

Cap-Shaped Gastropods from Upper Jurassic and Lower Cretaceous Deposits of Northern East Siberia

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Abstract—Cap-shaped gastropods are first identified in Upper Jurassic and Lower Cretaceous sections of northern East Siberia. They belong to three new genera of the subclass Pectinibrachia (*Boreioconus* gen. nov., *Nixepileolus* gen. nov., and *Taimyroconus* gen. nov.), which are identified at the species level (*B. bojarkensis* sp. nov., *N. depressus* sp. nov., *T. zakharovi* sp. nov.), and several species with the open nomenclature. The genus *Taimyroconus* attributed to the family Calyptraeidae is considered as an ancestral form of the genus *Crepidula*. The stratigraphic position of each taxon is determined for several sections. The facies confinement, habitat conditions, and ethology of defined genera are considered with the analysis of their geographic distribution.

Keywords: Gastropoda, Pectinibrachia, Calyptraeidae, Upper Jurassic, Lower Cretaceous, northern East Siberia, paleogeography, facies

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INTRODUCTION

The systematic investigations of the taxonomic composition of fossil marine invertebrates in Jurassic and Lower Cretaceous sections of northern areas of Siberia initiated at the end of the 1950s and beginning of the 1960s are still in progress, although they are now less intense as compared with the previous period. They resulted in the thorough study of practically all fossil cephalopod mollusks (ammonites and belemnites), most bivalves, and a substantial share of gastropods. Brachiopods were subjected to monographic description. The investigations included also the analysis of both microzoofossils (foraminifers, ostracods, radiolarians) and microphytobenthos (dinocysts, prasinophytes). The paleontological analysis was accompanied by stratigraphic, sedimentological, and paleogeographic investigations. They were culminated in development of zonal (or even infrazonal) scales on the basis of many fossil groups, which form a set of parallel scales that provide detailed chronological succession of beds and members. The available chronostratigraphic basis makes it possible to solve both geological and various paleontological problems. One of the important paleontological problems is connected with the further study of taxonomic diversity of the Arctic marine biota in the Mesozoic Era and specification of regional zoning within the Arctic paleogeographic realm established a half-century ago (Saks et al., 1971). This work contributes to the solution of

these problems. Three new genera of cap-shaped gastropods, two of which are now considered to be endemic to the Arctic region in the Late Jurassic and Early Cretaceous, are described.

MATERIALS AND METHODS

The collection of cap-shaped gastropod shells consisting of over 40 specimens originates from Upper Jurassic and Lower Cretaceous sections of the Khatanga Depression (Kheta River basin: Boyarka, Levaya Boyarka, Bol'shaya Romanikha rivers) and Taimyr Peninsula (Byrranga Mountains, Dyabaka-Tari River, Leningradskaya River basin, Kamennaya River) (Fig. 1). The fossils were collected during three interdisciplinary field expeditions (1961, 1963, 1964) organized by the Institute of Petroleum Geology and Geo-physics, Siberian Branch, USSR Academy of Sciences; Science Research Institute of Arctic Geology (NIIGA); and All-Union Research Institute of Geological Prospecting (VNIGRI). The bed-by-bed study of sections was accompanied by sedimentological and taphonomic observations for reconstructing depositional and fauna habitat environments (Zakharov, 1966a, 1995; Zakharov and Yudovnyi, 1974). The beds indicated in descriptions of taxa are shown in sections illustrated in (Zakharov, 1970; Mesezhnikov, 1984): section of the middle Volgian Substage, Dorsoplanoites maximus Zone at the Kamennaya River (Zakharov,

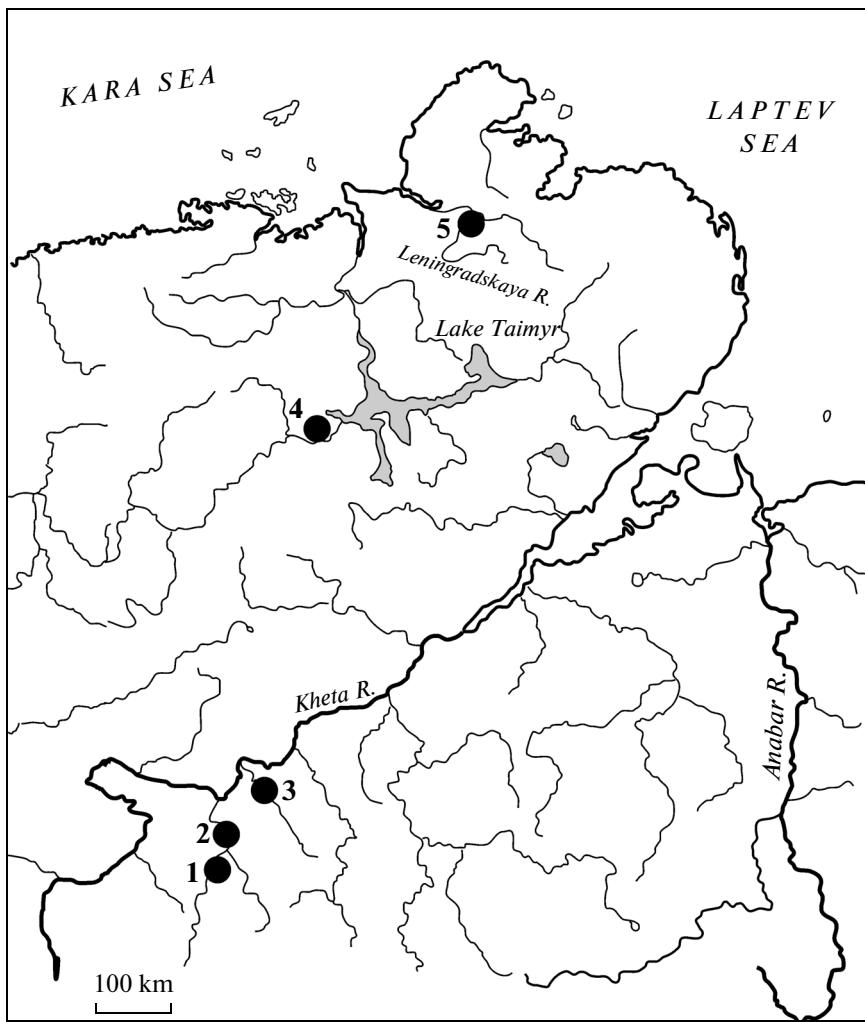


Fig. 1. Schematic location of Jurassic and Cretaceous sections in northern East Siberia with cap-shaped gastropods. (1) Levaya Boyarka River; (2) Boyarka River; (3) Bol'shaya Romanikha River; (4) Dyabaka-Tari River; (5) Kamennoy River, a tributary of the Leningradskaya River.

1970, fig. 20); Upper Jurassic—Lower Cretaceous section in the Boyarka River basin (Zakharov, 1970, fig. 27); lower Valanginian sections at the Bol'shaya Romanikha River (Zakharov, 1970, fig. 28); section of the middle Volgian Substage at the Dyabaka-Tari River (Mesezhnikov, 1984, fig. 19).

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTIONS OF CAP-SHAPED GASTROPODS

The earliest finds of cap-shaped gastropods originate from the integrated Upper Jurassic section located at the Levaya Boyarka River of the Kheta River basin in the eastern part of East Siberia (Fig. 2). The new genus *Taimyroconus* is found in the Oxfordian—Kimmeridgian Amoeboceras ravnii boundary zone and lower Kimmeridgian *Pictonia involuta* Zone and *Rasenia pseudouralensis* Subzone of the *Rasenia evoluta*

Zone (*Opornyi..., 1969*). The sections at the Dyabaka-Tari River (central Taimyr Peninsula) yielded *Nixipileolus* gen. nov. found in the *Dorsoplanites ilovaiskii* and *D. maximus* zones of the middle Volgian Substage, *Taimyroconus* gen. nov. recorded in the same zones and overlying *Taimyrosphinctes excentricus* Zone, and a form resembling *Boreoconus* species from the *Dorsoplanites ilovaiskii* Zone represented by two internal casts (“*Boreoconus*” sp. nov.). Fragments of shells probably belonging to the genera *Nixipileolus* and *Taimyroconus* are registered in the middle Volgian section (*Dorsoplanites maximus* Zone) at the Kamennoy River (Leningradskaya River basin, northern Taimyr) (Zakharov, 1970, fig. 20). The most diverse assemblage of cap-shaped gastropods was discovered in Lower Cretaceous (Valanginian and lower Hauterivian) sections of the Kheta River basin. This stratigraphic interval yielded type species of two new genera: *Boreoconus bojarkensis* occurring through the

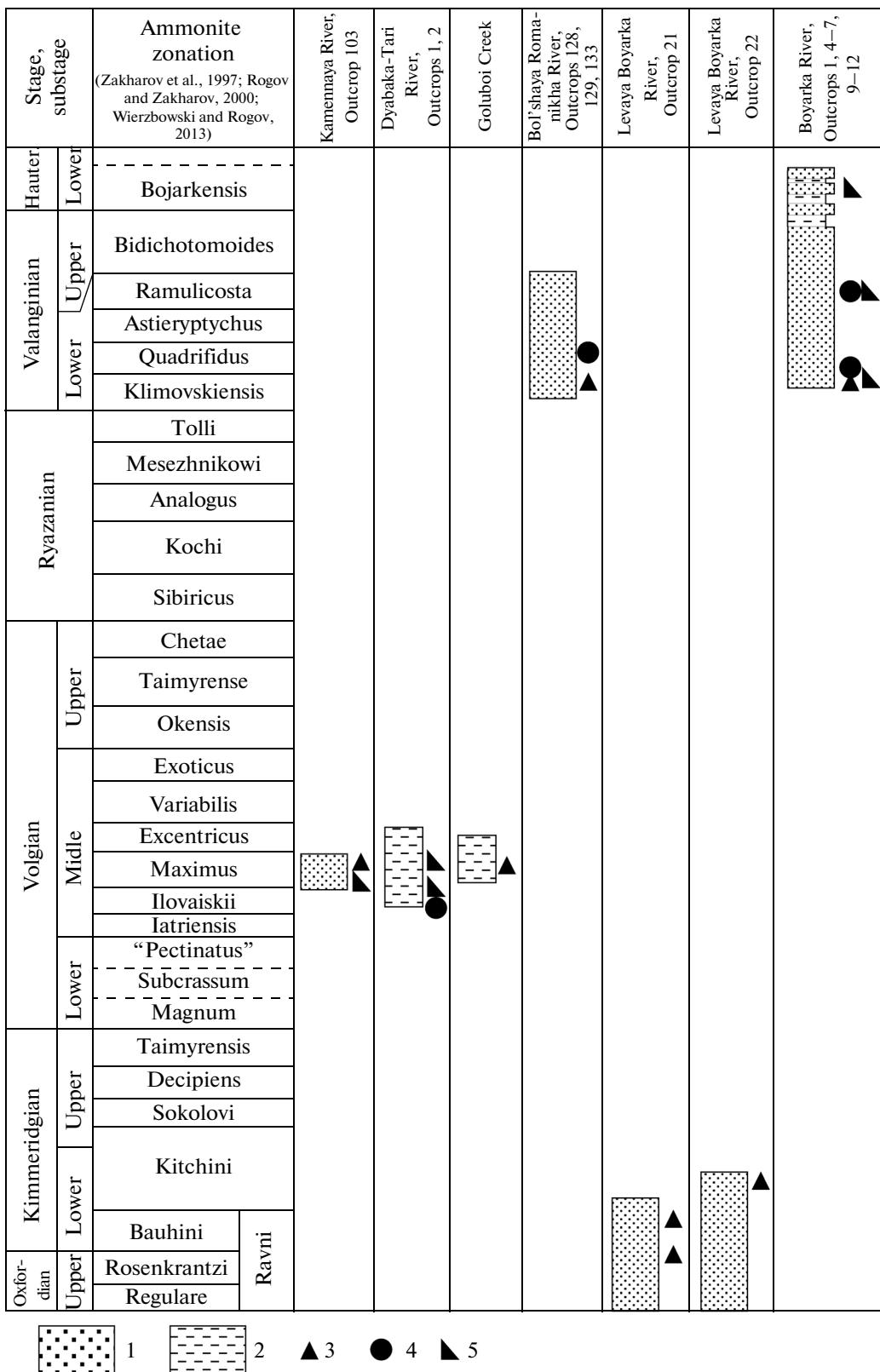


Fig. 2. Stratigraphic distribution of cap-shaped gastropod genera through zones in Upper Jurassic and Lower Cretaceous sections of northern East Siberia. (1) Sands and sandstones; (2) silts and siltstones; (3) genus *Taimyroconus*; (4) genus *Boreoconus*; (5) genus *Nixipileolus*.

entire Valanginian section and *Nixipileolus depressus* from the lower Valanginian Neotollia klimovskiensis and Siberites ramulicosta zones at the Boyarka River, the right tributary of the Kheta River. The lower Hauterivian interval of this section is characterized by a single *Nixipileolus* specimen similar to the species *N. depressus*. The genus *Taimyroconus* passes from the Upper Jurassic to the Lower Cretaceous strata. Single specimens of this genus are found in the lower Valanginian sections (Neotollia klimovskiensis Zone) at the Boyarka and Bol'shaya Romanikha rivers.

Thus, the stratigraphic range of cap-shaped gastropods encompasses the uppermost Oxfordian to basal Hauterivian stages. Their finds both in abundance and in taxonomic diversity are extremely irregular through the section. For example, a significant fraction of 40 specimens available in the collection belong to a single species: *Taimyroconus zakharovi* from the upper Oxfordian–lower Kimmeridgian Amoeboceras ravnii Zone. Most finds of individual species within ammonite zones are represented by one or several specimens. Cap-shaped shells are missing from the upper Kimmeridgian, lower Volgian and upper Volgian substages, and Boreal Berriasian (Ryazanian Stage) (Fig. 2). Taking into consideration the aforesaid, the significance of this Gastropoda family for stratigraphic purposes is for now uncertain.

FACIES CONFINEMENT AND HABITAT CONDITIONS

The sedimentological and paleoecological features indicate extremely or relatively shallow-water habitat environments of cap-shaped gastropods in the Late Jurassic epicontinental seas of northern East Siberia (Fig. 3). For example, abundant *Taimyroconus* remains found in the lower Kimmeridgian section at the Levaya Boyarka River (Kheta River basin) originate from fine-grained poorly sorted sands and glauconite–leptochlorite calcareous sandstones with coquina lenses consisting of isolated bivalve shells and fragments (Oporny..., 1969, pp. 25–26). Accumulations of vertically arranged large Pectinidae and rare *Ostrea* shells are observable along the strike of this bed. Such “rose”-type accumulations in recent seas are formed in the high-energy hydrodynamic zone (Zakharov, 1966a, p. 47). Substantially less abundant *Taimyroconus* and *Nixipileolus* representatives found in coquinas dwelt in hydrodynamically similar, although calmer, conditions of a sea bay in the northern Taimyr Peninsula (Zakharov, 1966a, p. 139; 1995, p. 90). The genera *Nixipileolus*, *Boreioco-nus*, and *Taimyroconus* populated approximately at the same time (middle Volgian) coastal biotopes of the Yenisei–Khatanga seaway in the northern (central Taimyr) part of the peninsula in the Dyabaka-Tari River basin, the left tributary of the Verkhnyaya Taimyr River. This area was likely dominated by relatively soft sediments populated by diverse large

bivalve forms (Pectinidae, *Ostrea*, *Isognomon*, *Oxitoma*, and others), which served as a substrate for cap-shaped gastropods (Fig. 4).

For interpreting habitat conditions of cap-shaped gastropods during the Early Cretaceous, it is reasonable to use the results of interdisciplinary facies investigations in the Valanginian–basal Hauterivian section in the Boyarka and Bol'shaya Romanikha river basins (Fig. 3a). This interval of the Boyarka River section composed mostly of sands with subordinate silt beds and thin coal seams is subdivided into 54 members attributed to nine elementary facies united into four complexes: lagoonal, lagoonal–marine, shallow marine to moderately deep, and internal relatively deep facies of the basin (Zakharov and Yudovnyi, 1974). Almost all finds of cap-shaped gastropods appeared to be confined to elementary facies of three types: lagoonal–marine facies of submarine sandy swells (*Taimyroconus*, *Nixipileolus*), sandy (*Boreioco-nus*, *Taimyroconus*) and muddy (*Nixipileolus*, *Boreioco-nus*, *Taimyroconus*) facies of marine shoals. Only a single specimen of the *Nixipileolus* form is found in the muddy facies of open lagoons (Fig. 3b).

These observations over the habitat depths of cap-shaped gastropods are of great significance. At the same time, this parameter may be estimated only qualitatively and by itself cannot be considered as decisive for benthos dispersion. Nevertheless, the depth controls to a significant extent main parameters of the medium: temperature, salinity, hydrodynamics, and, consequently, substrate type, pH, illumination, and, indirectly, quality and quantity of nutrients. The paleoecological analysis of marine Late Jurassic and Early Cretaceous invertebrates allowed an assumption of relatively high water temperatures in the Khatanga seaway close to subtropical values (Saks and Nal'nyaeva, 1964; Zakharov, 1966a). The subsequent study of stable oxygen isotopes revealed that average annual water temperatures in the Khatanga seaway were as high as 13–18°C (Zakharov, 1994; Žák et al., 2011; Dzyuba et al., 2013; Zakharov et al., 2014). Very high generic and species diversity of stenohaline mollusks (cephalopods, bivalves, gastropods), brachiopods, benthic and planktonic microzoofossils (foraminifers, radiolarian), and microphytobenthos (dinoflagellates) in the upper Oxfordian–Valanginian interval implies dominant normal salinity in the basin. The quantitative assessment of salinity by the Rucker–Valentine method yielded values ranging from 30 to 36‰ in the Early Cretaceous Khatanga sea (Zakharov and Radostev, 1975).

ETHOLOGY OF CAP-SHAPED GASTROPODS

The ethology of Late Jurassic–Early Cretaceous cap-shaped gastropods is derived from comparison with recent representatives of the same families and taphonomic observations along geological sections. The feature in common for all the described genera is the mode of their attachment to the solid substrate:

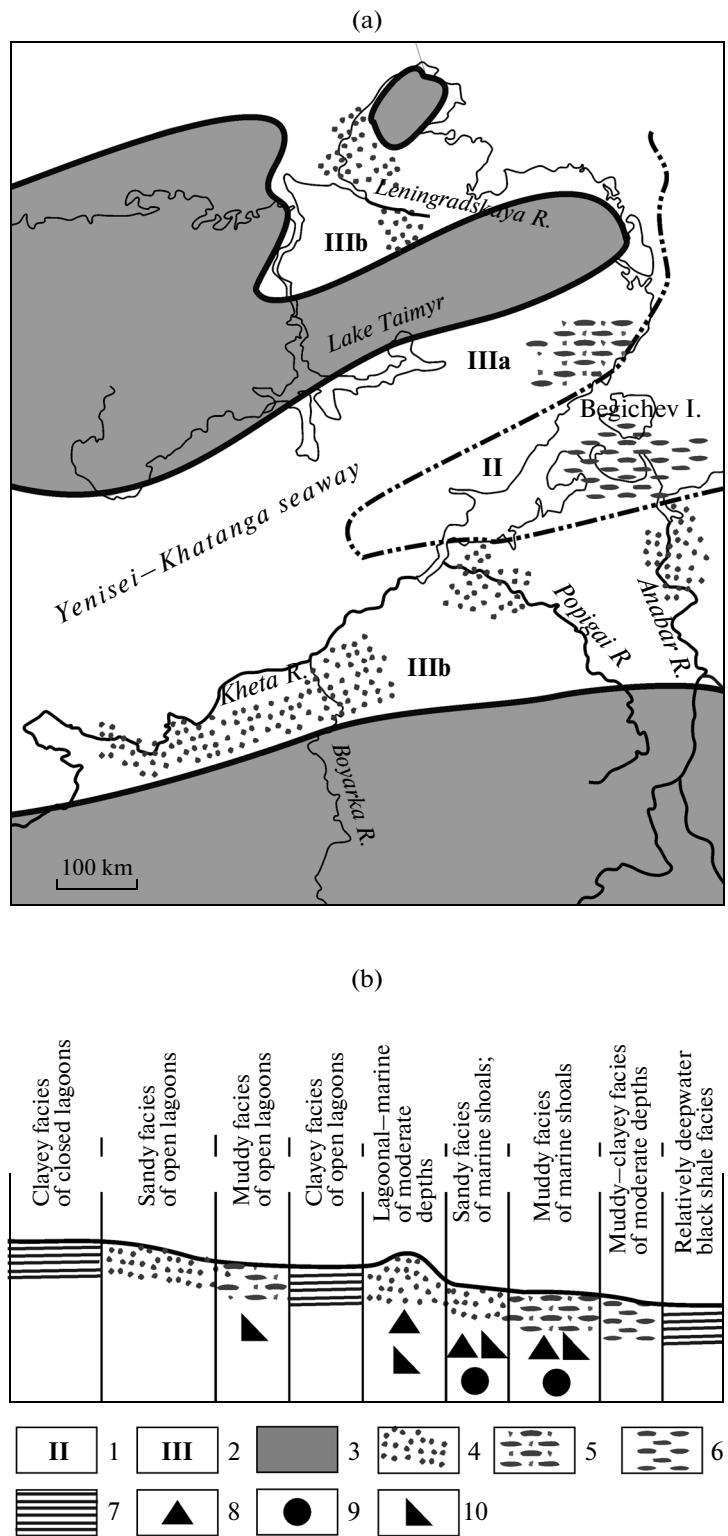


Fig. 3. (a) Schematic lithological–paleogeographic map of the Yenisei–Khatanga seaway in the early Valanginian time (Neotollia klimovskiensis phase) (Zakharov and Yudovnyi, 1974, fig. 12 modified); (b) generalized model of the bathymetric profile across facies zones of the Late Jurassic–Early Cretaceous Khatanga sea; the model shows the confinement of cap-shaped gastropods to particular facies. (1) Middle sublittoral settings; (2) upper sublittoral settings away from the shore (a) and close to the shore (b); (3) land; (4) sand; (5) sandy silt; (6) silt; (7) clay; (8) genus *Taimyroconus*; (9) genus *Boreoconus*; (10) genus *Nixipileolus*.

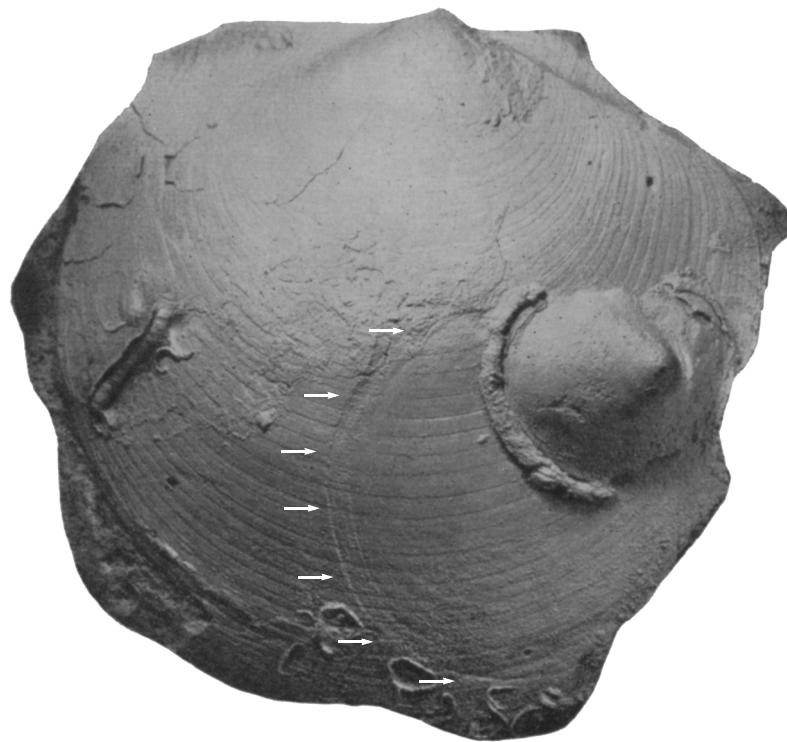


Fig. 4. Young *Boreioconus* on the shell of *Camptonectes (Maclearnia) imperialis* (Keyserling) (Zakharov, 1966b, plate 6, fig. 2), Boyarka River, Outcrop 13; lower Valanginian, Neotollia klimovskiensis Zone. Natural size. The shell surface exhibits distinct boundary of the gastropod grazing area (arrows).

like their recent analogs, they adhered to the substrate by podium.

The *Taimyroconus* ethology may be reconstructed by analogy with recent *Crepidula* representatives characterized by the same shell habit. This genus is accepted as being the ancestral taxon or the *Crepidula fornicate* group (Linnaeus, 1758) and the *Taimyroconus* ecology is interpreted using the data on ecology of present-day *Crepidula* forms (Fretter and Graham, 1962). It may be assumed that the *Taimyroconus* forms were most likely sestonophagous organisms. The significant size range of fossil shells implies their habitat in the form of groups on hard substrates (for example, on shell valves). Unfortunately, no *Taimyroconus* specimens are found in their intravital position.

As for the *Nixipileolus* and *Boreioconus* genera, the holotypes of both identified species were found attached to *Camptonectes (Maclearnia) imperialis* shells (Figs. 4, 5; Plate II, figs. 3b, 6a–6d). The following ethological properties are possible for these organisms: they were either sessile forms, which adhered to the surface of the pectinid valve and filtered suspended particulate matter, or scrapers of microalgae, bacteria, and other food material from the surface of different objects, including bivalve shells. For feeding, they most likely had to move between shells of pectinids, which densely populated the bottom surface (Zakharov, 1966a, figs. 10, 22). It is conceivable that after their “pasturing” the organisms returned to their previous place,

similar to recent *Patella* Linnaeus, 1758 representatives (Fretter and Graham, 1962, p. 498). At the same time, the third ethological mode is possible for *Nixipileolus* forms: commensalism on *Maclearnia* specimens. This mode is even most probable as compared with traveling in search of food. The present-day *Capulus ungaricus* (Linnaeus, 1758) is frequently attached to bivalve shells (*Pecten*, *Chlamys*, *Monia*, etc.). Using its long beak, this organism may capture food particles from their mantle cavity (Fretter and Graham, 1962, p. 506). In such a situation, *Capulus* specimens remain at the same place for a long time to leave a dissolved concentric scar. Two *Nixipileolus* specimens are found in their intravital positions on *Maclearnia* shells with eroded concentric scars beneath them (Fig. 5). It should be noted that these *Nixipileolus* specimens originate from lower Valanginian fine-grained sands (Boyarka River), where they occur together with many other invertebrate fossils buried in their intravital positions such as bivalves, brachiopods, bryozoans, worms, and foraminifers, which were commensal organisms like *Nixipileolus* forms (Zakharov, 1966b, plates 1–6).

Biogeographic significance of cap-shaped gastropods. The Upper Jurassic and Lower Cretaceous sections with finds of cap-shaped gastropods are located in the Kheta River basin of the Taimyr Peninsula. In the Kimmeridgian, Volgian, Boreal Berriasian (Ryazanian), Valanginian, and early Hauterivian ages, this region was an element of the North Siberian Province

of the Arctic paleozoogeographic region (Saks et al., 1971). The peculiar features of the taxonomic composition (mainly endemism) of invertebrates at the species level among ammonites (Mesezhnikov, 1984; Shul'gina, 1967), belemnites (Saks and Nal'nyaeva, 1964, 1966), several supraspecies taxa among bivalves (Zakharov, 1966a, 1970), and brachiopod family Boreiothyridae (Dagis, 1968) served as a basis for ranking the Arctic biochorema as a paleobiogeographic region at the initial stage of investigations (in the 1960s). Only later were endemic species and genera discovered and described among the above-mentioned groups and gastropods (Beizel, 1983), radiolarians (Bragin, 2009), and dinoflagellates (Nikitenko et al., 2008). The degree of domination of some groups, particularly among cephalopods, which never dominated in the Boreal-Atlantic and Boreal-Pacific paleobiogeographic realms, were taken into consideration as well.

Peculiar cap-shaped gastropods with the median septa described in this work, which were first (in the 1960s) conditionally attributed to the family Calyptraeidae (Saks et al., 1971, p. 194) and known only from the Soviet Arctic region, were considered as being endemic molluscan taxa of the Arctic biogeographic region. Our investigations show that the previous assumption of endemism of cap-shaped gastropods appeared to be to a significant extent valid and this group provides additional evidence for the high biogeographic rank of the Late Jurassic and Early Cretaceous Arctic biotas.

MORPHOLOGY OF CAP-SHAPED GASTROPOD SHELLS

The evolution of gastropods was accompanied by the appearance of forms with cap-shaped shells in their different groups. Their ancestral forms differed from each other in anatomy and shell appearance; therefore, the cap-shaped patterns of shells and their development were also different. This process resulted in different structure of shells in different cap-shaped gastropods.

Before going to interpretation of morphological features in fossils in question, let us briefly review the morphology of recent gastropods with cap-shaped or alike shells. Inasmuch as specimens from our collection demonstrate no features indicating forams and notches, such gastropods were omitted from this consideration. Most descriptions were provided by A.V. Guzhov when he studied shell collections stored at the Zoological Museum of Moscow State University and Zoological Institute of the Russian Academy of Sciences.

Cyclobranchia (Figs. 6a–6c). In Lotiidae, Acmaeidae, Nacellidae, and Patellidae representatives, the shell is shaped as a rounded to elongated cap covered by radial ornamentation or, less commonly, growth lines. The umbo is displaced to a variable extent to the anterior edge of the shell, being inclined

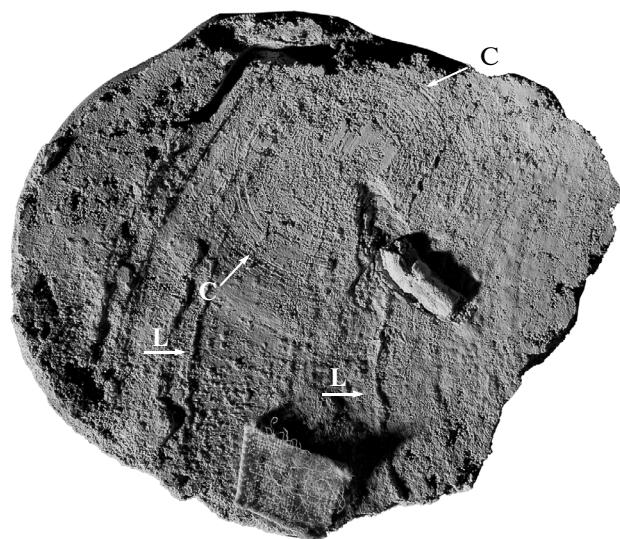


Fig. 5. The structure of the *Camptonectes (McLearnia) breviauris* valve beneath *Nixipileolus* sp. 1 aff. *depressus* sp. nov. (PIN, specimen 5524/17 (57 mm wide), Dyabaka-Tari River, Outcrop 8, Bed 1; middle Volgian Substage, Dorsoplaniates ilovaiskii Zone). Concentric circles (C) are traces of erosion on gastropod shell; arcuate lines (L) are growth lines on the shell.

anteriorly in some specimens. The spirally coiled stage is missing. On the inside, the shell is regularly conical with the ring-shaped impression in the middle of the shell height and parallel to its anterior edge. It consists of the posterior wide horseshoe-shaped impression, which comprises approximately 80% of the shell circumference and widens at the anterior ends, and the narrow pallial arcuate anterior impression, which passes between ends of the posterior impression. In large specimens, the posterior impression may be divided into several segments formed by separate bunches of the muscular complex. For example, in *Cellana testudinaria* (Linnaeus), it consists of the posterior twin segment (formed by two partly separated muscular bunches) and 12 lateral segments with the posterior penultimate one also being germinate.

Pectinibranchia

Capuloidea. Capulidae (Fig. 6d–6f). In *Capulus* Montfort, 1810, the shell is close to conical in shape with the umbo strongly inclined posteriorly and slightly sideways. The shell surface is covered by growth lines or ornamentation diverging in a fan manner from the umbo. The short plate, which is formed on the inside beneath the umbo, becomes reduced during development of the cap to a small ridge (for example, from *Capulus ungaricus* (Linnaeus) to *C. danieli* (Crosse)). The horseshoe-shaped muscular scar covers approximately 70% of the shell circumference. It is more or less well developed and passes parallel to the lower edge of the shell. The posterior, nar-

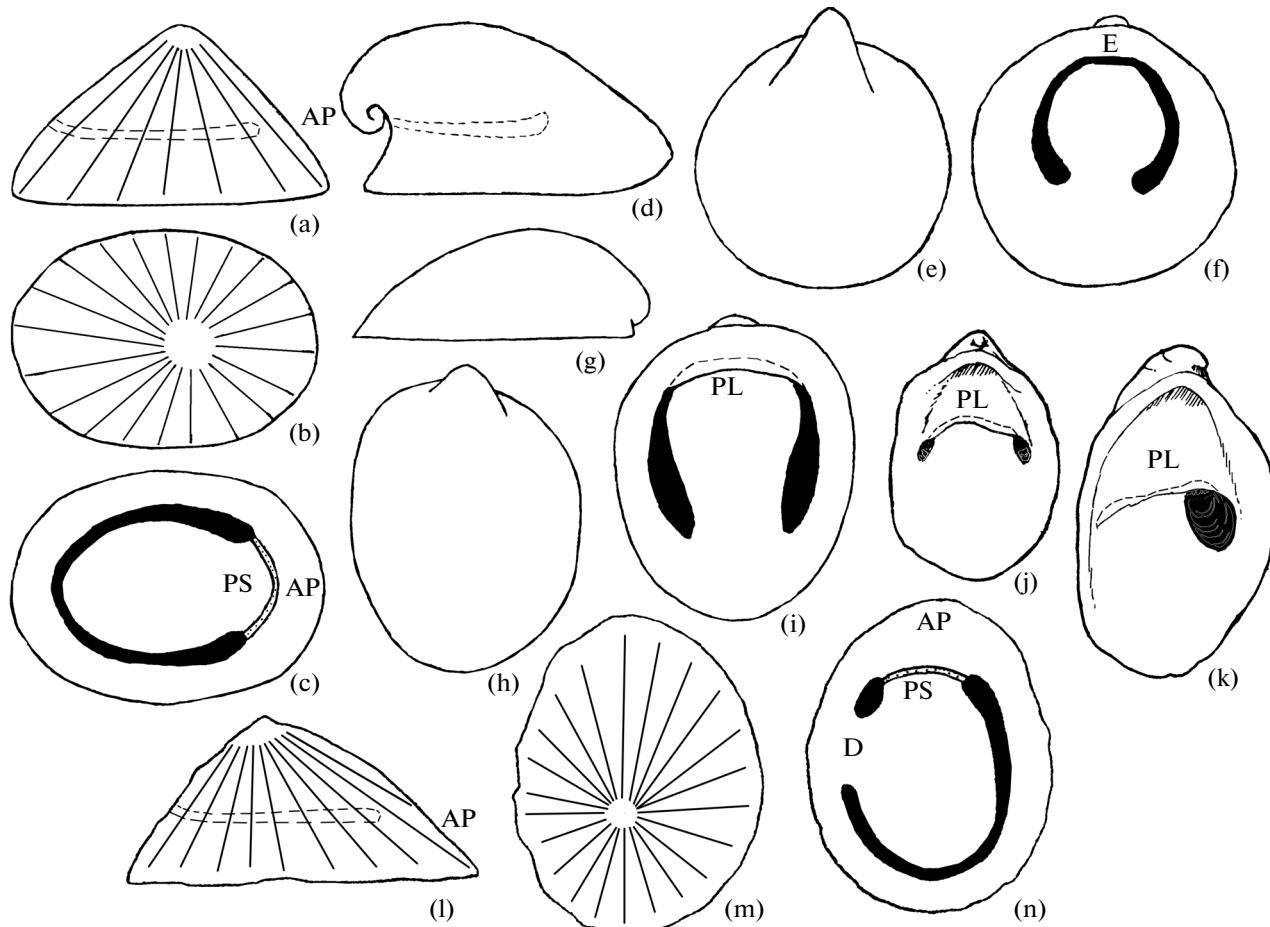


Fig. 6. Muscular scars on shells of recent and fossil gastropods. (a–c) *Acmaea*; (d–f) *Septaria*; (g, h) *Capulus*; (i, j) *Crepidula* (Hoagland, 1977, fig. 2, modified; (l–n) *Siphonaria*. (E) elevation; (D) diastema; (PL) plate; (AP) anterior part of the shell; (PS) pallial scar. Observable areas of muscular scars are shown in black; hidden areas are contoured by dashed line.

lower part of the scar with thickened ends is located on the upper side of the plate. A similar structure is characteristic of representatives of the genus *Trichamantina*, the shells of which demonstrate a large spire coiled posteriorly and slightly sideways. On the inside, the posterior part of the shell bears a flattened area. The muscular scar is horseshoe-shaped, but poorly expressed.

Velutoinioidea. Velutinidae. In *Piliscus commodus* (Middendorff), the shell is thin-walled, covered by growth lines and eccentric folds, with the posteriorly inclined umbo coiled into a small spire. The last whorl is conical, lacking a small inside ridge on the spire side; the muscular scar is similar to that in *Capulus* representatives, although being almost invisible owing to its poor development.

Vanicoroidea. Hipponicidae. The genus *Hipponix* Defrance, 1819 representatives are usually characterized by conical shells with the straight umbo slightly going beyond the edge of the shell, so that some shells look like a short horn. Less commonly, the umbo is small, displaced, and bent backward, not projecting

beyond the shell edge. Ornamentation is represented by radial or concentric ribs or their combinations. *Sabia* Gray, 1841 is characterized by a rounded cap-shaped shell with low strongly displaced and posteriorly oriented umbo and radial ornamentation. Both of these genera exhibit a horseshoe-shaped muscular scar located on the posterior side of the shell and becoming thicker anteriorly. It occupies 70 and 60% of the whorl circumference in the *Hipponix* and *Sabia*, respectively.

Neritoidea. Neritidae (Figs. 6g–6j). The *Septaria* Férrussac, 1807 shell is elongated, cone-shaped, with an umbo located near the posterior edge. The umbo is coiled into a short sideways bent spire. The column is transformed into a more or less long plate. It is located near the lower edge of the shell, being characterized by an even or concave anterior edge. The shell wall in front of the plate exhibits thickened ends of the well-developed horseshoe-shaped muscular scar. The scar is parallel to the shell edge. In the Late Jurassic–Early Cretaceous Epoch, the community of cap-shaped neritoids included forms of the genus *Pileolus* G.B. Sowerby, 1823. Their shells represent small caps usually with

well-developed radial ornamentation. The umbo position varies from subcentral to strongly displaced in the posteriorly direction. The column represents a plate that passes near the apertural edge. It is parallel to the lower edge of the shell with a narrow arcuate foramen in front of the latter. The anterior edge of the plate is usually concave, smooth, or dentate.

Calyptroidea. Calyptreidae (Figs. 6j, 6k). In *Crepidula* Lamarck, 1979 representatives, the shell is variable in shape from earlike, coiled in the posterior and rightward directions into a short spire (*C. fornicate* (Linnaeus)), to almost flat triangle–oval (*C. monoxyla* (Lesson)). Ornamentation is represented by growth lines or threads diverging from the umbo along the shell, with spines in some specimens. The column is transformed into a long thin plate in the posterior part of the shell, extending approximately to the middle of its height. The plate may be as long as half of the shell, usually being concave and with an anterior edge of variable configuration. The muscular scar is either unobservable or only with visible ends, located on the right or both sides in the conjunction area of the anterior edge of the plate and wall of the shell (Hoagland, 1977).¹ The *Calyptrea* Lamarck, 1799 representatives are characterized by rounded conical shells covered by concentric growth lines (*C. chinensis* Linnaeus) or their shells retain spiral coiled shapes (*C. calyptraeformis* Lamarck). *Trochita trochiformis* (Born) is characterized by a shell similar to that of *C. calyptraeformis*, which is, however, covered by transverse ribs. The species with the maximally reduced spiral–conical structure of the shell retains a column in the form of a spirally coiled denticle; therefore, the upper half of internal casts of *Calyptrea* representatives demonstrates a spiral furrow, which is left after dissolution of the column. In *Crucibulum* Schumacher, 1817, the shell is shaped as a rounded or oval cone with the small umbo more or less displaced toward the posterior edge. The shell is covered by radial threads (in some specimens with spines) diverging from the umbo or, less commonly, eccentric growth lines. On the inside, the shell bears the column rudiment in the form of a vertical triangle or oval cone in the posterior part of the shell. The cone is elongated transverse to the shell and its walls join each other on the right side at an acute angle.

Peltospiroidea. Peltospiridae (after McLean, 1989). Shells are variable in shape from earlike with a reduced spire coiled backward to the right to elongated–conical with a reduced spire, or with curved and strongly backward displaced umbo. Ornamentation is repre-

sented by rows of small spines and blade-shaped ribs resulting from the periostracum formation. The column is reduced to a short plate or transverse ridge beneath the umbo. Some specimens bear a horseshoe-shaped muscular scar, which passes behind along the internal side near the plate edge. Inasmuch as orientation of the muscular scar is not emphasized, it may be assumed that it is elongated anteriorly parallel to the apertural edge as in other secondary cap-shaped Pectinibranchia representatives.

Divasibranchia

Siphonarioidea. Siphonariidae (Figs. 6l–6n). *Siphonaria* G.B. Sowerby, 1823 has a round to oval cap-shaped shell usually with a posteriorly displaced umbo and covered on the outside by more or less rough radial ornamentation. The shell edge is marked in the right posterior by radially oriented projection of the shell surface (frequently, the latter coincides with one of the ribs in roughly ornamented forms). On the inside, the projection corresponds to a radial notch. A sinus in the anterior part of the shell encompasses breath foramen, anus, and retractive muscular system (Cottrell, 1911). As in patellogastropods, the muscular scar consists of a horseshoe-shaped posterior segment thickened along edges and a narrower semicircular anterior segment; because of the above-mentioned arrangement patterns of organs in the mantle cavity, it is interrupted in the sinus area. *Williamia* Monterosato, 1884 is characterized by a higher cone and posteriorly overhanging umbo; its shell is covered only by growth lines and has no distinct radial curve in the right posterior part. The muscular scar is similar to that in *Siphonaria*, although its interruption zone is wider (Keen and Coan, 1974, p. 18).

Incetae sedis. Anisomyon Meek et Hayden, 1860 (Fig. 7). Sohl (1967), who investigated the external and internal shell morphology of *A. borealis* (Morton, 1842), *A. centrale* Meek, 1871, and *A. patelliformis* (Meek et Hayden, 1856) (type species of the genus), attributed this Cretaceous genus to siphonariids. At the same time, the arrangement of muscular scars and some peculiarities in the internal surface of a shell differ substantially from these features in recent Siphonariidae. The author illustrated the morphology of these species by drawings of muscular scars (Sohl, 1967, p. B37, fig. 10; this work, Figs. 7a–7c). The drawings are made using specimens illustrated in the same work: *A. borealis* (Sohl, 1967, pl. 8, figs. 9, 10, 12, 13, 15); *A. patelliformis* (Sohl, 1967, pl. 11, figs. 12, 13, 16); *A. centrale* (Sohl, 1967, pl. 10, figs. 7, 8, 10–12). The drawings proposed for *A. centrale* with the chaotic changes in the thickness and orientation give rise to doubts in their interpretation. The photographs offer the opportunity to trace changes of scars in the first two species. All shells exhibit the umbo distinctly displaced to the shell edge. All the species in drawings with the displaced umbo are characterized by the well-

¹ Owing to high diversity of muscular scars in *Crepidula* representatives, some authors propose to divide them into several genera. For example, Marshall (2003) proposes the following genera: *Crepidula* without muscular scars; *Maoricrypta* Finlay, 1926 with two scars; *Grandicrepidula* MaLean, 1995 with the right scar. This classification gives birth to questions because of gradual variability of muscular fields among *Crepidula* s. l. species. Invalidity of subdivision of the genus *Crepidula* is also emphasized in several publications (Hoagland, 1977; Bandel and Riedel, 1994).

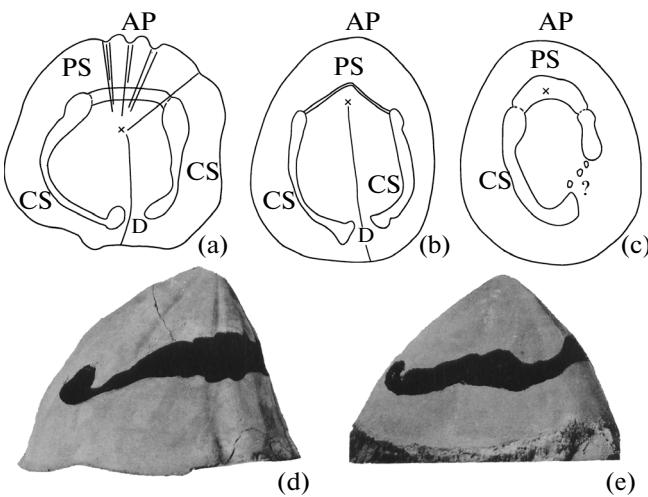


Fig. 7. Reconstruction of muscular scars for the genus *Anisomyon* (Sohl, 1967, modified). (a) *Anisomyon centrale* Meek, 1871; (b) *Anisomyon borealis* Morton, 1842; (c) *Anisomyon patelliformis* Meek et Hayden, 1856; (d, e) drawing of the posterior scar on shells of *A. centrale*. (a–c) Taken from (Sohl, 1967, p. B39, fig. 10); (d, e) taken from (Sohl, 1967, pl. 10, figs 7, 13). (x) umbo; (D) diastema; (CS) columellar scar; (AP) anterior part of the shell; (PS) pallial scar.

developed anterior pallial impression, which is located on the side with the displaced umbo. Such a position is characteristic of patellogastropods, not siphonariids. The anterior scar in *A. borealis* and *A. patelliformis* is substantially wider as compared with that in recent patellogastropods and siphonariids. In *A. centrale*, the scar passes immediately near the apex of the internal shell surface, while in *A. patelliformis* it crosses (!) the latter, which is also unusual. In addition, the species are highly different in the internal morphology: *A. patelliformis* exhibits no radial ornamentation; *A. borealis* has several radial ridges extending to the end opposite to the umbo; *A. centrale* has radial furrows oriented in the opposite direction in addition to ridges. No radial elements similar to those in *A. centrale* and *A. borealis* are known either in patellogastropods or in siphonariids.

The review of Jurassic and Cretaceous cap-shaped gastropods demonstrates the extreme scarcity and incompleteness of the data. Four groups of cap-shaped gastropods may be defined in addition to more or less undoubted patellogastropods. The first group unites cap-shaped shells barren of muscular scars: *Berlieria* Loriol, 1903 (Late Jurassic), *Brunonia* G. Müller, 1898 (Late Cretaceous), *Gigantocapulus* Hayami et Kanie, 1980 (Late Cretaceous). Some of such shells demonstrate peculiar radial structures: *Rhytidopilus* Cossmann, 1895 (Late Jurassic), *Pseudorhytidopilus* Cox, 1960 (Jurassic). The second group includes species attributed to the genus *Anisomyion*. The third group is represented by species of the genus *Pileolus*. The morphological features of the last two genera are discussed above. The last group includes internal casts of shells, some of which bear muscular scars. They

may belong to any of the above-mentioned groups, since neither shells nor scar patterns are known. During their description, these forms were attributed to known recent and fossil genera, mostly to patellogastropods.

Thus, gastropod species with the shell close to the cap-shaped one bear the posterior muscular scar shaped as a horseshoe with widened anterior ends. Patellogastropoda and Siphonarioidea shells are characterized also by a narrow arcuate anterior (pallial) scar. At the same time, the posterior scar in Siphonarioidea representatives is shortened on the right side or has a diastema. Patelloidea, Lottoidea, and Siphonarioidea shells have no projections or plates except for the radial sinus in Lottoidea representatives. Other gastropods retain a rudimentary column in form of a plate or elevation located in the posterior part of the shell. The shell umbo is anteriorly and posteriorly displaced in patellogastropods and other groups, respectively; i.e., the ends of the posterior muscular scar are oriented toward the umbo in the first group and in the opposite direction in the others. From other Pectinibranchia representatives, Neritoidea differ in the position of the plate close to the apertural edge of the shell.

INTERPRETATION OF FOSSIL MATERIAL

Shells attributed to the new genus *Taimyroconus* are characterized by a well-developed spire coiled posteriorly and displaced to the right. It projects beyond the posterior edge of the shell. The shell surface is covered by eccentric growth lines. The last whorl is cone-shaped with its internal space crossed in the posterior part by a downward inclined plate. Some most complete casts demonstrate that the plate projects for approximately 40% of the shell length. The casts bear traces of the muscular scar. They are represented by widened ends of the scar located on the wall of the shell above the plate. The scar terminates close to the junction of the plate with the wall of the shell and its ends extend forward and slightly upward. It seems that the muscular scar crossed strictly transverse to the plate as in all the above-mentioned recent gastropods with a similar shell. At the same time, in contrast to them, the muscular scar in the genus under consideration is located away from the plate edge and, thus, is completely hidden under the plate.

Externally, the *Taimyroconus* shells resemble recent *Crepidula* (group 1, after Holland, 1977; for example, *C. fornicata* Linnaeus, 1758). In our opinion, the similarity of fossil remains to recent *Crepidula* representatives is determined by their close ecology and ethology. Differences in the patterns and position of the muscular scar indicate the convergence of their external similarity. In *Crepidula* s. s., the muscular system was attached to the upper side of the plate along its anterior edge (with the larger and smaller bunches being attached to its right and left sides, respectively). With development of the muscular system, the muscular

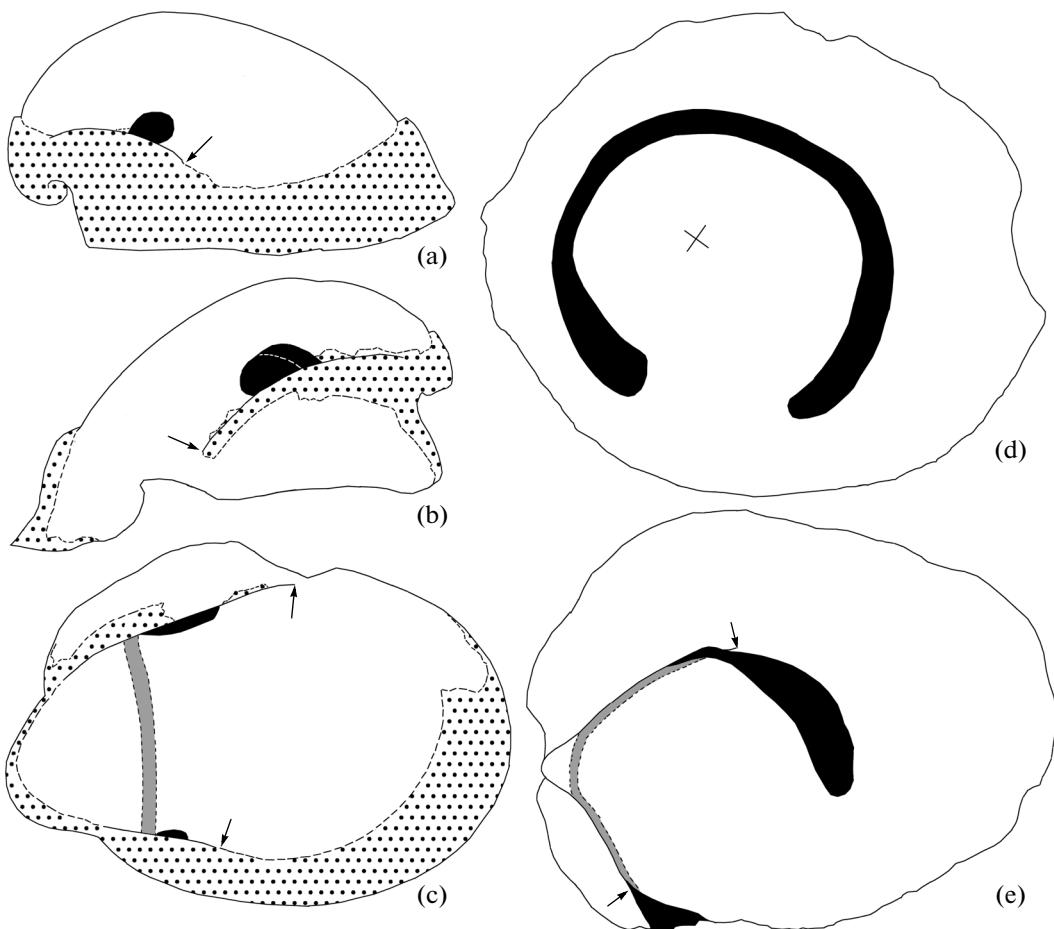


Fig. 8. Muscular scars of cap-shaped gastropods. (a–c) *Taimyroconus zakharovi* sp. nov., PIN, holotype specimen 5524/2: (a) right lateral view; (b) left lateral view; (c) view from above; (d) *Boreoconus bojarkensis* sp. nov., PIN, holotype specimen 5524/1; (e) *Nixipileolus depressus* sp. nov., PIN, holotype specimen 5524/3. (×) umbo; (solid line) contours of the specimen and slits left by dissolved plates visible on the internal cast; (black dashed line) contours of preserved shell; (speck fill) shell remains; (without fill) surface of the internal casts; (black fill) visible contours of muscular scars; (gray fill contoured by dashed line) assumed hidden areas of muscular scars; (white dashed line) boundary between scars of particular muscular bunches; (arrows) observable anterior boundaries of plates.

scar extended along the whole edge of the plate and then to the wall of the shell in front of the right end of the plate and, subsequently, in front of its left end. In *Taimyroconus*, the muscular scar is developed in accordance with the last variant, although the attachment area is displaced posteriorly (Figs. 8a–8c). Such a position of the plate is likely explained by its downward incline, while in *Crepidula* the plate is subparallel to the lower edge of the shell.

In the family Calyptraeidae, the cap-shaped aspect of the shell is likely determined by two modes of reduction of spiral coiling of the shell: (1) without changes of the coiling axis and (2) with the displacement of its incline relative to the horizontal plane. Owing to these peculiarities, the spire and inner wall of the whorl (column) are reduced in different ways. In shells developing in accordance with the first reduction mode, the umbo retains its subcentral position and the column becomes reduced up to a triangular

vertical cone (*Crucibulum*) or curved denticle (*Calyptraea*). In shells with the second reduction mode, the spire is displaced backward and the column is turned into a curved plate (*Crepidula*). Hoagland (1977) considers *Trochita* Schumacher, 1817, which has a spirally coiled column, as being the parental genus. In his opinion, this genus gave birth to *Calyptraea* with the column variable in shape from spirally coiled to denticle-shaped. *Crucibulum* and *Crepidula* are considered as its descendants that realized different modes of the transition to cap-shaped shells.

There are two versions of the *Taimyroconus* taxonomic position. According to the first one, *Taimyroconus* represents a final form that originated from an unknown Jurassic ancestor and yielded no descendants, although because of the similar mode of life it acquired a shell convergent with that of *Crepidula*. According to the second version, *Taimyroconus* could be a taxon which gave birth to Cenozoic *Crepidula*. In

such a situation, the assumption of *Crepidula* origin from *Calyptrea* is invalid, and calyptreids should be divided in two groups independently evolving for a long time. In the *Description* section, *Taimyroconus* is attributed to the family Calypraeidae.

Several specimens attributed to the new genus *Nixipileolus* are the most similar to *Taimyroconus* representatives. Unfortunately, our collections include no preserved shells of this genus, although their internal casts bear distinct traces of muscular scars and fissure left by the platy column. In contrast to *Taimyroconus*, the spire of *Nixipileolus* shells is strongly reduced; therefore, the umbo of the shell occupies the central position, being significantly displaced toward the posterior edge. The plate is less distinct and less inclined; therefore, the muscular scar is displaced forward. Its posterior part occupied the upper side of the plate along its anterior edge, while anterior ends are located on the wall of the shell next to the plate (Fig. 8e). The scar exhibits strong asymmetry between the crescent long narrow left and short wide right ends. The phylogenetic lineage in the genus *Nixipileolus* from the middle Volgian to early Hauterivian demonstrates a tendency for spire reduction, which results in shortening of the septa, decrease in its incline, and decrease in size and degree of the umbo development. By its features, *Nixipileolus* resembles none of the known genera: it may only be assumed that available fossils represent Pectinibranchia incertae sedis remains. The high position of the plate relative to the lower edge of the shell provides grounds for excluding relations between *Nixipileolus* and Neritidae representatives.

Other specimens are represented by circular caps with the central or slightly backward displaced apex covered by eccentric growth lines. The internal casts bear traces of strong muscular scars, which encompass 80% of the cone circumference (Fig. 8d). The muscular scar in the posterior part of the cap is narrower and crosses a more or less distinct depression; the posterior ends of the scar are widened and rounded. The scar is located in the middle of the cap height or slightly above. The observable features correspond ideally to their counterparts in Pectinibranchia taxa with the secondarily cap-shaped shell. Unfortunately, it is impossible to attribute these specimens to any known family/suprafamily. The presence of similar cap-shaped forms in different families of recent and Cenozoic gastropods implies that such a morphotype was repeatedly formed in phylogenetically distant groups. Unfortunately, no recent or fossil genera with such shells are known to us from the literature. Therefore, in this work, they are attributed to the new genus *Boreioconus*.

The last small group is represented by low-conical shells. The umbo is small, displaced, and bent backward. On the inside, short distinct elevation is developed under the umbo. The muscular scar is horse-shoe-shaped, mostly hidden under remains of the shelly layer. It is conceivable, that these remains belong to an additional gastropod genus, although

fragmentary material hampers the adequate description of the new taxon. In the *Description* section, it is presented as "*Boreioconus*" sp. nov.

PALEONTOLOGICAL DESCRIPTION

CLASS GASTROPODA

SUBCLASS PECTINIBRANCHIA BLAINVILLE, 1814

Genus Boreioconus Guzhov, gen. nov.

Name of the genus: from βόρειος (Greek)—north; and κώνος (Greek)—cone. Male.

Type species: *Boreioconus bojarkensis* sp. nov.; Lower Cretaceous, Valanginian; Russia, northeastern Siberia.

D i a g n o s i s. Shell large, cap-shaped, moderately thick, with umbo position changing from subcentral to posteriorly displaced. Spire reduced. The area under the umbo on the inside of the shell is occupied by transverse elevation, which served for attaching the retractive muscular system. Ornamentation represented by vague eccentric wrinkles, which are nevertheless seen on the inner surface of the shell. Muscular scar well developed, horseshoe-shaped. It passes slightly above the middle of the shell height, being oriented parallel to the apertural edge, and encompasses approximately three-fourths of the cap circumference.

C o m p o s i t i o n. Type species.

Boreioconus bojarkensis Guzhov, sp. nov.

Plate I, figs. 1–3.

Name orign: after the Boyarka River.

Holotype: PIN RAS, specimen 5524/1 (Plate I, fig. 1; Fig. 8d); Russia, northern East Siberia, Boyarka River (a right tributary of the Kheta River), Outcrop 4; Lower Cretaceous, Valanginian.

D e s c r i p t i o n. Shell large, up to 7–8 cm long, conical, with the subcentral umbo. Spire unobservable. The angle of the cap cone is approximately 100°–110°. Surface of the shell is covered by eccentric smoothed wrinkles and growth lines. Muscular scar horseshoe-shaped, distinct, occupies 80% of the shell diameter, and passes slightly above the middle of the shell height. Behind the apex, it is located on the vague transverse elevation. Owing to the dextral coiling mode, the right side of the scar, particularly its posterior part, is lower as compared with its left half. Elevation is also more distinct on the right side.

D i s t r i b u t i o n. Lower Cretaceous, Valanginian; Russia, northeastern Siberia.

M a t e r i a l. Lower Cretaceous, Valanginian, Neotollia klimovskiensis Zone: Boyarka River, Outcrop 14, Bed 4 (single specimen, internal cast); Propolypychites quadrifidus Zone: Bol'shaya Romanikhha River, Outcrop 129 (single specimen, internal cast), Outcrop 133 (two specimens, shell and internal cast); Sibirites ramulicosta Zone: Boyarka River, Out-

crop 4, Bed 4 (single specimen, shell fragment); Outcrop 6, Bed 7 (single specimen, internal cast); lower Valanginian: Boyarka River, Outcrop 4 (talus), Outcrop 6, Bed 7 (single specimen, internal cast); lower Valanginian: Boyarka River, Outcrop 5, Beds 8 and 9 (single specimen, internal cast); Valanginian: Boyarka River, Outcrop 4 (talus) (single specimen, internal cast with shell fragments), Outcrop 7 (talus) (single specimen, internal cast).

"Boreoconus" sp. nov.

Plate I, fig. 4

Description. Shell approximately 4.5 cm long, low conical, with the umbo located in one-third of the shell length from its posterior edge, bent backward in the internal cast. Its shape shows that the shell had a reduced backward coiled spire. On the inner side, area beneath the umbo is occupied by high elevation, which served as a substrate for attachment of the muscular system. In available specimens, scars are almost entirely hidden under remains of the shell layer. Visible areas of the internal cast are smooth; ornamentation is unknown.

Remarks. This form differs from *Boreoconus bojarkensis* in the backward bent and displaced umbo, lower wide-angle cone. In adult specimens of *Boreoconus bojarkensis*, umbo is not bent backward, although the area behind the umbo on the inner side may be marked by small elevation. From *Nixipileolus*, the species in question differs in a small backward bent umbo located far from the posterior edge of the shell. This form is close to representatives of the genus *Boreoconus* differing from the latter in several features; therefore, it is conditionally attributed to this genus.

Material. Upper Jurassic, middle Volgian Substage, Dorsoplaniites ilovaiskii Zone, Dyabaka-Tari River, Outcrop 1, Bed 1 (two internal casts).

Genus *Nixipileolus* Guzhov, gen. nov.

Name origin: from nix (Latin)—snow; and pileolus (Latin)—small circular cap. Male.

Type species. *N. depressus* sp. nov.; Lower Cretaceous, Valanginian; Russia, northeastern Siberia.

Diagnosis. Shell large, cupuliform to low elongated-conical, with umbo located near the posterior edge and projecting beyond the latter. Spire varies from well developed to highly reduced. On the inside, the area under the umbo is occupied by plate or high elevation. Ornamentation consists of vague eccentric wrinkles. The muscular scar is well developed, horse-shoe-shaped, oriented parallel to the apertural edge. It occupies three-fourths of the cap circumference with the posterior part located along the plate edge or on elevation.

Composition. Type species.

Comparison. From *Boreoconus*, the genus under consideration differs in the presence of spire,

the umbo displaced toward the posterior edge of the shell or protruding beyond the latter, and column in form of plate.

***Nixipileolus depressus* Guzhov, sp. nov.**

Plate I, fig. 6

Name origin: from *depressus* (Latin)—low.

Holotype: PIN RAS, specimen 5524/3 (Plate I, fig. 6; Fig. 8d); Russia, northeastern Siberia, Boyarka River (a right tributary of the Kheta River), originates from talus of Outcrop 12; Lower Cretaceous, lower Valanginian, Neotollia klimovskiensis Zone.

Description. Shell low, elongated-conical, from 5 to, presumably, 10 cm long. Surface of the internal cast covered by vague eccentric wrinkles. Spire dextral, reduced, looks like a beak-shaped downward-bent umbo on the cast. The spire slightly projected beyond the posterior edge of the shell. Plate-shaped column occupies approximately one-fourth of the shell length and is subparallel to the lower edge of the shell. Muscular scar large, horseshoe-shaped, encompasses approximately 70% of the shell circumference. It extends to the wall of the shell near conjunction of the plate with the shell wall. The left end of the muscular scar is long, narrow, arcuate, while the right one is very wide, short.

Comparison. From middle Volgian representatives, this species differs in less developed spire and, correspondingly, shorter plate, lower profile of the shell, and umbo not extending beyond the shell edge. Plate subparallel to the apertural edge is less inclined than in *N. sp. 1 aff. depressus*. From Hauterivian *N. sp. 2 aff. depressus*, the species under consideration differs in less reduced spire, more developed septa, and higher shell profile.

Material. Lower Cretaceous, lower Valanginian, Neotollia ramulicosta Zone, Boyarka River, Outcrop 9 (talus, single specimen), Outcrop 12 (talus, one specimen); Siberites ramulicosta Zone, Boyarka River, Outcrop 4, Bed 3b (one specimen).

***Nixipileolus* sp. 1 aff. *depressus* Guzhov, sp. nov.**

Plate II, fig. 1.

Description. Shell cupuliform, elongated in the width (specimen 5524/5 4.5 cm wide and 4.0 cm long; specimen 5524/17 5.0 cm long and 5.8 cm wide). External layers of the shell are destroyed. The surface of the internal cast covered by vague eccentric wrinkles. Umbo strongly displaced toward the posterior end of the shell, overhanging the latter. Plate short, bent downward (gentler on the left and steeper on the right), extends for one-fourth of the shell length. Muscular scar extends to the shell wall behind its junction with the plate. The left end of the muscular scar is extremely wide and well developed; right end is destroyed.

C o m p a r i s o n. *N. sp. 1 aff. depressus* is probably the ancestral form of lower Valanginian *N. depressus* forms differing from them in greater incline of the plate and wider shell. From *N. sp. 2 aff. depressus*, *N. sp. 1 aff. depressus* differs in wider shell, well-developed inclined plate, and spire projecting beyond the posterior edge of the shell.

M a t e r i a l. Upper Jurassic, middle Volgian Substage, Dorsoplanites ilovaiskii Zone, Dyabaka-Tari River, Outcrop 8, Bed 11 (one specimen, internal cast); Dorsoplanites maximum Zone, Dyabaka-Tari River, Outcrop 1, Beds 7, 8 (one specimen, shell).

***Nixipileolus* sp. 2 aff. *depressus* Guzhov, sp. nov.**

Plate I, fig. 5.

D e s c r i p t i o n. Single specimen with preserved shell except for the umbo and posterior slope. Shell elongated (4.3 cm long), with surface covered by eccentric growth lines and irregular small wrinkles. The umbo displaced toward the posterior edge of the shell, not reaching, however, the latter. Column is in the form of a very short plate. The area right of the umbo is occupied by a wide muscular scar developed near the conjunction between the anterior edge of the plate and wall of the shell.

C o m p a r i s o n. *N. sp. 2 aff. depressus* represents likely a descendant of lower Valanginian *N. depressus* forms differing from them in more reduced spire and plate.

M a t e r i a l. Lower Cretaceous, lower Hauterivian, Homolsomites bojarkensis Zone, Boyarka River, Outcrop 1, Bed 14 (one specimen).

S U P R A F A M I L Y CALYPTRAEOIDEA LAMARCK, 1809

FAMILY CALYPTRAEIDAE LAMARCK, 1809

Genus *Taimyroconus* Guzhov, gen. nov.

G e n u s n a m e: after the Taimyr Peninsula and κώνος (Greek)—cone. Male.

T y p e s p e c i e s. *T. zakharovi* sp. nov.; Upper Jurassic, upper Oxfordian–lower Kimmeridgian; Russia, northern East Siberia.

D i a g n o s i s. Shell *Crepidula*-shaped, with conical last whorl and small dextral-coiled spire located in

the posterior part of the shell. Shell is covered by eccentric growth lines. Plate-shaped column in the last whorl extends forward approximately to the middle of the last whorl cavity and is inclined toward the apertural edge. Muscular scar horseshoe-shaped with its posterior part crossing transverse to the upper side of the plate. End of the scar extends to the wall of the whorl above the plate. Left end of the scar is projected relative to its right end. The scar is entirely hidden under the plate.

C o m p o s i t i o n. Type species, *Crepidula gaultina* Buvignier, 1852 (Lower Cretaceous, Aptian–Albian), *Crepidula mniovnikensis* Gerasimov, 1992 (Upper Jurassic, middle Volgian Substage), *Crepidula janeti* Cossmann, 1897 (Upper Cretaceous, upper Senonian).

C o m p a r i s o n. From *Crepidula*, the species differs in the arrangement of the muscular scar and downward-inclined plate.

***Taimyroconus zakharovi* Guzhov, sp. nov.**

Plate II, figs. 2–6.

S p e c i e s n a m e: after V.A. Zakharov, a Russian paleontologist.

H o l o t y p e. PIN RAS, specimen 5524/2 (Plate II, fig. 2; Figs. 8a–8c); Russia, northern East Siberia, Boyarka River (right tributary of the Kheta River), originates from coquina of Outcrop 21; Upper Jurassic, upper Oxfordian–lower Kimmeridgian, Amoeboceras ravni Zone.

D e s c r i p t i o n. Shell *Crepidula*-shaped, from 2 to 4 cm long. Shell surface covered by eccentric growth lines. Plate extends forward to the middle of the whorl, simultaneously sloping to the shell aperture. The anterior part of the plate transversely wrinkled on both sides. Muscular scar horseshoe-shaped with its posterior part crossing transverse to the upper side of the plate in its middle. Widened ends of the scar located on the wall of the shell, above the plate. The right end shorter, being oriented at approximately 45° relative to the apertural plane of the last whorl. Muscular scar occupies approximately 60% of the circumference formed by plate and wall of the shell. Ends of the muscular scar never reach the anterior edge of the plate.

Plate I. Cap-shaped gastropods from the Lower Cretaceous sections at the Boyarka and Bol'shaya Romanika rivers (Kheta River basin) and middle Volgian Substage (Upper Jurassic) at the Dyabaka-Tari River (central Taimyr). Figs. 1–3. *Boreioconus bojarkensis* sp. nov.: (1) PIN, holotype 5524/1 (shell 71 mm long, 40 mm high), Boyarka River, talus of Outcrop 4, Lower Cretaceous, Valanginian: (1a) internal cast, view from above; (1b) internal cast with shell fragments, anterior view; (1c) the same, right lateral view; (2) PIN, specimen 5524/6 (shell 16 mm high and 38 mm long), Bol'shaya Romanika River, Outcrop 133, lower Valanginian, Propolyptychites quadrifidus Zone: (2a) view from above, (2b) lateral view; (3) PIN, specimen 5524/7 (shell 53 mm long), Kheta River, Outcrop 14, Bed 4, lower Valanginian, Neotollia klimovskiensis Zone: (3a) view from above, (3b) right lateral view. **Fig. 4.** “*Boreioconus*” sp. nov., PIN, specimen 5524/16 (shell 45 mm long and 17 mm high), Dyabaka-Tari River, Outcrop 1, Bed 1, middle Volgian Substage, Dorsoplanites ilovaiskii Zone: (4a) view from above, (4b) left lateral view, (4c) posterior view. **Fig. 5.** *Nixipileolus* sp. 2 aff. *depressus* sp. nov., PIN, specimen 5224/4 (shell 43 mm long), Boyarka River, Outcrop 1, Bed 14, lower Hauterivian, Homolsomites bojarkensis Zone: (5a) view from above, (5b) right lateral view, without sputtering. **Fig. 6.** *Nixipileolus depressus* sp. nov., PIN, holotype specimen 5224/3 (shell 51 mm long and 40 mm wide), Boyarka River, Outcrop 12, lower Valanginian, Neotollia klimovskiensis: (6a) view from above, (6b) posterior view, (6c) left lateral view, (6) right lateral view, without sputtering.

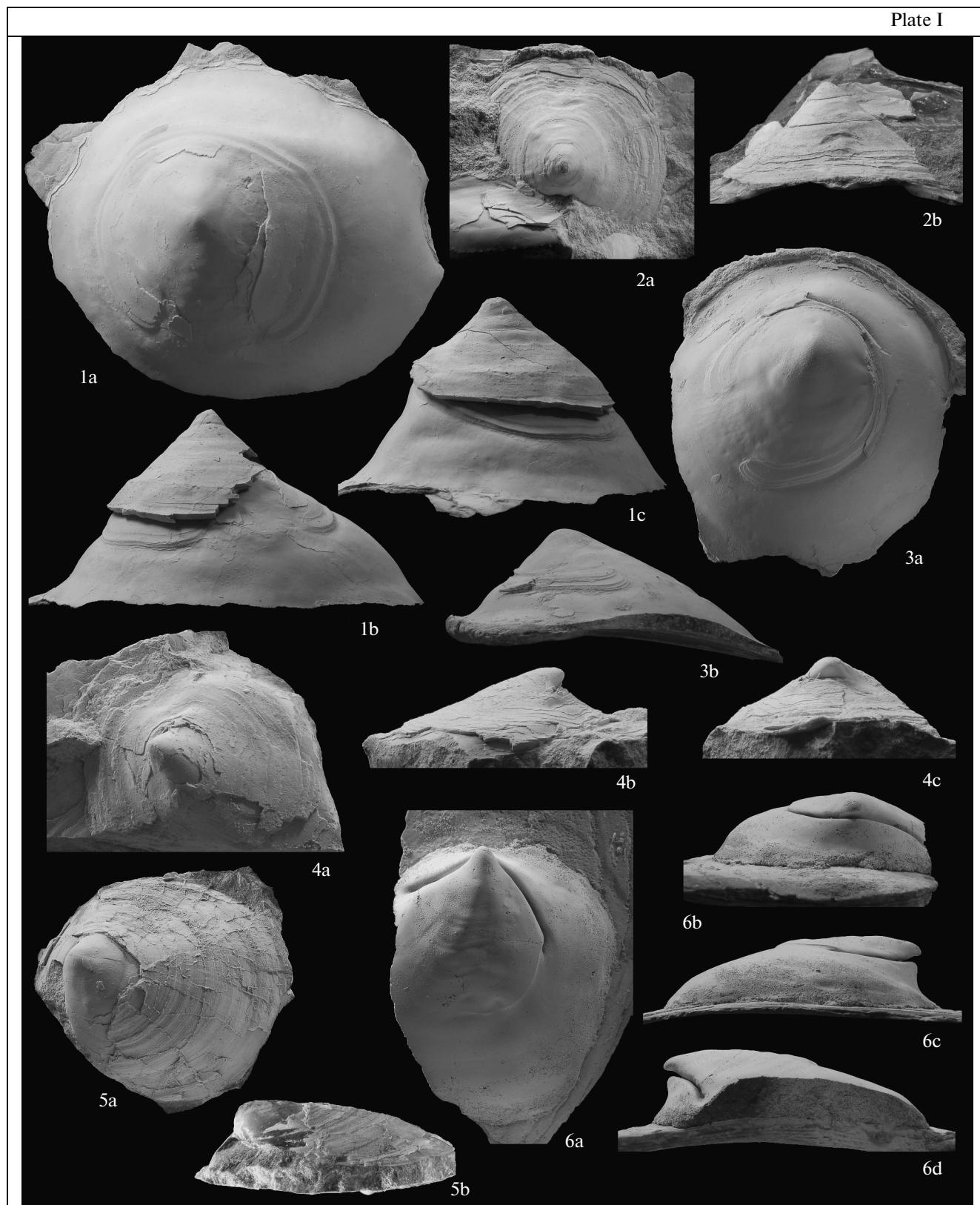


Plate II

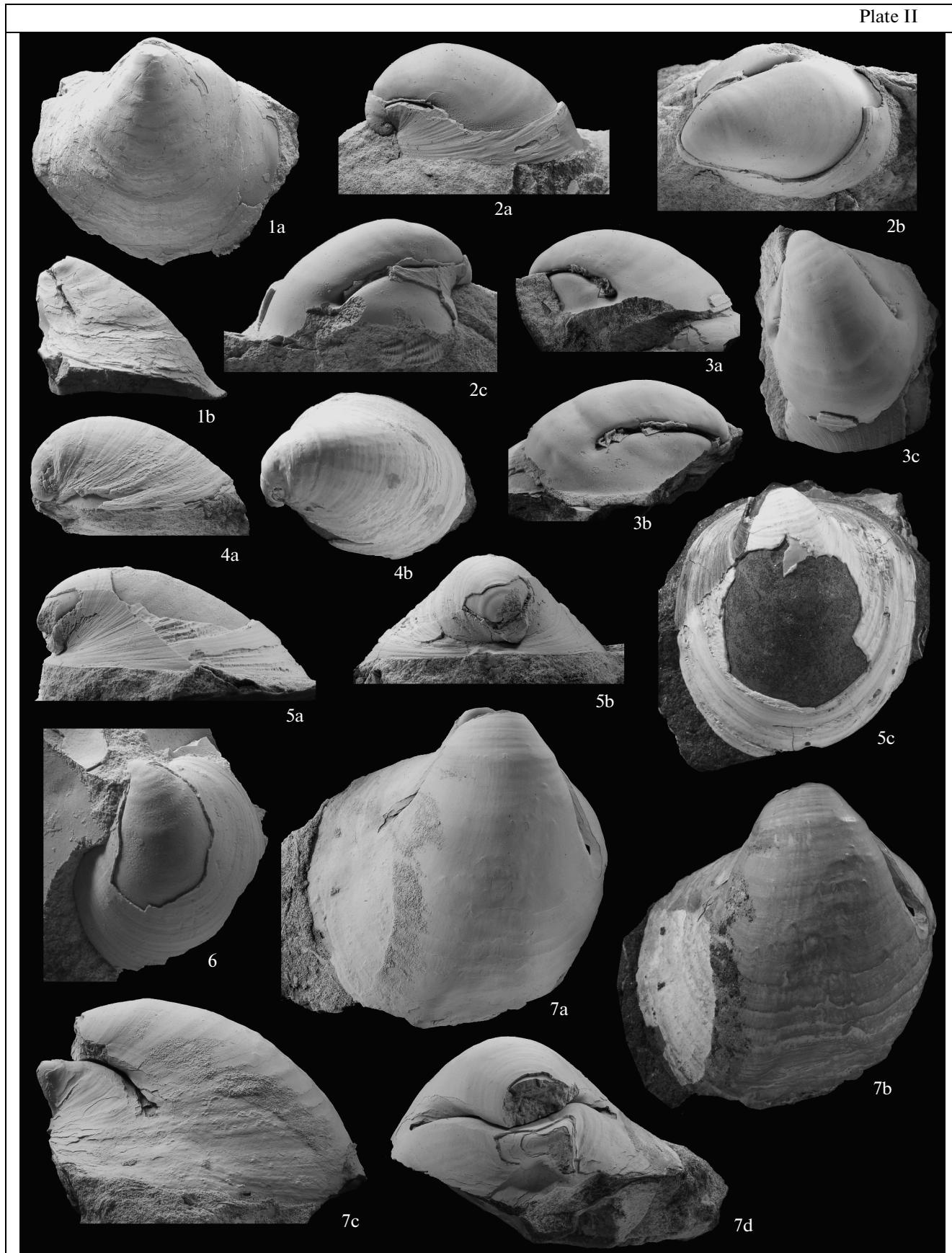


Plate II. Cap-shaped gastropods from the Upper Jurassic Cretaceous sections at the Dyabaka-Tari River (central Taimyr) and Levaya Boyarka and Boyarka rivers (Kheta River basin). **Fig. 1.** *Nixipileolus* sp. 1 aff. *depressus* sp. nov., PIN, specimen 5524/5 (shell 40 mm long and 45 mm wide), Dyabaka-Tari River, Outcrop 1, Beds 7, 8, middle Volgian Substage, Dorsoplanites ilovaiskii Zone: (1a) view from above, (1b) left lateral view. **Fig. 2–6.** *Taimyroconus zakharovi* sp. nov., PIN, holotype specimen 5524/2 (shell 20 mm long), Boyarka River, Outcrop 21, upper Oxfordian–lower Kimmeridgian, Amoeboceras ravnii Zone: (2a) right lateral view, (2b) view from above, (2c) left lateral view; (3) PIN, specimen 5524/9 (shell 38 mm long), age and locality the same: (3a) right lateral view, (3b) left lateral view, (3c) view from above; (4) PIN, specimen 5524/10 (shell 19 mm long), age and locality the same: (4a) right lateral view, (4b) view from above, without sputtering; (5) PIN, specimen 5524/8 (shell 34 mm long and 30 mm wide), Levaya Boyarka River, Outcrop 22, Bed 6, lower Kimmeridgian, Rasenia evoluta Zone, Rasenia pseudouralensis Subzone: (5a) right lateral view, (5b) posterior view, (5c) view from above, without sputtering; (6) PIN, specimen 5524/11 (shell 21 mm long along the diagonal), view from above, Levaya Boyarka River, Outcrop 21, Bed 2, lower Kimmeridgian, Pictonia involuta Zone. **Fig. 7.** *Taimyroconus* sp. 1 cf. *zakharovi* sp. nov., PIN, specimen 5524/12 (shell 60 mm long, 55 mm wide), Dyabaka-Tari River, Goluboi Creek, Outcrop 8, middle Volgian Substage, *Taimyrosphinctes excentricus*: (7a) view from above, (7b) view from above without sputtering, (7c) right lateral view, (7d) posterior view.

C o m p a r i s o n. Volgian *Taimyroconus* sp. 1 representatives are very close to *T. zakharovi*. At the same time, taking into consideration the absence of data on muscular scar patterns, spire form, and stratigraphic isolation, we consider it premature to speak about their identity.

D i s t r i b u t i o n. Upper Jurassic, upper Oxfordian–lower Kimmeridgian; Russia, northeastern Siberia.

M a t e r i a l. 18 specimens: Upper Jurassic, upper Oxfordian–lower Kimmeridgian, Amoeboceras ravnii Zone, Boyarka River, Outcrop 21 (14 specimens are represented by shells and internal casts); Levaya

Boyarka River, Outcrop 1, Bed 14 (one specimen, shell); lower Kimmeridgian, Pictonia involuta Zone, Levaya Boyarka River, Outcrop 21 (one specimen, shell); Rasenia evoluta Zone, Rasenia pseudouralensis Subzone, Levaya Boyarka River, Outcrop 22, Bed 6 (two specimens, shell and internal cast).

Taimyroconus sp. 1 cf. *zakharovi* sp. nov.

Plate II, fig. 7

D e s c r i p t i o n (Figs. 9a, 9b). Shell *Crepidula*-shaped, elongated, from 1.5 to >6 cm long. Shell surface covered by eccentric growth lines; the surface of

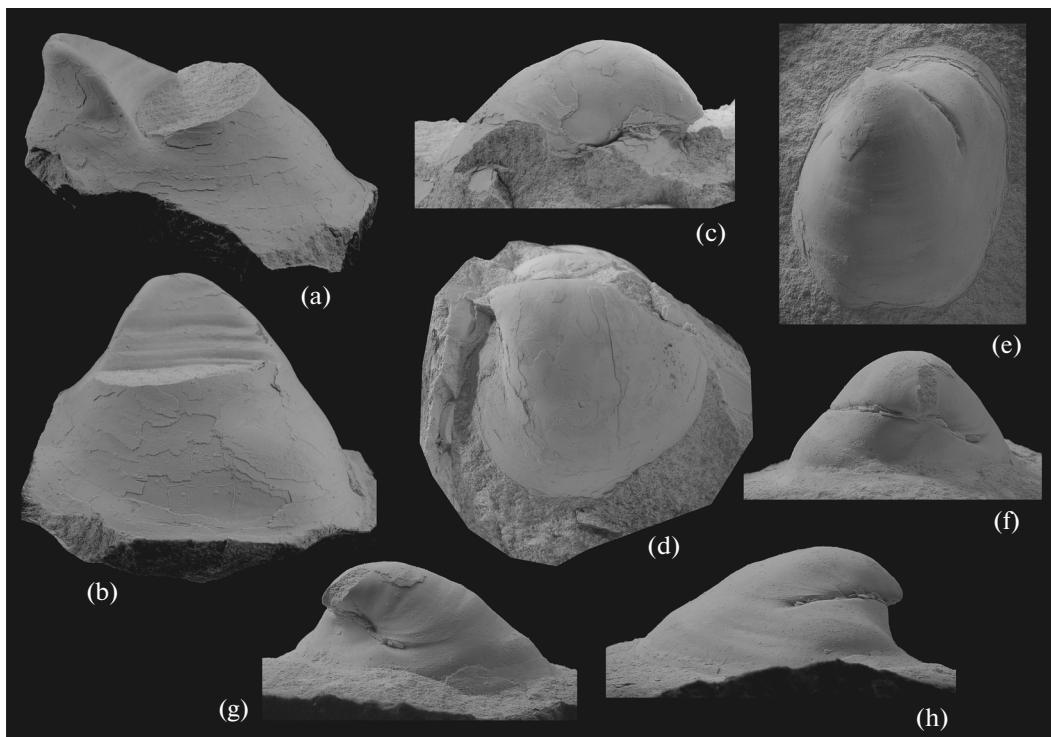


Fig. 9. Shells of Volgian and Valanginian *Taimyroconus* forms. (a, b) *Taimyroconus* sp. 1 cf. *zakharovi* sp. nov., PIN specimen 5524/13 (shell 30 mm long, 31 mm wide), Dyabaka-Tari River, Outcrop 2, Bed 2, Middle Volgian Substage, Dorsoplanites maximus Zone: (a) right lateral view, (b) anterior view; (c–h) *Taimyroconus* sp. 2 cf. *zakharovi* sp. nov.: (c, d) PIN specimen 5524/14 (shell 23 mm long), Bol'shaya Romanikha River, Outcrop 128, lower Valanginian: (c) left lateral view, (d) view from above; (e–h) PIN, specimen 5524/15 (shell 37 mm long, 28 mm wide), Boyarka River, Outcrop 9, Bed 6, lower Valanginian, Neotollia klimovskiensis: (e) view from above, (f) posterior view, (g) right lateral view, (h) left lateral view.

specimen 5524/12 is in addition covered by radial striation. Shell of the same specimen exhibits intravital patterns emphasizing eccentric growth and radial ornamentation. Plate extends forward up to the middle of the whorl, simultaneously descending to the shell aperture. Lower surface of the plate transversely wrinkled.

C o m p a r i s o n. See description of *T. zakharovi*.

M a t e r i a l. Upper Jurassic, middle Volgian Substage, *Dorsoplaniites ilovaikii* Zone, Dyabaka-Tari River, Outcrop 1, Bed 1 (one specimen, internal cast); *Dorsoplaniites maximus* Zone, Dyabaka-Tari River, Outcrop 2, Bed 2 (one specimen, shell); Taimyrosphinctes excentricus Zone, Dyabaka-Tari River, Goluboi Creek, Outcrop 8 (one specimen, shell).

Taimyroconus sp. 2 cf. *zakharovi* sp. nov.

D e s c r i p t i o n (Figs. 9c–9h). Shell *Crepidula*-shaped, presumably close to rounded (see undeformed specimen 5524/14, Fig. 8d), from 2 to 4 cm long. Surface patterns of the shell unknown. Surface of internal casts exhibits vague eccentric undulation. Plate extends forward to the middle of the whorl, simultaneously descending to the shell aperture.

C o m p a r i s o n. Shells of *T. sp. 2* exhibit peculiar features of the inner structure characteristic of *Taimyroconus*, although the absence of the data on scar patterns and poor preservation (including cast deforming) hamper its attribution to any species and comparison with shells from other stratigraphic intervals.

M a t e r i a l. Lower Cretaceous, lower Valanginian, *Neotollia klimovskiensis* Zone, Boyarka River, Outcrop 9, Bed 6 (one specimen, internal cast); lower Valanginian, Bol'shaya Romanikha River, Outcrop 128 (one specimen, shell).

CONCLUSIONS

The data discussed in this work provide additional substantiation for paleobiogeographic zoning of boreal regions in the Northern Hemisphere of the Earth during the Mesozoic, which was proposed almost half a century ago (Saks et al., 1971). These authors defined for the Jurassic and Cretaceous periods the Arctic paleobiogeographic realm despite the scarcity of reliable data at that time. This was particularly true of endemics of the supraspecies rank. Only several bivalve genera and subgenera, one ammonite subgenus, and new brachiopod genera were described by that time. The areas of distribution of separate genera and families of Boreal mollusks in the Arctic realm outlined its southern boundary only approximately. During the last half-century, new endemic genera of radiolarians (Bragin, 1009, 2011) and ammonoids (Repin, 2012; Wierzbowski and Rogov, 2013; Rogov, 2014) were discovered in the Arctic biogeographic realm. In this work, we publish descriptions of three genera of cap-shaped gastropods. It may be assumed

that the further investigation of other fossil groups, primarily microfossils, should increase the number of supragenus endemics. Nevertheless, it is clear that the Arctic paleobiogeographic realm defined half a century ago represents an objective category.

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REFERENCES

- Bandel, K. and Riedel, F., Classification of fossil and recent Calyptraeoidea (Caenogastropoda) with a discussion on neomesogastropod phylogeny, *Berliner Geowiss. Abh.*, 1994, no. 13, pp. 329–367.
- Beizel, A.L., Late Jurassic and Early Cretaceous gastropods of the north of Middle Siberia (systematic composition, paleoecology, stratigraphic and paleogeographic significance), in *Proc. Inst. Geol. Geophys. SB RAS*, 1983, no. 484, pp. 1–94.
- Bragin, N.Yu., Echinocampidae fam. nov., a new family of Late Jurassic-Early Cretaceous radiolarians of Arctic Siberia, *Paleontol. J.*, 2009, vol. 43, no. 4, pp. 356–369.
- Cottrell, A.J., Anatomy of *Siphonaria obliquata* (Sowerby), *Trans. Proc. N. Z. Inst.*, 1911, vol. 43, pp. 582–594.
- Dagis, A.S., Jurassic and Early Cretaceous brachiopods of northern Siberia, in *Proc. Inst. Geol. Geophys. SB RAS*, 1968, no. 41, pp. 1–169.
- Dzyuba, O.S., Izokh, O.P., and Shurygin, B.N., Carbon isotope excursions in boreal Jurassic–Cretaceous boundary sections and their correlation potential, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 2013, vols. 381–382, pp. 33–46.
- Fretter, V. and Graham, A., *British Prosobranch Molluscs. Their Functional Anatomy and Ecology*, London: Ray Soc., 1962.
- Hoagland, K.E., Systematic review of fossil and recent *Crepidula* and discussion of evolution of the Calyptraeidae, *Malacologia*, 1977, vol. 16, no. 2, pp. 353–420.
- Keen, M.A. and Coan, E., *Marine Molluscan Genera of Western North America: an Illustrated Key*, Stanford: Stanford Univ. Press, 1974.
- Marshall, B.A., A review of the recent and late Cenozoic Calyptraeidae of New Zealand (Mollusca: Gastropoda), *The Veliger*, 2003, vol. 46, no. 2, pp. 117–144.
- McLean, J.H., New archaeogastropod limpets from hydrothermal vents: new family Peltospiridae, new super-

- family Peltospiracea, *Zoologica Scripta*, 1989, vol. 18, no. 1, pp. 49–66.
- Mesezhnikov, M.S., *Kimeridzhskii i volzhskii yarusy severa SSSR* (Kimmeridgian and Volgian Stages of the Northern Part of the USSR), Leningrad: Nedra, 1984 [in Russian].
- Nikitenko, B.L., Pestchevitskaya, E.B., Lebedeva, N.K., and Ilyina, V.I., Micropalaeontological and palynological analyses across the Jurassic-Cretaceous boundary on Nordvik Peninsula, northeast Siberia, *Newslett. Stratigr.*, 2008, vol. 42, no. 3, pp. 181–222.
- Opornyj razrez verkhneyurskikh otlozhenii basseina r. Khetы (Khatangskaya vpadina)* (Reference Section of Upper Jurassic Deposits of the Kheta River Basin (Khatanga Depression)), Leningrad: Nauka, 1969 [in Russian].
- Repin, Yu.S., The endemic branch of the Phylloceratida (Ammonoidea) of Arctic Mesozoic, in *Sovremennye problemy izucheniya golovanogikh mollyuskov. Morfologiya, sistematika, evolyutsiya, ekologiya i biostratigrafiya. Vyp. 3* (Proc. Conf. “Contributions to Current Cephalopod Research: Morphology, Systematics, Evolution, Ecology, and Biostratigraphy.” (April 9–11, 2012, Moscow)), Moscow: PIN RAS, 2012, pp. 73–76.
- Rogov, M. and Zakharov, V., Ammonite- and bivalve-based biostratigraphy and Panboreal correlation of the Volgian Stage, *Sci. China Ser. D, Earth Sci.*, 2009, vol. 52, no. 12, pp. 1890–1909.
- Rogov, M.A., Khetoceras (Craspeditidae, Ammonoidea)—a new genus from the Volgian Stage of Northern Middle Siberia, and parallel evolution of Late Volgian boreal ammonites, *Paleontol. J.*, 2014, no. 5, pp. 457–464. http://jurassic.ucoz.ru/_fr/20/Rogov-2014_Khet.pdf
- Saks, V.N. and Nal’nyaeva, T.I., *Verkhneyurskie i nizhne-meloye belemnity severa SSSR. Rody Cylindroteuthis i Lagonibelus* (Upper Jurassic and Lower Cretaceous Belemnites of the Northern USSR. The Genera Cylindroteuthis and Lagonibelus), Leningrad: Nauka, 1964 [in Russian].
- Saks, V.N. and Nal’nyaeva, T.I., *Verkhneyurskie i nizhne-meloye belemnity severa SSSR. Rody Pachyteuthis i Acroteuthis* (Upper Jurassic and Lower Cretaceous Belemnites of the Northern USSR. The Genera Pachyteuthis and Acroteuthis), Moscow: Nauka, 1966 [in Russian].
- Saks, V.N., Basov, V.A., Dagis, A.A., et al., Paleozoogeography of seas of Boreal belt in Jurassic and Neocomian, in *Problemy obshchei i regional’noi geologii* (Problems of General and Regional Geology), Novosibirsk: Nauka, 1971, pp. 179–211.
- Shul’gina, N.I., Tithonian Ammonites from Northern Siberia, in *Problemy paleontologicheskogo obosnovaniya detal’noi stratigrafiyi mezozoya Sibiri i Dal’nego Vostoka* (Problems of Detailed Paleontological Substantiation of Mesozoic Stratigraphy in Siberia and Far East), Leningrad: Nauka, 1967, pp. 131–177.
- Sohl, N.F., Upper Cretaceous gastropods from the Pierre Shale at Red Bird, Wyoming, *U. S. Geol. Surv. Prof. Pap.*, 1967, no. 393-B, pp. 1–46.
- Wierzbowski, A. and Rogov, M.A., Biostratigraphy and ammonites of the Middle Oxfordian to lowermost Upper Kimmeridgian in northern Central Siberia, *Russ. Geol. Geophys.*, 2013, vol. 54, no. 9, pp. 1083–1102.
- Žák, K., Košťák, M., Man, O., et al., Comparison of carbonate C and O stable isotope records across the Jurassic/Cretaceous boundary in the Tethyan and Boreal realms, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 2011, vol. 299, nos. 1–2, pp. 83–96.
- Zakharov, V.A., *Pozdneiyurskie i rannemelovye dvustvorchatye mollyuski severa Sibiri i usloviya ikh sushchestvovaniya (otryad Anisomyaria)* (Late Jurassic and Early Cretaceous Bivalves of Northern Siberia and Conditions of Their Existence (Order Anisomyaria)), Moscow: Nauka, 1966a [in Russian].
- Zakharov, V.A., Invertebrates, buried during life-time in the Valanginian sands of the Khatanga Depression (Boyarka R.), in *Organizm i sreda v geologicheskem proshlom* (Organism and Environment in the Geological Past), Moscow: Nauka, 1966b, pp. 31–54.
- Zakharov, V.A., Late Jurassic and Early Cretaceous bivalves of north Siberia and their ecology. PT. 2. Family Astartidae, in *Proc. Inst. Geol. Geophys. SB RAS*, 1970, no. 113, pp. 1–144.
- Zakharov, V.A. and Yudovnyi, E.G., Conditions of sediment deposition and fauna existence in the Early Cretaceous sea of Khatanga depression, in *Tr. Inst. Geol. Geofiz. “Paleobiogeografiya Severa Evrazii v mezozoe”* (Proc. Inst. Geol. Geophys. SB RAS “Paleobiogeography of North Eurasia in the Mesozoic”), 1974, no. 80, pp. 127–174.
- Zakharov, V.A. and Radostev, I.N., The salinity of the early Cretaceous Sea in the north of Central Siberia, according to the paleobiogeochemical data, *Geol. Geofiz.*, 1975, no. 2, pp. 37–43.
- Zakharov, V.A., Climatic fluctuations and other events in the Mesozoic of the Siberian Arctic, *Proc. Int. Conf. on Arctic Margins.*, Thurston, D.K. and Fujita, K., Eds., Anchorage, 1994, pp. 23–28.
- Zakharov, V.A., Late Jurassic benthic assemblages of Siberia, *Stratigr. Geol. Correl.*, 1995, vol. 3, no. 5, pp. 504–509.
- Zakharov, V.A., Bogomolov, Yu.I., Il’ina, V.I., et al., Boreal zonal standard biostratigraphy of the Siberian Mesozoic, *Russ. Geol. Geophys.*, 1997, vol. 38, no. 5, pp. 965–993.
- Zakharov, V.A., Rogov, M.A., Dzyuba, O.S., et al., Paleoenvironments and paleoceanography changes across the Jurassic/Cretaceous boundary in the Arctic Realm: case study of the Nordvik section (North Siberia, Russia), *Polar Res.*, 2014, vol. 33, pp. 1–19.

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