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Bivalve-Based Stratigraphy of the Toarcian Deposits of Eastern Siberia and Northeastern Russia (Family Oxytomidae Ichikawa, 1958). Part 1. A Brief Outline of the Development of Views on the Toarcian Zonal Stratigraphy in Northeast Asia. History of the Study of Oxytomids. Materials and Methods of Fossil Study

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Abstract—Interpretations of the stratigraphic range of the Toarcian Stage in Northeast Asia are analyzed using the concept of historical dynamics of science. Although Lower-Middle Jurassic deposits have been studied for more than a hundred years, and the biostratigraphic framework has been developed, some problems of the Lower and Middle Jurassic stratigraphy of Eastern Siberia and Northeastern Russia remain unresolved. These include substantiation of the lower and upper boundaries of the Toarcian and analysis of the completeness of the Toarcian Stage represented in sections. It is shown that current bivalve zonal scales for Eastern Siberia and Northeastern Russia are based on different principles, constructed to successions of taxa belonging to different families, and are used independently in the two regions. By identifying the structural and logical components of the research process, three stages are recognized in the history of the study of the family Oxytomidae Ichikawa, 1958. The relevance of the study of the bivalve family Oxytomidae is substantiated. New methods are developed for studying bivalves with a pterineoid hinge: growth stages, typification of the hinge apparatus, zoning and morphometry. The method of growth periodization of mollusk shells makes it possible to identify oxytomid growth stages in shells of different sizes. Use of a shell zoning method allows the relative boundaries of shell parts to be determined, and development of a unified terminology for morphological traits used in describing taxa. The method of hinge typification facilitates the study of ontogenetic changes in bivalves with a pterineoid hinge and helps clarify the phylogeny of the group. The morphometric method allows for a quantitative assessment of the characters used in the description of taxa and statistical testing of hypotheses about evolutionary transformations.

Keywords: bivalves, taxonomy, age periodization, typification, zoning, morphometry, Jurassic system

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INTRODUCTION

This work is the result of a study of Mesozoic bivalves of the family Oxytomidae Ichikawa, 1958 and of the stratigraphy of Toarcian successions in Eastern Siberia and Northeastern Russia.

Interpretation of the geochronological range of the Toarcian deposits of the Lower and Middle Jurassic deposits of Eastern Siberia and Northeastern Russia has varied considerably over the history of their study. There has even been confrontation between representatives of different stratigraphic schools, seeking the dominance of their views. This is consistent with Kuhn's (1977) concept of the historical dynamics of science, that emergence of a hypothesis is followed by adoption of a paradigm, the adherents of which seek to marginalise researcher who do not accept it. The problems of zonal division of the Toarcian Stage, which arose when compiling stratigraphic schemes of sedimentary formations of Eastern Siberia and Northeastern Russia, are due to different approaches to the interpretation of geological and paleontological data, and, accordingly, different views on the history of the geological evolution of both regions. Due to the lack of finds of ammonites (orthostratigraphic group) at the base of the Toarcian in Siberia, the approved regional stratigraphic scheme of the Mesozoic of Central Siberia (*Resheniya*..., 1981) showed a regional hiatus at the Pliensbachian-Toarcian boundary corresponding to the stratigraphic range of the lowermost Toarcian zone. Due to different views on the taxonomy of Late

Toarcian ammonites, the ratified regional stratigraphic schemes of Mesozoic deposits of Siberia at the Lower-Middle Jurassic boundary showed either a regional hiatus of the entire Upper Toarcian (*Resheniya*..., 1981), or did not show any regional gap (*Reshenie*..., 2004). In the ratified stratigraphic scheme of Northeastern Russia (*Resheniya*..., 2009), the Upper Toarcian zones based on the succession of endemic ammonite species cannot be accurately correlated with global zones, hence their correlation is tentative (Repin and Polubotko, 2004). Determining the range of the Toarcian represented in sections is also difficult due to existing acceptance of a high degree of species endemism of Siberian, Northeastern and Far Eastern bivalves that dominate fossil cenoses (*Stratigrafiya*..., 1976). This work is the first to substantiate the effectiveness of parallel zonal scales of the Toarcian Stage of Eastern Siberia and Northeastern Russia, based on the evolutionary sequences of taxa of the subfamily Oxytominae. The discreteness of taxa was determined based on the study of the morphogenesis of the hinge plate and byssal block, as well as analysis of characters using a posteriori weighting. It has been established that Early Toarcian index species of oxyto-zones and Beds with oxytomids are ubiquitous in Boreal deposits. This allows for interregional correlation of Lower Toarcian deposits at the zonal level. For the Late Toarcian deposits of Eastern Siberia, the oxytomid scale allows for intraregional correlation at the zonal level, as well as interregional correlation of these deposits of Eastern Siberia and Northeastern Russia at the substage level. The identification of a continuous phyletic sequence of oxytomids at the Toarcian-Aalenian boundary in Eastern Siberia contributed to a more accurate fixation of the Lower and Middle Jurassic boundary drawn between the *Arctotis similis* and *Arctotis tabagensis* oxyto-zones.

In this paper, geographic zoning of Asian part of Russia follows that accepted in the geological literature. The territory located east of the Lena River is usually attributed to Northeastern Russia (*Resheniya*..., 2009), and the territory from the Urals to the Yenisei River is assigned to Western Siberia (*Reshenie*..., 2004). In my opinion, it is not logical to use the name "Central Siberia" for the territory from the Yenisei River to the Lena River (*Resheniya*..., 1981). In this work, the term Eastern Siberia introduced by Semenov-Tyan-Shansky (1873) is used instead, even though in a narrower sense. To unify the stratigraphic terminology, which has undergone changes in various editions of the "Stratigraphic Code," this work adopts the terminology recommended in its latest edition (*Stratigraficheskiy*..., 2019).

The object of study in this work was bivalve mollusks of the family Oxytomidae Ichikawa, 1958. The subject of study was the spatiotemporal relationships of the Toarcian deposits and the boundary intervals—the Upper Pliensbachian and Aalenian of Eastern Siberia and Northeastern Russia, containing species belonging to the same phyletic lineage of the family Oxytomidae.

Purpose of the study—revision of the system of the bivalve family Oxytomidae Ichikawa, 1958 (subfamily Oxytominae Ichikawa, 1958) and modernization of the bivalve zonal scale for the Toarcian deposits of Eastern Siberia and Northeastern Russia. The objectives of the study included a monographic study of the Toarcian-Aalenian taxa of the family Oxytomidae, as well as the division and correlation of sections of the Toarcian of Eastern Siberia and Northeastern Russia based on the author's zonal scale for bivalves of the family Oxytomidae.

Relevance of the work. Modern literature on the stratigraphy of the Toarcian of Eastern Siberia, Northeastern Russia, and the Far East contains descriptions of taxa that belong to the family Oxytomidae, but their systematic position and stratigraphic distribution are understood differently. The difficulty of using Early and Middle Jurassic bivalves in solving stratigraphic problems was due to the insufficient degree of their study by modern methods using SEM. The SEM study the hinge and shell microornamentation in this work and the study of the morphogenesis of the hinge plate and byssal block underlie the proposal of a revised systematics of the family Oxytomidae. Taxonomic data are decisive for modernizing the zonal scale for bivalves.

The regional stratigraphic scheme of the Lower and Middle Jurassic of Eastern Siberia, used to this day, was adopted at the 3rd Interdepartmental Regional Stratigraphic Meeting on the Mesozoic and Cenozoic of Central Siberia in 1978, more than 40 years ago (*Resheniya*..., 1981). The regional stratigraphic scheme of Northeastern Russia was adopted at the 3rd Interdepartmental Regional Stratigraphic Meeting on the Precambrian, Paleozoic and Mesozoic of Northeastern Russia in 2002, more than 20 years ago (*Resheniya*..., 2009). Both schemes require modernization due to the accumulation of new information on paleontology and biostratigraphy, which significantly changes the interpretations of the geochronological ranges of both regional and local stratigraphic units in these schemes. The proposed zonal scale for oxytomids will contribute to the detailing of new generation stratigraphic schemes for the Lower–Middle Jurassic of Eastern Siberia and Northeastern Russia. The results obtained can be used in large-scale mapping and in conducting exploration work related to the search for oil, gas and diamonds in the Lower-Middle Jurassic of Eastern Siberia.

PROBLEMS OF ZONAL STRATIGRAPHY OF THE TOARCIAN STAGE IN EASTERN SIBERIA AND NORTHEASTERN RUSSIA

In the current International Stratigraphic Scale, the Toarcian Stage is divided into two substages; the Toarcian Stage terminates the Lower Jurassic (*Zony*..., 1982). The substantiation of the completeness of the Toarcian Stage in Eastern Siberia and Northeastern Russia is a problematic issue of stratigraphy. The history of study of the Lower and Middle Jurassic of Eastern Siberia and Northeastern Russia is characterized by inconsistent interpretation of geochronology of the Toarcian Stage. There were several concepts that influenced views on the Toarcian stratigraphy of Northeast Asia. The controversy continues to this day. Discussions regarding the stratigraphic range of the Toarcian Stage in sections of Eastern Siberia and Northeastern Russia have been ongoing for more than 80 years (Bodylevsky, 1939, 1957; Sachs et al., 1963; Dagys and Dagys, 1965, 1967; Kirina, 1966, 1976; Polubotko and Repin, 1974, 1978, 1992, 1994; Knyazev, 1983, 1991, 1997; Knyazev et al., 1983b, 1984, 2002, 2003, 2007a, 2007b; Repin, 1991, 2016, 2017; Pein and Polubotko, 1993, 2004; Grinenko, 2010; etc.).

The study of the geological structure of the Mesozoic deposits of Eastern Siberia using biostratigraphic models first began in 1912–1917, with research of Rzhonsnitsky (1880–1920) in the Vilyui River basin. Toarcian ammonites found by A.G. Rzhonsnitsky in marine clayey sediments on the Vilyui River, were mistakenly identified by A.P. Pavlov as *Harpoceras (=Ludwigia) murchisonae* (Sow.), a species known from the Upper Aalenian deposits of Western Europe. As a result, the first stratigraphic scheme of the Mesozoic deposits of the Vilyui Depression was proposed (Rzhonsnitsky, 1923), in which the marine sequence of the Lower Dogger (=Aalenian) was identified above the fresh-water deposits of the Lias (=Pliensbachian) with a stratigraphic gap corresponding to the Toarcian Stage. Based on the conclusion about the Aalenian dating of marine sediments in the sections of the Vilyui and Tyung rivers, which immediately overlie the coastal-marine Pliensbachian sediments, a hypothesis was put forward suggesting discontinuous deposition in the Vilyui Depression. According to A.G. Rzhonsnitsky, marine transgression occurred in the Aalenian. This paradigm lasted for more than 20 years from 1917 to 1939.

In 1926 S.S. Kuznetsov conducted geological research along the Tyung River, a left tributary of the Vilyui River. Based on the fossils obtained, S.S. Kuznetsov identified three successive Jurassic series with marine fauna, which served as the basis for subsequent stratigraphic comparisons. A.P. Pavlov incorrectly identified Toarcian ammonites from the Tyung River as *Perisphinctes davidsoni* Buckm., a species characteristic of Bajocian of Western Europe. Based on this conclusion, beds with ammonites and belemnites, as well as underlying beds with bivalves identified as *Pseudomonotis echinata* (Smith) and *Pseudomonotis subechinata* Lah., were considered Middle Jurassic. Overlying beds with the bivalves *Pseudomonotis (Hinnites) lenaensis* Lah. were assigned to the Upper Jurassic (Kuznetsov, 1929).

The first reliable information about the presence of Toarcian deposits in Northeastern Russia comes from S.V. Obruchev, from whose collections (in 1929–1930) in the Yana River basin, V.I. Bodylevsky identified the Toarcian ammonites *Harpoceras, Coeloceras* (Obruchev, 1936, 1932).

Later V.I. Bodylevsky identified from the Munugudzhak River (Kolyma River basin) ammonites *Porpoceras verticosum* Buckm. and *Harpoceras* sp., also known from the Toarcian of Western Europe (Bodylevsky and Kiparisova, 1940). The first reliable information about the presence of Toarcian deposits in Eastern Siberia also belongs to V.I. Bodylevsky. He identified ammonites of the genus *Dactylioceras* from the collections of A.I. Berzin on the Nordvik Peninsula of 1935 (Bodylevsky, 1939). In 1937, the first zonal scale of Jurassic deposits in Eastern Siberia was proposed. It was proposed by V.I. Bodylevsky in a report to the 17th session of the International Geological Congress (Bodylevsky and Kiparisova, 1940). The scheme was based on ammonite finds in sections of the Anabar-Khatanga Trough. It contained the Middle Lias (Upper Pliensbachian), Upper Lias (Toarcian) and Aalenian (Fig. 1).

Based on the biostratigraphic model of V.I. Bodylevsky, a hypothesis of continuous deposition in the Early-Middle Jurassic Eastern Siberia arose in the 1930s.

In 1947, G.Ya. Krymgholz, G.T. Petrova and V.F. Pchelintsev re-examined the fossil collections from deposits in sections of the Vilyui Syneclise and the Verkhoyansk Trough.

Ammonites found by S.S. Kuznetsov on the Tyung River in “belemnite-Leda beds”, considered by A.P. Pavlov’s to represent the Middle Jurassic *Perisphinctes davidsoni* Buckm., G.Ya. Krymgholz re-identified as *Dactylioceras athleticum* (Simps.) and *Dactylioceras gracile* (Simps.), known from the Toarcian deposits of England and France (Krymgholz, 1950). Based on the redefinition of ammonites, G.Ya. Krymgholz recognized in Yakutia the Upper Lias (=Toarcian and Lower Aalenian) with *Dactylioceras* and the Upper Aalenian with *Ludwigia murchisonae* Sow. (*Atlas*..., 1947) (Fig. 2).

V.I. Bodylevsky, in a report at the Interdepartmental Meeting on the Unified Stratigraphic Schemes of Siberia (Leningrad, 1956), emphasized that the problem of identifying the Lower Aalenian is due to the fact that the section interval between two biostratigraphic levels with *Dactylioceras* (Lower Toarcian) and *Ludwigella concava* Sow. (Upper Aalenian) in northern Siberia is poorly characterized by ammonites. It is represented by a thick fossiliferous series with mainly bivalves and belemnites. The Toarcian-Aalenian boundary was drawn by V.I. Bodylevsky tentatively above the Beds with *Dactylioceras* (Bodylevsky, 1957). This highlighted the problem of recognizing the Upper Toarcian and substantiating the Lower-Middle Jurassic boundary in northern Siberia.

Geological age		Main index fossils
Middle Jurassic	Aalenian	*Ludwigia concava*, *Pseudomonotis lenaensis*
Lower Jurassic	Upper Lias	*Dactylioceras*, *Belemnites janus*, *B. tolli*, *B. brevis*, *Pseudomonotis vai*
	Middle Lias	*Amaltheus margaritatus*, *Harpax*, *Myophoria laevigata*

Fig. 1. Scheme of the stratigraphy of the Lower and Middle Jurassic of the Anabar-Khatanga Depression (according to Bodylevsky, 1939).

Northwestern Europe			Eastern Siberia							Northeastern USSR				
Arkell, 1956	Dean et al., 1961		*Atlas*..., 1947	Saks, 1962	Bidzhiev, 1965	Kirina, 1966	Dagys, A.A. and Dagys, A.S., 1967	*Resheniya*..., 1981		Tuchkov, 1962a	Dagys, A.A. and Dagys, A.S., 1965, 1967	Polubotko and Repin, 1966	*Resheniya*..., 1978	
Leioceras opalinum	Leioceras opalinum		Dactylioceras	Pseudolioceras maclintocki	Leioceras opalinum	Pseudolioceras maclintocki		Pseudolioceras maclintocki		Leioceras opalinum	Pseudolioceras maclintocki	Pseudolioceras maclintocki	Pseudolioceras maclintocki	
								Pseudolioceras alienum					Pseudolioceras beyrichi	
Lytoceras jurense	Dumortieria levesquei	Pleydellia aalensis		Pseudolioceras compactile	Pseudolioceras sp.	Pseudolioceras sp.				Pseudolioceras compactile				
		Dumortieria moorei												
		Dumortieria levesquei										Pseudolioceras wurttembergica	Pseudolioceras rosenkrantzi	
		Phlyseogrammoceras dispansum												
	Grammoceras thouarsense	Phlyseogrammoceras struckmanni												
		Grammoceras striatulum									Pseudolioceras rosenkrantzi			
	Haugia variabilis										Pseudolioceras compactile	Coeloceras spinatum	Porpoceras polare	
Hildoceras bifrons	Hildoceras bifrons	Zugodactylites braunianus		Dactylioceras spp.	?	Dactylioceras	Pseudolioceras alienum	Zugodactylites monestieri		Pseudolioceras witbiense	Zugodactylites braunianus	Pseudolioceras lythense	Zugodactylites monestieri	
		Peronoceras fibulatum					Dactylioceras commune	Dactylioceras athleticum			Dactylioceras commune	Dactylioceras commune	Dactylioceras athleticum	
		Dactylioceras commune												
Harpoceras falcifer	Harpoceras falcifer	Harpoceras falcifer			Dactylioceras spp.	Osperleioceras viluiense, Harpoceras	Osperleioceras viluiense	Harpoceras falcifer		Dactylioceras athleticum	Harpoceras sp.	Harpoceras exaratum	Harpoceras falcifer	Harpoceras falcifer
		Harpoceras exaratum							Harpoceras exaratum		Ovaticeras propinquum			Harpoceras exaratum
									Eleganticeras elegantulum			Harpoceras alajensis		Eleganticeras alajensis
Dactylioceras tenuicostatum	Dactylioceras tenuicostatum											Ovaticeras facetum	Tiltoniceras propinquum	

Fig. 2. Evolution of views on the zonal stratigraphy of Toarcian deposits in Eastern Siberia and the Northeastern USSR in the 1940–1970s.

In 1962 V.N. Sachs proposed a zonal scale of Toarcian in Siberia, the Northeastern USSR, and the Far East (Saks, 1962). Based on the ammonites, the index Toarcian fossils, he substantiated the Lower and Upper Toarcian. In the Lower Toarcian, he recognized one zone, Dactylioceras spp., corresponding to the Dactylioceras tenuicostatum, Harpoceras falcifer, and Hildoceras bifrons zones of the standard scale, for the Upper Toarcian, he recognized the Pseudolioceras compactile Zone, approximately corresponding to the Lytoceras jurense Zone of the zonal scheme of the Toarcian of the British Isles (Arkell, 1956). He provisionally correlated the series in the north of Siberia in the Yuryung-Tumus region and in the Far East, with the ammonites *Pseudolioceras* sp. (? cf. *beyrichi* Schloenb.) with the Pleydellia aalensis Zone, terminal in the Toarcian stratotype section in France (Gabilly, 1961), The concept of identifying the Upper Toarcian was based mainly on the appearance of ammonites of the genus *Pseudolioceras* in the section and the disappearance of ammonites of the genus *Dactylioceras* in the section (Saks et al., 1963) (Fig. 2).

In the same year I.I. Tuchkov proposed a different scheme for the zonal division of Lower Jurassic deposits for the Northeastern USSR. Based on occurrences of the ammonites *Dactylioceras athleticum* Simpson, *Pseudolioceras whitbiense* Buckm., *Ps. lectum* Simpson, *Pseudolioceras compactile* Simpson, which are index taxa of the Toarcian of Western Europe, the Toarcian Stage was subdivided into three zones (Tuchkov, 1962a) (Fig. 2). In the 1960–1970s, ideas about Early Jurassic ammonoids and bivalves of the Northeastern USSR were expanded by A.A. Dagys, A.S. Dagys, V.A. Zakharov, Yu.S. Repin, I.V. Polubotko, and I.I. Tuchkov.

Bidzhiev (1965) proposed a zonal scale for the north of the Verkhoyansk Trough, which he correlated with the British scale proposed by Arkell (1956). In Bidzhiev's zonal scale, the lower part of the Toarcian corresponded to the Dactylioceras spp. Zone, and the Upper Toarcian corresponded to the Pseudolioceras sp. Zone (Bidzhiev, 1965) (Fig. 2).

In 1965, at the Plenum of the Permanent Commission of the ISC, according to the recommendations of the First International Colloquium on the Jurassic System (Luxembourg, 1962), the Lower Jurassic in the USSR was subdivided into four stages (Hettangian, Sinemurian, Pliensbachian, and Toarcian). By the recommendations of the International Colloquium on the Jurassic System, the range of the Toarcian was defined from the D. tenuicostatum Zone to the D. levesquei Zone inclusive. This resolved the issue of the range of the Toarcian. The Toarcian zonal division scheme proposed by British stratigraphers (The decision..., 1965) was adopted as the standard ammonite succession. This scheme (Dean et al., 1961) integrated data on the ammonoid sequence established in Toarcian sections of England, France, and Germany, and began to be used as a standard for the subdivision and correlation of Toarcian deposits around the world (*Zony*..., 1982; Hillebrandt et al., 1992).

Dagys, A.A. and Dagys, A.S. (1966) developed a more detailed scheme of the Toarcian in the Northeastern USSR, based on the sequence of succession of ammonite asssemblages in sections of the Omolon Massif (Fig. 2). They proposed subdividing the Lower Jurassic Toarcian Stage of the Northeastern USSR into six ammonite zones. The division of the Toarcian in terms of refinement approached the Western European schemes for the Toarcian Stage.

Polubotko and Repin (1966) proposed their own version of the scheme for the zonal division of Toarcian deposits for the Omolon Massif (Fig. 2). Difference from the scheme of A.S. Dagys and A.A. Dagys consisted of selecting new zonal index species and subdividing the Harpoceras spp. Zone. into two local Harpoceratoides alajaensis and Harpoceras exaratum zones. The remaining zones had the same range and fossil characteristics as the zones established by Dagys and Dagys (Polubotko and Repin, 1965).

In 1957–1963 the main sections of the Jurassic of Eastern Siberia were studied by T.I. Kirina (Arctic Geology Research Institute, Leningrad). In 1966, ammonites *Pseudolioceras* spp., identified by T.I. Kirina on the Markha River from the clay series, attributed to the Toarcian, were revised by M.S. Mesezhnikov (All-Union Petroleum Research Exploration Institute, Leningrad). He attributed some specimens to *Pseudolioceras maclintocki* (Haughton), a characteristic species of the Early Aalenian deposits of Alaska (Mesezhnikov and Kirina, 1966). Based on these identifications in the sections of the Vilyui Syneclise, T.I. Kirina established four levels with ammonites (from bottom to top): (1) Beds with Osperleioceras viluiense and Harpoceras (Lower Toarcian), (2) Beds with Dactylioceras (Middle Toarcian), (3) Beds with Pseudolioceras sp. (Upper Toarcian), Pseudolioceras maclintocki (Lower Aalenian) (Kirina, 1966).

In 1967 A.A. Dagys described a new species *Pseudolioceras alienum* A. Dagys, the holotype of which came from an outcrop near the mouth of Lokhaiy Creek on the Markha River. A specimen from the same outcrop, identified by M.S. Mesezhnikov as *Pseudolioceras maclintocki* (Haughton) (Mesezhnikov and Kirina, 1966), A.A. Dagys included the new species in the synonymy. She also included specimens originating from the Zugodactylites monestieri Zone from sections of the Omolon Massif in Northeastern Russia as *Pseudolioceras alienum*. Based on this, the age of the sediments containing the ammonites *Pseudolioceras alienum* on the Markha River was dated Early Toarcian (Dagys, A.A. and Dagys, A.S., 1967).

Kalacheva and Sey (1967) studied the Jurassic sections of the Western Okhotsk region and came to the conclusion about the Early Aalenian age of the ammonites *Pseudolioceras beyrichi* in Western Europe, the Caucasus and the Eastern of the USSR. This became the reason for accepting the Aalenian age of the Beds with Pseudolioceras beyrichi in the stratigraphic schemes of the Northeastern USSR and Eastern Siberia (*Resheniya*..., 1978, 1981) (Fig. 2). The evolution of views on the zonal division of the Toarcian in Eastern Siberia and the North-East of the USSR in the 1940–1960s is shown in Fig. 2.

In 1977, N.G. Krymgholz (All-Union Geological Research Institute, Leningrad) revised the species *Pseudolioceras alienum* A. Dagys. She considered that specimens of *Pseudolioceras alienum* from Markha represent a different taxon from Lower Toarcian specimens from Omolon. The Beds with Pseudolioceras alienum on the Markha River she tentatively dated as Early Aalenian based on the correlation of belemnite assemblages and bivalves, which corresponded M.S. Mesezhnikov's views (Krymgholz, 1977).

In the 1960–1980s, Newton's concept of "absolute" time was mainly used as a methodological basis for the geochronometry of Jurassic deposits in Eastern Siberia. The standard Western European six-zone stratigraphic scale (Dean et al., 1961) was considered an external scale to regional events and a tool for external dating.

Most specialists who studied the Lower and Middle Jurassic deposits accepted the views of M.S. Mesezhnikov and N.G. Krymgholz about the absence of Late Toarcian ammonites in the sections of Eastern Siberia. Based on this, it was concluded that there was a Late Toarcian hiatus in sedimentation, as a result of which the Middle Jurassic sediments were separated from the Lower Jurassic by a large stratigraphic unconformity of regional rank (Kirina et al., 1978; Polubotko and Repin, 1978; Zinchenko et al., 1978). M.S. Mesezhnikov can be considered as the author of this paradigm. Paying attention to the determining role of biostratigraphic zones in identifying stratigraphic gaps, M.S. Mesezhnikov believed that the continuity of sedimentation can be controlled using zones accurate to the zonal moment (phase) (Mesezhnikov, 1966, 1969).

In preparation for the Third Interdepartmental Regional Stratigraphic Meeting on the Mesozoic and Cenozoic of Central Siberia (Novosibirsk, 1978), proposals for a new stratigraphic scheme for the Lower and Middle Jurassic deposits of Eastern Siberia were published (Kirina et al., 1978). A stratigraphic meeting on the Mesozoic of Central Siberia, held in Novosibirsk in 1978, confirmed the Early Aalenian age of the Beds with Pseudolioceras alienum, and the Beds with Pseudolioceras beyrichi were assigned to the basal Lower Aalenian (*Resheniya*..., 1981).

In 1978–1987, a special study on the stage stratigraphy of sections in Eastern Siberia was organized by the Siberian Research Institute of Geology, Geophysics and Mineral Resources (Novosibirsk). During this period, a group of specialists from the Mesozoic Stratigraphy Department of that institute studied the main Toarcian sections of Eastern Siberia and Northeastern Russia. The group included specialists in the following areas: V.P. Devyatov (lithology), V.G. Knyazev (ammonites), O.A. Lutikov (bivalves), E.N. Kiselman and V.V. Sapjanik (foraminiferas), K.N. Grigorieva (spores and pollen). As a result, new paleontological and lithological data were obtained, which made it possible to return to the debate around the hypothesis of a regional stratigraphic hiatus at the Lower-Middle Jurassic boundary.

In 1983, V.G. Knyazev described an ammonite he found in the section of the Markha River and identified it as *Pseudolioceras compactile* (Simps.), known from the Upper Toarcian of England. He substantiated the synonymy of *Pseudolioceras compactile* and *Pseudolioceras alienum* from the Markha River. On this basis, the age of the "Beds with Pseudolioceras alienum" was considered to be Late Toarcian (Knyazev, 1983; Knyazev et al., 1983b, 1984). The evidence provided by V.G. Knyazev et al. renewed interest in the hypothesis of a regional stratigraphic hiatus.

On March 2–3, 1988, a colloquium on the boundary of the Lower and Middle Jurassic was held in Leningrad with the participation of geologists and paleontologists from the All-Russia Petroleum Research Exploration Institute (VNIGRI, Leningrad), All-Union Geological Research Institute (Leningrad), VNIIOkeanologiya (Leningrad), NPO SIBGEO (Novosibirsk), A.A. Trofimuk Institute of Petroleum Geology and Geophysics, Siberian Branch, USSR Academy Sciences (IGiG, Novosibirsk), KAGE-3 (Moscow), PGO "Lenaneftegazgeologiya" (Yakutsk). At the colloquium, the problem of drawing the boundary of the Lower and Middle Jurassic in the northeast of the Siberian Platform was discussed. Most specialists in ammonoids—M.S. Mesezhnikov (VNIGRI), E.D. Kalacheva (Geological Research Institute), Yu.S. Repin (VNIGRI) recognized the separate taxonomic status of the species *Pseudolioceras alienum* A. Dagys. Other ammonite specialists did not agree with the taxonomic decision of V.G. Knyazev (NPO Sibgeo), who attributed the ammonites *Pseudolioceras* from the *alienum* group to the European Late Toarcian species *Pseudolioceras compactile* (Repin, 1991).

On the other hand, V.V. Grausman, a geologist from PGO "Lenaneftegazgeologiya" (Yakutsk) expressed doubts about the conclusions about a regional stratigraphic gap within the clay series filling the marginal troughs of the Siberian Platform. Yu.S. Repin (VNIGRI) reported on the Toarcian-Aalenian boundary deposits in the river basin. Berezovka (Kolyma River basin) and Kelimyar River (Olenek River basin). In the section of the Berezovka River between the Beds with Pseudolioceras rosenkrantzi (Upper Toarcian) and Pseudolioceras beyrichi (Lower Aalenian), he established two new biostratons with ammonites of the same phylogenetic line of the genus *Pseudolioceras*. Thus Y.S. Repin substantiated the presence of new biostratigraphic levels for Upper Toarcian ammonites in Northeastern Russia. From the section along the Kelimyar River, he found an ammonite between the level with Zugodacrilites braunianus and the level with Pseudolioceras beyrichi, which he attributed to *Pseudolioceras* ex gr. *alienum*. M.S. Mesezhnikov's views regarding the Aalenian age of the Beds with Pseudolioceras alienum were controversial for a number of subjective and objective reasons. Subjective contradictions were in different interpretation of the Lower and Middle Jurassic stratigraphy of Eastern Siberia among specialists in other faunal groups. For example, the consequence of accepting the

Aalenian age of the Beds with Pseudolioceras alienum was the inclusion of the level with the bivalves *Pseudomytiloides marchaensis*, accompanied by finds of *Pseudolioceras alienum* in the basin of the Markha and Kelimyar rivers, into the assemblage of the Early Aalenian Beds, although in the Northeastern USSR, the species *Pseudomytiloides marchaensis* was characteristic of the Upper Toarcian (*Stratigrafiya*..., 1976). The hypothesis of a regional hiatus within a uniform series objectively contradicted data on the transgressive-regressive depositional settings in the marginal troughs of the Siberian Platform in the Early Jurassic (Knyazev et al., 1983b, 1991). V.G. Knyazev's statement of the synonymy of *Pseudolioceras alienum* and *Pseudolioceras compactile* was not accepted due to disagreement between ammonite specialists.

Based on an agreement between specialists in different groups of fauna and flora, a compromise decision was made on the Late Toarcian age of the Beds with Pseudolioceras alienum and the presence in the sections of the Kelimyar and Markha rivers of sediments that can be attributed to the Upper Toarcian (Repin, 1991). Using the conventional approach, previous views were revised (*Resheniya*..., 1981) that the Middle Jurassic deposits are separated from the Lower Jurassic deposits by a large stratigraphic unconformity of regional significance in most areas of Eastern Siberia.

Knyazev (1991) developed a zonal scale for the Upper Toarcian substage, consisting of ammonite zones recognized on the basis of a sequence of three Western European species: *Pseudolioceras compactile, P. wuerttenbergeri*, and *P. falcodiscus*.

However, this ammonite scale was not taken into account for a long time by other specialists in the stratigraphy of the Lower and Middle Jurassic (*Zonalnaya*..., 1991; Polubotko and Repin, 1992). In 1993, Yu.S. Repin and I.V. Polubotko proposed a different scheme for the zonal division of the Upper Toarcian into three ammonite zones, characterized by local species: *Pseudolioceras rosenkrantzi, P. danilovi,* and *P. paracompactile* for the Kolyma region of Northeastern Russia (Repin and Polubotko, 1993; Polubotko and Repin, 1994).

Knyazev (1997) developed an assemblage of parallel Toarcian ammonite zonal scales for Northeast Asia based on the phylogenetic sequence of taxa of the subfamily Harpoceratinae and the family Dactylioceratidae (Knyazev, 1997). In the same year, a group of Siberian paleontologists led by V.A. Zakharov (IGiG) as the first to propose a boreal zonal standard for Jurassic deposits, in which a three-zone ammonite scale proposed by V.G. Knyazev was used for the Upper Toarcian. The substantiation of the recognition of the Upper Toarcian in the sections of Northeast Asia was facilitated by the comprehensive work of specialists on various fossil groups: bivalves, foraminifera, belemnites, ostracods, dinocysts, spores and pollen (Zakharov et al., 1997).

In 2002, at the Third Interdepartmental Regional Stratigraphic Meeting on the Precambrian, Paleozoic and Mesozoic Northeastern Russia, the Lower–Middle Jurassic scheme was adopted, the main compilers of which were Yu.S. Repin (VNIGRI, St. Petersburg) and I.V. Polubotko (All-Union Geological Research Institute, St. Petersburg). In the scheme, the Upper Toarcian included four ammonite zones (*Resheniya*..., 2009).

In 2003 V.G. Knyazev and co-authors proposed a new version of the zonal standard of the Toarcian Stage of Northeast Asia, which was based on the phylogenetic succession of European species of one subfamily Harpoceratinae (Knyazev et al., 2003).

In 2016, Yu.S. Repin proposed a new version of the ammonite scale of Northeast Asia. Its fundamental difference from all previous variants was the placement of the *Pseudolioceras replicatum* Zone from the Lower Aalenian to the Upper Toarcian (Repin, 2016). In this scheme, the Upper Toarcian is represented by five ammonite zones.

The evolution of views on the zonal subdivision of Toarcian in Eastern Siberia and the Northeastern USSR in the 1990s–2020s is shown in Fig. 3.

In the 1980s, event stratigraphy became a popular approach. It was believed that the most striking traces in the history of the Earth are left by geological events, regardless of their nature: eustatic cycles, impact elemental and isotopic anomalies, etc. (Zakharov, 1989). Hallam (1981) convincingly demonstrated the importance of eustatic transgressions for stratigraphy. Thanks to the works of E. Hallam, Eduard Suess' concept of the eustatic sea level movement became widespread in the USSR. In 1988 V.P. Devyatov, based on lithostratigraphic analysis of the sections of the Siberian Platform, and relying on data from paleontologists from Siberian Research Institute of Geology, Geophysics and Mineral Raw Materials (SNIIGGiMS), (NPO Sibgeo), established a regular sequence of presumably isochronous clayey series corresponding to transgressions (Golbert et al., 1985; Devyatov et al., 1988).

According to the concept of the occurrence of periodic global changes in the level of the world oceans, it was assumed that the reference horizons corresponding to the levels of maximum transgressions could be the event framework of the stratigraphic schemes of the Lower and Middle Jurassic of Eastern Siberia. Based on the sequence of clayey series of the Yenisei-Khatanga region, six reference horizons were recognized (in genetic terms, regional levels of clayey deposition): Early Hettangian, Sinemurian, Late Pliensbachian, Early Toarcian, Late Toarcian-Early Aalenian and Bajocian-Bathonian (Devyatov et al., 1988). At the end of the 20th century, the vertical and lateral differentiation of deposits of sedimentary basins was taken as the basis for the stratigraphic subdivision of the Lower and Middle Jurassic of Western and Eastern

Stage	Substage	Northeastern Europe (British Isles)		Boreal Standard	Northeast Asia	Northeastern Russia		Boreal Standard	Northeast Asia	
		Howarth, 1992		Zakharov et al., 1997	Knyazev et al., 2003	*Resheniya*..., 2009		Shurygin et al., 2011	Repin, 2016	
		Zone	Subzone	Zone	Zone	Zone, subzone		Zone	Zone, subzone	
Toarcian	Upper	Dumortieria levesquei	Pleydellia aalensis	Pseudolioceras falcodiscus	Pseudolioceras falcodiscus	Pseudolioceras paracompactile		Pseudolioceras falcodiscus	Pseudolioceras replicatum	
			Dumortieria moorei							
			Dumortieria levesquei						Pseudolioceras paracompactile	
			Phlyseogrammoceras dispansum			Pseudolioceras danilovi			Pseudolioceras danilovi	
		Grammoceras thouarsense	Pseudogrammoceras struckmanni	Pseudolioceras wurttenbergeri	Pseudolioceras wurttenbergeri			Pseudolioceras wurttenbergeri		
			Grammoceras striatulum			Pseudolioceras rozenkrantzi			Pseudolioceras rozenkrantzi	
		Haugia variabilis		Pseudolioceras compactile	Pseudolioceras compactile	Pseudolioceras spinatum		Pseudolioceras compactile	Pseudolioceras spinatum	
	Lower	Hildoceras bifrons	Catacoeloceras crassum	Peronoceras spinatum	Pseudolioceras lythense	Zugodactylites braunianus		Zugodactylites braunianus	Zugodactylites braunianus	
			Peronoceras fibulatum	Zugodactylites monestieri						
			Dactylioceras commune	Dactylioceras commune	Harpoceras subplanatum	Dactylioceras commune		Dactylioceras commune	Dactylioceras commune	
		Harpoceras falciferum	Harpoceras falciferum	Harpoceras falciferum	Harpoceras falciferum	Harpoceras falciferum	Harpoceras falciferum	Harpoceras falciferum	Harpoceras falciferum	Harpoceras falciferum
			Cleviceras exaratum		Harpoceras exaratum		“Cleviceras” exaratum			“Cleviceras” exaratum
				Eleganticeras elegantulum	Eleganticeras elegantulum	Eleganticeras elegantulum			Eleganticeras elegantulum	
		Dactylioceras tenuicostatum	Dactylioceras semicelatum	Tiltoniceras propinquum	Tiltoniceras antiquum	Tiltoniceras antiquum		Tiltoniceras antiquum	Tiltoniceras antiquum	
			Dactylioceras tenuicostatum							
			Dactylioceras semicelatum							
			Protogrammoceras paltum							

Fig. 3. Evolution of views on the zonal stratigraphy of Toarcian deposits in Eastern Siberia and the Northeastern USSR in the 1990–2000s.

Siberia. Vertical differentiation was observed in the regular repeatability in the section of transgressive clayey and regressive silty-sandy series, due to the periodicity of eustatic fluctuations, lateral differentiation—in the areal features of some landscapes: marine-transitional-continental. When reconstructing the time scale, the final objects of interpretation were regional chronostratigraphic units (horizons) recognized based on the data synthesis, uniting laterally coeval deposits of different facies (Surkov et al., 1998). The authors of new stratigraphic schemes calibrated the geological time coordinates based on an analysis of the cyclicity of geological processes, such as transgressions and regressions (Shurygin et al., 2000).

In 2003, at the VI Interdepartmental Stratigraphic Meeting in Novosibirsk, the Interdepartmental Stratigraphic Committee (ISC) approved the Regional Stratigraphic Scheme of Jurassic of Western Siberia (*Reshenie*..., 2004). The most significant advantage of the adopted scheme was the use of parallel (combined) biostratigraphic scales for several groups of macro- and microfossils to correlate different-facies deposits (Shurygin et al., 2011). The combined ammonite scale and scales for other faunal groups created a comprehensive biostratigraphic basis for providing high resolution in the stratigraphy of boreal deposits and provided the opportunity for international correlations (Nikitenko et al., 2013).

Despite the creation of a biostratigraphic framework for stratigraphic schemes of a new generation, the main problems of biostratigraphy of the Lower and Middle Jurassic of Eastern Siberia and Northeastern Russia still include the substantiation of the lower and upper boundaries of the Toarcian, the substantiation of the completeness of the Toarcian stage in some geological sections. The identification of Toarcian beds in most sections of the Lower Jurassic of Eastern Siberia by geologists is relatively easy, based on the characteristic finely exhumed clayey and bituminous formations in the lower part of these beds and specific fossils (Knyazev et al., 2003). Nevertheless, the issues of detailed subdivision of the Toarcian-Aalenian deposits and the dating of some formations remain the subject of debate (Shurygin et al., 2000; Repin and Polubotko, 2015).

The main method of parallelizing the regional horizons of Eastern Siberia and Northeastern Russia with stages of the International Stratigraphic Scale (ISC) is the correlation of ammonite zones. Global correlation of the upper part of the Pliensbachian sections with units of standard subboreal scales is problematic due to the difference in ammonite fauna in Northeast Asia (Repin, 1974; Dagys, 1976; Meledina and Shurygin, 2001) and in Western Europe (Page, 2003).

The complete endemism of species of the Pliensbachian terminal phase necessitated the identification of a local zone for Northeast Asia—Amaltheus viligaensis Zone (Dagys, 1976). Despite the good recognition of Early Toarcian mostly clayey deposits in the sections, the correlation of the lower part of the Toarcian is complicated by the different succession of biozones in zonal ammonite species in Northeast Asia and Europe. In Northwestern Europe, the base of the Toarcian is usually drawn at the base of the tenuicostatum Zone (Howarth, 1992), which is based on the first mass appearance of *Dactylioceras* after the disappearance of *Pleuroceras* (Elmi et al., 1997; Page, 2003). In the global stratotype of the lower boundary of the Toarcian Stage (TGSB, GSSP) on the Peniche Peninsula (Portugal), the Pliensbachian-Toarcian boundary is drawn by the appearance of the ammonites *Dactylioceras (Eodactylites) simplex* (Fucini) in association with *Protogrammoceras (Paltarpites)* cf. *paltum* (Buckman) and *Tiltoniceras* aff. *capillatum* (Denckmann). This level correlates with the Protogrammoceras paltum Biohorizon at the base of the Toarcian of Northwestern Europe (Rocha et al., 2016). In Northwestern Europe, the first *Tiltoniceras* do not appear at the base of the Toarcian. This level correlates with the *Protogrammoceras paltum* biohorizon at the base of the Toarcian of Northwestern Europe (Rocha et al., 2016). In Northwestern Europe, the first Tiltoniceras do not appear at the base of the Toarcian. In Germany, Tiltoniceras capillatum Subzone correlates with the upper half of the Dactylioceras tenuicostatum Zone (Hoffmann, 1968). In Spain, France and England, the Tiltoniceras antiquum Biohorizon corresponds to the upper part of the Dactylioceras semicelatum Subzone (Elmi et al., 1997; Page, 2003). In Northeastern Russia, in the sections of the Astronomicheskaya and Brodnaya rivers, between the levels with the Late Pliensbachian *Amaltheus extremus* Repin, *Amaltheus viligaensis* (Tuchkov), and the Toarcian *Tiltoniceras antiquum* (Wright) there is an interval without ammonites, which, according to some sources, is about 2–3 m (Dagys, A.A. and Dagys, A.S., 1965; Dagys, 1968, 1974), according to others—about 1 m (Knyazev et al., 2003). Most Russian experts draw the boundary between the Pliensbachian and the Toarcian based on the disappearance of species of the genus *Amaltheus* and the appearance of species of the genus *Tiltoniceras* (Dagys, 1974; Meledina, 2000; Knyazev et al., 2003). In the zonal scale of Yu.S. Repin, the lower boundary of the Toarcian is proposed to be drawn by the appearance of the endemic species *Lioceratoides asiaticus* Repin (Repin, 2016). In Eastern Siberia, due to the lack of finds of ammonites from the lower Toarcian zone, a regional hiatus was assumed at the Pliensbachian-Toarcian boundary (*Resheniya*..., 1981). For the geological correlation of Toarcian deposits of Eastern Siberia and Northeastern Russia, Russian authors have been developing and improving zonal ammonite scales for more than 50 years (Saks, 1962; Tuchkov, 1962a; Dagys, 1968, 1974; Zakharov et al., 1997; Knyazev et al., 2003; Shurygin et al., 2011; Repin, 2016; etc.).

Interdepartmental regional stratigraphic meetings approved two zonal Toarcian ammonite scales for these territories (*Reshenie*..., 2004; *Resheniya*..., 2009). The zonal division of the Lower Toarcian is almost identical in terms of the range of the zones and their comparison with the zones of the subboreal standard scale (Page, 2003). There are only differences in the understanding of the status and nomenclature of individual zones, as well as the degree of detailing of subzones and beds with ammonites. The zonal division of the Upper Toarcian fundamentally differs both in range and in the nomenclature of zones. Due to the rare occurrence of ammonites in the Toarcian of Eastern Siberia, it is difficult to use ammonite scales in the stratigraphy and correlation of both natural outcrops and sections of boreholes.

Ideas about the existence of a regional stratigraphic hiatus at the border of the Pliensbachian and Toarcian within the lower zone of the ammonite standard scale in northern Siberia still remain dominant (Shurygin et al., 2000; Grynenko et al., 2013). However, the absence of traces of a lithologically pronounced hiatus at the boundaries of the Kyra and Kelimyar formations, the Tyung and Suntary formations both in outcrops and in well sections (Devyatov, 1985) gives reason to question this interpretation.

The determination of the stratigraphic range of the Toarcian Stage in the Cis-Verkhoyansk Trough remains the subject of discussion. For the first time, the Toarcian Stage was recognized in the Zhigansk District in borehole cores and in the area of the Muna River (Test et al., 1962). And in the 1970s and 1980s, it was believed that the Lower Jurassic deposits (Motorchuna Formation) were separated from the Middle Jurassic beds (Syungyude Formation) by a stratigraphic hiatus with the erosion of the Toarcian sediments (Kiryna et al., 1978; *Resheniya*..., 1981; Zinchenko and Repin, 1982). The study of the sections along the Motorchuna, Syungyude, and Molodo rivers by a team of specialists of the Siberian Research Institute of Geology, Geophysics and Mineral Raw Materials (SNIIGGiMS), which included the present author, formed the basis of a review of the views on the stratigraphic range of the series overlying the Motorchuna Formation (Devyatov et al., 1988; Knyazev et al., 2007a). Kirina et al. (1977) recognized the "Syungyude" Formation with a stratotype on the Syungyuyude River. V.P. Devyatov et al. argued that the largely clayey deposits of the lower part of the "Syungyude" Formation correspond to the Suntary Formation (Devyatov et al., 1988; Knyazev et al., 2007a). Toarcian ammonites and bivalves were found in the lower part of this series on the Motorchuna River (Knyazev et al., 1991).

According to V.P. Devyatov et al., the middle and upper sub-formations of the "Syungyude" Formation correspond to the Nizhnyaya Kystatym Formation in section, according to the description previously given by Vakhrameev (1958). However, in the same district, but 10 years earlier, Dmitriev (1968) recognized the " Syungyude" Formation. It did not include the lower clay bed. This led to an opinion that the "Syungyude" Formation recognized by S.D. Dmitriev, may be accepted; it differs profoundly from the Kystatym Formation in composition, thickness, and stratigraphic position. Both formations form a consecutive series in the section (Repin and Polubotko, 2015).

For a long time, there was no evidence of the presence of Upper Toarcian deposits in the Vilyui Syncline and the adjacent part of the Cis-Verkhoyansk marginal trough. In the 1970s and 1980s, a view about a regional stratigraphic hiatus in the Upper Toarcian dominated and formed the basis of the "Regional Stratigraphic Scheme of the Jurassic Deposits of Middle Siberia" (*Resheniya*..., 1981). Proposals for the recognition of the Upper Toarcian in the eastern border of the Siberian Platform were based on the redefinition of previous ammonite occurrences and new finds (Knyazev, 1983, 1991; Knyazev et al., 1984), but were not universally accepted (Repin, 1991; Meledina, 2000).

The age of the upper part of the Suntary Formation remains debatable. According to the decision of the Siberian Branch of the Russian Stratigraphic Committee, the "Lokhaiy Beds" composed of shallow marine, partly deltaic sediments with shells of marine bivalves, interbeds of leptochlorite rocks were recognized in the lower part of the Yakut Formation in the northwest of the Vilyui Syncline (basins of the Vilyui, Markha, and Tyung rivers) as an independent lithostratigraphic unit, in contrast to the "continental" sands of the Yakut Formation., However, bivalves are found in marine interbeds within the Yakut Formation on the Tyung River (outcrop at Mount Tuk-Tuk) (Knyazev et al., 1991). Therefore, in the absence for the evidence for separation of this auxiliary stratigraphic unit in the rank of a local lithostratigraphic unit, it was proposed to consider the Lokhaiy Beds within the Yakut formation as a member (lens) (Shurygin et al., 2000).

The litho- and biostratigraphic subdivision of the Toarcian section in the basin of the Levy Kedon River (Astronomicheskaya, Saturn, Start, Brodnaya rivers), belonging to the Levy Kedon stratigraphic zone, is ambiguous. The Toarcian series was originally part of the Startian Horizon (*Zonalnaya*..., 1991). Repin and Polubotko (1993) considered the Lower-Middle Jurassic section along the Saturn River to be incomplete due to the absence of several local ammonite zones recognized in the adjacent area of the Berezovka River. Knyazev et al. (2003) substantiated the completeness of the Toarcian section on the Saturn River based on the ammonite sequence, similar to that in the Upper Toarcian sections of Western Europe. Siberian stratigraphers subdivided the section into two formations: Astronomicheskaya and Mrachnenskaya (Knyazev et al., 2003). The overlying Middle Jurassic beds represented by black tuffaceous sandstones with retroceramids, were attributed either to the Eksin Formation (Knyazev et al., 2003) or to the Saturn Formation (*Resheniya*..., 2009). The age of this formation is debatable. From the point of view of Koshelkina (1980) and Knyazev et al. (2003), these deposits are presumably dated Aalenian, from the point of view of Yu.S. Repin and I.V. Polubotko, they should be assigned to the Lower Bajocian (*Geologiya*..., 1970; *Resheniya*..., 2009). The beginning of the 21st century is connected with the further detailing of stratigraphic scales, the widespread introduction of event-stratigraphic, cyclo-, seismic-, chemo-, magnetostratigraphic and other methods into stratigraphic practice (Gladenkov, 2013). At the same time, modern discoveries in all Earth sciences confirm V.I. Vernadsky's concept of the geological eternity of the biosphere. For billions of years, the ongoing biogeochemical activity of the living matter of the biosphere confirm the planet-building significance of this component of the Earth's system (Aksenov, 2021). In V.I. Vernadsky's biosphere concept, time is strongly connected with the irreversibility of earthly events. Time and space are formed as a result of the sequential change of qualitatively new components of concrete material objects and processes (Vernadsky, 1932). V.I. Vernadsky's statements of the synchronicity of geological history and biosphere evolution emphasize the fundamental nature of the concept of biological time, which is used to measure the existence of planetary structures. The possibilities of the biostratigraphic method of stratigraphy and correlation of sections of marine origin are inexhaustible. This is supported by the conclusions of ammonite specialists working with biohorizons in Western and Eastern Europe, allowing subdivision of zones and subzones into smaller subdivisions—biohorizons—that can be traced over several thousand kilometers (Callomon, 1964; Kiselev, 2001; Rogov, 2017).

BIVALVE-BASED TOARCIAN ZONAL SCALES OF NORTHEAST ASIA

Along with ammonite scales, parallel scales based on bivalves were developed for the Lower Jurassic. Representatives of the class Bivalvia are the most numerous and diverse in macrobenthic assemblages in the Lower and Middle Jurassic of Eastern Siberia and Northeastern Russia. The first information about the Toarcian bivalves Eastern Siberia dates back to the second half of the 19th century (Schmidt, 1886).

The first bivalve-based biostratigraphic scheme of the Jurassic in the Vilyui River basin, which served as the basis for further stratigraphic constructions, was proposed by S.S. Kuznetsov. In 1926, he recognized several successive series containing bivalves in the Lower and Middle Jurassic deposits of the Tyung River: (1) *Pseudomonotis subechinata* Lahusen, (2) *Leda* and (3) *Pseudomonotis (=Hinnites) lenaensis* (Lahusen). He assigned the Beds with Pseudomonotis subechinata and the “belemnite-Leda Beds” to the Middle Jurassic. The overlying Pseudomonotis (Eumorphotis) lenaensis Beds he assigned to the Upper Jurassic (Kuznetsov, 1929).

In 1930 G.E. Frischenfeld recognized two paleontologically characterized horizons with bivalves within the marine Jurassic series on the Markha River: a horizon with massive *Leda* accumulations (thickness of 50–60 m), attributed by him to the Middle Jurassic, and a horizon with *Pseudomonotis lenaensis* and *Inoceramus lopatini* Schmidt (thickness of about 100 m), which he dated Late Jurassic (Frishenfeld, 1932).

In the first Toarcian zonal scheme of northern Siberia, proposed by V.I. Bodylevsky bivalves were together with ammonites, were used as index taxa: *Pseudomonotis vai* Bodyl. for the Upper Lias (= Toarcian) and *Pseudomonotis lenaensis* (Lahusen) for the Aalenian (Bodylevsky, 1939) (Fig. 1).

In 1941, G.Ya. Krymgholz, G.T. Petrova, V.F. Pchelintsev began joint work on the monographic study of faunal collections assembled by A.G. Rzhonsnytskyi, S.S. Kuznetsov and other geologists in the Vilyui River and Lena River basins (*Atlas*..., 1947; Krymgholz, 1950; Krymgholz et al., 1953). They were the first to recognize three stratigraphic levels in the Vilyui Basin with bivalve assemblages (from bottom to top): (1) Middle Lias *Pseudomonotis tiungensis* Petr. Beds, *Myophoria laevigata* Bronn., *Tancredia kuznetsovi* Petr., *T. securiformis* Dunk., *Pleuromya oleneki* Lah., *P. galathea* Ag., *Eumorphotis sparsicosta* Petr., *E. tabagensis* Petr., *Mytiloides marchaensis* Petr., *Harpax laevigatus* d’Orb., *H. terqumi* Desh.; (2) Upper Lias beds with *Leda acuminata* Goldf., *L. jacutica* Petr., *Tancredia stubendorfii* Schm., *T. namanaensis* Petr., *Modiola numismalis* Opp., *M. viluiensis* Khud., *Mytiloides amygdaloides* Goldf., *M. jacuticus* Petr.; (3) Upper Aalenian, *Eumorphotis lenaensis* Lah. Beds (Krymgholz, 1950).

In a report at the Interdepartmental Stratigraphic Conference on the Development of Unified Stratigraphic Schemes of Siberia (Leningrad, 1956), V.I. Bodylevsky expressed his opinion about the significance of bivalves of the genus *Eumorphotis,* representatives of which can form a genetic lineage from the Toarcian to the Valanginian, for the stratigraphy of Northern Siberia (Bodylevsky, 1957). In the period 1957–1960, geologists of VNIGRI, including T.I. Kirina, G.V. Demchenko, A.N. Dmitriev, and L.S. Velikzhanina collected bed-by-bed an abundant fauna of marine Early Jurassic bivalves from various areas of the Vilyui Syncline and the Cis-Verkhoyansk Trough. These collections enabled L.S. Velikzhanina in 1961 to considerably extend knowledge of the succession of bivalve assemblages in the Toarcian of the Vilyui Syncline and of the taxonomic diversity of bivalves in the Toarcian of Eastern Siberia. This research made a great contribution to the development of Toarcian biostratigraphy using bivalves. She included the following taxa in the lower assemblage: *Leda acuminata* (Goldf.), *L. jacutica* Petr., *Tancredia* cf. *stubendorfii* Schm., *Oxytoma* sp. 1, *Mytiloides marchaensis* Petr., *Pecten* sp. indet., *Modiola nitidula* Dunk. var. *tiungensis* Petr., *M. marchaensis* Khud. emend. Petr. Mass distribution of *Leda jacutica* Petr., and *Oxytoma* sp. 1 was a feature of the assemblage in all studied sections. The second assemblage contained: *Leda acuminata* (Goldf.), *L. jacutica* Petr., *Tancredia* cf. *stubendorfii* Schm., *T.* aff. *securiformis* (Dunk.), *Pseudomonotis* sp., *Arctotis* sp., *Oxytoma* sp. 2, *Mytiloides* aff. *sinctus* (Goldf.), *M. amygdaloides* (Goldf.), *M. marchaensis* Petr., *M. jacuticus* Petr., *M. oviformis* Khud. in collect. Krimh., *Modiola* aff. *viluense* Khud. var. *namanaensis* Petr., *M. nitidula* Dunk. var. *tiungensis* Petr. The assemblage was recognized based on the appearance of the new species *Oxytoma* sp. 2, *Mytiloides oviformis* Khud., *M. jacuticus* Petr., *M. marchaensis* Petr., *Modiola* aff. *viluensis* Khud. var. *namanaensis* Petr. And by the presence of the transitive taxa *Leda jacutica* Petr., *Tancredia studendorffi* Schm., *Modiola nitidula* Dunk. var. *tiungensis* Petr. The third assemblage contained: *Leda acuminata* (Goldf.), *Tancredia namanaensis* Petr., *T. stubendorffii* Schm., *T.* aff. *securiformis* (Dunk.), *Pleuromya* cf. *galathea* Agass., *Arctotis* sp. (aff. *sparsicosta* Petr.), *A.* cf. *marchaensis* Petr., *Pecten* sp. 2, *Modiola numismalis* Opp. The assemblage was characterized by the appearance of new species: *Arctotis* sp. (aff. *sparsicosta*

Petr.), *Modiola numismalis* Opp., *Tancredia namanaensis* Petr., and *T.* aff. *securiformis* (Dunk.). L.S. Velikzhanina drew attention to the fact that representatives of the genus *Mytiloides* are absent along the Vilyui River in the upper part of the section, and a common feature of the Vilyui, Ygyatta and Markha rivers is that the upper part of the sections is characterized by species of *Arctotis* sp. (aff. *sparsicosta* Petr.) and *Modiola numismalis* Opp. On the Ygyatta River, Velikzhanina (1961) recognized a level with *Mytiloides* cf. *jacuticus* (Petr.) below the level of *Arctotis* sp. (aff. *sparsicosta* Petr.) and *Modiola numismalis* Opp. In 1961, an interdepartmental conference on the development of unified stratigraphic schemes of the Yakutskaya ASSR was held in Yakutsk (Yakutsk, 1961) and a regional scheme of the Lower and Middle Jurassic sediments of Yakutia was adopted, in which for the first time characteristic assemblage of bivalves, which have stratigraphic significance for intraregional correlations of sections of Eastern Siberia. For the regions of Western Yakutia, the following Toarcian bivalves were considered characteristic: *Leda acuminata* Goldf., *Tancredia stubendorffi* Schm., *Inoceramus quenstedti* Pchel., *I. amygdaloides* Goldf., *Arctotis marchaensis* Petr. For the sections of the Anabar Bay, the bivalves *Leda jacutica* Petr. were included in the characteristic assemblages of the Lower Toarcian, and *Arctotis vai* Bodyl. was listed in the characteristic assemblage of the Upper Toarcian. *Arctotis vai* was considered to be a characteristic Toarcian bivalve for the lower reaches of the Olenek and Lena rivers; for the Zhigansk District—*Leda* cf. *acuminata, Leda jacutica*. On the Markha, Vilyui, and Ygyatta rivers, characteristic Toarcian fauna included *Arctotis* sp., *Camptonectes* sp., *Lima* sp., *Perna* sp., *Arctotis marchaensis*, *Inoceramus* sp. On the Aldan and Amga rivers, characteristic Toarcian bivalves included *Arctotis marchaensis* and *Inoceramus* sp. Areas on the right bank of the Lena River, characteristic Toarcian taxa included *Arctotis marchaensis, Tancredia curta, Modiola numismalis*; and in the Ust-Vilyu and Suntary districts—*Leda acuminata* (*Resheniya*..., 1963).

Tuchkov (1962b) was the first to identify assemblages of bivalves for the Toarcian of the Northeastern USSR. He included the following taxa in the Lower Toarcian assemblage: *Oxytoma* aff. *oppeli* Roll., *Trigonia (Lyrodon) similis* Agass., *Variamussium pumilum* Lam., and the flowing taxa in the Upper Toarcian assemblage—*Camptonectes aratus* Waagen., *Entolium demissium* Phill., *Aequipecten* aff. *acuticosta* Lam., *Arctotis marchaensis* Petr., *Leda acuminata* Goldf., and *Mytiloides amygdaloides* Goldf.

In the 1960s, information on the Toarcian-Aalenian bivalves of Eastern Siberia and the Far East was supplemented by the description of new taxa (Bodylevsky, 1960; Koshelkina, 1962; Pchelintseva, 1962; Bodylevsky and Glazunova, 1968; Bodylevsky et al., 1968; Okuneva, 1968; *Polevoi*..., 1968; Velikzhanina, 1973; etc.). During this period, some groups of Toarcian oxytomids were monographically studied (Koshelkina, 1963; Velikzhanina, 1966).

In 1968, I.V. Polubotko significantly extended knowledge on the succession of Toarcian and Aalenian bivalve assemblages in the Northeastern USSR. The assemblage from the two lower Toarcian ammonite zones, included: *Meleagrinella substriata*, *Pseudomytiloides* aff. *amygdaloides*, *Pseudomytiloides mytiliformis* Polub., *Lima* sp., *Pholadomya* sp. The assemblage of the two upper zones of the Lower Toarcian included: *Meleagrinella faminaestriata*, *Pseudomytiloides jacuticus*, *Variamussim pumilum*, *Goniomya rhombifera*. The Upper Toarcian assemblage included: *Myophorella (Vaugonia) literata*, *Meleagrinella faminaestriata* Polub., *Pseudomytiloides marchaensis* (Petr.), *Oxytoma startense* Polub., *Protocardia striatula* (Phill.), *Variamussim waageni* Polub. The Lower Aalenian assemblage is characterized by: *Leda subjacutica* Polub., *Nucula amydgaloides* Sow., *Nucula* aff. *palmae* Sow., *Trigonia* aff. *hemisphaerica* Lyc., *Oxytoma ferrugintum* Roll., *O. jacksoni* (Pomp.), *Retroceramus quenstedti* (Pchel.), *Variamussium oleneki* Bodyl., *Modiolus* sp., *Tancredia* sp., *Liostrea* sp. The second, younger faunal assemblage of the Aalenian stage includes: *Retroceramus menneri* Kosch., *R. popovi* Kosch., *R.* aff. *popovi* Kosch., *R. elegans* Kosch., *R. lungershauseni* Kosch., *R. ussuriensis* Vor. The genera *Arctotis*, *Variamussium*, *Phacoides*, *Tancredia* are less common (Polevoi..., 1968).

Okuneva (1973) was the first to recognize three assemblages of bivalves for the Toarcian of Eastern Transbaikalia. For the Lower Toarcian she indicated *Leda jacutica* Petr., *L. acuminata* (Goldf.), for the middle part of the Toarcian—*Nucula eudorae* var. *acuta* (Boriss.), *Leda acuminata* (Goldf.), *Oxytoma* sp. indet., *Eumorphotis* cf. *sparsicosta* Petr., *Galinia ovata* Okun., *G. dubiiformis* Okun., *G. acuta* Okun., *G. rhombica* Okun., *G. porrecta* Okun., *G. borsjaensis* Okun., *G. zabaikalica* Okun., *Posidonia buchi* Roemer, *P. bronni* Voltz, *P.* aff. *daghestanica* Uh1ig, *Entolium (Syncyclomena) demissum* Phill., *Quenstedtia cf. laevigata* Phill., *Chlamys textoria* Schloth., *Myopholas cf. baranovi* Sibirjakova, *Tancredia* cf. *stubendorffii* Schmidt, *T.* aff. *oblonga* Schmidt, *Plesiocyprina* cf. *rostralis* Peel., *Cardinia* sp., *C.* (?) sp., for the upper part of the Toarcian—*Quenstedtia* cf. *levigata* Phi11., *Q.* sp. indet., *Variamussium personatum* (Zieten), *Chlamys textoria* Schloth.

In the 1970s it was believed that the assemblages of Toarcian bivalves in Eastern Siberia, in the Northeastern USSR, and in the Far East differ significantly. Not a single genus has been identified that would mark the beginning of the Toarcian (*Stratigrafiya*..., 1976).

For the Northeastern USSR, regional biostratigraphic subdivisions of bivalves for Lower Jurassic sediments were adopted for the first time at the Second Interdepartmental Regional Stratigraphic Conference on the Precambrian and Phanerozoic of the

General stratigraphic scale			Regional stratigraphic units		
Stage	Substage	Zones	Zones and regional zones	Beds with ammonites	Beds with bivalves
Aalenian	Lower	Tmetoceras scissum	Pseudolioceras maclintocki	Pseudolioceras maclintocki	Mytiloceramus priscus
		Leioceras opalinum		Pseudolioceras beyrichi	Trigonia alta
Toarcian	Upper	Dumortieria levesquei	Pseudolioceras rosenkrantzi		
		Grammoceras thouarsense			
		Haugia variabilis	Porpoceras polare		Vaugonia literata
	Lower	Hildoceras bifrons	Zugodactylites monestieri		Meleagrinella faminaestriata
			Dactylioceras athleticum		
		Harpoceras falcifer	Harpoceras falcifer		"Pseudomytiloides" mytileformis
			Harpoceras exaratum		
			Eliganticeras alajaense		
		Dactylioceras tenuicostatum	Tiltoniceras propinquum	Arctomercaticeras costatum	
				Kedonoceras compactum	

Fig. 4. Regional stratigraphic units of the Toarcian-Aalenian deposits of the Northeastern USSR (*Resheniya*..., 1978).

North-East of the USSR (Magadan, 1974–1975). The Toarcian Stage was subdivided into two bivalve biostratons: Beds with “Pseudomytiloides” mytileformis corresponding to the two lower Toarcian zones—Tiltoniceras propinquum Zone and Harpoceras falcifer Zone, and the Beds with Meleagrinella faminaestriata corresponding to the lower Toarcian Dactylioceras athleticum, Zugodactylites monestieri, and Upper Toarcian zones. The Upper Toarcian Porpoceras polare Zone was correlated with one parallel biostraton—Beds with Vaugonia literata. In the Lower Aalenian, two biostratons were recognized—the Beds with Trigonia alta and Mytiloceramus priscus (*Resheniya*..., 1978) (Fig. 4).

In 1978, at the Third Interdepartmental Regional Stratigraphic Meeting on the Mesozoic and Cenozoic of Central Siberia (Novosibirsk, 1978), regional stratigraphic subdivisions for bivalves for Eastern Siberia were adopted for the first time. The Lower Toarcian included the Beds with Dacryomya inflata and Tancredia bicarinata (in the Harpoceras falcifer, Dactylioceras athleticum, and Zugodactylites monestieri zones). It was believed that the overlying beds containing the species *Oxytoma jacksoni*, are everywhere dated Aalenian (Kirina, 1976). Based on this consideration, the Beds containing *Oxytoma jacksoni* and the endemic ammonite species *Pseudolioceras alienum* in the Vilyui Syneclise were assigned to the Aalenian. Based on the paradigm of M.S. Mesezhnikov (VNIGRI, Leningrad) on the regional stratigraphic hiatus in the Vilyui Syneclise and marginal depressions of the Siberian Platform with the missing Upper Toarcian, the Early Aalenian age of the deposit, containing the assemblage of the bivalves *Pseudomytiloides marchaensis, Oxytoma jacksoni, Propeamussium olenekense, Arctotis marchaensis,* was approved at the meeting (*Resheniya*..., 1981). It was assumed that the Upper Toarcian is missing from the sections of the Vilyui Syncline and Cis-Verkhoyansk Trough. For the Upper Toarcian regional bivalve-based biostratons were not recognized (Fig. 5). Studies of numerous sections in Eastern Siberia and the Northeastern USSR have shown that the sequence of Early and Middle Jurassic bivalve assemblages is quite well maintained over a vast territory. In the 1980s and 1990s, autonomous zonal scales were proposed. Interregional correlation methods using autonomous zonal scales were based on the fundamental principles of stratigraphy: homotaxality and chronological interchangeability of features (Zakharov et al., 1997). The first bivalve zonal scales were introduced in the 1980s (*Resheniya*..., 1978; Shurygin, 1986) and were later further emended many times (Shurygin, 1987a, 1987b; Zonalnaya..., 1991; Polubotko and Repin, 1992, 1994; Repin and Polubotko, 1993, 1996; Nikitenko and Shurygin, 1994; Shurygin et al., 1998).

Modern bivalve scales for the Toarcian and Aalenian of Eastern Siberia and Northeastern Russia are based on sequences of taxa belonging to different families and are used independently in both regions (*Reshenie*..., 2004; *Resheniya*..., 2009).

In 2000, B.N. Shurygin developed a bivalve-based synthetic zonal scale for the Toarcian–Aalenian of Siberia and Northeastern Russia (Shurygin et al., 2000). The bivalve biostratons identified in it were considered as zones co-occurrence of taxa belonging to five different families. The boundaries of the zones were drawn both by the appearance of new taxa and by renewal of bivalve assemblages, including information on the epiboles of a number of characteristic species. The change in the assemblages of species chosen as indices was explained by the total effect of evolutionary change and the results of migrations. The following levels were taken as reference levels in the scheme: below, the lower Toarcian Dacryomya inflata b-Zone and the Tancredia bicarinata b-Zone and above, the Lower Aalenian Mytiloceramus elegans b-Zone. The isochronism of the reference levels along their entire duration was confirmed by ammonite occurrences. These reference levels were the basis for determining the stratigraphic position of other beds based on bivalves. Sequences and their correlation were analyzed without regard to the boundaries of zones and stages based on ammonites. In the Lower Toarcian, a single b-Zone was recognized (Dacryomya inflata, Tancredia bicarinata b-Zone). In parallel, the Meleagrinella faminaestriata Beds were recognized (top of the Lower Toarcian and base of the Upper Toarcian). The series, attributed to the Upper Toarcian and Lower Aalenian, was subdivided into three units: Pseudomytiloides marchaensis b-Zone, Arctotis marchaensis b-Zone, and Mclearnia kelimyarensis b-Zone. The parallel Dacryomya gigantea b-Zone corresponded to the Pseudomytiloides marchaensis b-Zone and the Arctotis marchaensis b-Zone. In subsequent versions of the scale, a new biostraton with bivalves—Corbilomima Beds—was recognized at the base of the Toarcian (Knyazev et al., 2003). In the modern version of the scale, the sequence of biostratons established earlier is preserved, but the stratigraphic ranges of zones and beds are specified (Shurygin et al., 2011) (Fig. 6).

The Toarcian zonal scale for bivalves, based on the sequence of taxa belonging to four different families, was introduced by I.V. Polubotko and Yu.S. Repin. In 2004, they proposed the Arctic Jurassic standard, in which six bivalve biostratons were recognized for the Toarcian (Fig. 7).

Bivalve zones were considered as intervals of phylogenetic lineages (phylozones), represented by gradually changing assemblages of genera. The change of assemblages within phylozones was explained by ecological and migration changes (Repin and Polubotko, 2004).

Modern bivalve zonal scales (Repin and Polubotko, 2004; Shurygin et al., 2011) are based on different principles and correlated with different ammonite scales. The eponymous zones in the Upper Toarcian based on bivalves have different stratigraphic range. Since none of the ammonite scales proposed as the North Asian standard (Zakharov et al., 1997; Knyazev et al., 2003; Shurygin et al., 2011; Repin, 2016) is still not universally accepted, the bivalve scales can be used only via the European ammonite scale.

As a parallel scale for the biozonal stratigraphy of the Toarcian Stage of Eastern Siberia and the Northeastern Russia, the monograph proposes a scale based on the phylogenetic sequence of species of the genera *Meleagrinella* and *Arctotis* (family Oxytomidae).

HISTORY OF STUDY OF OXYTOMIDAE

The bivalve family Oxytomidae is one of the most widespread faunal groups in the Jurassic of Russia. These are representatives of the genera *Meleagrinella* Whitfield, 1885; *Arctotis* Bodylevsky, 1960 and *Oxy-*

General stratigraphic scale				Regional stratigraphic units		
Stage	Substage	Zones		Zones and regional zones	Beds with ammonites	Beds with bivalves
Aalenian	Lower	Leioceras opalinum		Pseudolioceras maclintocki	Pseudolioceras maclintocki	Mytiloceramus elegans
						Propeamussium olenekense, Arctotis marchaensis
					Pseudolioceras alienum	
Toarcian	Upper	Dumortieria levesquei				
		Grammoceras thouarsense				
		Haugia variabilis				
	Lower	Hildoceras bifrons	Zugodactylites braunianus	Zugodactylites monestieri		Dacryomya inflata Tancredia bicarinata
			Peronoceras fibulatum			
			Dactylioceras commune	Dactylioceras athleticum		
		Harpoceras falcifer	Harpoceras falcifer	Harpoceras falcifer		
			Harpoceras exaratum		Harpoceras cf. exaratum	
					Eliganticeras elegantulum	
		Dactylioceras tenuicostatum				

Fig. 5. Regional stratigraphic units of the Toarcian-Aalenian deposits of Eastern Siberia (*Resheniya*..., 1981).

toma 1864. Oxytomids were listed both as part of characteristic assemblages in all previously accepted regional stratigraphic schemes, and as zonal index species in existing bivalve scales, therefore they are considered one of the most important groups for Toarcian-Aalenian stratigraphy deposits of Eastern Siberia and Northeastern Russia.

Oxytomids are well known from the Jurassic and Cretaceous of North America, Europe, Asia, Australia, and New Zealand, where they are frequently the dominant group of bivalves in oryctocenoses. Starting in 2009, the author began a monographic study of the family Oxytomidae (Lutikov et al., 2009, 2010; Lutikov and Shurygin, 2010; Lutikov and Arp, 2020a, 2020b, 2023a, 2023b; Lutikov, 2021; Rogov and Lutikov, 2022). At the same time, special attention was paid to the study of the bivalve hinge, as a structure that is least subject to variability. This work presents results of a revision of the genera *Meleagrinella* Whitfield, 1885 and *Arctotis* Bodylevsky, 1960.

Stage	Substage	Zone, subzone Howarth, 1992; Hillebrandt et al., 1992		Boreal standard Zakharov et al., 1997; Shurygin et al., 2011	Zonal scale of the Toarcian and Aalenian of Northern Siberia and Northeastern Russia	
					b-zones with bivalves and beds*	
Aalenian	Upper	Grafoceras concavum		Pseudolioceras (Tugurites) whiteavesi	Arctotis lenaensis	Retroceramus jurensis
		Brasilia bradfordensis				Retroceramus elegans
	Lower	Ludwigia murchisonae		Pseudolioceras maclintocki		
		Leioceras opalinum		Pseudolioceras beyrichi	Dacryomya gigantea	Mclearnia kelimyarensis
Toarcian	Upper	Dumortieria levesquei		Pseudoliocera falcodiscus		Arctotis marchaensis
		Grammoceras thouarsense		Pseudolioceras wuerttenbergeri		
		Haugia variabilis		Pseudolioceras compactile	Pseudomytiloides marchaensis	
	Lower	Hildoceras bifrons	Catacoeloceras crassum	Zugodactylites braunianus	Dacryomya inflata Tancredia bicarinata	Meleagrinella faminaestriata
			Peronoceras fibulatum			
			Dactylioceras commune	Dactylioceras commune		
		Harpoceras falciferum	Harpoceras falciferum	Harpoceras falciferum		
			Cleviceras exaratum			
		Dactylioceras tenuicostatum		Tiltoniceras antiquum		Corbulomima sp.*

Fig. 6. Toarcian–Aalenian zonal scale for bivalves of Northern Siberia and Northeast Asia (Shurygin et al., 2011; Nikitenko et al., 2013). Asterisks (*) indicate Beds with bivalves.

The main stages of the study of the family Oxytomidae Ichikawa, 1958 are conditionally recognized and are idenified by the main structural and logical components of the research process:

(1) development of the first typological classifications;

(2) modernization of typological classifications and construction of the first phylogenetic schemes;

(3) development of a family system.

The first stage (1753–1863) is characterized by the initial description of taxa based on the external morphology of shells and the creation of typological classifications. Initial information about the taxa attributed to the family under study dates back to the second half of the 18th century. Jurassic bivalves characterized by an unequal-sided oblique oval shell, a dysodont hinge, a straight hinge line, higher and more convex left valves, the presence of a byssal notch on the right valve, an elongated pointed posterior auricle, an oblique ligament pit, unequal muscle scars, the presence of a mantle scar, coming from Jurassic of England, France and Germany, mainly belonged to the extant genus *Avicula* Klein, 1753 (Smith, 1817; Sowerby, 1821; Phillips, 1829; Zieten, 1830; Goldfuss, 1835; Bronn, 1837; Orbigny, 1850; Morris and Lycett, 1854; Lycett, 1863; Schlönbach, 1863; Dumortier, 1869) and to a lesser extent to the Triassic genus *Mono-*

Stage	Zones	Bivalves	
		Zones, Beds*	Assemblages
Toarcian	Pseudolioceras replicatum	Arctotis marchaensis	Propeamussium olenekense, Arctotis marchaensis, Oxytoma muensteri, O. jacksoni, Trigonia alta, T.aff. nemisphaerica, Mytiloceramus (Lenoceramus) sp., "Retroceramus" subtilis, Modiolus ex gr. czekanowskii, Malletia amygdaloides, Dacryomya subjacutica
	Pseudolioceras paracompactile	Mytiloceramus (Lenoceramus) elongatus	Mytiloceramus (Lenoceramus) elongatus, M (L.) spp., Arctotis aff. marchaensis, Camptonectes sp., Mclearnia sp.
	Pseudolioceras danilovi		
	Pseudolioceras rosenkrantzi	Mytiloceramus (Pseudomytiloides) marchaensis	Mytiloceramus (Pseudomytiloides) marchaensis, Protocardia striatula, Vaugonia literata, Entolium kedonensis, Meleagrinella faminaestriata, Propeamussium pumilum, Oxytoma startensis, Astarte plana, Liostrea subtaimyrensis, Tancredia nalednensis, Cucullea saturnensis
	Peronoceras spinatum	Vaugonia* literata	
	Zugodactylites braunianus	Mytiloceramus (Pseudomytiloides) marati	Mytiloceramus (Pseudomytiloides) marati, Kedonella? tokurensis, K. dagysi, Mytiloceramus (Lenoceramus) vilujensis, Camptonectes aurites, Goniomya rhombifera, Meleagrinella faminaestriata, Propeamussium pumilum, Oxytoma startensis, Astarte plana, Liostrea subtaimyrensis, Tancredia nalednensis, Cucullea saturnensis
	Dactylioceras commune	Kedonella dagysi	Kedonella dagysi, Mytiloceramus (Lenoceramus) vilujensis, Meleagrinella faminaestriata, Propeamussium pumilum, Oxytoma startensis, Astarte plana, Cucullea saturnensis
	Harpoceras falcifer	Meleagrinella ex gr. substriata Kedonella mytileformis	Meleagrinella ex gr. substriata, Kedonella mytileformis, K. brodnensis, Kolymonectes toaricus
	Eleganticeras elegantulum		
	Tiltoniceras antiquum		

Fig. 7. Arctic standard of the Toarcian for ammonites and bivalves (Repin and Polubotko, 2004). Asterisks (*) indicate Beds with bivalves.

tis Bronn, 1830 (Münster, 1831; Goldfuss, 1835; Bronn, 1837; Quenstedt, 1858). Both genera were assigned to the family Aviculidae Lamarck, 1801.

In 1847 J.E. Gray established the family Pteriidae, to which he assigned several taxa, including the genus *Avicula* Klein, 1753 (Gray, 1847).

The second stage of the study of oxytomids (1864–1957) is characterized by the further development of the classification of the group, the identification of the taxa of *Oxytoma* (Meek, 1864 in Meek and Hayden, 1864) and *Meleagrinella* (Whitfield, 1885), the first reconstruction of the phylogeny of the genera *Pseudomonotis* and *Oxytoma* (Jackson, 1890). During this period, many works appeared describing oxytomids, but their generic affiliation was interpreted by taxonomists differently. During this period, many works appeared describing oxytomids, but their generic affiliation was interpreted by taxonomists differently. In 1864, F. Meek and F. Hayden, while revising the family Pteriidae Gray, 1847, established the subfamily Pteriinae, to which they assigned the genera *Pteria* Scopoli, 1777; *Eumicrotis* Meek, 1864 and *Monotis* Bronn, 1830. As part of the genus *Pteria*, F. Meek identified a new subgenus *Oxytoma* Meek, 1864 including one species *Avicula muensteri* Bronn, 1829, widespread in the Jurassic of Europe, to which F. Meek assigned his specimens from the Jurassic of South Dakota (USA) (Meek and Hayden, 1864). In the subfamily Pteriinae, F. Meek also included a new genus *Eumicrotis* Meek, 1864, to which he assigned the Permian species *Monotis hawni* Meek et Hayden, 1851 and the Jurassic *Avicula? custa* Hall, 1852. At the same time, F. Meek distorted the original name of the Jurassic species, naming it *Avicula curta* Hall (Meek and Hayden, 1864, p. 81). F. Mick designated the Permian species *Monotis hawni* as the type of the genus *Eumicrotis*. In 1880 R. Whitefield, studying collections of "*Eumicrotis*" from the Oxfordian of South Dakota (USA), collected by G. Newton, attributed some of the specimens to *Pseudomonotis (Eumicrotis) curta*, recognizing D. Hull as the author of the species (Whitfield, 1880). In 1885, R. Whitefield identified a new genus *Meleagrinella*, in which he included the Oxfordian species *Pseudomonotis (Eumicrotis) curta* and a new species *Pseudomonotis (Eumicrotis) orbiculata*, as well as the Upper Cretaceous *Avicula abrupta* Conrad (Whitfield, 1885).

During this same period, the earliest descriptions of *Arctotis* were published. These were based on the study of specimens from the Middle Jurassic of Eastern Siberia, which were assigned to the genus *Hinnites* De France, 1831 (Lahusen, 1886). Later, similar specimens from the Jurassic deposits of Eastern Siberia and the North-East of the USSR were presumably assigned to the genus *Eumorphotis* Bittner, 1901 and the subgenus *Pseudomonotis (Eumorphotis)* (Borissiak, 1914; Voronets, 1938; *Atlas*..., 1947; Krymgholz et al., 1953; Bodylevsky and Shulgina, 1958) or to the genus *Euchondria* Meek, 1874 (Voronets, 1938).

Specimens from the Jurassic of Europe and Asia similar to *Meleagrinella*, were mainly assigned to *Pseudomonotis* Beyrich, 1862 (Pompeckj, 1901; Borissiak, 1909; Rollier, 1914; Ivanov, 1915; Arkell, 1933; Voronets, 1936, 1938; Krymgholz, 1939; Krymgholz et al., 1953; *Atlas*..., 1947; Bodylevsky and Shulgina, 1958; etc.).

During this period, new taxa close to *Meleagrinella* were described. In 1908 E.M. Cossmann from the Bathonian deposits of France described the genus *Clathrolima* (Cossmann, 1908, p. 296), which was subsequently considered by some taxonomists as a synonym of *Meleagrinella* (Duff, 1978). In 1935 D. Marwick described the genus *Echinotis* from the Middle Jurassic of England, and designated *Avicula echinata* Smith, 1817 from the Bathonian-Callovian Cornbrash Formation as the type species (Marwick, 1935). In 1941 L. Cox, having studied collections of "avicula" from the Jurassic deposits of the state of South Dakota (USA), stored in the Natural History Museum, London, considered the genus *Echinotis* Marwick, 1935 a junior synonym of the genus *Meleagrinella* Whitfield, 1885 and indicated that *Avicula echinata* is not may belong to the genus *Pseudomonotis*, the type species of which is the Permian species *Gryphites speluncarius* Schlotheim (Cox, 1941). Based on the views of L. Cox, "*Pseudomonotis*" from the Hettangian, Pliensbachian, Lower Toarcian of Europe and Asia began to be considered as part of *Meleagrinella* Whitfield, 1885 (Hayami, 1959; Hoffmann and Martin, 1960; Koshelkina, 1963; Velikzhanina, 1966; *Polevoi*..., 1968; Urlichs, 1971; etc.). The third stage (from 1958 to the present) of the study of oxytomids is characterized by the creation of a system of the family Oxytomidae. During this period, new supraspecific taxa close to *Oxytoma* Meek, 1864 and *Meleagrinella* Whitfield, 1885 were described: *Hypoxytoma* Ichikawa, 1958; *Arctotis* Bodylevsky, 1960; *Palmoxytoma* Cox, 1962; *Malayomaorica* Jeletzky, 1963; *Boreioxytoma* Zakharov, 1966; *Arctotis (Canadarctotis)* Jeletzky et Poulton, 1987; *Canadotis* Jeletzky et Poulton, 1987.

In 1958 K. Ichikawa revised the family Aviculopectinidae based on the study of shell microsculpture. The genera *Oxytoma* Meek, 1864, *Meleagrinella* Whitfield, 1885 and *Maccoella* Etheridge, 1892 were united by him into an independent subfamily Oxytominae within the family Aviculopectinidae Etheridge, 1906. He considered the modern genus *Pteria* Scopoli, 1777, similar in appearance to *Oxytoma*, as part of the subfamily *Aviculopectininae* Newell, 1938. When interpreting phylogeny, K. Ichikawa considered the Triassic genus *Eumorphotis*, which he assigned to the subfamily Aviculopectininae, as the putative ancestor of *Oxytoma* and *Meleagrinella* (Ichikawa, 1958).

In the bivalve system developed by Soviet paleontologists, the genera *Oxytoma* Meek, 1864; *Meleagrinella* Whitfield, 1885; *Prooxytoma* Maslennikov, 1955; *Pseudomonotis* Beirich, 1862; *Eumorphotis* Bittner, 1901; *Monotis* Bronn, 1830; *Claraia* Bittner, 1901; *Otapiria* Marwick, 1935; *Pleuromysidia* Ichikawa, 1954 were considered as part of the family Monotidae Fischer, 1887 (*Osnovy*..., 1960). In 1960 V.I. Bodylevsky united a group of North Siberian species from the Jurassic and Cretaceous, previously classified as either *Pseudomonotis (Eumorphotis)* or *Eumorphotis* or *Eumorphotis (?),* into the genus *Arctotis* within the family Aviculopectinidae Etheridge, 1906 (Bodylevsky, 1960). Following V.I. Bodylevsky began to classify all Jurassic and Cretaceous "*Eumorphotis*" of Siberia and the Northeastern of the USSR as *Arctotis* Bodylevsky, 1960 (Koshelkina, 1960, 1963; Velikzhanina, 1966; Zakharov, 1966; *Polevoi*..., 1968). Unlike K. Ichikawa, V.I. Bodylevsky considered the genus *Oxytoma* Meek, 1864 as part of the family Monotidae Fischer, 1887 (Bodylevsky and Glazunova, 1968).

In 1961 L.R. Cox elevated the subfamily Oxytominae to the rank of the family Oxytomidae and considered it as part of the superfamily Pectinacea (Cox, 1961).

In 1965 N.D. Newell assigned the family Oxytomidae Ichikawa, 1958 together with the family Aviculopectinidae Meek et Hayden, 1864 to the superfamily Pectinacea Rafinesque, 1815 (Newell, 1965).

In 1966 V.A. Zakharov was the first to assign the genus *Arctotis* to the family Oxytomidae (Zakharov, 1966).

In 1967, when preparing the publication "Treatise on Invertebrate paleontology," G. Vokes proposed a new system of the class Bivalvia. He assigned 10 genera to the family Oxytomidae: *Arctotis* Bodylevsky, 1960; *Echinotis* Marwick, 1935; *Hypoxytoma* Ichikawa, 1958; *Maccoyella* Etheridge, 1892; *Malayomaorica* Jeletsky, 1963; *Meleagrinella* Whitfield, 1885; *Mimetostreon* Bonarelli, 1921; *Ostreavicula* Blanckenhorn, 1934; *Oxytoma* Meek, 1864; *Palmoxytoma* Cox, 1962 (Vokes, 1967). In the Treatise on Invertebrate Paleontology, only seven genera were included in the family Oxytomidae: *Oxytoma* Meek, 1864; *Meleagrinella* Whitfield, 1885; *Maccoyella* Etheridge, 1892; *Arctotis* Bodylevsky, 1960; *Pseudoavicula* Hadleston, 1890; *Cyrtorosta* Branson, 1930; *Avicularca* von Bubnoff, 1921. The genera *Hypoxytoma* Ichikawa, 1958; *Palmoxytoma* Cox, 1962 was considered as subgenera within the genus *Oxytoma* Meek, 1864 (*Treatise*..., 1969). The subgenus *Gryphaea* (Mimetostreon) Bonarelli, 1921 from the Cretaceous deposits of Patagonia was recognized as a subjective junior synonym of *Maccoyella* Etheridge, 1892 (Waterhouse and Riccardi, 1970).

Later, descriptions of new taxa appeared, the authors of which attributed them to the family Oxytomidae. In 1980 J. Chen and C. Chen established a new genus *Jianchuania* from the Late Triassic deposits of the Yunnan province of China (Chen Jin-hua and Chen Chu-zhen, 1980). In 1987, Yu. Yeletsky and T. Poulton described the subgenus *Arctotis (Canadarctotis)* and the monospecific genus *Canadotis* from the Volgian of Arctic Canada (Jeletzky et Poulton, 1987). In "A Synoptical Classification of Bivalves," (Carter et al., 2011) the family Oxytomidae, along with the families Buchiidae Cox, 1953 and Monotidae P. Fischer, 1886, is included in the hyporder Monotoidei Waterhouse, 2001. The family Oxytomidae Ichikawa, 1958 is divided into two subfamilies: Oxytominae Ichikawa, 1958 and Maccoyellinae Waterhouse, 2008 (Carter et al., 2011).

In the reference book "Bivalves of Russia and adjacent countries in the Phanerozoic" (Nevesskaja et al., 2013), the family Oxytomidae is considered as part of the superfamily Aviculopectinoidea Meek et Hayden, 1864 outside the superfamily Buchioidea Cox, 1953, which includes the families Buchiidae Cox, 1953 and Monotidae Fischer, 1887. The family Oxytomidae includes only four genera: *Oxytoma* Meek, 1864 (with the subgenera *Oxytoma* Meek, 1864, *Hypoxytoma* Ichikawa, 1958, *Palmoxytoma* Cox, 1962, *Boreioxytoma* Zakharov, 1966); *Cyrtorosta* Branson, 1930; *Meleagrinella* Whitfield, 1885; *Arctotis* Bodylevsky, 1960 (Nevesskaja et al., 2013).

The study of the family Oxytomidae has been going on for more than 60 years. Currently, the size of the family and its position in the Bivalvia class system is not generally accepted, i.e., the family in existing classifications includes a different number of genera; the family itself is classified either in the superfamily Pectinacea Rafinesque, 1815 (*Treatise*..., 1969), or in the superfamily Oxytomoidea Ichikawa, 1958 as part of the hypoorder Monotoidei Waterhouse, 2001 (Carter et al., 2011), or to the superfamily Aviculopectinoidea Meek et Hayden, 1864 (Nevesskaja et al., 2013). This paper presents the author's views on the taxonomy of bivalves of the family Oxytomidae.

PROBLEMS OF OXYTOMID TAXONOMY

Modern ideas about the size of the family Oxytomidae and its systematic position differ significantly due to different approaches to reconstructing the system of the class Bivalvia (typological, cladistic and evolutionary) (*Treatise*..., 1969; Carter et al., 2011; Nevesskaja et al., 2013). In the literature on Toarcian stratigraphy of Eastern Siberia, Northeastern Russia and the Far East, there are descriptions of the same taxa, which are classified as family Oxytomidae, but their taxonomic boundaries and stratigraphic distribution are understood differently (*Polevoi*..., 1968; Okuneva, 2002; Knyazev et al., 2003; *Atlas*..., 2004; Lutikov and Shurygin, 2010; etc.). Accordingly, the use of this group of bivalves for solving problems of detailed stratigraphy has been very limited.

Within the family, when diagnosing species, external characters were more often used—the size and outline of the shells, the number of radial ribs on the valves, the width of the interrib spaces, the width of the ribs, the ornamentation on the posterior ear, the convexity of the valves, the shape of the auricles, the symmetry of the shell, the size of the beaks (Krymgholz, 1939; *Atlas*..., 1947; Krymgholz et al., 1953; Koshelkina, 1963; Zakharov, 1966). To a lesser extent, the classification considered the structural characters of the hinge plate (Borissiak, 1909; Ivanov, 1915; Duff, 1978; Crame, 1985; Jeletzky and Poulton, 1987).

The continuous variability of most of the characteristics used for species identification creates the greatest difficulties in distinguishing species of the genus *Oxytoma*. Many specialists faced the problem of species identifications when studying *Oxytoma* (Waagen, 1901; Benecke, 1905; Gillet, 1924; Arkell, 1933; Duff, 1978; etc.). Some authors solved this problem by establishing different species for each formation (Rollier, 1914). Others considered most known species primarily as part of one variable, long-lived species (Waagen, 1901; Borissiak, 1909; Cox, 1940; Duff, 1978). Thus, L. Waagen attributed to the species *Avicula (Oxytoma) inaequivalvis* Sowerby a large group of species previously identified by various authors: *expansa* Phillips, *munsteri* Bronn, *macroptera* Roemer, *cornueliana* d'Orbigny, *semiradiata* Fischer, *signata* Rouillier, *russiensis* d'Orbigny, *triseriata* Gzapski, *sinemuriensis* d'Orbigny, *intermedia* Emmrich, *undulata* Schaffhautl, *bavarica* Schaffhautl, *interlaevigata* Quenstedt, *koessenensis* von Ditmar, *suecica* Hebert, *subinaurita* Lundgren, *transilis* Nikitin, etc. (Waagen, 1901). Among the representatives of the genus *Oxytoma* from several horizons of the Upper Jurassic of India, Cox (1940) listed species known from the Lower Jurassic of England, France and Germany. Parallelism creates the greatest difficulties in distinguishing species of the genus *Meleagrinella*. The species *Meleagrinella substriata* (Münster, 1831), characterized by small size, thin, often ribbed radial ornamentation and a highly unequal shell, was attributed to most of the *Meleagrinella* species from the Lower Toarcian of Northeastern Russia, Western Siberia, Eastern Siberia, the Far East and Germany. The generic affiliation of these oxytomids remained unclear for a long time due to poor knowledge of the hinge. Various authors referred to them as *Monotis, Avicula, Pseudomonotis, Pseudomonotis (Meleagrinella),* and *Meleagrinella* (Münster, 1831; Goldfuss, 1835; Bronn, 1837; Quenstedt, 1858; *Atlas*..., 1947; Bodylevsky and Shulgina, 1958; Hoffmann and Martin, 1960; *Polevoi*..., 1968; Urlichs, 1971; Stratigrafiya, 1976; Knyazev et al., 1991; Repin and Polubotko, 2004; etc.).

Continuous variability in such characters as the width of the posterior wing of the left valve, the degree of convexity of the left valve, the density of ribs and the width of interrib spaces presents the greatest difficulties in distinguishing closely related species of the genus *Arctotis*. Several species of the genus *Arctotis* are known from the Toarcian-Bajocian of Eastern Siberia and Northeastern Russia,: *Arctotis marchaensis* (Petrova), *Arctotis vai* (Bodylevsky), *Arctotis buschinskii* (Koschelkina), *Arctotis viluiensis* Velikzhanina, *Arctotis similis* Velikzhanina, *Arctotis tabagensis* (Petrova), *Arctotis lenaensis* (Lahuzen), *Arctotis tolmachevi* Koschelkina, *Arctotis gradiformis* Erschova, and *Arctotis sublaevis* (Bodylevsky) (Lahusen, 1886; *Atlas*..., 1947; Krymgholz et al., 1953; Bodylevsky and Shulgina, 1958; Koshelkina, 1960, 1963; Velikzhanina, 1966). There were no clear criteria for species delimitation; the stratigraphic position of the taxa of this group was assessed differently (Repin and Polubotko, 2004; *Resheniya*..., 2009; Lutikov and Shurygin, 2010; Shurygin et al., 2011).

Species diagnosis of oxytomids only based on external morphological characteristics can lead to erroneous conclusions. Thus, the species *Meleagrinella sparsicosta* (Petrova), the holotype of which comes from the Pliensbachian of the Tyung River section, was indicated as part of the Toarcian assemblages of bivalves of the Anabar Bay (*Stratigrafiya*..., 1976; Knyazev et al., 1983b). In terms of the type of ornamentation, the density of ribs, and the symmetry of the valves, specimens belonging to the Pliensbachian species *sparsicosta* have a great external resemblance to the Toarcian species *marchaensis*. One of the differences—the large convexity of the left valves in the species *marchaensis*—cannot be identified in crushed specimens. The hinge in these taxa was not studied; this was the reason for the formal combination of Toarcian and Pliensbachian forms belonging to different genera into one species.

In the 1960, the Beds with *Oxytoma jacksoni* were important for the correlation of Lower and Middle Jurassic deposits of Eastern Siberia and Northeastern Russia. The assignment of *Oxytoma* specimens from the Lower and Middle Jurassic of the Vilyui Syneclise and the Lena-Anabar Trough to *Oxytoma jacksoni* (Pompeckj), characteristic of the Aalenian of Franz Josef Land and Arctic Canada, led to the conclusion that the host sediments belong to the Aalenian and suggested the absence of Upper Toarcian in sections of Eastern Siberia (Krymgholz, 1977; *Resheniya*..., 1981). At the same time, it was not taken into account that representatives of the genus *Oxytoma* from Toarcian-Aalenian deposits may belong to different taxa (Pompeckj, 1900; Bodylevsky and Glazunova, 1968; Velikzhanina, 1973).

In 1958, while recognizing the subfamily Oxytominae, K. Ichikawa commented that members of Oxytominae are very similar in appearance to representatives of the Carboniferous—Triassic family Aviculopectinidae Meek et Hayden, 1864, but differ in a discrete pallial line and a regular radial arrangement of prisms in the ostracum (Ichikawa, 1958). Ichikawa (1958, p. 159) included such a morphological feature as a strongly elongated posterior auricle in the diagnosis of the genus *Oxytoma* Meek, 1864. However, the genus *Jianchuania* from the Upper Triassic of China, which has a highly elongated posterior auricle, is characterized by an entire pallial line (Chen Jin-hua and Chen Chuzhen, 1980). As our studies have shown, in small specimens of *Oxytoma* the posterior auricle does not protrude beyond the posterior margin of the shell, as in *Meleagrinella*. The locations of the exostracum prisms in the middle and lower parts of the right valve in *Meleagrinella (Praemeleagrinella?) tiungensis* from the Upper Pliensbachian deposits on the Anabar River and Tenkelyakh Site and in *Arctotis marchaensis* from the Upper Toarcian of the Tenkelyakh Site are not consistent, which complicates identification to genus based on these characteristics.

Thus, the use of only external characters when classifying oxytomids is not a sufficient condition for establishing the discreteness of taxa within the family Oxytomidae.

MATERIAL

The material for the research was collections of bivalves of the family Oxytomidae from the Mesozoic in the interval from the Norian to the Valanginian. The author conducted this research as part of scientific groups, starting from 1980. as part of the implementation of scientific programs and contractual work by SNIIGGiMS (Novosibirsk), NPO Sibgeo (Novosibirsk), OOO Inter-Geo (Novosibirsk), OOO NIIPSS (St. Petersburg, Novosibirsk) and Geological Institute Russian Academy of Sciences (GIN RAS) (Moscow). This work is based on the results of studies of Lower and Middle Jurassic sections of Eastern Siberia and Northeastern Russia from 1980 to 1987, carried out within the framework of the topic "Stage stratigraphy of Phanerozoic systems of Northern Siberia" during the author's work in the sector of stratigraphy and paleontology of the Mesozoic of Siberia SNIIGGiMS (Novosibirsk). In order to determine the stratigraphic range of the Siberian Toarcian, the author conducted detailed field lithological and stratigraphic work of the main Toarcian sections together with V.P. Devyatov (lithology), V.G. Knyazev (ammonites), and V.V. Sapyanik (foraminifera), (Knyazev et al., 1983a; Golbert et al., 1985). Materials from boreholes obtained by the author through his contractual work with OOO "Intergeo" and SNIIGGiMS in the period from 1990 to 2009 as well as data on Jurassic oxytomids and stratigraphy obtained during the author's work at the Geological Institute of the Russian Academy of Sciences (Moscow) from 2020 to 2023 as part of a research team (M.A. Rogov—ammonites, A.V. Ippolitov—belemnites, N.G. Zverkov—marine vertebrates). When conducting a revision of the family Oxytomidae, museum collections from various stratigraphic intervals from the Upper Triassic (Norian) to the Lower Cretaceous (Valanginian) were studied. Collections are housed in the TsNIGR Museum (St. Petersburg), the Center for Collective Use Geochron INGG SB RAS (Novosibirsk), the Bavarian State Repository of Paleontological and Geological Collections (Germany, Munich), the Goldfuß-Museum (Germany, Bonn), the National Museum of Natural History of the Smithsonian Institute (USA, Washington). Working collections from core depositories of the Geological Institute of the Russian Academy of Sciences (Moscow) and SNIIGGiMS (Novosibirsk) were also studied.

Main Material

The main material for the research included the author's own collections, collected in the period from 1980 to 1987 in the Toarcian-Aalenian outcrops in the coastal cliffs of Eastern Taimyr, Anabar Bay, in outcrops along the banks of the Anabar, Motorchuna, Markha, Vilyui, Kelimyar, and Kyra-Hos-Teryut-tyakh rivers, tributaries of the Levy Kedon river. The collections of colleagues at SNIIGGiMS were also studied, including those of V.G. Knyazev, collected from 1979 to 1982. in natural outcrops along the banks of the Tyung, Markha, Vilyui, Molodo, Sungyuyude rivers; I.V. Budnikov, V.P. Devyatov and I.S. Pavlukhin, collected from 1990 to 2009 when performing contractual work in the core of wells in the areas of exploratory drilling in the Vilyui-Lena interfluve. The main material comes from four sections of Northeastern Russia, 11 sections of Eastern Siberia and for exploration drilling sites (Fig. 8).

The total number of studied samples with bivalve mollusks from outcrops and wells is more than 150. In the author's own collections there are more than 2000 specimens of oxytomids of the genera *Oxytoma*, *Meleagrinella*, and *Arctotis*.

Supplementary Information

To clarify the systematic affiliation and stratigraphic position of some taxa, the following collections were examined: the collection of Gernot Arp (Georg-August University of Göttingen, Göttingen, Germany), collected by him in the period from 2010 to 2014 from natural outcrops of the lower Toarcian in the section of the Ludwig Canal (Dörlbach, Berg); the Stefan Seppelt collection (Wriesbergholz), from a temporary construction quarry in Lower Saxony (Adenstedt); collections of G. Münster, from natural outcrops of the Lower Toarcian of Germany (Mistelgau, Banz) (Fig. 9).

The type collection of R.P. Whitefield from the Oxfordian of South Dakota (USA) was examined to study the hinge in representatives of the nominative subgenus *Meleagrinella* s.str.

The syntypes of the type series of *Monotis substriata* from the collections of G. Münster, housed in the Bayerische Staatssammlung für Paläontologie und Geologie (Munich) and in the G. Goldfuss-Museum (Bonn) were studied from photographs, courtesy of Dr. W. Werner, Dr. G. Heumann and photographer G. Oleschinski.

The hinge structures of the holotype of *Clathrolima lamenti* from the Bathonian of the Côte d'Or area (Burgundy, France) were examined using photographs from the website of the National Museum of Natural History (Paris, France). The collection is housed therein.

The hinge structures of syntypes of *Pseudomonotis (Eumicrotis) curta*, which was included by Whitefield (1085) in the type group of the genus *Meleagrinella*, were studied using photographic images. The collection is housed at the Department of Paleobiology of the National Museum of Natural History, Smithsonian Institution (Washington DC, USA). Photos courtesy of Associate Manager of Invertebrate Collections, Division of Paleobiology, National Museum of Natural History, Smithsonian Institution, Mark S. Florence.

In order to study the morphogenesis of the hinge plate and byssal block in representatives of the family Oxytomidae, museum collections from the Triassic, Jurassic and Cretaceous of Eastern Siberia and Northeastern Russia, including those housed in the F.N. Tchernyshev TsNIGR Museum (St. Petersburg): A.A. Borissjak (Bajocian, Donetsk Region; Callovian,

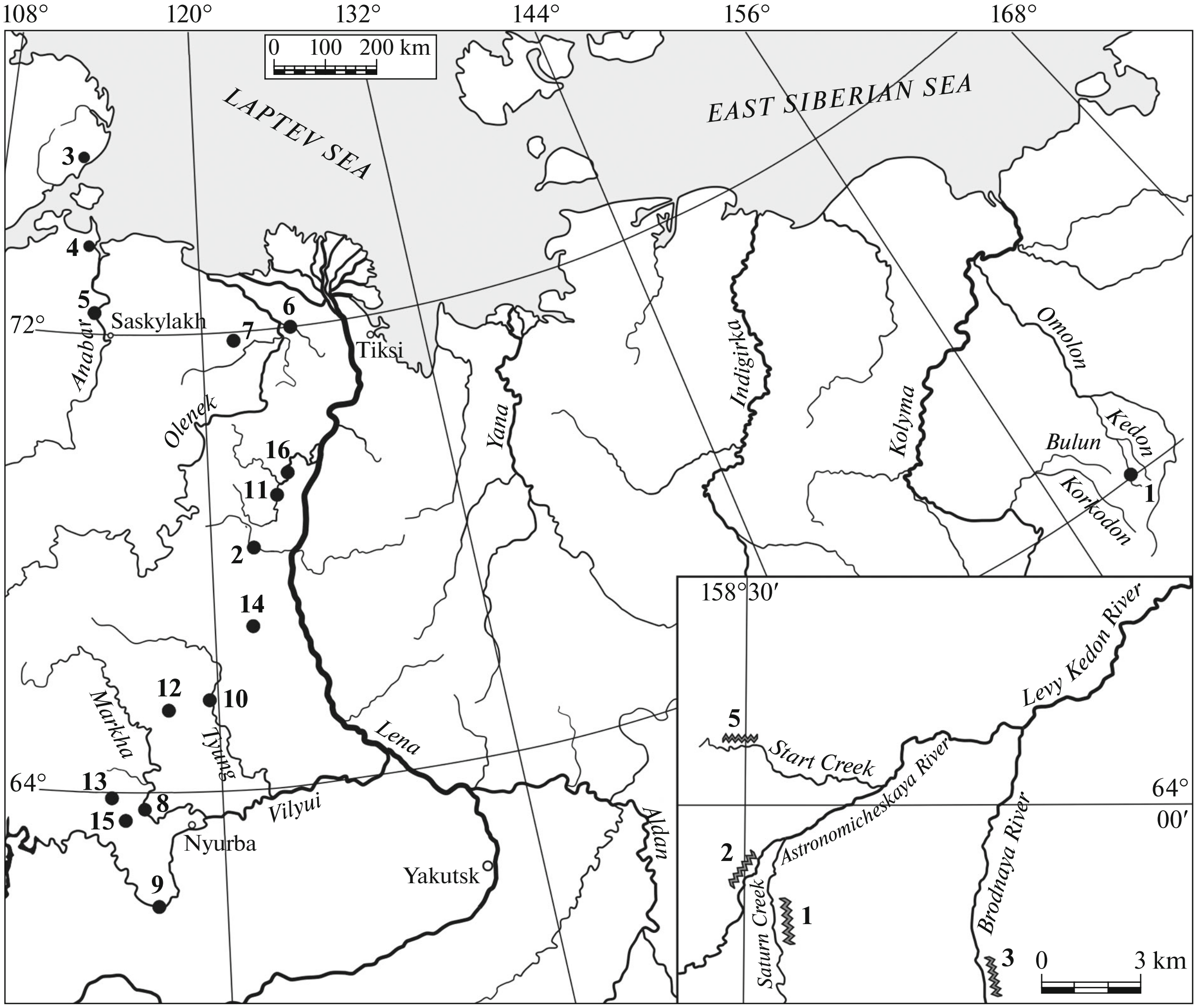

Fig. 8. Overview map of the studied Lower and Middle Jurassic sections in natural outcrops and drilling fields of Northeastern Russia and Eastern Siberia. 1—Northeastern Russia, Levyi Kedon River basin (shown in the inset field numbering of outcrops: 1—Saturn Creek, 2—Astronomicheskaya River, 3—Brodnaya River, 5—Start Creek); 2—11, 16—Eastern Siberia: 2—Motorchuna River, 3—Cape Tsvetkov (Eastern Taimyr), 4—Anabar Bay, 5—Anabar River, 6—Kelimyar River, 7—Kyra-Khos-Teryuttyakh, 8—Markha River, 9—Vilyui River, 10—Tyung, 11—Sungyuyude River, 16—Molodo River; 12—15—exploratory drilling areas: 12—Tenkelyakh (Tyukyan-Markha interfluve), 13—Pravoberezhnyi (Markha-Vilyui interfluve), 14—Serki-Lindensky (Tyung-Lena interfluve), 15—Ottursky (Markha-Vilyui interfluve).

Vladimir Region), N.S. Voronets (Oxfordian, Russian Far East), E.V. Ivanov (Bajocian, Kazakhstan), M.V. Korchinskaya (Norian, Spitsbergen), I.I. Lahusen (Callovian, Ryazan Region), G.T. Petrova (Pchelintseva) (Valanginian, Anabar River), V.F. Pchelintsev (Toarcian, Caucasus), I.V. Polubotko and Yu.S. Repin (Hettangian—Toarcian, Finish, Brodnaya, Astronomicheskaya, Start, Saturn, Paren, and Munugudzhak rivers), T.M. Okuneva (Toarcian, Gazimur River), G.A. Ivanov (Bathonian, Lena River), A.G. Rzhonsnitsky (Toarcian, Markha River), S.S. Kuznetsov (Pliensbachian, Tyung River). The collections housed in the Museum of the Mining University (St. Petersburg) were studied: V.I. Bodylevsky (Toarcian, Yuryung-Tumus Peninsula; Aalenian—Bajocian, Nordvik area), G.A. Ivanova (Bajocian—Bathonian, Lena River); collections housed in the VNIGRI museum (St. Petersburg): T.I. Kirina (Toarcian, Vilyui River, Markha River), Yu.S. Repin (Bajocian, Callovian, Magyshlak Peninsula), as well as collections housed in the laboratory of paleontology and stratigraphy of the Mesozoic and Cenozoic of Trofimuk Institute of Petroleum Geology and Geophysics of Siberian Branch Russian Academy of Sciences (IPGG SB RAS) and in the Central Siberian Geological Museum (Novosibirsk): V.A. Zakharov (Kimmeridgian—Volgian, Levaya Boyarka and Kamennaya rivers), B.N. Shurygin (Lower—Middle Jurassic, Yuryung-Tumus Peninsula, Anabar Bay) and the collections of A.S. Turbina in the core storage facility of SNIIGGiMS (Novosibirsk)—Kimmeridgian core from a borehole of the Yuzhno-Chulym deep drilling area.

Collections of Middle-Upper Jurassic oxytomids from areas of the European part of Russia, obtained during the author's work at the Geological Institute of the Russian Academy of Sciences (Moscow) from A.P. Ippolitov, A.A. Mironenko and M.A. Rogov from 2020 to 2023, were also studied.

The list of studied samples is presented in the author's publications (Lutikov and Shurygin, 2010; Lutikov et al., 2010, 2022; Lutikov, 2021; Lutikov and Arp, 2023a) and supplemented in the section "Description of zonal species" in this work. The samples are housed at the Department of Stratigraphy and Regional Geology of SNIIGGiMS (Novosibirsk), the Aprelevka Branch of the All-Russian Research Geological Oil Institute (VNIGNI) (Moscow) and in the Department of Phanerozoic Stratigraphy of the Geological Institute of the Russian Academy of Sciences (GIN RAS) (Moscow).

METHODS

Detailed biostratigraphy is necessary for conducting research on systematics and taxonomy (Zakharov, 1981). This paper on systematics and taxonomy is based on research carried out by the author from the 1980s to this day, together with colleagues at SNIIGGiMS (Novosibirsk) and at the GIN RAS (Moscow), research on the stratigraphy of the Lower and Middle Jurassic deposits of Eastern Siberia and the Northeastern USSR (Russia). The research methods used in the work were determined by the stages of work—field and laboratory. Field research was carried out directly by the author together with colleagues on natural outcrops of Jurassic sediments in remote areas of the Arctic. The author's laboratory research included taxonomic studies and general studies on taxonomy and biostratigraphy.

Fieldwork

Fieldwork included initial data collection, fossil collecting and description of geological sections. Stratigraphic division of natural outcrops of Jurassic deposits in Eastern Siberia and Northeastern Russia was carried out by the author based on the principles of layer-by-layer correlation of sections of rhythmic terrigenous series (Zakharov and Yudovny, 1967). When describing sections in the field, lithological, taphonomic and paleoecological observations were conducted in order to determine the autochthony or allochthony of fossil occurrences, fossil populations were identified in stratigraphic sections (Zakharov, 1974, 1975, 1984), and preliminarily identifications of species and generic affiliations of all fossils, including bivalves were made. Samples with bivalves were correlated with the lower boundary of the beds and relative to the levels of ammonoid horizons ("lower" or "higher" position). Samples with fossils from borehole cores were correlated to the base of beds established during the description of sections by SNIIGGiMS geologists, and in laboratory they were assessed by the boundaries of geological bodies (members) using geophysical methods.

Taxonomic Study

Species is the basic unit of classification and any system of biodiversity. The system of taxonomic hierarchy depends on defining the species boundaries. Currently, several concepts of the species are known: typological, nominalistic, Mayr's Biological Species Concept, Hennig's species-as-lineages concept, Mishler-Theriot and Wheeler–Platnick phylogenetic concepts, as well as the evolutionary concept of the species (Glushchenko et al., 2004). In the present study, I adhered to the evolutionary species concept proposed by G.G. Simpson. According to this concept, "a lineage (an ancestral–descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and with its own unitary evolutionary role and tendencies" (Simpson, 1961).

At the first stage of the primary diagnosis of taxa within the family Oxytomidae, specimens possessing a certain set of morphological characters were considered in accordance with the taxonomy adopted in the "Treatise on Invertebrate Paleontology" (*Treatise*..., 1969) (Lutikov and Shurygin, 2010).

At the second stage, a classification of the family was built, which included three procedures:

(1) the fossils were studied morphometrically for all possible morphological characters;

(2) without involving phylogenetic hypotheses, the taxonomic significance of the characters was assessed using the method of a posteriori weighing, based on the experience of assessing the amount of phylogenetically significant information contained in the selected character;

(3) the studied specimens were combined into species and supraspecific taxa based on the assembly of taxonomically significant characters; conclusions about family relationships were made based on the morphological similarity of homologous elements.

At the third stage, the system of the family Oxytomidae was proposed. The evolutionary approaches of G.G. Simpson (1951) and E. Mayr (1969) were used as a methodological basis), using the assumption that any trait is the result of evolution. The evolutionary approach, despite its relatively greater subjectivity, considers morphogenetic tendencies, the rate of divergence, and qualitative differences between taxa in the assemblage. In the evolutionary approach, the rank of taxa is judged by the degree of divergence from a common ancestor (Calow, 1986).

When choosing methods of systematics, the author followed the recommendations of V.E. Ruzhencev (1960) using Ruzhencev's ontogenetic principle, the principle of homology, and the principle of the main cluster. The study of new formations within the group was carried out by comparing homologous elements of

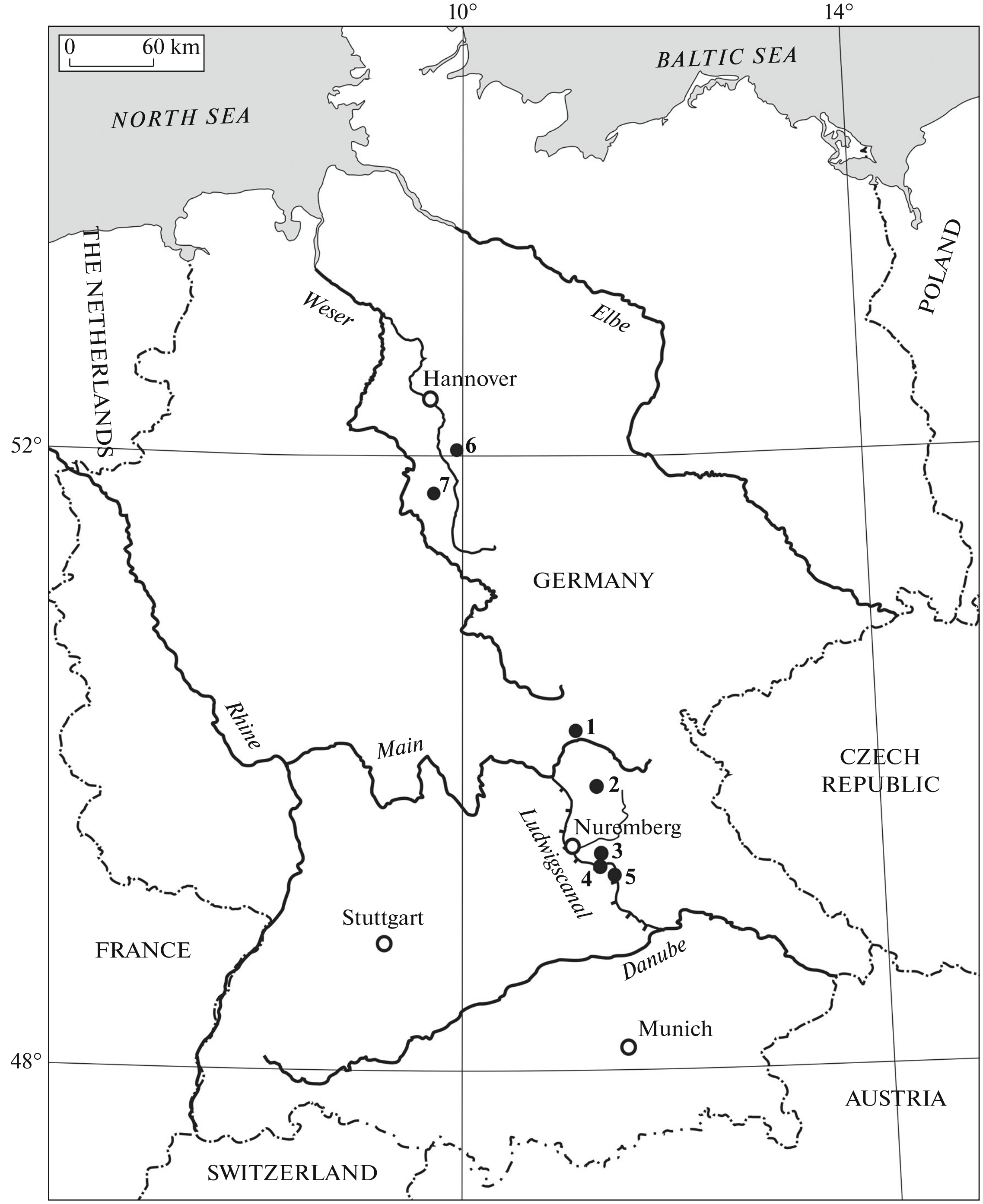

Fig. 9. Map of the location of the Toarcian sections of Germany, from which the studied collections. 1—5—Southern Germany: 1—Banz (place of origin of the lectotype and type collection of *Monotis substriata* (Münster, 1831), 2—Mistelgau, 3—Aldorf, 4—Dörlbach (place of origin of the holotype and type collections of *Meleagrinella golberti* (Lutikov and Arp, 2023a)), 5—Berg; 6, 7—Northern Germany: 6—Adenstedt, 7—Wellersen.

the hinge plate and byssal block of shells in samples from fossil populations separated in time.

After studying ontogenies in samples from fossil populations, phenoclines of the ligament pit and byssal ear were first constructed, then chronoclines of taxa were compiled taking into account their chronological sequence.

The change in the shape of the ligament pit was taken as the main cluster in evolutionary morphogenesis within the subfamily Oxytominae. Phylogeny was considered as a historical series of ontogenies selected in the process of evolution (Schmalhausen, 1982, p. 68). The systematization of taxa was based on a phylogenetic scheme. The sequence of transformations of

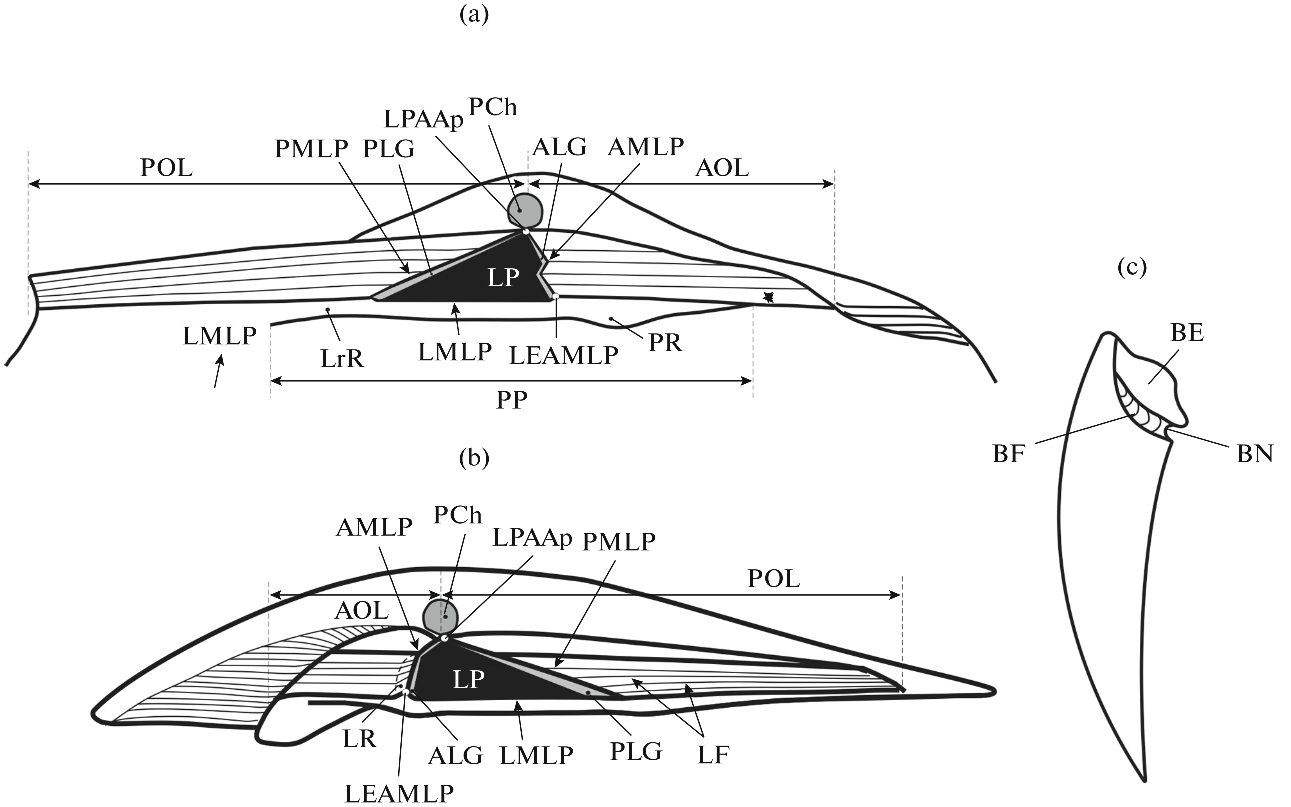

Fig. 10. Structure of the *Meleagrinella* hinge (a) left valve; (b, c) right valve; (a, b) hinge plate, (c) byssal block). Abbreviations: LP—ligament pit, ALG—anterior ligament groove, PLG—posterior ligament groove, LR—ligamental ridge, LF—ligament furrows, LMLP—lower margin of the ligament pit, PMLP—posterior margin of the ligament pit, AMLP—anterior margin of the ligament pit, BE—byssal ear, BF—byssal furrow, BN—byssal notch, LrR—lateral ridge, PR—protuberance, POL—posterior outer ligament, AOL—anterior outer ligament, POL—posterior outer ligament, PCh—prodissoconch, LPAAp—ligament pit apex, LEAMLP—the lower end of the anterior margin of the ligament pit.

the hinge plate was conventionally identified with the sequence of evolution of the family. The rank of taxa was proposed on the basis of identified morphogenetic trends in, taking into account established traditions in the study of the family (Ichikawa, 1958; *Treatise*..., 1969). The chronology of divergence nodes was calibrated by levels with ammonites.

Morphological Analysis Methods

The morphological characters of oxytomids underlie their taxonomy and serve as the basis for conclusions on lifestyle and ethology. Constructive-morphological study of oxytomids was conducted in laboratory, including measurements of morphological elements, the structure of the hinge plate and byssal block, ontogenetic changes and analysis of evolutionary trends. **Internal elements** of morphology include the hinge, pallial line and muscle scars. Oxytomids had a dysodont hinge of the "pterineoid type" (Nevesskaja et al., 1971). Based on the methodology for studying a similar hinge in buchiids (Zakharov, 1981), the elements of the hinge, mainly associated with the functioning of the ligament, are considered in this work as part of the hinge plate, and the elements, mostly associated with the byssal function, are considered as part of the byssal block. When describing the elements of the hinge plate and the byssal block, the author partially used the terminology proposed by Zakharov (1981) for the genus *Buchia* (Zakharov, 1981) as well as by Jeletzky and Poulton (1987) for the genus *Arctotis.*

The area of the shell on which the elements of the hinge plate are located, distinctly separated from most of the inner surface of the valves, is referred to as the hinge line. The oxytomid hinge plate includes: (1) elements of the ligament area—ligament pit, anterior and posterior ligament fields, ligament grooves, ligament ridge; (2) elements of the pseudoligamentous platform—lateral ridge, protuberance. The byssal block includes: byssal ear, byssal furrow and byssal notch (Fig. 10). The boundaries of the ligament area are determined by the field of distribution of ligament grooves on the hinge line. The margins of the oxytomid anterior outer ligament are separated from the anterior and posterior branches of the overlying area by sharp bends—ligament grooves. The area of articulation between the ligament pit and the anterior branch of the outer ligament in adult *Meleagrinella* and *Arctotis* has a raised area—a ligament ridge. In *Meleagrinella* and *Arctotis*, in contrast to *Buchia*, the lower border of the ligament area on both valves does not coincide with the lower hinge line. The smooth area of the hinge line between the ligament groove furthest from the umbo and the zone of articulation of the inner surface of the valve with the hinge line is called the pseudoligamentous platform (Lutikov and Shurygin, 2010). The area of articulation of the pseudoligamentous platform is limited from the inner surface of the valve by a lateral ridge formed by raising the inner surface of the valve. On the anterior branch of the lateral ridge in *Meleagrinella*, *Prearctotis* and *Canadotis* there is a semi-ellipsoidal or hemispherical protrusion called a "knotenartige Vorsprung" (Pompeckj, 1901), "tooth" (Borissjak, 1909), "protuberance" (Duff, 1978).

Without defining the functional purpose of this morphologically variable element, this work uses the term proposed by K. Duff.

The following terms are used to designate the elements of the ligament pit:

The lower margin of the ligament pit—the rim of the ligament pit, at the junction of the ligament area and the pseudoligamentous platform;

posterior margin of the ligament pit—the margin of the ligament pit formed by the intersection of the posterior outer ligament area and the posterior ligament groove;

the anterior margin of the ligament pit—the margin of the ligament pit, formed by the intersection of the anterior outer ligament and the anterior ligament groove. The ligament furrows are located on the ligament area and on the ligament pit parallel to each other and repeat the outlines of the lower margin of the ligament area.

The lamellar part of the oxytomid ligament was probably attached to the ligament grooves along the entire region of the overlying field. The ligament pit in oxytomids served to accommodate the fibrous part of the ligament. In Meleagrinella and Oxytoma, the ligament pit is a depression on the ligament platform, limited by grooves. The base of the ligament pit is flattened. In Arctotis, the base of the ligament pit is concave. The spoon-shaped structure for supporting the internal ligament, formed by the bending of the ligament platform, is called the resilifer.

The oxytomid byssal block is partially involved in the articulation of the valves. The upper part of the byssal ear is covered with ligament grooves. Probably, the lamellar part of the ligament extended to the byssal ear anterior to the ligament pit. The byssal ear is separated from the rest of the surface of the right valve by a deep byssal groove.

Shell Zoning

In the literature on the bivalves of the family Oxytomidae (Borissiak, 1909, 1914; Koshelkina, 1963; *Treatise*..., 1969; Nevesskaja et al., 2013), most of the terms denoting the names of the external elements of shell morphology are often ambiguous. In order to create relatively accurate concepts of morphological elements, zoning of the parallel projection of the valves onto a plane was applied using geometric figures. The shell zoning method makes it possible to determine the relative boundaries of shell zones and formulate terms to denote characteristics used in the description of taxa. A photograph of the valve, in the top view, was cut out to follow the outline of the valve in Photoshop and then imported to a Corel DRAW file.

Using Corel DRAW tools, the outer contour of the valve was fit into a large rectangle I. The horizontal sides of rectangle I were oriented parallel to the hinge line. The vertical sides of the outer rectangle I were drawn tangentially to the protruding shell margins. The photograph of the valve, in the anterior margin view was fit into small rectangle II. The two-dimensional projection of the shell was divided into sections using the inner rectangle III. The upper horizontal side of rectangle III was oriented parallel to the hinge line. One vertical side of rectangle III was drawn perpendicular to the hinge line tangent to the anterior end of the shell, the second vertical side was drawn perpendicular to the hinge line tangent to the notch of the posterior margin until it intersected with the valve contour. The lower horizontal side of rectangle III was drawn from the point of intersection with the valve contour and was oriented parallel to the hinge line (Fig. 11).

Most of the **external elements** of *Meleagrinella* and *Arctotis* have a similar morphology. Therefore, unified terms and designations are used for them.

The intersection points of the inner rectangle III with the contour of the shell are conventionally taken as the boundary points between the valve margins (Fig. 11):

The valve posterior margin (VPM) is a shell contour segment from the end of the posterior auricle to the point of intersection with rectangle III (between points 2–3); the valve ventral margin (VVM) is a shell contour segment between two points of intersection of the internal rectangle III with the external margin (between points 3–4); the valve anterior margin (VAM) is a shell contour segment between two points of intersection of the large internal rectangle with the external margin (between points 4–1); the valve's dorsal margin (VDM) is a shell contour segment between two points of intersection of the large internal rectangle with the external margin (between points 1–2).

The most protruding points of the anterior, posterior, ventral, and dorsal margins of the valve are designated as its anterior end (AE), posterior end (PE), lower end (LE) and upper end (UE).

Other characters are designated as follows:

Hinge line (HGL) is a straight line drawn through the point of the third bend of the anterior margin of the ligament pit, parallel to the upper margin of the posterior auricle;

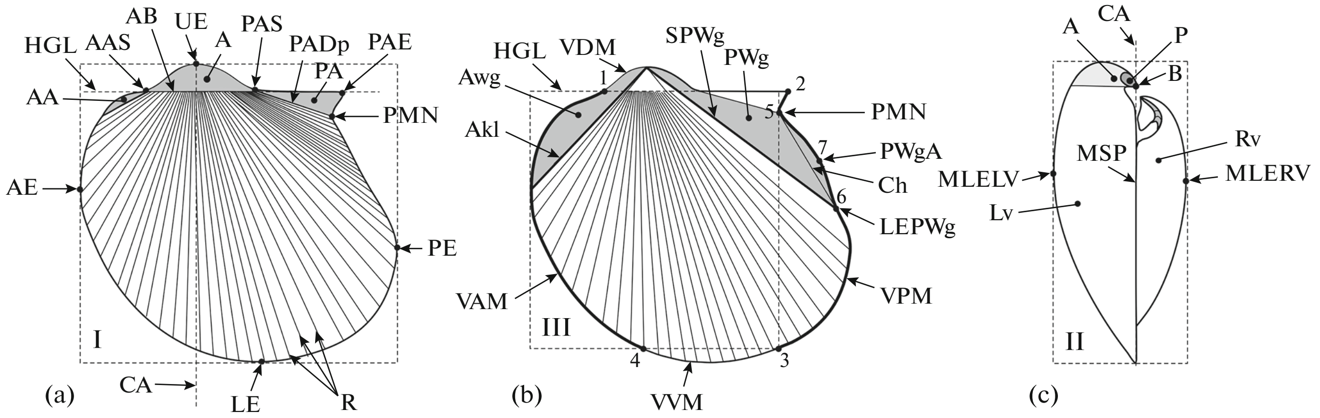

Fig. 11. Morphological elements of the *Meleagrinella* shell. (a, c) External view of the left valve; (b) lateral view of the shell, anterior margin. Abbreviations: Lv—Left valve, Rv—right valve, A—apex, B—beak, P—prodissoconch, Akl—valve anterior keel, PWg—posterior wing, Awg—anterior wing, CA—central axis; HGL—hinge line; UE—upper (dorsal) end of the valve; AE—anterior end of the valve; PE—posterior end of the valve; LE—lower (abdominal) end of the valve; MLELV—most lateral edge of the left valve, MLERV—most lateral edge of the right valve, VDM—valve dorsal margin (segment 1–2), VPM—valve posterior margin (segment 2–3), VVM—valve ventral margin (segment 3–4), VAM—valve anterior margin (segment 4–1), PA—posterior auricle, PAE—posterior auricle end, AA—anterior auricle; PADp—posterior auricle depression, SPWg—posterior wing sulcus, PMN—posterior margin notch, PWgA—posterior wing apex; LEPWg—lower end of the posterior wing, PwgA—posterior wing apex, Ch—posterior wing chord, R—ribs, MSP—midsagittal plane, AB—apex base, PAS—posterior auricle starting point, AAS—anterior auricle starting point.

Valve central axis (CA) is a straight line passing through the top end of the valve, perpendicular to the hinge line;

Beak (B) is a beak-shaped is a beak-shaped end of the left valve, with a prodissoconch (P) (primary veliger shell) at the apical point;

Apex (A)—part of the shell protruding over the hinge line. The apex has a top coinciding with the valve upper end (UE) and has an apex base (AB);

Apex base (AB) is the middle part of the hinge line limited by the valve dorsal margin;

Posterior auricle starting point (PAS) is the point of intersection of the hinge line with the apex base located closer to the posterior margin.

Anterior auricle starting point (AAS) is the point of intersection of the hinge line with the apex base located closer to the anterior margin of the valve;

Posterior auricle end (PAE) is an acute-angled bend (point 2) formed by the intersection of the upper and posterior margins of the valve;

Posterior margin notch (PMN) is a notch on the valve posterior margin below the posterior auricle end;

Posterior auricle (PA) is a triangular region in the posterior part of the valve near the hinge line, separated from the rest of the shell by a depression;

Posterior auricle depression (PADp) is a valve surface deflection line connecting the posterior auricle starting point (PAS) and the posterior margin notch (PMN) and separating the posterior auricle from the posterior wing;

Anterior wing (Awg) is a triangular area in the anterior part of the valve occupying a position between the anterior keel, anterior and upper margins of the valve;

Posterior wing (PWg) is a triangular undulating fold in the posterior part of the valve occupying a position between the posterior auricle and the main part of the valve, separated from above by the posterior auricle depression and by the posterior wing depression. The surface of the posterior wing is ornamented by tightly spaced radial ribs;

Anterior keel (Akl) is a valve surface inflection line connecting the upper and anterior ends of the valve;

Sulcus of posterior wing (SPWg) is a deflection line separating the fold of the posterior wing of the valve from the larger part of the valve on the side of the ventral margin (the term was introduced instead of the term "posterior keel" (Lutikov, 2021));

Lower end of posterior wing (LEPWg) is a notch (point 6) at the valve posterior end at the intersection of the sulcus of posterior wing (SPWg) and the valve posterior margin (VPM); the lower end of the posterior wing of the left valve can be located either above the posterior end of the valve or below it;

Posterior wing apex (PWgA) is a point (7) of maximum curvature of the posterior wing arc;

Posterior wing chord (Ch) is a line connecting the posterior margin notch (PMN) to the lower end of the posterior wing (LEPWg).

Most lateral edge of the left valve (MLELV) is a point of maximum curvature of the outer surface of the left valve;

Most lateral edge of the right valve (MLEKV) is a point of maximum curvature of the outer surface of the right valve;

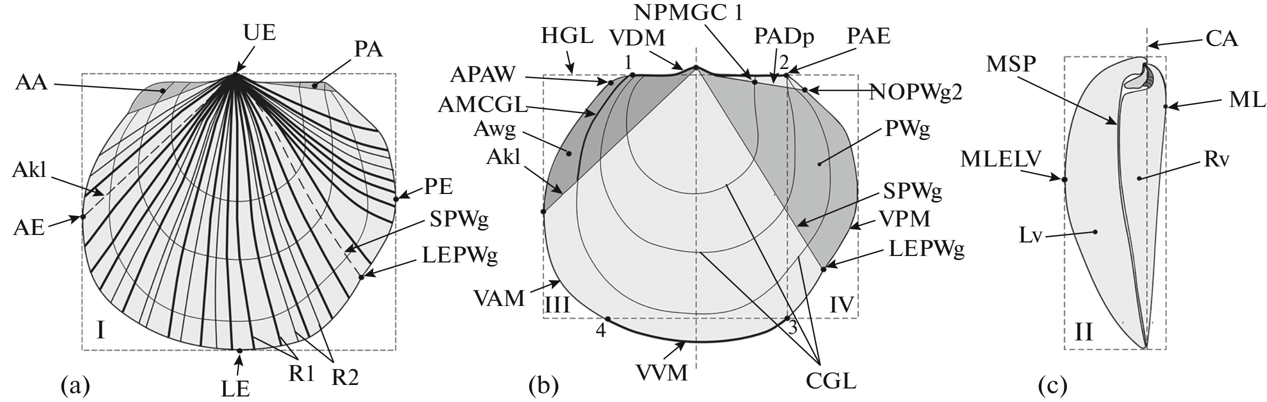

Fig. 12. Morphological elements of the *Arctotis* shell. (a, c) Left valve, external view, (b) anterior. Abbreviations: Lv—left valve, Pv—right valve, Akl—valve anterior keel, PWg—posterior wing, Awg—anterior wing, CA—central axis, HGL—hinge line, UE—upper (dorsal) end of the valve; AE—anterior end of the valve; PE—posterior end of the valve; LE—lower (abdominal) end of the valve; MLELV—most lateral edge of the left valve, MLERV—most lateral edge of the right valve, VDM—valve dorsal margin (segment 1—2), VPM—valve posterior margin (segment 2—3), VVM—valve ventral margin (segment 3—4), VAM—valve anterior margin (segment 4—1), PA—posterior auricle, PAE—posterior auricle end, AA—anterior auricle; PADp—posterior auricle depression, SPWg—sulcus of posterior wing, PMN—posterior margin notch, PWgA—posterior wing apex; LEPWg—lower end of the posterior wing, SPWg—sulcus of posterior wing, LEPWg—lower end of the posterior wing, R1—ribs of the first order, R2—ribs of the second order; MSP—midsagittal plane, CGL—concentric growth lines, AMCGL—anterior margin of the concentric growth line, APMAW—apical projection of the external margin of the anterior wing of the left valve, PMN 1—notch of the posterior margin of the concentric growth line, PMN 2—posterior margin notch, APAW—apical protrusion of the outer margin of the anterior wing .

For *Arctotis* shells, in addition to the basic morphological elements found in *Meleagrinella*, additional characters were introduced (Fig. 12):

anterior margin of the concentric growth line (AMCGL) is part of the growth con-center between the hinge line and the anterior keel;

concentric line notch (PMN 1) is a notch on teh posterior margin of the concentric growth line;

posterior wing notch (PWN) is a notch on the posterior margin of the valve below the end of the posterior auricle, lying at the intersection of the line connecting the notches of the growth con-centers and the valve posterior margin;

the apical protrusion of the outer margin of the anterior wing of the left valve (APAW) is the point of maximum distance of the interior margin valve from the anterior keel.

Ontogenetic Stages

A classification of ontogenetic stages in oxytomids has been proposed based on the study of ontogeny of the ligament area (Lutikov and Shurygin, 2010; Lutikov et al., 2010). In 2022, using SEM, new data on the morphology of the hinge in this bivalve group resulted in a profound change in the ontogenetic periodization compared to the previously existed one (Lutikov, 2023); this is emended in the present study. For the ontogenetic periodization of oxytomids, the general biological classification of ontogenetic development of animals was taken as a basis, distinguishing five stages—embryonic, nepionic, neanic, ephebic and gerontic (*Geologicheskii*..., 1978). Despite the fact that most of the growth stages identified in oxytomids only conditionally correspond to the generally accepted stages of ontogeny, their identification is fully justified by the fact that the appearance of new formations on shells of a fundamentally new nature as the shell grows emphasizes the staged nature of ontogeny and may be a consequence of natural rearrangements of genetic material in an organism (Glaser, 1998). The method of growth periodization of mollusk shells makes it possible to determine the boundaries of individual growth stages in oxytomids on shells of different sizes. One character was taken as the basis for growth periodization in the postembryonic phase—the position of the anterior margin of the ligament pit relative to the central axis of symmetry (Fig. 13).

The embryonic stage in modern bivalves covers the early period of shell ontogeny before the appearance of the first definite adult characters. This stage in general includes the formation of an egg, a trochophore-like larva and a veliger—a free-swimming larva. The veliger has a primary shell with two valves (prodissoconch). The anterior adductor appears at the veliger stage, (Nevesskaja et al., 2013). In the extant genus *Pteria*, which is similar in general morphology to *Oxytoma*, the pelagic larva at the embryonic stage reaches the size of a pinhead after 4—5 days and can settle on the substrate. However, the stage of a free-swimming larva can last much longer if there are no suitable conditions for settling (Davitashvili and Merklin, 1966). In heterogeneous bivalve families, larvae begin to settle after reaching different lengths: in Mytilidae—0.20—0.25 mm, in Ostreidae—0.20—0.40 mm (Zhilyakova, 2004), in Pectinida—0.13 mm (Sinelnikova, 1975). Oxytomid eggs and trochophore-like larvae are not known in fossils, and only the prodissoconch is known from embryonic stage fossils (Malchus, 2000). The dimensions of the prodissoconch measured in *Oxytoma* ex gr. *expansa* from the Middle Callovian (Erymnoceras coronatum Zone) (collections of A.A. Mironenko, Geological Institute of the Russian Academy of Sciences) in a sample of 15 specimens, vary—for the left valve from 0.27 to 0.35 mm, for the right valve from 0.29 to 0.37 mm. The hinge at the embryonic stage in bivalves has a distinct morphology (Malchus, 2004; Evseev and Kolotovkina, 2008; etc.), but in oxytomids it has not been studied. This stage of ontogeny of oxytomids is classified as the **larval stage.** The imprints that are sometimes preserved near the upper margin of the mold of the prodissoconch (Pl. I, fig. 1), show that the primary shell had a ctenodont-type provinculum (Nevesskaja, 2013) with one row of denticles, identical in shape and diverging in opposite directions sides from the apex. The succession of ligament pit shapes at subsequent ontogenetic stages was studied either on well-preserved adult shells (Pl. II, fig. 1) or on shells of different sizes in samples originating from the same core sample or from the same bed (Pl. II, figs. 5–7). The minimum length of oxytomid shells on which the hinge was examined was about 2.5 mm.

The nepionic stage in bivalves begins after the larva settles on the substrate and ends with the onset of puberty. Extant mollusks at this stage are characterized by relatively high rates of shell formation (Zolotarev, 1989). In oxytomids, this ontogenetic stage is divided into two periods—postlarval and juvenile.

The postlarval stage in *Oxytoma* and *Meleagrinella* begins after the shell length reaches 0.27–0.37 mm. In this period, as the mollusk increases in size, a triangular primary ligament pit is formed, a radially located prismatic microsculpture appears, and a byssal notch is formed. The size of the prodissoconch in *Arctotis* has not been measured, so the minimum shell size characterizing the beginning of the postlarval period in this genus has not yet been precisely established. The original shape of ligament pit, which appears in the postlarval period in *Oxytoma* and *Meleagrinella*, is preserved only on specimens smaller than 3.0 mm; in larger specimens it changes.

The juvenile stage in *Oxytoma* and *Meleagrinella* occurs after the shell reaches a length of about 1.0 mm. The beginning of the period is determined by the first bend of the anterior margin of the ligament pit. At this stage, as the ligament area expands and the size of the mollusk shell increases in different groups of taxa, subrectangular (Pl. I, fig. 1), wide-angled (Pl. I, fig. 2), subsymmetrical (Pl. I, fig. 3) 3) and acute-angled (Pl. I, fig. 4) types of ligament pit appear. The ligament pit outline, which was formed in the juvenile period, is preserved on specimens larger than 3.0 mm in *Meleagrinella (Praemeleagrinella)*. On specimens larger than 3.0 mm in *Meleagrinella* s.str. and *Meleagrinella (Clathrolima)* the outlines of the ligament pit change. Among the studied *Arctotis* shells, the minimum valve length was about 7 mm. This valve already shows all

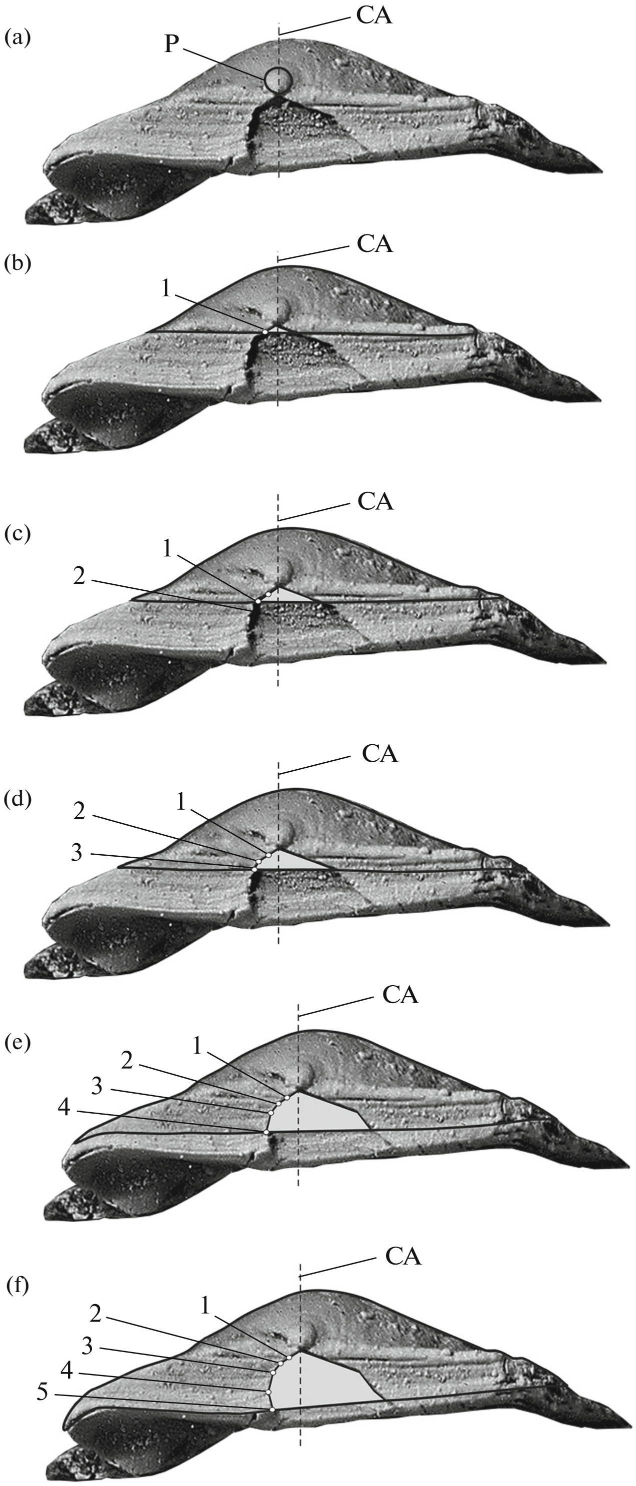

Fig. 13. External boundaries of the right valve and ligament pit in *Meleagrinella subolifex* at different growth stages: (a) larval, (b) postlarval, (c) juvenile; (d) subadult, (e) adult, (f) mature; CA—central axis, P—prodissoconch; 1–5—position of the lower end of the anterior margin of the ligament pit, fixing the growth stage boundaries: 1—postlarval, 2—juvenile, 3—subadult, 4—adult, 5—mature.

the characters of the subadult stage, so the size of the shell at the beginning of the juvenile period in *Arctotis* is not clearly established.

The neanic stage in extant bivalves begins with the onset of reproductive maturity. The size of the shell, the timing and duration of this stage can vary greatly among different families. For example, in Mediterranean and Black Sea Mytilidae, sexual maturity occurs during the first six months of life when the shell valves are 20–25 mm long (Zhilyakova, 2004). In Veneridae from the Sea of Japan, the minimum size of sexually mature mollusks is 40 mm at the age of 7–8 years, the maximum is 50–55 mm at the age of 9–10 years (Vlasenko and Kalinina, 2015). In sexually mature Tellinidae from the southern part of the Barents Sea, the shell length varies from 4.8 to 8.5 mm (Noskovich and Pavlova, 2017). The neanic stage of ontogeny of extant bivalves corresponds to the subadult period recognized in oxytomids.

The subadult stage in *Oxytoma* and *Meleagrinella* begins after the shell reaches a length of 2.5 mm and is fixed at the starting point of the second bend of the anterior margin of the ligament pit. As the ligament area expands, two subtypes of ligament pit can be distinguished: oblique (Pl. I, fig. 1) and expanding (Pl. I, fig. 3). In *Arctotis*, the minimum shell size at the beginning of the subadult stage is not clearly established; using the growth line on a specimen 7.0 mm long, it is fixed at the starting point of the second bend of the anterior margin of the ligament pit. As the ligament area expands, an inversed subtype of ligament pit is developed (Pl. II, fig. 3). At this stage, the angle of the ligament area to the midsagittal plane of increases, the byssal ear becomes subtriangular, the outline of the lower margin of the ligament pit changes from straight to curved, three subtypes of the lower margin of the ligament pit are formed: *straight* (Pl. II, figs. 1, 2, 5–7), *angular* (Pl. II, fig. 3) and *spoon-shaped* (Pl. II, fig. 4).

The ephebic stage of modern bivalves is characterized by the greatest changes in morphology. At this stage, sharp changes occur in the degree of inequivalvity, inequilaterality, elongation, and convexity of the shell in byssal-attached forms (Mytilidae, Dreissenidae) (Nevesskaja et al., 2013). At this stage, extant *Pteria* and *Pinctada*, which are close in morphology and ecology to oxytomids, lead a sessile lifestyle, attaching byssus to underwater rocks and stones. They grow very slowly: at 3 y.o. they reach a size of only 5–6 cm (*Zhizn'*..., 1968). The ephebic stage of ontogenesis of modern bivalves corresponds to the adult period recognized in oxytomids.

The adult stage in *Meleagrinella* and *Oxytoma* begins after reaching a length of 3.5 mm, in *Arctotis*—after reaching a length of about 7.0 mm and is fixed at the starting point of the third bend of the anterior margin of the ligament pit. This stage is characterized by significant changes occurring in the hinge plate and byssal block including many modifications of the ligament pit and the byssal ear.

The boundary between the adult and gerontic stages of ontogeny, even in modern bivalves, is not always clear. In long-lived bivalves, growth in most cases does not depend on age (Comfort, 1956). The gerontic stage in bivalves may be accompanied by the loss of some properties and functions or a slowdown in the rate of development. In some byssal Mytilidae from the Sea of Japan, the transition to this stage is marked by a sharp incurving of the valve margins, resulting in them becoming blunter and in the shell convexity increased.

It has been established that the onset of bending of the outer surface of molluskan shells occurs in years that are unfavorable for the growth of mollusks. This means that a slowdown in growth rates is a trigger for the processes of age-related changes in shell morphology (Zolotarev, 1989). The gerontic stage of ontogeny of modern bivalves conventionally corresponds to the mature period recognized in Oxytomidae. A meaningful description of maturity is difficult since the beginning of the period is not easy to determine.

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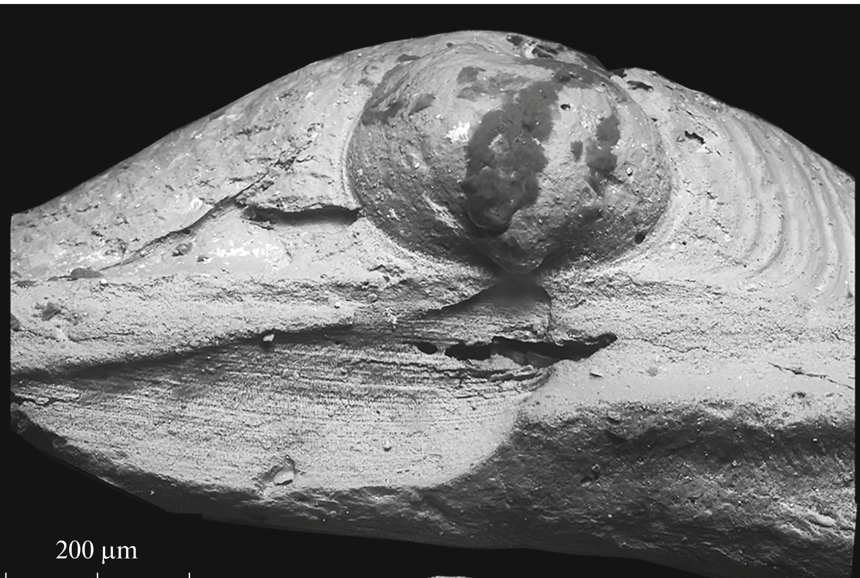
Plate I. fig. 1. *Oxytoma (Oxytoma)* ex gr. *expansa* (Phillips), specimen no. MB-1, ligament pit of the left valve of a subadult specimen; near the apex, on both sides, on the core of the prodissoconch, imprints from the denticles of the provinculum are preserved; primary pit is wide-angled—the outer angle of the front margin and the bottom margin of the ligament area form an obtuse angle (ca. 111°); after the first bend, the anterior margin of the ligament pit and the lower margin of the ligament area form a subright angle—rectangular ligament pit; after the second bend, the anterior margin of the ligament pit and the lower margin of the ligament area form an acute angle (ca. 52°)—oblique subtype of ligament pit, scale bar 0.2 mm; Ryazan Region, Mikhailov Cement Quarry; Middle Jurassic, Middle Callovian, Erymnoceras coronatum Zone (collections by A.A. Mironenko, GIN RAS). **fig. 2.** *Meleagrinella (Meleagrinella) prima* Lutikov, specimen no. TX-1/10. ligament pit of the left valve of a juvenile specimen; primary pit is subsymmetrical—the anterior margin of the ligament pit and the lower margin of the ligament area form an obtuse angle (ca. 155°); after the first bens, the anterior margin of the ligament pit and lower margin of the ligament area form an obtuse angle (ca. 108°)—wide-angled type of a ligament pit, scale bar 1.0 mm; Tenkelyakh Site, line 1060. Borehole 350. depth 31 m, Sample no. TX-1, Lower Jurassic, Lower Toarcian, Suntary Formation, third member (collected by I.V. Budnikov, SNIIGGiMS). **fig. 3.** *Arctotis (Arctotis) tabagensis* (Petrova), specimen no. MD-2/1, ligament area of the left valve of a small specimen (ca 10.0 mm); anterior margin of the ligament pit and lower margin of the ligament area form an obtuse angle (ca. 164°)—subsymmetrical ligament pit, scale bar 2.0 mm; Molodo River, Outcrop 8, Bed 2, Sample no. MD-2; Middle Jurassic, Lower Aalenian (collected by V.G. Knyazev, SNIIGGiMS). **fig. 4.** *Meleagrinella (Meleagrinella)* sp., specimen no. PZ/1–2, ligament pit of the left valve of a subadult specimen; primary pit is widely-angled—outer angle of the anterior margin and lower margin of the ligament area form an obtuse angle (ca. 113°); after the first bend, the anterior margin of the ligament pit and lower margin of the ligament area form an acute angle (82°)—acute-angled type of the ligament pit; scale bar 0.2 mm; Penza region, Pletnevsky Quarry, Member I; Middle Jurassic, Lower Bathonian (collected by A. Ippolitov).

Plate I

1



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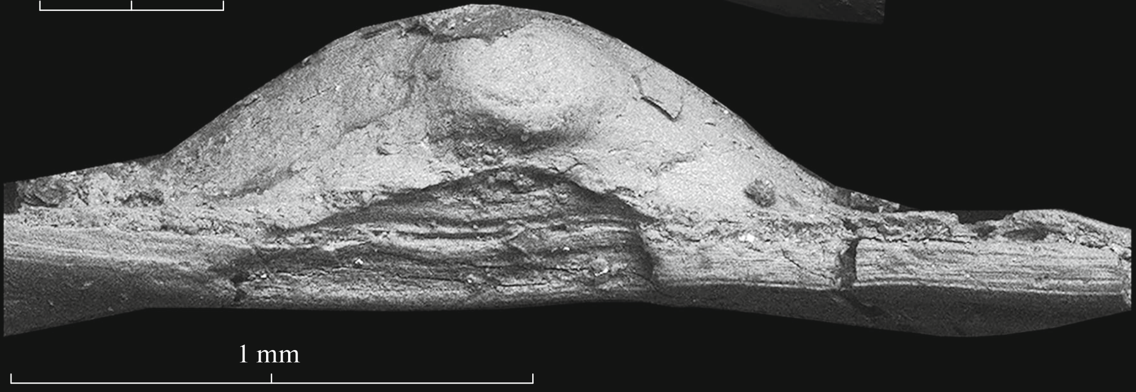

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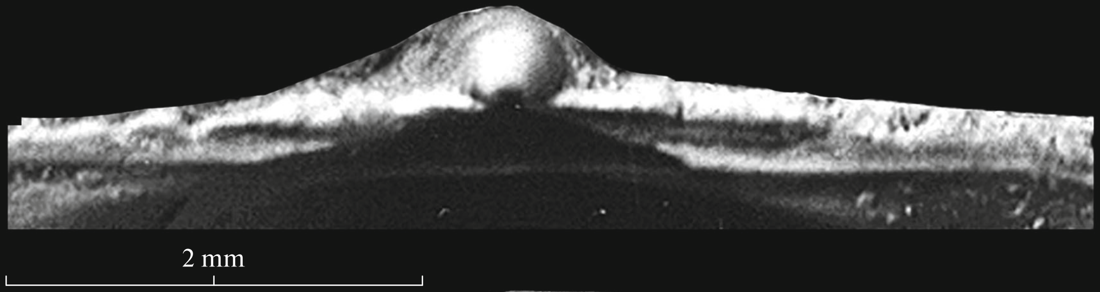

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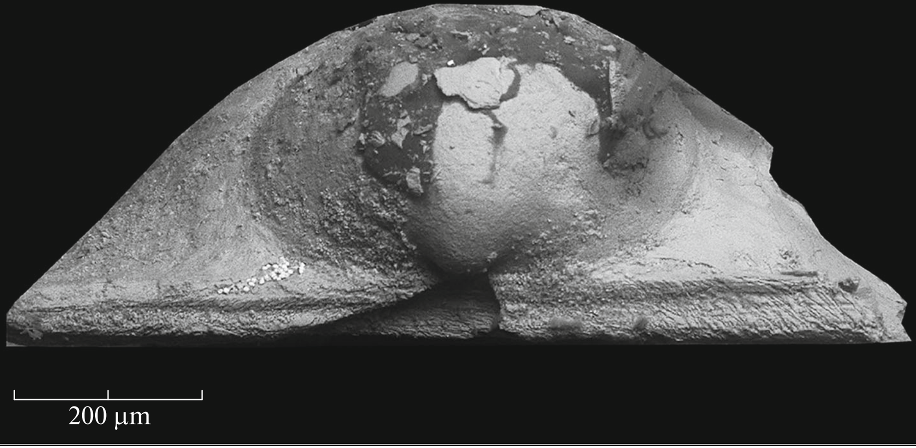

The mature stage in *Meleagrinella* is fixed by the starting point of the fourth bend of the anterior margin. During this age period, the most complex forms of ligament pit appear with several changes in the direction of movement of the lower end of the anterior margin. The mature period in *Praearctoris* is characterized by differentiation of the base of the ligament pit with the formation of a depression near the anterior margin. The mature period in *Arctotis* and *Oxytoma* is characterized by the loss of the triangular shape of the ligament pit—its upper part is rounded, resting on the umbo, the lateral sides of the pit diverge in the direction of the anterior and posterior margins of the valve. In *Arctotis* s. str. and *Arctotis (Canadarctotis)* in this period the byssal notch becomes overgrown, associated with the reduced ability of byssal attachment and the transition to cementation attachment strategy.

Typification of the Hinge Apparatus

The method of typification of the hinge, based on the establishment of typical characters for each growth stage, makes it possible to study ontogenetic changes in bivalves with a pterineoid type of hinge and to clarify the phylogenetic relationships between different taxa. The ligament pit of adult oxytomid shells retains traces of ontogenetic stages marked by sharp bends of the pit margins. The bends of later stages of ontogeny are clearly visible on the outer surface of the ligament platform; the bends of the initial stages are not always preserved on adult shells. Each bend corresponds to many seasonal growth lines located in parallel on the ligament site. The lines are preserved in the fossil state but are not always clearly visible. The sharp bends of the margins of the ligament pit are taken as the conventional boundaries of the life stages of the mollusk's ontogeny.

The ligament pit shape at the postlarval ontogenetic stage. A shared character in the structure of the ligament area in the entire family is the triangular shape of the primary ligament pit, the lateral margins of which diverge from the umbo in the direction of the anterior and posterior margins of the shell. The original triangular shape is preserved on shells 0.37–1.0 mm long. The angle between the lateral margins diverging from the apex of the ligament pit in the Callovian *Oxytoma* ex gr. *expansa* is about 105° (Pl. I, fig. 1), in the Pliensbachian *Meleagrinella (Praemeleagrinella) deleta* is about 110° (Pl. II, fig. 2), in the Toarcian *Meleagrinella (Meleagrinella) prima* is about 140° (Pl. I, fig. 3), in the Aalenian *Arctotis (Arctotis) tabagensis*—about 153° (Pl. I, fig. 3), in the Bathonian *Meleagrinella (Meleagrinella)* sp.—about 87° (Pl. I, fig. 4).

Ligament pit shape at the juvenile stage. The primary triangular shape of the ligament pit in oxytomids begins to change to a pentagonal shape already in very small shells 1.0–2.5 mm long. A shared character in the structure of the ligament at this stage is the formation of the first bend on the lateral margins of the ligament pit. Morphometric characteristics define four types of the ligament pit, which were determined by the outer angle formed by the anterior margin of the ligament pit and the lower margin of the ligament area. A ligament pit of a *rectangular type* is characterized by an angle of inclination of the anterior margin to the lower margin within the range of 85°–95° (Fig. 14a). A *wide-angled type* of the ligament pit is characterized by an angle of inclination of the anterior margin of the ligament pit to the lower margin within the range of 96°–155° (Fig. 14b). A *symmetrical type* of the ligament pit is characterized by an angle of inclination of the anterior margin of the ligament pit to the lower margin of more than 155° (Fig. 14c). An *acute-angled type* of the ligament pit is characterized by an angle of

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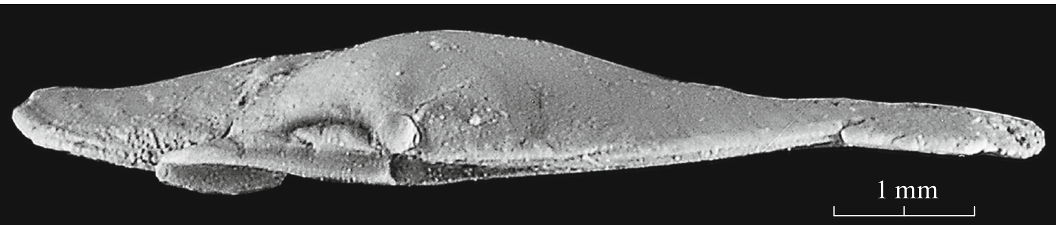
Plate II. fig. 1. *Oxytoma (Oxytoma) jacksoni* (Pompeckj), specimen no. AG-115/1, ligament area of the right valve of a juvenile specimen; anterior margin of the ligament pit and lower margin of the ligament area form an angle close to 90°—subrectangular ligament pit, scale bar 1.0 mm; Anabar Bar, west coast, Outcrop 5, Bed 90. Sample 115; Lower Jurassic, Upper Toarcian, *Pseudolioceras falcodiscus* Zone (coll. by O.A. Lutikov, core storage of GIN RAS). **fig. 2.** *Meleagrinella (Praemeleagrinella) deleta* (Dumortier), specimen no. Pr-21p/24, ligament pit of the left valve of a juvenile specimen; primary pit is widely-angled—anterior margin of the ligament pit and lower margin of the ligament area form an obtuse angle (ca. 137°); after the first bend, the anterior margin of the ligament pit form an obtuse angle (ca. 131°) with the lower margin—widely-angled type of a ligament pit, scale bar 0.2 mm; Pravobrezhnaya Field, line 524, Borehole 546.5, depth 18.6 m, Lower Jurassic, Upper Pliensbachian, Tyung Formation (coll. by I.V. Budnikov, SNIIGGiMS). **fig. 3.** *Arctotis (Paearctotis) marchaensis* (Petrova), specimen no. TX-1080-350-35/2, ligament area of the left valve of an adult specimen, angled subtype of the lower margin of a ligament pit, scale bar 2.0 mm; Tenkelyakh Site, line 1080, Borehole 350, depth 35 m, Sample no. TX-1080-1, Lower Jurassic, Upper Toarcian, Suntary Formation, Third Member (coll. by I.V. Budnikov, core storage of SNIIGGiMS). **fig. 4.** *Arctotis (Arctotis) tabagensis* (Petrova), specimen no. MD-2/2, ligament area of the right valve of a subadult specimen, spoon-like subtype of the lower margin of a ligament pit, scale bar 2.0 mm; Molodo River, Outcrop 8, Bed 2 (coll. by V.G. Knyazev, core storage of SNIIGGiMS); Middle Jurassic, Lower Aalenian. **figs. 5–7.** *Meleagrinella (Clarthrolima) subovalis* Zakharov, (5) specimen no. YuCh-3, ligament area of the right valve of a juvenile specimen; anterior margin of the ligament pit and the lower margin of the ligament area form an obtuse angle (ca. 139°)—widely-angled ligament pit, scale bar 1.0 mm; Chulym-Yenisei interfluve, Yuzhno-Chulym Field, Borehole 1, interval 1205.4–1213.4 m, Upper Jurassic, Kimmeridgian–Volgian (coll. by A.S. Turbina, core storage of SNIIGGiMS); (6) specimen no. YuCh-2, ligament area of the right valve of a subadult specimen; anterior margin of the ligament pit and lower margin of the ligament area in juveniles form an obtuse angle (ca. 87°)—subrectangular ligament pit, scale bar 1.0 mm; the same locality; (7) specimen no. YuCh-1, ligament area of the right valve of an adult specimen; anterior margin of the ligament pit and lower margin of the ligament area of the adult stage form an obtuse angle (ca. 52°)—acute-angled ligament pit, scale bar 2.0 mm; the same locality.

Plate II

1



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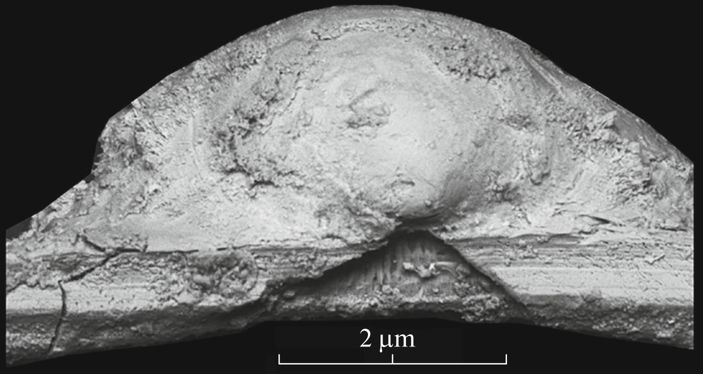

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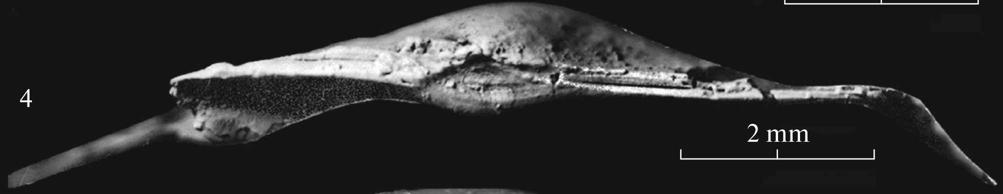

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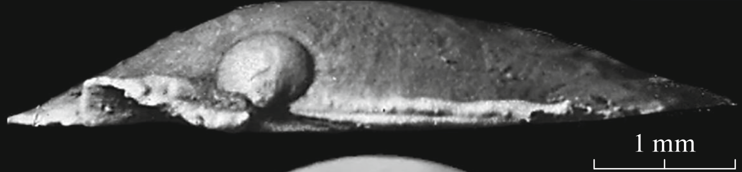

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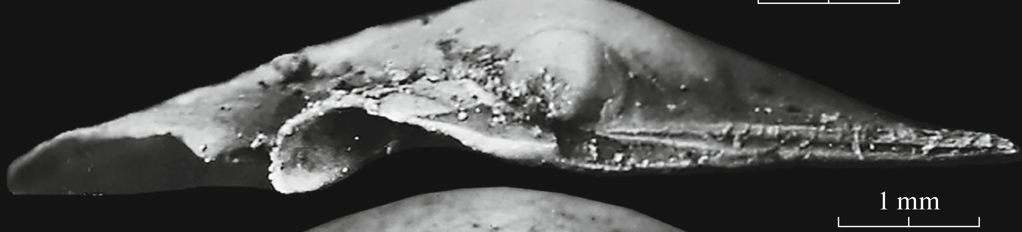

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Ligament pit types

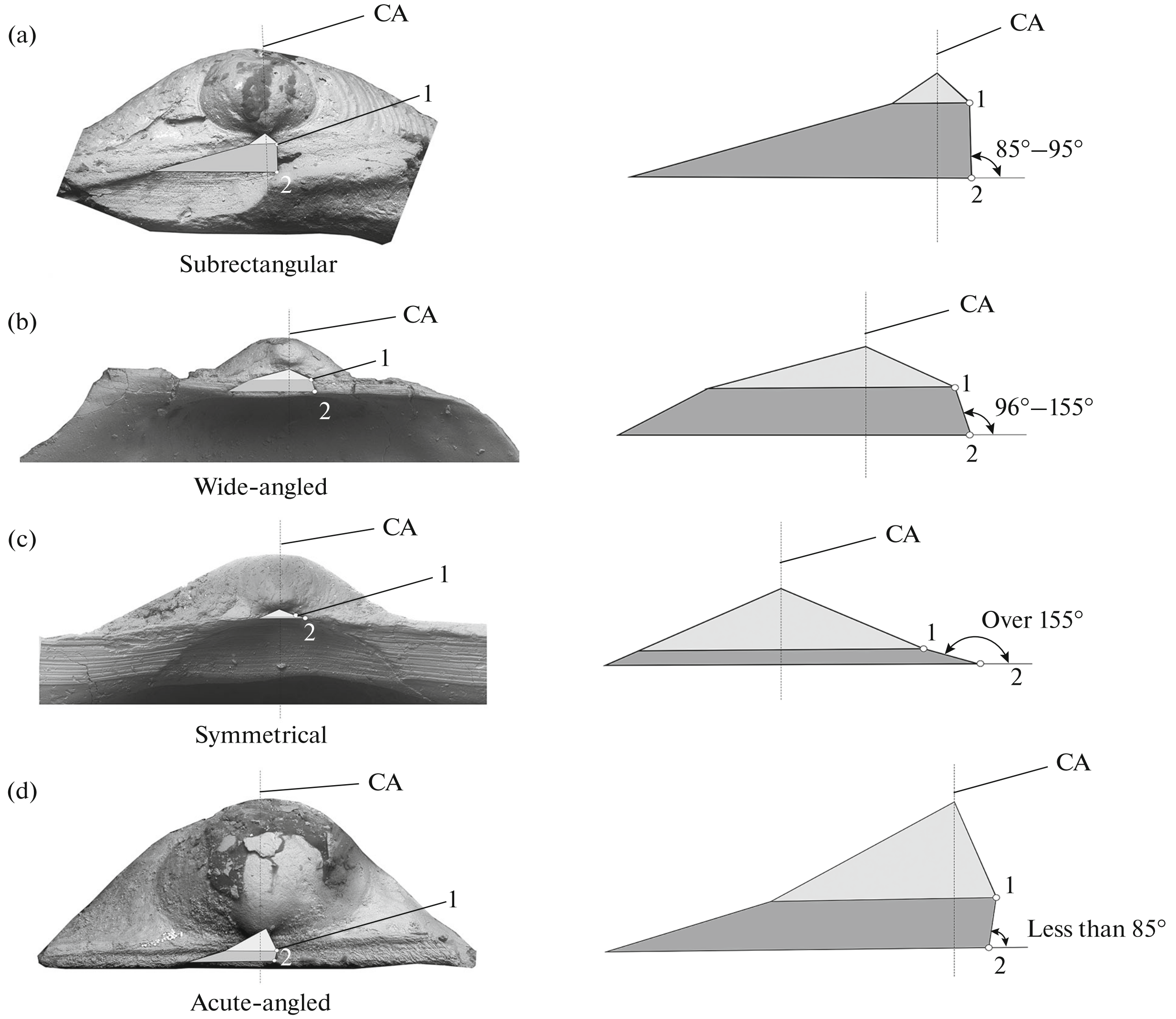


Fig. 14. Shape of the ligament pit at the juvenile stage; (a) subrectangular type (*Oxytoma* ex gr. *expansa*), (b) wide-angled type (*Meleagrinella prima*), (c) symmetrical type (*Arctotis sublaevis*), (d) acute-angled type (*Meleagrinella* sp.); CA—central axis; 1—lower end of the anterior edge of the ligament pit in the postlarval period, 2—lower end of the anterior edge of the ligament pit in the juvenile period; (a–c) growth stages of the ligament pit in two shades of gray: postlarval (light) and juvenile (dark).

inclination of the anterior margin of the ligament pit to the lower margin of less than 85° (Fig. 14c). The lower margin of the ligament pit at the postlarval and juvenile stages within the family has no bends and is of the *rectilinear type*.

Ligament pit shape at the subadult stage. At the subadult stage, the shape of the ligament pit in oxytomids begins to change already on very small shells about 2.5–3.0 mm long. During this period, a second bend is formed on the lateral margins of the ligament pit. Characteristics of the directions of movement of the lower end of the anterior margin of the ligament pit relative to the central axis define three subtypes of ligament pit. The pit, which after the first and second bend is characterized by a shift of the lower end of the anterior margin "right-to-right", belongs to the *oblique subtype* (Fig. 15a). The pit, characterized by a sequence of shifts of the lower end of the anterior margin "right-left," belongs to the *expanding subtype* (Fig. 15b). The pit, characterized by a sequence of shifts of the lower end of the anterior margin "left-right", belongs to the *inversed subtype* (Fig. 15c).

At the subadult stage, the outline of the lower margin of the ligament pit begins to change. The characteristics of the curvature of the lower margin of the ligament pit of the right valve define three subtypes of the lower margin. The *straight subtype* of the lower margin of the ligament pit is characterized by rectilinear outline (Fig. 15d). The *angular subtype* of the lower margin is characterized by knee-shaped asymmetrical outline (Fig. 15e). The *spoon-shaped* subtype of the lower

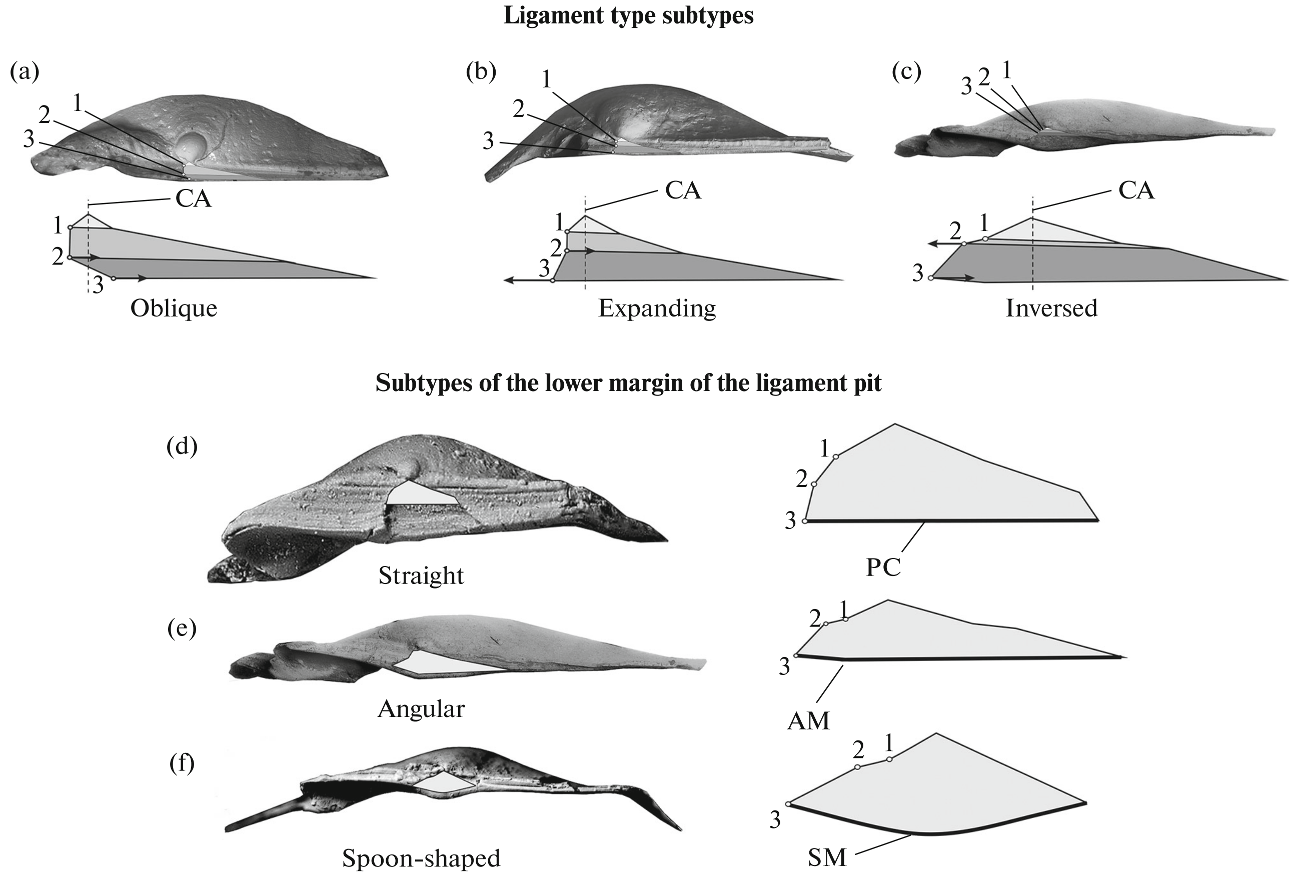


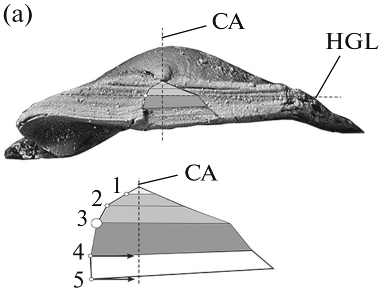
Fig. 15. Shape of the ligament pit at the subadult stage: (a–c) subtypes of the ligament pit (right valves): (a) oblique (*Oxytoma* ex gr. *expansa*); (b) expanding (*Meleagrinella doneziana*); (c) inversed (*Prearctotis marchaensis*); (d–f) subtypes of the lower margin of the ligament pit (right valves): (d) straight (*Praemeleagrinella subolifex*), (e) angular (*Prearctotis marchaensis*), (f) spoon-shaped (*Arctotis tabagensis*). CA—central axis of symmetry, PC—straight lower margin of the ligament pit, AM—angular lower margin of the ligament pit, SM—spoon-shaped lower margin of the ligament pit; (a–c) area of growth of the ligament pit in three shades of gray at three growth stage: postlarval (light-gray), juvenile (gray), subadult (dark gray); (d–f) the shape of the ligament pit at the subadult stage is shown in light gray. Circles with numbers indicate the bend points of the anterior margin.

margin is characterized by rounded symmetrical outline (Fig. 15f).

Ligament pit shape at the adult stage. At this stage, a third bend is formed on the lateral margins of the ligament pit. Characterization of the sequence of directions of shifts of the lower end of the anterior margin of the ligament pit on the right valve relative to the central axis gives an idea of the typical modifications of the ligament pit in adults. Typical forms of the ligament pit are represented by five modifications. After three bends of the anterior margin of the ligament pit, modification 1 is characterized by the sequence “right-right-right”, while the lower end of the anterior margin of the ligament pit of the right valve after the third bend is located to the left of the axis of symmetry (Figs. 16a, 16b). Modification 2 is characterized by a sequence of directions “right-left-right”, with the lower end of the anterior margin of the ligament pit after the third bend located to the left of the axis of symmetry (Fig. 16c). Modification 3 is characterized by a sequence of directions “left–right–right” (Fig. 16d). Modification 4 is characterized by the sequence “right–left–right”, with the lower end of the anterior margin of the ligament pit after the third bend located to the right of the axis of symmetry (Figs. 16e, 16f). Modification 5 is characterized by the sequence “right-right-right”, with the lower end of the anterior margin of ligament pit after the third bend located to the right of the axis of symmetry (Fig. 16g).

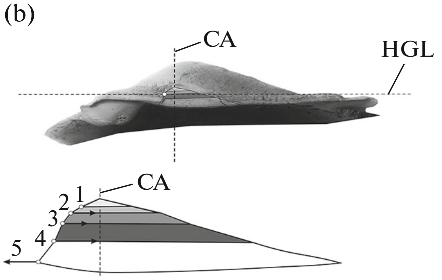
Shape of the ligament pit at the mature stage. At this stage, the fourth and subsequent bends are formed on the lateral margins of the ligament pit. In the mature period, the greatest variety of modifications occurs. At this age stage, from one to six changes in the direction of shifts of the lower end of the anterior margin of the ligament pit were recognized (Figs. 16a–16f). Typical forms of the ligament pit are represented by seven modifications. Modification 1a is characterized by the sequence of directions of movement of the lower end of the anterior margin ligament pit “right-right-right-right”, while the lower end of the anterior margin ligament pit of the right valve after the fourth bend is

(a)



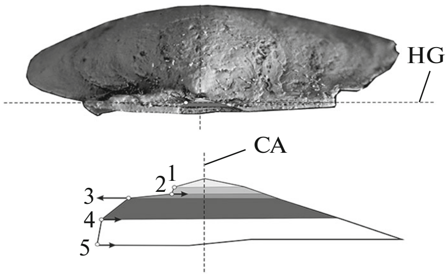
Modification 1a

(b)



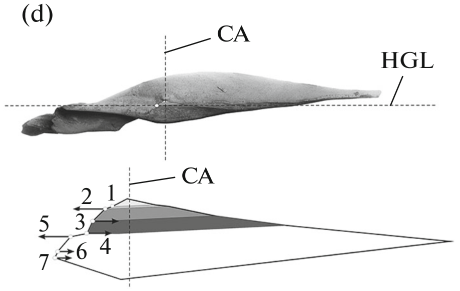
Modification 1b

(c)



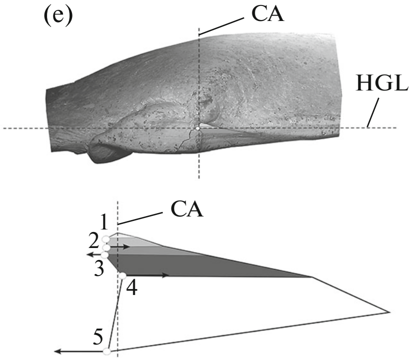
Modification 2

(d)



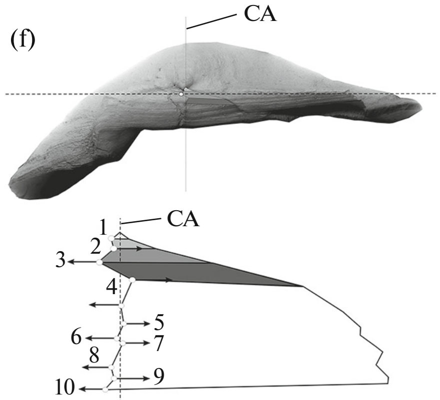
Modification 3

(e)



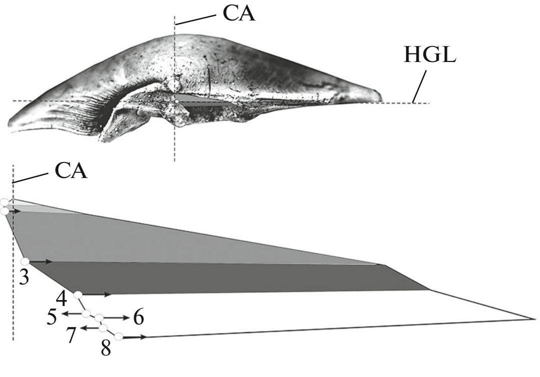
Modification 4a

(f)



Modification 4b

(g)



Modification 5

Fig. 16. Shape of the ligament pit at the adult and mature stages (right valve): (a) modification 1a (*Meleagrinella* (*Praemeleagrinella*) *subolifex*), (b) modification 1b (*Meleagrinella* (*Praemeleagrinella?*) *tiungensis*), (c) modification 2 (*Meleagrinella* (*Meleagrinella*) *prima*), (d) modification 3 (*Arctotis* (*Praearctotis*) *marchaensis*), (e) modification 4a (*Meleagrinella* (*Meleagrinella*) *doneziana*), (f) modification 4b (*Meleagrinella* (*Meleagrinella*) *ippolitovi* sp. nov.); (g) modification 5 (*Meleagrinella* (*Clathrolima*) *subovalis*). HGL—hinge line, CA—central axis; 1—10—lower end of the anterior margin of the ligament pit at the end of each growth stage: 1—postlarval, 2—juvenile, 3—subadult, 4—adult, 5—10—mature; arrows indicate the direction of bend of the anterior margin of the ligament pit at each growth stage; shades of gray indicate the corresponding growth stages of the ligament pit. The circles indicate the bend points of the anterior margin.

located to the left of the axis of symmetry (Fig. 16a). Modification 1b is characterized by the sequence “right-right-right-left”, with the lower end of the anterior margin ligament pit of the right valve after the fourth bend located to the left of the axis of symmetry (Fig. 16b). Modification 2 is characterized by the sequence “right—left—right—right” (Fig. 16c). Modification 3 is characterized by the sequence “left—

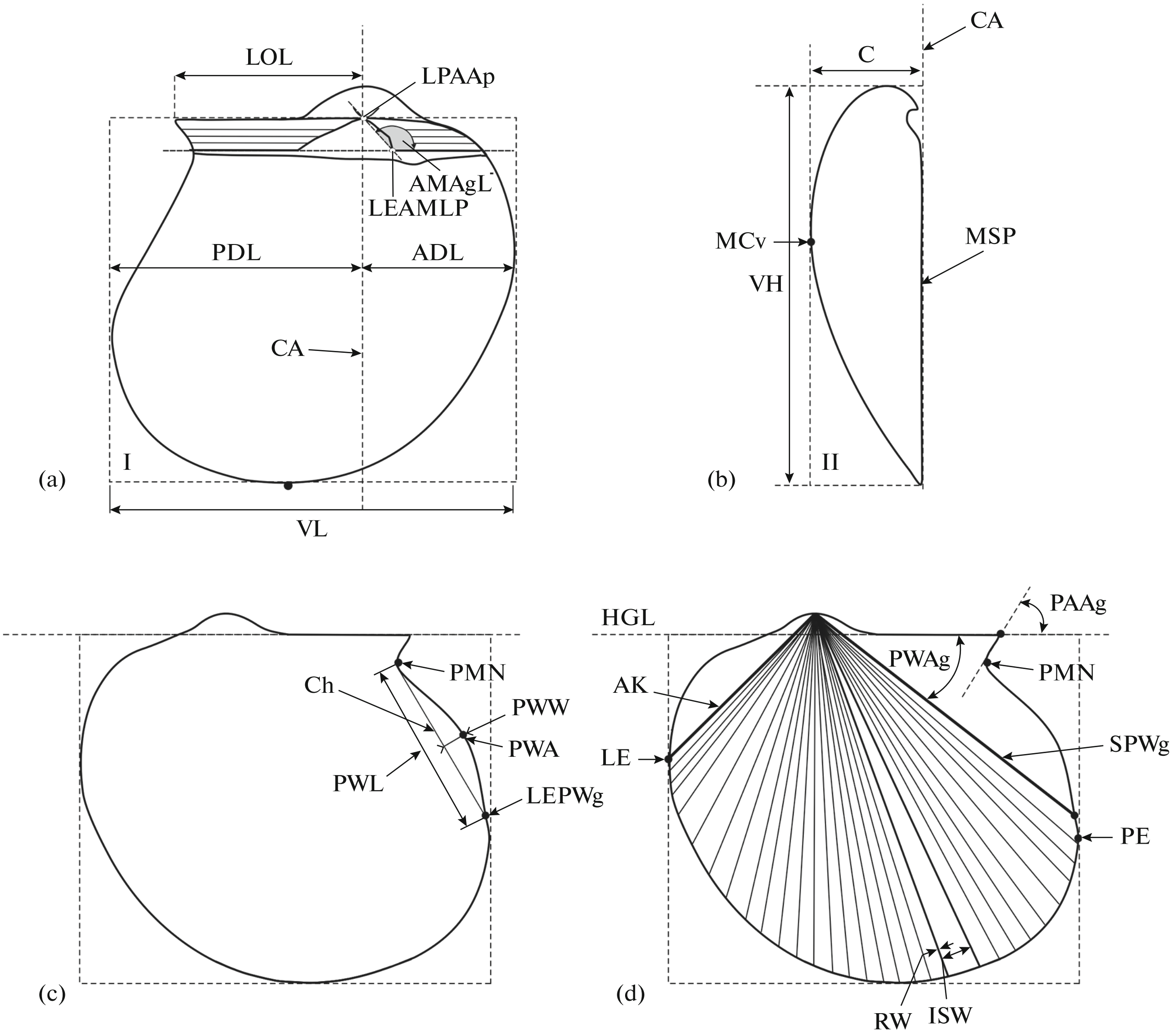


Fig. 17. Measurements of *Meleagrinella* shells. Morphological elements: LEPWg—lower end of the posterior wing, PMN—posterior margin notch, PWA—posterior wing apex, HGL—hinge line, AK—anterior keel, SPWg—posterior wing sulcus, Ch—posterior wing chord, MCv—maximum convexity of the valve. External metric characters: VH—valve height, VL—valve length, Cv—valve convexity, PDL—length of the posterior part of the valve, ADL—length of the anterior part of the valve, PWAg—posterior wing angle, PAAg—anterior auricle angle, RW—rib width, ISW—interrib space width, PWL—posterior wing length, PWW—posterior wing width. Internal metric characters: LOL—posterior outer ligament length, AMAgL—angle of the anterior margin of the ligament pit, LPAAp—ligament pit apex, LEAMLP—the lower end of the anterior margin of the ligament pit.

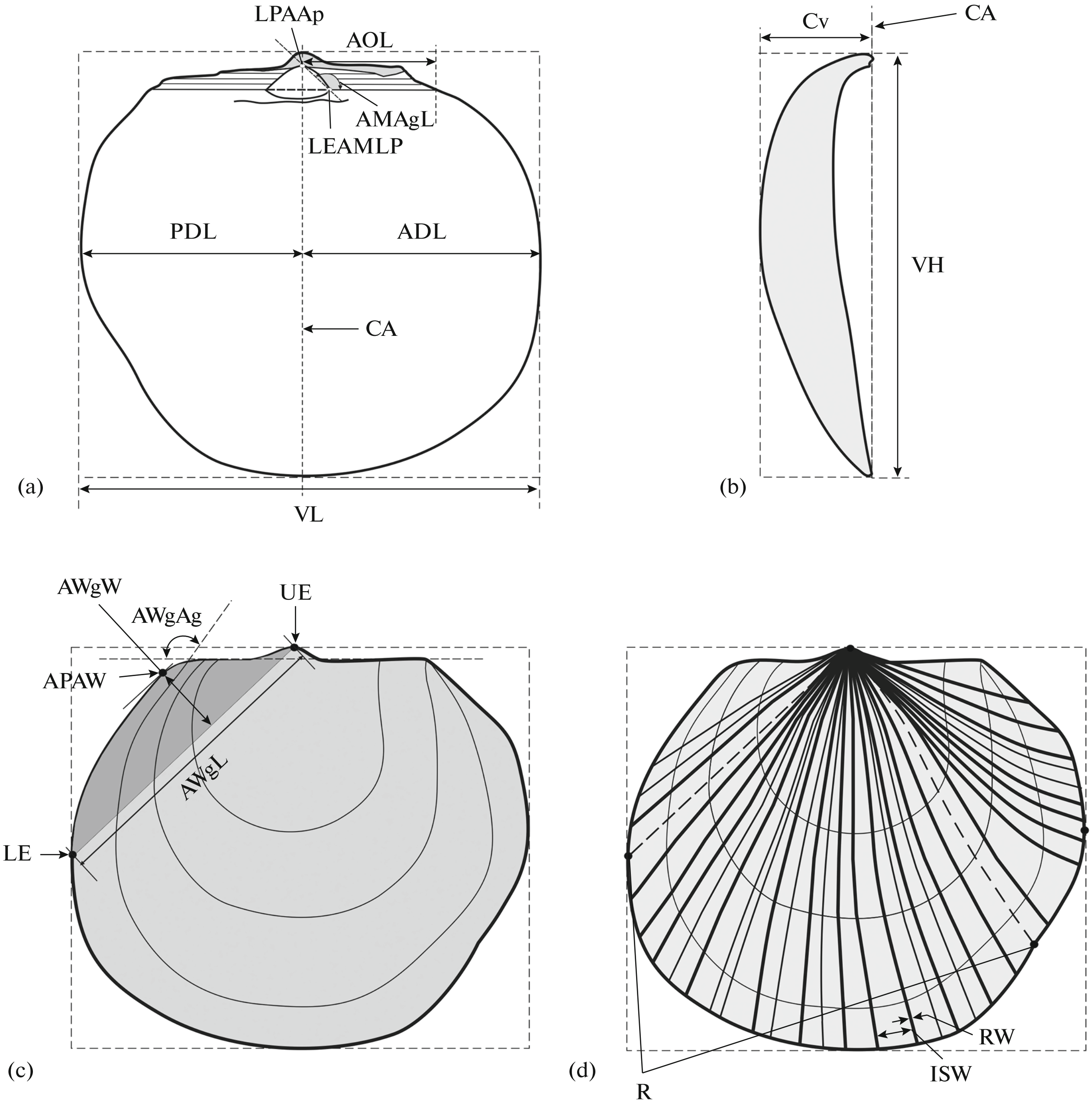


Fig. 18. Measurements of *Arctotis* shells. Morphological elements: CA—central axis, UE –upper end of the valve, AE—anterior end of the valve, APMAW—apical projection of the external margin of the anterior wing of the left valve. External metric characters: VH—height, VL—length, PDL—length of the posterior part of the valve, ADL—length of the anterior part of the valve, R—ribbing, ISW—interrib space width, Cv—convexity, RW—rib width, APAW—the apical protrusion of the outer margin of the anterior wing, AWgAg—anterior wing angle, AWgW—anterior wing width, AWgL—anterior wing length. Internal metric characters: AOL—length of the anterior outer ligament field, AMAgL—angle of the anterior margin of the ligament pit, LPAAp—ligament pit apex, LEAMLP—the lower end of the anterior margin of the ligament pit.

right–right–right" (Fig. 16d). Modification 4a is characterized by the sequence "right–left–right–left," while the outline of the ligament pit after the second bend is subrectangular (Fig. 16e). Modification 4b is characterized by the sequence "right–left–right–left," while the outline of the ligament pit after the second bend is oblique (Fig. 16f). Modification 5 is characterized by the sequence "right-right-right-right", with the lower end of the anterior margin of the ligament pit after the third bend located to the right of the axis of symmetry (Fig. 16g).

Morphometry

The morphometric method allows for a quantitative assessment of the characters used in the descrip-

Table 1. Gradations of the shells of *Meleagrinella* and *Arctotis*

Height (H), mm	Valve size gradations (1)	H/L	Valve outline gradations (2)	Angle of anterior margin of the ligament pit (AMLPAg)	Ligament pit shape gradations (3)
Less than 10	Very small	Less than 0.95	Very low	Less than 40°	Wedge-shaped
10.01–30	Small	0.95–0.97	Low	40°–84°	Acute-angled
30.01–50	Medium	0.98–1.02	Rounded	85°–95°	Subrectangular
50.01–70	Large	1.03–1.05	High	96°–155°	Widely-angled
Over 70	Very large	Over 1.05	Very high	Over 155°	Subsymmetrical
APL/VL	Valve symmetry gradations (4)	Cv/VH	Convexity gradations (5)	LOL/PDL	Length of the anterior outer ligament of the left valve gradations (6)
Lesss than 0.35	Strongly inequilateral	Less than 0.20	Weakly convex	Less than 0.6	Very short
0.35–0.40	Inequilateral	0.20–0.30	Moderately convex	0.60–0.70	Short
0.41–0.45	Moderately inequilateral	0.31–0.40	Strongly convex	0.71–0.80	Long
0.45–0.50	Equilateral	Over 0.40	Inflated	Over 0.80	Very long
Posterior wing angle (PWAg)	Posterior wing width of the left valve gradations (7)	PWgW/PWgL	Shape of posterior wing gradations (8)	RVH/LVH	Relative valve size gradations (9)
Less than 35°	Very narrow	Less than 0.05	Straight	Less than 0.80	Strongly inequilateral
35°– 40°	Narrow	0.05–0.10	Weakly concave	0.90–0.80	Moderately inequilateral
41°– 45°	Wide	0.11–0.15	Moderately concave	Over 0.90	Weakly inequilateral
Over 45°	Very wide	Over 0.15	Strongly concave		
Posterior auricle angle (PAAg)	Posterior auricle shape gradations (10)	R/VL	Ribbing density gradations (11)	(ISW/RW)	Interrib space gradations (12)
Less than 85°	Acute-angled	Less than 1.00	Sparsely ribbed	Less than 1.50	Very narrow
85°–105°	Subrectangular	1.00–2.00	Moderately ribbed	1.5–2.00	Narrow
Over 105°	Obtuse-angled	2.01–3.00	Medium-ribbed	2.01–2.50	Moderately wide
		3.01–4.00	Densely ribbed	2.51–3.00	Wide
		Over 4.00	Tightly ribbed	Over 3.00	Very wide
Anterior wing angle (AWgAg)	Gradations by the shape of the anterior wing of the left valve (13)	AAL / ADL	Anterior auricle of the left valve length gradations (14)	AWgW/AWgL	Anterior wing width of the left valve gradations (15)
Less than 80°	Acute-angled	Less than 0.45	Short	Less than 0.20	Narrow
85°–105°	Subrectangular	0.45–0.50	Long	0.21–0.22	Moderately wide
Over 105°	Obtuse-angled	Over 0.50	Very long	Over 0.22	Wide

tion of taxa and statistical testing of hypotheses about evolutionary transformations. To characterize the external morphological elements of *Meleagrinella* shells, measurements were taken using 12 characteristics. To characterize the internal characteristics of the elements of the ligament area, measurements were taken for four characteristics (Fig. 17). To characterize the external morphological elements of *Arctotis* shells, measurements were taken using 12 characteristics. To characterize the internal characteristics of the elements of the ligament area, measurements were taken for four characteristics (Fig. 18).

This method requires high quality material. Depending on the state of preservation of the material, when taking measurements using a caliper, only one parameter was measured—the height or length of the valve. To reduce the error, other parameters were measured from photographs of shells were vectorized using the tools of the Corel DRAW program.

The characters were assessed quantitatively on the basis of the gradation system used in the study of the genera *Arctotis* and *Meleagrinella* (Lutikov, 2023), with modifications. To characterize taxa based on quantitative assessment of characters, 15 sizes and ratios were used, converted into conditional gradations (Table 1):

(1) The size gradation of shells was based on the valve height (H).

(2) Height to length ratio (VH/VL) was used to gradate shells along the contour.

(3) Based on the magnitude of the external angle between the straight line connecting the top of the ligament pit and the lower end of the anterior margin ligament pit, and the lower margin of the ligament pad (UPCL), gradation was performed based on the shape of the ligament pit.

(4) The front length to length ratio (APL/VL) was used to grade shells based on symmetry.

(5) The ratio of convexity to valve height (Cv/VH) was used to gradate the degree of valve convexity.

(6) The ratio of the length of the posterior outer ligament to the length of the posterior part of the valve (LOL/PDL) was used for gradation along the length of the posterior auricle of the left valve.

(7) By the size of the posterior wing angle (PWAg) gradation was performed according to the width of the posterior wing of the left valve.

(8) The ratio of the width of the posterior wing to the length of the posterior wing (PWgW/ PWgL) was used for grading shells based on the shape of the posterior wing.

(9) Based on the ratio of the right valve height to the left valve height (RVH/LVH), valves were gradated using the ratio of the valve sizes.

(10) Based on the posterior auricle angle (PAAg) gradation was performed using the shape of the posterior auricle.

(11) The ratio of the number of ribs in the area between the anterior and posterior ends of the valve to the length of the valve (Rib/L) was used to estimate the ribbing density of the valves.

(12) The ratio of the width of the interrib spaces to the rib width (ISW/RW) was used to gradate shells using the width of the interrib spaces.

(13) Gradations by the shape of the anterior wing of the valves were determined by the angle (AWgAg) between the hinge line of the valve and the tangent to the anterior margin of the last visible growth con-center.

(14) Gradations by the length of the anterior auricle of the left valve were determined by the ratio of the length of the anterior outer ligament of the left valve to the length of the anterior part of the valve (POL/ADL).

(15) Gradations in the width of the anterior wing of the left valve were determined by the ratio of the anterior wing width to anterior wing of the left valve length (AWgW/AWgL).

(16) Gradations by ligament pit type were determined by the external angle of the anterior margin of the ligament pit to the lower margin of the ligament area (AngAMarLig) at the juvenile stage.

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CONFLICT OF INTEREST

The author of this work declares that he has no conflicts of interest.

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