The low belemnitellid diversity in the Cenomanian/Turonian boundary interval is presumably connected with a major Cm/T extinction. Only the highly endemic species *P. sozhensis* (Makhlin) survived this time interval in the area between the present Russia/Belarussia and the Russia/Kazakhstan borders.

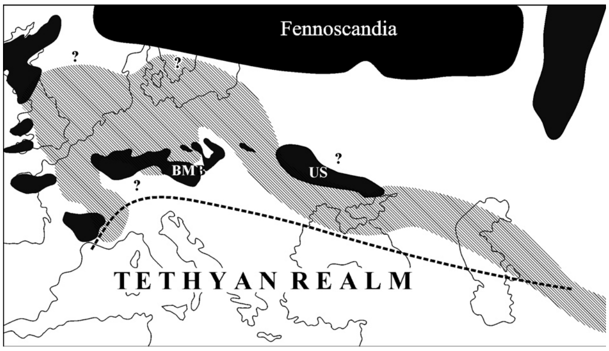
The eastern part of the European Paleobiogeographic Region can be considered an independent province (East European Pro-



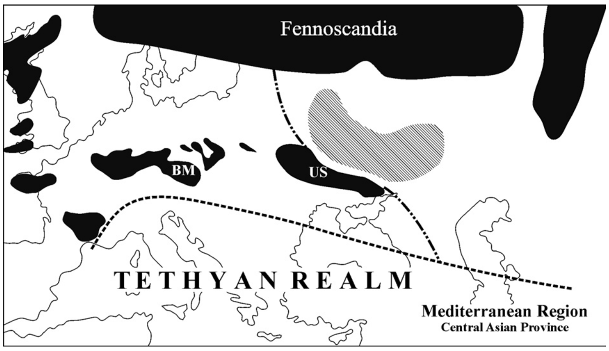
■ **Text-fig. 18.** Palaeobiogeographic distribution of *P. primus*. Middle Cenomanian. BM – Bohemian Massif, US – Ukrainian Shield.

vince, EEP) with respect to the occurrence of 100% endemic taxa in the latest Cenomanian through the earliest Coniacian. This province existed for about 5 million years. The Russian Central Subprovince is well distinguishable from the early Turonian to the earliest Coniacian. Communication with other areas is limited to the southeast (Transcaspian area), east (western Siberia, Yenisei River), and north (Russian Arctica – Taimyr Region).

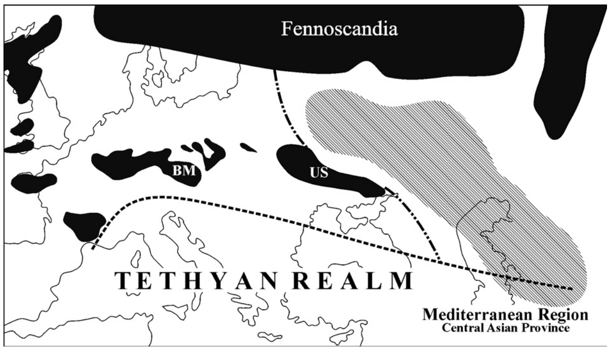
Praeactinocamax triangulus Naidin and *P. contractus* Naidin are now raised to the rank of independent species on the basis of their biometry, morphology, ontogeny and stratigraphy, and belong to taxa typical of the EEP in the early Turonian. Geographic distribution of *P. triangulus* extends from Belarussia in



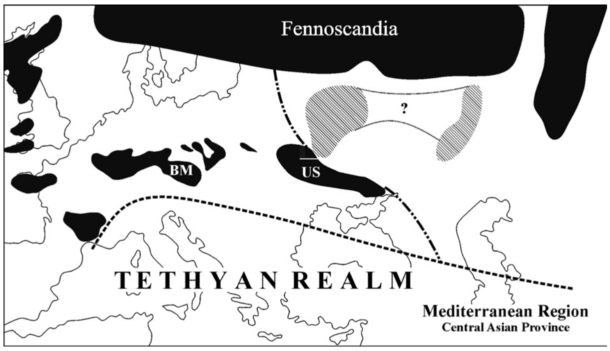
■ **Text-fig. 19.** Palaeobiogeographic distribution of *P. plenus*. Late Cenomanian. BM – Bohemian Massif, US – Ukrainian Shield.



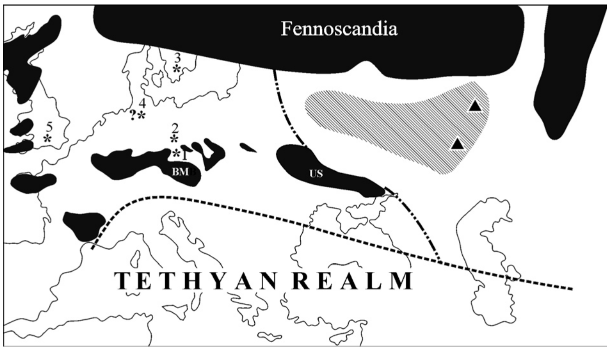
■ **Text-fig. 20.** Palaeobiogeographic distribution of *P. sozhensis*. Cenomanian/Turonian boundary interval. BM – Bohemian Massif, US – Ukrainian Shield.



■ **Text-fig. 21.** Palaeobiogeographic distribution of *P. triangulus*. Early Turonian. BM – Bohemian Massif, US – Ukrainian Shield.



■ **Text-fig. 22.** Palaeobiogeographic distribution of *P. contractus*. Early Turonian. BM – Bohemian Massif, US – Ukrainian Shield.



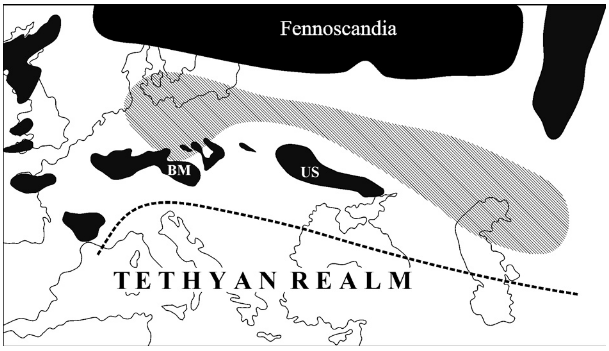
■ **Text-fig. 23.** Palaeobiogeographic distribution of *G. intermedius* (late middle to upper Turonian) and *G.* sp. (Δ; upper Turonian – the base of the Coniacian). The upper Turonian distribution of *P. bohemicus* (*) in Central and Northern Europe (1. Bohemian Cretaceous Basin, 2. Saxony, 3. S Sweden, 4. ?Münster Basin), 5. lower Coniacian in England (Yorkshire). BM – Bohemian Massif, US – Ukrainian Shield.

the west as far as to Uzbekistan and western Turkestan in the southeast.

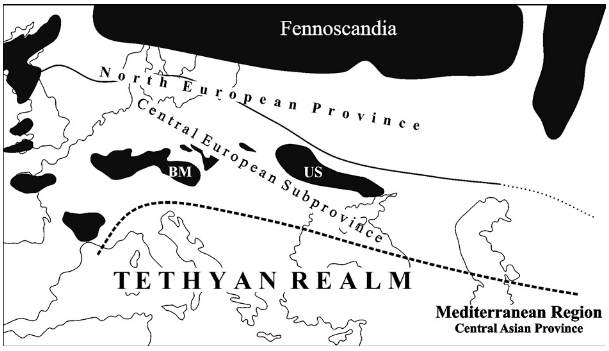
Goniocamax intermedius (Arkhangelsky) and G. sp. are the middle Turonian through the lowermost Coniacian endemics of the CRS.

Belemnitellids of the Central Russian Subprovince (genera *Actinocamax*, *Praeactinocamax*, and *Goniocamax* including 12 species) show high endemicity during the Turonian. They are not so much frequent and only rarely migrate into other regions. *Praeactinocamax matesovae* (Naidin) (or a very similar species) occurs on the Mangyshlak Peninsula (Caspian Sea, NW Kazakhstan). *Praeactinocamax* sp. is (this paper) recorded from Tuarkyr (W Turkestan). 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 Russian Arctic regions (Taimyr Region). Their occurrence probably proves the so-called North migration way (Naidin, 1978; Saks and Nal´nyaeva, 1975) across the Arctic circumpolar zones. This migration path could have connected the EEP with the North American Province in the Turonian (Košťák and Wiese, 2002).

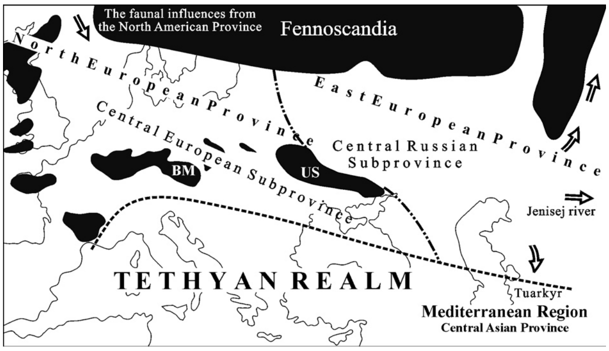
The Central European Subprovince (CES) is completely isolated from the EEP during the whole Turonian stage (see Text-fig. 26). It is obvious that the late Turonian belemnites from the CES show marked similarities to those from the North American Province (including North America and Greenland). The EEP and NEP resumed connection in the earliest Coniacian again (*G. lundgreni*, ?*A. verus* ssp.) and fused into a single North European Province (= North European Region) (Text-fig. 27). *Goniocamax lundgreni* (Stolley) is the first typical lower Coniacian species (Text-fig. 24) for this province



■ **Text-fig. 24.** Palaeobiogeographic distribution of *G. lundgreni*. Early Coniacian.



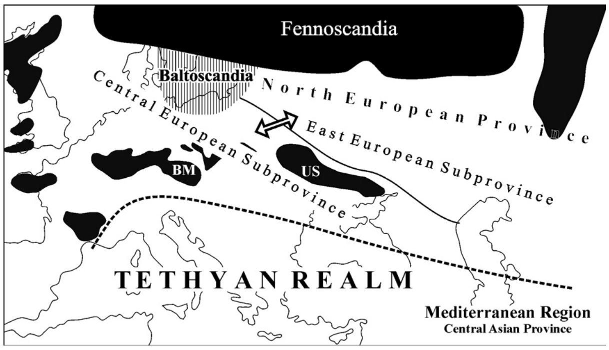
■ **Text-fig. 25.** Cenomanian belemnitellid Province distribution (after Christensen, 1976). BM – Bohemian Massif, US – Ukrainian Shield.



■ **Text-fig. 26.** Turonian belemnitellid Province distribution. BM – Bohemian Massif, US – Ukrainian Shield.

(region). The possibility of contemporaneous distribution of *G. lundgreni* in the Baltoscandia and CRS is the last remaining question. Some insinuations could prove that *G. lundgreni* occurred also in the CRS in the earliest Coniacian (see parts II Systematics and III Phylogeny). This problem should be studied in more detail, especially with the use of material from Russia.

Free belemnite migration continued during the Santonian, Campanian and Maastrichtian – genera *Gonioteuthis*, *Belemnitella* and Belemnella are almost cosmopolitan in the whole North European Region.



■ **Text-fig. 27.** Coniacian belemnitellid Province distribution (after Christensen, 1976 and 1997; Naidin &et al. 1993). BM – Bohemian Massif, US – Ukrainian Shield.

Palaeoecology and palaeobiology

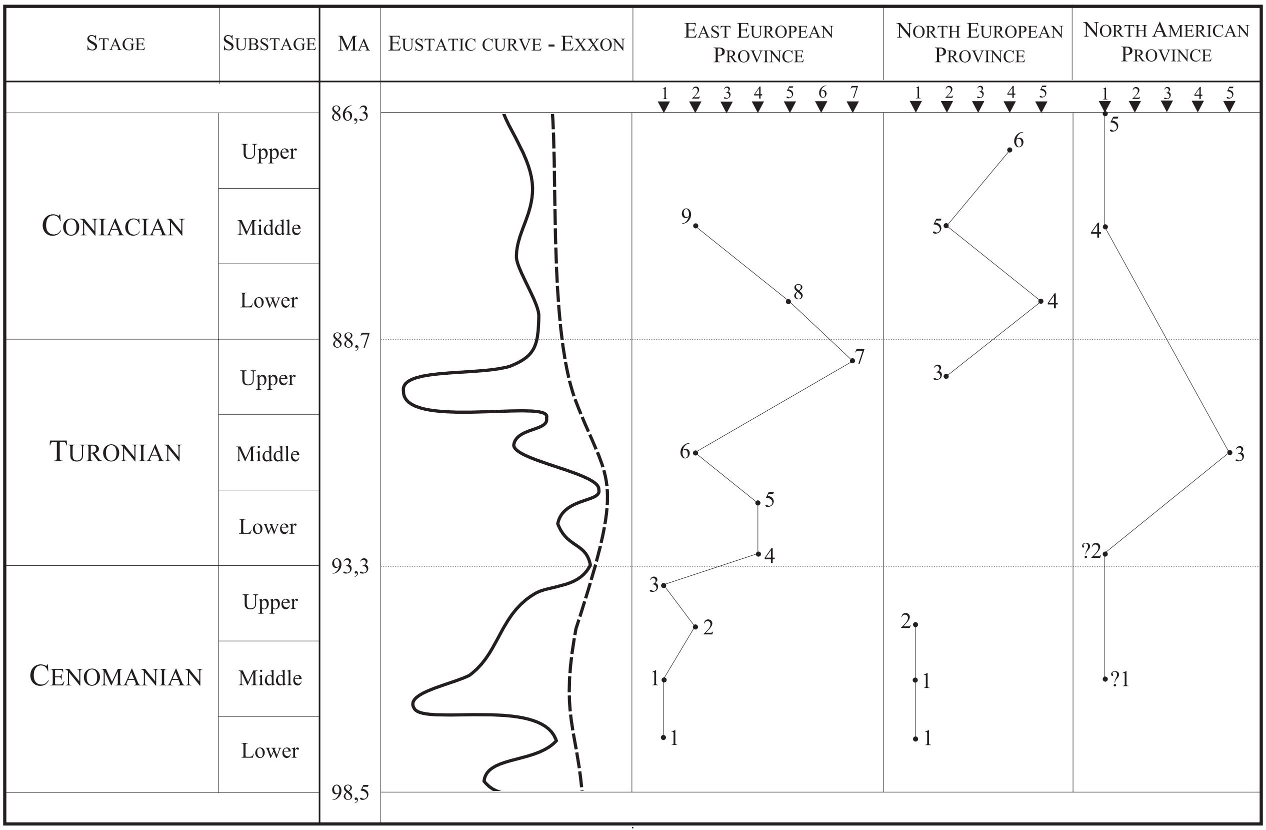
The depth of basins (100–200m) and the probable temperature of 12–17 °C (see Stevens 1965, Naidin 1969, more recently Voigt and al. 2001) of sea water were the limiting factors for belemnitellid evolution. Deeper water became a barrier for them. The depth and temperature are the reasons for belemnitellid absence in the Tethyan Realm. Belemnitellidae are distributed on the northern hemisphere only.

Progressive Cenomanian transgression affected large platform areas here and established suitable conditions for belemnitellid evolution. However, the origin and spread of larger oceans limited their migration especially towards the south. Family Dimitobellidae Whiteaves (derived from immigrants of northern hemisphere) developed on the southern hemisphere as independent belemnite fauna. The temperature, depth and physical/chemical properties of seawater combined with specific ecological and ethological characteristics of independent taxa caused their provinciality in the Late Cretaceous. Dependence on facies has not been proved (Naidin, 1969; Christensen, 1976).

Generally, belemnites can be considered inhabitants of shallower seas (nearshore areas) with the mean temperature of about 15 °C. Higher abundance of guards (so-called "battle fields") can be explained by actualistic model – by the comparison with the ethology of modern Coleoidea (common squids). Their mass dying is connected with copulation acts (see also Doyle and Mac Donald, 1993). Places of their reproduction are also looked for by many predators (especially sharks). Shark teeth are very frequent and abundant in deposits rich in guards. Shark fauna is usually the only common fauna preserved together with belemnites in the EEP (author's observation).

Eustasy and belemnitellid diversity in the East European Province during the Cenomanian to early Coniacian

Belemnitellids (Belemnitellidae, Pavlow) are common fossils of the Late Cretaceous shallow East European seas. The East European Province (EEP) was recently established by Naidin and Košťák (2000) on the basis of 100% occurrence of endemic belemnitellid taxa in the uppermost Cenomanian – lowermost Coniacian



■ **Text-fig. 28.** Eustasy and belemnitellid diversity (Cenomanian – Coniacian): ∇ 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.* sp., *Actinocamax verus* ssp. 8. *Goniocamax lundgreni*, *G. surensis*, *G.* sp., *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).

interval. Their stratigraphic ranges were revised and compared with the general eustatic curve (Exxon – Košťák 2003).
The most diversified belemnitellid fauna occurs in the upper Turonian of the EEP, middle Turonian of North American Province (NAP) and lower Coniacian of North European Province (NEP) in the upper Cenomanian through lower Coniacian interval. A revision of the systematics and stratigraphic ranges of belemnitellids from the EEP enabled a correlation between their occurrences and eustatic cycles in the EEP.

Low belemnitellid diversity is not influenced by the Cenomanian transgression (low diversity could have been connected with Oceanic Anoxic Event – OAE 2). A dependence of belemnitellid diversity on transgression/regression pulses is marked from the lower Turonian in the EEP. Belemnitellids are relatively well diversified here in the lower Turonian and in the lower/middle Turonian boundary interval. A decline in their diversity is recorded in the middle Turonian of the EEP (on the other hand, the maximum diversity of belemnitellids in the NAP culminated in the middle Turonian). An absolute absence of belemnitellids in the Central European Subprovince of the NEP was encountered in the lower to middle Turonian. The most diversified belemnitellid fauna occurs in the upper Turonian of the EEP. This phenomenon is probably connected with the late Turonian transgression pulse. Rare species of *P. bohemicus* and *P.* aff. *bohemicus* probably migrated from the NAP to the NEP in the late Turonian. Their similarities to representatives from the NAP were discussed by Jeletzky (1961), Naidin (1964), Christensen (1982), Košták (1996), Košťák and Wiese (2002). Interconnection of the NEP with the EEP started in the early Coniacian, and the NEP and EEP fused into a single North

European Province sensu Christensen (1976) or Region sensu Naidin (1978).

No evidence was found for the theory of different deeper-water dependences of belemnitellid species. Functional morphology and hydrodynamics could be the key to this problem.

? Sexual dimorphism

The sample of population was divided into two distinguishable parts by statistical program in some species – most notably in *P. plenus*. This phenomenon was observed in *P. plenus* from the Bohemian Cretaceous Basin, too (Košťák and Pavliš, 1997). The absence of the medium-size class, which is reported as the most numerous from England (Christensen, 1974), can be explained by the highest fitness, that is the lowest mortality of these specimens. Selection caused by different preservation of this class is impossible. Nevertheless, this size distribution may be also due to sexual dimorphism. The belemnite sexual dimorphism was described by some authors in the past, more recently by Doyle (1985) for the Jurassic belemnites. A. d´Orbigny (see Špinar, 1960, p. 466–467) considered smaller guards to belong to females and larger guards to males. It is very difficult to define sexual dimorphism in belemnites because it has very different forms in modern cephalopods – i.e., either larger males or females.

The L/DAMLD and MLD/DAMLD parameter ratios seem to be a key to the distinction of variability in the sample. Possible sexual dimorphism must be studied only in large sets (more than 50 specimens from the same locality and stratigraphic level). At the same time, ontogeny must be known, i.e., iso- and allometric growth phases.

Remarks to description of the Upper Cretaceous belemnites

Experience obtained during this revision and author's previous works in belemnites lead to several recommendations to be used in the description of Upper Cretaceous belemnites.

1. Population analysis – to analyse the set of belemnites from one locality or adjacent localities with known stratigraphic position means to grasp intraspecific variability.
2. Study of adult specimens should be performed especially on the medium-size class (juvenile and very old specimens are less significant).
3. Biometry analysis must be applied to well preserved and complete specimens only (it depends on the type of sediment and diagenesis).
4. Descriptions published by Naidin (1964) and Christensen and Schmidt (1987) were used, but the character of alveolar end (fracture) was given priority (cf. Košťák and Pavliš, 1997).
5. Parameters DAMLD/L and DAMLD/MLD can be used to distinguish the variability.
6. Description of new species: It is necessary to have a large sample set containing 20–30 specimens in the case of morphological similarity with a known species; at least 4–5 identical specimens from the same or adjacent location and the same stratigraphic level must be used in the case of clear morphological differences.

Conclusions

Seventeen species belonging to three genera of Belemnitellidae are redescribed here. Three of them are retained in the open nomenclature with respect to the lack of material. Upper Turonian/lowermost Coniacian species of *Goniocamax* sp. will be subsequently described (Kostak, in prep.) as a new taxon of the Central Russian Subprovince – EEP. A systematic revision combined with statistical analysis confirmed the independence of the species of *P. triangulus* and *P. contractus*. The important species of *P. sozhensis* was described by Makhlin (1973) but poorly cited in the past. It was considered to be conspecific with *P. plenus*. This also resulted in an incorrect stratigraphic interpretation of the distribution of *P. plenus*.

Phylogeny is based on the similar shapes and sizes of the guard, alveolar end character and ontogeny of specimens studied. The question is to what degree does this approach fit reality: the guard constitutes 1/5 to 1/8 of the total length of the animal. I did not use a cladistic model with respect to possible parallelism and convergence.

The present revision disproved theory of the lower Turonian occurrences of *P. plenus* in the East European basins. Geographic distribution of this species is also a surprise: it is shifted towards the south, which indicates either a southward shift of cool belts in the late Cenomanian or a higher temperature affinity of this species. Its occurrence is probably connected with current regime; however, the whole area is also its reproduction place. The geographic distribution and stratigraphic ranges of the studied species were re-evaluated and corrected, where possible. Four belemnite biozones are introduced for the EEP (*primus*, *plenus*, *triangulus*, *intermedius* – CRS only) and one (*lundgreni*) can be designated later in the Cenomanian – lower Coniacian interval.

An independent East European Province was established on the basis of the occurrence of 100% endemic taxa in the uppermost Cenomanian through the base of the Coniacian. This province existed for about 5 million years. The Russian Central Subprovince is well distinguishable from the lower Turonian through the lowermost Coniacian. Geographically it extends from the present Belarussia/Russia border in the west to the Mangyshlak Peninsula (NW Kazakhstan) and Tuarkyr (W Turkestan – Mediterranean region borders) in the south to southeast and to western Siberia (Yenisei River) in the east. Northern borders were defined by a large European land mass. Belemnitellids also penetrated to the Russian Arctic region (Taimyr Region) during the Turonian, probably across the Turgay channel. This migration path could have connected the EEP with the NAP. This possibility was formerly rarely discussed (see above). Other relationships among paleobiogeographic units are discussed for the northern hemisphere.

A theory of the influence of eustatic cycles on belemnitellid evolution in the EEP is introduced. This theory is supported by the comparison of the number of taxa with the transgressive/regressive pulses. The increase in belemnitellid diversity is connected with the rise of sea level in the EEP.

The question of sexual dimorphism in *P. plenus* was reopened. Statistical evaluation showed a marked division of the set into two clearly separated parts . Especially the L/MLD and

L/DAMLD ratios were used as significant for distinguishing the variability. This phenomenon does not seem to be connected only with iso- and allometric growth phases.

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Plate 1

- **Fig. 1**. *Actinocamax verus antefragilis* Naidin, 1964. Specimen No. Sav1999/1, upper Tuconian – Surskoe, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Lateral view.
- **Fig. 2.** *Actinocamax verus antefragilis* Naidin, 1964. Specimen No. Sav1999/2, upper Turonian – Surskoe, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Dorsal view.
- **Fig. 3.** *Actinocamax verus antefragilis* Naidin, 1964. Specimen No. Sav1999/3, upper Turonian – Surskoe, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Dorsal view.
- **Fig. 4.** *Praeactinocamax primus* (Arkhangelsky, 1912). Specimen No. 111/1, middle Cenomanian – Ozarinci, Ukraine. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – dorsal view. B – anterior end (x2).
- **Fig. 5.** *Praeactinocamax primus* (Arkhangelsky, 1912). Specimen No. 111/3, middle Cenomanian – Ozarinci, Ukraine. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – dorsal view. B – anterior end (x2).
- **Fig.** 6. *Praeactinocamax primus* (Arkhangelsky, 1912). Specimen No. 6316-1/1, middle Cenomanian – Pady, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – dorsal view. B – anterior end (x2).
- **Fig. 7.** *Praeactinocamax primus* (Arkhangelsky, 1912). Specimen No. 7253/5, middle Cenomanian – Tcherpetovo, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Dorsal view.
- **Fig. 8.** *Praeactinocamax primus* (Arkhangelsky, 1912). Specimen No. 12/20, middle Cenomanian – Kupol Troitskiy, Kazakhstan. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Dorsal view.
- **Fig. 9.** *Praeactinocamax primus* (Arkhangelsky, 1912). Specimen No. 7240/17, middle Cenomanian – Fokino, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – lateral view. B – anterior end (x2).
- **Fig. 10.** *Praeactinocamax primus* (Arkhangelsky, 1912). Specimen No. 7240/17, middle Cenomanian – Fokino, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – lateral view. B – anterior end (x2).
- **Fig. 11.** *Praeactinocamax primus* (Arkhangelsky, 1912). Specimen No. 7253/5, middle Cenomanian – Tcherpetovo, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – lateral view. B – anterior end (x2).
- **Fig. 12.** *Praeactinocamax plenus* (Blainville, 1825). Specimen No. KK 8/5, upper Cenomanian – Koksyirtau, Kazakhstan. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – ventral view. B – lateral view.
- **Fig. 13.** *Praeactinocamax plenus* (Blainville, 1825). Specimen No. 6767, upper Cenomanian – Koksyirtau, Kazakhstan. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – ventral view. B – lateral view.
- **Fig. 14.** *Praeactinocamax plenus* (Blainville, 1825). Specimen No. KK 8/8, upper Cenomanian – Koksyirtau, Kazakhstan. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – ventral view. B – lateral view.
- **Fig. 15.** *Praeactinocamax plenus* (Blainville, 1825). Specimen No. KK 8/6, upper Cenomanian – Koksyirtau, Kazakhstan. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – ventral view. B – lateral view.

■ Plate 1

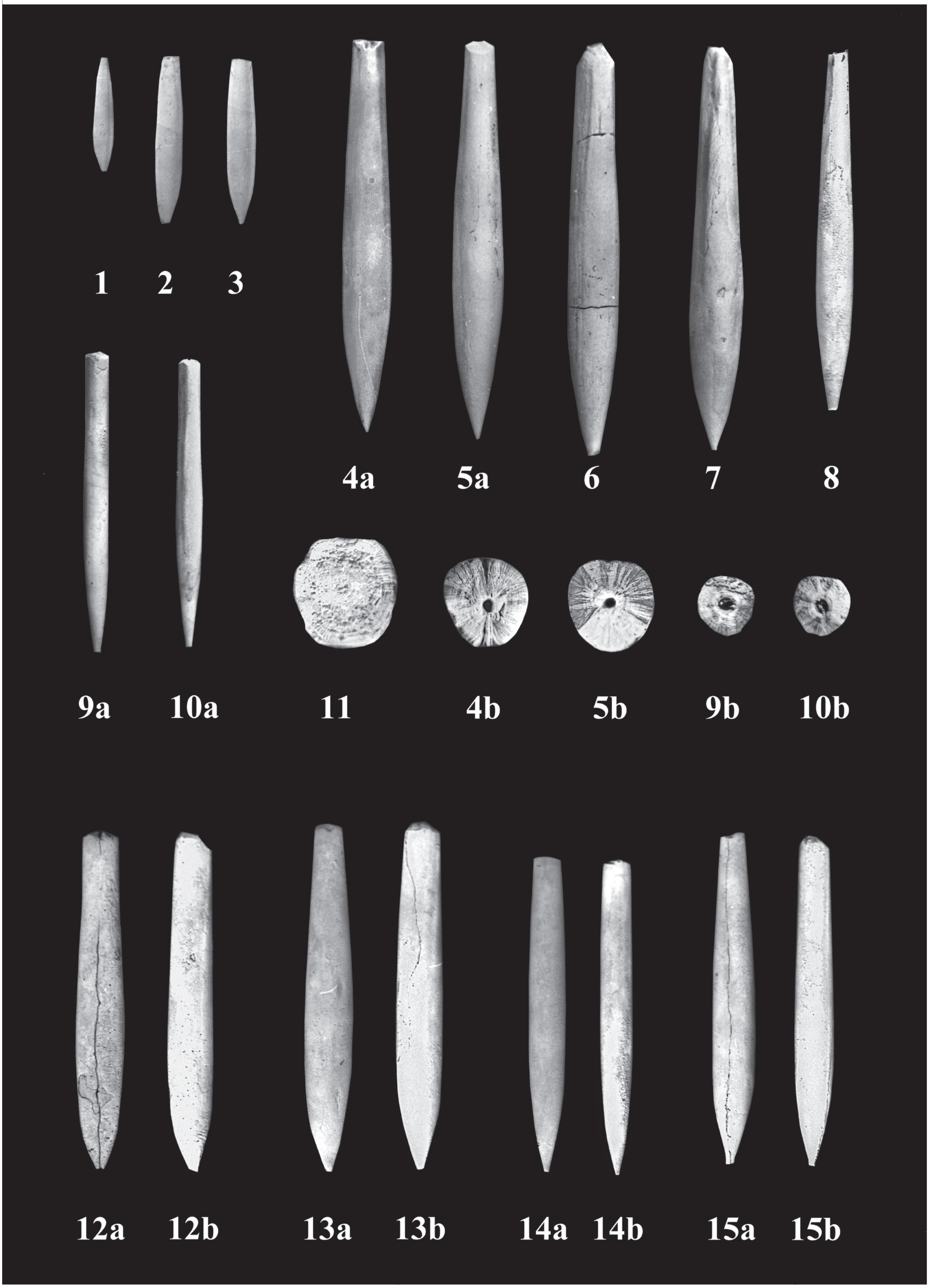
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Plate 2

- **Fig. 1.** *Praeactinocamax plenus* (Blainville, 1825). Specimen No. KK 8/3, upper Cenomanian – Koksyirtau, Kazakhstan. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Dorsal view.
- **Fig. 2.** *Praeactinocamax plenus* (Blainville, 1825). Specimen No. 901/2, upper Cenomanian – Valkininkai, Lithuania. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Dorsal view.
- **Fig. 3.** *Praeactinocamax plenus* (Blainville, 1825). Specimen No. 901/3, upper Cenomanian – Valkininkai, Lithuania. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Dorsal view.
- **Fig. 4.** *Praeactinocamax plenus* (Blainville, 1825). Specimen No. KK 8/5, upper Cenomanian – Koksyirtau, Kazakhstan. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – dorsal view. B – anterior end (x2).
- **Fig. 5.** *Praeactinocamax plenus* (Blainville, 1825). Specimen No. 6767, upper Cenomanian – Koksyirtau, Kazakhstan. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Dorsal view.
- **Fig. 6.** *Praeactinocamax plenus* (Blainville, 1825). Specimen No. KK 8/6, upper Cenomanian – Koksyirtau, Kazakhstan. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – dorsal view. B – anterior end (x2).
- **Fig. 7.** *Praeactinocamax sozhensis* (Makhlin, 1965). Specimen No. 7249/1, lower Turonian – Bryansk, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – dorsal view. B – lateral view (-1,2x).
- **Fig. 8.** *Praeactinocamax sozhensis* (Makhlin, 1965). Specimen No. 7253/1, lower Turonian – Tcherpetovo, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – dorsal view. B – lateral view (-1,2x).
- **Fig. 9.** *Praeactinocamax sozhensis* (Makhlin, 1965). Specimen No. 28-93/2, upper Cenomanian – lower Turonian – Fokino, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – dorsal view. B – lateral view (-1,2x).
- **Fig. 10.** *Praeactinocamax sozhensis* (Makhlin, 1965). Specimen No. 5/9, upper Cenomanian – lower Turonian – Gryaz, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – poorly calcified anterior part. B – anterior end (-1,2x).
- **Fig. 11.** *Praeactinocamax sozhensis* (Makhlin, 1965). Specimen No. 95-8/1, upper Cenomanian – lower Turonian – Fokino, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Anterior end (x2).

■ Plate 2

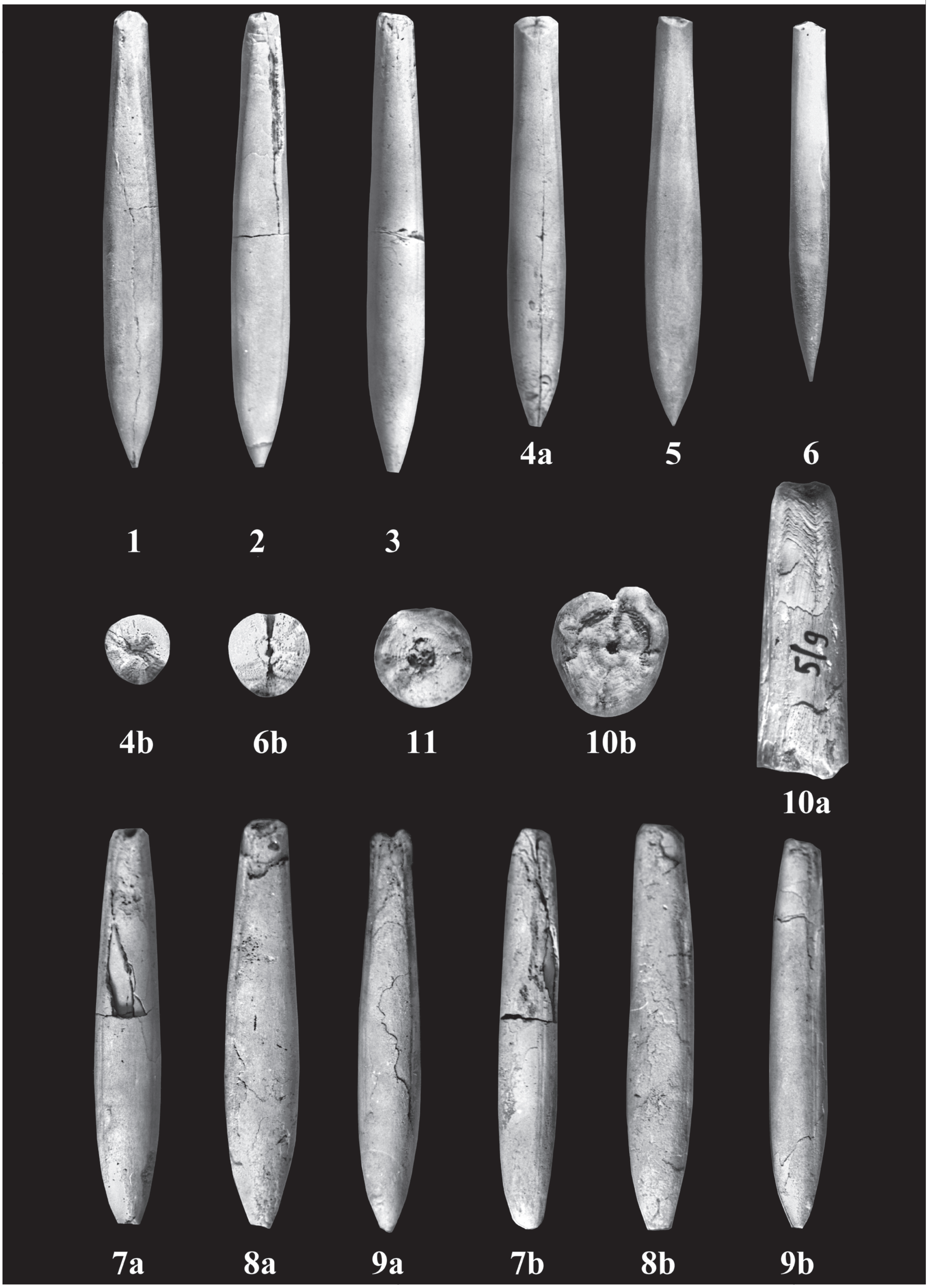


Plate 3

- **Fig. 1.** *Praeactinocamax primus* (Arkhangelsky, 1912). Specimen No. 7240/5, middle Cenomanian – Fokino, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Longitudinal section.
- **Fig. 2.** *Praeactinocamax plenus* (Blainville, 1825), Specimen No. KK 8/4, upper Cenomanian – Koksyirtau, Kazakhstan. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Longitudinal section.
- **Fig. 3.** *Praeactinocamax sozhensis* (Makhlin, 1965). Specimen No. 7247/1, upper Cenomanian – lower Turonian – Vygonitchi, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Longitudinal section.
- **Fig. 4.** *Praeactinocamax contractus* (Naidin, 1964). Specimen No. 97-6. lower Turonian – Vygonitchi, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Longitudinal section.
- **Fig. 7.** *Praeactinocamax sozhensis* (Makhlin, 1965). Specimen No. 5/7s, upper Cenomanian – lower Turonian – Gryaz, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Dorsal view.
- **Fig. 8.** *Praeactinocamax sozhensis* (Makhlin, 1965). Specimen No. 5302, upper Cenomanian – Nizhne Soinskiy, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Dorsal view.
- **Fig. 9.** *Praeactinocamax sozhensis* (Makhlin, 1965). Specimen No. 5305/26, lower Turonian – Medwedica, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Juvenile specimen – dorsal view (slightly enlarged).
- **Fig. 10.** *Praeactinocamax contractus* (Naidin, 1964). Specimen No. 6302/2, lower Turonian – Surskoe, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – dorsal view. B – anterior end.
- **Fig. 11.** *Praeactinocamax contractus* (Naidin, 1964). Specimen No. 5545, lower Turonian – Kamenka, Belarussia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – dorsal view. B – anterior end.
- **Fig. 12.** *Praeactinocamax contractus* (Naidin, 1964). Specimen No 5340-4/4, lower Turonian – Pudovkino, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Dorsal view.
- **Fig. 13.** *Praeactinocamax contractus* (Naidin, 1964), Specimen No. 8020-16/4, lower Turonian – Surskoe, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Dorsal view.

■ Plate 3

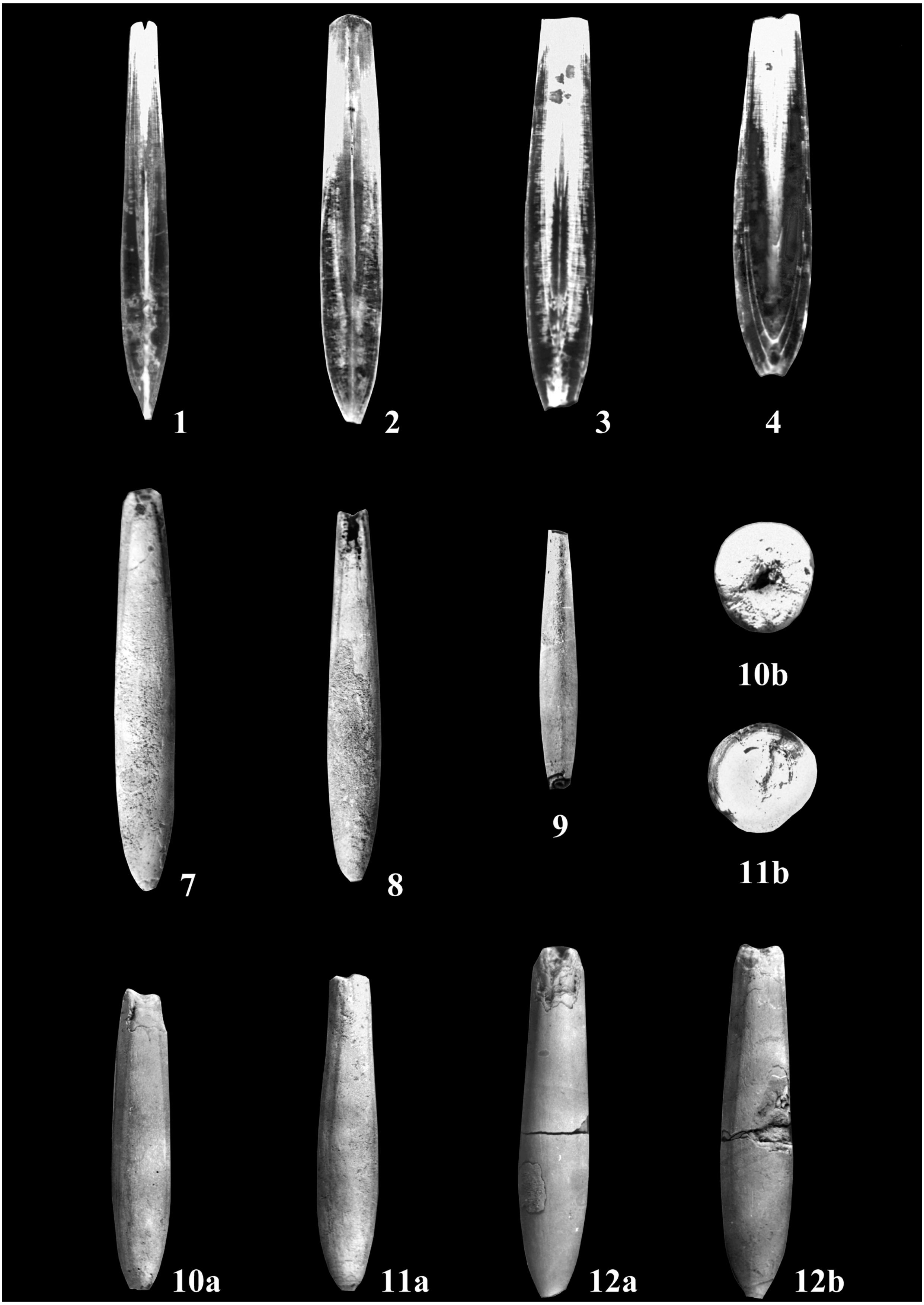


Plate 4

- **Fig. 1.** *Praeactinocamax triangulus* (Naidin, 1964). Specimen No. 101, lower Turonian – Semiluky, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – lateral view (-1.2x). B – ventral view. (-1.2x).
- **Fig. 2.** *Praeactinocamax triangulus* (Naidin, 1964). Specimen No. 5305/25. lower Turonian – Medwedica, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – dorsal view (slightly enlarged). B – anterior end.
- **Fig. 3.** *Praeactinocamax triangulus* (Naidin, 1964). Specimen No. 5/2, lower Turonian – Alexandrovka, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Dorsal view (slightly enlarged).
- **Fig. 4.** *Praeactinocamax triangulus* (Naidin, 1964). Specimen No. 5305/16. lower Turonian – Medwedica, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Ventral view (slightly enlarged).
- **Fig. 5.** *Praeactinocamax triangulus* (Naidin, 1964). Specimen No. 1082/1, lower Turonian – Kritchev, Belarussia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Longitudinal section (slightly enlarged).
- **Fig. 6.** *Praeactinocamax triangulus* (Naidin, 1964). Specimen No. 5544, lower Turonian – Kamenka, Belarussia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Anterior end.
- **Fig. 7.** *Praeactinocamax triangulus* (Naidin, 1964). Specimen No. 5296/2, lower Turonian – Nizhne Bezymyanny, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Anterior end.
- **Fig. 8.** *Praeactinocamax triangulus* (Naidin, 1964). Specimen No. 1745/1, lower Turonian – Ak/Kuly, Turkistan. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Anterior end.
- **Fig. 9.** *Praeactinocamax triangulus* (Naidin, 1964). Specimen No. 140/1, lower Turonian – Demorukoe, Russia. Collections of the Institute of Geology and Palaecntology, Charles University, Prague. Anterior end.
- **Fig. 10.** *Praeactinocamax triangulus* (Naidin, 1964). Specimen No. 5/2, lower Turonian – Alexandrovka, Russia. Collections of the Institute of Geology and Palaecntology. Charles University, Prague. Anterior end.
- **Fig. 11.** *Praeactinocamax planus* (Makhlin, 1965). Specimen No. B1999/2 upper Turonian – Boltaevka, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Dorsal view.
- **Fig. 13.** *Praeactinocamax planus* (Makhlin, 1965). Specimen No. B1999/3 upper Turonian – Boltaevka, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – (juvenile specimen) – dorsal wiew. B – anterior end (x2).
- **Fig. 14. (15)** *Praeactinocamax planus* (Makhlin, 1965). Specimen No. S1999/1 (B1999/4), upper Turonian – Boltaevka, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – dorsal view. B (15) – anterior end (x2).
- **Fig. 16.** *Praeactinocamax coronatus* (Makhlin, 1965). Specimen No. Bc1999/’. upper Turonian – Boltaevka, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – pseudoalveolus. B – anterior end (x1.5).

■ **Plate 4**

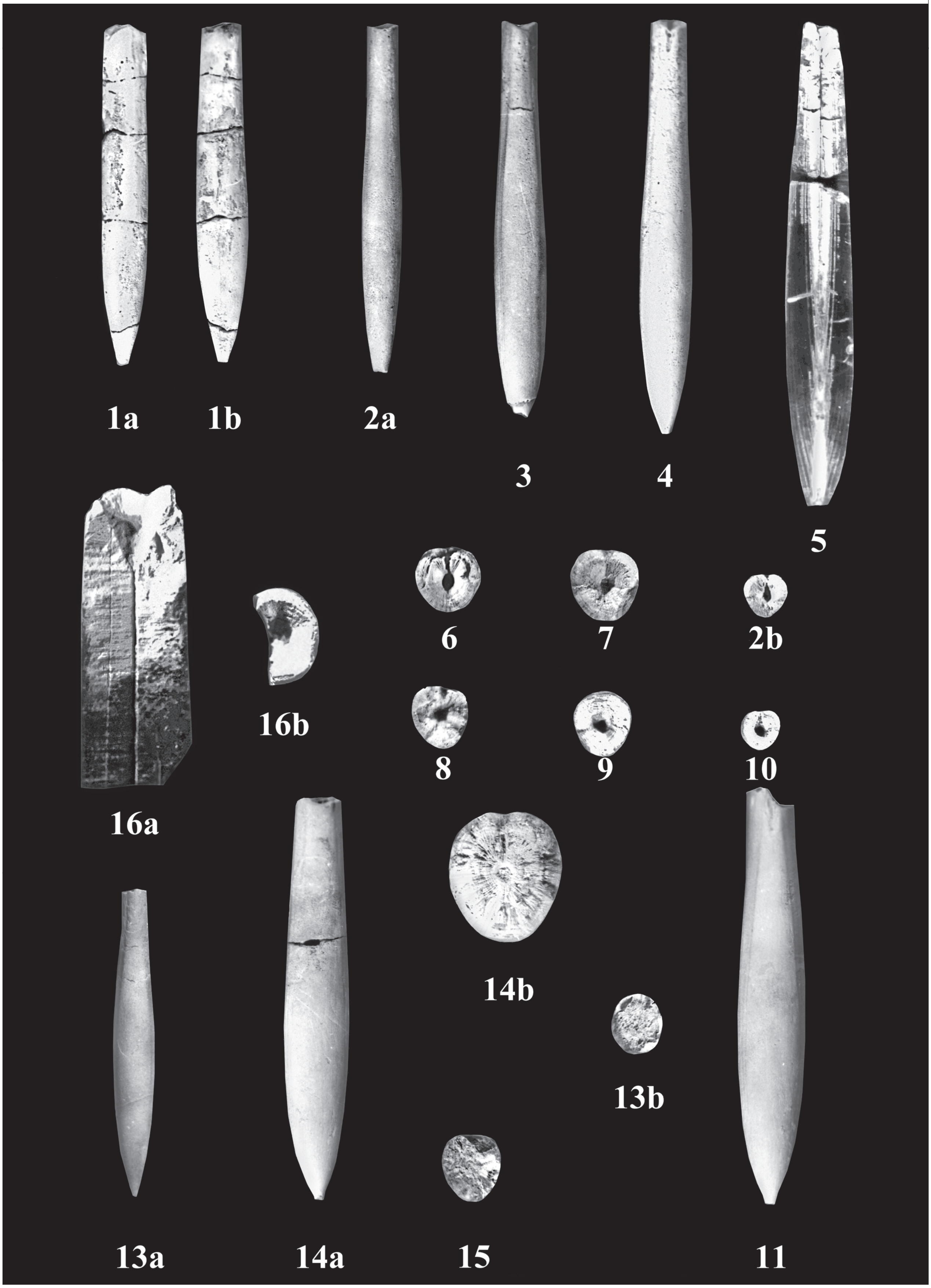


Plate 5

- **Fig. 1.** *Goniocamax intermedius* (Arkhangelsky, 1912). Specimen No. 250, upper Turonian – Novaya Derevna, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – ventral view. B – anterior end (x2).
- **Fig. 2.** *Goniocamax intermedius* (Arkhangelsky, 1912). Specimen No. 8016b1, upper Turonian – Boltaevka, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – ventral view. B – anterior end (x2).
- **Fig. 3.** *Goniocamax intermedius* (Arkhangelsky, 1912). Specimen No. 3171, upper Turonian – Kyrsanovsk, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – ventral view. B – lateral view.
- **Fig. 4.** *Goniocamax intermedius* (Arkhangelsky, 1912). Specimen No. 28-93, middle/upper Turonian – Kyrsanovsk, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – ventral view. B – lateral view.
- **Fig. 5.** *Goniocamax intermedius* (Arkhangelsky, 1912). Specimen No. 5545/2, middle/upper Turonian – Kamenka, Belarussia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Ventral view.
- **Fig. 6.** *Goniocamax intermedius* (Arkhangelsky, 1912). Specimen No. 5545/1, middle/upper Turonian – Kamenka, Belarussia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Ventral view.
- **Fig. 7.** *Goniocamax* sp. Specimen No. 253/1, lowermost Coniacian – Pudovkino, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A. – dorsal view. B – lateral wiew. C – anterior end. (x2).
- **Fig. 8.** *Goniocamax* sp. Specimen No. 249bg/1, upper Turonian – Pudovkino, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – Dorsal view. B – lateral view.
- **Fig. 9.** *Goniocamax* sp. Specimen No. 249bg/1, juvenile specimen, upper Turonian – Pudovkino, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. 9A – dorsal view (slightly enlarged). 9B – anterior end (x2).
- **Fig. 10–11.** Pseudoalveolus (x2) of the *Goniocamax* sp. (No. 253/1). 11 – lateral view (−1.3x).

■ **Plate 5**

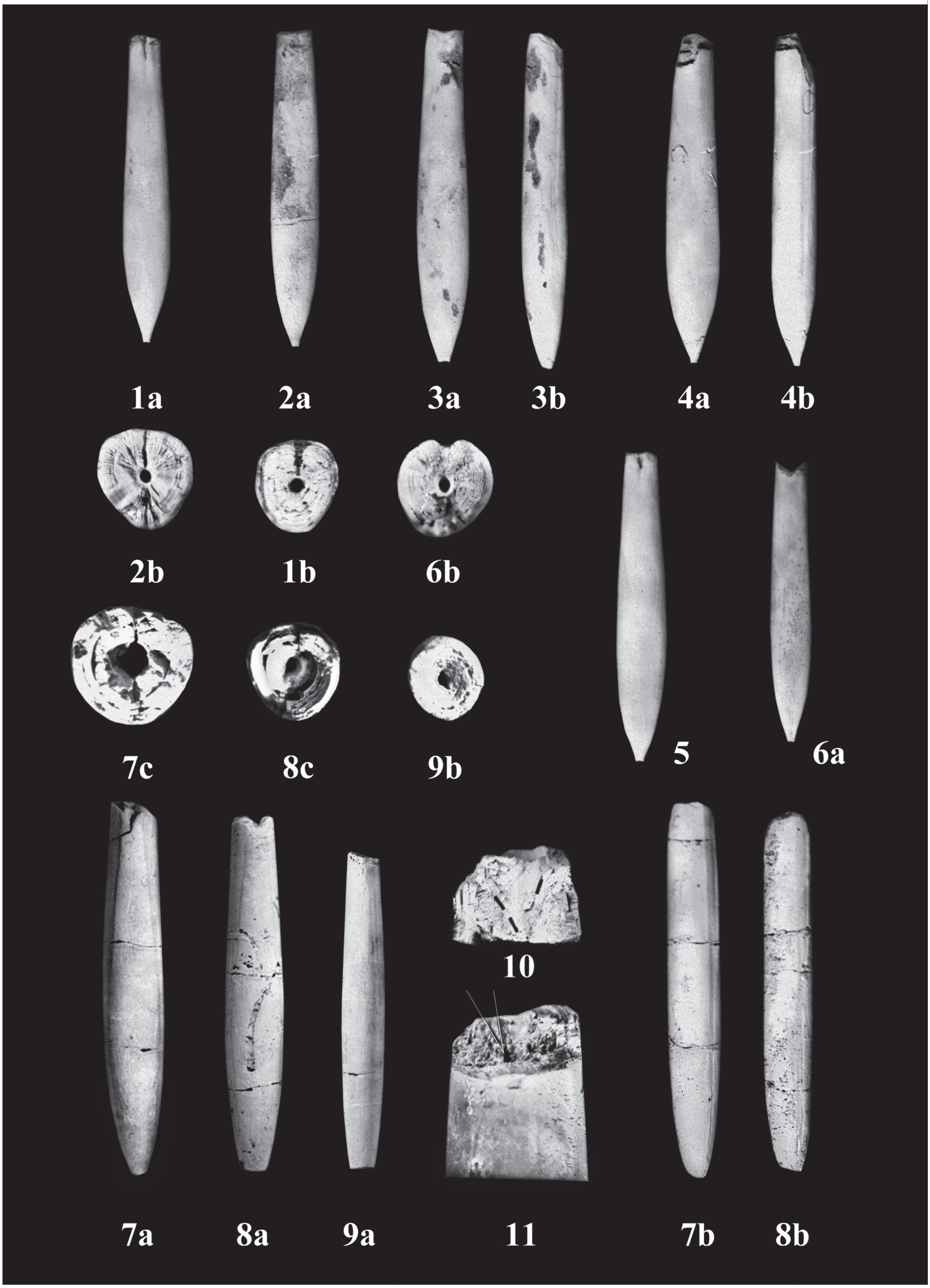
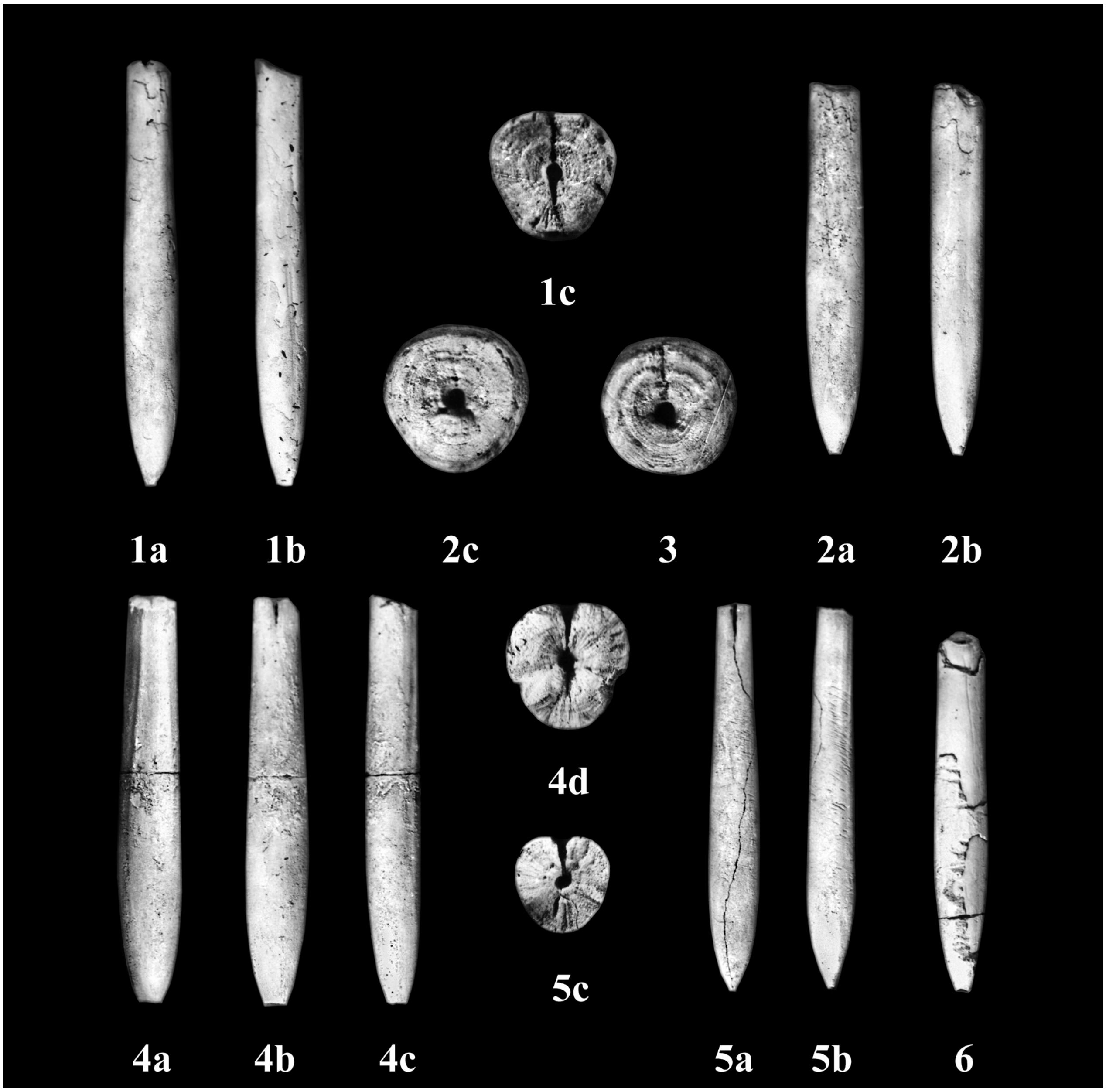


Plate 6

- **Fig. 1.** *Praeactinocamax* aff. *triangulus.* Specimen No. 7240, middle Cenomanian – Fokino, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – ventral view. B – lateral view. C – anterior end (x2).
- **Fig. 2.** *Praeactinocamax* sp. 1. Specimen No. 6302/1 a, lower Turonian – Surskoe, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – ventral view. B – lateral view. C – anterior end (x2).
- **Fig. 3.** *Praeactinocamax* sp. 1. Specimen No. 6302/2a, lower Turonian – Surskoe, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague.Anterior end (x2).
- **Fig. 4.** *Praeactinocamax* sp. 2. Specimen No. 672/62, upper Turonian/lower Coniacian – Tuarkyr, Turkistan. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – dorsal view. B – ventral view (-1.2x). C – lateral view (-1.2x). D – anterior end (x2).
- **Fig. 5.** *Praeactinocamax* cf. *strehlensis.* Specimen No. 170/7, upper Cenomanian – Koksyirtau, Kazakhstan. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. A – ventral view (-1.3x). B – lateral view (-1.2x). C – anterior end (x1.5).
- **Fig. 6.** *Praeactinocamax matesovae* (Naidin, 1964). Specimen No. Spm1999/10, upper Turonian – Surskoe, Russia. Collections of the Institute of Geology and Palaeontology, Charles University, Prague. Ventral view (-1.5x).

■ **Plate 6**



Appendix

No.	Item	L	MLD	DAMLD	LDAE	DVDAE	MDVD	Locality
1.	SAv1999/1	20	4.5	7			4.5	Boltaevka
2.	Sav1999/2		3	5			2.5	Boltaevka
3.	Sav1999/3		5	10			4.7	Surskoe
4.	Sav1999/4		5	12			5	Surskoe

■ **Tab. 1.** Table of measured dimensions in *A. verus antefragilis* in [mm].

No.	Item	L	MLD	DAMLD	LDAE	DVDAE	MDVD	Locality
1.	12/1	92	12.3	36.4	6.7	7	10.6	Kupol Troitskiy
2.	12/2	60	7.7	18	4.4	4.3	7	Kupol Troitskiy
3.	12/3	64	7.8	20	4.2	4.6	7.1	Kupol Troitskiy
4.	12/4	59.1	8.2	19	4.6	4.6	7.9	Kupol Troitskiy
5.	12/5	61	7.9	18	5	5*	7.1	Kupol Troitskiy
6.	12/6	65.4	7.7	33	5.7	5.7	7.4	Kupol Troitskiy
7.	12/7	56.8	6.2	23.7			5.8	Kupol Troitskiy
8.	12/9	64.8	7.6	27	5.5	5.1	7.2	Kupol Troitskiy
9.	12/13	62*	6.2	20	5		5.8	Kupol Troitskiy
10.	12/14	58.2	6.6	20	4.5		5.6	Kupol Troitskiy
11.	12/16	56.4	6.3	26.4	4.8		6	Kupol Troitskiy
12.	12/17	49.3	5.6	16.4	3.4	3.3	5.4	Kupol Troitskiy
13.	12/19a	54.1	6.5	19.8	4.1	4.3	5.8	Kupol Troitskiy
14.	12/19	51.1	6.9	17.4			7	Kupol Troitskiy
15.	12/20	60.2	6.4	28	3.8		5.8	Kupol Troitskiy
16.	12/21	47.1	5.5	20	4	4	4.8	Kupol Troitskiy
17.	12/23	51.2	5.8	20	4.4	4.5	5.5	Kupol Troitskiy
18.	12/24	54.8	6	17.2	4.1	4.1	6	Kupol Troitskiy
19.	12/26	58*	7.3	16	4		7.2	Kupol Troitskiy
20.	12/27	49.1	4.9	26.6			4.6	Kupol Troitskiy
21.	12/29	51.1	6.6	16			6.2	Kupol Troitskiy
22.	12/30		5.7	20			5.5	Kupol Troitskiy
23.	12/33	50.2	5.7	18.6	4.3	4.4	5.5	Kupol Troitskiy
24.	12/34	53.3	5.8	20.8			5.2	Kupol Troitskiy
25.	12/40	50	4.3	22.8	2.5	2.2	4	Kupol Troitskiy
26.	12/41		6.6	13.7			5.7	Kupol Troitskiy
27.	12/42	44.5	4.4	21.7	3.5	3.4	4.2	Kupol Troitskiy
28.	7240/x	73	9.8	25.1	5.6	5.7	9.1	Fokino
29.	7240/5	69	8.7	22.8	5.2	5.9	8.7	Fokino
30.	7240/10	85.2	11.6	36	7.5*	7.5	10.4	Fokino
31.	7240/17	50.1	4.4	22.9	4	4	4.3	Fokino
32.	7240/18	48.3	4.8	22.1	3.9	4.1	4.8	Fokino
33.	7253/2	73*	10.3	26*	6.2	6.5	10.1	Tcherpetovo
34.	7253/5	91.3	11.6	40.5	7.7	8	10.6	Tcherpetovo
35.	111/1	71.2	9.1	25.8	6.3	6.7	9.5	Ozarincy
36.	111/2	77.1	9.3	28.3	6.6	7.4	9.5	Ozarincy
37.	111/3	72	9.4	30	6	6.9	9.6	Ozarincy
38.	5300-2/1	53.5	7.8	19	5.5	6	7.3	Nizhne Soinskiy
39.	5300-2/2	58.9	7.6	21.6	5.5	6.3	7.4	Nizhne Soinskiy
40.	5300-2/4		5.6	26.6			5.5	Nizhne Soinskiy
41.	5300-2/5		7				7	Nizhne Soinskiy
42.	5300-2/6				5.9	6.2		Nizhne Soinskiy
43.	5300-2/7		6.1		6	5.7	6.4	Nizhne Soinskiy
44.	5300-2/8		6		5.3	5.4	5.7	Nizhne Soinskiy
45.	5300-2/9				5.6	6.3		Nizhne Soinskiy
46.	5300-2/12				5.1	5.9		Nizhne Soinskiy
47.	5300-2/13				5.3	5		Nizhne Soinskiy
48.	333/1		8.2				8.4	Aktulagai
49.	333/2		8.8				8.9	Aktulagai
50.	333/3				8*	7.7		Aktulagai

■ **Tab. 2.** Table of measured dimensions in *P. primus* in [mm].

No.	Item	L	MLD	DAMLD	LDAE	DVDAE	MDVD	Locality
51.	7259/4	46*	5.2	18	3.7		5	Betovo
52.	7259/5	53.8	7.4	19.4	4.7	5*		Betovo
53.	7259b/7		4.5		4.2	4.5	4.3	Betovo
54.	7259b/9	38.4	3.5	15.9	3.6	3.4	3.2	Betovo
55.	151/1	58*	7.1	22*	5.5	6	7.3	Vygonitchi
56.	151/2	41.2	4.4	19	3.1		4.2	Vygonitchi
57.	151/3				3.2	3.3		Vygonitchi
58.	295b/1	38.3	4.5	11.7	2.8		4.1	Pady
59.	259b/2		6		4.5	4.4	5.8	Pady
60.	259b/3	39.4	4	15.4			4	Pady
61.	296b				6.3	6.6		Pady
62.	6316-1/1	74.8	9.9	31	7.1	7.2	8.5	Pady
63.	6316-1/2	65*	7.9	22			7.9	Pady
64.	6316-1/3		7.6		6.7	6.9	7	Pady
65.	6316-1/4		8.5	21.5			8	Pady
66.	6316-1/5		6.7	30			7.2	Pady
67.	6316-1/6		7.7	30			7.2	Pady
68.	6316-1/7		8				6.8	Pady
69.	5286/6		10		7	7.4	8.5	Nizhne Bezymyan.
70.	5286/8		8.9		5.8	6.1	8.2	Nizhne Bezymyan.
71.	7246/1				4.7	4.7		Vygonitchi
72.	7246/2				2.4	2.4		Vygonitchi
73.	7249/7	44*	4	19	3.3	3.2	3.8	Bryansk
74.	7249/8				4.4	5		Bryansk
75.	7249/9				4.5	4.5		Bryansk

*estimated

■ **Tab. 2.** (*continued*) Table of measured dimensions in *P. primus* in [mm],.

No.	Item	L	MLD	DAMLD	LDAE	DVDAE	MDVD	Locality
1.	800-5/1	67.5	10	28.3	7.8	7.7	9.1	Aksyirtau
2.	800-5/2	55	7.8	23	4.7	4.8	7	Aksyirtau
3.	800-5/3	75.2	10.4*	30	7.4*	7.8	9.2	Aksyirtau
4.	800-5/4	75.2	13.2*	32	8.7*	8.1	12.2	Aksyirtau
5.	800-5/5	69.5	10*	28.7	8.4*	7.8	9.7	Aksyirtau
6.	800-5/6	80	10.6*	31.7	7.4*	7.9	10.1	Aksyirtau
7.	800-5/7				12.4*	11.8		Aksyirtau
8.	800-5/8	73.6	11.2*	24.5			10	Aksyirtau
9.	800-5/9	78.8	11.5	28.4	8.2	8.4	9.8	Aksyirtau
10.	86/440/1	74.2	8.2	32.4	6.4	6.7	7.5	Aksyirtau
11.	86/440/2				6.7	7		Aksyirtau
12.	86/440/3		11.7	35*			10.3	Aksyirtau
13.	86/440/5		9.8	26.8			8.8	Aksyirtau
14.	86/440/7	61.7	7.6	25.1	5.2	5.6	6.7	Aksyirtau
15.	86/440/8		7.1	22			6.9	Aksyirtau
16.	86/440/9				5.4	5.6		Aksyirtau
17.	86/440/10		10*	25			9.8	Aksyirtau
18.	86/440/11				9*	9.8		Aksyirtau
19.	86/440/12				7.6*	7.9		Aksyirtau
20.	86/440/13		11*	22.3			9.7	Aksyirtau
21.	86/440/14	67	9*	24.3	7.4*	7.3	9.3	Aksyirtau
22.	86/440/15	67*	11.4	26	8*	8	10.3	Aksyirtau
23.	KK 8/1	97.4	16.7	36.2	10.7	11	14.5	Koksyirtau
24.	KK 8/2	63.6	9.5	23	6.5	7	9.2	Koksyirtau
25.	KK 8/3	84.2	11.2	30.2	7	7	9.8	Koksyirtau
26.	KK 8/4	70	11	27.3	7.9	8.6	9.9	Koksyirtau
27.	KK 8/5	75.7	11.1	28.8	8.3	8.6	10.2	Koksyirtau
28.	KK 8/6	73.5	9.6	29	6.6	7.1	9.1	Koksyirtau
29.	KK 8/7	81.2	9.5	38	6.5	6.8	8.9	Koksyirtau
30.	KK 8/8	71	8.3	34.8	6.6	6.8	7.5	Koksyirtau

■ **Tab. 3.** Table of measured dimensions in *P. plenus* in [mm].

No.	Item	L	MLD	DAMLD	LDAE	DVDAE	MDVD	Locality
31.	KK 8/9	72.8	9.6	34	7.2	7.5	8.5	Koksyirtau
32.	KK 8/10	65.4	9.4	29	6.8	7.4	8.6	Koksyirtau
33.	KK 8/11	59.2	6.9	27	5.4	5.6	6.3	Koksyirtau
34.	KK 8/12	49	5.7	22			5	Koksyirtau
35.	KK 8/13	91.7	13.6*	33.7	9*	9.7	11	Koksyirtau
36.	KK 8/14	91.4	13.2*	28	9.4*	9.4	13.3	Koksyirtau
37.	KK 8/15	72	10.2*	21	7.4*	7.1	9.6	Koksyirtau
38.	2154/1		10*	27			10.3	Mangyshlak
39.	2154/2		11.2	29			11*	Mangyshlak
40.	2154/3	69	12*	27	8.2	8.5	10.8	Mangyshlak
41.	2154/4				6.7	7		Mangyshlak
42.	170/5	62.4	9.1	27.5	6.4	7.2	8.8	Mangyshlak
43.	170/6	67.5*	7.8	34*	6.6	6.5	7.2	Mangyshlak
44.	170/11	68	10.1	26.1	7.1	7.9	9.7	Mangyshlak
45.	170/12				8.8	8.8*		Mangyshlak
46.	170/14				6.4	8*		Mangyshlak
47.	170/15				7.6*	7.8		Mangyshlak
48.	133a	69.3	11.7	25	7.4	8.2	10.9	Mangyshlak
49.	133b	76	10	34	7.5	8	9.3	Mangyshlak
50.	849/1	70*	8.9	26.5	5.8	6.2	8.4	Kolodec Kemal
51.	849/2	70.5	10*	20	8*	6.8	8.6	Kolodec Kemal
52.	849/3		9.3		6.7	7	8.2	Kolodec Kemal
53.	849/4		11.2	31.7			9.6	Kolodec Kemal
54.	849/5		14*	31			12	Kolodec Kemal
55.	133/35	75	10.5	30.5	6.9	7.2	9.2	Aksyirtau
56.	133/35a	75*	11.6	23	8	8.5	10.8	Aksyirtau
57.	133/1				6	7*		Aksyirtau
58.	133/2/33				8*	7		Aksyirtau
59.	6767	77.3	11	31.4	7.8	8.8	10.7	Koksyirtau
60.	6767/1	69.4	10.5	25.6	8.1	8.4	9.2	Koksyirtau
61.	6767/2	55	7.2	21.6	5.1	5.7	6.5	Koksyirtau
62.	6001/1	72.6	10.5	26	7.4	8	9.5	Koksyirtau
63.	6001/2	78*	11.2	30	7.5	7.7	11.7	Koksyirtau
64.	6001/3	64.5	8	23.8	5.6	6	7	Koksyirtau
65	6001/4	71	10*	25.5	7.7	8	8.8	Koksyirtau
66.	6001/5	79.8	11.7	35	8.3	8.4	11	Koksyirtau
67.	6001/6	69.6	11*	22	8.2	8.3	9.8	Koksyirtau
68.	6001/7				7.6*			Koksyirtau
69.	31-5/1	84*	11	32*	7.9	8.3	9.9	Koksyirtau
70.	31-5/2	65*	9.5	27	6.9	7.4	8.7	Koksyirtau
71.	31-5/3				5.2	5.3		Koksyirtau
72.	31-5/4		4.2		3.2	3.4	3.8	Koksyirtau
73.	1805	82	15.5	30	8.5	8.3	14.4	Aktau
74.	1237/1	76	10.7	34	7.6	8.1	9.5	Aktau
75.	1237/2				6.7	7.8		Aktau
76.	150		13.8		9.2	10.6	12.3	Kelat
77.	6219/2	80*	9	32*	6.4	7.2	9	Donbas
78.	6404/1				6.4	7		Strypa
79.	901/2	83.7	11.8	28.2	6.7	7	10	Valkininkai
80.	901/3	85.5	10.9	30.5	7.3	7.1	10.4	Valkininkai

*estimated

■ **Tab. 3.** (*continued*) Table of measured dimensions in *P. plenus* in [mm].

sNo.	Item	L	MLD	DAMLD	LDAE	DVDAE	MDVD	LVF	Locality
1.	170/7	66.6	8.7	19.5	6.2	6.5	8.6	6	Koksyirtau

■ **Tab. 4.** Table of measured dimensions in *P. plenus* cf. *P. strehlensis* (Fr. et Schloen.) in [mm].

No.	Item	L	MLD	DAMLD	LDAE	DVDAE	MDVD	D	Locality
1.	1083/3	72	9.3	27	7.3	7		5	Kritchev
2.	56/1	88*	14.6	35	10.2	11.5		6	Khoper
3.	8023/1	81.7	11.5	34	9.6	10	10.5	5.5	Surskoe
4.	6/2	90	14.1	38	10	10.1	12.6	5.2	Gryaz
5.	1745/2	73	10.2	24	7.6	8.2	8.9	6	Tuarkyr
6.	8023/3	69	9.8	24	6.4	6.8	8.7	5.5	Surskoe
7.	5305/4	80*	18	23*	11.8	11.2	14.5	6.2	Medwedica
8.	5305/3	93*	18.3	25*	12	11.5	14.7	6.8	Medwedica
9.	5305/13	74	11	28	7.5	7	9.9	6.5	Medwedica
10.	5305/2	84.5	14.5	35	11	10.8		7	Medwedica
11.	1082				5	4.9		3.1	Kritchev
12.	1082/2				5.3	5.7		4.9	Kritchev
13.	1082/1	83*	12.2	33*	8.3	8.4	11		Kritchev
14.	1745/1	64	9.7	27	7.4	8.3	8.8	5.2	Ak/Kuly,
15.	1745/2	92*	16	36*			13.8		Tuarkyr
16.	5562/2				4.1	4.3		3.3	Fokino
17.	7254b	69	9.9	30	6.4	7.2	8.3	3.5	Tcherpetovo
18.	5544	76	9.7	34.5	8.3	8.3	8.5	5.1	Kamenka,
19.	28-93	70*	11.2		7.5	8	9.2	5.6	Fokino
20.	8025b/1				6.4	6.3		5.7	Boltaevka
21.	6241b				6	5.4		3.2	Shchigri
22.	140/1	74	10.5	33.7	7.7	8.4	9.6	3.4	Demorukoe
23.	5-2	71	11.8	29.6	8.4	8.8	9.7	5.1	Besh-Tyube
24.	5-2/1				8.6	9.2		4.4	Besh-Tyube
25.	5/9				8.4	8.6		5.8	Alexandrovka
26.	5/1	75.5	11.7	31.9	9.5	9.2	10.7	5	Alexandrovka
27.	5/7	77.6	13.2*	30	10*	10	11.4	6.2	Alexandrovka
28.	5/2	61.9	8	22.4	5.6	5.6	7.1	4	Alexandrovka
29.	24-150				10.5	10.9		6.3	S. Zviling
30.	5305/22	62	8.3	26	4.6	4.9	7.2	3.5	Medwedica
31.	5305/18	64	8.2	22.4	5.5	5.5	7.2	4.4	Medwedica
32.	5305/25	55*	6	21*	4.8	4.9	5.4	3.8	Medwedica
33.	5305/14	75*	10.5	26.3			9.6		Medwedica
34.	5305/30	45	6	21	3.8	3.9	5.6	1.3	Medwedica
35.	5305/24		7.4		5.8	5.8	6.9	3.1	Medwedica
36.	5305/16	61	9.6	27.4	7	7.4	9	2.5	Medwedica
37.	5305/15	61	8	27	6.4	6.4	7.2	3.7	Medwedica
38.	5305/7				8.6	8.7		3.6	Medwedica
39.	5305/1				11.2	11.8		5.6	Medwedica
40.	101	76	12	33.6	8.8	9.6	10.5	4	Semiluky
41.	5296/2	75.3	12.4	29.5	8.8	9.2	10.9	5.4	Nizhne Bezym.
42.	5296/1		14	34			12.7		Nizhne Bezym.
43.	7249/6	60	7.8	26.2	5.8	6.1	7	3	Bryansk
44.	249/5	66*	9.9	26*	7	7	9.2	4.2	Pudovkino
45.	5305/9	77	14	30	10.3	11.1	12.2		Medwedica

*estimated

■ **Tab. 5.** Table of measured dimensions in *P. triangulus* in [mm]. Holotype No. 1. 1083/3, paratypes No. 2–6. No. 7. 5305/4, holotype of *P. plenus crassus* and No. 9–10 – paratypes of *P. plenus crassus* Naidin, 1964.

No.	Item	L	MLD	DAMLD	LDAE	DVDAE	MDVD	D	Locality
1.	7240	80*	10.3	25*	8.1	8.4	9.8	3.8	Fokino

■ **Tab. 6.** Table of measured dimensions in *P.* aff. *triangulus* in [mm].

No.	Item	L	MLD	DAMLD	LDAE	DVDAE	MDVD	Locality
1.	7253/1	79.3	12.7	30	7.9	8.8	12	Tcherpetovo
2.	7249/1	81*	13.2	33*	8.4	8.5	11.8	Bryansk
3.	7249/3	71.5	10	28.9	6.4	7.1	9.7	Bryansk
4.	28-93/1	81.1	12.5	37	9	10.1	12	Fokino
5.	28-93/2	82	14.8	37.9	9.4	10.3	13.8	Fokino
6.	7249/2	76	11.4	30	8.4	8.8	10.2	Bryansk
7.	7247/1	75*	12.4	30*	9	9.8	11.7	Vygonitchi
8.	7261b	73*	13	28*	9	9.6	12.2	Betovo
9.	5305/11	77*	14.4	25	8.4	8.1	12	Medwedica
10.	5305/8	80*	13.5	30*			12	Medwedica
11.	5305/26	45	6.4	20	3.6	4.2	6	Medwedica
12.	28-93/3		12.6				11.4	Fokino
13.	7249/5		14.4	31			13.2	Bryansk
14.	7249/4		12.8				11.4	Bryansk
15.	95-8/1		10.8		8.4	8.6	10	Fokino
16.	95-8/2	70*	11.6	30*	7.6	8.9	10.7	Fokino
17.	95-8/3		10.5		7	7.4	10.1	Fokino
18.	95-8/4				9.3			Fokino
19.	249b9	70*	10.4	30*	7.8	7.8	9.5	Pudovkino
20.	5/6	67	11	25			10	Gryaz
21.	5302	75	11.4	27.6	7.2	7.2	10.4	N. Soinskiy
22.	5305/19	56	10.6	20	6.5	7	9.3	Medwedica
23.	5/1s	77*	12.4*	32	7.2*	8.2	11.3	Gryaz
24.	5/2s		13.8	26			12.8	Gryaz
25.	5/4s		10	28			9.4	Gryaz
26.	5/5s		12.9	38			12.1	Gryaz
27.	5/7s	78*	10.8	36	7.6	8.6	10	Gryaz
28.	5/8s	58	9.4	29	7	7.7	8.6	Gryaz
29.	5/9s				9.6	10.6	10	Gryaz
30.	40/726	87	14.5				12.2	Gryaz

*estimated

■ **Tab. 7.** Table of measured dimensions in *P. sozhensis* in [mm]. Holotype No. 30 – 40/726 (dimensions after Makhlin, 1973).

No.	Item	L	MLD	DAMLD	LDAE	DVDAE	MDVD	Locality
1.	6277/4	72.1	13.7	27	9.3	10.7	12.5	Kanyev
2.	8020-1b/4	71.7	14.8	24.6	10.5	10.9	13.1	Surskoe
3.	5340-4/4	72*	14.4	25*	10.5	11.5	12.8	Pudovkino
4.	5545	62*	11.8	26*	8.4	9.7	11	Kamenka
5.	146/1	70*	15	30*	11	11.9	14	Bryansk
6.	6302/2	63	12.5	20.6	8.1	8.5	11.4	Surskoe
7.	97-6	65*	14	26*	10.3	10	12.5	Vygonitchi
8.	249b/3		12.5	27.6			11.4	Pudovkino
9.	5341	54.6	10.5	21.4	7.5	7.2	9.2	Pudovkino
10.	8023	59	10.7	21	7.8	8.8	9.8	Surskoe

*estimated

■ **Tab. 8.** Table of measured dimensions in *P. contractus* in [mm]. Holotype No. 1. – 6277/4.

No.	Item	L	MLD	DAMLD	LDAE	DVDAE	MDVD	Locality
1.	B1999/1	80*	20.5	31.8	9.4	9.7	11.6	Boltaevka
2.	B1999/2	73.3	12.2	26	9	9.8	10.7	Boltaevka
3.	B1999/3	51.8	7.1	24.5	4.5	4.7	6.5	Boltaevka
4.	B1999/4		14	35*			12.6	Boltaevka
5.	B1999/6				4.9	5.7		Boltaevka

■ **Tab. 9.** Table of measured dimensions in *P. planus* in [mm].

No.	Item	L	MLD	DAMLD	LDAE	DVDAE	MDVD	D	Locality
1.	6302/1a	69	11	31	9.5	9.5	10.4	6.2	Surskoe
2.	6302/2a				9.3	9.4		6.1	Surskoe
3.	6302/3a	52*	5.5		4.8	4.8	5	2	Surskoe

■ **Tab. 10.** Table of measured dimensions in *P.* sp. 1 in [mm].

No.	Item	L	MLD	DAMLD	LDAE	DVDAE	MDVD	D	Locality
1.	672/62	71*	10.7	24*	8	8.5	9.6	4	Tuarkyr

■ **Tab. 11.** Table of measured dimensions in *P.* sp. 2 in [mm].

No.	Item	L	MLD	DAMLD	LDAE	DVDAE	MDVD	D	Locality
1.	5545/II	61	9.3	25	7.1	7.2	8.7	3.6	Kamenka
2.	3171	74	12	27	8.3	8.2	10.7	4*	Kyrsonovsk,
3.	5545/16	68.4	11.4	27.5	7,6	7.6	10	3.5	Kamenka
4.	250	67.7	10.9	25	7.3	7.4	9.7	4.2	Novaya Derev.
5.	8016b/1	69.8	11	27	8.7	8.6	9.5	3.7	Boltaevka
6.	28-93	73.2	11.8	27.7			10.3		Fokino
7.	6302/2	62.5	10.3	24.8	5.3	5.6	9.4	3.9	Surskoe
8.	7244/1	52.3	8.3	20	7.2	6.6	7.5		Fokino
9.	5340-4/5	63*	9.9	27*	7.5	8.1	9.3		Pudovkino
10.	7244/b				8.5	8.5			Fokino
11.	5545/a		11.7	31.4			10.8		Kamenka
12.	5545/c		12.7		9	9.4	11	5	Kamenka
13.	5340-8/3				7.8	8.2			Pudovkino
14.	249b11	52	7.2	22.4	5.6	6	7		Pudovkino
15.	8023-2b/1	60*	9.8	27*	7.3	7.8	9.2	3.2	Surskoe
16.	5340-4/7		12.7	22.8			11.3		Pudovkino
17.	5545/2	62.2	10.9	26	8	8.6	10.1		Kamenka

*estimated

■ **Tab. 12.** Table of measured dimensions in *G. intermedius* in [mm].

No.	Item	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

*estimated

■ **Tab. 13.** Table of measured dimensions in *G.* sp. in [mm]. Holotype No. 1. – 253/3, pratypes No. 2, 4.