

Report 1

Upper Cretaceous Ammonites and their extinction: interpretation of data from the Caucasus and comparison with Mangyshlak, the Crimea and the Maastricht area

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Abstract

Comparison of Upper Cretaceous ammonite faunas from the Caucasus, the Crimea, Mangyshlak and around Maastricht.

Key words: ammonites, Upper Cretaceous, distribution, evolution.

Résumé

Comparaison des ammonites du Crétacé supérieur du Caucase, de la Crimée, du Mangyshlak, et des environs de Maastricht.

Mots-clefs: ammonites, Crétacé supérieur, répartition, évolution.

Резюме

Сравнение аммонитов верхнего мела Кавказа, Крыма, Мангышлака и окрестностей Маастрихта.

Ключевые слова: аммониты, верхний мел, распределение, развитие

INTAS project 94-1414 studies the evolution of the faunas and their environments in three stratigraphically and palaeontologically important regions. A detailed comparison of latest data from the following regions is presented: 1. Mangyshlak (West Kazakhstan), 2. Upper Crimea, 3. The Maastricht type area (Belgium-the Netherlands).

The Upper Cretaceous ammonite fauna from the Caucasus forms a link between Mangyshlak and Upper Crimea, and its characteristics shall help to define faunistic relations. Even more so as the Upper Cretaceous Caucasian basins are restricted to shallow marine basins, a kind of environment in which the Cretaceous/Tertiary boundary has rarely been studied. In Georgia some continuous sections are known which are of interest from this point view.

Let us start with the **Northern Caucasus**.

In its central part the **Campanian** stage is represented by white limestones with stylolite horizons and thin clay marl beds. These strata contain echinoids (*Micraster schroederi* Stolley, *Echinocorys turrita* Lambert, *Pseudoffaster schmidtiae* Posl. & Moskvin, *Offaster pomeli* Munier-Chalmas), inocera-

mids (*Inoceramus azerbaijanensis* Aliev, *I. dariensis* Dobrov & Pavlova) and rare specimens of the ammonite *Eupachydiscus launayi* de Grossouvre - (thickness 30 to 40 m).

Higher up follows an alternation of white and light-creamy limestones with clay marls of increasing thickness (from 10 to 15 up to 70 to 80 cm), containing *Hauericeras pseudogardeni* Schlüter, *Inoceramus balticus* Boehm, *I. muelleri* Petrascheck, *Micraster coravium* Posl. & Moskvin, *Seunaster gillieronii* de Loriol, *Offaster pilula* Lamarck, *Galeola senonensis* d'Orbigny, *Conulus matesovae* Posl. & Moskvin. In the upper part *Pseudoffaster caucasicus* Druschitz (70 to 80 m.).

Beside these species, in the Campanian *Pachydiscus koeneni* de Grossouvre, *Bostrychoceras polyplacum* (Roemer), *Glyptoceras retrorsum* (Schlüter), *Menuites auritocostatus* (Schlüter), *Baculites vertebralis* Lamarck, *Inoceramus balticus*, *Micraster brongniarti* Hébert, *Pseudoffaster caucasicus*, *Galeola gauthieri* Lambert, and rare fragments of *Belemnitella mucronata* (Schlotheim) are found.

Eastwards, the Campanian sediments extend almost unchanged up to Malchick. Further to the East in the Lower Campanian *Offaster pomeli*, *Pseudoffaster schmidtiae*, *Inoceramus azerbaijanensis* are present; in the upper part *Micraster coravium*, *Seunaster gillieronii*, *Pseudoffaster caucasicus*, *Conulus matesovae*, *Inoceramus balticus*.

In the Ardon basin the Campanian was washed out.

To the west of the Bolshoi Zelenchuk River, sediments enriched with clays are of reduced thickness (15-20 m), but both substages of the Campanian are present: in the lower part: *Micraster schroederi*, *Pseudoffaster caucasicus*, *Conulus matesovae*; in the upper part *Micraster brongniarti*, *Galeola gauthieri*, *Pseudoffaster caucasicus*.

The **Maastrichtian** stage is characterised by an abundant fauna. The Lower Maastrichtian substage consists of clayey limestones with marly "interlayers" with numerous inoceramids (*Inoceramus alaeformis sensu* Tsagareli non Zekeli, *I. pertenuis* Meek & Hayden, *I. sagensis* Owen, *I. convexus* Hall & Meek), cephalopods [*Hoploscaphites constrictus* (J. Sowerby), *Hauericeras sulcatum* (Kner), *Didymoceras schloenbachi* (Favre), *Pseudokosmaticeras galicianum* (Favre), *P. brandti* (Redtenbacher), *Baculites vertebralis*, *B. anceps* Lamarck, rarely *Belemnitella conica obesa* Naidin], echinoids (*Micraster grimmensis* Nietsch., *Orthaster cipliensis* Lambert, *Coraster cubanicus* Posl. & Moskvin, *Galerites vulgaris* Leske) are present. Higher up these taxa occur more rarely, but we also find *Diplomoceras cylindraceum* (Defrance), *Belemnitella conica rotunda* (Naidin), *Guettaria rocardi* (Cotteau), *Stegaster chal-*

Stage	Substage	Maastricht area Kennedy, 1986a, b Naidin, 1978	Upper Crimea Maslakova, 1986	North Caucasus Moskvin, 1986	Transcaucasus Tsagareli, 1954 Gambashidze, 1979	Mangyshlak Atabekian, 1986
Maastrichtian	Upper	<i>Saghalinites</i> sp. <i>Baculites anceps</i> <i>B. vertebralis</i> <i>Nostoceras</i> sp. <i>Glyptoxoceras</i> cf. <i>subcompressum</i> <i>G.</i> cf. <i>circularis</i> <i>Diplomoceras cylindraceum</i> <i>Hoploscaphites constrictus</i> <i>H. pungens</i> <i>H. felderi</i> <i>Acanthoscaphites</i> cf. <i>verneuillianus</i> <i>Pachydiscus gollevillensis</i> <i>P. jacquoti</i> <i>Anapachydiscus fresvillensis</i> <i>Sphenodiscus binkhorsti</i>	<i>Hypophylloceras surya</i> <i>Hoploscaphites constrictus</i> <i>Pachydiscus neubergicus</i> <i>P. gollevillensis</i>	<i>Hypophylloceras surya</i> <i>Baculites anceps</i> <i>B. vertebralis</i> <i>Neancyloceras retrorsum</i> <i>Hoploscaphites constrictus</i> <i>Pachydiscus neubergicus</i> <i>P. gollevillensis</i> <i>P. colligatus</i>	<i>Diplomoceras cylindraceum</i> <i>Hoploscaphites constrictus</i> <i>Pachydiscus neubergicus</i> <i>P. gollevillensis</i> <i>P. subrobustus orientalis</i>	<i>Baculites anceps</i> <i>Hoploscaphites constrictus</i> <i>crassus</i>
	Lower	<i>Diplomoceras cylindraceum</i> <i>Hoploscaphites constrictus</i> <i>H. tenuistriatus</i> <i>Acanthoscaphites tridens</i>	<i>Diplomoceras cylindraceum</i> <i>Hoploscaphites constrictus</i> <i>Acanthoscaphites tridens</i> <i>Hauericeras sulcatum</i> <i>Pseudokossmaticeras galicianum</i>	<i>Baculites vertebralis</i> <i>B. anceps</i> <i>Didymoceras schloenbachi</i> <i>Diplomoceras cylindraceum</i> <i>Hoploscaphites constrictus</i> <i>Hauericeras sulcatum</i> <i>Pseudokossmaticeras galicianum</i> <i>P. brandti</i>	<i>Diplomoceras cylindraceum</i> <i>Hoploscaphites constrictus</i> <i>Acanthoscaphites tridens</i> <i>Hauericeras sulcatum</i> <i>Pseudokossmaticeras galicianum</i> <i>P. brandti</i> <i>Pachydiscus neubergicus</i> <i>Pa.</i> cf. <i>colligatus</i> <i>Pa. perfidus</i> <i>Pa. koeneni</i> <i>Anapachydiscus fresvillensis</i> <i>Parapachydiscus icenicus</i>	
Campanian	Upper	<i>Baculites</i> sp. <i>Trachyscaphites spiniger</i> <i>Hoplitoplacenticeras marroti</i> <i>H.</i> cf. <i>coesfeldiensis</i> <i>Pachydiscus colligatus</i>	<i>Baculites</i> ex gr. <i>anceps</i> <i>Hauericeras pseudogardeni</i> <i>Pachydiscus koeneni</i>	<i>Baculites vertebralis</i> <i>Bostrychoceras polyplacum</i> <i>Glyptoxoceras retrorsum</i> <i>Hauericeras pseudogardeni</i> <i>Pachydiscus koeneni</i> <i>Menuites auricostatus</i> <i>Eupachydiscus launayi</i>	<i>Bostrychoceras polyplacum schloenbachi</i> <i>Glyptoxoceras retrorsum</i> <i>Eupachydiscus levyi</i> <i>Scaphites</i> cf. <i>haugi</i> <i>Hoplitoplacenticeras vari</i>	<i>Pachydiscus stobaei</i>
	Lower	<i>Scaphites hippocrepis</i> <i>Pachydiscus duelmensis</i>			<i>Glyptoxoceras wernickei</i> <i>Discoscaphites gibbus</i> <i>Eupachydiscus levyi</i>	

masi Seunès, *Echinocorys pyramidata* Portlock, *Galeaster bertrandii* Seunès, *Homoeaster tunetanus* Pomel. (thickness of the Lower Maastrichtian: 200 to 250 m).

The Upper Maastrichtian consists of limestones interbedded with marls, and only in the upper part with thin stylolite horizons. The lower part contains: *Pseudofaster renngarteni* Schmidt, *Echinocorys pyramidata*, *Galerites vulgaris*. No inoceramids except rare *Inoceramus caucasicus* Dobrov [= *Spyridoceras tegulatus* (Ravn)]. The upper part contains: *Pachydiscus gollevillensis* (d'Orbigny), *P. neubergicus* (Hauer), *Pseudophyllites indra* (Forbes), *Phylloceras (Hypophylloceras) surya* (Forbes), *Baculites vertebralis*, *Neancyloceras retrorsum* (Schlüter), *Neobelemnella kazimiroviensis* Skolozdrowna, *Inoceramus "tegulatus" sensu Dobrov & Pavlova* (= *Tenuipteria argentea* Conrad), *Echinocorys perconica* von Hagenow, *E. cipliyensis* Lambert, *Cyclaster integer* Seunès, *Abathomphalus mayaroensis* Bolli. *Hoploscaphites constrictus* occurs throughout the Maastrichtian (MOSKVIN, 1986).

In Transcaucasian Georgia Late Cretaceous ammonites were studied by TSAGARELI (1954) and GAMBASHIDZE (1979). Koteishvili and Magalashvili provided supplementary data. Shallow marine environments dominate on the Georgian Block, and in the Artvin-Bolnisi Block and in the Adjara-Trialetian basin.

On the Georgian Block three facies types were distinguished in calcareous-marly sediments by GAMBASHIDZE (1979). In the uppermost part of the **Campanian**, in one of the blocks, *Bostrychoceras polyplacum schloenbachi* (Favre) was found. In the Transcaucasus during the **Maastrichtian** ammonites are more abundant: in the lower part of the substage *Pachydiscus neubergicus*, *Acanthoscaphites tridens* (Kner), *Hoploscaphites constrictus*, *Diplomoceras cylindraceum* were found, whereas in the upper part *Pachydiscus neubergicus*, *Hoploscaphites* cf. *constrictus* were collected. In the Dzirula type in the Lower Maastrichtian *Hauericeras sulcatum*, *Pseudokossmaticeras galicianum* and *P. brandti* were observed; in the Upper Maastrichtian only *Pachydiscus neubergicus* was noticed.

In the Ajara-Trialeti basin the Campanian is represented only by limestones and variegated marls, and it is defined only by inoceramids: *Inoceramus pseudoregularis* Sornay, *I. alaeformis sensu Tsagareli non Zekeli*, *I. convexus*, *I. georgicus* Tsagareli, *I. cf. adjakendensis* Aliev, *I. salisburgensis* Fugger & Kastner, in the lower part, and *I. balticus*, *I. alaeformis sensu Tsagareli non Zekeli*, *I. barabini* Morton, *I. proximus* Tuomey, *I. georgicus*, *I. colchicus* Tsagareli in the upper part.

The Maastrichtian is represented by marly limestones and in places by variegated marls. In the Lower Maastrichtian we found: *Pachydiscus neubergicus*, *P. cf. subrobustus* Seunès, *Hauericeras* sp., *Inoceramus nahorianensis* Kotsyubinskij, *I. colchicus*, *I. simonovitchi* Tsagareli, *I. salisburgensis*, *I. cf. nebrascensis* Owen, *Echinocorys* cf. *elatus* Arnaud, and the microfossils *Arenobulimina obliqua* (d'Orbigny), *Bolivina in-crassata* (Reuss), *Anomalina clementiana* (d'Orbigny), *Cyroidina caucasica* Subbotina.

In the Upper Maastrichtian *Pachydiscus neubergicus*, *P. subrobustus orientalis* Tsagareli, *Diplomoceras cylindraceum*, *Hoploscaphites constrictus*, *Coraster vilanovae* Cotteau, *Ornithaster anthulai* (Lambert), *Seunaster georgicus* Rouch., *Cardiotaxis heberti* Cotteau, *Galeaster seunesi* Lambert, *Ventilab-*

rella carseyae (Plummer), *Globotruncana stuarti* (de Lapparent), *Globotruncana coronata* Bolli, *Bolivinoidea draco* Mars-son, *Inoceramus tenuilineatus* Hayden & Meek, *I. incurvus* Meek, *I. tegulatus sensu Tsagareli non von Hagenow* (= *Tenuipteria argentea* (Conrad)), *I. georgicus*.

In the Somkhiti block Campanian and Maastrichtian stages are represented by limestones, in places with variegated tuffs. In the Lower Campanian we found *Glyptoxoceras retrorsum* (Schlüter) and almost the same complex of inoceramids and echinoids as in Ajara-Trialeti. In the Upper Campanian only inoceramids were found. In the Lower Maastrichtian we recognised *Pachydiscus perfidus* de Grossouvre, *P. fresvillensis* Seunès, *Parapachydiscus icenicus* (Sharpe) and *Inoceramus* cf. *salisburgensis* Fugger & Kastner, *Austinocrinus erckerti* Dames, and in the Upper Maastrichtian only *Pachydiscus neubergicus*.

In the Lesser Caucasus, in the Debeda-Terter facies type, which is represented in a calcareous marly facies, and in which, according to GAMBASHIDZE (1979) the Lower and Upper Campanian are each divided into two parts.

The lower Lower Campanian is characterised by: *Inoceramus sarumensis* Woods, *I. subsarumensis* Renngarten, *I. convexus*, *I. balticus*, *I. prons* Renngarten, *I. adjakendensis* Aliev, *I. cf. lingua* Goldfuss, *I. cf. mitraikyensis* Sornay, *Pseudofaster caucasicus*, *Caronaster cupuliformis* Airaghi, *Echinocorys ovatus* Leske, *E. cf. pyramidatus*, *Isomicraster fraasi* Rouch., *Galeola senonensis*.

The upper Lower Campanian contains: *Glyptoxoceras wernickei* (Wolleman), *Discoscaphites* cf. *gibbus* (Schlüter), *Inoceramus decipiens* Zittel, *I. tausensis* Aliev.

The lower Upper Campanian yielded *Hoplitoplacenticeras coesfeldiense* (Schlüter), *Scaphites* cf. *haugi* de Grossouvre, *Belemnitella mucronata* (Schlotheim), *Inoceramus balticus*.

The upper Upper Campanian *Inoceramus regularis* d'Orbigny non Münster (= *Selenoceras sornayi* Dhondt). In the Lower Maastrichtian were observed: *Pachydiscus neubergicus*, *Diplomoceras cylindraceum* Ivovense Mich., *Belemnella lanceolata* (Schlotheim), *Inoceramus colchicus*, *I. nebrascensis* Owen.

In the Upper Maastrichtian *Pachydiscus gollevillensis*, *Pachydiscus colligatus* (Binkhorst), *Pachydiscus haueri haueri* Collignon, *P. egertoni jacquoti* Seunès, *Pseudokossmaticeras brandti*, *Diplomoceras cylindraceum*, *Inoceramus regularis* d'Orbigny non Münster, *Guettaria rocardi*, *Echinocorys duponti* Lambert, *Austinocrinus meyni* Stolley.

In Upper Crimea the **Campanian** stage is represented mainly by white marls, and the upper part by light grey chalky marls.

The Lower Campanian is divided into two zones: lowermost is the *Micraster schroederi* Zone and above it the *Hauericeras pseudogardeni* Zone:

– the *schroederi* Zone is characterised by the following foraminifers: *Globotruncana arca* Cushman, *Bolivinoidea decoratus* Jones, *Gavelinella clementiana* (d'Orbigny), *Orbignyana inflata* (Reuss);

– the *pseudogardeni* Zone contains: rare *Hauericeras pseudogardeni*, *Belemnitella* ex gr. *mucronata* (Schlotheim), *Inoceramus balticus*, *I. azerbaijanensis*, and the foraminifers *Globotruncanita elevata* Brotzen, *Rugoglobigerina kelleri* (Subbotina), *Cibicidoides aktulagayensis* Vassilenko; in the Lower Campanian *Inoceramus dariensis* was also observed (65 - 70 m).

The Upper Campanian is divided into two zones based on belemnites:



Fig. 1 — Maastrichtian and Campanian ammonites species from the Maastricht area, from Upper Crimea, from the Caucasus and from Mangyshlak.

– the lower Upper Campanian Zone contains *Belemnitella mucronata senior*

– the upper Upper Campanian Zone contains *Belemnitella langei*. The lower Upper Campanian Zone further contains *Inoceramus balticus*, rare *Pachydiscus koeneni*, *Globotruncana morozovae* Vassilenko, *G. majzoni* Sac. & Deb., *Brotzenella menneri* Keller, *B. monterelensis* Marie, *Stensioeina pommerana* Brotzen.

The upper Upper Campanian further contains *Baculites* ex gr. *anceps*, *Pachydiscus koeneni*, *Inoceramus buguntaensis* Dobrov, *I. caucasicus* Dobrov (??), *Cibicidoides voltzianus* (d'Orbigny), *Bolivina kalinini* Vassilenko, *B. incrassata* (Reuss). In the uppermost part of the section were found: *Bolivinoidea miliaris* Hiltermann & Koch, *Globotruncana contusa* Cushman, *Neoflabellina praereticulata* Hiltermann.

In the **Crimean lowland** the **Campanian** is divided into two parts for foraminifers: the Lower Campanian contains *Globotruncana arca* Cushman, *Globotruncanella elevata* Brotzen, *Rugoglobigerina kelleri* Subbotina, *Bolivinoidea decoratus* Jones; the Upper Campanian is characterised by *Globotruncana morozovae* Vassilenko, *Stensioeina pommerana* Brotzen, *Brotzenella menneri* Keller, *Cibicidoides voltzianus* (d'Orbigny), *Bolivina incrassata* (Reuss).

The **Maastrichtian** stage is widespread in the **Crimea**, where it is represented by grey sandy marls and sandstones.

The Lower Maastrichtian substage is characterised by the *Belemnella lanceolata* - *Acanthoscaphites tridens* Zone - this is the equivalent of the *Globotruncanella stuarti* Zone. Also observed in this zone are: *Belemnella sumensis* Jeletzky, *Hoploscaphites constrictus*, *Diplomoceras cylindraceum*, *Hauericeras sulcatum*, *Pseudokossmaticeras galicianum*, and foraminifers, bivalves, brachiopods and echinoids.

The Upper Maastrichtian is represented by the *Neobelemnella kazimiroviensis* Zone, or the equivalent *Abathomphalus mayaroensis* Zone. Herein occur *Hoploscaphites constrictus*, *Pachydiscus neubergicus*, *P. gollevillensis*, *Phyllopachyceras* (?) *surya*, inoceramids, other bivalves, gastropods, brachiopods, Bryozoa, Foraminifera.

Near Bakhchisaray remains of a dinosaur (*Orthomerus weberi* Rjab.), near Skalistoe fragments of a mosasaur (*Tylosaurus* cf. *anceps* Owen) and near Sevastopol fragments of a crocodile (*Thoracosaurus macrorhynchus* Blainville) were found.

On the Crimean lowland Maastrichtian the following foraminifers were recognised: *Raceguembelina fructuosa* Egger, *Bolivinoidea draco*, *Globotruncanella stuarti* etc. (500 to 800 m on Tarkhankut peninsula).

In the **Mangyshlak** peninsula (W. Kazakhstan) the **Campanian** is represented by chalks and chalk-like limestones, which north-eastwards (in Central Usturt) become marls and clayey limestones (thickness 30 to 150 m). Four zones, recognised in the Kopet-Dagh are confirmed in Mangyshlak: *Offaster pomeli* Zone, *Eupachydiscus levyi* Zone, *Hoplitoplacentoceras coesfeldiense*/*Stegaster gillieronii* Zone, *Bostrychoceras polyplacum* Zone. All four zones are also characterised by inoceramids, echinoids, belemnites, brachiopods and foraminifers. In the uppermost zone *Pachydiscus stobaei* Nilsson has been found.

The Mangyshlak **Maastrichtian** is represented by rocks which are similar to those of the Campanian: chalk-like limestones and chalks, in places with flint nodules and in the upper part enriched with "aleurites" (10 to 30 to 175 m). The Lower Maastrichtian contains *Belemnella lanceolata* (Schlotheim), *Inoceramus oviformis* Arzum., *I. buguntaensis* Dobrov & Pavlova, *Micraster grimmensis* Nietsch., *Echinoc-*

orys lamberti Smiser, *E. conica* Agassiz, *E. belgica* Lambert and also foraminifers are numerous.

Sometimes an Upper Maastrichtian hardground rests on the Lower Maastrichtian. The lower Upper Maastrichtian strata correspond to the Kopet-Dagh *Diplomoceras cylindraceum* Zone and contain *Baculites anceps*, *Echinocorys ciplensis*, *E. belgica* Lambert, *E. lamberti*, *Conulus magnificus* d'Orbigny, rare *Neobelemnella kazimiroviensis*. The *Tenuipteria argentea* Zone, besides the zonal species, contains: *Hoploscaphites constrictus* crassus Lopuski, *Oxytoma danica* (Ravn), *Echinocorys ciplensis*, *E. pyramidata*, *Galerites sulcatus* d'Orbigny, *G. vulgaris* Leske, *Cyclaster integer* Seunès and also foraminifers: *Bolivina incrassata crassa* Vassilenko, *B. plaita* Carsey, *Karrerella fallax* Rzeh.

When we compare the three main localities of the Alpine line: Upper Crimea, the Caucasus and Mangyshlak, we can see that in – the **Campanian** the genera *Hauericeras*, *Baculites* and *Pachydiscus* occur both in the Crimea and the Caucasus; *Pachydiscus* was also found in Mangyshlak, where it is the only Campanian ammonite genus known so far.

– in the **Maastrichtian** the genera common between the Caucasus and the Crimea are: *Hoploscaphites*, *Diplomoceras*, *Hauericeras*, *Pseudokossmaticeras*. Thus the Campanian-Maastrichtian Crimean ammonite complex contains taxa also known from the Caucasus, and has no distinctive elements.

In Mangyshlak two genera were observed: *Baculites* and *Hoploscaphites*. Both are also known in the Caucasus and the Crimea.

In the **Maastricht type area** the following genera are known: – in the **Campanian**: *Baculites*, *Scaphites*, *Trachyscaphites*, *Hoplitoplacentoceras*, *Pachydiscus*. Only *Trachyscaphites* is not known from the Caucasus.

– in the **Maastrichtian**: *Saghalinites*, *Baculites*, *Nostoceras*, *Glyptoxoceras*, *Diplomoceras*, *Hoploscaphites*, *Acanthoscaphites*, *Pachydiscus*, *Anapachydiscus*, *Sphenodiscus*. *Saghalinites*, *Nostoceras* and *Sphenodiscus* are not known from Crimea nor from the Caucasus nor from Mangyshlak.

Ammonites are a group of organisms which went extinct at the end of the Maastrichtian. The Late Cretaceous is the last epoch of their existence. How were they distributed during this time?

Usually it is accepted that the stratigraphic importance of ammonites in the Late Cretaceous is decreasing - more precisely they decrease in number and there are hiatuses in their distribution. Therefore belemnites, inoceramids, echinoids and foraminifers become stratigraphically more important.

In the Caucasus already in the Albian zonation only with ammonites is impossible.

In order to have a complete view of the distribution and extinction of the ammonites, we review them for the complete Upper Cretaceous:

CENOMANIAN

Caucasus - 19 - *Hypophylloceras*, *Gaudryceras*, *Tetragonites*, *Sciponoceras*, *Baculites*, *Anisoceras*, *Hypoturritites*, *Turritites*, *Bostrychoceras*, *Scaphites*, *Puzosia*, *Austenicerias*, *Latidorsella*, *Schloenbachia*, *Mantelliceras*, *Calycoceras*, *Acanthoceras*, *Cunningtoniceras*, *Couloniceras*.

Crimea - 6 - *Mesogaudryceras*, *Sciponoceras*, *Scaphites*, *Puzosia*, *Schloenbachia*, *Mantelliceras*.

Mangyshlak - 14 - *Sciponoceras*, *Anisoceras*, *Idiohamites*, *Neostlingoceras*, *Turritites*, *Scaphites*, *Worthoceras*, *Hypophylites*, *Schloenbachia*, *Submantelliceras*, *Acompsoceras*, *Acanthoceras*, *Euomphaloceras*, *Karamaites*.

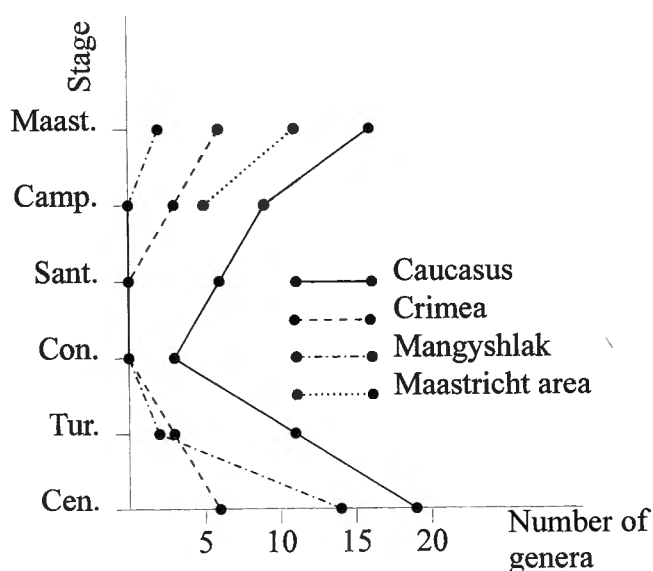


Fig. 2 — Number of ammonite genera in the Upper Cretaceous of the studied regions.

TURONIAN

Caucasus - 11 - *Neogaudryceras*, *Sciponoceras*, *Tetragonites*, *Scaphites*, *Puzosia*, *Lewesiceras*, *Romaniceras*, *Mammites*, *Collignoceras*, *Subprionocyclus*, *Arkhangelskiceras*.

Crimea - 3 - *Hypanthoceras*, *Scaphites*, *Lewesiceras*.

Mangyshlak - 6 - *Sciponoceras*, *Hypanthoceras*, *Scaphites*, *Lewesiceras*, *Metoicoceras*, *Collignoceras*.

CONIACIAN

Caucasus - 3 - *Baculites*, *Eubostriyoceras*, *Nowakites*.

Crimea - 0.

Mangyshlak - 0.

SANTONIAN

Caucasus - 6 - *Gaudryceras*, *Scaphites*, *Puzosia*, *Hauericeras*, *Nowakites*, *Eupachydiscus*.

Crimea - 0.

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Mangyshlak - 0.

CAMPANIAN

Caucasus - 9 - *Baculites*, *Bostriyoceras*, *Glyptoxoceras*, *Discoscaphites*, *Hauericeras*, *Pachydiscus*, *Menuites*, *Eupachydiscus*, *Hoplitoplacenticeras*.

Crimea - 3 - *Baculites*, *Hauericeras*, *Pachydiscus*.

Mangyshlak - 1 - *Pachydiscus*.

Maastricht - 5 - *Baculites*, *Scaphites*, *Trachyscaphites*, *Hoplitoplacenticeras*, *Pachydiscus*.

MAASTRICHTIAN

Caucasus - 16 - *Hypophylloceras*, *Helicoceras*, *Baculites*, *Didymoceras*, *Diplomoceras*, *Neancyloceras*, *Hoploscaphites*, *Acanthoscaphites*, *Hauericeras*, *Kossmaticeras*, *Discoscaphites*, *Pachydiscus*, *Parapachydiscus*, *Pseudophyllites*, *Discohoplites*, *Pseudokossmaticeras*.

Crimea - 6 - *Phyllopachyceras*, *Diplomoceras*, *Hoploscaphites*, *Hauericeras*, *Pachydiscus*, *Pseudokossmaticeras*.

Mangyshlak - 2 - *Baculites*, *Hoploscaphites*.

Maastricht - 11 - *Saghalinites*, *Baculites*, *Nostoceras*, *Glyptoxoceras*, *Diplomoceras*, *Scaphites*, *Hoploscaphites*, *Acanthoscaphites*, *Pachydiscus*, *Anapachydiscus*, *Sphenodiscus*.

To summarize:

	Caucasus	Crimea	Mangyshlak	Maastricht
Maastrichtian	16	6	2	11
Campanian	9	3	0	5
Santonian	6	0	0	—
Coniacian	3	0	0	—
Turonian	11	3	6	—
Cenomanian	19	6	14	—

In the Cenomanian the maximum number of genera was present; during the Turonian it decreased. In the Coniacian and Santonian (two short stages) the number of ammonite genera was minimal, and in Crimea and Mangyshlak they were not found. From the Campanian upwards the number of genera increased again and reached (except in Mangyshlak) in the Maastrichtian a level comparable to that known from the Cenomanian. Thus shortly before the complete extinction of the ammonites in the Maastrichtian they knew a last expansion.

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Addendum

Stratigraphic distribution of Upper Cretaceous ammonite genera from the Caucasus, the Crimea, Mangyshlak and the Maastricht area

1. *Phyllopachyceras* Spath, 1925, br - m
2. *Hypophylloceras* Salfeld, 1924, h - m
3. *Neogaudryceras* Shimizu, 1935, tur - m (= *Gaudryceras*)
4. *Mesogaudryceras* Spath, 1927, cen
5. *Gaudryceras* de Grossouvre, 1894, tur - m
6. *Tetragonites* Kossmat, 1895, al₂ - cen₃
7. *Pseudophyllites* Kossmat, 1895, camp - m
8. *Helicoceras* d'Orbigny, 1842, al₂ [= *Hamites* (*Hamitella*)]
9. *Sciponoceras* Hyatt, 1894, al₃ - tur₂
10. *Baculites* Lamarck, 1799, tur₂-m
11. *Anisoceras* Pictet, 1854, al₃ - tur₃
12. *Idiohamites* Spath, 1925, al₃ - cen
13. *Hypoturrites* Dubourdieu, 1953, cen
14. *Neostilingoceras* Klinger & Kennedy, 1978, cen₁₋₂
15. *Turritites* Lamarck, 1801, cen-tur₁
16. *Bostrychoceras* Hyatt, 1900, cen-m₁
17. *Eubostrychoceras* Matsumoto, 1967, al - sant (? camp)
18. *Hyphantoceras* Hyatt, 1900, tur-sant
19. *Didymoceras* Hyatt, 1884, camp - m (= *Ciroceras* Conrad, 1868)
20. *Nostoceras* Hyatt, 1884, camp
21. *Diplomoceras* Hyatt, 1900, camp
22. *Neancyloceras* Spath, 1926, camp₂-m
23. *Glyptoxoceras* Spath, 1925, sant - m
24. *Scaphites* Parkinson, 1811, al₃ - m
25. *Hoploscaphites* Nowak, 1911, camp - m
26. *Discoscaphites* Meek, 1870, camp - m
27. *Acanthoscaphites* Nowak, 1911, camp
28. *Trachyscaphites* Cobban, 1964, camp - m
29. *Worthoceras* Adkins, 1928, al₃ - tur₂
30. *Puzosia* Bayle, 1878, al₁ - tur₂
31. *Austiniceras* Spath, 1922, cen₃ - tur₂ (= *Parapuzosia*)
32. *Latidorsella* Jacob, 1908, al₃ - cen (= *Desmoceras* Zittel)
33. *Hauericeras* de Grossouvre, 1894, con - m
34. *Kossmaticeras* de Grossouvre, 1901, tur₂ - camp
35. *Pseudokossmaticeras* Spath, 1922, camp₂ - m
36. *Brahmaïtes* Kossmat, 1897, m
37. *Lewesiceras* Spath, 1939, cen₃ - con
38. *Nowakites* Spath, 1922, con-sant
39. *Pachydiscus* Zittel, 1884, camp-m
40. *Parapachydiscus* Hyatt, 1900, "Senonian"
41. *Anapachydiscus* Yabe & Shimizu, 1926, con-m
42. *Menuites* Spath, 1922, sant - camp
43. *Eupachydiscus* Spath, 1922, con - camp
44. *Pseudophyllites* Spath, 1926, con
45. *Hoplitoplacenticeras* Spath, 1922, camp₁ - m
46. *Discohoplites* Spath, 1925, al₃
47. *Hypoplites* Spath, 1922, al₃ - cen₃
48. *Schloenbachia* Neumayr, 1875, al₃ - cen₃
49. *Mantelliceras* Hyatt, 1903, cen₁
50. *Sharpeiceras* Hyatt, 1903, cen
51. *Submantelliceras* Spath, 1923, cen₁ (= *Mantelliceras*)
52. *Acompsoceras* Hyatt, 1903, cen₁
53. *Calycoceras* Hyatt, 1900, cen - tur₁ (= *Newboldiceras*)
54. *Acanthoceras* Neumayr, 1875, cen₁ - cen₃
55. *Euomphaloceras* Spath, 1923, cen₃
56. *Cunningtoniceras* Collignon, 1937, cen₃ (= *Euomphaloceras*)
57. *Romaniceras* Spath, 1923, cen₃ - tur₂
58. *Metoioceras* Hyatt, 1903, tur₁
59. *Mammites* Laube & Bruder, 1886, tur
60. *Collignoniceras* Breistroffer, 1947, tur
61. *Prionotropis* Meek, 1878, tur
62. *Subprionocyclus* Shimizu, 1932, tur₂
63. *Barroisiceras* de Grossouvre, 1894, con
65. *Arkhangelskiceras* Iljin, 1957, cen?
66. *Couloniceras* Busnardo, 1966, cen
67. *Karamaïtes* Sokolov, 1961, cen