Евгению Ю. Барабошкину с глубоким уважением

Ecology of Caucasian Callovian Ammonitida

(Ökologie kaukasischer Callovium-Ammoniten)

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With 2 Text Figures

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Abstract: Reconstruction of the ecology and behaviour of the Callovian Ammonitida and the supposed bathymetry of the Callovian marine basin in the Caucasus area, allows us to suppose that Callovian ammonites generally belong to two ecological groups: nectonics and nectobenthonics. They inhabited shallow areas of the sea with the most favourable depths not exceeding 100 m. Temperature was a decisive factor in habitat selection of these ammonites.

Kurzfassung: Die Rekonstruktion der Lebens- und Verhaltensweisen der Callov-Ammoniten und die vermutete Bathymetrie des kaukasischen Callov-Beckens erlauben es, die Callov-Ammoniten zwei Lebensräumen zuzuordnen: dem Nekton und dem Nektobenthos. Sie bewohnten flache Schelfmeere mit einer optimalen Wassertiefe bis zu 100 m. Temperatur spielte eine entscheidende Rolle bei der Wahl des Habitats.

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1. Burial conditions

The structure and shape of ammonite shells is closely related to their habitat, therefore it would be impossible to reconstruct the mode of life led by these animals without first studying the habitat in which they lived. However, in order to reconstruct their mode of life, one must be sure that the shells were buried close to their habitat. Otherwise, it would be unreasonable to consider a group of ammonites as an indicator of certain environmental conditions.

The hypothesis of *postmortem* transport of ammonite shells is called in question by the fact that the orictocenosis of one site are assemblages of variously sized shells. Indirect evidence against this hypothesis is that neither in the Caucasus nor on the Russian Platform do the Callovian Ammonitida shells have any signs of rounding caused by tidal action.

This hypothesis is further contradicted by the fact that numerous ammonites are confined to certain facies, by the existence of some forms of these animals in different climatic conditions, and by their mixing only on the borders of these provinces.

It appears, however, that it would be rash to completely deny the possibility of *postmortem* transport; nonetheless, if we overrate its importance we may arrive at the wrong conclusion.

Ammonite burial in some areas of the Caucasian Callovian sea proceeded quickly, as the traces of boring organisms on the shells are extremely rare and the presence of small forms of ammonites and bivalves in body chambers indicates burial under conditions of a relatively unstable marine environment.

2. Mode of life

The variability and diversity of shell structures in different groups of ammonites enable us to assume that individual forms differed from one another in their mode of life. Among modern Cephalopoda we distinguish five major life forms: nectonic, benthonic, nectobenthonic, pelagic, and planktonic (Nesis 1975). The majority of Callovian Ammonitida seem to have belonged to two life forms — nectonic and nectobenthonic.

3. On the shell injuries of living Callovian ammonites

Observations of shell damage incurred during an ammonite's lifetime tell much about the enemies of Ammonitida. In some cases, shell-damaged Ammonitida can no longer swim, therefore the study of damage inflicted during life plays an important role in interpreting their mode of life.

All damage and anomalies found by us on *Macrocephalites, Hecticoceras, Perisphinctes,* etc. are divided into three main groups: 1. minor damage of the shell (without involving the mantle), which heals fast; 2. significant damage of the shell which affects the mantle's edge (in this case, though, regeneration of the damaged sculpture occurs, but it rarely assumes its normal shape; such damage frequently affects the animal's subsequent mode of life); 3. small anomalies in the sculpture, keel displacement, shifting in the normal location of partitions and in spiral symmetry caused by the damaged state of the mantle or by the environment (Lominadze 1982).

4. Habitat

For paleoecologic observations, the most favourable sites are Callovian sediments of the Northern Caucasus which extend over a large area along the Caucasian Range and contain a rich complex of Ammonitida skeletal fossils. We investigated the ammonite habitats predominantly in this area of the Caucasian Callovian marine basins.

Insufficient research has been done so far on the following problem: at what water depth were the optimum conditions for the existence of Ammonitida

groups? Because water depth affects temperature, lighting, feeding patterns, etc., its study is important for the reconstruction of their habitat.

Ammonites are free-swimming animals. The water depth which they inhabited can be ascertained both by the character of sediments deposited in the given basin and by the assemblage of organisms (predominantly benthonic) found in these sediments.

An attempt has been made here to reconstruct the bathymetry of the basin, using a method developed by Ziegler (1967) and to reproduce the environment of Ammonitida in the Callovian.

Early Callovian

With the advent of the Lower Callovian transgression, a large part of the Caucasus became submerged. Although the transgression continued into the Middle Callovian in some places in the Caucasus, in other places the Lower Callovian deposite became eroded.

The early Callovian marine basin of the North Caucasus was the region where Boreal and Mediterranean faunas met and where *Macrocephalites* and *Cadoceras* developed extensively.

Macrocephalitidae are the largest group of ammonites in the Lower Callovian sediments of the Caucasus.

In the North Caucasus, during the existence of Macrocephalitidae in a shallow, very warm sea, carbonate sediments were deposited which contained terrigenous material and a large amount of iron oxides. A shallow depth is indicated by the presence of *Pholadomya, Ceromya, Ctenostreon,* and *Pecten* bivalves found in association with Macrocephalitidae. The Callovian sediments (in areas where Macrocephalitidae are numerous) consist mainly of ferruginous, oolitic, coarse-grained, calcareous arenaceous rocks with plant remains. To the west of these areas, where shallow water facies are replaced by deep water, Macrocephalitidae are not found in such large amounts.

The same picture can be seen in the eastern part of the North Caucasus. This is confirmed by investigations carried out in Georgia. In the environs of Tsessi village, where there is an abundance of Macrocephalitidae, patterns of Callovian sediments and fauna indicate the proximity of the shore and shallow depth of the basin. Also, the observed regularity is found in Abkhazia and South Osetia (Georgian SSR).

It seems that the representatives of Macrocephalitidae inhabited shallow water environment and lived in hydrodynamically active parts of the basin, which is confirmed by the considerable thickness of these animals' shell walls and their confinement to shallow water sediments.

Macrocephalitidae existed only in certain facies. They are found most frequently in sediments rich in iron and calcium carbonate. This is clearly seen in the Caucasus and is confirmed by their wide distribution in similar rocks in other areas of the Soviet Union and elsewhere.

Macrocephalitidae flourished mostly in Early Callovian seas in the southern region in waters which seem to have been distinguished by rather high temperatures. This is indicated by the massiveness of the mollusk shells in the deposits, the pre-

dominance of carbonates, and by a large amount of ferruginous oolites in the North Caucasus Callovian (Lominadze 1967).

The Early Callovian Sea of the North Caucasus was connected in today's vicinity of the Georgian Military Road with warm early Callovian seas of the southern slope by a wide sound. At the same time, an extensive distribution in the North Caucasus of ammonites belonging to typical Boreal genera corroborates the theory that the Early Callovian sea in the north was linked with shallow seas on the Russian Platform.

Cadoceras are rather common in clays and have never been found in any other Callovian rock. Thus we may assume that *Cadoceras* preferred deeper water. This is also supported by their presence in clay facies of the Russian Platform. The habitat of *Cadoceras* in deep water can also be accounted for by the lower temperatures (as compared to warmer, shallower water). Since the *Cadoceras* came from Boreal seas where they flourished most, then they needed low temperature conditions in their new Tethyan habitat.

In comparatively shallow areas of the Callovian marine basin of the North Caucasus we come across numerous *Kepplerites* and *Sigaloceras*. *Kepplerites* have a rather heavy shell, apparently indicating their adaptation to life at a short distance from the shore.

Similarity between numerous species of Early Callovian Ammonitida from the North Caucasus, Transcaucasia, Russian Platform, Crimea, and Soviet Middle Asia shows that communication between the Early Callovian marine basins in these areas was rather extensive.

Middle Callovian

The entire northeastern Caucasus was covered by a shallow shelf sea during the Callovian. The depth of the sea over a large part of the region seems to have been 40 to 50 m, never exceeding 100-200m. To the north there was a landmass whose proximi-

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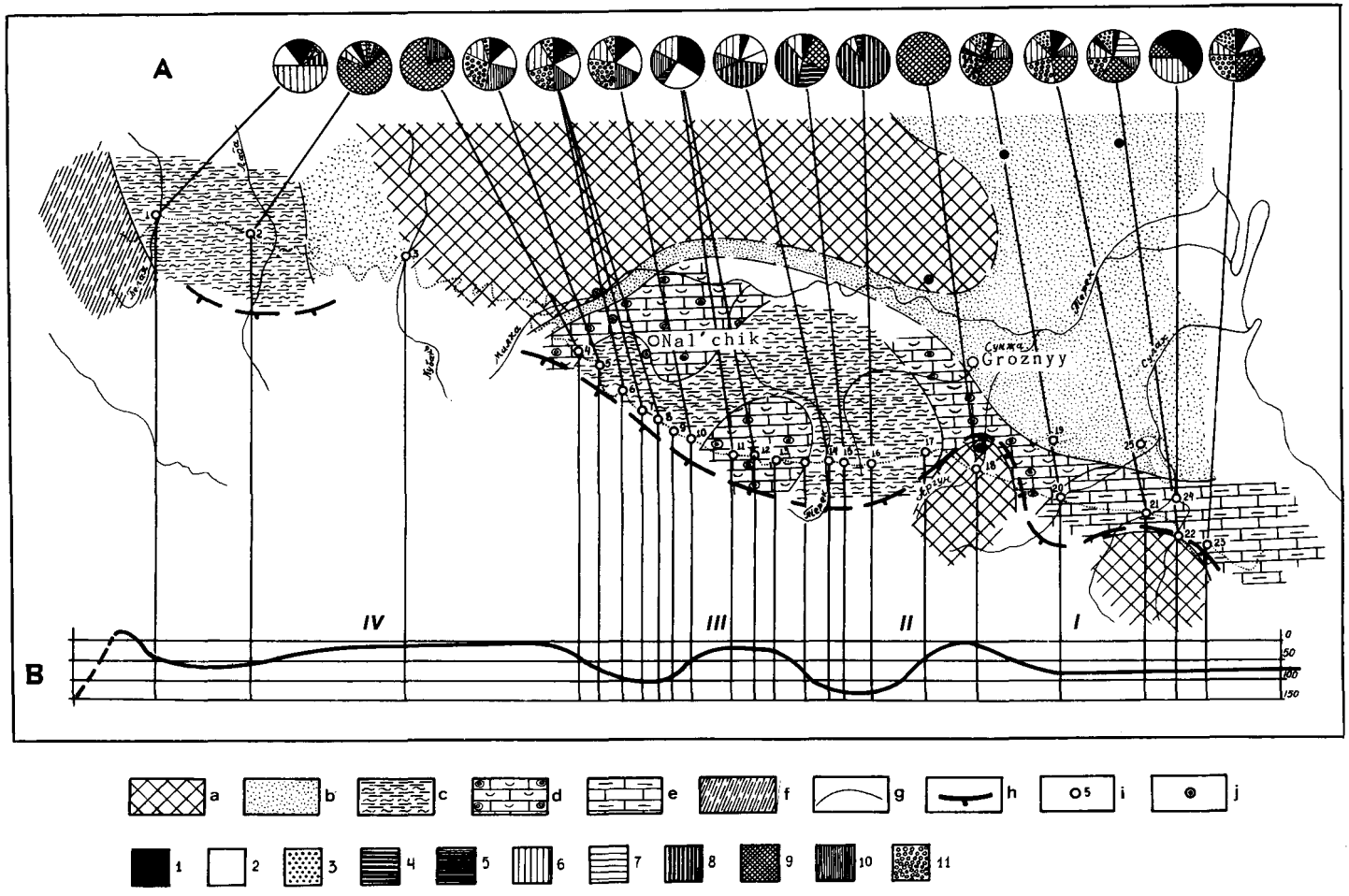
Text Fig. 1. Spectra of skeletal remains in the Middle Callovian deposits of the North Caucasus.
Localities: 1 - the Belaya; 2 - the Malaya Laba; 3 - the Kuban; 4 - the Baksan; 5 - the Cheghem; 6 - the Chereck Khulamski; 7 - the Chereck Balkarski; 8 - the Psigansu; 9 - Vaza-Hoh Mountain; 10 - the Urukh; 11 - Kioni Pass; 12 - the Ardon; 13 - the Fiagdon; 14 - the Terek; 15 - Gherchech; 16 - Otzik village; 17 - the Ghekhi; 18 - the Chanti-Argoon; 19 - the Kharachai; 20 - Ghigatli village; 21 - Golotle village; 22 - Gunib village; 23 - Tsudakhar; 24 - Irganai village; 25 - Salatau Ridge.
A - Paleogeographic scheme.
a - supposed land; b - f - depositional areas of: b - sandy sediment; c - carbonaceous clayey silt; d - carbonaceous silt with leprochloritic oolites and shells of mollusks, Brachiopoda, and Echinodermata; e - carbonaceous clayey and sandy silt which formed concretionary limestone; f - flysch sediment; g - boundary between heterofacies areas; h - southern boundary of *Kosmoceras's* range; i - outcrops; j - prospecting boreholes.
Faunal spectra: 1 - *Kosmoceras;* 2 - Hecticoceratinae; 3 - *Erymnoceras;* 4 - *Cadoceras;* 5 - *Reineckeia;* 6 - Perisphinctidae; 7 - *Peltoceras;* 8 - thin-shelled bivalves (*Posidonia, Entolium*); 9 - coarse-shelled bivalves (*Pholadomya, Aequipecten*); 10 - Brachiopoda; 11 - Echinida.

B - Bathymetric profile of the North Caucasian marine basin of Middle Callovian age, based on faunal spectra and lithological composition of sediments.
I-IV see text.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ty can be inferred from the presence (in the north) of sandy material in the Middle Callovian sediments. At first, sedimentation occurred because of the washing out and removal of Lower Callovian terrigenous rocks, as seen in the presence of numerous resedimented Lower Callovian ammonites in terrigenous carbonate formations of the Middle Callovian as well as in the character of the sediments (Text Fig. 1).

In the second half of the Middle Callovian, the water depth seems to have reached 100-150 m. At that time, clay carbonate or pelitic and sandy material admixtures were deposited. The most widely occurring organisms then are thin-walled *Posidonia, Entolium,* and thin-ribbed, small Perisphinctidae. *Kosmoceras* were less frequent (Lominadze & Sakharov 1971).

The North Caucasus central areas are distinguished by the prevalence of carbonate sediments. To the west, limy aleurolites were deposited; this region seems to have been the farthest from land.

Thus, in the North Caucasus in the Middle Callovian the sea gradually deepened. Early in the Middle Callovian, sandy and pelitic material formed a large part of the sediments; at the end of the Middle Callovian, sandy material almost completely disappeared, giving way to clay and carbonate silt.

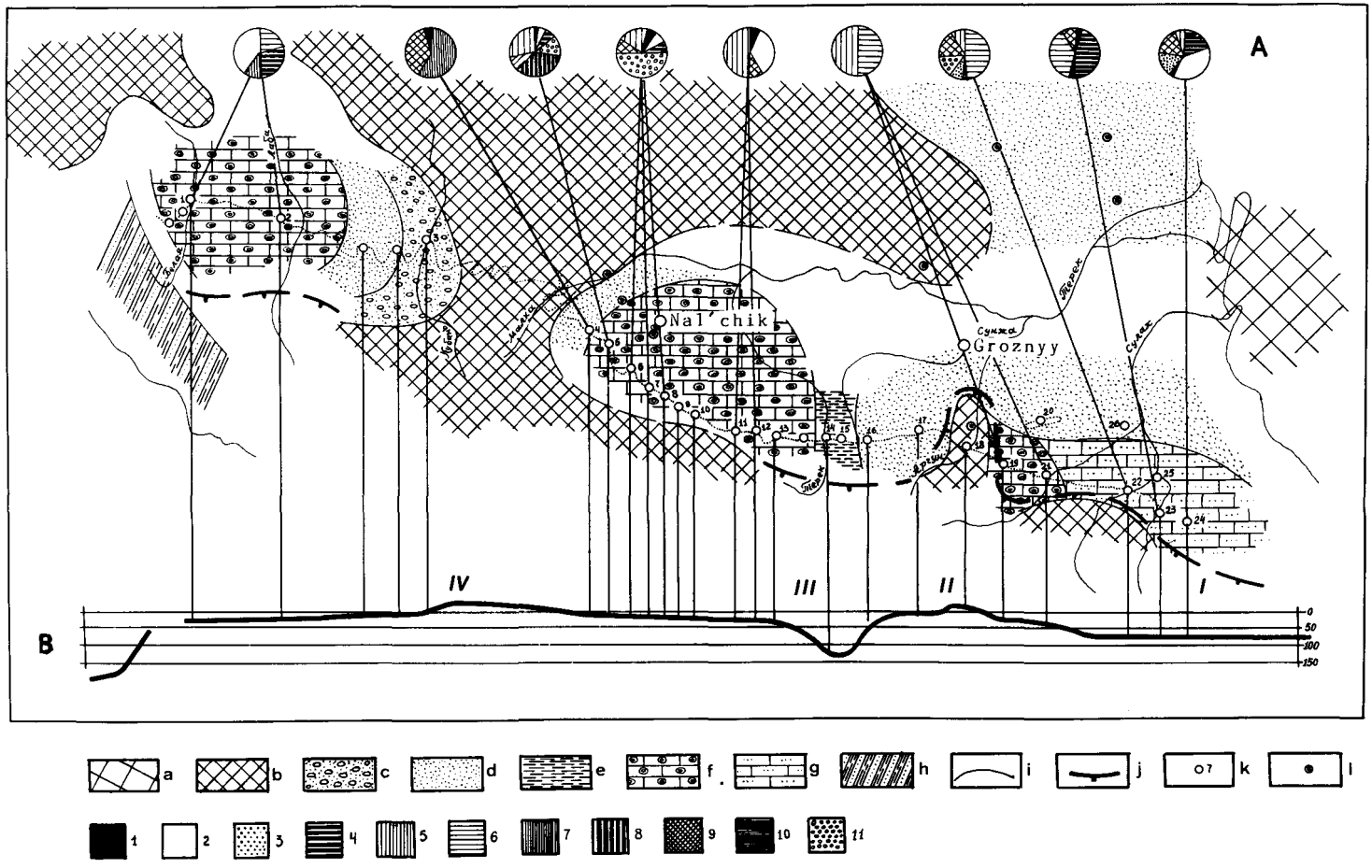
The fauna underwent an important change. In the early Middle Callovian, *Perispinctes, Reineckeia,* and *Kosmoceras* were present. Brachiopods and echinoids were greatly abundant. However, the second half of the Middle Callovian saw an extensive flourishing of *Erymnoceras, Kosmoceras,* and *Peltoceras.* Among them are found hecticoceratids and perisphinctids. Echinoidea and bivalves abounded.

Based on the character of the fauna and sediments in the Middle Callovian, the North Caucasus can be subdivided into four major regions:

I. Daghestan - ammonites are widespread (*Kosmoceras, Erymnoceras, Rollierites, Hecticoceras,* Perisphinctidae, etc.); echinoids, bivalves with thick shells (*Pholadomya, Aequipecten, Ceratomya, Gervillia,* etc.) and brachiopods are present. The water depth did not exceed 100 m.

Text Fig. 2. Spectra of skeletal remains in the Late Callovian deposits of the North Caucasus.
Localities: 1 - the Belaya; 2 - the Malaya Laba; 3 - the Kuban; 4 - the Baksan; 5 - the Cheghem; 6 - the Chereck Khulamski; 7 - the Chereck Balkarski; 8 - the Psigansu; 9 - Vaza-Hoh mountain; 10 - the Urukh; 11 - Kioni Pass; 12 - the Ardon; 13 - the Fiagdon; 14 - the Terek; 15 - Gherchech Pass; 16 - Otzik village; 17 - the Ghekhi; 18 - the Chanti-Argoon; 19 - the Sharo-Argoon; 20 - Kharachai village; 21 - Ghigatli village; 22 - Golotle village; 23 - Gunib village; 24 - Tsudakhar village; 25 - Irganai village; 26 - Salatau Ridge.
A - Paleogeographic scheme.
a - supposed land; b - land; c-i - depositional areas of: c - conglomerate; d - sandy material; e - carbonaceous clayey silt; f - carbonaceous silt with leptochloritic oolites and shells of mollusks, Brachiopoda, and Echinodermata; g - carbonaceous and sandy silt; h - flysch sediment; i - boundary between heterofacies areas; j - southern boundary of *Kosmoceras'* range; k - outcrops; l - prospecting boreholes.
Faunal spectra: 1 - *Kosmoceras;* 2 - Hecticoceratinae; 3 - *Oppelia;* 4 - *Quenstedtoceras;* 5 - *Peltoceras;* 6 - Perisphinctidae; 7 - Brachiopoda; 8 - Porifera; 9 - coarse-shelled bivalves; 10 - thin-shelled bivalves; 11 - Echinida.

B - Bathymetric profile of the North Caucasian marine basin of Late Callovian age, based on faunal spectra and lithological composition of sediments.
I-IV see text.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II. Ingush - ammonites are less frequent and represented by *Hecticoceras* and thin-ribbed Perisphinctidae; the bivalves *Posidonia* and *Entolium* are found. The water depth did not exceed 150-200 m.

III. North Osetia and Kabardino-Balkaria - echinoids, bivalves with thick shells and ammonites (Hecticoceratinae, *Kosmoceras*, Perisphinctidae) exist in great number. The water depth did not exceed 50 m.

IV. Northwest Caucasus - ammonites are numerous (Perispinctidae, *Kosmoceras, Hecticoceras,* etc.) as well as brachiopods and thick-walled bivalves. The water depth did not exceed 100 m.

Late Callovian

In the central part of mountainous Daghestan, the depth of the basin deepened somewhat. In central areas of the North Caucasus, carbonate clays and oolitic limestones are found. Conglomerates underlying these sediments consist of rounded and semi-rounded cores of ammonites and limy pebbles. To the west, Late Callovian deposits are represented by oolitic and poorly bedded limestone and sandstone containing beds of aleurolite (Text Fig. 2).

The Late Callovian sea in the North Caucasus was shallow and warm, and its bottom seems to have been rather flat. The size of the Late Callovian marine basin did not change as compared to that of the Middle Callovian basin. *Kosmoceras* and *Hecticoceras* continued to flourish, and *Peltoceras* and *Quenstedtoceras* emerged. In biocenoses of the late Callovian marine basin Boreal influence is noticeable.

In the North Caucasus seas in the Late Callovian, four regions are again distinguished, based on the faunal spectra and lithologic composition of the sediments:

I. Daghestan - ammonites (*Quenstedtoceras, Peltoceras, Kosmoceras,* etc.), thick-walled bivalves (*Anisocardia, Modiola, Protocardia,* etc.), and gastropods are present. The water depth did not exceed 80 m.

II. Ingush - there are ammonites of the genera *Putealiceras, Brightia,* and *Okaites;* very rare are *Quenstedtoceras* and thick-walled bivalves. The water depth did not exceed 50 m.

III. North Osetia and Kabardino-Balkaria - ammonites are rare; there are numerous thin-walled bivalves (*Chlamys, Entolium,* etc.), brachiopods (*Praecyclothyris, Holcothyris, Zeilleria,* etc.), and echinoids. The water depth did not exceed 150 m.

IV. Northwest Caucasus - there are numerous thick-walled ammonites (*Peltoceras, Quenstedtoceras, Lunuloceras,* Perispinctidae), bivalves, brachiopods, gastropods. The water depth did not exceed 50 m.

Boreal influence on the fauna in the Callovian marine basin in the North Caucasus is noticeable for the entire age.

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