ISSN 0869-5938, Stratigraphy and Geological Correlation, 2024, Vol. 32, No. 7, pp. 851–928. © Pleiades Publishing, Ltd., 2024.

Bivalve-Based Stratigraphy of the Toarcian of Eastern Siberia and Northeastern Russia (Family Oxytomidae Ichikawa, 1958). Part 2. Ontogeny. Classification and Taxonomic Assessment of Characters. Phylogeny. System of the Family Oxytomidae. Taxonomic Descriptions

O. A. Lutikov*

Geological Institute, Russian Academy of Sciences, Moscow, 119017 Russia

**e-mail: niipss@mail.ru*

Received October 16, 2023; revised January 25, 2024; accepted February 1, 2024

Abstract—The system of the family Oxytomidae (subfamily Oxytominae) was revised based on Mesozoic material from different stratigraphic levels, using our own and museum collections. Variability of the hinge plate and byssal block of shells in the ontogeny of these mollusks was assessed using the age periodization method. Taxa were classified using a posteriori character weighting. Relationships between taxa were established by the constant presence of a character or assembly of characters in morphologically similar taxa. To establish the relationship, the similarity of homologous characters was used—the shape of the ligament pit at the postlarval stage, the type of the ligament pit at the juvenile stage, the subtype of the ligament pit and the subtype of the lower margin of the ligament pit at the subadult stage, the type of the byssal furrow, the type of the byssal notch, the presence of a protuberance, the presence of an inclination of the ligament area relative to the shell axis. The phenoclines of these characters were identified and the directions of morphological evolution within the subfamily Oxytominae were reconstructed based on the study of ontogenetic and evolutionary variability in the shape of the ligament pit, byssal ear, and the anterior and posterior wing of the left valve. The chronoclines were reconstructed based on the chronological succession of taxa with unidirectional changes in characteristics. When the phenocline and chronocline coincided, probable phylogenetic relationships between the taxa were suggested. The transformation of the ligament pit of the Jurassic-Cretaceous *Meleagrinella* and *Arctotis* is accepted as the main cluster of the phylogeny of the family Oxytomidae in the Jurassic. Based on the phylogenetic reconstruction, the composition of the subfamily Oxytominae was emended. It contains three genera—*Oxytoma, Meleagrinella,* and *Arctotis*. Using the method of morphometric assessment of morphological characteristics, the index species of the Pliensbachian-Aalenian oxyto-zones and of the Beds with oxytomids were systematically described and compared with other species in the taxonomic clade.

Keywords: bivalves, classification, ontogeny, phylogeny, Jurassic System

DOI: 10.1134/S0869593824700023

INTRODUCTION

The structure of the hinge in the family Oxytomidae with description of the main morphological characteristics of the hinge plate was first studied by Pompeckj (1901). Based on the presence of similar elements in the hinge plate in *Pseudomonotis echinata* (Smith) from the Bathonian (Wiltshire, England) and in some “*Aucella*”, I. Pompeckj suggested a direct genetic connection between *Pseudomonotis* and *Aucella*. The genus *Pseudomonotis (=Meleagrinella)* was identified by him as the most likely ancestor of *Aucella* (=*Buchia*). Subsequent criticism of these views was based on evidence that the Early Oxfordian “*Aucella*” *impressae* Quenst. and *“A”. radiata* Trautsch., considered by I. Pompeckj to be the initial forms in the lineage of *Buchia*, in fact belonged to the genus *Meleagrinella* (Sokolov, 1912), as well as on finds of *Buchia* in the Middle Jurassic (Zakharov, 1981). Studies of the hinge structure in *Pseudomonotis (=Meleagrinella) echinata* var. *doneziana* Borissjak from the Bajocian of the Donetsk region (Kovalevka) and *Pseudomonotis (=Meleagrinella) subechinata* Lahuzen and *Oxytoma inaequivalvis* var. *borealis* Borissjak from the Callovian of the Vladimir region (Dmitrievy Gory) were conducted by A.A. Borissjak. When comparing Bajocian and Callovian taxa, he was the first to show differences in the shape of the ligament pit in *Pseudomonotis (=Meleagrinella)* from different stratigraphic levels (Borissjak, 1909). E.V. Ivanov discovered differences in the morphology of the ligament pit in *Pseudomono-*

tis (=Meleagrinella) doneziana, from the Bajocian of Western Kazakhstan, and in *Pseudomonotis (=Meleagrinella) echinata* from the Bathonian of England (Pompeckj, 1901). According to E.V. Ivanova, the shaped of the ligament pit in *Pseudomonotis (=Meleagrinella) echinata* is more similar to that of *Pseudomonotis (=Meleagrinella) subechinata* Lahusen, recorded by A.A. Borissjak from the Callovian, than to *Pseudomonotis (=Meleagrinella) doneziana* Borissjak (Ivanov, 1915). The structure of the hinge plate in *Eumorphotis (= Arctotis)* was first studied by A.A. Borissjak. He conducted studies of age-related changes in the ligament pit of *Eumorphotis (=Arctotis) lenaensis* Lahuzen from the Bajocian-Bathonian deposits of the Anabar River based on specimens from the collections of I.P. Tolmachev and E.V. Toll. A.A. Borissjak found differences in the shape of the ligament pit in small, larger and large specimens of *Eumorphotis (=Arctotis)* (Borissjak, 2014).

Further development of the systematics of *Meleagrinella* and *Oxytoma* was associated with studies of the pallial line and shell microstructure. Ichikawa was the first to establish that *Oxytoma* differs from Aviculopectinidae primarily in the discontinuous pallial line. He studied the mineral composition of valves in the species *Avicula (=Oxytoma) muensteri* (Goldfuss, 1835), which is the type species of the genus *Oxytoma*, and compared it with modern representatives of the genus *Pteria* Scopoli, 1777, which originally included the subgenus *Oxytoma* (Meek and Hayden, 1864). The genus *Pteria*, in the family Pteriidae Gray, 1847, has an aragonite inner layer. Unlike in *Pteria*, the endostracum of the left valve in *Oxytoma* is calcitic. In *Oxytoma* the prismatic layer is present only in the right valve, while in *Pteria* it is present in both valves. Based on these differences, K. Ichikawa assigned the genera *Oxytoma* Meek, 1864, *Meleagrinella* Whitfield, 1885, and *Maccoella* Etheridge, 1892 to the subfamily Oxytominae. K. Ichikawa considered the smaller byssal ear and radially oriented arrangement of prisms on the right valve to be additional diagnostic characters of the subfamily. K. Ichikawa included the characters of the hinge plate and byssal block as generic characters, pointing out that the ligament pit in *Oxytoma* is slanted from the apex towards the posterior margin of the shell, and the byssal ear is nearly tubular. When interpreting the phylogeny, K. Ichikawa considered the Triassic genus *Eumorphotis* from the subfamily Aviculopectininae Newell, 1938. as the putative ancestor of oxytomids. Following K. Ichikawa, in the second half of the twentieth century, generic affiliations of the North Siberian "*Pseudomonotis*" and "*Eumorphotis*" from the Jurassic and chalk (Ichikawa, 1958) have significantly changed. Based on the study of the structure of the hinge plate V.I. Bodylevsky recognized the genus *Arctotis*, which included a group of Jurassic and Cretaceous North Siberian species, previously classified either in *Pseudomonotis (Eumorphotis),* or in *Eumorphotis* and *Eumorphotis* (?) (Bodylevsky, 1960). All "*Pseudomonotis*" from the Hettangian, Pliensbachian, Lower Toarcian of Siberia, Northeastern Russia and the Far East were classified within *Meleagrinella* (Hayami, 1959; Koshelkina, 1963; Velikzhanina, 1966; *Polevoi*..., 1968). Following V.I. Bodylevsky, all "*Eumorphotis*" from the Upper Toarcian, Aalenian, Bajocian and Bathonian of Eastern Siberia, Northeastern Russia were classified within *Arctotis* Bodylevsky, 1960 (Koshelkina, 1960, 1963; Velikzhanina, 1966; Zakharov, 1966; Polevoy..., 1968; etc.). The morphology of the hinge plate and byssal block in *Arctotis* from the Late Jurassic of Antarctica was examined in detail by Crame (1985) and from the Late Jurassic deposits of Arctic Canada by Jeletzky and Poulton (1987). Ontogenetic and evolutionary transformations of oxytomid hinge plate were first described by the present author (Lutikov et al., 2009, 2010).

In order to unify some of the terminology used in this work, the following definitions are accepted: morphogenesis—the process of the emergence of new forms and structures in an individual and evolutionary development of organisms (Belousov, 1987). Phene is a distinct (profoundly different from others), hereditarily determined trait; phenotype is the totality of all morphological and physiological traits of an individual (Zavertyaev, 1983). Phenocline—phenetic series; chronocline—a succession of taxa that replace each other in successive beds, having unidirectional changes in the characteristic (Krassilov, 1977).

The material for studying morphogenesis was our own and museum collections collected at different stratigraphic levels. At the initial stage of research, taxa with a certain set of morphological characters were considered within the genera *Oxytoma, Meleagrinella, Arctotis*, based on the classification adopted in the "Treatise on Invertebrate Paleontology" (*Treatise*..., 1969). At the final stage, the classification was based on new data on the study of the hinge plate and byssal block in 29 taxa and a priori weighing of 31 characters. The hinge plate and byssal block were studied:

In five species of *Oxytoma*: Norian *Oxytoma czekanowskii* Teller, 1886; Early-Late Toarcian *Oxytoma kirina* Velikzhanina, 1973; Late Toarcian *Oxytoma startense* Polubotko, 1968; Late Toarcian-Aalenian *Oxytoma jacksoni* (Pompeckj, 1899); Callovian *Oxytoma* ex gr. *expansa* (Phillips), 1829;

In four species of *Praemeleagrinella*: Hettangian *Meleagrinella (Praemeleagrinella) subolifex* Polubotko, 1968; Late Pliensbachian *Meleagrinella* (*Praemeleagrinella*) *deleta* (Dumorter), 1869; *Meleagrinella* (*Praemeleagrinella?*) *tiungensis* (Petrova), 1947; *Meleagrinella* (*Praemeleagrinella*) *sparsicosta* (Petrova), 1947;

In six species of *Clathrolima*: Early Toarcian *Meleagrinella* (*Clathrolima*) *substriata* (Muenster), 1831, *Meleagrinella* (*Clathrolima*) sp.; Bathonian *Meleagrinella* (*Clathrolima*) *lamenti* Cossman, 1908, Middle Callovian *Meleagrinella (Clathrolima) braamburiensis* (Phillips), 1829; Late Callovian *Meleagri-*

nella (*Clathrolima*) *subechinata* (Lahusen), 1883; Kimmeridgian-Volgian *Meleagrinella* (*Clathrolima*) *subovalis* Zakharov, 1966;

In five species of *Meleagrinella* s.str.: Early-Late Toarcian *Meleagrinella* (*Meleagrinella*) *prima,* Lutikov, 2023; Bajocian *Meleagrinella* (*Meleagrinella*) *doneziana* (Borissjak), 1909; Bathonian *Meleagrinella* (*Meleagrinella*) sp.; Oxfordian *Meleagrinella (Meleagrinella) curta* (Whitfield), 1880;

In two species *Praearctotis*: Late Toarcian *Arctotis (Praearctotis) marchaensis* (Petrova), 1947, *Arctotis (Praearctotis) similis* Velikzhanina, 1966;

In three species of *Arctotis* s.str.: Aalenian *Arctotis* (*Arctotis*) *tabagensis* (Petrova), 1953; Aalenian-Bajocian *Arctotis* (*Arctotis*) *sublaevis* (Bodylevsky), 1958; Bajocian-Bathonian *Arctotis* (*Arctotis*) *lenaensis* (Lahuzen), 1886;

In two species of *Canadotis*: Oxfordian *Arctotis* (*Canadotis*) *simkini* (Voronetz), 1938; Volgian *Arctotis* (*Canadotis*) *canadese* Jeletzky et Poulton, 1987;

In two species of *Canadarctotis*: Volgian *Arctotis* (*Canadarctotis*) *intermedia* Bodylevsky, 1960; Berriasian-early Valanginian *Arctotis (Canadarctotis) anabarensis* (Petrova), 1953.

Using photographs, the hinge structures of the species *Meleagrinella* (*Meleagrinella*) *curta, Meleagrinella* (*Clathrolima*) *substriata,* and *Meleagrinella* (*Clathrolima*) *lamenti* were studied.

METHODS

Ontogeny was studied using methods of age periodization and typification of the hinge apparatus. Using the method of age periodization, the boundaries of individual ontogenetic stages in oxytomids were determined on shells of different sizes. Changes in the hinge plate in ontogeny in each taxon were studied by comparing the typical forms of the ligament pit for each growth stage.

In this work, when classifying organisms within the family Oxytomidae, character weighting, i.e., differentiated assessment of their taxonomic significance, was used as a key operation.

Phylogeny of the family Oxytomidae in historical (evolutionary) development was assessed by comparing the ontogenies of taxa from successive geological beds. To determine the direction of evolution of traits, several approaches were used, including the ontogenetic method, based on the basic biogenetic law—the transformation series of character states was polarized in accordance with the ontogenetic sequence of character states in the putative descendant. Along with it, a paleontological method was used, based on the assertion that the transformational series of characters should be polarized in accordance with the paleontological succession of character states. The third method of phylogenetic analysis used is the method of analogies. It is based on Vavilov's "Law of Homologous Series in Variation": if the phenocline is successfully polarized in one group, the direction of transformations in the other group should be considered similar (Rasnitsyn, 2002). All of these methods provide some scientific support for the proposed phylogeny of the family Oxytomidae, until and unless convincing evidence to the contrary is presented.

ONTOGENY

Ontogeny was reconstructed primarily through the study of samples consisting of shells of varying sizes from very small to large. Shells were studied at different stages of individual development, from the postlarval stage, which arose after the formation of the prodissoconch, to the mature stage, when the shape of the ligament pit changed greatly compared to the shape at early stages. Ontogenetic or age-related variability was interpreted as natural changes in the body that occurred during its individual development (ontogeny). Ontogenetic (age-related) variability was established based on a comparison of the typical forms of ligament pits of each ontogenetic stage.

Age-Related Variability of the Hinge Plate in Meleagrinella

The variability of the hinge plate in ontogeny in *Meleagrinella (Praemeleagrinella) subolifex* was studied using two samples from the Hettangian deposits of different facies of the Nordvik (Anabar Bay) and Lena-Anabar regions (Kyra River, Olenek River basin). The samples come from the lower parts of the Zimny and Kyrin formations, respectively. About 20 specimens were studied in each sample.

Postlarval stage. Measurements were taken along growth lines on a specimen from the Hettangian deposits of the Kyra River (basin of the Olenek River). The ligament pit is wide-angled. The outer angle of the anterior margin of the ligament pit is 146° (Pl. II, fig. 1).

Juvenile stage. Wide-angle ligament pit. The external angle of the anterior margin of the ligament pit is 145°.

Subadult stage. Oblique subtype of the ligament pit. External angle of the anterior margin of the ligament pit is 117°. Straight subtype of the lower margin of the ligament pit.

Adult stage. The external angle of the anterior margin of the ligament pit is about 100°. The ligament pit shape in all samples is represented by modification 1a.

Mature stage. Measurements were taken along growth lines on a specimen from the Hetthangian of the Kyra River (Olenek River basin) and Anabar Bay. The anterior margin forms an angle of 79°–90° with the lower margin of the ligament area. The posterior margin of the ligament pit of the left valve forms an angle of 90°–135° with the lower margin of the ligament area. The lower margin of the ligament pit in specimens from both samples is straight; the ligament area of the left valve lies in the midsagittal plane. The protuberance is semi-ellipsoidal, almost equal to the length of the anterior outer ligament (Pl. I, figs. 1, 2; Pl. II, figs. 1, 2).

The variability of the hinge plate in ontogeny in *Meleagrinella (Praemeleagrinella) sparsicosta* was studied using two samples from the Upper Pliensbachian of the Suntary region (Tyung River, Tenkelyakh Site). The samples come from the upper part of the Tyung Formation. About 10 specimens were studied in each sample.

Juvenile stage. No measurements taken.

Subadult stage. The measurements were taken from a specimen with a height of 10.0 mm. Straight subtype of the lower margin of the ligament pit. External angle of the anterior margin of the ligament pit 133°.

Adult stage. The measurements taken from a specimen 32 mm high from the Upper Pliensbachian deposits of the Tyung River. External angle of the anterior margin of the ligament pit 123°. The ligament pit form in all samples is represented by modification 1 (Pl. I, fig. 3).

Mature stage. The external angle of the anterior margin of the ligament pit is 90°. The lower margin of the ligament pit is straight, the ligament area of the left valve lies in the midsagittal plane. The protuberance is hemispherical, equal to half the length of the anterior outer ligament (Pl. I, fig. 3).

The variability of the hinge plate in ontogeny of *Meleagrinella (Praemeleagrinella?) tiungensis* was studied using two samples from the Upper Pliensbachian deposits of the Nordvik Region (Anabar River) and the Suntary region (Tenkelyakh Site). The samples come from the upper part of the Tyung Formation. About 10 specimens were studied in each sample.

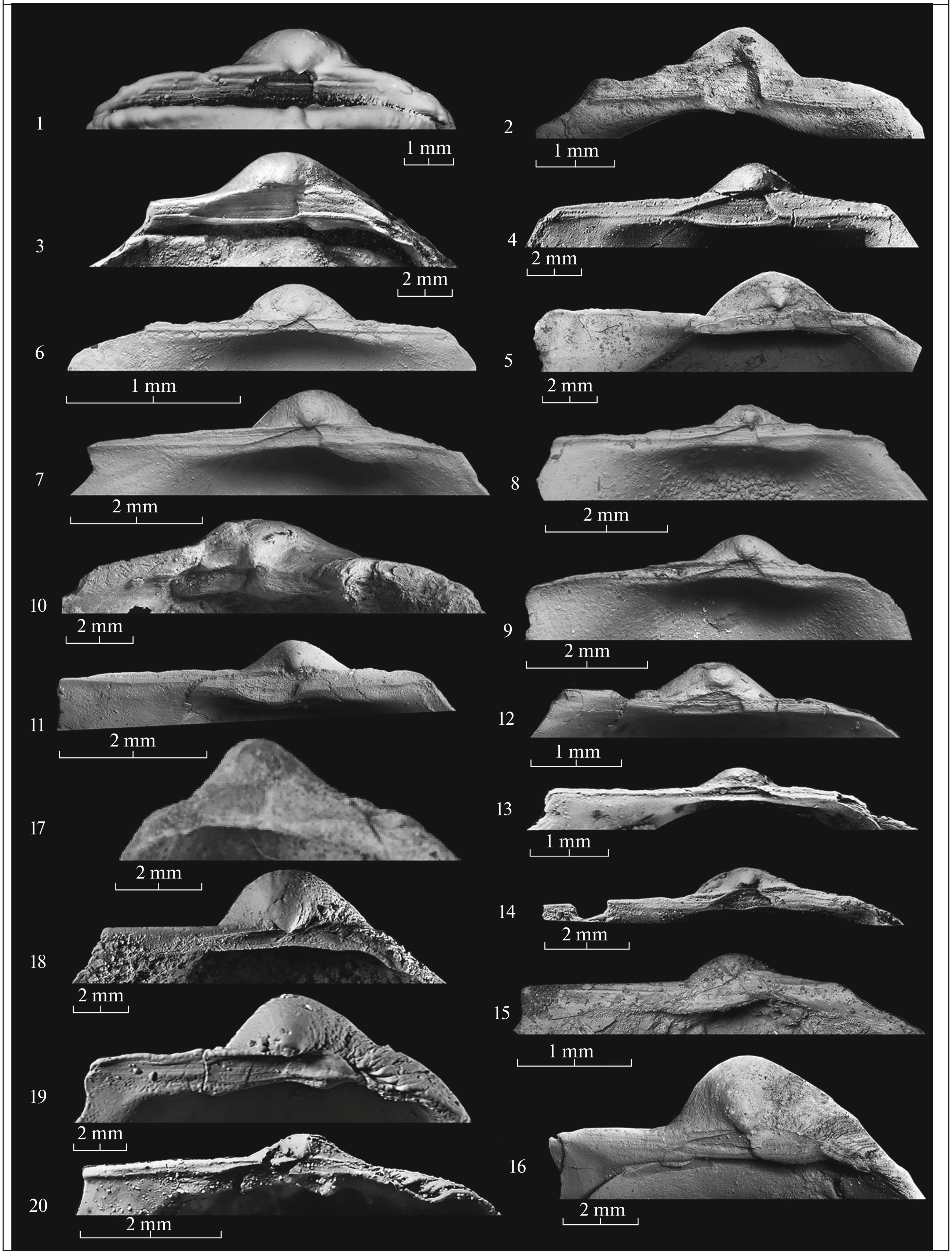
Postlarval stage. Ligament pit wide-angled.

Juvenile stage. Measurements were taken along growth lines on specimens from the Upper Pliensbachian of the Tenkelyakh Site. Wide-angle ligament pit. The external angle of the anterior margin of the ligament pit is 142°.

→

Plate I. Figs. 1, 2. *Meleagrinella (Praemeleagrinella) subolifex* Polubotko, (1) specimen no. KR-119/44, hinge plate of the left valve of a mature specimen, ligament pit, modification 1a, scale bar 1.0 mm; Kyra-Khos-Teryuteekh River, Outcrop 3, Kyra Formation, Bed 1, Sample 119; Lower Jurassic, Hettangian; (2) specimen no. AG-60/68, hinge plate of the left valve of a mature specimen, ligament pit, modification 1a, scale bar 1.0 mm; Anabar Bay, Outcrop 5, Zimnyaya Formation, Bed 18; Lower Jurassic, Hettangian. Fig. 3. *Meleagrinella (Praemeleagrinella) sparsicosta* (Petrova), specimen no. T-165/2, hinge plate of the left valve of a mature specimen, ligament pit, modification 1a, scale bar 2.0 mm; Tyung River, Outcrop 9, Bed 4, Sample 165; Lower Jurassic, Upper Pliensbachian. Figs. 4, 5. *Meleagrinella (Praemeleagrinella?) tiungensis* (Petrova), (4) specimen no. AN-15/2, hinge plate of the left valve of a mature specimen, ligament pit, modification 1b, scale bar 2.0 mm; Anabar River, Outcrop 3, Bed 1, Sample AN-15; Lower Jurassic, Upper Pliensbachian; (5) specimen no. TX 160-36-102.7/1, hinge plate of the left valve of a mature specimen, ligament pit, modfication 1b, scale bar 2.0 mm; Tenkelyakh Site, line 160, Borehole 36, depth 102.7 m, Tyung Formation, Lower Jurassic, Upper Pliensbachian. Figs. 6–9. *Meleagrinella (Praemeleagrinella) deleta* (Dumortier), (6) specimen no. Pr-21p/24, hinge plate of the left valve of a juvenile specimen, wide-angled type of the ligament pit, scale bar 1.0 mm; Pravobrezhnyi Site, line 524, Borehole 546.5, depth 18.6 m, Tyung Formation, Lower Jurassic, Upper Pliensbachian (coll. by I.V. Budnikov); (7) specimen no. no. Pr-21p/23, hinge plate of the left valve of a mature specimen, ligament pit, modification 1a, scale bar 2.0 mm; the same locality; (8) specimen no. Pr-21p/26, hinge plate of the left valve of a mature specimen, ligament pit, modification 1b, scale bar 2.0 mm; the same locality; (9) specimen no. Pr-21p/25, The hinge plate of the left valve of a mature specimen, ligament pit, modfication 1b, scale bar 2.0 mm; the same locality. Fig. 10. *Meleagrinella (Clathrolima) substriata* (Münster), syntype, specimen no. AS-VII-2087a, hinge plate of the left valve of a mature specimen, ligament pit, modification 5, scale bar 2.0 mm; Mistelgau, Germany, Lower Jurassic, Lower Toarcian (G. Münster collection). Fig. 11. *Meleagrinella (Clathrolima)* sp., specimen no. P-470-521/1, hinge plate of the left valve of a mature specimen, ligament pit, modification 5, scale bar 2.0 mm; Pravoberezhnyi Site, line 470, Borehole 521, depth 21.9 m, Suntary Formation, Lower Toarcian. Figs. 12–14. *Meleagrinella (Meleagrinella) prima* Lutikov, (12) specimen no. TX-1/10, The hinge plate of the left valve of a juvenile specimen, wide-angled type of the ligament pit, scale bar 1.0 mm; Tenkelyakh Site, line 1060, Borehole 350, depth 31 m, sample no. TX-1, Suntary Formation, Lower Toarcian; (13) specimen no. AG-103/1, hinge plate of the left valve of a subadult specimen, expanding subtype of the ligament pit, scale bar 1.0 mm; Anabar Bay, western coast, Outcrop 5, Eren Formation, Bed 76, sample no. AG-103, Lower Toarcian, Zugodactylites braunianus Zone; (14) specimen no. AG-103/2, hinge plate of the left valve of a mature specimen, ligament pit, modification 2, scale bar 2.0 mm, Anabar Bay, western coast, Outcrop 5, Eren Formation, Bed 76, sample no. AG-103, Lower Toarcian, Zugodactylites braunianus Zone. Fig. 15. *Meleagrinella (Meleagrinella) doneziana* (Borissjak), specimen no. MK-142/1, hinge plate of the left valve of a subadult specimen, expanding subtype of the ligament pit, scale bar 1.0 mm; Mangyshlak Peninsula, Bajocian (collected by L.F. Romanov L.F., coll. of Repin Yu.S.). Fig. 16. *Meleagrinella (Meleagrinella)* sp., specimen no. PZ/1-2, hinge plate of the left valve of a mature specimen, ligament pit, modification 4a, scale bar 2.0 mm; Lower Bathonian, Penza Region, Pletnevsky Quarry (coll. by A.P. Ippolitov). Fig. 17. *Meleagrinella (Clathrolima) lamenti* Cossman, specimen no. MNHN.F.J08231, holotype. Ligament plate of the left valve of a mature specimen, ligament pit, modification 5, scale bar 2.0 mm; Bathonian, Côte-d'Or, Burgundy, France (collection of M. Cossmann, Muséum national d'Histoire naturelle, France). Figs. 18, 19. *Meleagrinella (Clarthrolima) braamburiensis* (Phillips), (18) specimen no. MK-152/2, hinge plate of the left valve of a mature specimen, ligament pit, modification 5, pseudoligament platform with an underdeveloped protuberance, scale bar 2.0 mm; (19) specimen no. MK-152/4, hinge plate of the left valve of a mature specimen, ligament pit, modification 5, pseudoligamentous platform with a developed protuberance, scale bar 2.0 mm; Middle Callovian; Mangyshlak Peninsula (coll. by L.F. Romanov). Fig. 20. *Meleagrinella (Clarthrolima) subovalis* Zakharov, specimen no. YuCh-2, hinge plate of the left valve of a mature specimen, ligament pit, modification 5, scale bar 2.0 mm, South Chulyms area, Borehole 1, interval 1205.4–1213.4 m; Upper Jurassic, Kimmeridgian (coll. by A.S. Turbina, Siberian Research Institute of Geology, Geophysics and Mineral Resources (SNIIGGiMS)).

Plate I


1
1 mm
2
1 mm
3
2 mm
4
2 mm
6
1 mm
5
2 mm
7
2 mm
8
2 mm
10
2 mm
9
2 mm
11
2 mm
12
1 mm
17
2 mm
13
1 mm
18
2 mm
14
2 mm
19
2 mm
15
1 mm
20
2 mm
16
2 mm

Subadult stage. Measurements were taken along growth lines on specimens from the Upper Pliensbachian deposits of the Tenkelyakh Site, Anabar River and Tyung River. Oblique subtype ligament pit. The external angle of the anterior margin of the ligament pit is 106°–120° (Pl. I, figs. 4–5). Angular subtype of the lower margin of the ligament pit (Pl. II, figs. 4–5).

Adult stage. The external angle of the anterior margin of the ligament pit is 104°. The ligament area of the left valve lies in the midsagittal plane. The ligament pit form in all samples is represented by modification 2.

Mature stage. External angle of the anterior margin of the ligament pit is 121°. The protuberance is semi-ellipsoidal, almost equal to the length of the anterior outer ligament (Pl. I, figs. 4–5; Pl. II, figs. 4–5).

The variability of the hinge plate in ontogeny in *Meleagrinella (Praemeleagrinella) deleta* was studied using a sample (about 20 specimens) from the Upper Pliensbachian of the Vilyui region (Markha-Vilyui interfluve; Pribrezhnyi drilling site, line 524, Borehole 546.5, depth 18.6 m). The sample comes from the Tyung Formation.

Postlarval stage. Measurements were taken from one juvenile specimen (Pl. I, fig. 6). The primary ligament pit is wide-angle—the anterior margin and the lower margin of the ligament area form an angle of 137°.

Juvenile stage. Measurements were taken from one juvenile specimen (Pl. I, Fig. 6). The external angle of the anterior margin of the ligament pit is 131°. Wide-angle ligament pit.

Subadult stage. The measurements were taken from three adult specimens, represented by the left valves. The external angle of the anterior margin of the ligament pit is 134°, 106° and 112°, respectively (Pl. I, figs. 7, 8, 9). Oblique subtype of the ligament pit. The lower margin of the ligament pit is of a straight subtype.

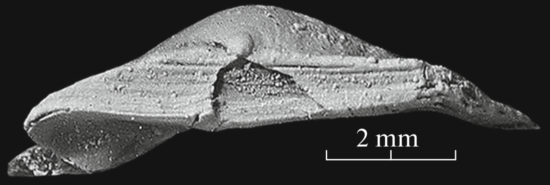
Adult stage. The measurements were taken from three adult specimens, represented by left valves. The external angle of the anterior margin of the ligament pit is 128°, 94° and 118°, respectively (Pl. I, figs. 7, 8, 9). The ligament pit form is represented by modification 1.

Mature stage. The ligament pit in the samples is represented by two modifications. In some specimens, the anterior margin of the ligament pit bends towards the posterior margin of the shell and forms an angle of 92° with the lower margin of the ligament area (Pl. I, fig. 7). The ligament pit form is represented by modification 1a. In other specimens, the anterior margin of the ligament pit bends towards the anterior margin of the shell and forms angles of 110° and 134° with the lower margin of the ligament area (Pl. I, figs. 8, 9). The ligament pit form is represented by modification 1b. The ligament area of the left valve lies in the midsagittal plane. The protuberance is semi-ellipsoidal, almost equal to the length of the anterior outer ligament (Pl. I, figs. 4–5; Pl. II, figs. 4–5).

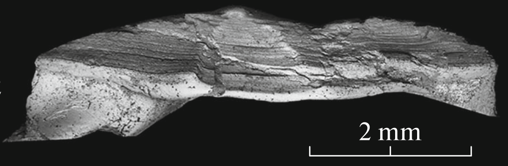
→

Plate II. Figs. 1, 2. *Meleagrinella (Praemeleagrinella) subolifex* Polubotko, (1) specimen no. KR-120/43, hinge plate of the right valve of a mature specimen, ligament pit, modification 1a, scale bar 2.0 mm, Kyra-Khos-Teruteekh River, Outcrop 3, Bed 1, Sample 119; Lower Jurassic, Hettangian; (2) specimen no. AG 60/72, hinge plate of the right valve of a mature specimen, ligament pit, modification 1a, scale bar 2.0 mm; Anabar Bay, Outcrop 5, Bed 18; Lower Jurassic, Hettangian. Fig. 3. *Meleagrinella (Praemeleagrinella) sparsicosta* (Petrova), specimen no. TX-160-38/81-1, hinge plate of the right valve of a mature specimen, ligament pit, modification 1a, scale bar 2.0 mm; Tenkelyakh Site, line 160, Borehole 38, depth 81.0 m, Upper Pliensbachian, Tyung Formation. Figs. 4, 5. *Meleagrinella (Praemeleagrinella?) tiungensis* (Petrova), (4) specimen no. T-94/2, The hinge plate of the right valve of a mature specimen, ligament pit, modification 1b with a curved lower margin, scale bar 2.0 mm, Tyung River, Outcrop 4, Bed 8, Tyung Formation, Lower Jurassic, Upper Pliensbachian (coll. by V.G. Knyazev), (5) specimen no. TX-160-36-102.7/2, hinge plate of the right valve of a mature specimen, ligament pit, modification 1b with a curved lower margin, scale bar 2.0 mm; Tenkelyakh Site, line 160, Borehole 36, depth 102.7 m, Tyung Formation, Lower Jurassic, Upper Pliensbachian. Figs. 6–8. *Meleagrinella (Praemeleagrinella) deleta* (Dumortier), (6) specimen no. Pr-21p/23, hinge plate of the right valve of a juvenile specimen, scale bar 1.0 mm; Pravoberezhnyi Site, line 524, Borehole 546.5, depth 18.6 m, Tyung Formation, Upper Pliensbachian; (7) specimen no. Pr-21p/24, hinge plate of the right valve of a mature specimen, modification 1b, scale bar 1.0 mm; the same locality; (8) specimen no. Pr-21p/25, hinge plate of the right valve of a mature specimen, modification 1a, scale bar 1.0 mm; the same locality. Figs. 9, 10. *Meleagrinella (Meleagrinella) prima* Lutikov, (9) specimen no. TX-1/2, hinge plate of the right valve of a mature specimen, ligament pit, modification 2 with a curved lower margin of the ligament pit, scale bar 1.0 mm; Tenkelyakh Site, line 1060, Borehole 350, depth 31 m, sample no. TX-2, Suntary Formation, Lower Toarcian; (10) specimen no. TX-1/3, hinge plate of the right valve of a mature specimen, ligament pit, modification 2 with a curved lower margin of the ligament pit, scale bar 2.0 mm; the same locality. Fig. 11. *Meleagrinella (Meleagrinella) doneziana* (Borissjak), specimen no. MK-142/2, hinge plate of the right valve of a mature specimen, ligament pit, modification 4a, scale bar 2.0 mm; Mangyshlak Peninsula, Bajocian (collected by L.F. Romanov, coll. of Yu.S. Repin). Fig. 12. *Meleagrinella (Meleagrinella)* sp., specimen no. PZ/1-1, hinge plate of the right valve of a mature specimen, ligament pit, modification 4b, scale bar 2.0 mm; Lower Bathonian, Pletnevsky stone quarry, Penza Region (coll. by A.P. Ippolitov). Fig. 13. *Meleagrinella (Clarthrolima) subechinata* (Lahusen), specimen no. DG/1-1, hinge plate of the right valve of a subadult specimen, oblique subtype of the ligament pit, scale bar 2.0 mm; Sample DG/4, horizon 3, Upper Callovian, Vladimir Region, Dmitrievy Gory. Fig. 14. *Meleagrinella (Meleagrinella) curta* (Whitfield), hypotype of specimen no. USNM PAL 12322b, hinge plate of the right valve of a mature specimen, ligament pit, modification 4b, scale bar 2.0 mm, South Dakota, Black Hills, USA, Oxfordian (collected by G. Newton, coll. of R.P. Whitefield, Smithsonian Museum, Washington, USA). Figs. 15, 16. *Meleagrinella (Clarthrolima) subovalis* Zakharov, (15) specimen no. 150/4138, hinge plate of the right valve of a mature specimen, ligament pit, modification 5, scale bar 2.0 mm, Lower Kimmeridgian, Levaya Boyarka River (collections by V.A. Zakharov, Center for Collective Use "Collection GEOCHRON", INGG SB RAS), (16) specimen no. 150/4145, type specimen, hinge plate of the right valve of an adult specimen, scale bar 2.0 mm, the same locality.

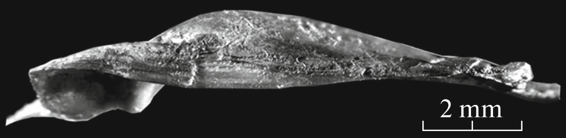
Plate II



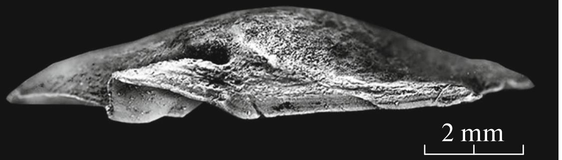
1



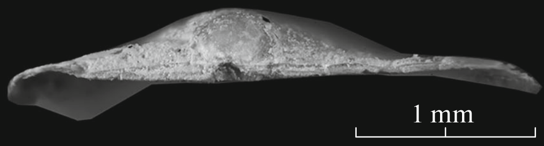
2



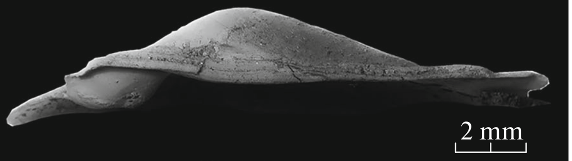
3



4

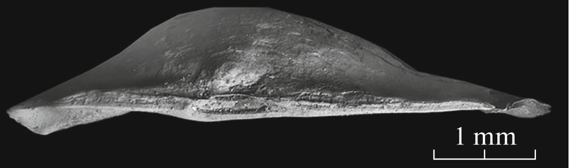


6

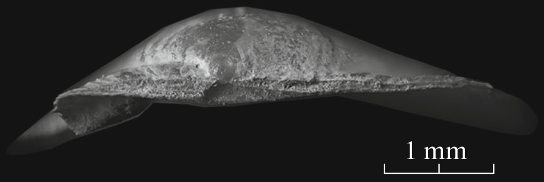


5

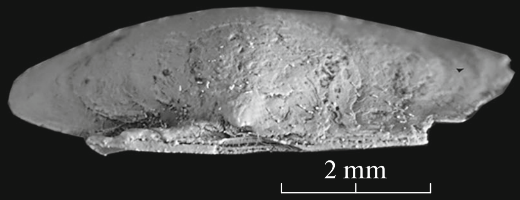
7



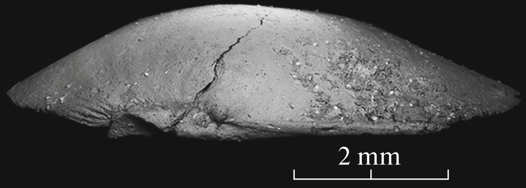
9



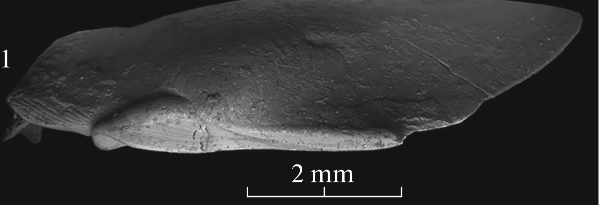
8



10



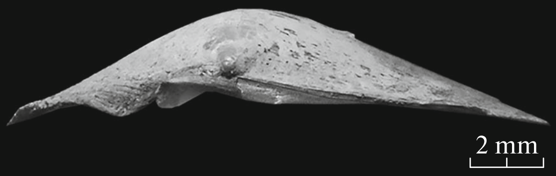
13



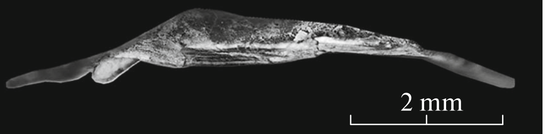
11

15

12



16



14

The ontogenetic variability of the ligament area in *Meleagrinella (Praemeleagrinella?) golberti* and *Meleagrinella (Clathrolima) substriata* has not been studied due to the unsatisfactory preservation of material from the lower part of the Toarcian—specimens are found either in concretions, and their hinge plates cannot be prepared, or in foliated shales, and their shells are severely deformed. A large specimen (about 32 mm) of *Meleagrinella (Clathrolima) substriata* from the Lower Toarcian of southern Germany (Banz, Posidonian Schist formation, Hildoceras bifrons Zone, Dactylioceras commune Subzone) has a preserved hinge plate. The ligament pit is characterized by oblique outline at all visible stages and is represented by modification 6. The anterior margin of the pit forms an acute angle of 72° with the lower margin of the ligament area. The lower margin of the ligament pit is almost straight; the ligament area of the left valve lies in the midsagittal plane. A hemispherical protuberance, which occupies about half the length of the anterior outer ligament, is present on the pseudoligamentous platform of the left valve, between the anterior margin of the ligament pit and the anterior margin of the valve (Pl. I, fig. 10). The variability of the hinge plate in ontogeny in *Meleagrinella (Meleagrinella) prima* was studied in three samples (about 20 specimens each) from the Lower Toarcian (Zugodactylites braunianus Zone) of the Nordvik region (Anabar Bay), Vilyui Region (Markha River and the Hannya-Tyukyan interfluve, Tenkelyakh drilling site, 1060, Borehole 350, depth 31 m). The samples come from the middle parts of the Eren and Suntary formations.

Postlarval stage. The primary ligament pit is subsymmetrical. In the Anabar specimen, the anterior margin of the ligament pit angle is 160° (Pl. I, fig. 12). The Tenkelakh specimen has an anterior margin of the ligament pit angle of 158° (Pl. I, fig. 13).

Juvenile stage. Measurements at the juvenile stage were taken from two left valves from sections of Anabar Bay and the Tenkelyakh Site, which have a width of less than 3 mm. Wide-angle ligament pit. In the Anabar specimen the angle of the anterior margin of the ligament pit is 120° (Pl. I, fig. 14), and in the Tenkelakh specimen it is 114° (Pl. I, fig. 13).

Subadult stage. Expanding subtype of the ligament pit. The anterior margin of the ligament pit angle is 148° (Pl. I, fig. 14).

Adult stage. The external angle of the anterior margin of the ligament pit is 92°. The ligament pit has modification 3 (Pl. I, fig. 14; Pl. II, figs. 9, 10). The lower margin of the ligament pit is slightly curved.

Mature stage. The lower end of the anterior margin forms an angle of 93° with the lower margin of the ligament area. The lower margin of the ligament pit in specimens from both samples is slightly curved.

The variability of the hinge plate in ontogeny in *Meleagrinella (Meleagrinella) doneziana* was studied in four samples: from the Bajocian of the Mangyshlak Peninsula (5 specimens; collection of Yu.S. Repin, housed at the department of Phanerozoic stratigraphy of the Geological Institute (GIN), Moscow); from the Bajocian deposits of the Donetsk Region (6 specimens; collection no. 311 of A.A. Borissjak, housed in the TsNIGR museum, St. Petersburg), from the Bajocian of western Kazakhstan (7 specimens; collection no. 2008 of E.V. Ivanov, housed in the TsNIGR museum, St. Petersburg), from the Bajocian of the Saratov Trans-Volgian region (Perelyubsky District).

Postlarval stage. The primary ligament pit is wide angled. The specimen from the Perelyubsky District has an anterior margin of the ligament pit angle of 132° (Pl. III, fig. 2).

Juvenile stage. Measurements at the juvenile stage were taken a specimen from the Perelyubsky District, which has a width of about 2 mm. Wide-angled ligament pit. The anterior margin of the ligament pit angle is 97° (Pl. III, fig. 2).

Subadult stage. Expanding subtype of the ligament pit. The angle of the anterior margin of the ligament pit in the specimen from the Bajocian of the Perelyubsky District is about 109° (Pl. III, figs. 1, 2).

Adult stage. The external angle of the anterior margin of the ligament pit is about 73°. The ligament pit of the specimen from the Bajocian of the Mangyshlak Peninsula has modification 3 (Pl. III, fig. 3).

Mature stage. The external angle of the anterior margin of the ligament pit is 106°. The lower margin of the ligament pit is straight (Pl. III, fig. 3).

Similar changes in ontogeny are observed in specimens from the Donetsk Region (Kovalevka Village), assigned by Borissjak (1909) to *Pseudomonotis echinata* var. *doneziana*, and *Meleagrinella* specimen from the Bajocian of western Kazakhstan (Ural River), which were attributed by E.V. Ivanov (1915) to *Pseudomonotis doneziana*. On the pseudoligamentous platform of the left valve, between the anterior margin of the ligament pit and the anterior margin of the valve, a

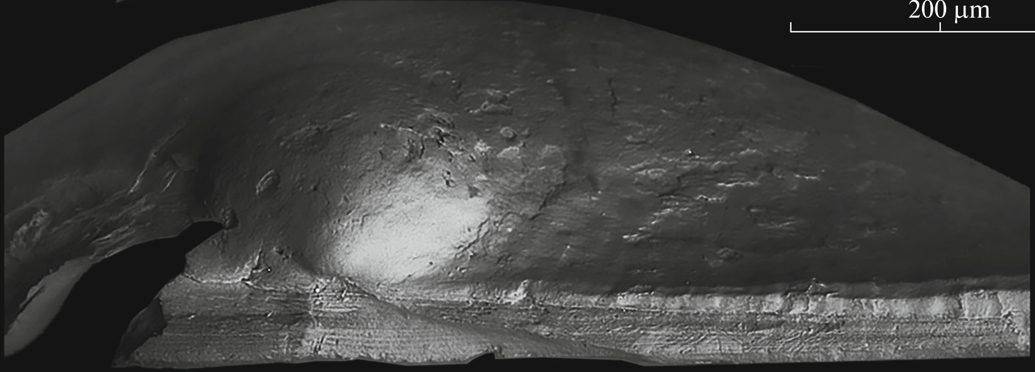
→

Plate III. Figs. 1–3. *Meleagrinella (Meleagrinella) doneziana* (Borissjak), (1) specimen no. PB-95/1, hinge plate of the left valve of a subadult specimen, expanding subtype of the ligament pit; scale bar 0.2 mm, Saratov Trans-Volga Region, Perelyubsky District, Borehole 103, depth 214 m, sample no. PB-95, Upper Bajocian; (2) specimen no. PB-95/2, hinge plate of the right valve of a subadult specimen, expanding subtype of the ligament pit, scale bar 0.5 mm, Saratov Trans-Volga Region, Perelyubsky District, Borehole 103, depth 214 m, sample no. PB-95, Upper Bajocian; (3) specimen no. MK-142/2, hinge plate of the right valve of a mature specimen, ligament pit, modification 4a, scale bar 1.0 mm; Mangyshlak Peninsula, Bajocian (collected by L.F. Romanov.). Fig. 4. *Meleagrinella (Meleagrinella) curta* (Whitfield), hypotype, specimen no. USNM PAL 12322b, hinge plate of the right valve of a mature specimen, ligament pit, modification 4b; scale bar 1.0 mm, South Dakota, Black Hills, USA, Oxfordian (collected by G. Newton, coll. of R.P. Whitefield, Smithsonian Museum, Washington, USA).

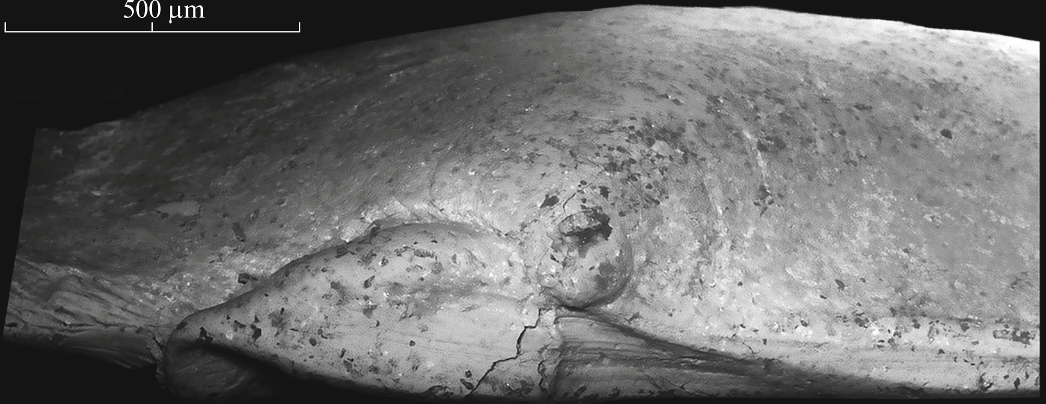
Plate III

1

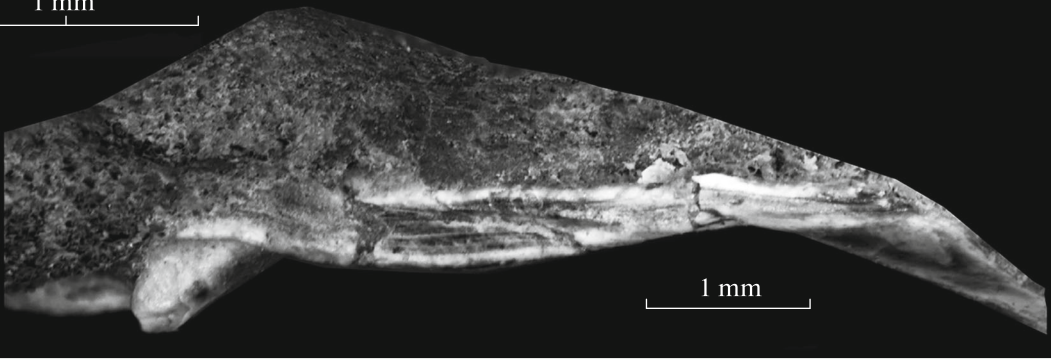
2



3



4



hemispherical protuberance is present occupying more than half the length of the anterior outer ligament.

The hinge plate in *Meleagrinella (Clarthrolima) braamburiensis* was studied using a sample from the Middle Callovian of the Mangyshlak Peninsula (collections of L.F. Romanov, collection of Y.S. Repin). It was not possible to observe the complete succession of ontogenetic changes in the ligament pit. The primary and juvenile ligament pit is not preserved in adult specimens. The ligament pit is of modification 5 (Pl. I, figs. 18, 19). The hinge plate of the type species *Meleagrinella (Meleagrinella) curta* was studied using photographs of type specimens from the Oxfordian of the Black Hills Mountains (South Dakota, USA; collection of H. Newton, housed in the National Museum of Natural History, USA, Washington). It was not possible to observe the complete sequence of ontogenetic changes in the ligament pit. The primary and juvenile ligament pit is not preserved in adult specimens. In adult specimens, the ligament pit is of modification 5 (Pl. II, fig. 14).

The hinge plate in the type species of the subgenus *Clathrolima—Meleagrinella (Clathrolima) lamenti—* from the Bathonian of the Côte-d'Or (Burgundy, France) was studied using photographs of the holotype, no. MNHN.F.J08231, illustrated on the website of the National Museum of Natural History (Paris, France). The ligament pit is of modification 5. The lower margin of the ligament pit in this specimen is almost straight, the ligament area of the left valve lies in the midsagittal plane. On the pseudoligamentous platform of the left valve, near the anterior margin of the ligament pit, a hemispherical protuberance is present, which is almost equal to the length of the anterior outer ligament (Pl. I, fig. 17).

The variability of the hinge plate in ontogeny in *Meleagrinella (Clathrolima) subovalis* was studied in a sample from the Kimmeridgian of the Chulym-Yenisei interfluve (Yuzhno-Chulymskaya area, Borehole 1, interval 1205.4–1213.4 m; 5 specimens; collection of A.S. Turbina, core storage facility of the Siberian Research Institute of Geology, Geophysics and Mineral Resources (SNIIGGiMS, Novosibirsk) and in a sample (30 specimens) from the Lower Kimmeridgian of the Boyarka River (collection of V.A. Zakharov, Central Collective Use Center "Collection GEOKHRON", INGG SB RAS, Novosibirsk).

Postlarval stage. The observation were made of a specimen from the South Chulym area, which has a width of about 5 mm. The primary ligament pit is wide-angled (Lutikov, 2024, Pl. II, fig. 5).

Juvenile stage. The ligament pit is wide-angled.

Subadult stage. Tapering subtype of the ligament pit. The outline of the pit is subrectangular (Lutikov, 2024, Pl. II, fig. 6).

Adult and mature stages. The outer angle of the anterior margin of the ligament pit is acute (Pl. I, fig. 20; Lutikov, 2024, Pl. II, fig. 7). The ligament pit in a specimen from the Kimmeridgian-Volgian deposits of the South Chulym area and specimens from the lower Kimmeridgian of the Levaya Boyarka River is of modification 5 (Pl. I, fig. 20). Some adult specimens retain subrectangular outlines that arose in the subadult stage (Pl. II, fig. 16). The ligament pit is of modification 5. On the pseudoligamentous platform of the left valve, near the anterior margin of the ligament pit, a hemispherical protuberance is present, which is equal to half the length of the anterior outer ligament.

Age-Related Variability of the Byssal Block in Meleagrinella

The byssal block of *Meleagrinella (Praemeleagrinella) subolifex* was studied using two samples from the Hettangian-Sinemurian of different facies of the Nordvik (Anabar Bay) and Lena-Anabar regions (Kyra River, Olenek River basin).

Juvenile stage. Byssal ear is quadrangular, rhomboid (Pl. IV, fig. 4).

Adult and mature stages. The byssal ear is quadrangular and has the shape of an inverted trapezoid. The upper margin of the ear is five times longer than the lower one. The anterior margin of the ear forms an acute angle with the hinge line. The byssal furrow is open, the byssal notch is 3.6 times shorter than the anterior auricle (Pl. IV, fig. 5). The variability of the byssal block in ontogeny in *Meleagrinella (Meleagrinella) prima* was studied in a sample (about 20 specimens) from the Lower Toarcian of the Hannya-Tyukyan interfluve (Tenkelyakh drilling site, 1060, Borehole 350, depth 31 m).

Juvenile stage. The byssal ear is quadrangular rhomboid (Pl. VI, fig 1a).

Subadult stage. The upper margin of the auricle extends in the direction of the anterior margin of the shell (Pl. VI, fig. 1a).

Adult and mature stages. The byssal ear is quadrangular, has the shape of an inverted trapezoid with a shortened base. The byssal furrow is open, the anterior auricle is 10.7 times longer than the byssal notch (Pl. VI, fig. 1b).

The variability of the byssal block in ontogeny in *Meleagrinella (Clarthrolima) subovalis* was studied in two samples: from the Kimmeridgian deposits of the Chulym-Yenisei interfluve (South Chulym area, interval 1205.4–1213.4 m; 5 specimens; collection of A.S. Turbina) and in a sample (30 specimens) from the Lower Kimmeridgian deposits of the Boyarka River (collection of V.A. Zakharov).

Juvenile stage. The byssal ear is quadrangular, the anterior margin forms an angle close to 90° with the lower and upper margins (Lutikov, 2024, Pl. II, fig. 5).

Subadult stage. The lower margin of the auricle extends in the direction of the anterior margin of the shell (Lutikov, 2024, Pl. II, fig. 6).

Adult and mature stages. The byssal ear is rhomboid, with an elongated lower margin (Lutikov, 2024, Pl. II, fig. 7). The anterior margin of the ear forms an acute angle with the lower margin. The byssal furrow is open, the anterior auricle is 3 times longer shorter than the byssal notch (Pl. IV, figs. 13a, 13b).

Age-Related Variability of the Hinge Plate in Arctotis

The variability of the hinge plate in ontogeny in *Arctotis (Praearctotis) marchaensis* was studied in three samples from the Late Toarcian of Eastern Siberia: Tenkelyakh Site (line 1080, Borehole 350, depth 35 m; 15 specimens), Anabar Bay (20 specimens) and the Markha River (20 specimens).

Postlarval stage. Measurements were taken along the growth lines of a 6.5 mm long specimen from the Upper Toarcian of the Tenkelyakh Site. Wide-angled ligament pit. The external angle anterior margin of the ligament pit 152°.

Juvenile stage. Measurements were taken along the growth lines of a specimen 12.3 mm long. Symmetrical ligament pit type. The anterior margin of the ligament pit angle is 169° (Pl. V, fig. 2).

Subadult stage. Inversed subtype of the ligament pit. The anterior margin of the ligament pit angle is 130°. Angular subtype of the lower margin of the ligament pit (Pl. V, fig. 2). The ligament area is inclined relative to the midsagittal plane.

Adult and mature stages. In all studied specimens, the ligament pit has modification 4. The length of the ligament pit is 0.38 times the length of the ligament area. In specimens originating from the upper part of the Toarcian section on the Markha River, the base of the ligament pit is heterogeneous, has a deepened area adjacent to the anterior margin of the ligament pit and a flattened area near the posterior margin of the ligament pit (Pl. V, fig. 3). A similar differentiation of the ligament pit was observed in specimens from the Nordvik region (Anabar Bay) (Pl. V, fig. 4). This depressed area is presumably the first stage of resilifer formation. The ligament area is three times wider than the pseudoligamentous platform (Pl. V, fig. 1). The lower margin of the pseudoligamentous platform of the left valve has a concavity corresponding to the geniculate bend of the lower margin of the ligament area of the right valve. On the pseudoligamentous platform of the left valve, near the anterior margin of the ligament pit, a hemispherical protuberance is present, which is equal to a quarter of the length of the anterior outer ligament. The inclination of the ligament area increases compared to the juvenile stage (Pl. V, fig. 1).

The variability of the hinge plate during ontogeny in *Arctotis (Praearctotis) similis* was studied in two samples from the Upper Toarcian deposits of the Motorchuna River and Cape Tsvetkov.

Postlarval stage. Measurements were taken from large specimens along growth lines. Wide-angled ligament pit. The external angle of the anterior margin of the ligament pit is about 153° (Pl. V, fig. 3).

Juvenile stage. Symmetrical ligament pit type. External angle of the anterior margin of the ligament pit is 156° (Pl. V, fig. 3).

Subadult stage. Inversed subtype of the ligament pit. Spoon-shaped subtype of the lower margin of the ligament pit (Pl. V, fig. 9). The ligament area is inclined towards the midsagittal plane.

Adult and mature stages. The ligament pit in specimens from both samples has modification 4. The base of the ligament pit of the right valve is heterogeneous, has a depression near the anterior margin, and a flattened part near the posterior margin (Pl. V, figs. 6, 7). The length of the ligament pit is 0.18 times the length of the ligament pit. The ligament area of the left valve is two as wide as the pseudoligamentous platform (Pl. V, fig. 5). A ligament ridge appears on the anterior branch of the ligament area, separating the ligament pit from the ligament field. The slope of the hinge plate increases (Pl. V, fig. 5).

The variability of the hinge plate in ontogeny in *Arctotis (Arctotis) tabagensis* was studied in two samples from the lower Aalenian deposits of Anabar Bay (20 specimens) and the Molodo River (15 specimens).

Postlarval stage. Measurements were taken from specimens 10.0 mm long from the Lower Aalenian deposits of the Molodo River. Wide-angled ligament pit. The external angle anterior margin of the ligament pit is about 165° (Pl. V, fig. 8).

Juvenile stage. The symmetrical type of the ligament pit is established based on the growth lines. The external angle anterior margin of the ligament pit is about 165°.

Subadult stage. Inversed subtype of the ligament pit. The external angle anterior margin of the ligament pit is about 150°. Spoon-shaped subtype of the lower margin of the ligament pit. The length of the ligament pit is 0.20 times the length of the ligament area (Pl. V, fig. 9). The ligament area is inclined relative to the midsagittal plane.

Adult and mature stages. The ligament pit in specimens from both samples has modification 4. The ligament pit of the right valve is heterogeneous, differentiated into two parts—it has a depression located closer to the anterior margin of the ligament pit, and a flattened part closer to the posterior margin of the ligament pit (Pl. V, figs. 6, 7). The width of the pit at the adult stage is 1/4–1/5 the length of the ligament area. The ligament area of the left valve is twice as wide as the pseudoligamentous platform (Pl. V, fig. 5). The length of the ligament pit is 0.28 times the length of the ligament pit. The slope of the ligament area increases (Pl. VII, fig. 10).

Variability of the hinge plate during ontogeny in Arctotis (Arctotis) sublaevis was studied in two samples from the Aalenian-Bajocian of the Anabar River.

Postlarval stage. No measurements were taken.

Juvenile stage. The symmetrical type of the ligament pit is recognized based on the growth lines. The external angle anterior margin of the ligament pit is about 165°.

Subadult stage. Inversed subtype of the ligament pit. Spoon-shaped subtype lower margin of the ligament pit.

Adult and mature stages. The ligament pit in specimens from both samples has modification 4. The length of the pseudoligamentous platform is 1/3 of the length of the hinge margin. The ligament area is 2.4 times wider than the pseudoligamentous platform. The length of the ligament pit of the right valve is 0.30 times the length of the hinge plate. The ligament area is three times wider than the pseudoligamentous platform (Pl. V, fig. 13).

The hinge plate of *Arctotis (Canadotis) canadense* was studied in a sample (about 40 left and 25 right valves) from the Volgian of Northern Taimyr (Anzhelika–Pakhra interfluve) (collections by G.V. Schneider). It was not possible to observe the complete sequence of changes in the ligament pit in ontogeny.

Adult and mature stages. The length of the pseudoligamentous platform of the left valves is 1/2 the length of the hinge line. The ligament area is more than 1.2 times wider than the pseudoligamentous platform (Pl. V, fig. 14, 15).

The hinge plate of *Arctotis (Canadarctotis) intermedia* was studied in a sample (20 specimens) from Volgian deposits (Dorsoplanites maximus Zone) of the Taimyr Peninsula (Dyabaka-Tari, Kamennaya rivers) (collection of V.A. Zakharov). It was not possible to observe the complete sequence of changes in the ligament pit in ontogeny.

Adult and mature stages. The length of the pseudoligamentous platform of the left valves is 1/2 the length of the ligament area; the ligament area is more than 1.2 times wider than the pseudoligamentous platform (Pl. V, fig. 18). The length of the ligament pit of the right valve is 0.32 times the length of the ligament area (Pl. V, fig. 19). The ligament areas of the left valves have a very large inclination relative to the midsagittal plane.

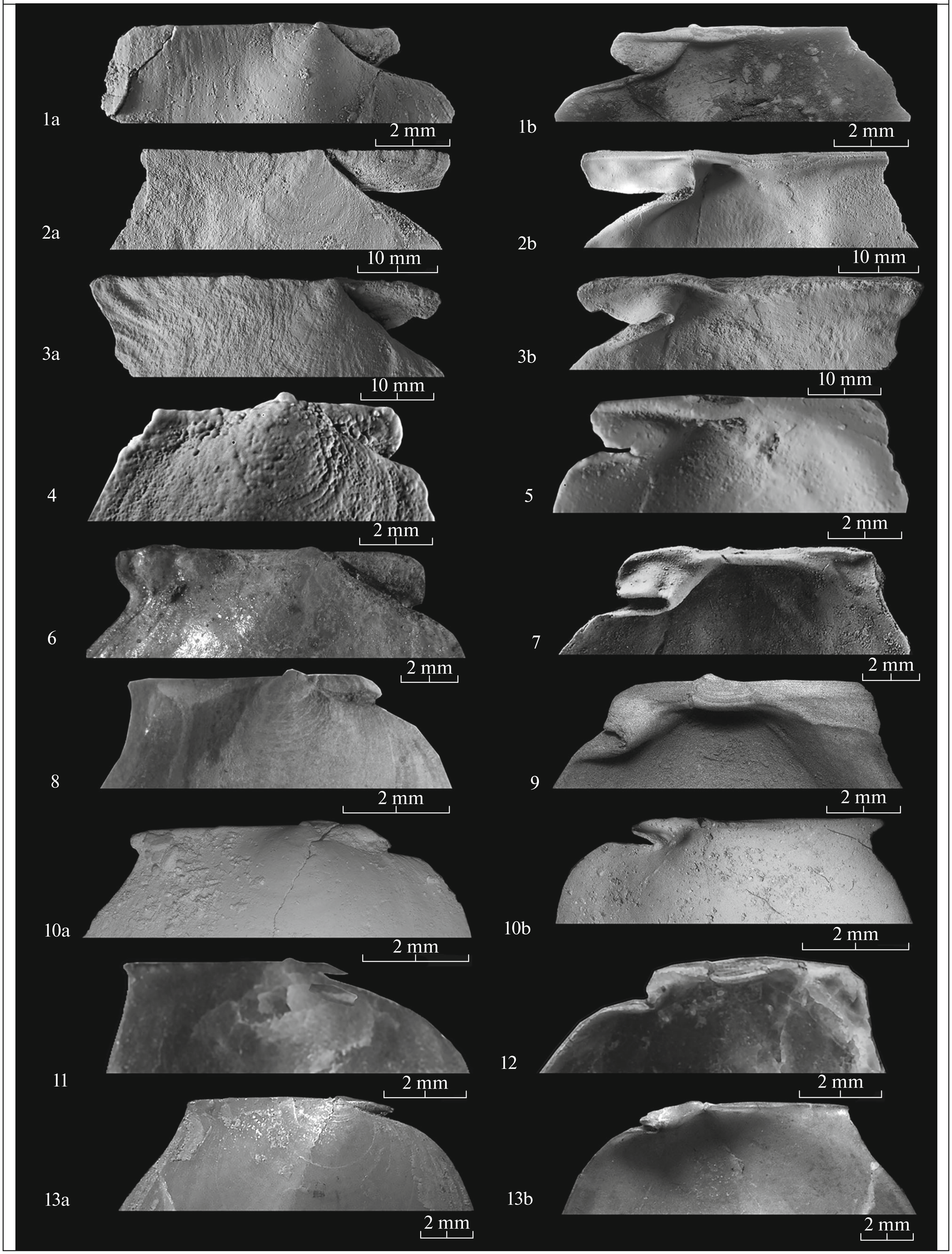
The hinge plate of *Arctotis (Canadarctotis) anabarensis* was studied in a sample (20 specimens) from the Lower Valanginian of the Khatanga Depression (Boyarka River) (collection of V.A. Zakharov). It was not possible to observe the complete sequence of changes in the ligament pit in ontogeny.

Adult and mature stages. The length of the pseudoligamentous platform of the left valves at the adult stage is 1/2 the length of the hinge margin; the width of the pseudoligamentous platform is more than 1.9 times greater than the width of the ligament area. The ligament areas of the left valves have a very large inclination relative to the midsagittal plane. The pseudoligamentous platform of the left valve almost merges with the inner surface of the valve (Pl. V, fig. 20). The length of the ligament pit of the right valve is 0.23 times the length of the ligament area (Pl. VII, fig. 21).

→

Plate IV. Fig. 1. *Oxytoma (Oxytoma) jacksoni* (Pompeckj), specimen no. AG-115/1, umbonal region of the right valve of a juvenile specimen, rhomboid byssal ear, scale bar 2.0 mm; (a) shell exterior, (b) shell interior; Anabar Bay, western coast, Outcrop 5, Bed 90, Sample 115; Lower Jurassic, Upper Toarcian, Pseudolioceras falcodiscus Zone. Figs. 2, 3. *Oxytoma (Oxytoma) kirinae* Velikzhanina, (2) specimen no. TX-870-505/1-1, umbonal region of the right valve of a mature specimen, falcate byssal ear, (a) shell exterior, (b) shell interior, scale bar 10.0 mm; Tenkelyakh Site, line 870, Borehole 505, depth 9 m, sample no. 505/1, Suntary Formation, third member, Lower Jurassic, Lower–Upper Toarcian; (3) specimen no. TX-870-505/1-2, umbonal region of the right valve of a mature specimen, falcate byssal ear, (a) shell exterior, (b) shell interior, scale bar 10.0 mm; the same locality. Figs. 4, 5. *Meleagrinella (Praemeleagrinella) subolifex* Polubotko, (4) specimen no. AG 60/70, umbonal region of the right valve of a mature specimen, trapezoid byssal ear, shell exterior; scale bar 2.0 mm, Anabar Bay, Outcrop 5, Bed 18, level 0.7 m, Sample 60; Lower Jurassic, Hettangian; (5) specimen no. AG 60/71, umbonal region of the right valve of a mature specimen, shell interior, scale bar 2.0 mm; the same locality. Figs. 6, 7. *Meleagrinella (Praemeleagrinella?) tiungensis* (Petrova), (6) specimen no. 160-38-81/1, umbonal region of the right valve of a mature specimen, shell exterior, scale bar 2.0 mm; Tenkelyakh Site, line 160, Borehole 38, depth 81 m (coll. by I.V. Budnikov); Lower Jurassic, Upper Pliensbachian; (7) specimen no. T-94/2, umbonal region of the right valve of a mature specimen, rhomboid byssal ear, shell interior, scale bar 2.0 mm; Tyung River, Outcrop 4, Bed 8, Lower Jurassic, Upper Pliensbachian (collected by V.G. Knyazev). Figs. 8, 9. *Meleagrinella (Meleagrinella)* sp., (8) specimen no. PZ/1-1, umbonal region of the right valve of a mature specimen, rhomboid byssal ear, shell exterior, scale bar 2.0 mm; Lower Bathonian, Penza Region, Pletnevsky Quarry (collected by A.P. Ippolitov); (9) specimen no. PZ/1-2, umbonal region of the right valve of a mature specimen, rhomboid byssal ear, shell interior, scale bar 2.0 mm; the same locality. Fig. 10. *Meleagrinella (Clarthrolima) subechinata* (Lahusen), specimen no. DG/4/1-1, umbonal region of the right valve of a subadult specimen, rhomboid byssal ear, (a) shell exterior, (b) shell interior, scale bar 2.0 mm; horizon 3, Sample DG/4; Upper Callovian, Vladimir region, Dmitrievy Gory. Figs. 11, 12. *Meleagrinella (Meleagrinella) curta* (Whitfield), (11) hypotype specimen no. USNM PAL 12322c, umbonal region of the right valve of a mature specimen, very short byssal ear, shell exterior, scale bar 2.0 mm; uth Dakota, Black Hills, USA, Oxfordian (collected by G. Newton, coll. of R.P. Whitefield, Smithsonian Museum, Washington, USA); (12) hypotype specimen no. USNM PAL 12322b, umbonal region of the right valve of a mature specimen, rhomboid byssal ear with a very short byssal notch, shell interior, scale bar 2.0 mm, the same locality. Fig. 13. *Meleagrinella (Clarthrolima) subovalis* Zakharov, type specimen no. 150/4141, umbonal region of the right valve of a mature specimen, rhomboid byssal ear, scale bar 2.0 mm; (a) shell exterior; (b) shell interior; Lower Kimmeridgian, Levaya Boyarka River (collections by V.A. Zakharov, Center for Collective Use “Collection GEOCHRON”, INGG SB RAS).

Plate IV


1a
2 mm
1b
2 mm
2a
10 mm
2b
10 mm
3a
10 mm
3b
10 mm
4
2 mm
5
2 mm
6
2 mm
7
2 mm
8
2 mm
9
2 mm
10a
2 mm
10b
2 mm
11
2 mm
12
2 mm
13a
2 mm
13b
2 mm

Age-Related Variability of the Byssal Block in Arctotis

The variability of the byssal block in ontogeny in *Arctotis (Praearctotis) marchaensis* was studied in three samples: from the Upper Toarcian of the Tenkelyakh Site, Anabar Bay and the Markha River.

Juvenile stage. The byssal ear is quadrangular, rhomboid.

Subadult stage. The byssal ear is quadrangular, has the shape of an inverted trapezoid with a small notch on the anterior margin and is slightly turned towards the midsagittal plane (Pl. VI, figs. 2a, 2b).

Adult and mature stages. The byssal ear is drop-shaped, with a smoothly outlined anterior margin, located in a plane parallel to the ligament area (Pl. VI, fig. 3, 4a, 4b).

The variability of the byssal block during ontogeny in *Arctotis (Arctotis) tabagensis* was studied in two samples: from the Lower Aalenian of the Molodo River and Anabar Bay.

Subadult stage. The byssal ear is falcate, with a smoothly outlined lower margin and a gaping byssal notch (Pl. VI, fig. 6).

Adult and mature stages. In specimens from the Lower Aalenian of the Anabar Region, the byssal ear is falcate, with a smoothly outlined lower margin, and the gaping byssal notch (Pl. VI, fig. 5).

The byssal block of Arctotis (Arctotis) sublaevis was studied in a sample (10 specimens) from the Aalenian-Bajocian of the Anabar River.

Subadult stage. The byssal ear is falcate.

Adult stage. The byssal ear is falcate with a wide notch (Pl. VI, fig. 8).

Mature stage. In very large specimens, the byssal ear is fused with its lower margin to the anterior part of the upper margin of the valve, the byssal furrow is closed (Pl. VI, fig. 7), and the byssal notch is overgrown (Pl. VI, fig. 9).

The byssal block of *Arctotis (Canadotis) canadense* was studied in a sample (15 specimens) from the Volgian of Northern Taimyr (Anzhelika–Pakhra interfluve) (collections by G.V. Schneider).

Subadult stage. The byssal ear is falcate, with a smoothly outlined lower margin and a gaping byssal notch (Pl. VI, fig. 10a).

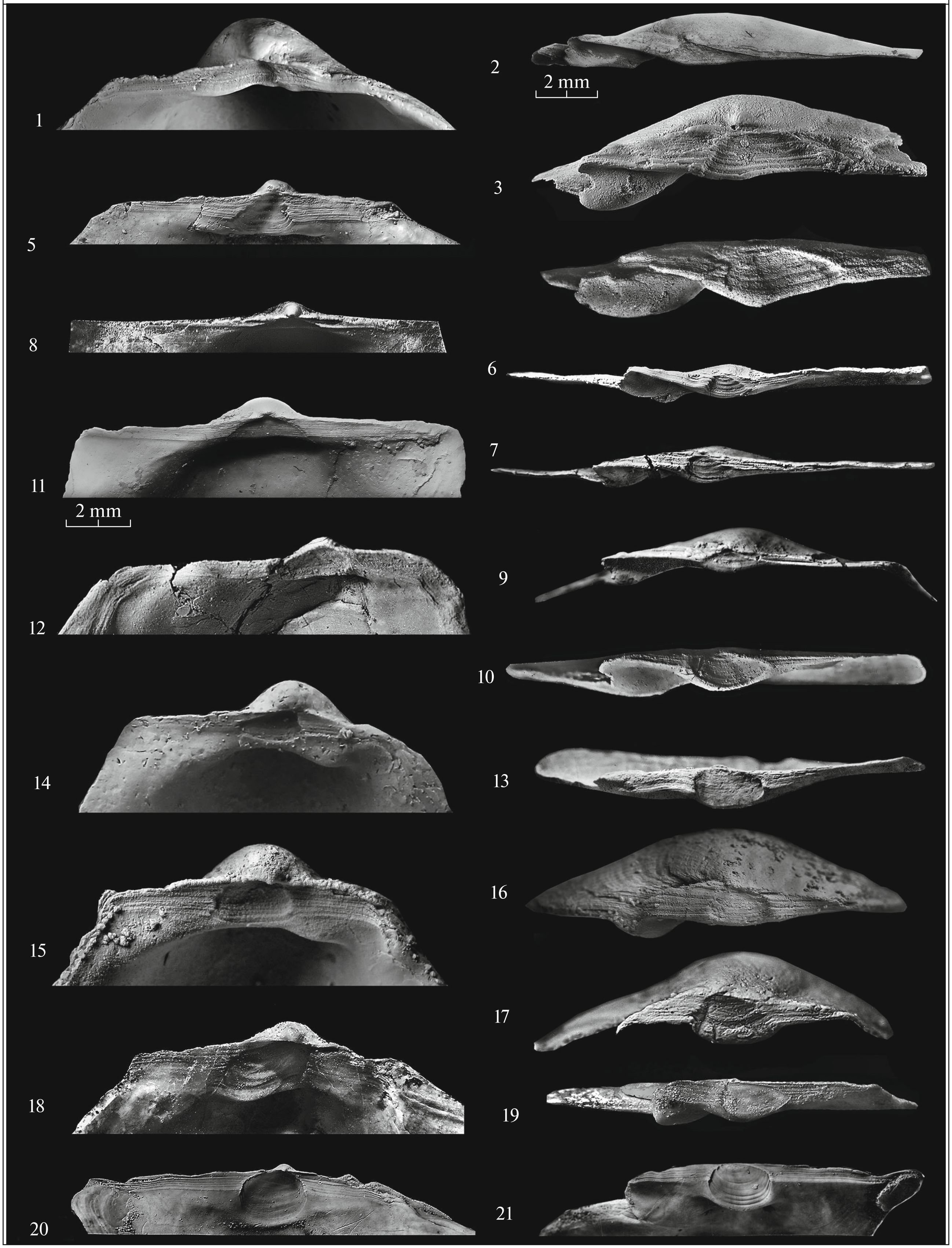
Adult and mature stages. The byssal ear is crescent-shaped, the byssal furrow is open (Pl. VI, fig. 10a), the byssal notch is gaping, long (Pl. VI, fig. 10b).

The byssal block of *Arctotis (Canadarctotis) intermedia* was studied in a sample (20 specimens) from Volgian deposits (Dorsoplanites maximus Zone) of the Taimyr Peninsula (Dyabaka-Tari, Kamennaya rivers) (collection of V.A. Zakharov).

⟶

Plate V. Figs. 1–4. *Arctotis (Praearctotis) marchaensis* (Petrova), **(**1) specimen no. MX-111/2, hinge plate of the left valve of a mature specimen, ×4; Markha River, Outcrop 4, scree of Beds 2–4, Sample 111, Lower Jurassic, Upper Toarcian, collected by V.G. Knyazev; (2) specimen no. TX–1080-350-35/2, hinge plate of the left valve of an adult specimen, modification 3, angular subtype of the ligament pit, uniform base of the 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; (3) specimen no. MX-111/1, hinge plate of the right valve of a mature specimen, angular subtype of the ligament pit with a differentiated ligament pit, ×4, the same locality; (4) specimen no. AG-37/1, hinge plate of the right valve of a mature specimen, angular subtype of the ligament pit with a differentiated ligament pit, ×4, Anabar Bay, Outcrop 4, Bed 18; Lower Jurassic, Upper Toarcian. Figs. 5–7. *Arctotis (Praearctotis) similis* Velikzhanina, **(**5) specimen no. MH-216/1, hinge plate of the left valve of an adult specimen, ×2.5; Motorchuna River, Outcrop 4, Bed 2, Sample 216; Lower Jurassic, Upper Toarcian, Pseudolioceras falcodiscus Zone; (6) specimen no. MH-216/2, hinge plate of the right valve of a mature specimen, spoon-shaped subtype of the ligament pit, ×2.5; the same locality; (7) specimen no. TR-19/1, hinge plate of the right valve of an adult specimen, spoon-shaped subtype of the ligament pit, ×2; Eastern Taimyr (Cape Tsvetkov), Lower Jurassic, Upper Toarcian, Pseudolioceras falcodiscus Zone. Figs. 8–10. *Arctotis (Arctotis) tabagensis* (Petrova), **(**8) specimen no. MD-2/1, hinge plate of the left valve of a juvenile specimen, symmetrical type of the ligament pit, ×10; sample no. MD-2, Molodo River, Outcrop 8, Bed 2, collected by V.G. Knyazev; Middle Jurassic, Lower Aalenian; (9) specimen no. MD-2/2, hinge plate of the right valve of a subadult specimen, uniform base of the ligament pit, spoon-shaped subtype of the ligament pit ×10, the same locality; (10) specimen no. AG-116/1, hinge plate of the right valve of an adult specimen with a resilifer, ×1.7, Anabar Bay, western coast, Outcrop 5, Bed 92, Sample 116; Middle Jurassic, Lower Aalenian. Figs. 11–13. *Arctotis (Arctotis) sublaevis* (Bodylevsky), (11) specimen no. KM-v/1, hinge plate of the left valve of an adult specimen, inverse subtype of the ligament pit, scale bar 2.0 mm; Lena River, Cape Kystatym, Outcrop 5, Nizhnyaya Kystatym Subformation, collected by V.V. Zabaluev, Middle Jurassic, Upper Aalenian; (12) specimen no. AN-18/1 l, hinge plate of the left valve of a mature specimen, ×2; Anabar River, Outcrop 3, Bed 8, Sample 18, Middle Jurassic, Upper Aalenian–Lower Bajocian (?); 13—specimen no. AN-18/1 r, hinge plate of the right valve of the same specimen ×2, the same age and locality. Figs. 14–17. *Arctotis (Canadotis) canadensis* (Jeletzky et Poulton), (14) specimen AZh-1, hinge plate of the left valve of an adult specimen, ×7; Northern Taimyr, Anzhelika–Pakhra interfluve, Lower Volgian Substage, collected by G.V. Schneider; (15) specimen AZh-2, The hinge plate of the left valve of a mature specimen, ×4; the same age and locality; (16) specimen AZh-3, hinge plate of the right valve of an adult specimen, ×3; the same age and locality; (17) specimen no. 171/872, hinge plate of the right valve of an adult specimen, ×3, Graham-Bell Island, Franz Josef Land, Lower Volgian substage, collection of Yu.S. Repin. Figs. 18, 19. *Arctotis (Canadarctotis) intermedia* Bodylevsky, **(**18) specimen no. 150 KM-2, hinge plate of the left valve of a mature specimen, ×6; Kamennaya River, Taimyr District, Outcrop 121, Bed 4, collected by V.A. Zakharov, collection B.N. Shurygin, INGG SO RAN, Novosibirsk; Upper Jurassic, Volgian Stage; (19) specimen no. KM-1, hinge plate of the right valve of a mature specimen ×2, the same locality. Figs. 20, 21. *Arctotis (Canadarctotis) anabarensis* (Petrova), **(**20) specimen no. BK-1, hinge plate of the left valve of a mature specimen, ligament pit inverse-tapering ontogeny ×2, Boyarka River; Lower Cretaceous, Upper Berriasian; collected by V.A. Zakharov, INGG SB RAS, Novosibirsk; (21) specimen no. BK-2, hinge plate of the right valve of a mature specimen ×2, the same locality.

Plate V



Subadult stage. The byssal ear is crescent-shaped, the byssal furrow is open (Pl. VI, fig. 10a).

Adult and mature stages. The byssal ear subtriangular. The byssal notch is wide, gaping and short (Pl. VI, fig. 10b).

The byssal block of *Arctotis (Canadarctotis) anabarensis* was studied in a sample (20 specimens) from the Lower Valanginian of the Khatanga Depression (Boyarka River) (collection of V.A. Zakharov).

Subadult stage. The byssal ear is subtriangular, byssal furrow is open.

Adult stage. The byssal ear subtriangular.

Mature stage. The byssal furrow is closed (Pl. VI, fig. 11a). The byssal notch is overgrown and short (Pl. VI, fig. 11b).

CLASSIFICATION AND TAXONOMIC ASSESSMENT OF CHARACTERS

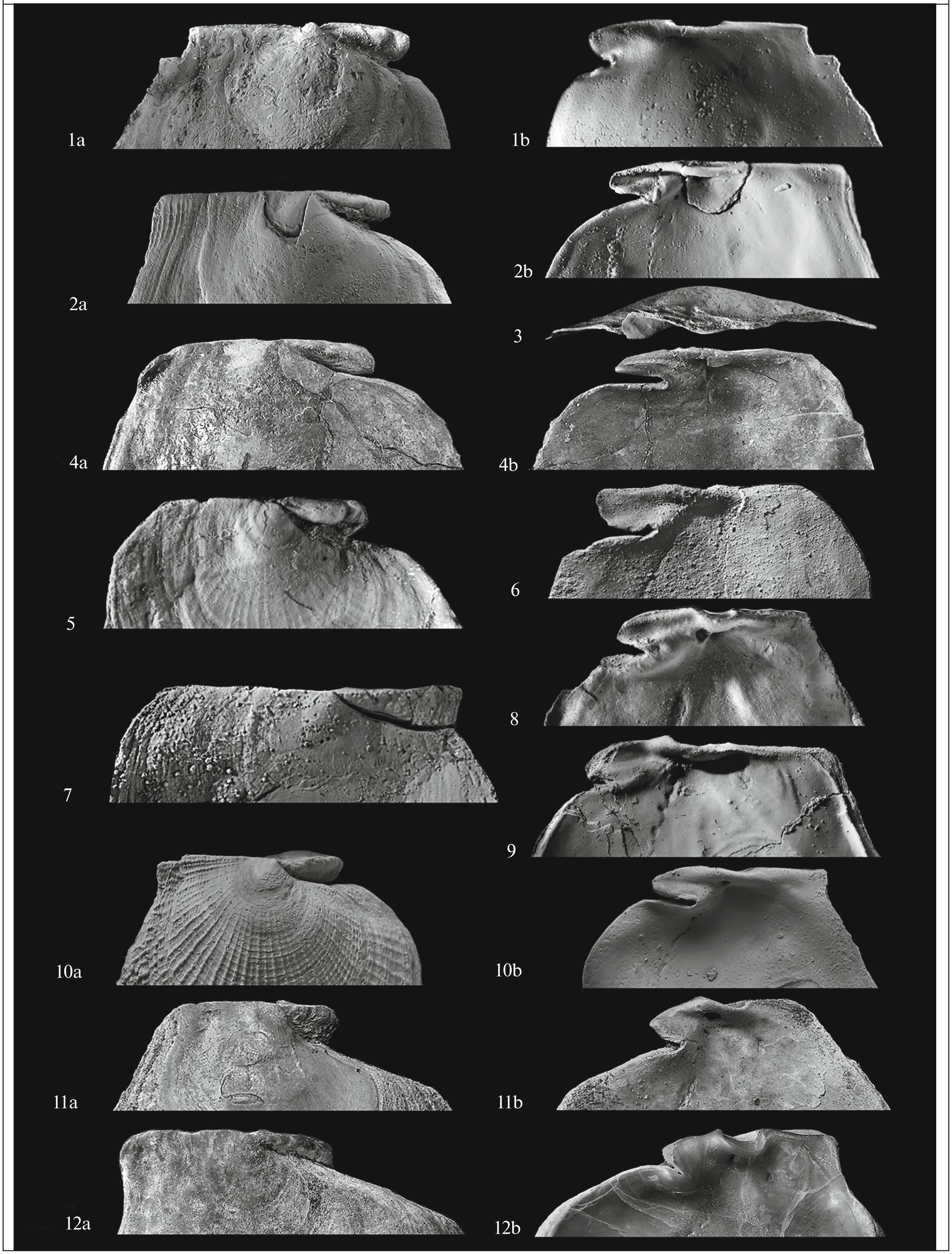
Classification here refers to the division of all extant and extinct groups of organisms into classes based on their common characters. Typological classifications not only historically, but also logically preceded evolutionary ones (Pavlinov, 2005). When classifying mollusks within the family Oxytomidae, such characteristics as valve symmetry, auricle shape, hinge plate width, ligament pit width, relative length of the hinge line, degree of development of the notch of the posterior margin of the posterior auricle, degree of radial ribbing, relative size of the shell, length of the hinge line (Krymgholz, 1939; *Atlas*..., 1947; Krymgholz et al., 1953; Pchelintseva, 1962; Koshelkina, 1963; Velikzhanina, 1966, 1973; Zakharov, 1966; *Polevoi*..., 1968; Nevesskaja et al., 2013; etc.). The structure of the hinge plate was described in detail by many researchers, but the variability and taxonomic weight of the elements of the hinge plate and byssal block were not assessed (Pompeckj, 1901; Borissjak, 1909; Ivanov, 1915; Ichikawa, 1958; Duff, 1978; Crame, 1985; Crame et al., 1993; Jeletzky and Poulton, 1987). In evolutionary taxonomy, classification is based on a combination of genealogy and the degree of similarity and difference, reflecting the level of divergence (Keylow, 1986). Relationships are judged by similarity. The latter means that first diversity is ordered typologically, and then this identified order is given one or another evolutionary interpretation (Pavlinov, 2005).

Taxonomic Assessment of Characters

A priori approaches to weighting features are based on the assumption that some are more important than others. The taxonomic weight of a character is understood as a state of a trait, which reflects the ability, using this trait, to unambiguously define the position of a taxon in the system. It is assumed that some features adequately reflect the essences of objective groups, while others reflect properties that are not entities (Pavlinov, 2009). When studying the family as a whole, large series of specimens originating from deposits of different geological ages were carefully studied in order to find out within which groups the characters are "fairly constant" or "repeating cyclically." Taxa were then classified into genera and subgenera. The taxonomic significance of the characters was determined by the stability of the characters in the selected groups. Based on the study of age-related variability of morphological characters in the geochronological sequence of taxa, the characters were

Plate VI. Fig. 1. *Meleagrinella (Meleagrinella) prima* Lutikov, specimen no. TX-1060-1/2, umbilical part of the right valve of an adult specimen with a trapezoid byssal ear and a very short byssal notch; (a) shell exterior; (b) shell interior, ×9; Tenkelyakh Site, line 1060, Borehole 350, depth 31 m (coll. by I.V. Budnikov), Lower Jurassic, Lower Toarcian. Figs. 2–4. *Arctotis (Praearctotis) marchaensis* (Petrova), (2) specimen no. TX-1080-1-35/2, umbonal region of the right valve of an adult specimen with a drop-shaped byssal ear; (a) shell exterior, ×4; (b) shell interior, ×4; Tenkelyakh Site, line 1080, Borehole 350, depth 35 m, sample no. TX-1080-1, Lower Jurassic, Upper Toarcian, Suntary Formation, third member; (3) specimen no. TX-1080-1-35/3, drop-shaped byssal ear and ligament area of the right valve of an adult specimen, ×4; the same locality; (4) specimen no. MX-210, umbonal region of the right valve of a mature specimen drop-shaped and incurved byssal ear; (a) shell exterior, ×4; (b) shell interior ×4; Markha River, Outcrop 5, Bed 7 (collected by V.G. Knyazev), Lower Jurassic, Upper Toarcian. Figs. 5, 6. *Arctotis (Arctotis) tabagensis* (Petrova), (5) specimen no. AG-116/2, umbonal region of the right valve of a mature specimen with a subtriangular falcate byssal ear and a wide byssal furrow, shell exterior, ×1, Anabar Bay, western coast, Outcrop 5, Bed 92, Sample 116, Middle Jurassic, Lower Aalenian (?); (6) specimen no. AG-116/3, umbonal region of the right valve of a subadult specimen with a falcate byssal ear and a long byssal notch, shell interior, ×4, the same locality. Figs. 7–9. *Arctotis (Arctotis) sublaevis* (Bodylevsky), (7) specimen no. AN-18/2, umbonal region of the right valve of a mature specimen with subtriangular byssal ear and overgrown byssal furrow, shell exterior, ×1.2, Anabar River, Outcrop 3, Bed 8, Sample 18, Middle Jurassic, Upper Aalenian–Lower Bajocian (?); (8) specimen no. AN-18/3, umbonal region of the right valve of a mature specimen with byssal notch overgrown to 1/2 length, shell interior, ×2, the same locality; (9) specimen no. AN-18/3, umbonal region of the right valve of an adult specimen with a byssal notch growing over 2/3 of its length, shell interior, ×2, the same locality. Fig. 10. *Arctotis (Canadotis) canadensis* (Jeletzky et Poulton), specimen no. AZh-4, umbonal region of the right valve of an adult specimen with a rhomboid byssal ear and a gaping byssal notch, (a) shell exterior ×3, (b) shell interior, ×3; Northern Taimyr, Anzhelika–Pakhra interfluve, Lower Volgian Substage, collected by G.V. Schneider. Fig. 11. *Arctotis (Canadarctotis) intermedia* Bodylevsky, specimen no. KM-1, umbonal region of the right valve of a mature specimen with triangular byssal ear, (a) shell exterior ×3.5; (b) shell interior, ×3.5; Kamennaya River, Taimyr Peninsula, Outcrop 121, Bed 4, Upper Jurassic, Volgian Stage (collected by V.A. Zakharov, Institute of Oil and Gas Geology and Geophysics, Novosibirsk). Fig. 12. *Arctotis (Canadarctotis) anabarensis* (Petrova), type specimen no. 643/5393, umbonal region of the right valve of a mature specimen with triangular byssal ear and overgrown byssal notch, (a) shell exterior ×1.5; (b) shell interior, ×1.5; R. Lyungdyul, Lower Cretaceous, Valanginian (collection of G.T. Petrova (Pchelintseva), F.N. Chernyshev TsNIGR Museum, St. Petersburg).

Plate VI



conditionally divided into three categories—with low, medium and high weight. Only after this were the characteristics of various taxa established.

Character of hight weight include:

(1) ***Type of the pallial line.*** The type of the pallial line was determined by its structure. The entire pallial line has a continuous linear scar running on the inner surface of the valves, located parallel to the anterior, lower and posterior margins of the valves. The discrete pallial line is discontinuous, represented by a series of pits located parallel to the anterior, ventral and posterior margins of the valves. Based on a discrete pallial line, a phylogenetic relationship has been established between *Oxytoma, Meleagrinella, Arctotis* and *Maccoyella*. The character is shared within the family Oxytomidae. In the family Aviculopectinidae, which is closest to Oxytomidae in terms of the general plan of shell structure, the pallial line is entire.

(2) ***Sculpture.*** The sculpture of oxytomids is represented by radial ribs and concentric growth lines. This character is present in all members of the family Oxytomidae. Only in the Canadian species *A. rugosa*, judging by the images published by Jeletzky and Poulton (1987), the differentiation of the ribs is not pronounced, which may be the result of abrasion of the shells when growing to each other. In *Meleagrinella* s.str., *Praemeleagrinella*, and *Clathrolima*, the ribs are differentiated by one or two orders of magnitude in thickness. In *Praearctotis* and *Canadotis*, the radial ribs are differentiated by two orders of magnitude. In *Oxytoma, Arctotis* s.str., and *Canadarctotis*, the radial ribs are differentiated by three to four orders of magnitude due to the intercalation of additional ribs.

(3) ***Shape of the ligament pit at the postlarval stage.*** The triangular shape of the ligament pit in the postlarval stage is a shared character in the family Oxytomidae. The apical angle of the ligament pit was determined by the angle between the lateral margins originating from the beak at the postlarval stage. In Callovian *Oxytoma* ex gr. *expansa* it is about 105°, in the Pliensbachian *Meleagrinella (Prameleagrinella) deleta* it is about 110°, in the Toarcian *Meleagrinella (Meleagrinella) prima* it is about 140°, in the Aalenian *Arctotis (Arctotis) tabagensis* it is about 153°, in the Bathonian *Meleagrinella (Meleagrinella)* sp. about 87°. Based on the apical angle of the ligament pit, close phylogenetic connections have been established between *Prameleagrinella* and *Oxytoma*, and between the Toarcian *Meleagrinella* s.str. and *Praearctotis*.

(4) ***Ligament pit type***. The type of the ligament pit was determined by the relative position of the sides of the pit at the juvenile stage. The ligament pit of subrectangular type is characteristic of *Oxytoma, Clathrolima, Bajocian Meleagrinella* s.str.; the ligament pit of the wide-angled type is characteristic of *Praemeleagrinella, Toarcian Meleagrinella* s.str.; the ligament pit of the symmetrical type is characteristic of *Praearctotis, Arctotis* s.str., *Canadotis*, and *Canadarctotis*. The oblique ligament pit type is observed in the Bathonian *Meleagrinella* s.str. Based on the type of the ligament pit in the chronological series of taxa, the morphogenetic trends within the family Oxytomidae were established.

(5) ***Ligament pit subtype.*** The oblique subtype of the ligament pit is characteristic of the Jurassic *Oxytoma, Praemeleagrinella,* and *Clathrolima*. The expanding subtype is characteristic of *Meleagrinella* s.str. The inversed subtype is characteristic of *Arctotis*. Based on the ligament pit subtype in the chronological series of taxa, the directions of morphogenesis in parallel lines in *Meleagrinella* were established.

(6) ***Subtype of the lower margin of the ligament pit.*** The straight subtype is characteristic of *Oxytoma* s.str., *Praemeleagrinella, Meleagrinella* s. str,. and *Clathrolima*. The angular subtype is characteristic of early *Praearctotis*. The spoon-shaped subtype is characteristic of late *Praearctotis*, *Arctotis* s.str., *Canadotis*, and *Canadarctotis*. Based on the angular subtype in the chronological series of taxa, phylogenetic relationships between the Toarcian *Meleagrinella* s.str. and early *Praearctotis*, based on the spoon-shaped subtype, phylogenetic connections have been established between the late *Praearctotis* and *Arctotis* s.str., *Canadotis,* and *Canadarctotis*.

(7) ***Byssal notch type.*** The byssal notch in oxytomids is formed by the bend of the anterior margin byssal ear and serves for the exit of the byssus. In *Oxytoma* s.str., *Praemeleagrinella*, *Meleagrinella* s.str., *Clathrolima,* and *Canadotis*, the byssal notch is gaping. In *Arctotis* s.str. and *Canadarctotis* in adult shells the byssal notch is overgrown.

(8) ***Byssal ear type.*** Based on the number of sharp bends formed by the margins of the byssal ear, two types of byssal ear are distinguished—subquadrangular and subtriangular. The subquadrangular ear is characteristic of *Praemeleagrinella, Meleagrinella* s.str., *Clathrolima, Canadotis* and early *Praearctotis*, the subtriangular byssal ear is characteristic of late *Praearctotis*, *Arctotis,* and *Oxytoma*.

(9) ***Byssal furrow type.*** The byssal furrow is formed by the byssal ear fold running from the prodissoconch to the byssal notch. It is limited on one side by the anterior margin of the byssal ear of the right valve, on the other side by the bend of the outer surface of the byssal ear. Based on the relative position of the furrow margins, two types of byssal furrow are distinguished—open and closed. Open is characteristic of *Oxytoma, Praemeleagrinella, Meleagrinella* s.str., *Clathrolima, Canadotis,* and *Praearctotis*. A closed byssal furrow is characteristic of *Arctotis* and *Canadarctotis*.

(10) ***Position of the ligament area relative to the midsagittal plane.*** The ligament area, which is a bound element in the hinge plate, retains the shape of a wide-angled triangle within the fossil populations of all genera included in the family, changing its inclination relative to the midsagittal plane. The ligament area of the left valve in *Oxytoma* s.str., *Praemeleagrinella, Melea-*

grinella s.str. and *Clathrolima* lies in the midsagittal plane at all growth stages. The ligament area of the left valve in *Praearctotis, Arctotis, Canadotis,* and *Canadarctotis* is inclined towards the midsagittal plane. The slope increases in the phylogeny from *Praearctotis* to *Canadarctotis*.

(11) ***Length of ligament area.*** In the diagnosis of the genus *Arctotis*, Bodylevsky (1960) included the relative length of the ligament area, indicating that compared with the ancestral genus, the Triassic *Eumorphotis*, *Arctotis* has a hinge margin that is shorter than the length of the shell. A shorter length of the ligament area compared to the length of the shell is characteristic of the entire family. The relative length of the ligament area within the family was estimated using the following gradations: very short 0.40–0.60, short 0.61–0.80, long 0.81–1.00, very long more than 1.00. The ratio of the length of the ligament area to the length of the right valve of adult specimens varied within the following limits: *Praemeleagrinella*—0.54–0.70; *Meleagrinella* s.str.—0.65–0.71; *Clathrolima*—0.43–0.65; *Paearctotis*—0.50–0.67; *Arctotis*—0.60–0.74; *Canadotis*—0.54–0.68; *Canadarctotis*—0.60–0.76; *Oxytoma* s.str.—0.85–0.94. The length of the ligament area in relation to the length of the shell changes during ontogeny and decreases with shell growth in *Praemeleagrinella* and *Oxytoma*. In juvenile specimens of some *Oxytoma* species, the length of the ligament area of the right valve is greater than the length of the shell (Pl. XVI, fig. 9); in adults, the length of the ligament area is almost equal to the length of the shell (Pl. XVI, figs. 7, 8) or less than it (Pl. XVI, figs. 5, 6).

(12) ***Comparative valve convexity.*** Biconvex valves are characteristic of *Praemeleagrinella, Meleagrinella* s.str., *Clathrolima* and early *Praearctotis*. Convex left valves and flat right valves are characteristic of *Oxytoma* s.str., late *Praearctotis*, early Aalenian *Arctotis* s.str. Convex-concave valves are characteristic of Aalenian-Bajocian representatives of the subgenus *Arctotis* s.str. and *Canadarctotis*.

(13) ***Comparative valve size.*** Strongly inequivalve shells are characteristic of *Oxytoma*, moderately inequivalve shells are characteristic of *Meleagrinella*, and somewhat inequivalve shells are characteristic of *Arctotis*. The ratio of the height of the right valve to the left valve of adult specimens varies: in *Meleagrinella* within 0.77–0.83, in *Arctotis* within 0.85–0.95; in *Oxytoma* s.str. it is about 0.66.

Characters with medium weight include:

(14) ***Shape of the ligament pit base of the right valve.*** In *Oxytoma* and *Meleagrinella,* the base of the ligament pit is a flattened depression, bounded anteriorly and posteriorly by ligament grooves. In *Praearctotis*, the base of the ligament pit is heterogeneous and differentiated into a flattened posterior part and a depression in the anterior part. In *Arctotis* s.str., *Canadotis*, and *Canadarctotis*, the base of the ligament pit is uniform and is a spoon-shaped depression occupying the entire area of the pit.

(15) ***Presence of protuberance***. The presence of protuberance on the pseudoligamentous area is considered a characteristic of the genus *Meleagrinella* (*Treatise*..., 1969; Duff, 1978). However, this morphological element is not always expressed in shells of even one species within the same sample, as was observed in the Hettangian-Sinemurian *Praemeleagrinella* and Callovian *Clarthrolima* (Pl. I, figs. 18, 19). This may be due to sexual dimorphism. The protuberance is present in *Praemeleagrinella*, *Meleagrinella* s.str., *Clarthrolima, Praearctotis,* and *Canadotis*, but its degree of expression and form are different. In *Arctotis* s.str. and *Canadarctotis,* the protuberance is absent.

(16) ***Microsculpture of mesostracum of the right valve.*** The microsculpture of the mesostracum of the right valve in all studied *Meleagrinella* and *Oxytoma* in the middle and lower parts of the right valve consists of quadrangular and hexagonal prisms located parallel to the radial ribs. The microsculpture of the ostracum of the right valve in *Arctotis (Praearctotis) marchaensis* is represented by hexagonal prisms arranged in a mosaic pattern. Hexagonal prisms arranged in a mosaic pattern are also present in the Late Pliensbachian *Meleagrinella (Praemeleagrinella?) tiungensis* and *Meleagrinella (Praemeleagrinella) sparsicosta*. It is possible that the polygonal shape of the prisms and their mosaic arrangement in *Meleagrinella* was the result of adaptation to temperature fluctuations or changes in salinity.

(17) ***Presence of ligament ridge.*** The presence of a ligament ridge near the anterior margin of the ligament pit was considered by Jeletzky and Poulton (1987) as a generic character in *Arctotis*. This character is present on the right valve of the Hettangian *Praemeleagrinella* (Pl. II, fig. 1, 2), Toarcian *Praearctotis* (Pl. V, fig. 6), and Volgian *Canadotis* (Pl. V, fig. 16), but not always well expressed. The ridge is absent in all known species of *Oxytoma* (Pl. VII, figs. 4–8) and in *Meleagrinella* s.str. (Pl. III, figs. 2, 3).

(18) ***Length of the posterior outer ligament of the left valve (=length of posterior auricle)***. Ichikawa (1958) included the character "long posterior auricle" in the diagnosis of the genus *Oxytoma*. According to the gradation of characters adopted in this work in the studied samples, in *Oxytoma* the posterior outer ligament varies from long to very long (LOL/PDL = 0.92–0.74). The posterior outer ligament in *Praemeleagrinella* is very short to very long (LOL/PDL = 0.48–0.81); in *Meleagrinella* s.str. short to long (LOL/PDL = 0.61–0.72); in Clathrolima from very short to long (LOL/PDL = 0.49–0.77). The posterior outer ligament in *Paearctotis* is very short to long (LOL/PDL = 0.55–0.72); in *Arctotis* s.str. very short (LOL/PDL = 0.51–0.55); in *Canadotis* it is very short (LOL/PDL = 0.49–0.54); in *Canadarctotis* from very short to long (LOL/PDL = 0.77–0.57). A long posterior auricle is not always a characteristic of the family

Oxytomidae. This trait is characteristic of the genus *Jianchuania* (Chen Jin-hua and Chen Chu-zhen, 1980) from the Upper Triassic of China. However, the presence of a solid pallial line on the valves does not allow this genus to be assigned to the family Oxytomidae.

(19) ***Posterior auricle outline.*** The outline of the posterior auricle is determined by the depth of the notch on the posterior margin of the valve. Specimens of *Meleagrinella (Praemeleagrinella) deleta* from the Upper Pliensbachian of the Tyung Formation have acute-angled posterior auricles on both valves (Pl. IX, figs. 2–6). Specimens of *Meleagrinella (Praemeleagrinella?) golberti* from the Tiltoniceras antiquum and Harpoceras falciferum zones (Kelimyar, Tyung, Astronomicheskaya, Motorchuna rivers) are characterized by an acute-angled auricle (Pl. X, figs. 7–11). Specimens from the Cleviceras elegans Subzone (Dörlbach, Ludwigskanal) have an acute-angled or subrectangular auricle (Pl. X, figs. 1–6). Specimens of *Meleagrinella (Clathrolima) substriata* from the Hildoceras bifrons Zone (Dactylioceras commune Subzone) have an obtuse-angled auricle (Pl. XI, figs. 1–10). Specimens of *Meleagrinella (Meleagrinella) prima* from the Zugodactylites braunianus Zone (Markha River, Anabar Bay) are characterized by a change in the outline of the posterior auricle during ontogeny. At the early stages the auricle is acute-angled, at the final stages it is subrectangular (Pl. XII, figs. 1–10).

Bodylevsky (1960) in his diagnosis of the genus *Arctotis* indicated a weakly expressed notch of the posterior auricle as a character of the genus. The absence of a deep notch under the posterior auricle and the blunt-pointed posterior auricle in adult specimens distinguish *Arctotis* from most species of *Meleagrinella*. However, in *Meleagrinella (Clathrolima) substriata* from the Hildoceras bifrons Zone (Dactylioceras commune Subzone), the posterior auricle is obtuse-angled, the notch under the auricle is weakly expressed. In adult specimens of *Oxytoma (Oxytoma) inequivalvis* from the Sinemurian of England, the notch of the posterior margin of the auricle is weakly expressed (Hodges, 2022). In juvenile shells of *Oxytoma (Oxytoma) jacksoni* from the Upper Toarcian of Anabar Bay, the notch of the posterior margin of the auricle is also weakly expressed (Pl. IV, fig. 1a).

(20) ***Byssal ear outline.*** Jeletzky and Poulton (1987) considered the outline of the byssal ear to be the main distinguishing characters of *Arctotis, Canadotis* and *Canadarctotis*. The rhomboid and trapezoidal byssal ear is characteristic of the genus *Meleagrinella*. Drop-shaped, crescent-shaped and triangular byssal ears are characteristic of *Arctotis*. A crescent-shaped byssal ear, sometimes with a notch on the lower margin, is characteristic of adult specimens of the genus *Oxytoma* (Pl. IV, figs. 2, 3; pl. XVII, figs. 7, 8). The states of the trait change during ontogeny.

Low weight characters include:

(21) ***Posterior wing type.*** The type of the posterior wing was determined by a combination of two characters: the outline of the outer margin of the posterior wing and the outline of the posterior auricle (Fig. 1).

Specimens of *Meleagrinella (Praemeleagrinella) deleta* from the Upper Pliensbachian of France and Eastern Siberia have a “straight” type of the posterior wing of the left valve (Fig. 1a). They are characterized by the absence of a bend in the posterior wing and an acute-angled posterior auricle (Pl. IX, figs. 1, 2, 3, 6, 7).

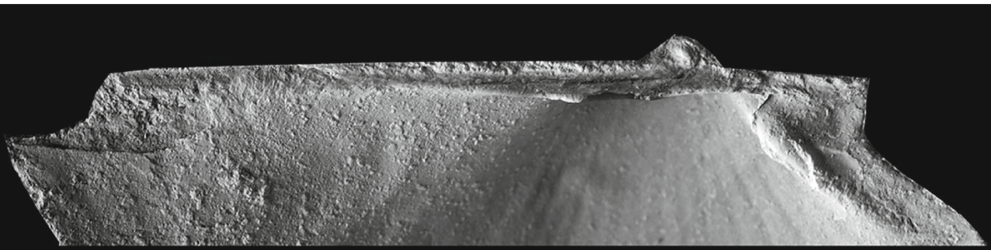
Specimens of *Meleagrinella (Praemeleagrinella?) golberti* from the *Tiltoniceras antiquum* and *Harpoceras falciferum* zones of Germany and Eastern Siberia (Kelimyar, Tyung, Motorchuna rivers, Anabar Bay, Ottursky area) are characterized by a bow type of the posterior wing (Fig. 1b). They are characterized by bow-shaped posterior wing and an acute-angled or sub-rectangular posterior auricle (Pl. X, figs. 1–11). The same type of the posterior wing is found in specimens from the *Harpoceras falciferum* Zone of England (Morris et al., 2019) (Pl. X, fig. 12), from the Dactylioceras kanense Zone (Harpoceras serpentinum Subzone) of Western Canada (Martindale and Aberhan, 2017) (Pl. X, fig. 13).

Specimens of *Meleagrinella (Clathrolima) substriata* from the Hildoceras bifrons Zone (Dactylioceras commune Subzone) of Germany and the Dactylioceras commune Zone of Eastern Siberia have an “S-

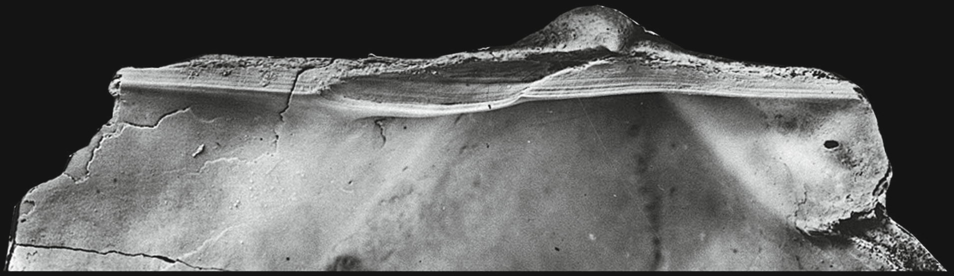
Plate VII. Fig. 1. *Oxytoma (Oxytoma) startense* Polubotko, specimen no. CA-34/2, hinge plate of the left valve of a mature specimen, ×3; Saturn River, Outcrop 1, Bed 18, base, Sample 34, Lower Jurassic, Upper Toarcian, Pseudolioceras compactile Zone. Fig. 2. *Oxytoma (Oxytoma) kirinae* Velikzhanina, specimen no. MX-506/ 1, hinge plate of the left valve of a mature specimen, ×3; Markha River, sample no. 506, scree of Outcrop 13 (after Knyazev et al., 1991), Suntary Formation, Lower Jurassic, Lower–Upper Toarcian. Fig. 3. *Oxytoma (Oxytoma) jacksoni* (Pompeckj), specimen no. K-186/2, hinge plate of the left valve of a mature specimen, ×3; Kelimyar River, Outcrop 16, Bed 8; Lower Jurassic, Upper Toarcian. Figs. 4–6. *Oxytoma (Oxytoma) kirinae* Velikzhanina, (4) specimen no. TX-870-505/1-3, hinge plate of the right valve of an adult specimen with an acute angular ligament pit, ×3; Tenkelyakh Site, line 870, Borehole 505, depth 9 m, sample no. 505/1, Suntary Formation, third member, Lower Jurassic, Lower–Upper Toarcian; (5) specimen no. MX-506/ 2, hinge plate of the right valve of a mature specimen, ×3, the same locality; (6) specimen no. TX-870-505/1-1, hinge plate of the right valve of an adult specimen with wedge-shaped ligament pit, ×3.5; Markha River, sample no. 506, scree of Outcrop 13 (after Knyazev et al., 1991), Suntary Formation, Lower Jurassic, Lower–Upper Toarcian. Figs. 7, 8. *Oxytoma (Oxytoma) jacksoni* (Pompeckj), (7) specimen no. AG-115/1, hinge plate of the left valve of a juvenile specimen, scale bar 2.0 mm; Anabar Bay, western coast, Outcrop 5, Bed 90, Sample 115; Lower Jurassic, Upper Toarcian, Pseudolioceras falcodiscus Zone; (8) specimen no. K-186/1, hinge plate of the right valve of a mature specimen, ×3; Kelimyar River, Outcrop 16, Bed 8; Upper Toarcian.

Plate VII

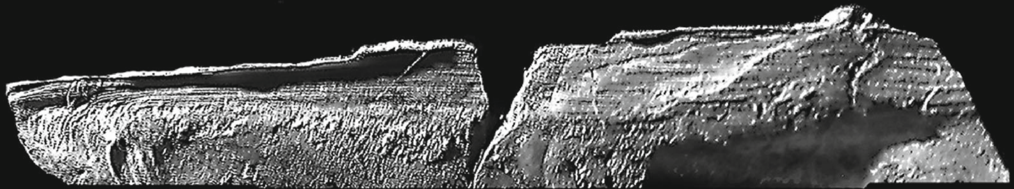
1



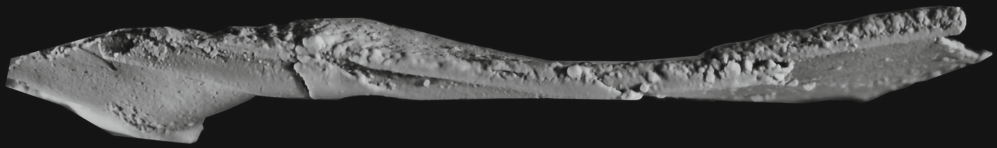
2



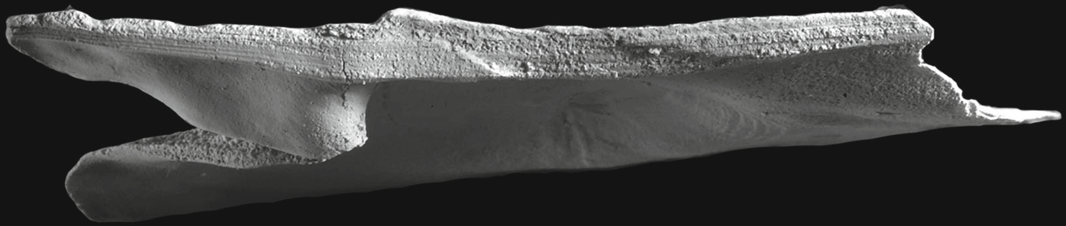
3



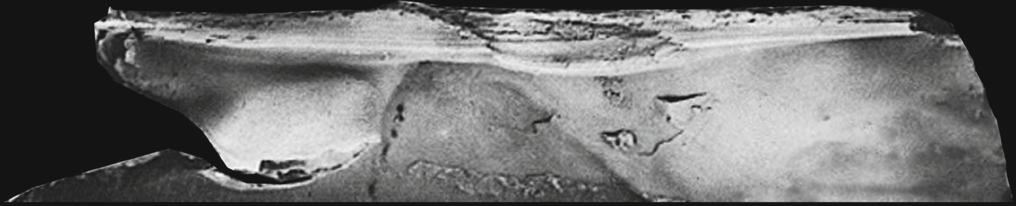
4



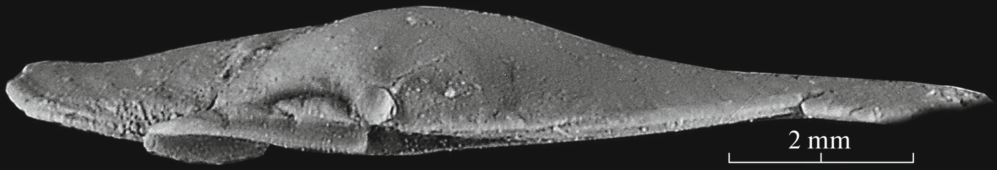
5



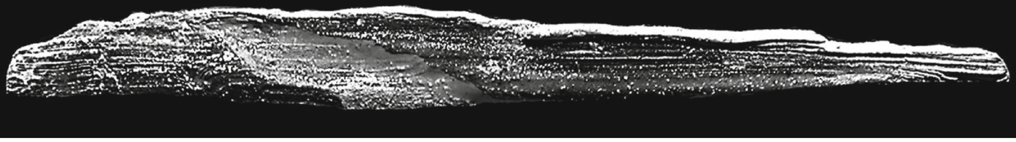
6



7



8



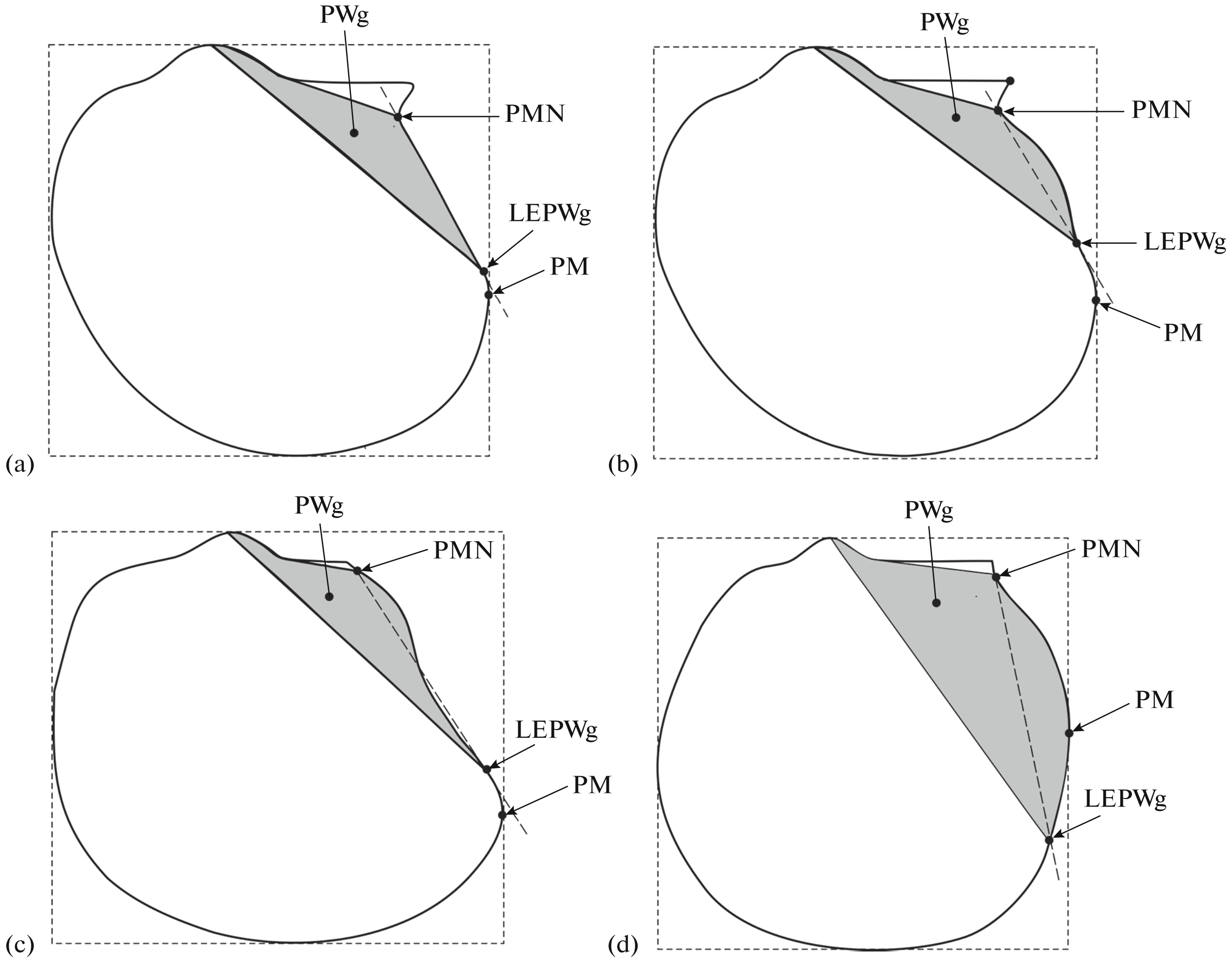


Fig. 1. Types of the posterior wing of the left valve of *Meleagrinella*. (a) Straight type (*Meleagrinella* (*Praemeleagrinella*) *deleta*); (b) bow-shaped type (*Meleagrinella* (*Praemeleagrinella?*) *golberti*), (c) S-shaped type (*Meleagrinella* (*Clathrolima*) *substriata*), (d) arched type (*Meleagrinella* (*Meleagrinella*) *prima*). Morphological elements: PWg—posterior wing, PM—posterior margin of the valve, PMN—posterior margin notch, LEPWg—lower end of the posterior wing

shaped" type of the posterior wing (Fig. 1c). They are characterized by an S-shaped bend of the posterior wing and an obtuse-angled posterior auricle (Pl. XI, figs. 1–12). This character was found in the lectotype (Pl. XI, fig. 2), in specimens from the "Dactylioceras-Monotis-Bed" Member of the Ludwigskanal section (Dörlbach, Southern Germany) (Pl. XI, fig. 6–8), in specimens from the second member of the Suntary Formation of the section of the Tyung and Vilyui rivers (Dactylioceras commune Zone) (Pl. XI, figs. 10–12), in specimens from the upper subformation of the Start Formation of the section of the Astronomicheskaya River (Dactylioceras commune Zone) (Pl. XI, fig. 9).

Specimens of *Meleagrinella (Meleagrinella) prima* from the Zugodactylites braunianus Zone of Eastern Siberia and the Zugodactylites braunianus, Pseudolioceras compactile zones of Northeastern Russia have an "arched" type of the posterior wing of the left valve (Fig. 1d). They are characterized by an arched curve of the posterior wing and a subrectangular or acute-angled posterior auricle. Unlike the bow-like type, which is characterized by a higher position of the lower end of the posterior wing relative to the posterior end of the valve, in the arched type, the lower end of the posterior wing is located below the posterior end of the valve. This character was observed in specimens from the third member of the Suntary Formation (Markha River, Tenkelyakh Site) (Pl. XII, figs. 1–7, 9), the middle part of the Eren Formation (Anabar Bay) (Pl. XII, fig. 8) and upper subformation of the Start Formation (Saturn River) (Pl. XII, figs. 11, 12).

Some types of posterior wing occur at different stratigraphic levels.

(22) ***Anterior wing type.*** The type of the anterior wing was determined by a combination of three characteristics: the length of the anterior outer ligament, the ratio of the width of the anterior wing to the length of the anterior wing, and the angle of the anterior

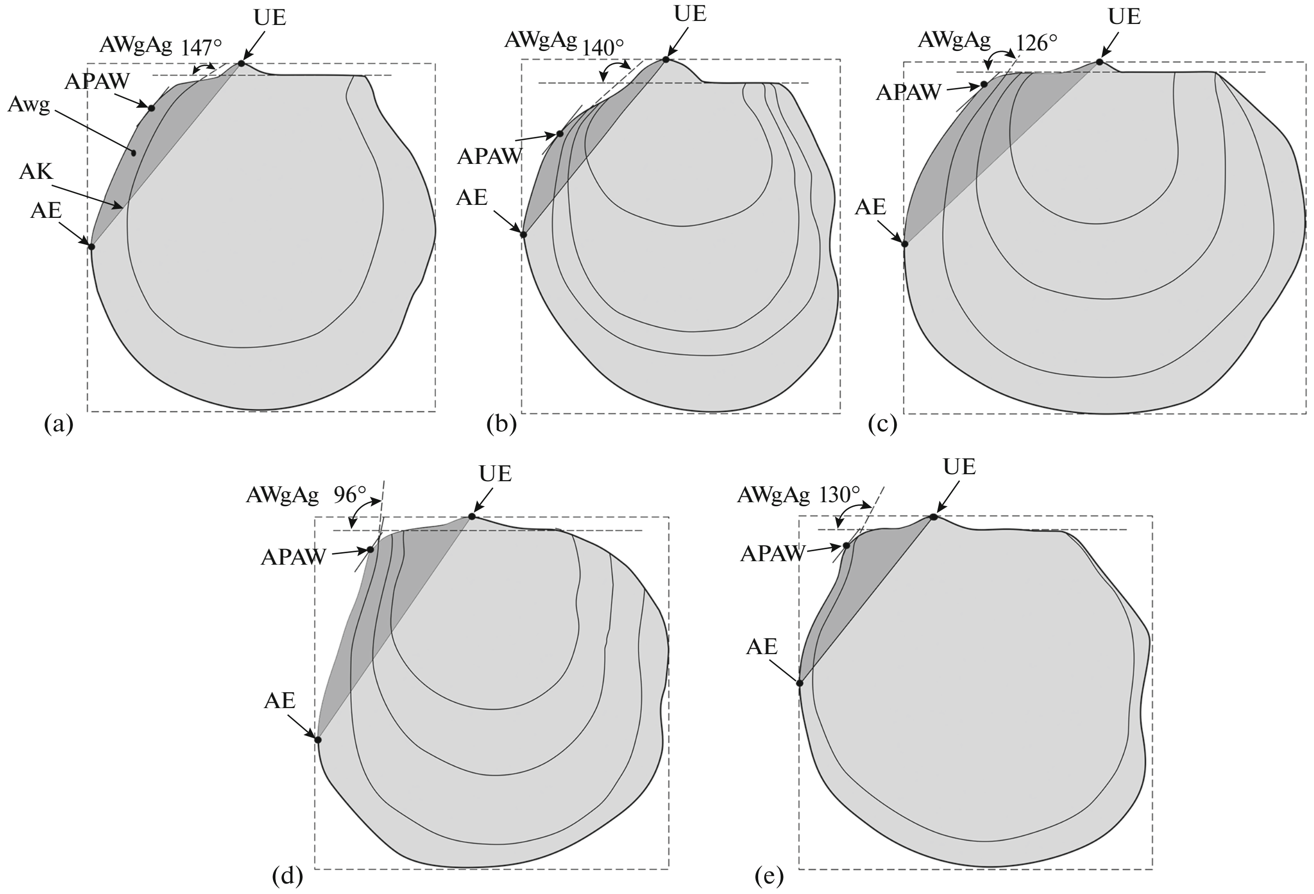


Fig. 2. Types of the anterior wing of the left valve of *Meleagrinella* and *Arctotis*. (a, b) Paraboloid type: (a) *Meleagrinella (Meleagrinella) prima*, (b) *Arctotis* (*Praearctotis*) *marchaensis*; (c) trapezoid type (*Arctotis* (*Praearctotis*) *similis*); (d) hyperboloid type (*Arctotis (Arctotis) tabagensis*), (e) S-shaped type (*Arctotis* (*Arctotis*) *sublaevis*). Morphological elements: Awg—anterior wing, Akl—anterior keel, AWgAg—anterior wing angle, UE—upper end of the valve, AE—anterior end of the valve, APAW—apical protrusion of the outer margin of the anterior wing of the left valve.

wing. *Meleagrinella* and *Arctotis* have four types of anterior wing (Fig. 2).

The "paraboloid" type in *Meleagrinella (Meleagrinella) prima* and *Arctotis (Praearctotis) marchaensis* is characterized by a short outer ligament (AOL/ADL less than 0.45), a narrow anterior wing (AWgW/AWgL less than 0.15) and an obtuse-angled anterior wing (AWgAg more than 105°).

The "trapezoidal" type in *Arctotis (Praearctotis) similis* is characterized by a long outer ligament (AOL/ADL = 0.45–0.50), a moderately wide anterior wing (AWgW/AWgL = 0.15–0.20) and an obtuse-angled anterior wing (AWgAg more than 105°).

The "hyperboloid" type in *Arctotis (Arctotis) tabagaensis* is characterized by a very long outer ligament (AOL/ADL more than 0.50), wide anterior wing (AWgW/AWgL more than 0.20), subrectangular (AWgAg = 85°–105°) or acute-angled anterior wing (AWgAg less than 85°).

The "S-shaped" type in *Arctotis (Arctotis) sublaevis* is characterized by a very long outer ligament (AOL/ADL more than 0.50), a wide anterior wing (AWgW/AWgL more than 0.20) and an inverted anterior wing with subrectangular (AWgAg = 85°–105°) outlines in the early stages of growth and with obtuse-angled (AWgAg more than 105°) outlines in the later stages of growth.

The "paraboloid" type of the anterior wing is characteristic of *Meleagrinella* s.str. and *Praearctotis*, "trapezoidal" type—for *Praearctotis*, "hyperboloid" and "S-shaped" types—for *Arctotis* s.str.

(23) ***Outline of the posterior wing outer margin.*** This character is determined by the contour of a segment of the posterior margin located between the point of the posterior auricle notch and the lower end of the posterior wing. The straight posterior wing of the left valve is characteristic of *Praemeleagrinella*, Middle Jurassic *Meleagrinella* s.str., the curved posterior wing of the left valve is characteristic of *Clathrolima, Praearctotis, Arctotis*, Toarcian *Meleagrinella* s.str. Similar character states occur at different stratigraphic levels.

(24) ***Anterior outer ligament length (= anterior auricle length).*** The length of the anterior outer ligament is a stable character in *Meleagrinella*.

(25) ***Anterior wing width.*** A narrow wing is characteristic of *Meleagrinella, Canadotis* and early *Praearctotis*, a moderately wide anterior wing is characteristic of late *Praearctotis*, a wide anterior wing is characteristic of *Oxytoma* s.str. and *Arctotis*.

(26) ***Anterior wing angle of the left valve.*** In *Praemeleagrinella, Meleagrinella* s.str., *Clathrolima, Praearctotis, Canadotis,* and *Canadarctotis*, the angle of the anterior wing of the left valve is obtuse. In *Oxytoma* and *Arctotis*, the angle of the anterior wing of the left valve changes from obtuse to straight and acute at different age stages.

(27) ***Valve convexity***. The convexity of the shells of *Meleagrinella* varies with age; juvenile shells have a greater convexity compared to adult specimens. For *Meleagrinella* this trait is not species specific. Taxa with smaller sizes have a greater convexity of the left valves. The convexity of the valves does not depend on an increase in the angle of inclination of the ligament area relative to the midsagittal plane. For example, *Praearctotis marchaensis* has more convex left valves than *Praearctotis similis*, but the ligament platform of the left valve in *Praearctotis marchaensis* has a lesser slope.

The convexity of shells increases in the geochronological sequence from the Late Pliensbachian *Meleagrinella* of the *sparsicosta* group (Pl. IX, figs. 8c, 10b) to the Late Toarcian *Praearctotis* of the *marchaensis* group (Pl. XIII, figs. 1b, 3b, 4b, 5b), as well as in the sequence from Late Toarcian *Praearctotis* of the *similis* group (Pl. XIV, fig. 5b) to Bajocian-Bathonian *Arctotis* of the *lenaensis* group (Pl. XV, fig. 5b). The increased convexity of the valves may have contributed to an increase in the strength of the shells and was a useful adaptation in shallow water conditions with higher-energy aquatic environment.

(28) ***Ribbing density.*** The trait is stable within fossil populations of the same species. In different populations, as a rule, there is variability of the trait. The degree of ribbing was influenced by the type of soil. In clay facies, forms with strongly ribbed shells are more common; in sandy facies, forms with weakly ribbed shells are more common. The width of the ribs was influenced by hydrodynamics: in near-shore facies, the relative width of the ribs at shells is greater than in off-shore facies.

(29) ***Shell shape.*** The shape of the shell in oxytomids is determined by the relative position of the sides of the valves and can be described using well-known geometric figures. Among the Hettangian–Pliensbachian *Meleagrinella*, oval-trapezoidal outlines predominate (*Meleagrinella subolifex, M. ptchelincevae, M. tiungensis, M. deleta*). Oval-triangular (*M. sparsicosta, M. ansparsicosta*) and elongated oval outlines (*M. oxytomaeformis*) are less common. Among the Early Toarcian *Meleagrinella*, oblique-oval (*M. golberti, M. substriata*) and, to a lesser extent, rounded outlines (*M. prima*) predominate. Among the Middle and Late Jurassic *Meleagrinella*, oblique-oval (*M. doneziana, M. braamburensis, M. subovalis*) and, to a lesser extent, rounded outlines (*M. echinata*) predominate. Among the Late Toarcian *Praearctotis*, oval-triangular (*Praearctotis marchaensis*) and elongated oval (*P. similis*) outlines are dominant. Among the early Aalenian *Arctotis*, oval and round shapes predominate (*Arctotis tabagensis, A. sublaevis*). Taxa with similar shell shapes occur at different stratigraphic levels.

(30) ***Size.*** Large and very large shell sizes are characteristic of some species of *Oxytoma* s.str., *Arctotis* s.str. and *Canadarctotis*, medium sizes for *Praearctotis* and *Canadotis*, very small, small and medium for *Praemeleagrinella, Clathrolima* and *Meleagrinella*. The size of the shell varies among different species of the same genus.

(31) ***Symmetry.*** In the diagnosis of the genus Oxytoma, Ichikawa (1958) included such a character as strong inequilaterality. *Oxytoma* and most Hettangian-Toarcian *Meleagrinella* have a strongly inequilateral shell (*Meleagrinella subolifex, M. ptchelincevae, M. tiungensis, M. ansparsicosta, M. deleta, M. golberti*), which indicates the low taxonomic weight of this character for generic diagnosis. An equilateral shell is characteristic of some Pliensbachian–Toarcian *Meleagrinella* (*M. sparsicosta, M. oxytomaeformis, M. prima*). *Praearctotis* shells have both equilateral valves (*Praearctotis similis*) and inequilateral valves (*Praearctotis marchaensis*). Symmetry is very variable in most taxa of the family, even within the same sample.

Identification of Taxa

Due to the absence of a permanently established weight for each character, they are assessed for identification (Meyen, 1989). The main task of classification within the family Oxytomidae was to select as few characters as possible to establish the discreteness of each category of taxa.

Based on the weighing of 31 characteristics, the characteristics of genera, subgenera and species were established. Supraspecific taxa were identified using a combination of characters with high and medium weight. To establish the degree of discreteness of species, a set of any characters with medium and low weight was determined, which was necessary and sufficient to describe the species as a closed system. The data obtained as a result of taxonomic studies were compared with data from the phylogenetic study.

Generic characters. Genera were identified by combining morphological characteristics of the hinge plate and byssal block with data on the reconstruction of phylogeny and ecological adaptations. The main generic characteristics include the type of sculpture, type and subtype of the ligament pit, type of the byssal notch, type of the byssal ear, type of the byssal furrow, position of the ligament area relative to the midsagittal plane, and the length of the ligament area. Auxiliary characters include: the presence of protuberance, the presence of a ligament ridge, the ratio of valve sizes, the posterior auricle length, the shape and location of prisms in the ectostracum of the right valve, and the outline of the byssal ear.

Subgeneric characters. Subgenera were identified by combining morphological characteristics of the hinge plate and byssal block, taking into account data on the study of the evolution of the ligament pit. The main subgeneric characters include the subtype of the ligament pit lower margin, shape of the ligament pit base, and the ligament area length. Auxiliary subgeneric characters include the subtype of the ligament pit, valve convexity ratio.

Species characters. Species were identified based on an assessment of the signs of external morphology, taking into account data on the study of the ontogeny of the hinge plate and byssal block and chorology. The main species traits include the anterior wing type and posterior wing type, outline of the posterior auricle, outline of the outer margin of the posterior wing, length of the anterior auricle, width of the anterior wing, angle of the anterior wing of the left valve, length of the anterior outer ligament. Auxiliary species traits include the ribbing density, valve convexity, shape of the valve contour, symmetry, shell size, and shell shape.

PHYLOGENY

Phylogeny is understood as a sequence of changing ontogenies. The evolution of the family Oxytomidae in the Mesozoic occurred through changes in the ontogenetic cycle in each successive generation. The new phenotype began with the destabilization of the previous phenotype and the emergence of deviations and then the stabilization of these deviations as the new norm. Reconstruction of the phylogeny imprinted in the shells of fossil lineages is the result of reconstructions based on phenetic and chronological relationships (Krassilov, 1977).

The first reconstruction of the phylogeny of the subfamily Oxytominae was based on evolutionary and cladistic approaches. When creating a phylogenetic system of the family using an evolutionary approach, already known superspecies groups were considered as equivalent unranked supraspecific taxa. Phylogenetic constructions and conclusions about the rank of taxa were made after studying the trends in the hinge plate and byssal block in successive geological beds. The relative taxonomic significance of the characters was determined by the stability of the characters in the identified supraspecific groups. The sequence of character transformations was conventionally identified with the history of evolution of a taxonomic group. For cladistic analysis a matrix of 10 morphological characters was analyzed using the criterion of parsimony (parsimony) of transformations of character states. Preliminary weighting of features and establishment of the order of the transformation series were not used. To polarize the cladogram, the oldest genus *Oxytoma* was chosen as an outgroup. As a result, two variants of phylogenetic reconstruction at the genus level were obtained for the genera *Meleagrinella* and *Arctotis*. The evolutionary reconstruction was generally consistent with the reconstruction based on the results of cladistic analysis. The main difference was the position of the supraspecific taxon *Meleagrinella* s.str., originating either from *Praemeleagrinella*, based on the evolutionary approach, or from *Praearctotis*, in accordance with the cladistic method (Lutikov et al., 2010).

In this work, an evolutionary approach was used to reconstruct the phylogeny of the subfamily Oxytominae. When constructing a phylogenetic system, a typological classification was first carried out based on weighted characters, then the phenoclines of some characters were reconstructed. Taking into account the pronounced trends in quantitative and qualitative changes in characters, such as subtype of the ligament pit, subtype of the lower margin of the ligament pit, presence of protuberance, shape of the byssal ear, phylogenetic relationships were determined in the ontogeny of taxa of different geological ages. At the same time, the taxonomic weight of some characters (type and subtype of the ligament pit) decreased for parallel phylogenetic branches (*Oxytoma* and *Meleagrinella*, *Clathrolima* and *Meleagrinella* s.str.). The amount of phyletic information contained in the characters was determined by the degree of relationship between the compared groups. Degree of relatedness was determined by the constant presence of the character in question or a stable complex of several characters in the taxa being compared, and especially in taxa that differ greatly in their lifestyle (Mayr, 1971). The identification of relatedness was carried out by establishing the similarity of homologous components in specimens belonging to different fossil populations. Homology criteria were used as proposed by A. Remane (Severtsov, 1987). The presence of parallelism in variation was considered as additional evidence of phylogenetic relatedness (Meyen, 1988). Similarity was used as a criterion defining the system, relatedness was used as a criterion controlling the quality of the system. Taxa were identified by tracing gaps in similarity, and then tested for unity of origin using a phylogenetic scheme (Rasnitsyn, 2008).

Phenoclines

The phenoclines were identified by recognizing the sequence of characters of the same growth stage in taxa originating from different geological beds. Shell shapes that replace each other in successive layers, characterized by a change in one of the characteristics, form a phenocline.

Phenoclines of the Ligament Pit

The ligament pit in Oxytomidae is a bound element in the hinge plate and has a triangular shape at the postlarval stage in all studied fossil populations. A change in the shape of the ligament pit is the main characters by which the direction of phenocline is determined.

Reconstructions of both phenoclines from *Asoella* to *Oxytoma* and *Meleagrinella* in the Jurassic reveal a tendency for increasing asymmetry in the outlines of the ligament pit. The phenocline of the ligament pit in the series from the Middle Triassic *Asoella* to the Middle Jurassic *Oxytoma* is based on the ontogeny of the Callovian *Oxytoma* ex gr. *expansa*. The outlines of the pit in this taxon, during the transition from the postlarval to the juvenile stage, successively change from wide-angled to subrectangular and then to acute-angled (Lutikov, 2024, Pl. I, fig. 1). The transformation of the ligament pit from the wide-angle type in the Norian *Oxytoma czekanowskii* Teller (Mojsisovics, 1886) to the subrectangular type in *Oxytoma inequivalvis* (Hodges, 2022) probably happened in the Hettangian. An increase in the inclination of the ligament pit and a change in its shape to a wedge-shaped one is reliably established in the early Toarcian in *Oxytoma kirinae* (Pl. VII, fig. 1). A change in the ligament pit from a subrectangular to an acute-angled shape is present in ontogeny in the Toarcian-Aalenian *Oxytoma jacksoni* (Pl. VII, figs. 7, 8). During its evolution in the Norian—Callovian interval, the ligament pit in *Oxytoma* was transformed tending to increase obliquity.

The phenocline of the ligament pit in the series from the Late Triassic *Asoella confertoradiata* Tokuyama, 1959 to the Hettangian *Meleagrinella (Praemeleagrinella)* is interpreted based on the ontogeny of the Hettangian species *Meleagrinella (Praemeleagrinella) subolifex*. In the ontogeny of *Meleagrinella (Praemeleagrinella) subolifex*, during the transition from the postlarval to the mature stage, the pit outline successively changed from subsymmetrical to subrectangular. The ligament pit in the Norian—Hettangian interval in *Praemeleagrinella* gradually changed towards increased pit asymmetry and bringing the anterior margin pit closer to the symmetry axis (Pl. I, figs. 1, 2; Pl. II, figs. 1, 2).

Two phenoclines are constructed from the Hettangian to the Late Pliensbachian *Praemeleagrinella*. One phenocline of the ligament pit was based on the ontogeny of the Late Pliensbachian species *Meleagrinella (Praemeleagrinella) sparsicosta*. During the ontogeny of *Meleagrinella (Praemeleagrinella) sparsicosta*, in the transition from the postlarval to the mature state, the outline of the pit successively changed from wide-angled to subrectangular. In samples from Upper Pliensbachian sections along the Tyung River and in the Tyukyan—Markha interfluve (Tenkelyakh Site), *Meleagrinella (Praemeleagrinella) sparsicosta* is dominated by specimens with a subrectangular ligament pit at the mature stage of ontogeny (Pl. I, fig. 3; Pl. II, fig. 3). There was no transformation of the ligament pit in the *Meleagrinella (Praemeleagrinella) subolifex* (Pl. I, fig. 2)—*Meleagrinella (Praemeleagrinella) sparsicosta* series; the ligament pit remained subrectangular (Pl. I, fig. 3).

The second phenocline ligament pit from the Hettangian to the Late Pliensbachian *Praemeleagrinella* is based on the ontogeny of the Late Pliensbachian species Meleagr*inella (Praemeleagrinella) deleta.* During the individual development of *Meleagrinella (Praemeleagrinella) deleta*, during the transition from the postlarval to the adult stage, the outline of the pit consistently changed from wide-angled to subrectangular. In the sample from the Upper Pliensbachian section in the Markha—Vilyui interfluve (Pravoberezhnyi Site), *Meleagrinella (Praemeleagrinella) deleta* is dominated by specimens in which at the mature stage there is a change in the direction of growth of the ligament pit towards its expansion (Pl. I, figs. 8, 9). Specimens with subrectangular ligament pits are present in smaller numbers (Pl. I, fig. 7). In the Late Pliensbachian species *Meleagrinella (Praemeleagrinella?) tiungensis* in samples from the Anabar River section and in the Tyukyan—Markha interfluve (Tenkelyakh Site), similar age variability was observed with a predominance of specimens with an expanding ligament pit at the mature stage (Pl. I, fig. 4, 5). The ligament pit in the series *Meleagrinella (Praemeleagrinella) subolifex—Meleagrinella (Praemeleagrinella?) tiungensis—Meleagrinella (Praemeleagrinella) deleta* changed towards its expansion.

The phenocline of the ligament pit from Early Jurassic *Praemeleagrinella* to Late Jurassic species of the subgenus *Clathrolima* is based on the ontogeny of the Kimmeridgian-Volgian species *Meleagrinella (Clathrolima) subovalis*. In this taxon, the shape of the ligament pit changed from wide-angle outlines at the postlarval stage to subrectangular outlines at the juvenile stage and to acute angular outlines at the subadult and adult stages. At the mature stage, the ligament pit transformed with a reversal of the direction of growth, and then became even more oblique (Pl. II, fig. 16). The ligament pit in the series *Meleagrinella (Praemeleagrinella) sparsicosta* (Upper Pliensbachian)—*Meleagrinella (Clathrolima) substriata* (Lower Toarcian) (Pl. II, fig. 9)—*Meleagrinella (Clathrolima) lamenti* (Bathonian) (Pl. II, fig. 17)—*Meleagrinella (Clathrolima) braamburensis* (Middle Callovian) (Pl. II, figs. 18, 19)—*Meleagrinella (Clathrolima) subovalis* (Kimmeridgian—Volgian) (Pl. II, fig. 20) gradually became more oblique.

The phenocline of the ligament pit in the series from Late Pliensbachian *Praemeleagrinella* to the Bathonian *Meleagrinella* s.str. is based on the ontogeny of the Bathonian *Meleagrinella (Meleagrinella)* sp. The ontogeny of this taxon was studied on postlarval, juvenile, juvenile, adult and mature specimens in a sample from the Lower Bathonian deposits of the Pletnevsky quarry in the Penza region. The shape of the ligament pit changed from wide-angled at the postlarval stage to oblique at the juvenile stage and widening outlines at the subadult stage. At the adult stage, the pit changed in the direction of increasing obliqueness; at the mature stage, the pit expanded again (Pl. II, fig. 12). The same character of ontogenetic variability was established in the Bajocian *Meleagrinella (Meleagrinella) doneziana* (Pl. III, figs. 1–3) in a sample from the Bajocian (?) deposits of the Perelyubsky District of the Saratov region and, judging by photographs obtained from the Smithsonian Museum, in the type species *Meleagrinella (Meleagrinella) curta* from the Oxfordian of the USA (Pl. II, fig. 14). The ligament pit in the series *Meleagrinella (Meleagrinella) prima* (Lower Toarcian)—*Meleagrinella (Meleagrinella) doneziana* (Bajocian)—*Meleagrinella (Meleagrinella)* sp. (Lower Bathonian)—*Meleagrinella (Meleagrinella) curta* (Oxfordian) changed its shape towards its gradual expansion.

The phenocline of the ligament pit in the succession from the Early Toarcian *Meleagrinella* s.str. to the Late Toarcian *Praearctotis* is based on the ontogeny of the Late Toarcian species *Arctotis (Praearctotis) marchaensis*. In this taxon, the first expansion of the ligament pit is observed already at the juvenile stage. Further changes in the shape of the ligament pit from a subsymmetrical outline at the juvenile stage to oblique outline at the subadult and adult stages. At the mature stage, there was a repeated change in the direction of growth of the ligament pit (Pl. V, fig. 2). The ligament pit in the series *Meleagrinella (Meleagrinella) prima* (Lower Toarcian)—*Arctotis (Praearctotis) marchaensis* (Upper Toarcian) showed a trend to expand. The appearance of the first *Arctotis (Praearctotis)* is associated with the transition of the expansion phase of the ligament pit to an earlier age stage compared to *Meleagrinella*.

The phenocline of the ligament pit in the series from *Praearctotis* to Middle Jurassic *Arctotis* s.str. is based on the sequence of changes in ligament pit in the series *Arctotis (Praearctotis) marchaensis* (Upper Toarcian, Pseudolioceras wuerttenbergeri Zone)—*Arctotis (Praearctotis) similis* (Upper Toarcian, Pseudolioceras falcodiscus Zone)—*Arctotis (Arctotis) tabagensis* (Lower Aalenian). The ligament pit changed from the angular subtype lower margin of the ligament pit in *Arctotis (Praearctotis) marchaensis* (Pl. V, figs. 2, 3, 4) to the spoon-shaped subtype of the lower margin of the ligament pit in *Arctotis (Praearctotis) similis* (Pl. V, figs. 6, 7) and then to the formation of resilifer in *Arctotis (Arctotis) tabagensis* (Pl. V, figs. 9, 10).

Comparison of the shape of the ligament pit in the series *Arctotis (Arctotis) tabagensis* (Lower Aalenian) (Pl. V, fig. 10)—*Arctotis (Arctotis) sublaevis* (Upper Aalenian, Lower Bajocian) (Pl. V, fig. 13)—*Arctotis (Canadotis) canadense* (Volgian stage) (Pl. V, figs. 16, 17)—*Arctotis (Canadarctotis) anabarensis* (Valanginian) (Pl. V, fig. 21) shows that the ligament pit transformation did not occur in this series.

Phenoclines of the Byssal Ear

The compilation of phenoclines of the byssal ear in *Meleagrinella* and *Arctotis* was based on a comparison of the shape and length of the byssal ear in taxa that successively replaced each other in geological sections. The phenoclines of byssal ear outlines in the series from Hettangian to Late Pliensbachian *Praemeleagrinella* are based on the ontogenies of *Meleagrinella (Praemeleagrinella) sparsicosta* and *Meleagrinella (Praemeleagrinella) deleta*. In the Hettangian *Meleagrinella (Praemeleagrinella) subolifex,* the byssal ear is trapezoidal, the anterior margin of the ear forms an obtuse angle with the lower margin (Pl. IV, fig. 4, 5). There was no transformation of the byssal ear in the series *Meleagrinella (Praemeleagrinella) subolifex* (Pl. I, fig. 1)—*Meleagrinella (Praemeleagrinella) sparsicosta* (Pl. I, fig. 3).

The trapezoidal shape of the ligament pit in *Meleagrinella (Praemeleagrinella) sparsicosta* was preserved. In *Meleagrinella (Praemeleagrinella) deleta*, at the early ontogenetic stages, the byssal ear is trapezoidal, at the mature stage it is rhomboid, the anterior margin of the ear forms an acute angle with the lower margin (Pl. IX, fig. 5). The same character of changes in the byssal ear is observed in the late Pliensbachian *Meleagrinella (Praemeleagrinella?) tiungensis* (Pl. II, fig. 4), which arose in the *Amaltheus margaritatus phase*. The transformation of the byssal ear in the series *Meleagrinella (Praemeleagrinella) subolifex*—*Meleagrinella (Praemeleagrinella?) tiungensis*—*Meleagrinella (Praemeleagrinella) deleta* proceeded in the direction of a change in outline from trapezoidal to rhomboid. The phenocline of the byssal ear outlines in the series from the Late Pliensbachian *Praemeleagrinella* to the Kimmeridgian–Volgian *Clathrolima* is based on the ontogeny of *Meleagrinella (Clathrolima) subovalis*. The outline of the byssal ear in the series *Meleagrinella (Praemeleagrinella) sparsicosta* (Upper Pliensbachian) (Pl. II, fig. 3)—*Meleagrinella (Clathrolima) subechinata* (Middle Callovian) (Pl. II, fig. 13)—*Meleagrinella (Clathrolima) subechinata* (Late Callovian)—*Meleagrinella (Clathrolima) subovalis* (Kimmeridgian–Volgian) (Pl. II, figs. 15, 16) changed from trapezoid to rhomboid.

The phenocline of byssal ear outlines in the series from Late Pliensbachian *Meleagrinella (Praemeleagrinella) deleta* to Early Toarcian Meleagrinella s.str. is based on the ontogeny of *Meleagrinella (Meleagrinella) prima*. The transformation of the byssal ear in *Meleagrinella* in the Late Pliensbachian–Early Toarcian went in the direction of a change in outline from rhomboid to trapezoid.

The phenocline of the byssal ear outlines in the series from the Early Toarcian *Meleagrinella (Melea-*

grinella) prima to the Late Toarcian *Arctotis* is based on the ontogeny of *Arctotis (Praearctotis) marchaensis*. The transformation of the byssal ear in *Meleagrinella* went in the direction of a change in outline from trapezoid to drop-shaped.

The phenocline of the byssal ear outline from the Late Toarcian *Praearctotis* to Aalenian *Arctotis* s.str. is based on the series *Arctotis (Praearctotis) marchaensis* (Upper Toarcian)—*Arctotis (Praearctotis) similis—Arctotis (Arctotis) tabagensis*. The transformation of the byssal ear went in the direction of changing the outline from drop-shaped to falcate.

The phenocline of the byssal ear outline from Aalenian to Bathonian *Arctotis* s.str. is based on the series *Arctotis (Arctotis) tabagensis* (Pl. VI, fig. 5)—*Arctotis (Arctotis) sublaevis* (Pl. VI, fig. 7)—*Arctotis (Arctotis) lenaensis*. The transformation of the byssal ear went in the direction of changing the outline from falcate to triangular.

The phenocline of the byssal ear outlines from the Volgian *Canadotis* to the Valanginian *Canadarctotis* is based on the series *Arctotis (Canadotis) canadense* (Volgian Stage) (Pl. VI, fig. 10)—*Arctotis (Canadarctotis) intermedia* (Volgian Stage) (Pl. VI, fig. 11)—*Arctotis (Canadarctotis) anabarensis* (Valanginian) (Pl. VI, fig. 12). The transformation of the byssal ear went in the direction of changing the outline from rhomboid to triangular.

The phenocline of the byssal ear length from Late Pliensbachian *Praemeleagrinella* to Oxfordian *Meleagrinella* s.str. Is based on the series *Meleagrinella (Praemeleagrinella) deleta* (Pl. IX, fig. 5)—*Meleagrinella (Meleagrinella) doneziana* (Pl. II, fig. 11)—*Meleagrinella (Meleagrinella)* sp. (Bathonian) (Pl. IV, fig. 9)—*Meleagrinella (Meleagrinella) curta* (Pl. IV, fig. 12). The byssal ear changed from a long one in *Meleagrinella (Praemeleagrinella) deleta* to a very short in *Meleagrinella (Meleagrinella) curta*.

Phenocline of the Posterior Wing Type

The phenocline of the posterior wing type from Late Pliensbachian *Praemeleagrinella* to Early Toarcian *Clathrolima* is composed of the series *Meleagrinella (Praemeleagrinella) deleta* (Pl. IX, figs. 1, 2, 3, 6, 7)—*Meleagrinella (Praemeleagrinella?) golberti* (Pl. X, figs. 1–13)—*Meleagrinella (Clathrolima) substriata* (Pl. XI, figs. 1–12)—*Meleagrinella (Clathrolima)* sp. (Pl. XI, fig. 13). The posterior wing changed from a straight type to a bow-like type, S-shaped type and an arched type.

Phenocline of the Anterior Wing Type

The phenocline of the anterior wing type phenocline from the Early Toarcian *Meleagrinella* s.str. to the Aalenian-Bajocian *Arctotis* s.str. is based on the series *Meleagrinella (Meleagrinella) prima—Arctotis (Praearctotis) marchaensis—Arctotis (Praearctotis) similis—Arctotis (Arctotis) tabagensis—Arctotis (Arctotis) sublaevis*. The anterior wing changed from paraboloid type to trapezoid type, hyperboloid type and S-shaped type.

Chronoclines

Chronoclines make it possible to establish chronological relationships between phenes that arose in the series of fossil populations. The chronological sequence does not always correspond to the phylogenetic one since ancestors could exist simultaneously with their descendants or even outlive them. Chronoclines illustrate the direction of evolution of certain parts of shells, which may be common to parallel lineages (Krassilov, 1977). Hypotheses about the direction of the chronocline were controlled by levels with ammonites.

The chronocline *Asoella—Oxytoma—Meleagrinella* corresponds to the chronological sequence of the appearance of the genera *Oxytoma* and *Meleagrinella* during the formation of the family but does not record the genetic relationships between these taxa. The basal levels of the lineages of Oxytoma and Meleagrinella do not show gradual transitions from ancestral taxa; they correspond to gaps in the clinal sequence in the Triassic and Early Jurassic.

The chronocline *Meleagrinella (Praemeleagrinella) subolifex* (Hettangian)—*Meleagrinella (Praemeleagrinella) sparsicosta* (Late Pliensbachian) corresponds to the chronological sequence of appearance of taxa. The evolution of ontogenies of *Praemeleagrinella* in Hettangian—Pliensbachian in this series represented a phase of relative stability. The ligament pit in *Meleagrinella (Praemeleagrinella) subolifex* and in *Meleagrinella (Praemeleagrinella) sparsicosta* at the mature stage is represented by modification 1a. The chronocline *Meleagrinella (Praemeleagrinella) subolifex—Meleagrinella (Praemeleagrinella?) tiungensis—Meleagrinella (Praemeleagrinella) deleta* demonstrates directional changes in the ligament pit and byssal ear. Presumably, in the *Amaltheus margaritatus* phase, *Meleagrinella (Praemeleagrinella?) tiungensis* separated from *Meleagrinella (Praemeleagrinella) sparsicosta* as a result of divergence, and then in the *Amaltheus viligaensis* phase, *Meleagrinella (Praemeleagrinella) deleta* separated. The ligament pit in *Meleagrinella (Praemeleagrinella?) tiungensis* and *Meleagrinella (Praemeleagrinella) deleta* at the mature stage is represented by modification 1b, the byssal ear is rhomboid.

In the Early Toarcian, the evolution of the genus *Meleagrinella* represented a phase of directed changes in the ligament pit. At the end of the Pliensbachian (*Amaltheus viligaensis* phase), the species group of the subgenus *Praemeleagrinella* with a subrectangular ligament pit was replaced by a group of species of the subgenus *Clathrolima* with an acute-angled ligament pit (Dactylioceras commune Phase). In parallel with it, a group of species of the subgenus *Meleagrinella* s.str. with a wide-angle ligament pit replaced the *Praemeleagrinella* group with a subrectangular ligament pit (Zugodactylites braunianus Phase).

The chronocline *Meleagrinella (Praemeleagrinella) sparsicosta* (Late Pliensbachian)—*Meleagrinella (Praemeleagrinella?) golberti* (Tiltoniceras antiquum and Harpoceras falciferum phases)—*Meleagrinella (Clathrolima) substriata* (Dactylioceras commune Phase)—*Meleagrinella (Clathrolima)* sp. (Zugodactylites braunianus and Pseudolioceras compactile phases) demonstrates directional changes in the posterior wing type and ligament pit shape. The chronocline corresponds to a continuous clinal sequence of posterior wing types from straight to arcuate and ligament pit shapes from subrectangular to acute-angled. Presumably, in the Dactylioceras commune Phase *Meleagrinella (Praemeleagrinella?) golberti* gave rise to *Clathrolima substriata* as a result of divergence. The chronocline of the posterior wing type of the left valve of *Meleagrinella* is taken as the basis for the periodization of the biochronological scale in the Late Pliensbachian—Late Toarcian (Lutikov and Arp, 2023a).

The chronocline *Meleagrinella (Praemeleagrinella) deleta* (Amaltheus viligaensis Phase)—*Meleagrinella (Praemeleagrinella?)* aff. *golberti* (Harpoceras falciferum Phase)—*Meleagrinella (Meleagrinella) prima* (Zugodactylites braunianus and Pseudolioceras compactile phases) corresponds to the chronological sequence of appearance of taxa but does not record genetic relationships between these taxa. The base of the *Meleagrinella* s.str. lineage does not have a gradual transition from ancestral taxa; it corresponds to a gap in the clinal sequence in the Dactylioceras commune Phase. Presumably, *Meleagrinella (Meleagrinella) prima* diverged from *Meleagrinella (Praemeleagrinella?)* aff. *golberti* in the Zugodactylites braunianus Phase.

In the Late Toarcian, communication between the seas of Eastern Siberia and the basins of Northeast Russia and the Far East decreased. Representatives of *Clathrolima*, which probably includes *"Monotis" elegans* (Quenstedt, 1858), continued to exist in the seas of Western Europe. In the Northeastern Russia, the adaptive zone, which was previously occupied by species of the genus *Meleagrinella* s.str., was occupied in the Late Toarcian by representatives of *Praebuchia (?)* - *"Meleagrinella" faminaestriata* (Polevoy..., 1968). In the seas of Eastern Siberia in the Late Toarcian (Pseudolioceras wuerttenbergeri Phase), *Meleagrinella* s.str. gave rise to *Praearctotis*, in which the hinge plate changed to form an angular and then a spoon-shaped subtype of the ligament pit (Pl. V, figs. 3–7). The group of species of the subgenus *Meleagrinella* s.str., which probably includes *Meleagrinella milovae, Meleagrinella okayamensis*, continued to exist in the seas of the Far East and Japan (Hayami, 1961; Okuneva, 2002).

The chronocline of *Meleagrinella prima—Praearctotis marchaensis—Arctotis tabagensis* is characterized by a gradual change in the shape of the ligament pit towards the formation of resilifer. The emergence of new structural types at the superspecies level corresponds to the continuous clinal sequence of this feature in the Late Toarcian—Early Aalenian. The phenocline of the ligament pit shape records the phylogenetic relationships between these three taxa. The wide-angled ligament pit arose in *Meleagrinella (Meleagrinella) prima* at the end of the Early Toarcian (Zugodactylites braunianus Phase). In the Late Toarcian (Pseudolioceras wuerttenbergeri Phase), the shell size of *Arctotis (Praearctotis) marchaensis* increased, the ligament pit expanded, a depression formed near the anterior margin pit, and an angular subtype of the ligament pit emerged (Pl. V, figs. 3, 4). In the terminal Toarcian, in *Arctotis (Praearctotis) similis*, the depression near the anterior margin began to occupy most of the area of the ligament pit, and a spoon-shaped subtype of the ligament pit arose (Pl. V, figs. 5, 6).

The chronocline *Arctotis (Praearctotis) marchaensis—Arctotis (Praearctotis) similis—Arctotis (Arctotis) tabagensis—Arctotis (Arctotis) sublaevis* is characterized by a gradual change in the shape of the anterior wing. The emergence of new species taxa corresponds to the continuous clinal sequence of this character in the Late Toarcian—Late Aalenian. The phenocline of the anterior wing type of the left valve of *Arctotis* is taken as the basis for the periodization of the biochronological scale in the Late Toarcian—Bajocian (Lutikov, 2021).

The chronocline *Meleagrinella (Meleagrinella) doneziana (Bajocian)—Meleagrinella (Meleagrinella)* sp. (Early Bathonian)—*Meleagrinella (Meleagrinella) curta* (Oxfordian) corresponds to the chronological sequence of taxa but does not record genetic relationships between these taxa. The base of the *Meleagrinella (Meleagrinella) doneziana* lineage does not have a gradual transition from ancestral taxa; it corresponds to a gap in the clinal sequence in Aalenian. Presumably, in the Aalenian, *Meleagrinella (Meleagrinella) doneziana* diverged from Western European taxa of the *Meleagrinella* s.str. lineage. In the Bajocian, the species group of the subgenus *Meleagrinella* s.str. with a ligament pit represented by modification 4a, replaced the species group of the subgenus *Meleagrinella* s.str. with modification 2. In the Bajocian, Bathonian, Callovian and Oxfordian, the evolution of Meleagrinella s.str. represented a phase of relative stability. There were no significant changes in the ontogenetic sequence from the Bajocian *Meleagrinella (Meleagrinella) doneziana* to the Oxfordian *Meleagrinella (Meleagrinella) curta*. In Bathonian, a ligament pit with modification 4b appeared in *Meleagrinella (Meleagrinella)* sp.

The chronocline *Meleagrinella (Clathrolima) substriata* (Lower Toarcian)—*Meleagrinella (Clathrolima) lamenti* (Bathonian)—*Meleagrinella (Clathrolima)* *braamburensis* (Middle Callovian)–*Meleagrinella (Clathrolima) subechinata* (Late Callovian)–*Meleagrinella (Clathrolima) subovalis* (Kimmeridgian–Volgian) coincides with the phenocline and corresponds to the chronological sequence of the taxa. The lineage has gaps in clinal sequence in the Aalenian, Bajocian, and Oxfordian and probably does not record genetic relationships between all taxa. In the Toarcian–Kimmeridgian, the evolution of *Clathrolima* represented a phase of stability. In all taxa, the ligament pit is represented by modification 5. In the direction from *Meleagrinella (Clathrolima) substriata* to *Meleagrinella (Clathrolima) subovalis*, there was a slight increase in the obliqueness of the ligament pit.

The chronocline *Arctotis (Canadotis) simkini* (Oxfordian)–*Arctotis (Canadotis) canadense* (Volgian)–*Arctotis (Canadarctotis) intermedia* (Volgian)–*Arctotis (Canadarctotis) anabarensis* (Valanginian) corresponds to the chronological sequence of taxa. The base of the lineage *Arctotis (Canadotis) simkini* does not have a gradual transition from ancestral taxa; it corresponds to a gap in the clinal sequence in the Callovian. In Oxfordian, the subgenus *Arctotis* s.str. was replaced by a group of species of the subgenus *Canadotis*, which includes Oxfordian-Volgian oxytomids with a relatively wider ligament area than that of *Arctotis* s.str. This group is close in hinge plate structure to the Toarcian *Paearctotis*. Despite having certain characters in common with *Arctotis* s.str., the species group of *Canadotis* was not previously considered a derivative of the genus *Arctotis* and was considered as a genus in its own right (Jeletzky and Poulton, 1987). The presence of protuberance on the pseudoligamentous platform of the left valves of Volgian *Canadotis canadense* (Pl. V, figs. 14, 15) confirms the phylogenetic relationship of the subgenus *Canadotis* with *Praearctotis*. In the Volgian, the subgenus Canadarctotis diverged from the *Canadotis* lineage. The subgenus *Canadarctotis* unites Volgian-Valanginian taxa that have a strong slope of the ligament platform of the left valve and a wide pseudoligamentous platform close to the inner side of the left valve.

Phylogenetic Hypotheses

Interpretations of the phylogeny of the family Oxytomidae are hypothetical. Using the method of typifying of the hinge, the patterns of evolutionary variability of mollusk shells were studied. Extrapolation of conclusions about phylogeny from characters to a taxon, requires two implied procedures: (1) extrapolation from characters to the historical series of ontogenies and (2) extrapolation from the morphological trend in the historical series of ontogenies to a taxon of the corresponding rank (Severtsov, 1987). Evolutionary taxonomy is based on the principles that genetic distances are inadequate to chronological distances and that when reconstructing phylogeny, similarity and relatedness should be maximized simultaneously (Krassilov, 1977). The coincidence of phenoclines and chronoclines increases the reliability of phylogenetic reconstruction (Krassilov, 1976). The phylogenetic interpretation of phenoclines is based on the predominance of certain trends in the evolution of the trait. The initial state of a trait is considered to be the least specialized (Krassilov, 1977).

Reconstruction of phylogeny within the family Oxytomidae was done in two stages. At the first stage, an archetype was identified in the putative ancestral taxa—a set of unspecialized ancestral characters. For the Jurassic *Oxytoma* and *Meleagrinella*, these are characters present in the subgenus *Asoella* (Tokuyama, 1959), which appeared in the Triassic. For the Middle Jurassic and Cretaceous *Arctotis*, this is a set of characters of the subgenus *Meleagrinella* s.str., which appeared in the Early Jurassic. At the second stage, the components of the hypothetical archetype were compared with the corresponding homologated components of shells belonging to other taxa. The transformation of the ligament pit in the Jurassic-Cretaceous *Meleagrinella* and *Arctotis* is taken as the main link in the reconstruction of the phylogeny of the family Oxytomidae in the Triassic and Jurassic. The sequence of states of this character is conventionally correlated with the sequence of evolution of the family Oxytomidae (Fig. 3).

Jackson (1890) was the first to propose a reconstruction of the phylogeny of the genera *Pseudomonotis* (including *Meleagrinella* (author's comm.) and *Oxytoma* in the Phanerozoic.

It was assumed that these genera arose in the Devonian and Triassic, respectively, from a common ancestor—the genus *Avicula*. Modern ideas about the phylogenetic relationships of Jurassic oxytomids with Triassic ancestors are mainly based on the hypotheses of K. Ichikawa. The genus *Oxytoma* Meek, 1864 is the earliest genus in the lineage of the family Oxytomidae. It was assumed that the splitting of the lineage Aviculopectinidae happened in the Middle Triassic as a result of the emergence of the "Oxytomini" group among the Triassic aviculopectenids, characterized by a discrete pallial line and a calcitic rather than aragonitic endostracum. The Triassic genus *Eumorphotis* Bittner, 1901, assigned to the group "Aviculopectinini", was proposed as a probable ancestor of *Oxytoma* (Ichikawa, 1958). Hypotheses of the structure of the hinge plate in *Eumorphotis* s.str. are based on an image of the hinge of the left valve of an adult specimen of the species *Eumorphotis multiformis* (Bittner), originating from the Lower Triassic of the USA. The shape of the ligament pit of this specimen is subrectangular (Waterhouse, 2008, p. 164, text-fig. 96).

Later, within the genus *Eumorphotis*, A. Tokuyama proposed a group of species from the Middle and Upper Triassic of Japan and assigned it to the subgenus *Asoella*. The structure of the hinge plate of *Asoella* is illustrated in the drawings of the hinges of the left valve of *Asoella confertoradiata* Tokuyama and the

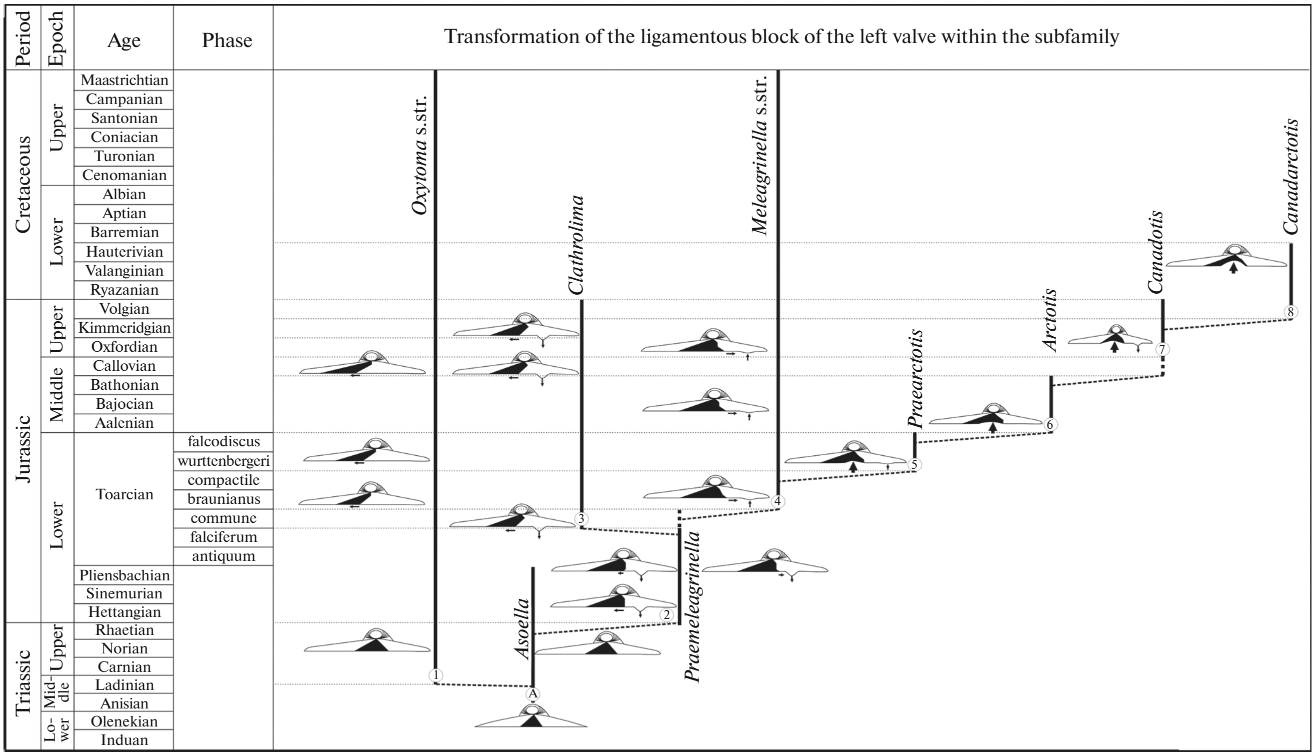


Fig. 3. Scheme of directions of ligament pit transformation in the phylogeny of the subfamily Oxytominae. A—archetype phylogenetic lineage, numbers in circles reflect the sequence of emergence of new lineage. Black color shows the shape of the ligament pit of the left valve, horizontal arrows show the tendency of the lower end of the anterior margin of the ligament pit to move in each lineage, vertical down arrows show the tendency of increasing protuberance, vertical arrows up show the tendency of reducing protuberance. Bold vertical arrows show the tendency of increasing inclination of the ligament pit relative to the midsagittal plane.

right valve of *Asoella laevigata* Tokuyama from the Norian of Japan (Tokuyama, 1959, text-figs. 1, 2). The shape of the ligament pit in *Asoella* is subsymmetrical. The earliest representatives of *Asoella* are known from the Anisian of Alaska (Verma, 1968) and China (Ros-Franch et al., 2014).

The earliest *Oxytoma* are known from the Middle Triassic (Dagys and Kurushin, 1985). Images of specimens of *Oxytoma* sp. were published from the Upper Ladinian of a section on the Dzhugadzhak River (Korkodona River basin), but their hinge was not studied (*Atlas*..., 1976). The only known image of the hinge plate of an adult specimen of *Oxytoma czekanowskii* Teller from the Norian of the Yana River basin, the ligament pit looks like an isosceles triangle (Mojsisovics, 1886, pl. XIX, fig. 4). SEM studies of the ligament pit have shown that in the Jurassic *Oxytoma* and *Meleagrinella*, the wide-angled triangular ligament pit first appears at the postlarval stage (Lutikov, 2024, pl. I, fig. 1; pl. I, fig. 6). The shape of the ligament pit at this stage is close to the shape of the pit of the Triassic adult specimen of *Asoella confertoradiata* (Tokuyama, 1959).

In accordance with the recapitulation hypothesis, the probable ancestor of *Oxytoma* and *Meleagrinella* could be a taxon belonging to *Asoella* Tokuyama, 1959. The hypothesis of Ichikawa (1958) of the origin of *Oxytoma* and *Meleagrinella* directly from *Eumorphotis* s.str., apparently, cannot be supported.

According to Ichikawa (1958), the genera *Oxytoma* and *Meleagrinella* evolved from different ancestral species. It is obvious that the formation of the family Oxytomidae by iterative branching of the genera *Oxytoma* and *Meleagrinella* at different times from the lineage *Asoella* can only be explained from the perspective of the theory of polyphyletic origin or based on the concept of broad monophyly (Simpson, 2006).

According to Verma (1968), the genus *Eumorphotis* flourished in the Early Triassic and continued to exist until the end of the Triassic. Findings of "*Meleagrinella*" in association with *Eumorphotis* are known from the Upper Norian of British Columbia. There is evidence of joint findings of "*Meleagrinella*" in association with *Oxytoma* in the Upper Triassic of Japan and the Queen Elizabeth Islands, so an alternative hypothesis has emerged about the origin of *Meleagrinella* from *Oxytoma* (Verma, 1968). This hypothesis can be explained from the perspective of the theory of monophyletic origin, but requires verification based on the study of the hinge plate and byssal block of the Triassic representative of *Oxytoma* and "*Meleagrinella*".

According to Ichikawa, the *Meleagrinella* evolved from *Eumorphotis* in Rhaetian. However, the structure of the hinge plate in the Triassic "*Meleagrinella*" is not known. Part of the Boreal Triassic "*Meleagrinella*" (Voronets, 1936; Korchinskaya, 1980; Dagys and Kurushin, 1985; *Triasovaya*..., 1996) apparently belongs to the subgenus *Eumorphotis (Asoella),* widespread in the Middle and Upper Triassic of Japan (Tokuyama, 1959), Middle and Upper Triassic of Western Canada (Verma, 1968). This conclusion is indirectly confirmed by a re-examination of the type specimens of *"Meleagrinella" boehmi* Korchiskaya, 1980 from the lower Norian of the Spitsbergen archipelago (Korchinskaya, 1980). Unlike the genus *Meleagrinella*, which is characterized by an "aviculoid" oblique shell shape with an elongated posterior auricle, *Asoella* have a "pectinoid" shell shape with equal-sized auricles (Pl. XVIII, fig. 1).

In this work, the phylogeny of the family Oxytomidae in the Triassic is reconstructed on the basis of the hypothesis of the morphological similarity of *Eumorphotis (Asoella)* and Oxytomidae (Fig. 4).

The phylogeny of the family was reconstructed by identifying the relationships between different groups of fossils and constructing the process by which the phyletic lineage of the family Oxytomidae branched through time. Genealogical relationships between taxonomic groups were identified based on recognized similar characters in the structure of the hinge plate and byssal block, including the type and subtype of the ligament pit, the presence or absence of protuberance, the presence or absence of inclination of the ligament area relative to the shell axis, and the type byssal notch and the type of the byssal furrow.

The family Oxytomidae evolved in the Ladinian as a result of *Oxytoma* separating from *Asoella*. The main characters that influenced the separation of the family were the appearance in the ancestral forms of a discrete pallial line and the calcitic shell. The ligament pit in the Late Triassic *Oxytoma* remained symmetrical during the adult stage (Mojsisovics, 1886). The evolution of the genus *Oxytoma* in the Jurassic followed the evolution of the byssal attachment to a solid substrate. The expansion of the byssal notch was probably facilitated by an increase in the number of byssal threads or their fusion to increase the strength of attachment to mobile algae. The elongated posterior auricle of *Oxytoma* was directed upward at an angle comparable to the angle formed by the lateral branches of the algae. The appearance of the oblique subtype of the ligament pit in the Early Jurassic was apparently correlated with the orientation of the shell valves relative to the vertical stem of algae (similar to modern pteriids—*Pteria colymbus*) (Stanley, 1970).

Presumably, the separation of *Meleagrinella (Praemeleagrinella)* from *Eumorphotis (Asoella)* occurred in the Hettangian. New formations in *Praemeleagrinella* were an asymmetrical ligament pit and a short ligament area. Although in the past the subgenus *Asoella* was thought to have disappeared at the end of the Late Triassic, its presence has recently been reported in Sinemurian and Pliensbachian sediments of South America (Ros-Franch et al., 2014). The genus *Meleagrinella* was reliably established only in the Hettangian (Pl. XVIII, figs. 2, 3). This conclusion is based on the presence of an asymmetric ligament pit and protuberance at the juvenile stage of ontogeny in *Meleagrinella (Praemeleagrinella) subolifex* Polubotko, 1968 (Pl. II, figs. 1, 2).

In the Hettangian–Pliensbachian, morphogenesis in *Meleagrinella* represented a phase of relative stability—the change in the shape of the ligament pit in most taxa went in the direction of increasing skewness. A weakly sloping ligament pit at the adult stage is present in *Meleagrinella (Praemeleagrinella) subolifex* in the Hettangian (Pl. I, figs. 1, 2; Pl. II, figs. 1, 2) and in *Meleagrinella (Praemeleagrinella) sparsicosta* in the late Pliensbachian (Pl. I, fig. 3; Pl. II, fig. 3). More significant changes occurred in the byssal block. The transformation of the byssal block went in the direction of changing the outlines of the byssal ear from trapezoid to rhomboid. In the Hettangian *Meleagrinella (Praemeleagrinella),* the *subolifex* byssal ear has a trapezoidal outline—the anterior margin of the ear forms an obtuse angle with the lower margin (Pl. II, figs. 1, 2; Pl. IV, figs. 4, 5), in the late Pliensbachian *Meleagrinella (Praemeleagrinella) sparsicosta* and *Meleagrinella (Praemeleagrinella?) tiungensis*, the byssal ear is rhomboid (Pl. II, figs. 3, 4, 5; Pl. IV, figs. 6, 7), in the later *Meleagrinella* (*Praemeleagrinella*) *deleta*, the byssal ear is rhomboid—the anterior margin of the ear forms an acute angle with the lower margin (Pl. IX, fig. 5). During life, the hinge line of *Meleagrinella* was oriented at an angle to the base of the attachment surface. The specialization of the organism went in the direction of strengthening the byssal method of attaching shells to a solid substrate or to each other, similar to modern *Pinctada radiata* (Stanley, 1970).

In the terminal part of Pliensbachian (Amaltheus viligaensis Zone), *Praemeleagrinella* developed deviations in the general form of ligament pit. At mature ontogenetic stage in *Meleagrinella (Praemeleagrinella) deleta,* the ligament pit in some specimens has modification 1a (Pl. I, fig. 7), in others—modification 1b (Pl. I, figs. 8, 9). The expanding ligament pit is also characteristic of the ate Pliensbachian *Meleagrinella (Praemeleagrinella?) tiungensis* (Pl. I, fig. 4). The transformation of the ligament pit at the end of the Pliensbachian towards its expansion apparently preceded the formation in the Toarcian of taxa with an expanding ligament pit, which appeared already at earlier ontogenetic stages, and the separation of *Meleagrinella* s.str. in the phylogeny of the genus *Meleagrinella*.

Meleagrinella (Praemeleagrinella?) golberti is the earliest representative of the genus *Meleagrinella* in the Toarcian. This species appeared in the Dactylioceras tenuicostatum Phase and was characterized by the appearance of a new phene—a curved posterior wing. The biozone of the species covers the Dactylioceras

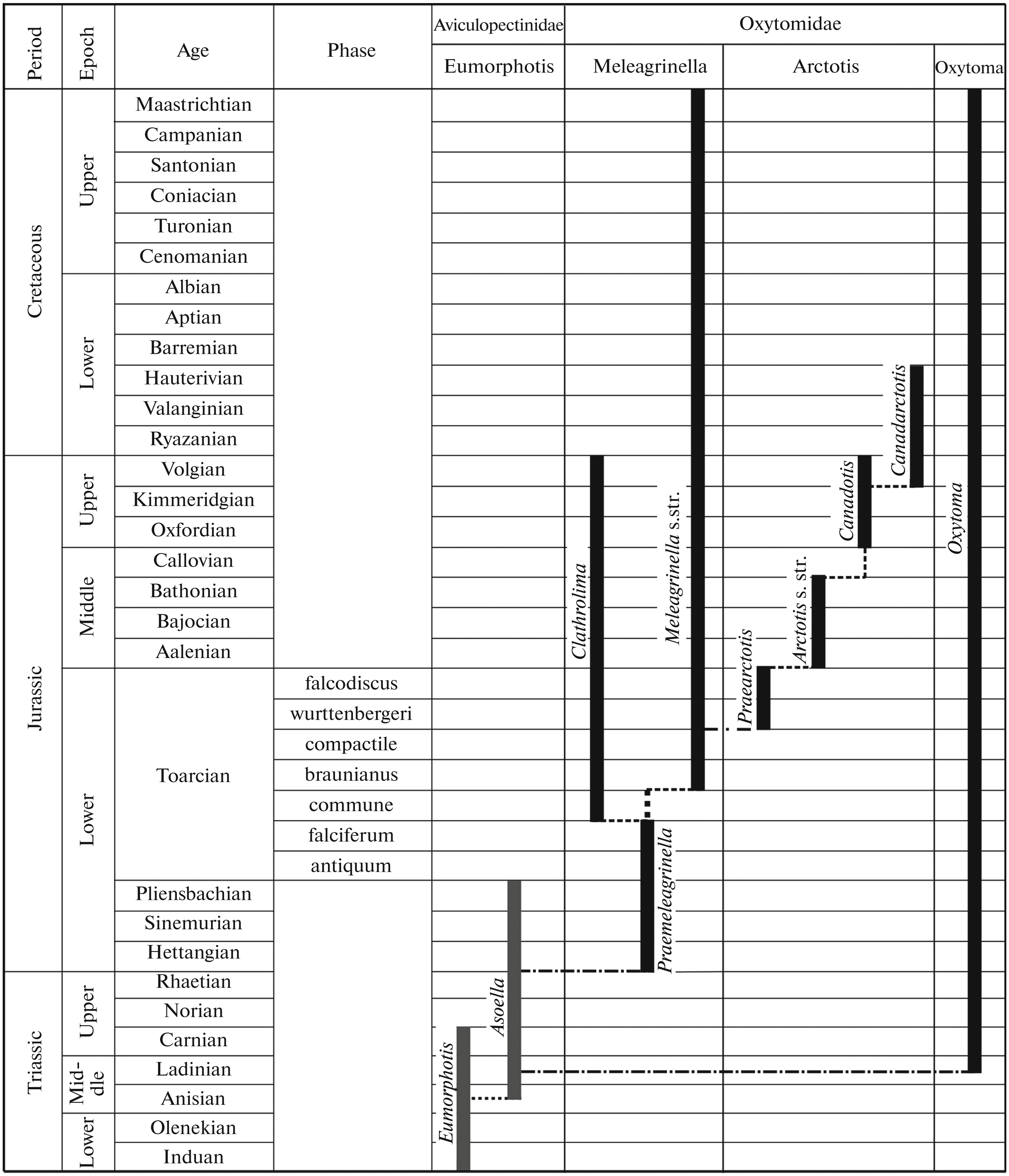


Fig. 4. Scheme of reconstruction of the phylogeny of the genera *Eumorphotis, Oxytoma, Meleagrinella* and *Arctotis*. Wide gray vertical lines indicate the stratigraphic range of the putative oxytomid ancestor. Wide black vertical lines indicate the stratigraphic range of subgenera, dashed lines show family relationships between subgenera, and dash-dot lines between genera.

tenuicostatum–Harpoceras serpentinum ammonite zones of the Subboreal standard scale and the Tiltoniceras antiquum–Harpoceras falciferum zones of the Boreal standard scale of the same age. The structure of the hinge plate in this taxon is unknown.

In the early Toarcian, *Praemeleagrinella* split into two phylogenetic groups—*Clathrolima* and *Meleagrinella* s.str. Presumably, the *Clathrolima* separated during the Dactylioceras commune Phase. An increase in the obliqueness of the ligament pit was a new acquired character (Pl. I, figs. 10, 11). Presumably, in the Zugodactylites braunianus Phase, the lineage *Meleagrinella* s.str separated. The expanding subtype of the ligament pit was a new character. The successive taxa in successive Jurassic beds of the demonstrate a multidirectional change in the shape of ligament pit. In the lineage of specialization *Meleagrinella (Praemeleagrinella) deleta–Meleagrinella (Clathrolima) substriata* the shape of the ligament pit changed in the direction of the formation of acute-angled outlines. In the Middle and Late Jurassic, evolutionary morphogenesis in the *Clathrolima* group was reflected in the increased obliqueness of the ligament pit in the ontogeny of the Callovian *Meleagrinella (Clathrolima) braamburensis* and Kimmeridgian *Meleagrinella (Clathrolima) subovalis*. Ethological specialization went towards the development of the byssal method of attachment to algae. In the line of specialization *Meleagrinella (Praemeleagrinella) deleta–Meleagrinella (Meleagrinella) prima*, the shape of the ligament pit changed in the direction of its expansion. The expansion of the fibrous ligament was a more effective adaptation for living in shallow-water high energy near-shore environments in the Zugodactylites braunianus Phase. The rounded shape and weak sculpture of the upper umbilical part of the right valve in *Meleagrinella (Meleagrinella) prima* indicate the close adhesion of the shells to the substrate (Pl. XII, fig. 10). Ethological specialization followed the direction of increasing attachment to the ground.

If Meleagrinella (Clathrolima) substriata was indeed the ancestral species for Meleagrinella (Meleagrinella) prima, then the expansion of the ligament pit took place rapidly. The angle of the anterior margin of the ligament pit to the lower margin of the ligament pit at the adult stage of ontogeny increased from 65° to 150°. In this case, the process of transforming the hinge plate of *Meleagrinella (Meleagrinella) prima* from the ancestral species *Meleagrinella (Clathrolima) substriata* should have occurred relatively quickly—within one ammonite phase. It seems more likely that the ligament pit of *Meleagrinella (Meleagrinella) prima* was gradually evolved from an intermediate taxon of the subgenus *Praemeleagrinella*. In *Meleagrinella (Praemeleagrinella) deleta*, the ligament pit expands at the mature stage. The expansion of the ligament pit in *Meleagrinella (Meleagrinella) prima* begins already at the subadult stage. Presumably, the closest ancestor was the species *Meleagrinella (Praemeleagrinella?)* aff. *golberti*, which is reliably present in the Harpoceras falciferum Zone (Brodnaya River). The presence of *Praemeleagrinella* in the Dactylioceras commune Zone has not been established. The appearance of *Meleagrinella* s.str. could have happened either in the Harpoceras falciferum Phase or in the Zugodactylites braunianus Phase.

Specialization of *Meleagrinella* s.str. in the shallow seas of Eastern Siberia showed the trend to expand the ligament pit. The specialization of *Meleagrinella (Clathrolima)* in deeper seas of Western Europe followed a trend towards increased obliqueness of the ligament pit. In this scenario, both phyletic lineages originating from the common ancestral lineage of *Praemeleagrinella* synchronously evolved in the Toarcian. This variant of the phylogeny is supported by the findings of *Meleagrinella* with mixed characters in the upper part of the Suntary Formation of the Pravoberezhnyi Site (Pl. XI, fig. 11). In *Meleagrinella (Clathrolima)* sp., the hinge plate structure corresponds to that of *Clathrolima*, all other external characters, including species-specific ones—a notch below the posterior auricle and a strongly curved posterior wing, correspond to those of *Meleagrinella (Meleagrinella) prima*. Because of homologous mutation and parallelism of closely related lines of *Clathrolima* and *Meleagrinella* s.str., the characteristic traits of the species *Meleagrinella (Meleagrinella) prima* appeared not in one, but in several populations (Anabar, Tenkelyakh and Pravoberezhnyi sites). The appearance in large numbers of certain phenes in parallel closely related phylolines may look like instantaneous dispersal of the species (Krassilov, 1977). For the Lower Toarcian (Harpoceras falciferum, Dactylioceras commune phases) with a high position of the global sea level, an explanation of the parallel sequence of species of the genus *Meleagrinella* in various sections is also possible using the Darwin-Huxley concept, according to which the dominant progressive species quickly spread from the center of origin and everywhere replaced more primitive ancestral species (Darwin, 1991).

In the Zugodactylites braunianus and Pseudolioceras compactile phases, the hypothesis of the simultaneous competitive replacement of ancestral taxa by descendent taxa may raise objections. It is unlikely that there were good connections between basins in the Arctic and Boreal-Atlantic paleobiogeographic regions, since the benthic fauna assemblages of Eastern Siberia, Northeastern Russia and Germany have little in common.

Phylogenetic position of the species group *Meleagrinella* s.str. has previously been interpreted ambiguously using evolutionary and cladistic approaches. The difference between the reconstructions was different conclusions about the origin of *Meleagrinella* s.str.—either from *Praemeleagrinella* or *Praearctotis* (Lutikov et al., 2010). At the same time, the shape of the ligament pit in the type species of the genus—*Pseudomonotis (Eumicrotis) curta* Whitfield, 1880 from the Oxfordian of the USA –seemed symmetrical based on uninformative images given by Whitfield (1880). Studies conducted in 2022 showed that ligament pit in the type species *Meleagrinella curta* (Pl. II, fig. 14), as well as in the Early Toarcian, *Meleagrinella (Meleagrinella) prima* (Pl. I, fig. 14), Bajocian *Meleagrinella doneziana* (Pl. II, fig. 11; Pl. III, figs. 1–3) and Early Bathonian *Meleagrinella* sp. (Pl. II, fig. 12) belongs to the expanding subtype. This allows these species to be considered as part of one phylogenetic group—the subgenus *Meleagrinella* s.str.

In the Late Toarcian (Pseudolioceras wuerttenbergeri Phase), the phylogenetic group *Arctotis (Praearctotis)* separated from *Meleagrinella* s.str. New formations in *Praearctotis* were a spoon-shaped depression in the anterior part of the ligament pit of the right valve, an angular subtype of the lower margin of the ligament pit of the right valve, and an inclination of the ligament area of the left valve.

Supposedly, the ancestral form of *Arctotis (Praearctotis) marchaensis* is the species *Meleagrinella (Meleagrinella) prima*, which in the ligament block has morphological characters inherent in *Arctotis*. The presence of a subsymmetrical pit in *Meleagrinella (Meleagrinella) prima* at the postlarval stage (Pl. I, fig. 12), as in *Arctotis* s.str. (Pl. V, fig. 8), indicates the proximity of *Meleagrinella* s.str. and *Arctotis*. The relationship between *Arctotis* and *Meleagrinella* is also supported by the presence of residual protuberance on the pseudoligamentous platform in *Praearctotis* (Pl. V, figs. 1, 2) and *Meleagrinella* s.str. (Pl. I, fig. 14) and the appearance of a weak bend of the lower margin of the ligament pit of the right valve in *Meleagrinella* s.str. (Pl. II, figs. 9, 10).

An indication of the relationship between *Meleagrinella (Praemeleagrinella?) tiungensis* and *Arctotis (Praearctotis) marchaensis* may be the same type of microsculpture of the endostracum in the middle part of the right valve. In *Meleagrinella (Praemeleagrinella?) tiungensis* (Pl. VIII, figs. 3, 4) *and Arctotis (Praearctotis) marchaensis* (Pl. VIII, fig. 8), the microsculpture is characterized by hexagonal prisms arranged in a disorderly manner. However, this morphological character could have arisen under the influence of cooling water and a decrease in its salinity in sea basins, and therefore was not associated with kinship. The levels with *Meleagrinella (Praemeleagrinella?) tiungensis* and *Arctotis (Praearctotis) marchaensis* are associated with interbeds with glendonites, indicators of cold water (Rogov et al., 2021). In *Meleagrinella (Meleagrinella) prima*, the closest putative ancestor of *Arctotis* from the Zugodactylites braunianus Zone, the microsculpture of the ostracum mainly consists of quadrangular prisms located parallel to the radial ribs in the direction from the crown to the lower margin (Pl. VIII, fig. 6).

The hypothesis about the origin of *Arctotis* during the periods of the most significant isolation of the Arctic basin in the Middle Jurassic, following iterative evolution from the genus *Meleagrinella*, was proposed by V.A. Zakharov and B.N. Shurygin (Zakharov et al., 2002). New paleontological data further develop this idea. In the Early Jurassic, the appearance of *Arctotis* was preceded by the emergence of new phenes in the ligament block among oxytomids. The angular subtype of the lower margin of the ligament pit arose in *Meleagrinella (Praemeleagrinella?) tiungensis* in a local population on the Tyung River in the late Pliensbachian (Pl. II, fig. 4) and reappeared in the Late Toarcian in several populations of *Arctotis (Praearctotis)* relatively simultaneously (Pseudolioceras wuerttenbergeri Phase) on the territory of the Vilyui (temperate latitude) and Nordvik (north latitude) epicontinental seas (Pl. V, figs. 3, 4). The expanding subtype of the ligament pit, which arose in *Meleagrinella (Meleagrinella) prima* in the Early Toarcian, and the inversed type of the ligament pit, which appeared in *Arctotis (Praearctotis) marchaensis*, could be the result of phylogenetic variability with a shift in the final states of characters that arose in ancestors to more and more early stages in descendants.

The initial stage of the formation of a new adaptive type in *Arctotis* was characterized by a high rate of morphogenesis. In the Pseudolioceras wuerttenbergeri Phase, *Arctotis (Praearctotis) marchaensis* developed a depression at the base of the ligament pit, which was the prototype of the resilifer (Pl. V, fig. 3). Against the background of an increase in the size of the shell, the growth of the ligament area in the direction from the beak to its lower margin contributed to the expansion of the pit and the formation of an angular subtype of its lower margin.

In the Pseudolioceras falcodiscus Phase, the angular lower margin of the ligament pit subtype in *Arctotis (Praearctotis) marchaensis* was replaced by a spoon-shaped subtype in *Arctotis (Praearctotis) similis*. The ligament pit of this taxon has a depression that occupies most of the base of the pit (Pl. V, figs. 6, 7).

The spoon-shaped resilifer (Pl. V, fig. 10) appeared in *Arctotis* in the Aalenian (Pseudolioceras maclintocki Phase). An increase in the curvature of the outer margin of the resilifer on the right valve affected the increased inclination of the ligament pit and ligament area towards the inner surface of the left valve. The change in the position of the parts of the hinge plate in relation to each other determined the emergence of a new shell structure in oxytomids and, accordingly, led to the separation of the subgenus *Arctotis* s.str. Among the diversity of Early and Middle Jurassic *Arctotis*, two main adaptive types can be distinguished: with a gaping byssal notch (*Praearctotis*) and with an overgrown byssal notch (*Arctotis* s.str.). The appearance of *Arctotis* s.str. was not accompanied by an abrupt change in the adaptive type in oxytomids. The appearance of a new morphotype in Aalenian is associated with new ethological adaptations—a very weak byssal attachment, which allows the organism to be in different orientations relative to the attachment surface and form groups of closely adjacent shells under conditions of active hydrodynamics. The transition period from one adaptive type to another was relatively long. Evolutionary transformations from taxa with an exclusively byssal attachment method (*Meleagrinella prima*) to taxa with a very weak byssal attachment (*Arctotis sublaevis*), in which animals could live in different orientations relative to the attachment surface and form groups of shells tightly adjacent to each other, began in the late Toarcian and ended in the early Bajocian (about 11.4 Ma).

The hypothesis of the origin of *Canadotis* from Late Triassic or Early Jurassic "Meleagrinella-form" bivalves belong to Yu. Eletsky and T. Poulton. They also suggested the existence of a direct phylogenetic relationship between the Middle Jurassic *Arctotis* and the *Cretaceous* Canadarctotis, uniting the group of Cretaceous species into the subgenus *Arctotis* (*Canadarctotis*) (Jeletzky and Poulton, 1987). V.A. Zakharov and B.N. Shurygin suggested that *Canadotis* and *Canadarctotis* formed due to terative evolution, the phyletic lineage of which was represented by the genus Meleagrinella (Zakharov et al., 2002). O.A. Lutikov and B.N. Shurygin suggested that *Canadotis* is a synonym of *Meleagrinella* (Lutikov and Shurygin, 2010).

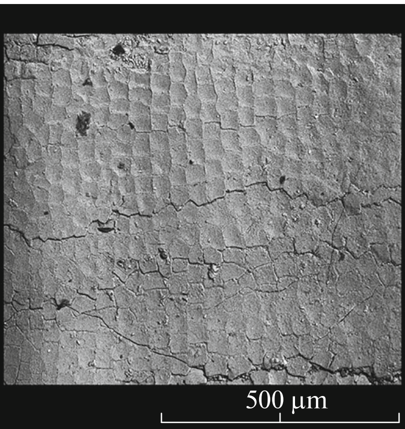
New data on the structure of the ligamentous and byssal blocks in *Canadotis*, obtained on material from the Lower Volga sediments of (collection of Yu.S. Repin) and the Oxfordian of the Amur oblast (collection of N.S. Voronets, TsNIGR Museum, St. Petersburg), develop these views. *Canadotis* has a spoon-shaped resilifer on the ligamentous platform of the right valve (pl. V, figs. 16, 17). According to this character, *Canadotis* should be referred to *Arctotis*. *Canadotis* has a protuberance on the pseudoligamentous platform. According to this character, this taxon is close to *Meleagrinella* and *Praearctotis*. The oldest *Canadotis* have been discovered in the Oxfordian. *Canadotis simkini* (Voronetz) from Oxfordian deposits of the Far East (Voronets, 1938), the ligament block of which has a spoon-shaped resilifer (Lutikov and Shurygin, 2010, pl. II, fig. 3), should be referred to this group. Possibly, the East Siberian and Far Eastern Bathonian—Kimmeridgian specimens belong to *Canadotis*, referred to *Meleagrinella ovalis*, the hinge of which has not yet been studied (Zakharov, 1966; Zakharov and Shurygin, 1978; Sei and Kalacheva, 1980; Paraketsov and Paraketsova, 1989; *Atlas*..., 2004). The Oxfordian *Avicula ovalis* from England (Phillips, 1829; Arkell, 1933) may also belong to the same group. The species *Canadotis simkini* (Oxfordian) and *Canadotis canadensis* (Volga Stage) reliably belong to the *Canadotis* group. Taxa belonging to this group have a protuberance developed on the pseudoligamentous platform of the left valve (pl. V, figs. 14, 15), the byssal block is characterized by diamond-shaped outlines of the byssal auricle (pl. VI, fig. 10).

The hypothesis of the origin of *Canadotis* from *Arctotis* rather than from *Meleagrinella* in Callovian seems more reasonable on the following grounds. The repeated transformation of the direct subtype of the lower margin of the ligamentous fossa in *Meleagrinella* to the spoon-shaped subtype and the formation of a more complex structure—the resilifer in *Canadotis*—has not yet been confirmed. The transformation of the subtriangular auricle in the Bathonian Arctotis to the rhomboidal byssal auricle in *Canadotis* through transitional stages of the byssal block in "*Meleagrinella*" *ovalis* seems more natural. The plasticity of the byssal auricle could be the reason for the multiple changes in byssal auricle shape in the Middle and Late Jurassic, as observed in Hettangian-Toarcian *Meleagrinella*. The appearance of the protuberance in *Canadotis* can be explained by evolutionary inertia (Krassilov, 1977). This character went into a dormant state in Middle Jurassic *Arctotis* s. str. and reappeared during the Oxfordian.

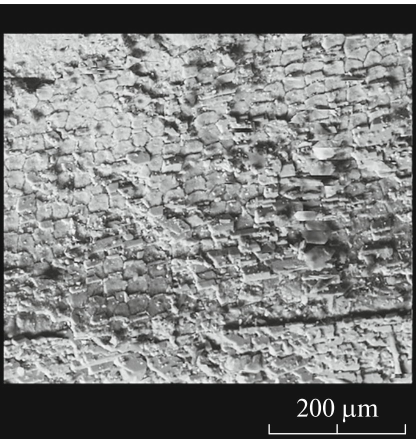
The hypothesis that *Canadarctotis* originated during the Volgian age from *Canadotis* and not from Arctotis s. str. seems more reasonable. In the Upper Jurassic, except for *Canadotis simkini* and *Canadotis kanadense*, no other taxa with a similar shape to Canadarctotis have been found so far. The ligamentous fossae in *Arctotis* s. str. and *Canadactotis* have not

Plate VIII. Fig. 1. *Meleagrinella (Praemeleagrinella) subolifex* Polubotko, specimen no. AG- 60/1, part of the surface of the prismatic layer of the right valve, scale bar 0.5 mm; Sample AG-60, Anabar Bay, Outcrop 5, Bed 18, Zimnyaya Formation, Lower Jurassic, Hettangian. Fig. 2. *Meleagrinella (Praemeleagrinella) deleta* (Dumortier), specimen no. AG 94/1, part of the surface of the prismatic layer of the right valve, scale bar 0.5 mm; Sample AG-94, Anabar Bay, Outcrop 5, Bed 63, level 1.8 m, Airkat Formation, Lower Jurassic, Upper Pliensbachian. Figs. 3, 4. *Meleagrinella (Praemeleagrinella?) tiungensis* (Petrova), (3) specimen no. 160-36-102.7/2, part of the surface of the prismatic layer of the right valve, scale bar 0.2 mm, Tenkelyakh Site, line 160, Borehole 36, depth 102.7 m; Tyung Formation, Lower Jurassic, Upper Pliensbachian; (4) specimen no. 745/16, part of the surface of the prismatic layer of the right valve, scale bar 0.5 mm; Sample A-15, Anabar River, Outcrop 3, Bed 1, Airkat Formation, Lower Jurassic, Upper Pliensbachian. Fig. 5. *Oxytoma (Oxytoma) kirinae* Velikzhanina, specimen no. TX-870-505/2, part of the surface of the prismatic layer of the right valve, scale bar 0.5 mm; Tenkelyakh Site, line 870, Borehole 505, depth 9 m, Suntary Formation, Lower Jurassic, Upper Toarcian. Fig. 6. *Meleagrinella (Meleagrinella) prima* Lutikov, specimen no. MX-237/10, part of the surface of the prismatic layer of the right valve, scale bar 0.2 mm; Markha River, Outcrop 10, Bed 9, Sample 237-B, Suntary Formation, Lower Toarcian. Fig. 7. *Oxytoma (Oxytoma)* ex gr. *expansa* (Phillips), specimen no. PCh/1, part of the surface of the prismatic layer of the right valve, scale bar 0.2 mm; Nizhny Novgorod region, village of Pochinki, Middle Jurassic, Lower Callovian, Cadochamoussetia subpatruus Zone. Fig. 8. *Arctotis (Praearctotis) marchaensis* (Petrova), specimen TX no. 1080-350-1/1, part of the surface of the prismatic layer of the right valve, scale bar 0.5 mm; Tenkelyakh Site, line 1080, Borehole 350, depth 35 m, Suntary Formation, Lower Jurassic, Upper Toarcian.

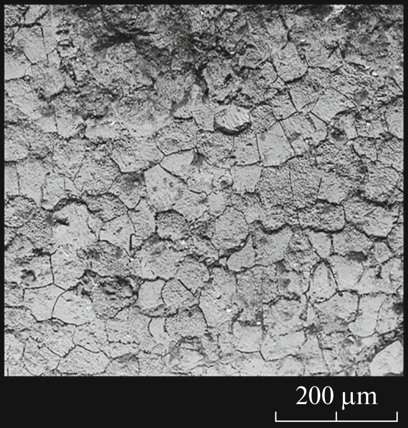
Plate VIII



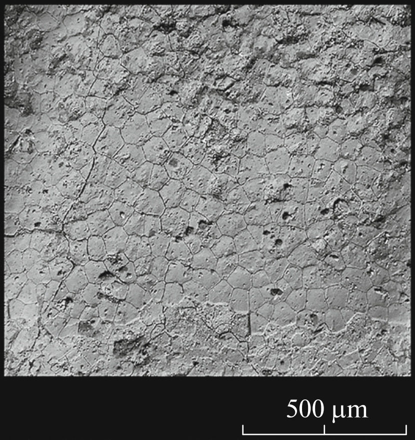
1



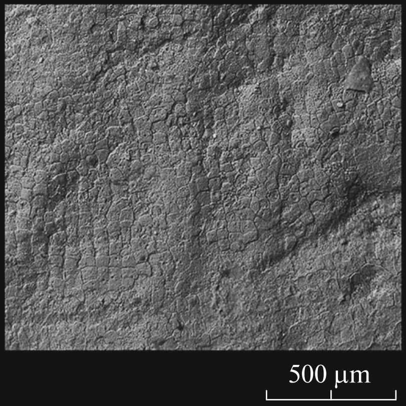
2



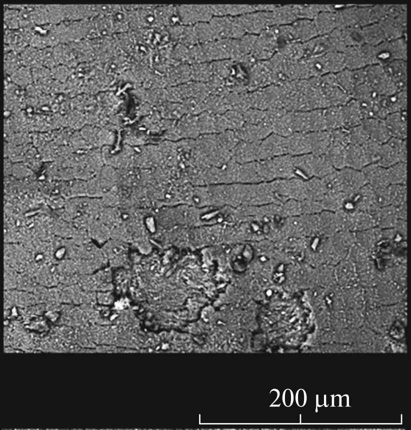
3



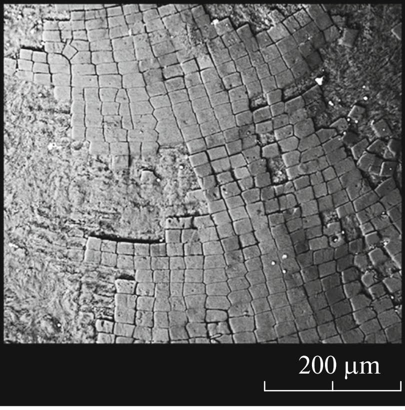
4



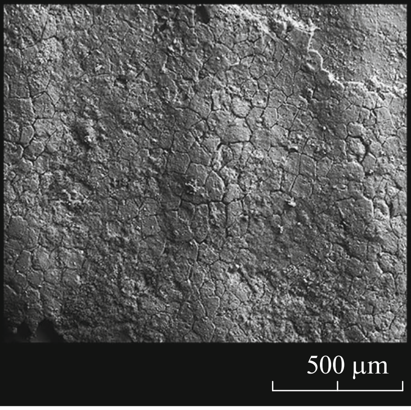
5



6



7



8

undergone significant changes. The main morphogenetic changes occurred during the formation of a triangular auricle in *Canadarctotis* and a change in the slope of the byssal notch. All the main generic features present in the ligament and byssal blocks of *Canadotis* and *Canadarctotis* (such as the spoon-shaped type of ligamentous fossa, the gaping and overgrowing types of the byssal notch, the type of the byssal auricle, the type of byssal groove, the inclined position of the ligamentous platform relative to the commissure plane, the presence of a protuberance, and the presence of the ligament ridge) are not newly formed structures and occurred in *Praearctotis* and *Arctotis* s. str. All these groups are considered subgenera of the genus *Arctotis*.

TAXONOMY OF THE FAMILY OXYTOMIDAE

The methodology for constructing a phylogenetic system is based on generally accepted principles, such as ontogeny, homology, the key link, and chorology (Ruzhentsev, 1960). A system in this context is understood as an arrangement of groups of organisms in a specific order, which is established during the classification process, based on the relationships between these groups. Despite this, there is still no single universally accepted classification system for bivalves.

Ichikawa (1958) first proposed the idea of uniting the genera *Oxytoma*, *Meleagrinella*, and *Maccoyella* into a new subfamily, Oxytominae, which he included in the family Aviculopectinidae. He considered as distinctive characters of this group the reduced right anterior muscular impression, calcitic internal ostracum with cross-plate structure, not aragonitic, as in Aviculopectinidae. The pallial line in *Oxytoma*, *Meleagrinella*, and *Maccoyella* is discontinuous and divided into small fossae, similar to that of modern Pteriidae. In contrast, in Aviculopectinidae, the pallial line is continuous (Ichikawa, 1958). L.R. Cox (1961) believed that these features were significant enough to elevate the Oxytominae to the rank of the family Oxytomidae within the superfamily Pectinacea. He considered the similarity in the structure of the pallial line in Oxytomidae to that of representatives of the superfamily Pteriidae to be the result of parallel evolution (Cox, 1961).

In the modern American "Synoptical Classification of the Bivalvia" (Carter et al., 2011), the family Oxytomidae is considered as part of the hyporder Monotoidei Waterhouse, 2001 and occupies the following position in the system of the class Bivalvia:

Class Bivalvia Linnaeus, 1758 in 1758–1759
  Grade Euprotobranchia Nevesskaja, 2009 (paraphyletic taxon)
  Clade Eubivalvia Carter, 2011
  Subclass Autobranchia Grobben, 1894
  Infraclass Pteriomorphia Beurlen, 1944
  Cohort Ostreomorphi Férussac, 1822
  Subcohort Ostreioni Férussac, 1822
  Megaorder Ostreata Férussac, 1822
  Superorder Ostreiformii Férussac, 1822
  Order Pectinida J. Gray, 1854
  Suborder Anomiidina J. Gray, 1854
  Hyporder Monotoidei Waterhouse, 2001
      Superfamily Oxytomoidea Ichikawa, 1958
    Family Oxytomidae Ichikawa, 1958
    Subfamily Oxytominae Ichikawa, 1958
    Subfamily Maccoyellinae Waterhouse, 2008

In the modern Russian reference book "Phanerozoic Bivalves of Russia and Surrounding Countries" (Nevesskaya et al., 2013), the family Oxytomidae is considered as part of the suborder Aviculopectinidina Waterhouse, 2001 and occupies the following position in the system of the class Bivalvia:

  Class Bivalvia Linnaeus, 1758.
Suborder Autobranchia Grobben, 1894
  Order Pectinida H. et A. Adams, 1857 (sensu Newell et Boyd, 1995)
  Suborder Aviculopectinidina Waterhouse, 2001
  Superfamily Aviculopectinoidea Meek et Hayden, 1864 (sensu Waterhouse, 2001)
  Family Oxytomidae Ichikawa, 1958

The creation of a phylogenetic system for the class Bivalvia was based on cladistic analysis, as proposed by J. Carter and colleagues. The rank of taxa was determined by their position on the cladogram, which showed the order of branching. A larger number of Linnaean ranks were used to accurately describe the phylogenetic relationships. However, in order to reduce the number of ranks, some were ignored with the understanding that this might obscure some of the relationships, as noted by Carter et al. (2011).

The creation of the phylogenetic system for the class Bivalvia, by L.A. Nevesskaya et al., was based on the methods of evolutionary taxonomy. The system was developed through a comprehensive study of the gill apparatus, digestive system, and hinges, taking into account the evolutionary development of individual groups (Nevesskaya et al., 2013).

The principal difference between the two systems is the different views on the position of the family Oxytomidae. Carter et al. considered that this family is phylogenetically similar to the family Monotidae Fischer, 1887 (Carter et al., 2011). Nevesskaya et al. (2013) considered that the family Oxytomidae is phylogenetically similar to the family Aviculopectinidae Meek et Hayden, 1864. The family included five genera: *Oxytoma* Meek, 1864; *Meleagrinella* Whitfield, 1885; *Arctotis* Bodylevsky, 1960; *Maccoyella* Etheridge, 1892; *Cyrtorostra* Branson, 1930 (=*Prooxytoma* Maslennikov, 1952) (Nevesskaya et al., 2013). These views are based on the ideas presented in (*Treatise*..., 1969) and on Waterhouse's views, who demonstrated that the Oxytomidae are closely related to the Aviculopectinidae, particularly the Etheripectinidae group.

He divided the Family Oxytomidae into two subfamilies, Oxytominae and Maccoyellinae (Waterhouse, 2008).

The information provided on the composition of the Oxytomidae family requires correction. Some experts have expressed doubts about the assignment of the genus Cyrtorostra Branson, 1930 (=Prooxytoma Maslennikov, 1952) to the family Oxytomidae (Marwick, 1935; Newell and Boyd, 1995). Based on images of *Cyrtorostra arctica* Logan from Permian deposits in Canada, it appears that the ligamentous platforms of both valves of this genus are located in the commissural plane (Logan, 1970). Based on this, this genus is well beyond the boundaries of the Oxytomidae family.

The genus *Maccoyella* Etheridge, 1892 was assigned to a separate Subfamily Maccoyellinae (Waterhouse, 2008).

The Jurassic and Cretaceous representatives of the genus *Arctotis* include four phylogenetically related groups, considered as subgenera: *Arctotis (Praearctotis), Arctotis* s.str., *Arctotis (Canadotis)* and *Arctotis (Canadarctotis)*. The subgenus *Arctotis* s.str. includes Aalenian-Bathonian taxa that have a greater inclination of the ligament area of the left valve relative to the midsagittal plane than that of *Praearctotis* (Pl. V, fig. 12). The byssal block in *Arctotis* s.str. is characterized by a closing byssal furrow (Pl. VI, fig. 7) and an overgrown byssal notch (Pl. VI, fig. 9). Apparently, the high adaptive value of these adaptations ensured the dominance of *Arctotis* in shallow coastal environments in Eastern Siberia in the Middle Jurassic.

The subgenus *Canadarctotis* includes the Volgian–Valanginian taxa, which have a wider pseudoligamentous area than that of *Canadotis*, a triangular byssal ear and a closed byssal furrow (Pl. VI, figs. 11, 12). The triangular outline of the byssal ear with an overgrown byssal notch at the adult stage in the Volgian and Cretaceous representatives of *Canadarctotis* brings this group closer to the Bajocian-Bathonian group of *Arctotis* s.str. The expansion of the ligament area and the reduction of the byssal notch and the transition to an incremental method of attachment to the substrate by the right valve were useful adaptations for a high-energy environment.

Based on the research of Ichikawa (1958), Waterhouse (2008) and Nevesskaja et al. (2013), the author classifies the family Oxytomidae within the superfamily Aviculopectinoidea Meek et Hayden, 1864. The composition of the family, taking into account the partial revision proposed in this work, is presented as follows:

- Class Bivalvia Linnaeus, 1758
- Superorder Autobranchia Grobben, 1894
  - Order Pectinida H. et A. Adams, 1857 (sensu Newell et Boyd, 1995)
    - Suborder Aviculopectinidina Waterhouse, 2001
- Superfamily Aviculopectinoidea Meek et Hayden, 1864 (sensu Waterhouse, 2001)
  - Family Oxytomidae Ichikawa, 1958
    - Subfamily Oxytominae Ichikawa, 1958
      - Genus *Meleagrinella* Whitfield, 1885
        - Subgenus *Praemeleagrinella* Lutikov et Schurygin, 2010 (Hettangian–Pliensbachian, Lower Toarcian?)
        - Subgenus *Meleagrinella* s.str. (Lower Toarcian–Maastrichtian)
        - Subgenus *Clathrolima* Cossmann, 1908 (Lower Toarcian–Upper Jurassic)
      - Genus *Arctotis* Bodylevsky, 1960
        - Subgenus *Praearctotis* Lutikov et Schurygin, 2010 (Upper Toarcian)
        - Subgenus *Arctotis* s.str. (Lower Aalenian–Bathonian)
        - Subgenus *Canadotis* Jeletzky et Poulton, 1987 (Callovian?, Oxfordian–Volgian)
        - Subgenus *Canadarctotis* Jeletzky et Poulton, 1987 (Volgian–Hauterivian)
      - Genus *Oxytoma* Meek, 1864 (Ladinian–Maastrichtian)
        - Subgenus *Oxytoma* s.str. (Ladinian–Maastrichtian)
        - Subgenus *Hypoxytoma* Ichikawa, 1958 (Lower–Upper Cretaceous)
        - Subgenus *Palmoxytoma* Cox, 1961 (Upper Triassic–Lower Jurassic)
        - Subgenus *Boreioxytoma* Zakharov, 1966 (Upper Jurassic)
    - Subfamily Maccoyellinae Waterhouse, 2008
      - Genus *Maccoyella* Etheridge, 1892
      - Genus *Zelotypia* Waterhouse, 2001

SYSTEMATIC PALEONTOLOGY

Genus *Meleagrinella* Whitfield, 1885

Meleagrinella: Whitfield, 1885, p. 354.

Type species—*Pseudomonotis (Eumicrotis) curta* Whitfield, 1880, p. 354, pl. 3, figs. 20–25; Upper Jurassic, Oxfordian Stage, USA.

Remarks on the type species. While studying fossils from the Late Jurassic deposits of Utah (USA), D. Hull described a taxon of dubious systematic affiliation, *Avicula? custa* Hall, 1852 (Hall, 1852, p. 412, pl. IV, figs. 1a, 1b). The understanding of this species is based on two drawings, in which only the oval outline of a shell with a high crown is visible. From the short description it is clear that the shell is oblique, the hinge line of the specimens is much shorter than the length of the shell, the upper margin is curved, and the sculpture is represented by thin, even grooves. Later F.B. Meek, establishing the genus

Eumicrotis Meek, 1864, included in its composition the Permian species *Monotis hawni* Meek, Hayden, 1858 and the Jurassic species *Avicula custa* Hall, 1852. *Avicula custa* Hall, 1852 is a lapsus by F.B. Meek for *Avicula curta* Hall, 1852 (Meek et Hayden, 1864, p. 81). He chose the Permian species *Monotis hawni* Meek et Hayden, 1858 as the type species of the genus *Eumicrotis*. In 1885 R.P. Whitefield, studying the collections of G. Newton from the Jurassic deposits of the Black Hills, identified the genus *Meleagrinella* (Whitfield, 1885). He included the species *Pseudomonotis (Eumicrotis) curta* (Whitfield, 1880), *Pseudomonotis (Eumicrotis) orbiculata* (Whitfield, 1877) from the Oxfordian sediments of South Dakota (USA), as well as the species *Avicula abrupta* (Conrad, 1853) from the Cretaceous sediments of the state New Jersey (USA). He indicated both Late Jurassic species as types of the genus *Meleagrinella* (Whitfield, 1885, p. 71). The author of the name of the species *Pseudomonotis (Eumicrotis) curta* is R.P. Whitefield recognized D. Hull, apparently focusing on the works of F.B. Mika and F.V. Hayden (Meek and Hayden, 1860, 1864). This subsequently led to confusion in fixing the name for the type species of the genus *Meleagrinella*. Specimens by D. Hull, described under the name *Avicula? custa*, and specimens described by R.P. Whitefield as *Pseudomonotis (Eumicrotis) curta*, come from different places and have obvious morphological differences. This circumstance allows us to doubt the correctness of the attribution of R.P. Whitefield of his specimens to the taxon of D. Hull. L.R. Cox (1941), studying the collection of Late Jurassic "*Meleagrinella*" from South Dakota and "*avicula*" from the Middle Jurassic of England at the British Museum of National History, came to the conclusion that the American specimens of R.P. Whitefield and the English species *Avicula braamburensis* (Phillips, 1829). The species *Avicula curta* Hall, 1852 was adopted by L.R. Cox as the type species of the genus *Meleagrinella* (Cox, 1941, p. 134). Undoubtedly, L. Cox, when establishing the type of the genus, did not take into account the work of H. Stransbury, where a specimen of *Avicula? custa* was illustrated. He took into account only the works of F.B. Mika and R.P. Whitefield, otherwise there would not have been an error in correct type identification. The assignment of *Avicula? custa* to bivalve mollusks is doubtful, therefore, in accordance with Article 70.3.2 of the International Code of Zoological Nomenclature the type of the genus *Meleagrinella* should be fixed in the following way: "If an author discovers that a type species was misidentified the author may select, and thereby fix as type species, the species that will, in his or her judgment, best serve stability and universality... the taxonomic species actually involved in the misidentification (Meyen, 1999). Since the understanding of the type species of the genus is based on the drawings and descriptions of R.P. Whitefield, the name of the type species as written by R.P. Whitefield should be recognized as correct: *Pseudomonotis (Eumicrotis) curta* Whitfield, 1880 and this case is to be submitted to the International Commission on Zoological Nomenclature.

Diagnosis. Shell oval-trapezoidal, oval-triangular, elongated-oval, oblique-oval or round; moderately irregular, very small to medium-sized. Ligament area of the left valve positioned in the midsagittal plane at all age stages. Sculpture of radial ribs of one or two orders and concentric growth lines. Anterior auricle shorter than shell anterior margin. Wide-angled, sub-rectangular or acute-angled ligament pit type. Expanding or oblique subtype of the ligament pit. Straight subtype of lower margin of ligament pit. Protuberance hemispherical or semi-ellipsoidal, rarely absent. Ligament area long. Byssal ear quadrangular, trapezoid (with a shortened lower margin) or rhomboid, separated from right valve by a deep byssal furrow. Byssal furrow open. Byssal notch gaping.

Comparison. This genus is distinguished from the genus *Oxytoma* Meek, 1864 by the quadrangular outline of the byssal ear, narrow byssal notch, less developed auricles in the subadult and adult ontogenetic stages, a short byssal ear. It differs from the genus *Arctotis* Bodylevsky, 1960 by the wide-angled ligament pit type and the straight subtype lower margin of the ligament pit, the presence of the protuberance, and the quadrangular outline of the byssal ear.

Composition. In addition to the nominative, it includes the subgenera *Clarthrolima* Cossmann, 1908; *Praemeleagrinella* Lutikov et Schurygin, 2010. More than 40 species are known in the literature, which are considered as part of the genus.

Remarks. It was assumed that the genus *Canadotis* Jeletzky et Poulton, 1987 is a junior synonym of the genus *Meleagrinella* Whitfield, 1885 (Lutikov et al., 2010). After re-examining the hinge plate in the type species of the genus *Meleagrinella* Whitfield, 1885 using photographs of specimens of the type species from the original collection of R. Whitefield, large differences in the structure of the hinge plate were revealed between *Meleagrinella* s.str. and *Canadotis* Jeletzky et Poulton, 1987. Hence, the synonymy of these genera has been reconsidered. The genus *Canadotis* Jeletzky et Poulton, 1987 is considered here as a subgenus of *Arctotis* Bodylevsky, 1960.

Occurrence. Hettangian–Volgian of Siberia and Northeast Russia; Bajocian–Oxfordian of the Far East; Bajocian–Callovian of Ukraine, Turkmenistan, Kazakhstan and Uzbekistan; Hettangian–Tithonian of Europe; Bathonian–Callovian of China; Hettangian–Toarcian of Japan; Hettangian–Cretaceous of Canada and USA, Toarcian–Bajocian of New Zealand.

Subgenus *Praemeleagrinella* Lutikov et Schurygin, 2010

Type species: *Meleagrinella subolifex* Polubotko, 1968 (*Polevoi*..., 1968, pl. 2, text-figs. 6–8,

Table 1. Dimensions in mm and ratios

Coll. no., valve	Locality	VL	VH	VH/VL	Cv	Cv/VH	ADL	ADL/VL	PDL	PDL/VH	LOL	LOL/PDL	PWAg	R	R/VL	ISW/RW	PAAg	PWW/PWL
GZG.INV.70490, holotype, left	Dörlbach, Germany, Ludwigskanal, “Laibstein II” Member, Harpoceras serpentinum Zone (Cleviceras elegans Subzone)	21.78	21.5	0.99	–	–	8.99	0.41	12.79	0.59	7.01	0.55	46°	66	3.03	2.88	96°	0.16
GZG.INV.70640, left	The same	8.81	8.57	0.97	–	–	3.48	0.40	3	0.62	3.05	0.59	45°	54?	6.35	2.66	88°	0.10
GZG.INV.70641, left	The same	11.67	10.6	0.97	–	–	4.45	0.38	7.22	0.68	3.91	0.54	42°	61	5.23	2.86	–	0.13
GZG.INV.70642, left	The same	12.83	13.0	1.01	–	–	4.4	0.34	8.43	0.65	4.95	0.59	44°	83	6.47	2.05	81°	0.14
GZG.INV.70650, right	Berg, Germany,“Laibstein II” Member, Harpoceras serpentinum Zone (Cleviceras elegans Subzone)	14.44	11.69	0.81	–	–	6.36	0.44	8.08	0.69	7.50	0.93	42°	28	1.92	4.17	24°	0.06
BSPG 2008 XXIX 1d, left	Altdorf, Germany, Harpoceras serpentinum Zone (Cleviceras elegans Subzone)	14.2	13,33	0.94	–	–	6.14	0.43	8.06	0.60	5.71	0.71	48°	67	4.72	2.23	93°	0.10
GZV.INV.70649 left	Adenstedt, Germany, Harpoceras serpentinum Subzone (Cleviceras exaratum Subzone)	14.44	14.34	0.99	–	–	5.58	0.38	8.86	0.62	5.12	0.58	43°	52	3.60	3.41	75°	0.09
K-1098/1, left	Kelimyar River, Kelimyar Formation, Kurung Member, Outcrop 16, Bed 3, level 0.7–0.8 m, sample no. 1098, Tiltoniceras antiquum Zone	17.45	15,8	0.91	4.74	0.30	6.28	0.36	11.17	0.71	7.75	0.76	42°	48	2.75	2.47	62°	0.06
K-1097/1, left	Kelimyar River, Outcrop 16, Bed 3, level 0.1–1.2 m, sample no.1097, Harpoceras falciferum Subzone (Cleviceras exaratum Subzone)	10.96	8.8	0.81	–	–	3.88?	0.35	7.08?	0.80?	5.25	0.74?	43°	35?	3.09	2.8	69°	–
K-1097/2, left	The same	7.67	7.2	0.94	2.19	0.28	3.25	0.42	4.42	0.61	3,32	0.75	45°	47	6,40	2.92	61°	0.10
K-1069/1, left	Kelimyar River, Kelimyar Formation, Kurung Subformation, Outcrop 11b	13.83	12.4	0.90	–	–	–	–	–	–	–	–	–	50?	3.61	3.50	69°	–
MT-213/3, left	Motorchuna River, Outcrop 3, Bed 2, Sample 213, Suntary Formation	6.98?	7.3	1.02?	–	–	2.46	0.35	4.52	0.62	3.07	0.70?	42°	42	4.63	2.76	67°	0.10
AC-72/1 left	Astronomicheskaya River, Outcrop 2, Bed 14, base, Sample 72, Harpoceras falciferum Subzone (Cleviceras exaratum Subzone)	7.40	7.8	1.05	–	–	3.00	0.41	4.40	0.56	2.51	0.57	48°	52	7.01	2.08	68°	0.12
166/1/238 left	Ust-Yenisei District, Borehole 3-p, depth 1029.1–1030.7 m; Kiterbyut Formation	6.25	6.32	1.01	–	–	2.57	0.41	3.68	0.58	2.86	0.78	40°	42?	6.72?	–	–	–
166/3/238 left, external imprint	The same	6.04	5.75	0.95	–	–	2.75	0.46	3.29	0.57	2.72	0.83	42°	42?	6.95?	–	70°	0.06

pp. 38–39). Hettangian–Sinemurian, Northeastern Siberia, Kedon River, Finish Creek

Diagnosis. Shell inequilateral, very small to medium-sized. Sculpture of radial ribs of one or two orders and growth co-centers. Wide-angled ligament pit type. Oblique subtype of ligament pit. At the mature stage, ligament pit wide-angled, modifications 1a and 1b. Lower end of the anterior margin of ligament pit of right valve after the third bend located to the left of the axis of symmetry. Hemispherical or semi-ellipsoidal protuberance present on pseudoligamentous platform of the left valve, near anterior margin of ligament pit. Byssal ear rhomboid or trapezoid

Comparison. This subgenus differs from *Meleagrinella* s.str in the oblique subtype of the ligament pit, with a more prominent protuberance. It differs from *Meleagrinella (Clarthrolima)* Cossmann, 1908 in the wide-angled type of the ligament pit at the juvenile stage and the less slanted ligament pit at the adult stage.

Species composition. The following species are assigned to this subgenus based on the hinge morphology: Hettangian *Meleagrinella subolifex* (*Polevoi…*, 1968), Late Pliensbachian *Avicula deleta* (Dumortier, 1869), *Pseudomonotis (Eumorphotis) sparsicosta* (*Atlas…*, 1947). Presumably the subgenus also includes: Hettangian *Monotis olifex* (Quenstedt, 1858); Sinemurian *Meleagrinella ferniensis* (Aberchan, 1998, non McLearn, 1924); Pliensbachian *Meleagrinella ansparsicosta*, *M. pthelincevae*, *M. oxytomaeformis* (*Polevoi…*, 1968), *Meleagrinella japonica* (Hayami, 1959), *Meleagrinella golberti* (Lutikov and Arp, 2023a).

Remarks. The species *Pseudomonotis tiungensis* (*Atlas…*, 1947) assigned to the subgenus conditionally due to the presence of microsculpture on the right valve, which is not typical of the subgenus.

Occurrence. Hettangian–Pliensbachian, Lower Toarcian(?) Eastern Siberia, Northeastern Russia, Russian Far East, Europe, Japan, Canada.

Meleagrinella (Praemeleagrinella?) golberti Lutikov et Arp, 2023

Plate X, figs. 1–13

Pseudomonotis substriata: Bodylevsky and Shulgina, 1958, pp. 48–49.

Meleagrinella substriata: Caswell et al., 2009, text-fig. 5C (here Pl. I, fig. 12); Teichert and Nützel, 2015, text-fig. 4B (here Pl. I, fig. 4); Arp and Gropengiesser, 2016, text-figs. 2f (here Pl. I, fig. 1), 2g; Morris et al., 2019, text-figs. 9.6H, I.

Meleagrinella (Praemeleagrinella) aff. *substriata*: Lutikov and Shurygin, 2010, pl. III, fig. 10 (here Pl. I, fig. 7).

Meleagrinella sp.: Martindale, Aberhan, 2017, text-figs. 4O (here Pl. I, fig. 13), 4P, 4Q, 4R; Muscente et al., 2019, text-fig. 3H.

Meleagrinella (Praemeleagrinella) sp. 1: Lutikov and Arp, 2020, pl. I, figs. 1–4.

Arctotis (Praearctotis) sp. 1: Lutikov and Arp, 2020, pl. I, figs. 5–8.

Meleagrinella (Praemeleagrinella?) golberti: Lutikov and Arp, 2023a, pl. I, figs. 1–13.

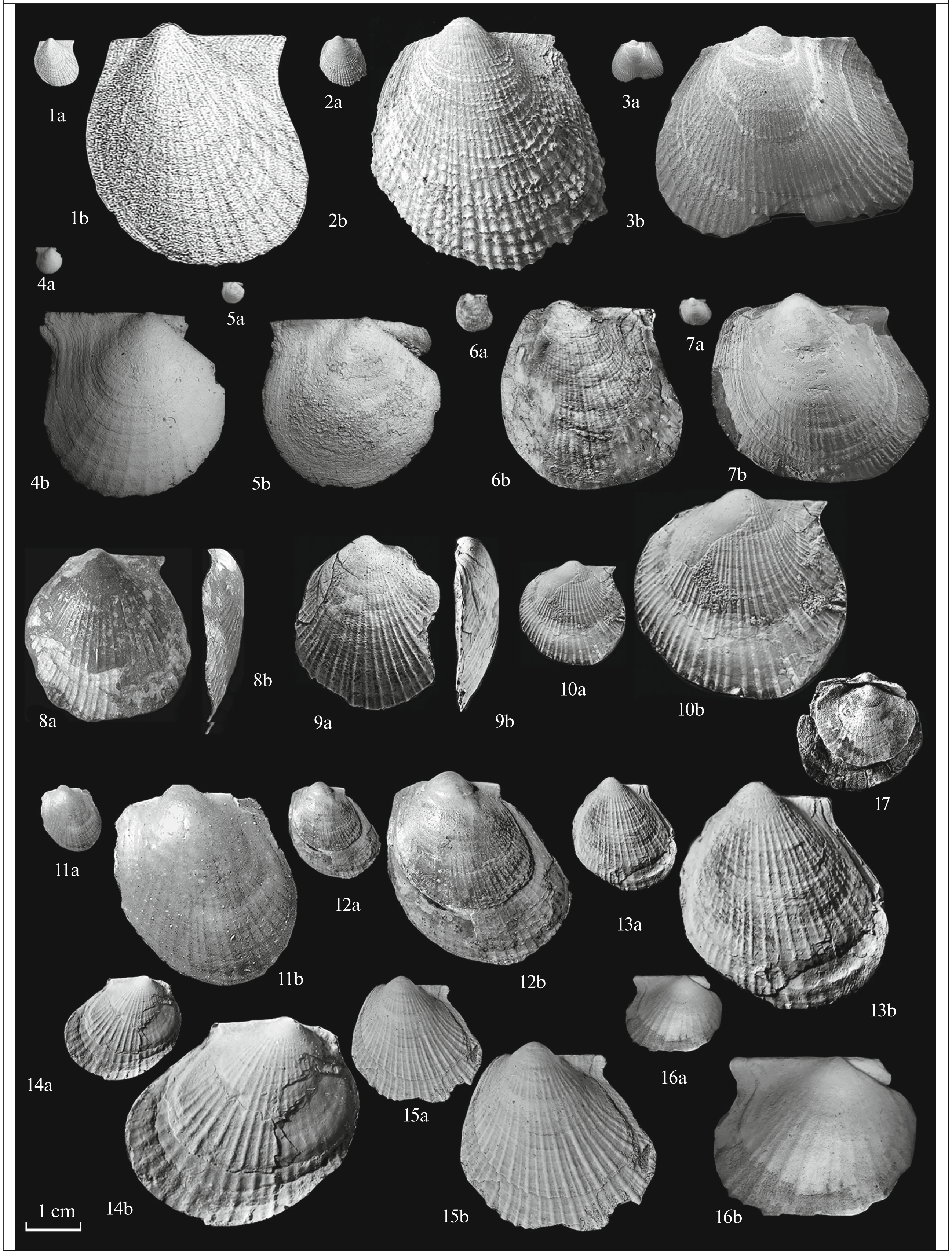
Etymology. The name is given in memory of the Russian researcher of Mesozoic deposits, geologist Arkady Viktorovich Golbert.

Holotype. Geological Museum of the University of Göttingen, specimen no. GZG.INV.70490, left valve. Lower Toarcian, Harpoceras serpentinum Zone (Cleviceras elegans Subzone), Dörlbach, Germany, Ludwig Canal, "Laibstein II" Member. Figured: Pl. I, fig. 1.

Material. About 20 left and right valves from the Lower Toarcian of the Ludwigskanal section in the area of Dörlbach (southern Germany), photographs of samples from the lower Toarcian of the Altdorf area section (southern Germany), one left valve from a

Plate IX. Figs. 1–7. *Meleagrinella (Praemeleagrinella) deleta* (Dumortier), (1) syntype, (a) left valve, ×1, (b) the same, ×5 (Dumortier, 1869, pl. XXXV, fig. 5), Giverdy, Burgundy, France, Upper Pliensbachian; (2) specimen no. Pr-21p/23, (a) left valve of a mature specimen, ×1, (b) the same, ×5; Pravoperezhnyi Site, line 524, Borehole 546.5, depth 18.6 m, Tyung Formation, Upper Pliensbachian; (3) specimen no. Pr-21p/26, (a) left valve of a mature specimen, ×1, (b) the same, ×5; the same locality; (4) specimen no. Pr-21p/27, (a) right valve of a mature specimen, ×1, (b) the same, ×7; the same locality; (5) specimen no. Pr-21p/28, (a) right valve of a mature specimen, ×1, (b) the same, ×8; the same locality; (6) specimen no. K-1012/202, (a) left valve of a mature specimen, ×1; (b) the same, ×7; Kelimyar River, Outcrop 5, Bed 2, sample no. K-1012, Kyra Formation, Upper Pliensbachian; (7) specimen no. 12/66/8, (a) left valve of a mature specimen, ×1; (b) the same, ×7; Anabar Bay, Outcrop 5, Bed 64, sample no. 12/66, Airkat Formation, Upper Pliensbachian (collected by B.N. Shurygin). Figs. 8–10. *Meleagrinella (Praemeleagrinella) sparsicosta* (Petrova), (8) holotype, specimen no. 689/5393, F.N. Chernyshev TsNIGR Museum (St. Petersburg), mold of the left valve of mature specimen, (a) shell exterior, ×1, (b) the same lateral view, ×1; Tyung River, Sabyki-Khaya Mount; Lower Jurassic, Upper Pliensbachian; collection of G.T. Petrova (Pchelintseva); (9) specimen no. T-165/2, (a) external view of the left valve of a mature specimen, ×1; (b) external view of a left valve, ×1; Tyung River, Outcrop 9, Bed 4, Sample 165; Tyung Formation, Lower Jurassic, Upper Pliensbachian, collected by V.G. Knyazev; (10) specimen no. T-165/10, (a) left valve of an adult specimen, ×1, (b) the same, ×5, the same age and locality. Figs. 11–17. *Meleagrinella (Praemeleagrinella?) tiungensis* (Petrova), (11) holotype, specimen no. 446/5393, F.N. Chernyshev TsNIGR Museum (St. Petersburg), (a) external view of the left valve of an adult specimen, (b) the same, ×3; Tyung River, Sabyki-Khaya Mount; Lower Jurassic, Upper Pliensbachian; collection of G.T. Petrova (Pchelintseva); (12) type specimen no. 451/5393, F.N. Chernyshev TsNIGR Museum (St. Petersburg); (a) view of a left valve of a mature specimen, ×1; (b) the same, ×2, the same locality; (13) specimen no. 745/15, (a) view of the left valve of a mature specimen, (b) the same, ×2; Sample A-15, Anabar River, Outcrop 3, Bed 1, Airkat Formation, Lower Jurassic, Upper Pliensbachian; (14) specimen no. 745/16, (a) view of the right valve of a mature specimen, (b) the same, ×2; the same locality; (15) specimen no. 160-36-102.7/1, (a) view of the left valve of a mature specimen, (b) the same, ×1.5, Tenkelyakh Site, line 160, Borehole 36, depth 102.7 m; Tyung Formation, Lower Jurassic, Upper Pliensbachian, coll. by I.V. Budnikov; (16) specimen no. 160-36-102.7/2, (a) view of the right valve of a mature specimen, (b) the same, ×2; the same locality; 17—specimen no. T-94/144, right valve view, ×1, Tyung River, Outcrop 4, Bed 8; Tyung Formation, Lower Jurassic, Upper Pliensbachian, collected by V.G. Knyazev.

Plate IX


1a
1b
2a
2b
3a
3b
4a
4b
5a
5b
6a
6b
7a
7b
8a
8b
9a
9b
10a
10b
17
11a
11b
12a
12b
13a
13b
14a
14b
15a
15b
16a
16b
1 cm

construction pit in the area of Adenstedt (Northern Germany), one right valve from the area of Berg (southern Germany). About 15 molds of left and right valves from nodules of the Kurung Member of the Kelimyar Formation of the section of the Kelimyar River, more than 20 deformed molds of left and right valves with remains of a shell layer from clays of the Kurung Member of the Kelimyar Formation of the Kelimyar river; 1 deformed mold of the left valve from the section of the lower Toarcian of the Motorchuna River, about 10 molds and imprints of left and right valves from nodules of the Start Formation of the Lower Toarcian section of the Saturn and Astronomicheskaya rivers. Five specimens from the monographic collection of V.I. Bodylevsky "Jurassic and Lower Cretaceous faunas of the lower reaches of the Yenisei", housed in the Mining Museum of the St. Petersburg Mining University.

Diagnosis. Shell low, moderately inequilateral. Posterior wing wide, moderately curved. Lower end of posterior wing of the left valve located above the posterior end of the valve. Posterior auricle of both valves acute-angled.

Dimensions in mm and ratios: see Table 1.

Description. The shell is small, up to 22 mm in height. The left valve is low, inequilateral, moderately convex. The posterior wing is wide, moderately curved. The posterior outer ligament of the left valve is short. The posterior auricle is acute-angled or subrectangular. The left valve is densely ribbed. The area between the projections of the anterior and posterior ends of the valve is covered with radial ribs of two orders (from 42 to 60), irregularly distributed along the valve, with interrib spaces of varying widths. The ribs of the second order are irregularly wedged into the interrib spaces. On the posterior wing the number of radial ribs is up to 24. On the anterior wing there are up to 10 ribs. On the mold near the anterior and posterior margins, the ribs are weakly expressed. The interrib spaces in different parts of the left valve vary in width from moderately wide to wide, rarely exceeding the width of the ribs by more than twice. The right valve is very low, moderately inequilateral. The posterior overlying field of the right valve is very long. The posterior wing of the right valve is slightly convex. The posterior auricle of the right valve is acute-angled. The radial sculpture is weakly expressed. The interrib spaces along the lower margin are very wide.

Comparison. It differs from *Meleagrinella (Praemeleagrinella) deleta* (Dumortier, 1869) from the upper Pliensbachian of France and Eastern Siberia (Pl. IX, figs. 1–7) in its large size, low contour of the left valve, moderately curved posterior auricle, irregular differentiation of the ribs by two orders of magnitude, higher density of ribs.

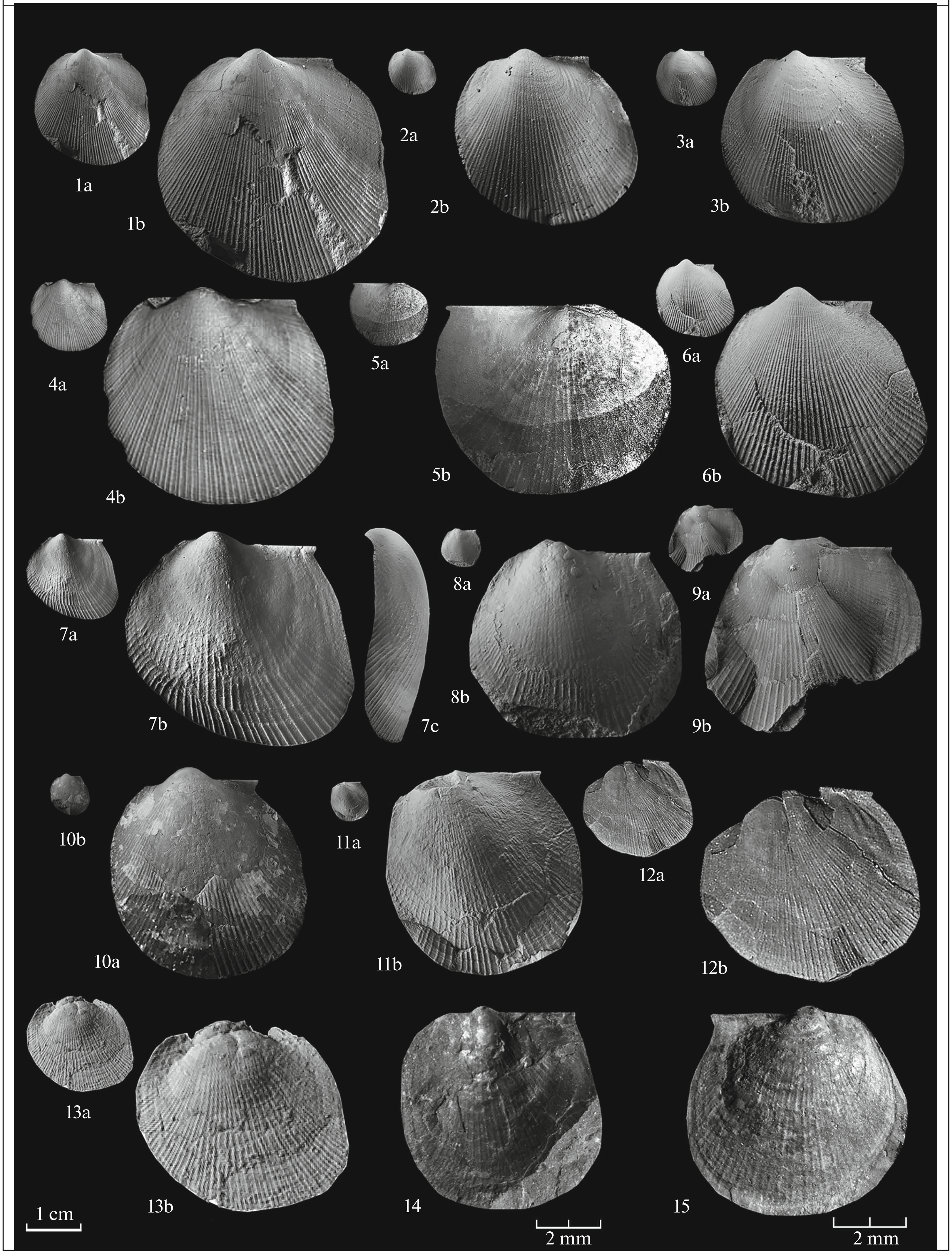
It differs from *Meleagrinella (Praemeleagrinella) sparsicosta* (Petrova) from the upper Pliensbachian of Eastern Siberia (Pl. IX, figs. 8–10) in its smaller size, low contour of the left valve, moderately curved posterior auricle, greater density of ribs, and greater inequivalve left valve.

It differs from *Meleagrinella (Praemeleagrinella?) tiungensis* (Petrova) from the upper Pliensbachian of Eastern Siberia (Pl. IX, figs. 11–16) in its smaller size, low contour of the left valve, moderately curved posterior auricle, and greater density of ribs.

By the contour of the left valve, the shell symmetry and the shape of the posterior wing of the left valve, it

Plate X. Figs. 1–15. *Meleagrinella (Praemeleagrinella?) golberti* Lutikov et Arp, (1) holotype, specimen no. GZG.INV.70490 (after Arp and Gropengiesser, 2016, text-fig. 2f): (a) left valve of a mature specimen, ×1, (b) the same ×2; Dorlbach Ludwigskanal, Harpoceras serpentinum Subzone (Cleviceras elegans Subzone); (2) specimen no. GZG.INV.70640, (a) left valve, ×1, (b) the same, ×4; the same locality; (3) specimen no. GZG.INV.70641, (a) left valve, ×1, (b) the same, ×3; the same locality; (4) specimen no. BSPG 2008 XXIX 1d (after Teichert and Nützel, 2015, text-fig. 4B), (a) left valve, ×1, (b) the same, ×3; Altdorf, Germany, Lower Toarcian, Harpoceras serpentinum Subzone (Cleviceras elegans Subzone); (5) specimen no. GZG.INV.70650, (a) right valve, ×1, (b) the same, ×3; Berg, Germany, Lower Toarcian, Harpoceras serpentinum Subzone (Cleviceras elegans Subzone); (6) specimen no. GZV.INV.70649, (a) left valve, ×1, (b) the same, ×2.5; Adenstedt, Germany, Harpoceras serpentinum Subzone (Cleviceras exaratum Subzone); (7) specimen no. K-1098/1, (a) mold of the left valve with remains of the shell layer, ×1, (b) the same, ×2.5, (c) lateral view from anterior margin, × 2.5; Kelimyar River, Outcrop 16, Bed 3, level 0.7–0.8 m, sample no. 1098, Kelimyar Formation, Kurung Subformation, Lower Toarcian, Tiltoniceras antiquum Zone; (8) specimen no. K-1097/2, (a) mold of the left valve with remains of the shell layer, ×1, (b) the same, ×5; Kelimyar River, Outcrop 16, Bed 3, level 1.0–1.2 m; Kelimyar Formation, Kurung Subformation, Lower Toarcian, Harpoceras falciferum Subzone, Harpoceras (=Cleviceras) exaratum–Harpoceras falciferum subzones; (9) specimen no. K-1069/1, (a) mold of the left valve with remains of the shell layer, ×1, (b) the same, ×5; Kelimyar River, Outcrop 11b, Kelimyar Formation, Kurung Subformation, Lower Toarcian; 10—specimen no. AC-72/1, (a) mold of the left valve with remains of the shell layer, ×1, (b) the same, ×5; Astronomicheskaya River, Outcrop 2, Bed 14, sample no. 72, base, Start Formation, lower subformation, Lower Toarcian, Harpoceras falciferum Subzone, Harpoceras (=Cleviceras) exaratum Subzone; (11) specimen no. MT-213/3, (a) mold of the left valve with remains of the shell layer, ×1, (b) the same, ×5; Motorchuna River, Outcrop 3, Bed 2, sample no. 213, level 4.0 m, Suntary Formation, Lower Toarcian; (12) specimen no. BM PI MB 991 (after Caswell et al., 2009, text-fig. 5C), (a) left valve, ×1, (b) the same, ×2; Port Mulgrave, England, Lower Toarcian, Harpoceras serpentinum Subzone (Cleviceras exaratum Subzone); (13) specimen no. L2430, TMP 2015.051.0096, (a) cast of the left valve, ×1, (b) the same, ×2 (after Martindale and Aberhan, 2017, text-fig. 4O); Alberta, Western Canada, Lower Toarcian, Harpoceras serpentinum Subzone; 14—specimen no. 166/1/238, left valve, partly covered by the rock matrix, scale bar 2.0 mm; Ust-Yenisei district, Borehole 3-p, depth 1029.1–1030.7 m; Kiterbyut Formation, Lower Toarcian; Mining Museum of St. Petersburg Mining University, monographic collection of V.I. Bodylevsky "Jurassic and Lower Cretaceous faunas of the lower reaches of the Yenisei"; (15) specimen no. 166/3/238, external imprint of the left valve, scale bar 2.0 mm; the same age and locality.

Plate X


1a
1b
2a
2b
3a
3b
4a
4b
5a
5b
6a
6b
7a
7b
7c
8a
8b
9a
9b
10b
10a
11a
11b
12a
12b
13a
13b
14
15
1 cm
2 mm
2 mm

is closest to *Meleagrinella oxytomaeformis* Polub. from the upper Pliensbachian of Northeastern Russia (*Polevoi*..., 1968, pl. 22, figs. 1–5). The new species is distinguished by irregular differentiation of the ribs into two orders of magnitude.

In Eastern Siberia, the new species includes specimens from the Kurung Subformation of the Kelimyar River section (Pl. X, figs. 7–9). The species is distributed in the lower part of the Suntary Formation in the sections of the Motorchuna River (Pl. X, fig. 11), Tyung River, in the Ygyatta River basin (Ottur drilling site).

In the North-East of Russia, the new species includes specimens from shell rocks of the lower subformation of the Start Formation (Harpoceras exaratum Subzone) in the Astronomicheskaya River (Pl. X, fig. 10), Saturn, and Brodnaya sections.

In Western Siberia, the Kiterbyut Formation contains bivalves, which V.I. Bodylevsky identified as *Pseudomonotis substriata* (Münster) (Bodylevsky and Shulgina, 1958, pp. 48–49), and later they were assigned to *Praearctotis milovae* (Lutikov and Shurygin, 2010). Five specimens under no. 166/238 from Borehole 3-r in the Ust-Yenisei region from a depth of 1029.1–1030.7 m, housed in the Mining Museum of the St. Petersburg Mining University, re-examined by the author in 2023, using an Olympus microscope. The left valve is characterized by very small size (up to 7 mm), dense sculpture of the entire surface (up to 60 ribs, including the anterior and posterior wings), and a curved posterior auricle. The lower end of the posterior wing of the left valve is located above the posterior end of the valve. Based on these characteristics, the specimen is assigned to the described species.

In Germany, *Meleagrinella (Praemeleagrinella?) golberti* Lutikov et Arp includes specimens from the Dörlbach locality (Ludwigskanal, "Laibstein II" Member, Harpoceras serpentinum Subzone, Cleviceras elegans Subzone) (Arp and Gropengiesser, 2016, text-fig. 2f; here Pl. X, fig. 1), previously referred to as "*Meleagrinella substriata*", specimens from the Altdorf area (Harpoceras serpentinum Subzone, Cleviceras elegans Subzone) (Teichert and Nützel, 2015, text-fig. 4B; here Pl. X, fig. 4), as well as a specimen from the Berg locality (Harpoceras serpentinum Subzone, Cleviceras elegans Subzone) (Pl. X, fig. 5) and a specimen from a construction pit in the Adenstedt locality, found in the same sample with *Hildaites murleyi* (Moxon) (here Pl. X, fig. 6).

In England, the described species includes specimens from Yorkshire (Port Mulgrave, Whitby Mudstone Formation, Harpoceras serpentinum Subzone, Cleviceras exaratum Subzone) (Caswell et al., 2009, text-fig. 5C, here plate X, fig. 12; Morris et al., 2009, text-fig. 5C, here Pl. X, fig. 12; Morris et al., 2019, text-figs. 9.6 H, I).

In Western Canada, the described species includes "*Meleagrinella* sp." from the Alberta area (Scalp Creek River, Fernie Formation, Harpoceras serpentinum Subzone) (Martindale and Aberhan, 2017, text-figs. 4O (here plate X, fig. 13), 4P, 4Q, 4R; Muscente et al., 2019, text-fig. 3H).

Remarks. Hinge structure is unknown. The assignment to the subgenus *Praemeleagrinella* is tentative.

In the last decade, *Meleagrinella substriata* (Münster) has been reported from various Toarcian ammonite zones both in the type locality (Bavaria, Germany) (Teichert and Nützel, 2015; Arp and Gropengiesser, 2016) and in other areas of Europe (England, Poland, Hungary) (Caswell et al., 2009; Morris et al., 2019; Hesselbo and Pieńkowski, 2011; Szente, 2015), and on the Arctic islands (Rogov and Lutikov, 2022). There is information about the occurrence of *Meleagrinella* sp. that are similar in external morphology in the Lower Toarcian in Western Canada (Martindale and Aberhan, 2017). From the above it follows that *Meleagrinella*, classified as *Meleagrinella substriata*, are distributed in all zones of the Lower Toarcian in the territory classified as the Panboreal paleobiogeographical superregion (Zakharov et al., 2003).

Bivalves belonging to "*Meleagrinella* cf. *substriata*", were first cited by B.N. Shurygin from the upper member of the Airkat Formation in the section of Anabar Bay, represented by light gray siltstones, intensely jarositized, containing stellate calcitic structures (*Stratigrafiya*..., 1976). These forms are very small in size, have a straightened posterior wing type, an acute-angled posterior auricle with a deep notch, and are close to *Praemeleagrinella deleta* (Dumortier, 1869, pl. 35, fig. 5). Based on the structure of the hinge plate, these bivalves belong to the subgenus *Praemeleagrinella* (Lutikov and Shurygin, 2010). Representatives of *Praemeleagrinella deleta* are close in outline to specimens from the Toarcian clays of the Kurung Subformation of the Kelimyar River section, previously assigned to "*Meleagrinella* aff. *substriata*" (Lutikov and Shurygin, 2010), but differ in the absence of a bend on the outer margin of the posterior wing. The species *Praemeleagrinella deleta* and *Meleagrinella (Praemeleagrinella?) golberti* Lutikov et Arp (="*Meleagrinella* aff. *substriata*") presumably form a single phylogenetic series.

In Northeastern Russia (Brodnaya River), in the Harpoceras falciferum Subzone, there are specimens that are characterized by wider interrib spaces. They are tentatively assigned to *Meleagrinella (Praemeleagrinella?)* aff. *golberti* Lutikov et Arp (Lutikov and Arp, 2023a). In Eastern Siberia, similar *Meleagrinella* were found in coquinae in the lower part of the Suntary Formation on the Motorchuna River (Pl. X, fig. 15), where confirmed *M. (P.?) golberti* (Pl. X, fig. 11) were found together with them.

Facies association and taphonomic characteristics. On the Kelimyar River, molds of individual valves with remains of a shell layer were found in carbonate concretions and in schistose thin-platy clays of the Kurung Member of the Kelimyar For-

Table 2. Dimensions in mm and ratios

Coll. no., valve	Locality	VL	VH	VH/VL	Cv	Cv/VH	ADL	ADL/VL	PDL	PDL/VH	LOL	LOL/PDL	PWAg	R	R/VL	ISW/RW	PAAg	PWW/PWL
Meleagrinella (*Clathrolima*) *substriata*																		
IGPB-Goldfuss-729 a/1, lectotype, left	Banz, Germany, Posidonienschiefer Formation	11.5	10.09	0.88	–	–	4.31	0.37	7.19	0.71	3.28	0.46	34°	60	5.22	1.76	134°	0.10
no. AS-VII-2087a syntype, right	Mistelgau, Germany, Posidonienschiefer formation	16.26	14.03	0.86	–	–	7.24	0.45	9.02	0.64	4.11	0.46	35°	31	1.91	2.20	131°	0.11
no. AS-VII-2087a syntype, left	The same	–	32.84	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
GZG. INV.70643, left	Ludwigskanal, Dörlbach, Germany, Posidonienschiefer Formation, Member 14, Hildoceras bifrons Zone, Dactylioceras commune Subzone	13.30	12.0	0.90	–	–	4.95	0.37	8.35	0.70	3.31	0.40	34°	46	3.46	3.22	143°	0.12
GZG. INV.70644, left	The same	12.33	12.0	0.97	–	–	4.00	0.32	8.33	0.69	4.04	0.48	32°	65	5.27	3.5	144°	0.09
GZG.INV.70646, left	The same	9.96	9.0	0.90	–	–	3.15	0.32	6.81	0.76	2.49	0.37	25°	65	6.53	2.13	-	0.18
AK-77/1, left	Astronomicheskaya River Outcrop 2, Bed 17; Dactylioceras commune Zone, Start Formation, upper subformation	9.49	9.06	0.95	2.96	0.33	3.47	0.36	5.93	0.65	3.37	0.57	39°	35?	3.69	1.91	114°	0.09
T-254/6, left	Tyung River, Outcrop 15a, scree of Beds 3–4, Sample 254, Dactylioceras commune Zone, Suntary Formation, second member	11.77	12.1	1.03	–	–	4.34	0.37	7.43	0.61	4.28	0.57	40°	48	4.08	2.31	100°	0.06
T-254/17, left	The same	10.38	9.8	0.89	–	–	3.97	0.38	6.61	0.65	3.94	0.60	35°	58	5.59	1.87	112°	0.07
T-254/30, left	The same	10.98	11.1	1.01	–	–	4.21	0.38	6.77	0.61	4.13	0.61	38°	50	4.55	2.35	–	0.08
Meleagrinella (*Clathrolima*) sp.																		
P-470-521/1, left	Pravoberezhnyi Site, line 470, Borehole 521, depth 21.9 m, Suntary Formation, third member	7.40	7.53	1.02	–	–	3.24	0.44	4.16	0.55	3.26	0.79	49°	30	4.05	1.17	67°	0.12

mation. Meleagrinella form shell accumulations in clays together with ammonites and *Kedonella*. The cores of individual valves are found in calcareous concretions together with oysters near the base of the Kurung Member. The type of fossil cenosis is slightly displaced thanatocenosis.

On the Motorchuna River, individual valves occur in concretions together with *Kedonella*. The type of fossil cenosis is slightly displaced thanatocenosis.

On the Astronomicheskaya River, in the silts of the lower subformation of the Start Formation, entire individual valves in places form local coquinae and are buried together with ammonites, *Kedonella*, *Lima* and *Entolium*. The type of fossil cenosis is slightly displaced thanatocenosis.

Lifestyle and habitats. Representatives of the species in question could lead a pseudoplanktonic lifestyle, attaching to floating algae or shells of living ammonites. This view is supported by some researchers of the Toarcian bituminous shales of Germany (Röhl, 1998; Teichert and Nützel, 2015). They were classified as suspension feeders that were tolerant of hypoxic environments (Caswell et al., 2009). If they were torn away from the place of attachment and fell to the bottom, unable to exist for a long time in anoxic conditions on the ground, they could probably move to the place of re-attachment due to the collapse of the valves. The pseudoplanktonic lifestyle with the possibility of active movement was a necessary adaptation of *Meleagrinella* to the hypoxic conditions in the Early Toarcian seas.

Geological age and geographical distribution. Lower Toarcian Substage, Tiltoniceras antiquum, Harpoceras falciferum zones of the Boreal scale; Dactylioceras tenuicostatum, Harpoceras serpentinum zones of the Subboreal scale.

Western Siberia: Ust-Yenisei District, Kiterbyut Formation. Eastern Siberia: Kelimyar River, Kelimyar Formation, Lower Toarcian; Anabar Bay, Anabar River, Kiterbyut Formation; Motorchuna River, Suntary Formation; Tyung River, Ottur section (Ygyatta River basin), Suntary Formation. Northeastern Russia: Saturn, Astronomicheskaya, Brodnaya rivers, Start Formation (lower subformation). Germany: Dörlbach, Berg, Altdorf, Adenstedt, Posidonienschiefer Formation. England: Yorkshire, Whitby Mudstone formation. Western Canada: Alberta, Fernie Formation.

Subgenus *Clathrolima* Cossman, 1908

Echinotis: Marwick, 1935, p. 34.

Type species: *Clathrolima lalmenti* (Cossmann, 1908, pl. II, fig. 8, text-fig., pp. 296–297).

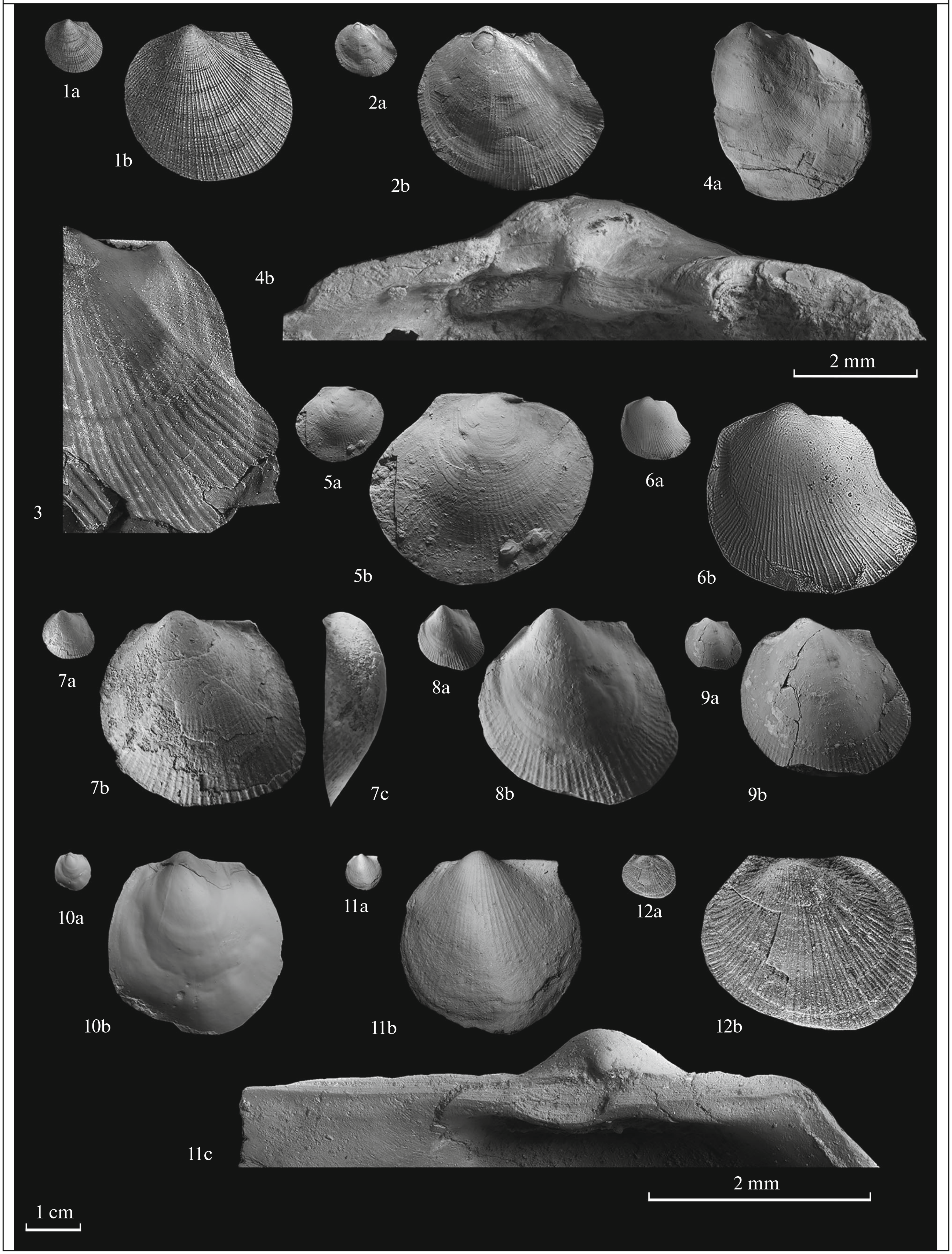
Diagnosis. Shell inequilateral, very small to medium-sized. Sub-rectangular ligament pit type. Oblique subtype of the ligament pit. At the mature stage, ligament pit acute-angled, modification 5; lower end of anterior margin of ligament pit of right valve after the third bend located to the right of axis of symmetry. Hemispherical protuberance present, rarely absent. Byssal ear rhomboid.

Species composition. Based on the hinge, the following species are classified within this subgenus: the Toarcian *Monotis substriata* (Münster, 1831; Goldfuss, 1835, non Zieten, 1830), the Bajocian *Pseudomonotis subechinata* (Lahusen, 1883), Bathonian *Avicula echinata* (Smith, 1817), Callovian *Avicula braamburensis* (Phillips, 1829), Kimmeridgian-Volgian *Meleagrinella subovalis* (Zakharov, 1966).

Remarks. Possibly this subgenus should also include the Aalenian *Monotis elegans* (Quenstedt, 1858) non *Avicula elegans* Muenster (Goldfuss, 1835); Bajocian *Pseudomonotis quenstedti* (Rollier, 1914), *Pseudomonotis lycetti* (Rollier, 1914), *Avicula decussata* Muenster (Goldfuss, 1835); Bathonian-Callovian *Pseudomonotis umaltensis* (Krymgholz, 1939); Callovian *Pseudomonotis ferniensis* (McLearn, 1924); Oxfordian *Monotis ornate* (Quenstedt, 1858), *Pseudomonotis laevis* (Arkell, 1933), *Pseudomonotis maltonensis* (Arkell, 1933), *Pseudomonotis greppini* (Rollier, 1914), *Pseudomonotis lorioli* (Rollier, 1914); Kimmeridgian-Volgian *Meleagrinella recta* (=*lata*) (Turbina, 1984).

Plate XI. Figs. 1–10. *Meleagrinella (Clathrolima) substriata* (Münster), (1) syntype (Goldfuss, 1835, p. 138, pl. CXX, figs. 7a, 7b), (a) left valve, ×1, (b) the same, ×3; Posidonienschiefer Formation, Banz, Germany; (2) lectotype, specimen no. IGPB-Goldfuss-729a/1, (a) left valve, ×1, (b) the same, ×3; the same locality; (3) syntype, specimen no. IGPB-Goldfuss-729a/3, mold of a left valve, view of a posterior auricle and posterior wing, ×7; the same locality; (4) syntype, specimen no. AS-VII-2087a, (a) left valve of a mature specimen, ×1, (b) view of a ligament area, scale bar 2.0 mm; Mistelgau, Germany; (5) syntype, specimen no. AS-VII-2087b, (a) right valve, ×1, (b) the same, ×2.5; the same locality; (6) specimen no. GZG.INV.70646, (a) left valve, ×1, (b) the same, ×4; Dörlbach Ludwigskanal, Germany, Posidonienschiefer Formation, Member 14 ("Monotis-Bank"), Hildoceras bifrons Zone (Dactylioceras commune Subzone); (7) specimen no. AS-77/1, (a) left valve, ×1, (b) the same, ×4, (c) the same, lateral view, ×4; Astronomicheskaya River, Outcrop 2, Bed 17; sample no. AC-77, Start Formation, upper subformation, Lower Toarcian, Dactylioceras commune Zone; (8) specimen no. T-254/6, (a) mold of a left valve, ×1, (b) the same, ×3; Tyung River, Outcrop 15a, sample no. 254, scree of Beds 3–4, Suntary Formation, second member, Lower Toarcian; (9) specimen no. T-254/17, (a) mold of a left valve, ×1, (b) the same, ×3; the same locality; Fig. 10. *Meleagrinella* cf. *substriata* (Münster), specimen no. B-5a/38-1, (a) mold of a left valve, ×1, (b) the same, ×5; Vilyui River, Iligir Creek, Outcrop 5a, Sample B-5a-38/2, scree of Bed 24, Suntary Formation, second member, Lower Toarcian. Fig. 11. *Meleagrinella (Clathrolima)* sp., specimen no. P-470-521/1, (a) left valve of a mature specimen, ×1, (b) the same, ×5, (c) view of a ligament area, scale bar 2.0 mm; Pravoberezhnyi area, line 470, Borehole 521, depth 21.9 m, Suntary Formation, third member, Lower–Upper? Toarcian. Fig. 12. *Otapiria substriata* (Zieten), specimen GZG.INV.70639, (a) mold of a left valve, ×1, (b) the same, ×4; Wellersen, Germany, Lower Sinemurian.

Plate XI


1a
1b
2a
2b
4a
4b
3
2 mm
5a
5b
6a
6b
7a
7b
7c
8a
8b
9a
9b
10a
10b
11a
11b
12a
12b
11c
2 mm
1 cm

Comparison. From *Meleagrinella* s.str. it is distinguished by a tapering subtype of the ligament pit at the juvenile stage, a more developed protuberance.

Geological age and geographical distribution. Lower Toarcian—Volgian stage of Eastern Siberia, Northeast and Far East of Russia. Lower Toarcian—Tithonian of Europe, Canada.

Meleagrinella (Clathrolima) substriata **(Münster, 1831)**

Plate XI, figs. 1–10

Monotis substriata: Münster, 1831, p. 406.

Monotis substriata: Goldfuss, 1835, p. 138, pl. CXX, figs. 7a–7f.

Arctotis (Praearctotis) substriata: Lutikov and Arp, 2020, pl. I, figs. 9–12.

Meleagrinella (Clathrolima) substriata: Rogov, Lutikov, 2022, text-figs. 4I–4N.

Meleagrinella (Clathrolima) substriata: Lutikov and Arp, 2023a, pl. II, figs. 1–11.

Holotype. Not designated. The type series was partially illustrated by Goldfuss (1835). The author and G. Arp selected a specimen from type series no. as the lectotype, IGPB-Goldfuss-729 a/1. Illustrated here at Pl. XI, fig. 2, stored at the Institute of Geosciences (Germany, Bonn). Posidonienschiefer Formation, Dactylioceras commune Subzone, Banz locality, Germany.

Material. More than 20 molds and individual valves from Toarcian of sections of Anabar Bay, the Astronomicheskaya, Saturn, Tyung, and Vilyui rivers. Also 23 imprints and individual valves, about 150 fragments from the Toarcian of the Ludwigskanal (Dörlbach) and the Berg area, Germany. Photographs of syntypes from the type collection of G. Münster, from the Posidonienschiefer Formation, Dactylioceras commune Subzone (Banz, Mistelgau, Germany); one specimen with a preserved shell, six molds and valve imprints from the Toarcian of the Agard Bay section, Spitsbergen.

Diagnosis. Shell very low, strongly inequilateral. Posterior wing narrow, moderately-concave. Posterior margin with a S-like curvature. Posterior auricle in both valves obtuse-angled, without a notch.

Dimensions in mm and ratios: See Table 2.

Description. The shell is small, mostly up to 15 mm in height, one syntype is up to 33 mm high. The left valve is very low, inequilateral, strongly convex. The posterior wing of the left valve is narrow, moderately convex. The posterior margin forms an S-shaped curve. The lower end of the posterior wing of the left valve is located above the posterior end of the valve. The posterior outer ligament of the left valve is very short. The posterior auricle is obtuse-angled, without a notch. The left valve is densely ribbed. The area between the ends of the anterior and posterior margins is covered with radial ribs of the same order, ranging from 35 to 60, irregularly distributed along the valve, with interrib spaces varying in width. The ribs of the second order are irregularly wedged into the interrib spaces. On the posterior wing, the number of radial ribs is more than 20. On the anterior wing, the number of radial ribs is more than 10. On the mold of the left valve in the area of the beak, near the anterior and posterior margins, the ribs are weakly expressed. The interrib spaces along the lower margin are moderately wide.

The right valve is low. The posterior outer ligament of the right valve is very long. The posterior auricle of the right valve is acute-angled. The posterior wing is narrow, moderately curved towards the posterior end of the valve. The right valve is moderately ribbed. The interrib spaces along the lower margin are moderately wide.

Variability. The contour of the left valve varies from very low to high. The symmetry of the left valves varies from moderately unequal to strongly unequal. The posterior outer ligament of the left valve varies from very short to long. The radial sculpture of the left valve varies from frequently ribbed to densely ribbed.

Comparison. This species differs from *Meleagrinella (Clathrolima)* sp. from the third member of the Suntary Formation of the Pravoberezhnyi Site (Pl. XI, fig. 11) in the more strongly inequivalve shells, an S-shaped posterior margin of the left valve, the position of the end of the posterior wing of the left valve above the posterior end of the valve, and an obtuse-angled posterior auricle without a notch.

It differs from *Meleagrinella (Praemeleagrinella?)* aff. *golberti* Lutikov et Arp, 2023 from the Tiltoniceras antiquum and Harpoceras falciferum zones (Pl. X, figs. 14, 15) in the more strongly iequivalve shells, an S-shaped posterior margin of the left valve, and an obtuse-angled posterior auricle without a notch.

Remarks. Researchers' views on the systematic affiliation of this taxon have changed many times. It was considered as part of the genera *Monotis* (Münster, 1831; Quenstedt, 1858), *Pseudomonotis* (*Atlas*..., 1947; Bodylevsky and Shulgina, 1958), *Pseudomonotis (Meleagrinella)* (Hoffmann and Martin, 1960), *Meleagrinella* (*Polevoi*..., 1968; Urlichs, 1971).

Based on photographs of several specimens from the type collection of the species *Monotis substriata*, stored in the Goldfuß-Museum (Bonn, Germany), a specimen from the Banz locality (Posidonienschiefer Formation, Dactylioceras-Monotis-Bed Member, Hildoceras bifrons Zone, Dactylioceras commune Subzone) was designated as the lectotype of the species (Pl. XI, fig. 2). The specimen depicted in the drawings in the monograph by Goldfuss (1835, p. 138, pl. CXX, figs. 7a, 7b; here Pl. XI, fig. 1) is very similar to the lectotype. The syntypes illustrated in other figures in the monograph by Goldfuss (1835, p. 138, pl. CXX, figs. 7c, 7e, here Pl. XI, figs. 4, 5) come from the Mistelgau area (Posidonienschiefer formations, Lias epsilon) and are stored in the Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany) under no. AS-VII-2087. The ligament pit of the left valve syntype no. AS-VII-2087a has an acute angular outline (Pl. XI, fig. 4b). According to this characteristic, the species of G. Munster belongs to the subgenus *Meleagrinella (Clathrolima)*. Right valve syntype no. AS-VII-2087b has an obtuse-angled posterior auricle shape (Pl. XI, fig. 3).

Specimens from the Dactylioceras-Monotis-Bed Member of the Ludwigskanal section in the Dörlbach locality (Pl. XI, fig. 6) and from the Dactylioceras commune Zone of the Astronomicheskaya River (Pl. XI, fig. 7) and Tyung River (Pl. XI, figs. 8, 9), have an obtuse-angled outline of the posterior auricle of the left valve, an S-shaped bend of the posterior margin, and a very short posterior outer ligament. Based on these characteristics, they belong to the species *Meleagrinella (Clathrolima) substriata*. The only specimen from the Vilyui River section (Pl. XI, fig. 10), found in the scree of Beds with Dactylioceras spp., is represented by a mold with the remains of a shell layer, has an obtuse-angled outline of the posterior auricle of the left valve, an S-shaped bend of the posterior margin and is assigned to *Meleagrinella* cf. *substriata*.

The species *"Avicula" substriata* (Zieten, 1830), originating from the Arietenkalk Formation (Lower Sinemurian, Stuttgart Region, Southern Germany), was presumably considered part of the subgenus *Meleagrinella (Praemeleagrinella)* (Lutikov and Shurygin, 2010). In coeval deposits of the Arietenton Formation in Northern Germany, G. Arp discovered specimens belonging to this species (clay quarry in the Wellersen area, Markoldendorf Syncline) (Pl. XI, fig. 12). Based on the outline of the anterior auricle of the left valve, the location at an angle to the hinge margin of the byssal ear, and the geniculate radial ribs at the lower margins of the Sinemurian species, *"Avicula" substriata* belongs to the genus *Otapiria* (Marwick, 1935), therefore, for the Toarcian species, the name *Meleagrinella substriata* is valid.

Facies association and taphonomic characteristics. On the Tyung River, specimens are represented by complete shells with two valves in concretions with shell rocks. *Meleagrinella* specimens were buried together with ammonites, *Dacryomia, Lyostria, Oxytomes, Lenoceramus, Modiolus,* and *Tankredia*. The type of fossil cenosis is slightly displaced thanatocenosis. The burial took place near habitats. On the Astronomicheskaya River and Saturn, shells form nest-like shell accumulations in massive nodules. *Meleagrinella* specimens are represented by scattered valves of poor preservation, buried with ammonites, belemnites, *AStart, Entolium, Cucullaea* rare *Propeamussium*, *Oxytoma*, *Lyostrea*, *Goniomia*. The type of fossil cenosis is a displaced thanatocenosis.

Lifestyle and habitats. They lived at shallow depths away from the shore (Tyung River, Astronomicheskaya, Saturn, Ludwigskanal). They settled in colonies. They were attached by byssus to algae and driftwood. They could form "benthic islands" by attaching to hard parts of the shells of dead other organisms, including ammonites (Schmid-Rohl and Rohl, 2003). No accumulations were found in near-shore environments (Vilyui River, Anabar Bay) or in off-shore settings (Cape Tsvetkov).

Geological age and geographical distribution. Lower Toarcian Substage, Dactylioceras commune Zone—Boreal standard scale; Hildoceras bifrons Zone, Dactylioceras commune Subzone—standard scale of Northwestern Europe.

Eastern Siberia: Tyung River, Vilyui, Suntary Formation; Anabar Bay, Eren Formation. Northeastern Russia: Saturn, Astronomicheskaya, Brodnaya rivers, Start Formation (upper subformation). Southern Germany: Banz, Mistelgau, Dörlbach, Posidonienschiefer Formation; England; Spitsbergen; Iran; Japan.

Subgenus *Meleagrinella* s.str.

Type species Subgenus: *Pseudomonotis (Eumicrotis) curta* (Whitfield, 1880, p. 354, pl. 3, figs. 20–25); Upper Jurassic, Oxfordian, USA.

Diagnosis. Shell equilateral, very small to medium-sized. Subrectangular or acute angular ligament pit type. Expanding subtype of the ligament pit. At the mature stage, ligament pit wide-angled, of modifications 2, 4a, 4b. Semiellipsoidal protuberance poorly developed, rarely absent. Byssal ear rhomboid or trapezoid.

Species composition. The following species are assigned to the subgenus based on the hinge structure: Toarcian *Meleagrinella (Meleagrinella) prima* (Lutikov and Arp, 2023a), Bajocian *Pseudomonotis echinata* var. *doneziana* (Borissjak, 1909); Early Bathonian *Meleagrinella (Meleagrinella)* sp. (here, Pl. III, fig. 16), Oxfordian *Pseudomonotis (Eumicrotis) curta* (Whitfield, 1877), *Pseudomonotis (Eumicrotis) orbiculata* (Whitfield, 1880).

Remarks. The following taxa should probably be assigned to this subgenus: Toarcian *Meleagrinella milovae* (Okuneva, 2002), *Meleagrinella okayamensis* (Hayami, 1961); Upper Callovian *Avicula pectiniformis* (Bronn, 1837), *Pseudomonotis? oblanceolata* (Voronets, 1938); Kimmeridgian *Pseudomonotis kiliani* (Rollier, 1914), Maastrichtian *Avicula abrupta* (Conrad, 1853). Since these species do not have a description of the hinge plate, they are tentatively assigned to the nominative subgenus.

Comparison with *Meleagrinella (Clathrolima)* Cossmann, 1908 (see above).

Geological age and geographical distribution. Bajocian–Kimmeridgian of European Russia, Lower Toarcian–Kimmeridgian of Western and Eastern Siberia, Northeast and Far East of Russia, Bathonian–Kimmeridgian of Europe, Oxfordian–Upper Cretaceous of the USA.

Meleagrinella (Meleagrinella) prima Lutikov, 2023

Plate XII, figs. 1–12

Meleagrinella substriata: *Polevoi...*, 1968, p. 42, pl. 39, figs. 1–2.

Meleagrinella faminaestriata: Knyazev et al., 2003, p. 90, pl. 6, fig. 1.

Arctotis (Praearctotis) milovae: Lutikov and Shurygin, 2010, Pl. III, figs. 12–14 (part.); Lutikov et al., 2010, Pl. I, fig. 9, Pl. II, fig. 2; Lutikov, 2021, Pl. I, fig. 1.

Arctotis (Praearctotis) substriata: Lutikov and Arp, 2020, Pl. I, figs. 15–17 (part.).

Meleagrinella (Meleagrinella) prima: Lutikov and Arp, 2023a, pl. III, figs. 1–11.

Etymology. From the Latin *prima* (first).

Holotype. Vernadsky State Geological Museum (GGM), Moscow, specimen no. MX-237/5, Markha River, Outcrop 10, Bed 9, sample no. MX-237-B, Lower Toarcian, Zugodactylites braunianus Zone.

Material. More than 700 individual valves, molds with remains of a shell layer from the sections of the Astronomicheskaya, Saturn, Start, Markha rivers, Anabar Bay, Tenkelyakh exploration drilling site (Hannya-Tyukyan interfluve).

Diagnosis. Shell round, moderately inequilateral. Posterior wing very wide, strongly convex towards valve posterior. Lower end of posterior wing of the left valve located below valve posterior end. Posterior auricle of both valves subrectangular or acute-angled, with a notch. Byssal ear trapezoid, with a short byssal notch.

Dimensions in mm and ratios: see Table 3.

Description. The shell ranges from very small to small. The left valve is rounded, moderately inequilateral, moderately convex. The posterior wing of the left valve is very wide, strongly convex towards the posterior end of the valve. The lower end of the posterior wing of the left valve is located below the posterior end of the valve. The posterior outer ligament of the left valve is short. The posterior auricle of the left valve is subrectangular, with a notch. The left valve is densely ribbed. The area between the apical projections of the anterior and posterior margins is covered with radial ribs of the same order, numbering from 37 to 38, irregularly distributed along the valve, with interrib spaces varying in width. On the posterior wing, the number of radial ribs is more than 12. On the anterior wing, the number of radial ribs is more than 10. On the core of the left valve in the area of the beak, near the anterior and posterior margins, the ribs are weakly expressed. On some specimens, in the interrib spaces there are ribs of the second order, differing in degree of expression from the ribs of the first order. The interrib spaces along the lower margin are narrow. The right valve is low, inequilateral. The posterior outer ligament of the right valve is very long. The posterior auricle of the right valve is acute-angled. The posterior wing is very wide, strongly convex towards the posterior end of the valve. The right valve is moderately ribbed.

Variability. Shell sizes range from very small (less than 10 mm) to small (up to 30 mm). The contour of the left valve varies from very low to high. The symmetry of the left valves varies from inequilateral to moderately inequilateral. The posterior outer ligament of the left valve varies from very short to long. The rib density of the left valve varies from frequently ribbed to densely ribbed.

Comparison. This species is distinguished from *Meleagrinella (Clathrolima) substriata* (Münster) from the Hildoceras bifrons Zone (Dactylioceras commune Subzone) by a subrectangular posterior auricle and a notch below the posterior auricle.

Plate XII. Figs. 1–12. *Meleagrinella (Meleagrinella) prima* Lutikov, **(**1) holotype, specimen no. MX-237/5, (a) left valve of a mature specimen, ×1, (b) the same, ×4; sample no. MX-237-B, Markha, Outcrop 10, Bed 9, Suntary Formation, third member, Lower Toarcian, Zugodactylites braunianus Zone; (2) specimen no. MX-237/4, (a) left valve of a mature specimen, ×1, (b) the same, ×4; the same locality; (3) specimen no. MX-237/3, (a) left valve of a mature specimen, ×1, (b) the same, ×4; the same locality; (4) specimen no. MX-309/17, (a) mold of a left valve of a mature specimen with an external imprint of the right valve, ×1, (b) the same, × 4; sample no. MX-309, Markha, Outcrop 8, Bed 7, Lower Toarcian, Zugodactylites braunianus Zone; (5) specimen no. MX-309/18, (a) mold of a left valve of a mature specimen, ×1, (b) the same, ×4; sample no. MX-309, the same locality; (6) specimen no. MX-229/1, (a) left valve of a mature specimen, ×1, (b) the same, ×4, (c) view of the posterior wing of a left valve, ×7; sample no. MX-229, Markha, Outcrop 6, Bed 3, Suntary Formation, Lower Toarcian, Zugodactylites braunianus Zone; (7) specimen no. MX-229/2, (a) mold of a left valve of a mature specimen, ×1, (b) the same, ×4; sample no. MX-229, the same locality; (8) specimen no. AG-103/4, (a) left valve of a mature specimen, ×1, (b) the same, ×4; Anabar Bay, western coast, Outcrop 5, Bed 76, sample no. AG-103, Eren Formation, Lower Toarcian, Zugodactylites braunianus Zone; (9) specimen no. TX-1/3, (a) left valve of a mature specimen, ×1, (b) the same, ×5; (c) the same, lateral view from the anterior margin, ×5, Lower Toarcian, third member of the Suntary Formation, Tenkelyakh Site, line 1060, Borehole 350, depth 31 m; (10) specimen no. TX-1/1, (a) right valve of a mature specimen, ×1, (b) the same, ×5; the same locality; (11) specimen no. Sa-1/18-1, (a) mold of a left valve, ×1, (b) the same, ×5; Sample 34, Lower Toarcian, Start Formation, upper subformation, Saturn River, Outcrop 1, Bed 18; (12) specimen no. Sa-1/18-2, (a) mold of a left valve, ×1, (b) the same, ×4; Sample 34, the same locality. Figs. 13, 14. *Meleagrinella (Meleagrinella)* aff. *prima* Lutikov, **(**13) specimen no. St-1/1, mold of a left valve of a mature specimen, (a) shell exterior, ×1, (b) the same, ×2.0; (c) lateral view from the anterior margin, ×2.0; Start River, Start Formation, upper subformation, scree of Bed 2, Outcrop5, Pseudolioceras compactile Zone; (14) specimen no. 24/12566, F.N. Chernyshev TsNIGR Museum (St. Petersburg), mold of a left valve of a mature specimen with remains of shell layer, shell exterior, ×1. Munugudzhak, collected by B.A. Snyatkov, Yu.S. Repin, Upper Toarcian. Figs. 15, 16. *Meleagrinella (Meleagrinella?) milovae* Okuneva, 2002, (15) specimen no. 44/12919, F.N. Chernyshev TsNIGR Museum (St. Petersburg), (a) imprint of a left valve, ×1; (b) the same, ×3; Gazimur River basin, Bolshaya Kulinda valley, collected by T.M. Okuneva, Upper Toarcian, Beds with *Meleagrinella milovae*; (16) specimen no. 46/12919, F.N. Chernyshev TsNIGR Museum (St. Petersburg), coquinae of molds of the left and right valves; the same locality, ×1.

Plate XII

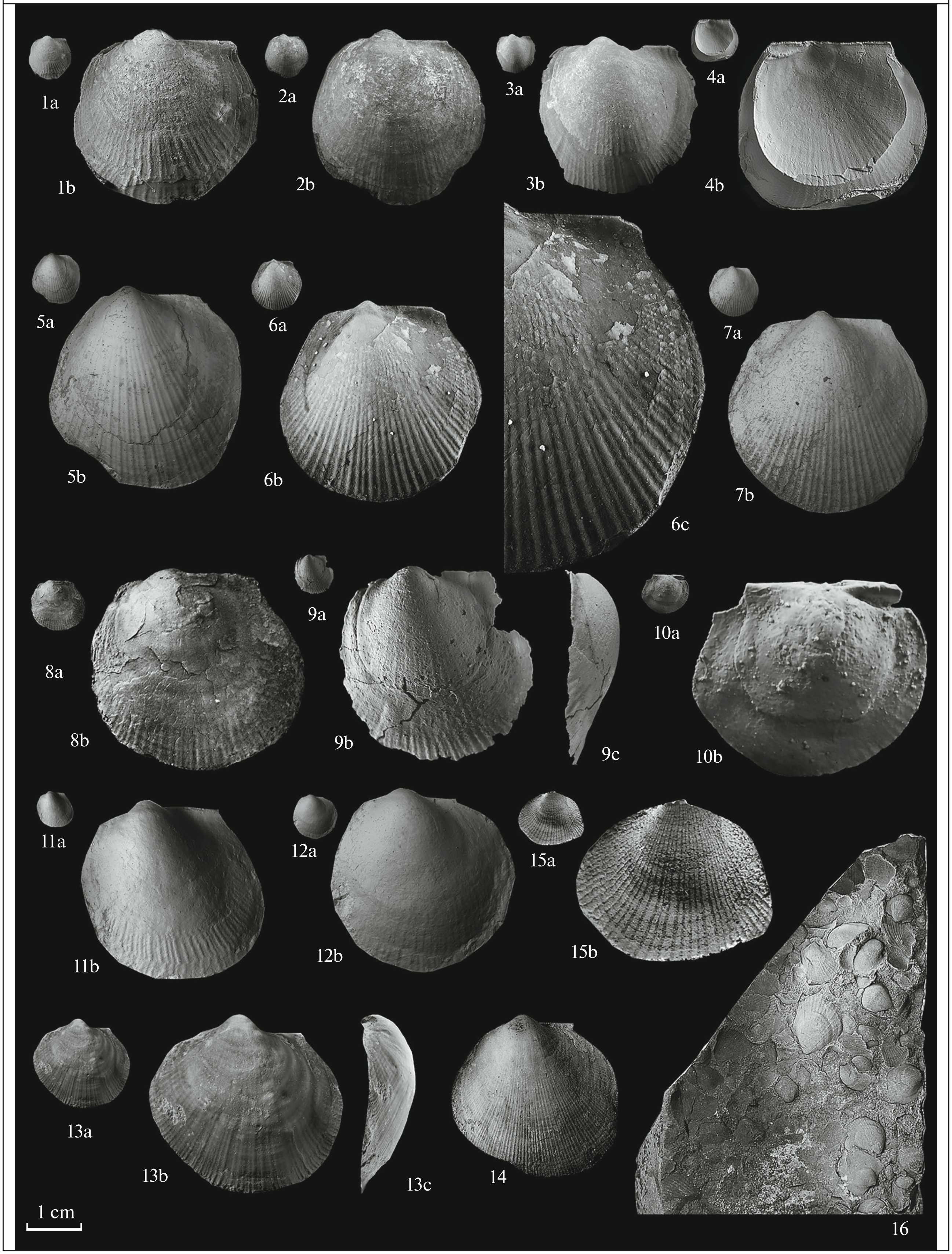

1a
1b
2a
2b
3a
3b
4a
4b
5a
5b
6a
6b
6c
7a
7b
8a
8b
9a
9b
9c
10a
10b
11a
11b
12a
12b
15a
15b
13a
13b
13c
14
16
1 cm

Table 3. Dimensions in mm and ratios

Coll. no., valve	Locality	VL	VH	VH/VL	RVH/RVL	Cv	Cv/VH	ADL	ADL/VL	PDL	PDL/Cv	LOL	LOL/PDL	PWAg	R	R/VL	ISW/RW	PAAg	PWW/PWL
Meleagrinella (*Meleagrinella*) *prima*																			
MX-237/5, holotype, left	Markha River, Outcrop 10, Bed 9, sample no. MX-237-B, Suntary Formation, Lower Toarcian, Zugodactylites braunianus Zone	7.89	8.1	1.03	–	–	–	3.42	0.43	4.47	0.55	3.56	0.78	56°	37?	4.69	2.00	90°	0.16
MX-237/4, left	The same	8.00	8.1	1.01	–	–	–	3.49	0.44	4.51	0.56	3.03?	0.67?	–	–	–	–	–	0.24
MX-237/3, left	The same	7.38	7.3	0.99	–	–	–	2.96	0.40	4.42	0.61	3,51	0.79	–	–	–	–	–	–
M-309/16, left	Markha River, Outcrop 8, Bed 7, Suntary Formation, Lower Toarcian, Zugodactylites braunianus Zone	8.84	8.80	1.00	–	2.55	0.29	3.42	0.38	5.42	0.62	3.49	0.64	52°	38	4.27	1.68	–	0.17
M-309/17, left right	The same	8.68 77.00	7.80 6.72	0.90 0.96	0.86	– –	– –	3,58 2.81	0.41 0.40	5.10 4.19	0.65 0.62	3.48 3.48	0.68 0.83	50° 50°	– 19	– 2.71	– –	– –	0.17 0.19
MX-229/19, left	Markha River, Outcrop 6, Bed 3, sample no. MX-229, Suntary Formation Lower Toarcian, Zugodactylites monestieri Zone	9.37	9.4	1.00	–	–	–	3.92	0.42	5.45	0.58	3.49	0.64	49°	38	4.06	2.00	–	0.16
AG-103/4, left	Anabar Bay, western coast, Eren Formation, Outcrop 5, Bed 76; Zugodactylites braunianus Zone	9.93	9.30	0.94	–	2.67	0.29	3.66	0.37	6.22	0.67	4.04	0.65	–	–	–	1.95	–	–
AG-103/2, left	The same, subadult stage, adult stage	–	9.50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
AG-103/1, left	The same juvenile stage	–	2.50	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
TX-1/3, left	Tenkelyakh Site, line 1060, Borehole 350, depth 31 m; Lower Toarcian, Suntary Formation	7.21	7.20	0.99	–	–	–	2.75	0.38	4.52	0.63	3.01	0.67	–	–	–	1.58	–	–
TX-1/1, right	The same	8.83	7.20	0.81	–	1.86	0.21	3.62	0.40	5.21	0.72	–	–	–	–	–	–	–	–
TX-1/10, left	The same, juvenile stage, subadult stage	3.00	2.50	0.80	–	–	–	1.26	0.41	1.84	0.74	0.93	0.51	–	–	–	–	–	–
Meleagrinella (*Meleagrinella*) aff. *prima*																			
Ct1/1, left	Start River, Outcrop 5, Start Formation, scree of Bed 2, Pseudolioceras compactile Zone	17.77	16.5	0.93	–	5.08	0.31	8.30	0.47	9.47	0.57	5.67	0.60	53°	56	3.05	1.81	–	0.17

Remarks. Specimens of *Meleagrinella*, identified as a new species, were previously identified as either *Meleagrinella faminaestriata* (Knyazev et al., 2003) or *Arctotis (Praearctotis) milovae* (Okuneva) (Lutikov and Shurygin, 2010; Lutikov, 2021). Very small sizes (up to 10 mm), a subrectangular posterior auricle and dense ribbing bring together representatives of the new species from the Zugodactylites braunianus Zone (Markha River, Anabar Bay) with the species *Meleagrinella milovae* from the Upper Toarcian of Eastern Transbaikalia (Okuneva, 2002, p. 379, pl. CXXIV, figs. 15–18). In 2022, the author re-examined the standard collection of T.M. Okuneva, stored in the F.N Tchernyshev TsNIGR Museum (St. Petersburg), using a new system of grading characters. The left valves in representatives of the Far Eastern population are characterized by a less curved posterior auricle; the lower end of the posterior wing of the left valve is located above the posterior end of the valve (Pl. XII, fig. 15). The exact genus of the taxon cannot be determined due to the poor preservation of fossil material. A typical sample is represented by coquina, consisting of scattered very small, poorly preserved valves of approximately the same size (Pl. XII, fig. 16). Taking into account the evidence of the existence of an extended land area that separated the East Siberian and Far Eastern seas in the Toarcian (Devyatov et al., 2011), it can be assumed that the population from the Gazimur River basin was isolated and belongs to an independent species. This local population occupies a stratigraphic level higher in the section than the Beds with Pseudolioceras rosenkrantzi, and may belong to *Arctotis (Praearctotis) marchaensis*, but this assumption requires verification and additional collecting.

The holotype of the species *“Meleagrinella” faminaestriata* Polubotko, 1968 comes from the section of the Tokur-Yuryakh River (*Polevoi*..., 1968). Specimens of the species *“Meleagrinella” faminaestriata* Polubotko, 1968 were studied from the type region along the tributaries of the Levy Kedon River. Their byssal ear has a tubular shape, the ligament area of the right valve is oriented parallel to the midsagittal plane, the sculpture is represented by radial grooves rather than ribs (Pl. XVIII, figs. 4–5). Based on these characters, this species belongs to a group not related to Oxytomidae Ichikawa, 1958. It is tentatively assigned to the genus *Praebuchia* Zakharov, 1981.

Representatives of the described taxon in the sample from the third member of the Suntary Formation (Tenkelyakh Site, Markha River) have a subsymmetrical ligament pit shape at the postlarval stage, and wide-angled at the juvenile stage (Pl. I, fig. 13). At the juvenile stage, the ligament pit expands (expanding subtype) (Pl. I, fig. 14). Based on this feature, the taxon belongs to the subgenus *Meleagrinella* s.str. The microsculpture of the ostracum in the lower part of the right valve is represented mainly by quadrangular prisms, which are located parallel to the radial ribs from the beak towards the lower margin (Pl. VIII, fig. 6).

In contrast to the described taxon, in representatives of *Arctotis (Praearctotis) marchaensis* in the sample from the fourth member of the Suntary Formation, the ostracum of the right valves is characterized by hexagonal prisms arranged in a disorderly manner (Pl. VIII, fig. 8). Based on this feature, populations from the Pseudolioceras wuerttenbergeri Zone belong to the subgenus *Arctotis (Praearctotis)* Lutikov et Schurygin.

Specimens of *Meleagrinella* were found in Northeastern Russia (Munugudzhak, Start rivers) in the Pseudolioceras compactile Zone, which are similar in external morphology to the described species, but differing in large size (up to 30 mm in height) (*Polevoi*..., 1968, pl. 39, figs. 1–2) (Pl. XII, figs. 13, 14). Given their higher stratigraphic position and size, these specimens are assigned to *Meleagrinella (Meleagrinella)* aff. *prima*.

Facies association and taphonomic characteristics. On the Markha River and in Anabar Bay, shells form shell accumulations. The shells are ungraded, but the radial ribs show signs of wear. *Meleagrinella* are found together with ammonites, *Dacryomia, Lyostria, Oxytoma, Lenoceramus*, *Modiolus* and *Tankredia*. The type of fossil cenosis is slightly displaced thanatocenosis. The burial took place near the habitat. On the Astronomicheskaya River and Saturn, shells form nest-like shell accumulations in massive nodules. Scattered, poorly preserved valves were buried with ammonites, belemnites, *AStart, Entolium, Cucullaea, Propeamussium, Oxytoma, Liostrea*, and *Goniomia*. The type of fossil cenosis is displaced thanatocenosis. In the Hannya-Tyukyan interfluve (Tenkelyakh Site), shells form shell accumulations of whole shells and individual well-preserved valves, represented by both adult and juvenile specimens. The burial took place at the place of residence. The type of fossil cenosis is autochthonous thanatocenosis.

Lifestyle and habitats. These mollusks lived on fine sandy soils, at shallow depths near the shore. Attached by byssus to a solid substrate. Settled in colonies.

Geological age and geographical distribution. Eastern Siberia, Anabar Bay, Markha River, Hannya-Tyukyan interfluve, Northeastern Russia, Astronomicheskaya, Saturn, Start rivers; Lower Toarcian, Zugodactylites braunianus, Pseudolioceras compactile zones.

Genus Arctotis Bodylevsky, 1960

Arctotis: Bodylevsky, 1960, p. 44.

Type species. *Hinnites lenaensis* Lahusen, 1886, pl. 1, figs. 3, 3a. Middle Jurassic, Eastern Siberia, Lena River.

Diagnosis. Shell moderately inequilateral or equilateral from small to very large in size. Sculpture of radial ribs of two or three orders and growth co-centers. Symmetrical ligament pit type. Inversed subtype of the ligament pit. At the mature stage, ligament pit wide-angled, characterized by modification 3. At the postlarval stage, anterior edge of the pit forms an angle close to 150° with the continuation of the lower margin of the ligament pit, and more than 155° at the juvenile stage. Spoon-shaped subtype of the ligament pit. Ligament area of the left valve located at an angle of more than 40° to midsagittal plane. Byssal ear subtriangular, with a rounded lower margin, separated from the right valve by a deep byssal furrow and byssal notch. The byssal notch gapes in the early growth stages. Byssal furrow open at early stages. Protuberance sometimes present on pseuoligament platform of the left valve. Ligament ridge present on the ligament area of the right valve.

Comparison. Differences from *Meleagrinella* Whitfield, 1885 are listed above. It differs from *Oxytoma* Meek, 1864 in the symmetrical type of the ligament pit, with an overgrown byssal furrow.

Composition. Apart from the nominative subgenus includes the subgenera *Praearctotis*, *Canadotis,* and *Canadarctotis*.

Geological and geographical distribution. Toarcian–Hauterivian of Eastern Siberia, Russian Far East, Europe, Arctic Canada; Berriasian of Antarctica.

Subgenus *Praearctotis* Lutikov et Schurygin, 2010

Type species. *Pseudomonotis (Eumorphotis) marchaensis* Petrova, 1947. Upper Toarcian of Eastern Siberia.

Diagnosis. Shell moderately inequilateral from small to medium in size. Sculpture represented by radial ribs of two orders and growth centers. Angular or spoon-shaped subtype of the ligament pit. Ligament pit with a heterogeneous structure, with a depression and a flattened part. The outer margin of the ligament area of the right valve is geniculate or rounded in the anterior part. The ligament area of the left valve is long. Protuberance is semi-ellipsoidal. Byssal ear drop-shaped.

Description. The ligament area of the left valve is located at an angle of about 25° to the midsagittal plane of the shell. On the pseudoligamentous platform of the left valve, the semi-ellipsoidal weak protuberance is present, extended along the anterior branch of the ligamental platform. The shell is thin-walled, from small to moderately large, rounded or high, slightly unequal. The left valve is strongly convex, the right valve is slightly convex or flat. The anterior auricle of the left valve is obtuse-angled at all stages, the posterior auricle is acute-angled at the juvenile and subadult stages, obtuse-angled at the adult stage. The byssal ear of the right valve is trapezoid with a shortened base, has a gaping byssal notch and an open byssal furrow, the posterior auricle of the right valve has the shape of an obtuse triangle at the juvenile stage and has an S-shaped bend of the posterior margin at the adult stages, indistinctly separated from the valve by a depression. The sculpture consists of radial ribs of one or two orders, strongly weakened on the right valve, and concentric growth lines are also clearly visible.

Comparison. In terms of structure, the hinge plate occupies an intermediate position between the Early Toarcian *Meleagrinella* s.str. and early Aalenian *Arctotis* s.str. Differs from *Meleagrinella* in the angular subtype of the ligament pit (Pl. V, fig. 2) and the inclination of the ligament area of the left valve in relation to the midsagittal plane (Pl. V, fig. 1).

It differs from the nominative subgenus by the homogeneous base of the ligament pit with a depression in the anterior part (Pl. V, figs. 3, 4), the presence of a weak semi-ellipsoidal protuberance on the pseudoligamentous platform of the left valve, and a

Plate XIII. Figs. 1–13. *Arctotis (Praearctotis) marchaensis* (Petrova), (1) holotype, specimen no. 574/5393-1, left valve of an adult specimen, (a) shell exterior, ×1, (b) lateral view from the anterior margin, ×1; (c) paratype, specimen no. 574/5393-2, right valve of an adult specimen, shell interior; Markha River, Upper Toarcian (collection of A.G. Rzhonsnitsky, F.N. Chernyshev TsNIGR Museum (St. Petersburg)); (2) specimen no. MX-111/2, external view of a left valve of a mature specimen, ×1; Markha River, Outcrop 4, scree of Beds 2–3, Sample 111, Upper Toarcian; (3) specimen no. MX-111/3, left valve of a mature specimen, (a) shell exterior, ×1, (b) lateral view from the anterior margin, ×1; Markha River, Outcrop 4, loose, Upper Toarcian; (4) specimen no. MX-220/6 l, left valve of a mature specimen, (a) shell exterior, ×1, (b) lateral view from the anterior margin, ×1; Markha River, Outcrop 5, loose, Sample 220, Upper Toarcian; (5) specimen no. MX-233/2, (a) external view of a left valve of a mature specimen, ×1, (b) lateral view from the anterior margin, ×1, (c) posterior margin view, ×2.5; Markha River, Outcrop 10, Bed 8, Upper Toarcian; (6) specimen no. MX-233/1, external view of a left valve of a mature specimen, ×1; Markha River, Outcrop 10, Bed 8, Upper Toarcian; (7) specimen no. TX-1/5, (a) external view of a left valve of an adult specimen, ×1, (b) the same, ×2; Tenkelyakh Site, line 1080, Borehole 350, depth 35 m, Upper Toarcian; (8) specimen no. TX-1/2, (a) external view of a right valve of an adult specimen, ×1, (b) the same, ×2; Tenkelyakh Site, line 1080, Borehole 350, depth 35 m, Upper Toarcian; (9) specimen no. AG-37/1, external view of the distorted left valve of a mature specimen, ×1, Anabar Bay, Outcrop 4, Bed 18, Upper Toarcian; (10) specimen no. AG-37/2, external view of the right valve of a mature specimen, ×1, Anabar Bay, Outcrop 4, Bed 18, Upper Toarcian; (11) specimen no. 7/306, holotype "*Arctotis vai*" Bodylevsky, (a) external view of a left valve of a mature specimen, ×1, (b) lateral view from the anterior margin, ×1; Yuryung-Tumus Peninsula, Upper Toarcian, Mining Museum of St. Petersburg Mining University, collection of the "Atlas of index forms of Jurassic deposits"; (12) specimen no. 8/306, inside view of the right valve of a mature specimen, ×1, Yuryung-Tumus Peninsula, Upper Toarcian, Mining Museum of St. Petersburg Mining University, collection of the "Atlas of index forms of Jurassic deposits"; ×1; (13) specimen no. N-73/ 2913/1 l, (a) view of the mold of the left valve of a mature specimen, ×1, (b) side view of the mold from the anterior margin, ×1, (c) view of the mold of the right valve, ×1; Yuryung-Tumus Peninsula, Upper Toarcian, collection of B.N. Shurygin, INGG SO RAN, Novosibirsk.

→

Plate XIII

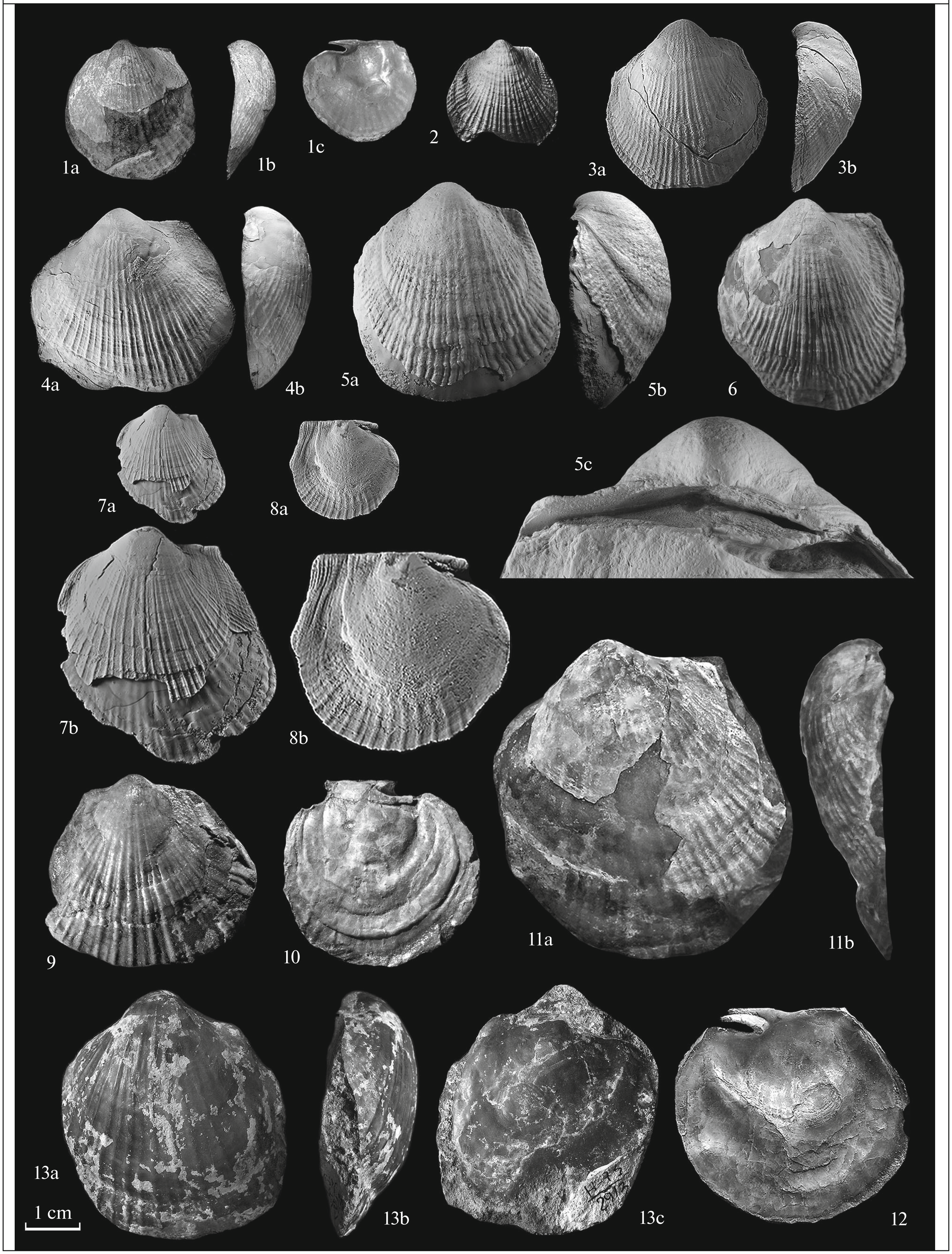

1a
1b
1c
2
3a
3b
4a
4b
5a
5b
6
5c
7a
8a
7b
8b
9
10
11a
11b
13a
13b
13c
12
1 cm

Table 4. Dimensions in mm and ratios

Coll. no., valve	Locality	VL	VH	VH/VL	C_v	C_v/VH	ADL	ADL/VL	AOL	AOL/ADL	AW_gA_g	R	R/VL	ISW/RW	AW_gW/AW_gL
574/5393 l, holotype	Markha River, Upper Toarcian, Museum TsNIGR, St. Petersburg, coll. A.G. Rzhonsnitsky	24.07	26.0	1.08	9.36	0.36	10.63	0.44	3.68	0.35	132°	32	1,33	1.10	0.17
574/5393 r, type specimen	The same	21.2	19.0	0.90	–	–	11.9	0.56	6.9	0.58	–	–	–	–	–
MX-111/2 l	Markha River, Outcrop 4, scree of Beds 2-3, Sample 111, Upper Toarcian	20.70	19.6?	0.95?	6.0	0.31	10.20	0.49	3.60	0.34	126°	26	1.26	1.06	0.15
MX-111/3 l	The same	30.41	31.6	1.09	13.07	0.42	14.52	0.48	–	–	121°	45	1.55	1.23	0.16
MX-220/6 l	Markha River, Outcrop 5, scree, Sample 220, Upper Toarcian	38.02	34.1	0.90	13.22	0.39	16.38	0.43	6.52	0.40	127°	41	1.10	1.64	0.09
MX-233/1 l	Markha River, Outcrop 10, Bed 8, Sample 233, Upper Toarcian	35.00	39,1	1.12	–	–	16.3	0.47	–	–	130°	43	1.23	0.92	0.15
MX-233/2 l	The same	38.25	40.5	1.06	18.97	0.47	17.57	0.46	7.28	0.41	119°	44	1.17	0.53	0.15
TX-1/5 l	Tenkelyakh Site, line 1080, Borehole 350, depth 35 m	21.8	22.6	1.04	6.5	0.29	9.5	0.44	3.81	0.40	144°	37	1.70	1.49	0.17
TX-1/2 r	The same	20.55	18.9	0.92	2.8	0.15	9.02	0.50	5.04	0.56	–	33	1.62	1.50	–
AG-37/1 l	Anabar Bay, Outcrop 4, Bed 18, Upper Toarcian	39.08	35.7	0.95	–	–	16.72	0.43	–	–	135°	34	0.90	1.28	0.20
AG-37/2 r	The same	36.27	34.7	0.96	–	–	16.30	0.45	–	–	–	28	0.77	–	–
7/306 l, holotype “*Pseudomonotis (Eumorphotis) vai*”	Yuryung-Tumus Peninsula, Upper Toarcian, Mining Museum of the St. Petersburg Mining University coll. V.I. Bodylevsky	55.48	59.2	1.06	17.36	0.29	21.21	0.38	–	–	119°	30	0.87	1.03	0.13
8/306 r, type specimen	The same	43,52	40.18	0.92	–	–	21.46	0.49	12.57	0.59	–	–	–	–	–
H-73/ 2913/1 l	Yuryung-Tumus Peninsula, Upper Toarcian, INGG SB RAS, Novosibirsk, coll. B.N. Shurygin	42.06	46.3	1.10	14.27	0.31	18.84	0.45	7.66	0.41	144°	22	–	2.14	0.15
H-73/ 2913/1 r	The same	37.80	36.20	0.96	4.11	0.11	17.48	0.46	–	–	–	–	–	–	–
no. 20/653, holotype “*Arctotis viluiensis*”	Vilyui River, Outcrop 54-56, Sample 1394, Upper Toarcian, VNIGRI Museum, coll. T.I. Kirina	39.33	36.2	0.92	13.89	0.38	18.33	0.47	6.78	0.37	135°	35	0.89	1.13	0.17

smaller angle of inclination of the ligament area of the left valve in relation to the midsagittal plane.

It differs from *Canadotis* in a smaller slope of the ligament area, a less developed pseudoligamentous platform, and a teardrop-shaped byssal ear.

Species composition. The subgenus includes *Pseudomonotis (Eumorphotis) marchaensis* (Atlas..., 1947), *Arctotis similis* (Velikzhanina, 1966) are classified as Subgenus. Presumably *Otapiria*? *frenguellii* (Damborenea, 1987) is also classified within this subgenus.

Occurrence. Upper Toarcian of Eastern Siberia, Northeastern Russia, Toarcian–Aalenian of Argentina.

Arctotis (Praearctotis) marchaensis **(Petrova, 1947)**

Plate XIII, figs. 1–13

Pseudomonotis (Eumorphotis) marchaensis Petrova: *Atlas*..., 1947, p. 123, pl. XII, figs. 13–15.

Pseudomonotis (Eumorphotis) vai Bodylevsky: *Atlas*..., 1947, p. 124, pl. XII, figs. 20–23.

Eumorphotis marchaensis: Krymgholz et al., 1953, p. 40, pl. IV, figs. 1–4.

Eumorphotis sparsicosta: Krymgholz et al., 1953, pl. V, figs. 7a, 7b, 7c, 8 (only).

Arctotis marchaensis: Koshelkina, 1963, p. 119, pl. II, figs. 4a–4c; Velikzhanina, 1966, p. 86, pl. I, fig. 15, pl. II, figs. 1–8; Polevoy..., 1968, pl. 40, fig. 5; Knyazev et al., 2003, p. 90, pl. 6, figs. 5, 7, 10.

Meleagrinella buschinskii Koschelkina: Koshelkina, 1963, p. 116, pl. II, figs. 3a, 3b.

Arctotis viluiensis Velikzhanina: Velikzhanina, 1966, pp. 89–90, pl. III, figs. 1–6 (only).

Praearctotis marchaensis: Lutikov et al., 2010, pl. I, fig. 10.

Praearctotis vai: Lutikov et al., 2010, pl. I, fig. 11.

Arctotis (Praearctotis) vai: Lutikov and Shurygin, 2010, pl. III, figs. 21–22.

Arctotis (Praearctotis) marchaensis: Lutikov and Shurygin, 2010, pl. III, figs. 16–20; Lutikov, 2021, pl. II, figs. 1–13; pl. III, fig. 1.

Holotype: F.N. Tchernyshev TsNIGR Museum, St. Petersburg, specimen no. 574/5393, collection of A.G. Rzhonsnitsky (1915), illustrated in: *Atlas*..., 1947, p. 123, pl. XII, fig. 14; Krymgholz et al., 1953, p. 40, pl. IV, fig. 2; here, Pl. II, fig. 1; Eastern Siberia, Markha River, Lower Jurassic, Upper Toarcian.

Material. More than 100 whole shells and individual valves from the Suntary Formation of the Markha River section; the type collection of *Pseudomonotis (Eumorphotis) marchaensis* from the Markha River, about 100 distorted shells and individual valves from the Eren Formation of Anabar Bay; molds of left valves from the upper Toarcian of the Saturn River; about 10 left and right well-preserved valves from wells in the Tenkelyakh Site; type collection of the species *Pseudomonotis (Eumorphotis) vai* from the Yuryung-Tumus Peninsula of V.I. Bodylevsky; collection of B.N. Shurygin—about 20 molds from the section of the Yuryung-Tumus Peninsula; type collection of *Arctotis viluiensis* from Vilyui River of T.I. Kirina.

Diagnosis. Shell commonly of medium size. Anterior wing of "paraboloid" type. Anterior wing obtuse-angled, narrow or very narrow. Anterior outer ligament of the left valve is short. Left valve strongly convex or inflated, right valve slightly convex. Radial ribs of two orders, up to 45 in number, interrib spaces narrow. Posterior wing of the left valve with up to 15 thin radial ribs. Ligament area of the left valve located at a slight inclination to midsagittal plane. Angular subtype of ligament area of the right valve. Spoon-shaped depression occupying a smaller part of ligament pit.

Dimensions in mm and ratios: See Table 4.

Variability. The sizes of specimens from sections of the Markha River, Anabar Bay, and boreholes of the Tenkelyakh Site are mostly medium-sized, with small (subadult) specimens less than 30 mm in size. Height varies from 19.6 to 40.5 mm. The holotype of "*Praearctotis vai*" (Pl. XIII, fig. 11) from the section of the Yuryung-Tumus Peninsula, has large dimensions—height 59.2 mm, which is not characteristic of the described taxon. The samples from the type locality of "*Praearctotis vai*" are dominated by medium-sized shells up to 46.0 mm, close in size to those from the Markha River. Perhaps only individual specimens reached large sizes, their height exceeding the limits of the range of variability of this trait. The contours of the left valves vary from very low to very high. The VH/VL coefficient varies from 0.90 to 1.12. With respect to the axis of symmetry, the left valve varies from moderately inequilateral to equilateral. The ADL/VL coefficient varies from 0.43 to 0.48. The contours and symmetry of shells were presumably influenced by the density of colonies of bivalve mollusks in the local areas they occupied. Shell contour and symmetry are variable and are not considered species-specific characters.

The left valves of the studied specimens from the Markha River sections, Anabar Bay, and Tenkelyakh Site are weakly ribbed. The R/VL ratio varies from 1.06 to 1.90. In the holotype of *Praearctotis vai*, the R/VL coefficient is 1.03. In terms of this characteristic value, these specimens are similar. The density of shell ribbing is correlated with the composition of sediments. Presumably, the state of the trait depends on the remoteness of the organisms' habitat relative to the shore and depth. In Early Toarcian oxytomids from the more clayey parts of the section—*Meleagrinella (Clathrolima) substriata* (Muenster), *Meleagrinella (Meleagrinella) prima* Lutikov—the ribbing coefficient is higher than that of the described taxon. The width of the interrib spaces is correlated with the thickness of the ribs and the degree of ribbing. The ISW/RW coefficient for specimens from the Markha River sections, Anabar Bay, and Tenkelyakh Site varies from 0.53 to 1.64. The taxon is characterized by narrow interrib spaces and wide radial ribs. In the holotype of "*Praearctotis vai*", the ISW/RW coefficient is 1.03. In this characteristic value, these specimens are similar. In some specimens from the type locality of the species "*Praearctotis vai*", the interrib spaces on the molds are moderately wide, the ISW/RW coefficient is 2.14,

Table 5. Dimensions in mm and ratios

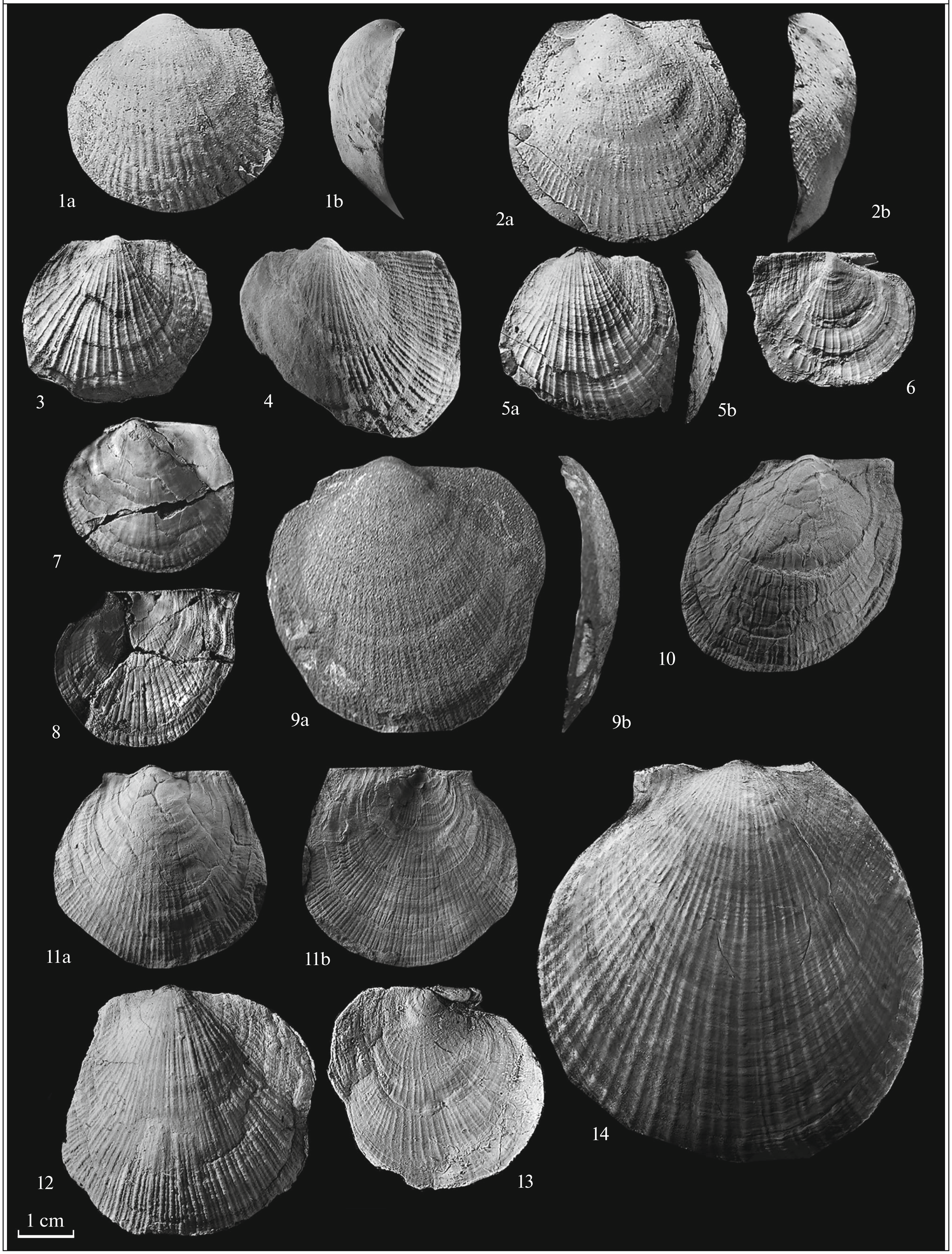
Coll. no., valve	Locality	VL	VH	VH/VL	Cv	Cv/VH	ADL	ADL/VL	AOL	AOL/ADL	AWgAg	R	R/VL	ISW/RW	AWgW/AWgL
MH-216/1 l	Motorchuna River, Outcrop 4, Bed 2, Upper Toarcian	32.81	31.5	0.96	8.0	0.25	14.52	0.44	6.35	0.44	146°	26	0.79	2.02	0.16
MH-216/2 r	The same	30.69	24.6	0.80	2.0	0.08	15.5	0.50	8.3	0.54	115°	25	0.81	3.28	0.20
TR-19/1 l	Eastern Taimyr, Outcrop 5, Bed 3, Lower Jurassic, Upper Toarcian	34.71	30.6	0.88	–	–	17.02	0.49	9.10	0.53	136°	25	0.72	4.79	0.22
f-113/1 l	Eastern Taimyr, Outcrop 5, Bed 5, sample no. f-113, Lower Jurassic, Upper Toarcian	40.00	–	–	–	–	–	–	–	–	115°	–	–	1.14	–
AG-114/1 l	Anabar Bay, western coast, Outcrop 5, Bed 89, Upper Toarcian	31.28	28.4	0.91	–	–	13.25	0.42	6.27	0.47	112°	40	1.28	1.24	0.16
AG-114/2 r	The same	33.95	29.0	0.93	–	–	13.0	0.42	5.88	0.45	–	40	1.28	–	–
no.14/653, holotype	Vilyui River, Outcrop 54, Sample 1953, Upper Toarcian, VNIGRI museum, coll. T.I. Kirina	42.96	41.6	0.97	12.54	0.30	18.84	0.44	10.20	0.54	131°	40	0.93	2.03	0.20

which is probably explained by the lower density of radial ribs on the internal cores. Presumably, the state of the feature depends on the physical properties of the soil. In the described taxon, which lived on clayey-silty soils, the interrib spaces are narrow.

The left valve is strongly convex or inflated. The Cv/VH coefficient varies from 0.31 to 0.47. The convexity of the left valves in taxa belonging to the phyletic lineage of the genus *Arctotis* varies. In addition to the described taxon, strongly convex or inflated left valves are characteristic of the shells of the Bajocian-Bathonian *Arctotis (Arctotis) lenaensis* (Lahuzen) and the Volgian *Arctotis (Canadarctotis) intermedia* (Bodylevsky). Presumably, forms that live under conditions of strong wave action have a highly convex or inflated shell. Weak ribbing density and a highly convex left valve are specific to species-rank taxa living in near-shore shallow-water environments.

Plate XIV. Fig. 1. *Arctotis (Praearctotis) marchaensis* (Petrova), specimen no. 20/653 (holotype "*Arctotis viluiensis*" Velikzhanina), VNIGRI museum, coll. of T.I. Kirina, left valve of a mature specimen, (a) shell exterior, ×1, (b) lateral view from the anterior margin, ×1; Vilyui River, Outcrop 54–56, Sample 1394, Upper Toarcian. Figs. 2–8. *Arctotis (Praearctotis) similis* Velikzhanina, (2) holotype, specimen no. 14/653, VNIGRI museum, coll. of T.I. Kirina, left valve of a mature specimen, (a) shell exterior, ×1, (b) lateral view from the anterior margin, ×1; Vilyui River, Outcrop 54, Sample 1953, Upper Toarcian; (3) specimen no. TR-19/1, external view of a left valve of a mature specimen, ×1; Eastern Taimyr, Cape Tsvetkov, Outcrop 5, Bed 3, Sample TF-19, Lower Jurassic, Upper Toarcian; (4) specimen no. f-113/1, external view of a left valve of a mature specimen, ×1; Eastern Taimyr, Cape Tsvetkov, Outcrop 5, Bed 5, Sample f-113, Lower Jurassic, Upper Toarcian, coll. of A.N. Aleynikov; (5) specimen no. MH-216/1, (a) external view of a left valve of a mature specimen, ×1, (b) lateral view of the left valve, ×1; Motorchuna River, Outcrop 4, Bed 2, Lower Jurassic, Upper Toarcian; (6) specimen no. MH-216/2, external view of the right valve of a mature specimen, ×1; the same locality, the same age; (7) specimen no. AG-114/1, external view of a mold of the left valve of a mature specimen, ×1; Anabar Bay, western coast, Outcrop 5, Bed 89; Middle Jurassic, Upper Toarcian; (8) specimen no. AG-114/2, imprint of the right valve of a mature specimen, ×1, the same locality. Figs. 9–14. *Arctotis (Arctotis) tabagensis* (Petrova), (9) holotype, specimen no. 602/5393, mold of a left valve of a mature specimen, (a) shell exterior, ×1, (b) lateral view from the anterior margin, ×1; Lena River, Tabaginskiy Cape (Verkhniy Kangallassky Kamen),Middle Jurassic, Aalenian; F.N. Chernyshev TsNIGR Museum (St. Petersburg); (10) specimen no. TF-26/1, mold of a left valve of a mature specimen, shell exterior, ×1; Eastern Taimyr, Cape Tsvetkov, Outcrop 5, Bed 8, Sample TF-26, Middle Jurassic, Lower Aalenian; (11) specimen no. 82 f/1, (a) mold of a left valve of a mature specimen, ×1; (b) internal imprint of the same valve, ×1; Eastern Taimyr, Cape Tsvetkov, Outcrop 7/1, Bed 3, top, Sample 82f, Middle Jurassic, Lower Aalenian, collected by A.N. Aleynikov; (12) specimen no. AG-116/1, external view of a left valve of a mature specimen, ×1, Anabar Bay, western coast, Outcrop 5, Bed 92, Middle Jurassic, Lower Aalenian; (13) specimen no. AG-116/2, external view of the right valve of a mature specimen, ×1, the same locality; (14) specimen TX-160-36-26/1, view of a mold of a left valve of a mature specimen, ×1, Tenkelyakh Site, line 160, Borehole 36, depth 26 m.

Plate XIV



The anterior outer ligament of the left valve is short. The AOL/ADL coefficient varies between 0.35–0.41. The anterior wing of the left valve is narrow. Coefficient AWgW/AWgL from 0.09 to 0.20. The anterior wing is obtuse-angled. The anterior wing angle of the left valve (AWgAg) varies from 121° to 144°. A short outer ligament, a narrow anterior wing and an obtuse angle of the anterior wing of the left valve characterize the "paraboloid" type of the anterior wing. The "paraboloid" type is specific to the Late Toarcian species group and to the taxon being described.

Comparison. In its shell outline, symmetry, and the angle of the anterior left wing, the species is closest to the holotype of *Arctotis (Praearctotis) similis* Velikzhanina, 1966 (Velikzhanina, 1966, pp. 90–92, Pl. II, fig. 9). It is distinguished by a narrower anterior wing, a short anterior outer ligament of the left valve, an angular subtype of the ligament pit, and narrower interrib spaces.

Remarks. Based on the anterior wing type, an angular subtype of the ligament area in the holotype of *Praearctotis marchaensis* from the Upper Toarcian of the Lena–Vilyui region (Markha River) (*Atlas*..., 1947, p. 123, pl. XII, fig. 14; this work, Pl. II, fig. 1) and the holotype of *"Pseudomonotis (Eumorphotis) vai* Bodylevsky*"* from the Upper Toarcian of the Nordvik Region (Yurung-Tumus Peninsula) (*Atlas*..., 1947, p. 124, pl. XII, fig. 20; this work, pl. XIII, fig. 11) belong to the same taxonomic group. Bodylevsky's species was previously assigned to the subgenus *Arctotis (Praearctotis)* (Lutikov and Shurygin, 2010). Since the size and width of the interrib spaces on the left valve are variable in samples and are not species-specific, *"Arctotis (Praearctotis) vai"* is considered in this paper as a junior synonym of *Arctotis (Praearctotis) marchaensis*.

According to the type of anterior wing, the left-valve convexity, the holotype *Arctotis* (*Praearctotis*) *marchaensis* from the Upper Toarcian of the Lena–Vilyui region (Markha River) and the holotype "*Arctotis viluiensis*" from the Upper Toarcian of the Lena–Vilyui region (Vilyui River) (Velikzhanina, 1966, pp. 89–90, pl. III, fig. 1, and this work, pl. XIV, fig. 1, belong to the same group. Velikhanina's species was previously considered an independent species by Lutikov and Shurygin (2010). Due to the similarity in the values of convexity and anterior outer ligament length in the left leave in the holotypes of the species describe dby G.T. Petrova and L.S. Velikzhanina, "*Arctotis viluensis*" is considered a junior synonym for *Arctotis* (*Praearctotis*) *marchaensis*.

The species *Meleagrinella buschinskii* is known from the Lena-Vilyui region (Markha River) (Koshelkina, 1963, p. 38, Pl. II, fig. 3). The type collection of G.I. Bushinsky, including the holotype, comes from ferruginous sandstones of the Suntary Formation with *Arctotis (Praearctotis) marchaensis*. Based on the type of the anterior wing, the outlines of the valves, convexity and sculpture, the view is Z.V. Koshelkina is close to *Arctotis (Praearctotis) marchaensis* and, obviously, is its junior synonym.

Geological age and geographical distribution. Lower Jurassic, Upper Toarcian, Western and Eastern Siberia, Northeastern Russia.

Arctotis (Praearctotis) similis Velikzhanina, 1966

Plate XIV, figs. 1–8

Pseudomonotis aff. *elegans*: Pchelintsev, 1933, p. 47, pl. III, text-fig. 45.

Arctotis similis Velikzhanina: Velikzhanina, 1966, p. 89, pl. II, figs. 9–10 (only).

Arctotis viluiensis Velikzhanina: Velikzhanina, 1966, p. 89, pl. III, figs. 7 (only).

Meleagrinella cf. *echinata* (Smith): Wierzbowski et al., 1981, p. 219, pl. 8, figs. 6–8.

Arctotis (Praearctotis) viluiensis: Lutikov and Shurygin, 2010, pl. I, fig. 8; pl. II, fig. 4; pl. III, figs. 23–26.

Praearctotis viluiensis: Lutikov et al., 2010, pl. I, fig. 12.

Arctotis (Arctotis) tabagensis: Lutikov and Shurygin, 2010, pl. IV, figs. 1–2.

Arctotis (Arctotis) viluiensis: Lutikov and Shurygin, 2010, pl. III, figs. 23–26.

Arctotis (Arctotis) similis: Lutikov, 2021, pl. III, fig. 2–8.

Holotype: specimen no. 14/653, left valve, VNIGRI Museum, St. Petersburg, collection of T.I. Kirina (1961). Illustrated: Velikzhanina, 1966, pl. II, fig. 9; here, pl. XIV, fig. 2; Eastern Siberia, Vilyui River. Lower Jurassic, Upper Toarcian.

Material. About 10 left and right well-preserved valves from the upper member of the Korotkiy Formation (Member 18) of the Cape Tsvetkov section (East-

→

Plate XV. Figs. 1, 2. *Arctotis (Arctotis) sublaevis* (Bodylevsky), (1) specimen no. AN-18/1, left valve of a mature specimen, (a) shell exterior ×1, (b) lateral view from the anterior margin, Anabar River, Outcrop 3, Bed 8, Sample 18, Arangastakh Formation, Middle Jurassic, condensed bed at the base of the formation, Upper Aalenian–Lower Bajocian (?); (2) holotype, specimen no. 123/238, left valve of a mature specimen, (a) shell exterior, ×1, (b) lateral view from the anterior margin, Nordvik Peninsula, Borehole 1-p, depth 92.5 m, Upper Aalenian–Lower Bajocian (?), Mining Museum of St. Petersburg Mining University, monographic collection of V.I. Bodylevsky "Jurassic and Lower Cretaceous faunas of the lower reaches of the Yenisei." Figs. 3–5. *Arctotis (Arctotis) lenaensis* (Lahuzen), (3) holotype, specimen no. 5/10942, adult specimen, (a) external view of the left valve, (b) external view of the right valve, (c) lateral view from the posterior margin, ×1; Lena River, Tongus-Apata Creek; Horongho Formation, Middle Jurassic, Upper Bajocian–Bathonian; F.N. Chernyshev TsNIGR Museum (St. Petersburg); (4) type specimen no. 6/1094, external view of a mold of the valve of a mature specimen, ×1, the same locality; (5) type specimen no. 5/509, (a) external view of the mold of the left valve of a mature specimen, (b) lateral view of the mold of the left valve, ×1, Lena River, Tongus-Apata Creek; Horongho Formation, Middle Jurassic, Upper Bajocian–Bathonian; Mining Museum of St. Petersburg Mining University, collection of A.L. Chekanovsky "Duplicates to the original material of I.I. Lagusen to the paper "Die Inoceramen-Schichten an dem Olenek und der Lena".

Plate XV

ern Taimyr); five left valves, two right valves, several molds and imprints of left and right valves from shell rocks of the Horgo Formation of Anabar Bay section; about 10 well-preserved left and right valves from the upper part of the Suntary Formation on the Motorchuna River; type collection of "*Arctotis similis*" from the Suntary Formation of the Vilyui River section by T.I. Kirina.

Diagnosis. Shell commonly medium-sized. Anterior wing of "trapezoid" type. Anterior wing obtuse-angled, moderately wide. Anterior outer ligament of the left valve is long or very long. Left valve moderately convex, right valve flat. Radial ribs of two orders in number from 25 to 40, interrib spaces commonly very wide. Posterior wing of the left valve with up to 16 thin radial ribs. Ligament area of the left valve strongly inclined to midsagittal plane. Spoon-shaped subtype of ligament pit. Spoon-shaped depression occupies most of ligament pit. Ligament area of right valve long.

Dimensions in mm and ratios: See Table 5.

Variability. The left valves in specimens from the Motorchuna River, Cape Tsvetkov (Eastern Taimyr) and Anabar Bay sections are small or medium-sized. The height of the left valve varies from 28.4 to 31.5 mm.

The contours of the left valves are variable: from very low to equal in size. The VH/VL coefficient varies from 0.88 to 0.96. In specimens from the Vilyui River section (collection of T.I. Kirina), the VH/VL coefficient is 0.99. The symmetry of the left valve is variable: from moderately inequilateral to equilateral. The ADL/VL coefficient varies from 0.42 to 0.49.

The left valves of specimens from the Motorchuna River and Vilyui River, Cape Tsvetkov sections (middle part of the Korotkiy Formation) are sparsely ribbed. The ribbing ratio (R/VL) varies from 0.72 to 0.99. In specimens from Anabar Bay section (Horgo Formation) (Pl. III, figs. 7, 8), the ribbing density is higher—up to 1.28. Interrib spaces in specimens from the Motorchuna River, Cape Tsvetkov and Vilyui River sections are moderately wide to very wide. The ISW/RW ratio varies from 2.02 to 4.79. In specimens from Anabar Bay section (Horgo Formation) and one specimen from the Cape Tsvetkov section (upper part of the Korotkiy Formation) (Pl. III, fig. 4), the interrib spaces are narrow, the ISW/RW coefficient varies from 1.14 to 1.24. In terms of the density of ribs and the width of interrib spaces, specimens from Anabar Bay section and a specimen from the upper member of the Korotkiy Formation of the Cape Tsvetkov section are close to *Arctotis (Arctotis) tabagensis* but differ in the anterior wing type. Probably, with further research, these forms will be separated within the same phylogenetic line, as a taxon occupying an intermediate position between *Arctotis (Praearctotis) similis* and *Arctotis (Arctotis) tabagensis*.

The left valve is moderately convex. The convexity coefficient (Cv/VH) was measured in only one specimen and is 0.25.

The anterior outer ligament of the left valve is long. The AOL/ADL coefficient varies between 0.44–0.54. The anterior wing of the left valve varies from narrow to moderately wide. The coefficient AWgW/AWgL varies from 0.16 to 0.22. The anterior wing is obtuse-angled. The anterior wing angle of the left valve (AWgAg) varies between 112°–146°.

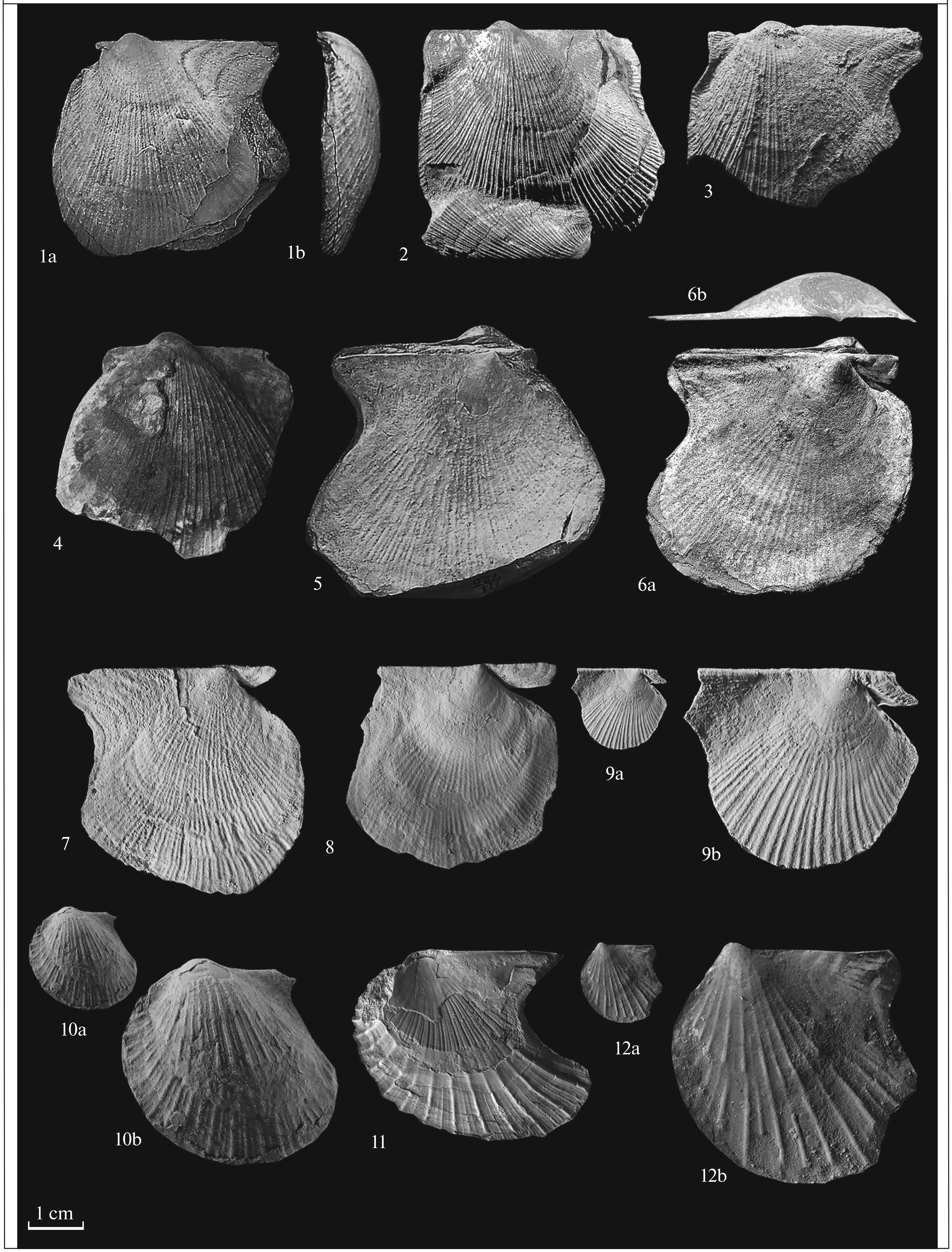
A long outer ligament, narrow or moderately wide anterior wing, and an obtuse angle of the anterior wing of the left valve characterize the "trapezoid" type of the anterior wing. The "trapezoid" type is specific only to the described taxon.

Comparison. Based on the spoon-shaped subtype of the ligament pit of the right valve and the convexity of the left valve, the described species is most close to *Arctotis (Arctotis) tabagensis* (Petrova, 1953 in Krymgholz et al., 1953, pp. 89–90, pl. IV, figs. 6–7). It is distinguished by a longer ligament platform of the

→

Plate XVI. Figs. 1–9. *Oxytoma (Oxytoma) kirinae* Velikzhanina, (1) holotype, specimen no. 4/720, left valve of a mature specimen, (a) shell exterior, ×1, (b) lateral view from the anterior margin; Markha River, Lower Jurassic, Lower–Upper Toarcian, collected by T.I. Kirina, 1960, core storage facility of the Aprelevsky branch of VNIGNI; (2) specimen no. MX-207v/1, left valve of a mature specimen, ×1; Markha River, Outcrop 5 (after Knyazev et al., 1991), Bed 5; Lower Jurassic, Lower–Upper Toarcian, collected by V.G. Knyazev; (3) specimen no. TX-870-535/1, external view of the left valve of a mature specimen, ×1; line 870, Borehole 535, depth 18 m, Sample 1, Suntary Formation, fourth member, Lower Jurassic, Lower–Upper Toarcian; (4) specimen no. MX-506/1, external view of the left valve of a mature specimen, ×1; Markha River, sample no. 506, scree of Outcrop 13 (after Knyazev et al., 1991), Suntary Formation, Lower Jurassic, Lower–Upper Toarcian; (5) type specimen no. 6/720, right valve of a mature specimen, external view, ×1, Markha River, Lower–Upper Toarcian, collected by T.I. Kirina, 1960, core storage facility of the Aprelevsky branch of VNIGNI; (6) specimen no. MX-228/1, (a) view from the right valve of a mature specimen, ×1, (b) upper view, ×1; Markha River, Outcrop 6, Bed 3, Sample 228; Upper Toarcian, collected by V.G. Knyazev; (7) specimen no. TX-870-505/1-4, external view of the right valve of a mature specimen, ×1; Tenkelyakh Site, line 870, Borehole 505, depth 9 m, sample no. 505/1, Suntary Formation, third member, Lower Jurassic, Lower–Upper Toarcian; (8) specimen no. TX-870-505/1-1, external view of the right valve of a mature specimen, ×1; the same age and locality; (9) specimen no. TX-870-505/1-3, (a) external view of the right valve of a mature specimen, ×1; (b) the same, ×2.5. Fig. 10. *Oxytoma (Oxytoma)* ex gr. *kirinae* Velikzhanina, specimen no. TF-15-1/6, (a) left valve of an adult specimen, ×1; (b) the same, ×2; Eastern Taimyr, Cape Tsvetkov, Outcrop 4, Bed 18, level 2.0 m from the base of the bed, Sample TF-15/1. Fig. 11. *Oxytoma (Oxytoma) startense* Polubotko, specimen no. CA-34/1, view of the left valve of a mature specimen, ×1; Saturn River, Outcrop 1, Bed 18, base, Sample 34, Lower Jurassic, Upper Toarcian, Pseudolioceras compactile Zone. Fig. 12. *Oxytoma (Oxytoma)* aff. *startense* Polubotko, specimen no. K-1015/1, left valve af an adult specimen, (a) shell exterior, ×1; (b) the same, ×2, Kelimyar River, Outcrop 5, Bed 4, Sample 1015; Kelimyar Formation, Lower Jurassic, Upper Toarcian, Pseudolioceras compactile Zone.

Plate XVI



right valve, an obtuse-angled anterior wing, and wide interrib spaces. It differs from *Arctotis frenguellii* (Damborenea, 1987, pl. 6, figs. 7–8; Damborenea et al., 2013, p. 124, fig. 6.1p) from the Toarcian-Aalenian of Argentina in a narrower anterior wing (in the Argentine species AWgW /AWgL = 0.26), with significantly fewer ribs.

Remarks. L.S. Velikzhanina, when describing the *Arctotis similis*, chose as a holotype the specimen represented by the left valve (Velikzhanina, 1966, Pl. II, fig. 9), originating from the Toarcian-Aalenian boundary beds (Suntary Formation) of the Vilyui River. The left valves of our specimens from the upper parts of the Toarcian of the Zhigansk, Lena-Anabar and East Taimyr regions belong to this species based on the similarity with the holotype in the outline of the anterior wing.

From a member of sands and ferruginous sandstones with a thin conglomerate at the base, located in the upper part of the Suntary Formation of the Vilyui River section, L.S. Velikzhanina recorded *Arctotis similis* Velikzh. (Velikzhanina, 1966, p. 89, Pl. II, figs. 9–11) and *A. viluiensis* Velikzh. (Velikzhanina, 1966, p. 89, Pl. III, figs. 1–7). The holotype of *Arctotis similis* comes from Outcrop 54 on the Vilyui River. The of "*Arctotis viluiensis*" is recorded from outcrops 54–56 on the Vilyui River (Velikzhanina, 1966; Kirina, 1966). Previously, both species were considered as synonyms (Lutikov and Shurygin, 2010). When studying the original collection of T.I. Kirina, stored in the VNIGRI museum, it was established that the holotype *Arctotis similis* has a moderately convex left valve, very long anterior outer ligament (Pl. XIV, fig. 2). In the holotype of "*Arctotis viluiensis*" the left valve is strongly convex, the anterior outer ligament is short (Pl. XIV, fig. 1).

According to the description, L.S. Velikzhanina considered the differences in sculpture to be the main difference between these two species: in "*A. viluiensis*" ribs of the first order are very strong, distinct, almost three times thinner than the wide interrib spaces in which the ribs of the second order are located. According to this feature, some of our specimens from the sections of Eastern Taimyr and Motorchuna River (Pl. XIV, figs. 3, 5) are close to the specimen "*Arctotis viluiensis*" from the Markha River (Velikzhanina, 1966, Pl. III, fig. 7). Another differing character in these species was considered to be the wavy growth wrinkles characteristic of *Arctotis similis*. Based on this character, all our specimens from the Korotkiy Formation of Eastern Taimyr, the Horgo Formation of Anabar Bay and the Suntary Formation of the Motorchuna River (Pl. XIV, figs. 3–8) are close to *Arctotis similis* in the description of Velikzhanina (1966, Pl. II, figs. 9–11). In some specimens from the section of Eastern Taimyr, originating from the upper half of Unit 18, the sculpture is represented by a large number of radial ribs (Pl. XIV, fig. 4). In the section of Anabar Bay in the Horgo Formation there are specimens with frequently spaced ribs (Pl. XIV, figs. 7, 8). These specimens have narrow interrib spaces and were tentatively classified as *Arctotis tabagensis* (Lutikov and Shurygin, 2010, pl. IV, figs. 1–2). Since the degree of ribbing may depend on facies, this feature is not considered species specific. In terms of anterior wing type, *Arctotis similis* occupies an intermediate position between the Late Toarcian species *Arctotis marchaensis* with a narrow wing and the Aalenian species *Arctotis tabagensis* with a wide anterior wing. All morphological varieties with an obtuse-angled and moderately wide anterior wing of the left valve, a long or very long anterior outer ligament are classified as *Arctotis (Praearctotis) similis* Velikzh. The species "*Arctotis viliuensis*" (Velikzhanina, 1966) is included in the synonymy of *Arctotis (Praearctotis) marchaensis* (*Atlas*..., 1947). Based on the presence of a weakly expressed protuberance on the left valve, established on specimens from the Suntary Formation of the Motorchuna River section (Pl. VI, fig. 5) and the Korotkiy Formation of the Cape Tsvetkov section, the species *Arctotis similis* should be attributed to subgenus *Praearctotis*.

Plate XVII. Figs. 1–7. *Oxytoma (Oxytoma) jacksoni* (Pompeckj), (1) specimen no. K-187/1, left valve of a mature specimen; (a) shell exterior, (b) lateral view, (c) upper view, ×1; Kelimyar River, Locality 5, scree; Lower Jurassic, Upper Toarcian; (2) specimen no. K-1084/1, left valve of a mature specimen, ×1; Kelimyar River, Outcrop 16, Sample 1084; Lower Jurassic, Upper Toarcian; (3) specimen no. K-1084/2, external view of the left valve of a mature specimen, ×1; the same locality; (4) specimen no. K-1084/3, external view of the right valve of a mature specimen, ×1; the same locality; (5) specimen no. 12/234, type specimen *Oxytoma kelimiarensis* Bodylevsky (Bodylevsky and Glazunova, 1968, pl. 41, fig. 2), left valve of a mature specimen, ×1; Kelimyar River; Lower Jurassic, Upper Toarcian; Mining Museum of St. Petersburg Mining University, collection "New Aalenian and Neocomian *Oxytoma* of the Olenek River basin and the Russian Platform" (St. Petersburg); (6) specimen no. 81f/2, mold of the right valve of a mature specimen with remains of the shell layer, ×1; Eastern Taimyr, Cape Tsvetkov, Outcrop 7/1, Bed 3, VII concretionary horizon, Sample 81f; Upper Toarcian–Lower Aalenian (?), coll. by A.N. Aleynikov; (7) specimen no. AG-111/1, mold of a left valve of a mature specimen with remains of shell layer, ×1; Anabar Bay, western coast, Outcrop 5, Bed 80, Sample 111, level 2.9 m; Lower Jurassic, Upper Toarcian, Arctotis marchaensis Oxyto-Zone. Fig. 8, specimen no. AG-115/1, (a) external view of the left valve of a juvenile specimen, ×1; (b) the same, ×4; Anabar Bay, western coast, Outcrop 5, Bed 90, Sample 115; Lower Jurassic, Upper Toarcian, Pseudolioceras falcodiscus Zone. Figs. 9–11. *Oxytoma* ex gr. *jacksoni* (Pompeckj), (9) specimen no. Sa-39/1, (a) left valve of an adult specimen, ×1, (b) the same, ×3; Saturn River, Bed 19, level 1.0 m, Sample 39, Lower Jurassic, Upper Toarcian, Pseudolioceras falcodiscus Zone; (10) specimen no. Sa-39/2, (a) left valve of a subadult specimen, ×1, (b) the same, ×5; the same locality; (11) specimen no. Sa-39/3, (a) left valve of a subadult specimen, ×1, (b) the same, ×5; the same locality.

Plate XVII

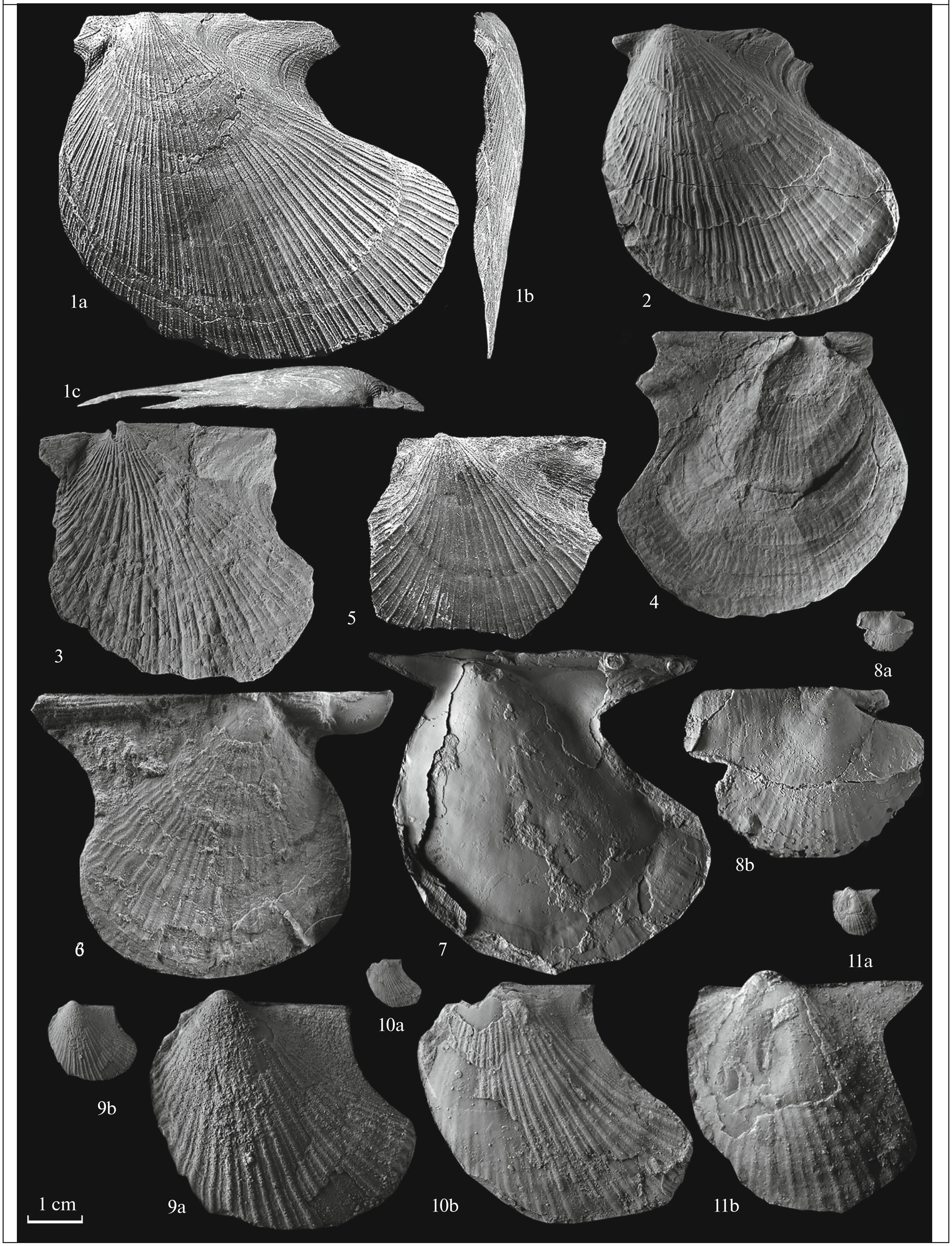


Table 6. Dimensions in mm and ratios

Coll. no., valve	Locality	VL	VH	VH/VL	Cv	Cv/VH	ADL	ADL/VL	AOL	AOL/ADL	AWgAg	R	R/VL	ISW/RW	AWgW/AWgL
602/5393 l holotype	Lena River, Upper Tabaginskiycliff, Lower Aalenian	49.50	48.85	0.98	–	–	22.42	0.45	–	–	97°	60	1.28	–	–
AG-116/1 l	Anabar Bay, west coast, Outcrop 5, Bed 92, base, Sample 116, Lower Aalenian	46.14	47.8	1.04	–	–	19.68	0.43	12.62	0.64	96°	68	1.47	1.14	0.26
AG-116/2 r	The same	40.49	38.2	0.94	–	–	21.91	0.54	10.20	0.47	–	38	0.94	1.20	–
TX/160/36 -26/1 l	Tenkelyakh Site, line 160, Borehole 36, depth 26.0 m, Lower Aalenian	–	73.2	–	–	–	36.37	–	19.43	0.53	90°	46	–	1.25	0.23
f/82-26/1 l mold	Eastern Taimyr, Outcrop7/1, Bed 3, Sample 82, Lower Aalenian	38.62	36.8	0.95	–	–	17.82	0.46	9.02	0.51	89°	63	1.63	1.05	0.20
f/82-26/2 l imprint	The same	38.87	–	–	–	–	–	–	–	–	89°	72	1.85	1.22	0.24

Geological age and geographical distribution. Lower Jurassic, Upper Toarcian, Pseudolioceras falcodiscus Zone. Upper Toarcian Eastern Siberia, Spitsbergen, Russian Far East, Caucasus.

Subgenus *Arctotis* s.str.

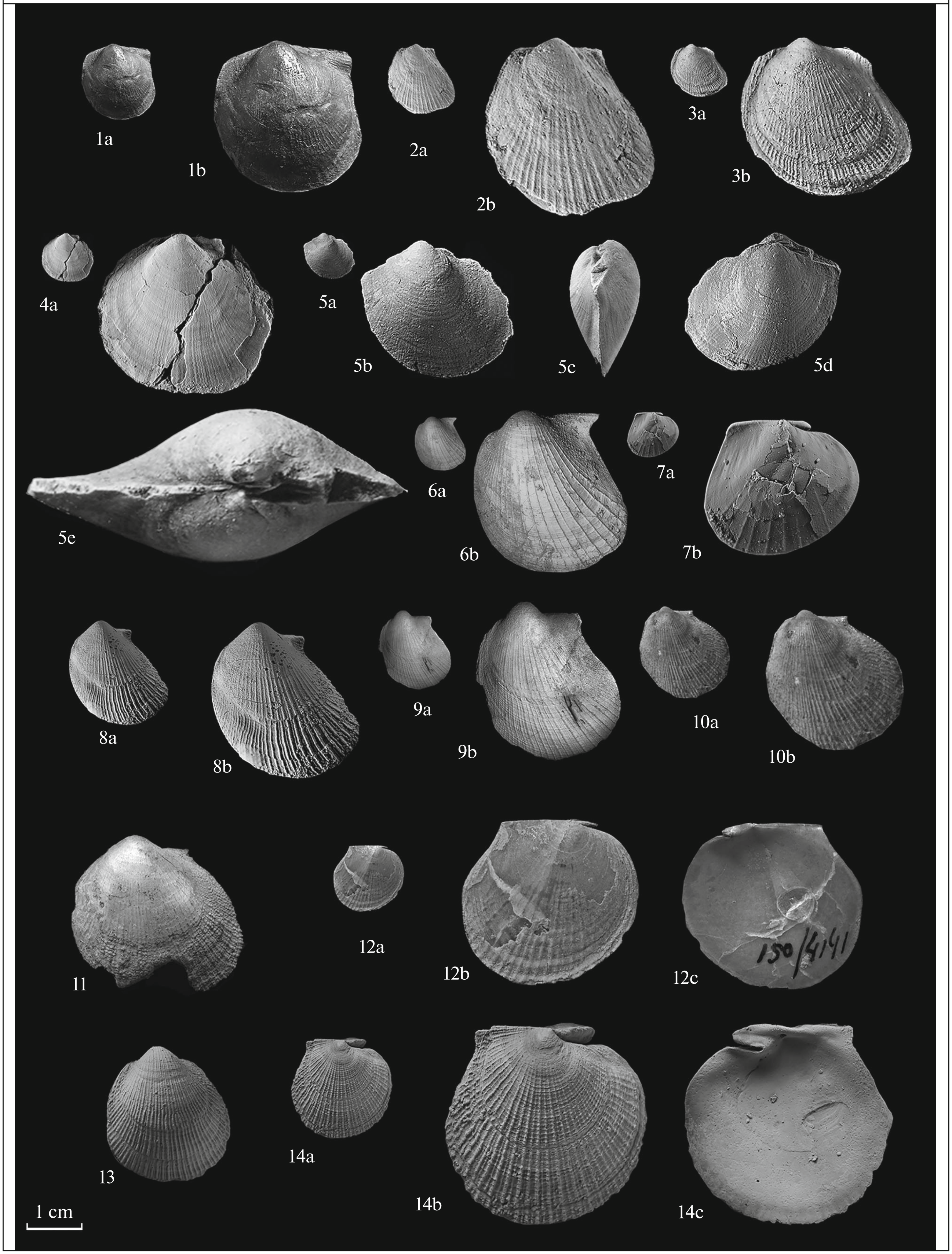
Type species. *Hinnites lenaensis* (Lahusen, 1886). Upper Bajocian–Lower Bathonian of Eastern Siberia.

Diagnosis. Shell equilateral from medium to very large sizes equilateral from medium to very large sizes. The sculpture is represented by radial ribs of three orders and growth co-centers. Byssal ear crescent-shaped. Spoon-shaped subtype of the ligament pit. Hinge margin short. The resilifer twice as wide as the ligament platform. Protuberance absent.

Description. The ligament area of the left valve is located at an angle of about 35° to the midsagittal plane of the shell. The pseudoligamentous platform of the left valve is not developed, the protuberance is absent. The shell is thick-walled, medium to very large, round or high, inequivalve. The left valve is highly convex or inflated, the right valve is flat or con-

Plate XVIII. Fig. 1. *Eumorphotis (Asoella) boehmi* (Korchinskaya), specimen no. 31/1187, type specimen, external view of a mold of the left valve, ×1, (b) the same, ×2; Sample 9B-13-12; Spitsbergen, Nadezhda Island, Wyche Bay, Upper Triassic, Norian; TsNIGR Museum, St. Petersburg (collection of M.V. Korchinskaya). Figs. 2, 3. *Meleagrinella (Praemeleagrinella) subolifex* Polubotko, (2) specimen no. AG-63/2, (a) external view of the left valve, ×1; (b) the same, ×3; Anabar Bay, Outcrop 5, Bed 20; Lower Jurassic, Hettangian; (3) specimen no. KR-119/44, (a) view from the left valve; (b) the same, ×3; Kyra River-Khos-Terytekh, Outcrop 3, Bed 1; Lower Jurassic, Hettangian. Figs. 4, 5. *Praebuchia? faminaestriata* (Polubotko), (4) specimen no. SA-39/2, (a) external view of the left valve, ×1, (b) the same, ×3; Saturn River, Outcrop 1, Bed 19, Lower Jurassic, Upper Toarcian; (5) specimen no. SA-39/1, (a) external view of a mold of the left valve, ×1; (b) the same, ×3; (c) view of the mold from the anterior margin, ×3; (d) external view of a mold of the right valve, ×3; (e) view of a mold from hinge line, ×7.5; the same locality. Fig. 6, 7. *Meleagrinella (Meleagrinella) doneziana* (Borissjak), (6) specimen no. PB-95/3, (a) external view of the right valve; ×1; (b) the same, ×3; Saratov Trans-Volga, Perelyubsky District, Borehole 103, depth 214 m, sample no. PB-95, Middle Jurassic, Upper Bajocian; (7) specimen no. MK- 142/1, (a) external view of the right valve; ×1; (b) the same, ×3; Mangyshlak Peninsula; Chom-Tarym, Sample 142; Middle Jurassic, Upper Bajocian (collection of Yu.S. Repin). Fig. 8. *Meleagrinella (Clarthrolima) braamburiensis* (Phillips), specimen no. MK-152/4, (a) external view of the left valve; ×1; (b) the same, ×1.5; Mangyshlak Peninsula; Sample 3431; Upper Jurassic, Middle Callovian (collected by L.F. Romanov, collection of Yu.S. Repin). Fig. 9. *Meleagrinella (Meleagrinella)* sp., specimen no. PZ/1-1, (a) external view of the left valve; ×1; (b) the same, ×2; Middle Jurassic, Lower Bathonian, Pletnevsky stone quarry, Penza Region (coll. by A.P. Ippolitov). Fig. 10. *Meleagrinella (Meleagrinella) curta* (Whitfield), holotype, specimen no. 29319, (a) external view of the left valve; ×1; (b) the same, ×1.5; South Dakota; Upper Jurassic, Oxfordian; National Museum of Natural History, Smithsonian Institution (USA, Washington). Figs. 11, 12. *Meleagrinella (Clarthrolima) subovalis* Zakharov, (11) specimen no. 150/5252, external view of the left valve, ×1; Levaya Boyarka River, Upper Jurassic, Lower Kimmeridgian, collection of V.A. Zakharov, Center for Collective Use "Collection GEOKHRON", INGG SO RAN (Novosibirsk); (12) specimen no. 150/4141, (a) external view of the right valve; ×1; (b) the same, ×2.5; (c) internal view of the right valve, ×2.5, the same locality. Figs. 13, 14. *Arctotis (Canadotis) canadensis* (Jeletzky et Poulton), (13) specimen no. AZh-2, external view of the left valve, ×1; Northern Taimyr, Anzhelika–Pakhra interfluve, Lower Volga Substage, collections by G.V. Schneider; (14) specimen AZh-4, (a) external view of the right valve, ×1; (b) the same, ×2; (c) internal view of the right valve, ×2.

Plate XVIII


1a
1b
2a
2b
3a
3b
4a
5a
5b
5c
5d
5e
6a
6b
7a
7b
8a
8b
9a
9b
10a
10b
11
12a
12b
150/4141
12c
13
14a
14b
14c
1 cm

cave. The anterior auricle of the left valve is rectangular or obtuse-angled, the posterior auricle is rectangular at the juvenile and subadult stages, obtuse-angled at the adult stage. The byssal ear of the right valve is crescent-shaped, with a rounded base, gaping or overgrown. byssal furrow is open or closed. The posterior wing of the right valve has the shape of an obtuse triangle at the juvenile stage and has an S-shaped bend of the posterior margin at the adult stages, clearly separated from the valve by a depression. The sculpture consists of radial ribs of two or three orders, strongly weakened on the right valve, and concentric growth lines are also clearly visible.

Comparison. It differs from *Canadotis* in the absence of protuberance and a less developed pseudoligamentous platform. It differs from *Canadarctotis* by a smaller slope of the ligament area and a less developed pseudoligamentous area.

Species composition. The nominative subgenus includes the Aalenian *Eumorphotis tabagensis* (Krymgholz et al., 1953); Aalenian-Bajocian *Pseudomonotis lenaensis* var. *sublaevls* (Bodylevsky and Shulgina, 1958), *Arctotis gradiformis* (Velikzhanina, 1966); Bajocian-Bathonian *Arctotis tolmatchevi* (Koshelkina, 1960), Bathonian *Hinnites lenaensis* (Lahusen, 1886).

Remarks. From the Aalenian-Bathonian deposits, mainly two species are recorded—*Arctotis lenaensis* (Lahusen) and Arctotis *sublaevis* (Bodylevsky) (*Stratigrafiya*..., 1976). I.I. Laguzen made the first description of the species *lenaensis* from the collections of A.L. Chekanovsky from siltstones and sandstones of the Horongho Formation in the lower reaches of the Lena River (Lahusen, 1886). Studying *arctotis* from the Nordvik region, V.I. Bodylevsky concluded that the massive distribution of morphological varieties of the *lenaensis* group in the North of Siberia belongs to Aalenian (Bodylevsky and Shulgina, 1958). In accordance with the modern scheme of comparison of the standard ammonite scale of the Middle Jurassic of Western Europe and the standard Boreal ammonite scale (Morton et al., 2020), the Horong Formation based on finds of ammonites *Cranocephalites* spp. (Kirina et al., 1978) should belong to the Upper Bajocian, therefore, V.I. Bodylevsky's interpretation of the stratigraphic position of the species *lenaensis* goes beyond the actual stratigraphic position of the species suggested in the original description by I.I. Lahusen.

Occurrence. Aalenian—Bathonian of Eastern Siberia, Northeastern Russia.

Arctotis (Arctotis) tabagensis (Petrova, 1953)

Plate XIV, figs. 9–14

Eumorphotis tabagensis Petrova: Krymgholz et al., 1953, pp. 89–90, pl. IV, figs. 6–7.

Arctotis (Arctotis) tabagensis: Lutikov and Shurygin, 2010, pl. IV, figs. 3–7.

Arctotis (Arctotis) tabagensis: Lutikov, 2021, pl. III, figs. 9–14.

Holotype. F.N. Tchernyshev TsNIGR Museum, St. Petersburg, specimen no. 602/5393, mold of the left valve, collection of Ivanov (1925). Illustrated: Krymgholz et al., 1953, pl. IV, fig. 6; here, Pl. III, fig. 9; Eastern Siberia, Lena River, Tabaginsky cliff. Middle Jurassic, Lower Aalenian.

Material. About a dozen whole shells and several molds of left valves from the Kystatym Formation of the Syungyude and Molodo river sections, right valve and an imprint of the left valve from siltstones of the Syungyude Formation of the Motorchuna River section; about 10 shells from the lower Arangastakh Formation of Anabar Bay, about 15 molds from the Aprelevsky Formation of Eastern Taimyr, type collection of G.T. Petrov from the Suntary Formation from the Lena River, housed in the TsNIGR museum.

Diagnosis. Shell from medium-sized to very large. Anterior wing type "hyperboloid". Anterior wing subrectangular and wide. Anterior outer ligament of the left valve very long. Left valve moderately convex, right valve flat. Radial ribs of three orders in number from 50 to 60, interrib spaces very narrow. Posterior wing of the left valve covered with up to 20 radial ribs. Ligament area of the left valve strongly inclined to midsagittal plane. Spoon-shaped subtype of ligament area of right valve. Spoon-shaped depression completely occupies the ligament fossa. Ligament area of the right valve short.

Dimensions in mm and ratios: See Table 6.

Variability. The dimensions of the left valves of the studied specimens from sections of the Lena River, Anabar Bay and Cape Tsvetkov are predominantly small or medium-sized, ranging from 30.0–50.0 mm. Some specimens from boreholes from the Tenkelyakh Site (Pl. XIV, fig. 14) are very large in size—more than 70.0 mm. Perhaps only some specimens reached large sizes, their height exceeding the limits of the range of variability of this trait. The forms from the Tenkelyakh Site boreholes are close in size to the Aalenian-Bajocian taxon *Arctotis (Arctotis) sublaevis* but differ in the anterior wing type. Perhaps, with further research, these forms will be isolated within the same phylogenetic line, as a taxon occupying an intermediate position between *Arctotis (Praearctotis) similis* and *Arctotis (Arctotis) sublaevis*.

The contours of the left valves are variable: from very low to high. The VH/VL coefficient varies from 0.95 to 1.04.

With respect to the axis of symmetry, the left valve is variable: from moderately inequilateral to equilateral. The ADL/VL coefficient varies from 0.43 to 0.46.

The left valves are slightly ribbed. The ribbing coefficient (R/VL) varies from 1.28 to 1.85.

This taxon is characterized by the appearance of intercalating ribs of the third order in the spaces between the ribs of the second order over the entire surface of the shell. Interrib spaces in specimens from sections of the Lena River, Cape Tsvetkov and Tenke-

Table 7. Dimensions in mm and ratios

Coll. no., valve	Locality	VL	VH	VH/VL	Cv	Cv/VL	ADL	ADL/VL	AOL	AOL/ADL	AWgAg°	R	R/VL	ISW/RW	AWgW/AWgL
Oxytoma (*Oxytoma*) *jacksoni*															
K-187/1 l	Kelimyar River, loc. 5, scree, Sample 187, Upper Toarcian	73.91	63.97	0.87	9.61	0.15	16.81	0.22	–	–	28.3	87	1.18	1.88	–
AG-116/1 l	Anabar Bay, western coast, Outcrop 5, Bed 80, 2.9 m from base, Sample 111, Upper Toarcian	62.1	60.5	0.97	–	–	17.9	0.29	22.18	1.24	29.2?	–	–	–	1.61
Oxytoma (*Oxytoma*) ex gr. *jacksoni*															
Sa-39/1	Saturn River, Bed 19, level 1.0 m, Sample 39, Upper Toarcian, Pseudolioceras falcodiscus Zone	16.47	14.82	0.90	–	–	4.57	0.28	–	–	–	38	2.31	1.29	–
Oxytoma (*Oxytoma*) *kirinae*															
Holotype 4/720 l	Markha River, Lower–Upper Toarcian, coll. T.I. Kirina, 1960	43.65	41.5	0.95	12.11	0.29	15.03	0.34	–	–	–	50 ?	1.14 ?	–	–
MX-207v/1 l	Markha River, Outcrop 5 (after Knyazev et al., 1991), Bed 5; Lower–Upper Toarcian, coll. V.G. Knyazev	45.51	39.88	0.88	–	–	15.62	0.34	13.08	0.84	118.0	78	1.71	1.51	0.37
Oxytoma (*Oxytoma*) *startense*															
CA-34/1 l	Saturn River, Outcrop 1, Bed 18, base, Sample 34, Upper Toarcian, Pseudolioceras compactile Zone	44.28	35.39	0.80	–	–	13.55?	0.31	–	–	–	57	1.29	–	–

lyakh section are very narrow. ISW/RW ratio varies from 1.05 to 1.25.

The left valve is moderately convex. The convexity coefficient (Cv/VH) was measured in only one specimen and is 0.26.

The anterior outer ligament of the left valve is very long. The AOL/ADL coefficient varies within 0.51–0.64. The anterior wing of the left valve is wide. The coefficient AWgW/AWgL varies from 0.20 to 0.26. The anterior wing is subrectangular. The anterior wing angle of the left valve (AWgAg) varies within 89°–104°.

A very long outer ligament, a wide anterior wing, and a subrectangular anterior wing of the left valve characterize the "hyperboloid" type of the anterior wing. The "hyperboloid" type is specific only to the taxon under description.

Comparison. The described species differs from *Arctotis (Arctotis) sublaevis* (Pl. XV, figs. 1, 2) from the Upper Aalenian and Lower Bajocian of the Nordvik, Zhigansk, Lena-Anabar and Eastern Taimyr regions in the subrectangular anterior wing of the left valve at all stages of growth (in the species *sublaevis* anterior wing at the later stages of growth is obtuse-angled), a flat right valve (in the species *sublaevis* right valve it is concave), an open byssal furrow at all age stages (in the species *sublaevis* the byssal furrow is closed at the later stages of growth in large shells). It differs from *Arctotis frenguellii* (Damborenea et al., 2013, p. 124, text-fig. 6.1p) from the Toarcian-Aalenian deposits of Argentina in the hyperboloid anterior wing type of the left valve (in the Argentine species there is a trapezoid anterior wing type).

It differs from *Arctotis (Arctotis) lenaensis* (Pl. XV, figs. 3–5) from the Upper Bajocian and Lower Bathonian of the Zhigansk region in having a smaller convex left valve and a flat right valve (in the species *lenaensis* the right valve is concave).

Remarks. The holotype of *Arctotis tabagensis* (Petrova, 1953 in Krymgholz et al., 1953) is represented by the mold of the left valve and comes from the Aalenian Yakut Formation (Pl. XIV, fig. 9). Based on the subrectangular shape of the anterior wing, our specimens from the Aalenian of Anabar Bay (Pl. XIV, fig. 12) and Eastern Taimyr (Pl. XIV, figs. 10, 11) are identical to the holotype.

Geological age and geographical distribution. Aalenian Stage, lower substage, Pseudolioceras maclintocki Zone, Western Siberia, Eastern Siberia: Anabar Bay, Eastern Taimyr, Lena, Molodo, Motorchuna, Vilyui, Markha, and Tyung river basins.

Genus Oxytoma Meek, 1864

Oxytoma: Meek, Hayden, 1864, p. 80.

Type species. *Avicula muensteri* Goldfuss, 1835; Middle Jurassic, Aalenian, Germany.

Remarks. F. Meek (Meek and Hayden, 1864) originally attributed the authorship of the species *Avicula muensteri* to G.G. Bronn, who gave the taxon its original name, but since G.G. Bronn did not describe this taxon (Bronn, 1829), G.A. Goldfuss should be considered as he was the first to describe and figured *Avicula muensteri* (Goldfuss, 1835, p. 131).

Diagnosis. Shell strongly inequilateral from small to very large. Sculpture of radial ribs of three to four orders and growth centers. Subrectangular type of ligament pit; oblique subtype of ligament pit; straight subtype of lower margin of ligament pit; falcate byssal ear; open byssal furrow at all age stages; protuberance absent; byssal notch wide gaping; ligament area equal to or longer than the length of left valve.

Remarks. No revision has been undertaken. The composition of the genus is given in accordance with the family system proposed by Nevesskaja et al. (2013). The genus includes the following subgenera: *Oxytoma* s.s. (Middle Triassic–Upper Cretaceous, Maastrichtian), *Palmoxytoma* L. Cox, 1962 (Lower Jurassic, Hettangian–Pliensbachian), *Hypoxytoma* Ichikawa, 1958 (Lower–Upper Cretaceous), *Boreioxytoma* Zakharov, 1966 (Upper Jurassic, Volgian).

Occurrence. Middle Triassic, Ladinian–Upper Cretaceous, Maastrichtian.

***Oxytoma (Oxytoma) jacksoni* (Pompeckj, 1899)**

Plate XVII, figs. 1–10

Pseudomonotis jacksoni Pompeckj: Pompeckj, 1899, p. 60–62, text-fig. 9, pl. IV, figs. 13–14, 16.

Oxytoma jacksoni: Frebold, 1958, pl. VI, figs. 1–3.

Oxytoma kelimiarensis Bodylevsky: Bodylevsky and Glazunova, 1968, pl. 41, fig. 2.

Oxytoma ex gr. *jacksoni*: Lutikov et al., 2022, Pl. II, figs. 1–3.

Holotype. Holotype not designated. Hypotypes of the left and right valves are illustrated by Frebold (1958, figs. 1–2). Canadian Arctic, Middle Jurassic, Lower Aalenian.

Material. About 50 complete shells and individual valves from the Kelimyar Formation of the Kelimyar River section; 1 mold of the left valve from the top of the Eren Formation of Anabar Bay, one right valve of a juvenile specimen from the Horongho Formation of Anabar Bay, two left and two right valves from the Korotkiy Formation of the Cape Tsvetkov section of Eastern Taimyr, two left valves from the Start Formation of the Saturn River section, collection "New Aalenian and Neocomian *Oxytoma* of the Olenek River basin and the Russian Platform", housed in the Mining Museum of the St. Petersburg Mining University (St. Petersburg).

Diagnosis. The shell is medium to very large in size. The anterior auricle of the left valve is subtriangular, the anterior margin of the auricle and the hinge line form an acute angle, the left valve is slightly convex. The byssal ear in adult specimens is falcate, in juvenile specimens it is rhomboid.

Dimensions in mm and ratios: See Table 7.

Variability. The length of the byssal ear relative to the length of the anterior part of the right valve varies within one sample from not protruding beyond the anterior end of the valve to protruding beyond the anterior end of the valve.

Comparison. The described species differs from *Oxytoma (Oxytoma) kirinae* from the Lower–Upper Toarcian of the Suntary region (Pl. XVI, figs. 1–9) in the slightly convex left valve (in the species *kirinae* the left valve is moderately convex), the acute angular outlines of the anterior auricle of the left valve (in the species *kirinae* anterior ear obtuse-angled).

It differs from *Oxytoma (Oxytoma) startense* from the Upper Toarcian (*Pseudolioceras compactile* Zone) of the Levy Kedon stratigraphic region (Pl. XVI, fig. 11) by straight ribs on the entire surface of the left valve (in the species *startense* the ribs are fan-shaped).

Remarks. V.I. Bodylevsky, when comparing *Oxytoma kelimiarensis* Bodylevsky (Bodylevsky and Glazunova, 1968, pl. 41, fig. 2), the type specimens of which were described by him from the Kelimyar River section, with the species *Oxytoma jacksoni* in the description of G. Frebold on material originating from Canada, considered the greater number of ribs in the Siberian species to be a differentiating character. However, an image of a complete specimen from Cameron Island shows more than 80 ribs on the surface of the left valve and more than 20 ribs on the posterior auricle (Frebold, 1958, pl. VI, fig. 1). Based on this characteristic, our large specimens from Kelimyar River (Pl. XVII, figs. 1–3) and specimen of Bodylevsky (Pl. XVII, fig. 4), having 60–87 ribs on the left valves, do not differ significantly from the Canadian specimens. Bodylevsky, when comparing his species with *Oxytoma jacksoni* in the description of I. Pompeckj based on materials from Franz Josef Land, considered a significantly less wide ligament area as a differentiating character. According to this character, our large specimens from the Kelimyar River (Pl. VII, fig. 3), with a wide ligament area, do not differ significantly from the specimens of I. Pompeckj. The obliquity of the shell in oxytomids is a highly variable character; comparison on this basis is possible only in large samples. Hence, Bodylevsky's species is identical to *Oxytoma (Oxytoma) jacksoni* and is its junior synonym.

Specimens classified as *Oxytoma (Oxytoma)* ex gr. *jacksoni* from the Upper Toarcian (Pseudolioceras falcodiscus Zone) of the Levy Kedon stratigraphic region, based on the outlines of the left valve and sculpture they are close to *Oxytoma (Oxytoma) jacksoni* of the Lena-Anabar structural-facies zone, but differ in smaller sizes (Pl. XVII, figs. 9–11). Beds with Oxytoma (Oxytoma) ex gr. jacksoni in the Saturn River section have a higher stratigraphic position (Pseudolioceras wuerttenbergeri–Pseudolioceras falcodiscus zones) than the Beds with Oxytoma (Oxytoma) startense (Pseudolioceras compactile Zone). Presumably *Oxytoma (Oxytoma)* ex gr. *jacksoni* and *Oxytoma (Oxytoma) jacksoni* belong to the same evolutionary lineage.

Geological age and geographical distribution. Upper Toarcian–Lower Aalenian, Eastern Siberia: Eastern Taimyr, basins of the Kelimyar, Molodo, Motorchuna rivers; Northeastern Russia: Levy Kedon, Viliga rivers. Lower Aalenian of the Canadian Arctic; Aalenian? Of Franz Joseph Lands.

FUNDING

This work was supported by ongoing institutional funding. No additional grants to carry out or direct thisparticular research were obtained.

CONFLICT OF INTEREST

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

Reviewer V.A. Zakharov

REFERENCES

Aberchan, M., Early Jurassic Bivalvia of western Canada. Part I. Subclasses Palaeotaxodonta, Pteriomorphia and Isofilibranchia, *Beringeria*, 1998, vol. 21, pp. 57–150.

Arkell, W.J., *A monograph of British Corallian Lamellibranchia*, *Palaeontogr. Soc. Monogr. (London)*, 1933, pp. 181–228.

Arp, G. and Gropengiesser, S., The Monotis–Dactylioceras Bed in the Posidonienschiefer Formation (Toarcian, southern Germany): condensed section, tempestite, or tsunami-generated deposit? *Paläontol. Z.*, 2016, vol. 90, pp. 271–286.

Atlas mezozoiskoi morskoi fauny Dal'nego Vostoka Rossii (Atlas of Mesozoic Marine Fauna of the Far East of Russia), Sey, I.I., Okuneva, T.M., Zonova, T.D., Kalacheva, E.D., and Yazykova, E.A., Eds., St. Petersburg: Vseross. Nauchno-Issled. Geol. Inst., 2004 [in Russian].

Atlas rukovodyashchikh form iskopaemykh faun SSSR. T. 8. Nizhnii i srednii otdely yurskoi sistemy (Atlas of Index Forms of Fossil Faunas of the USSR. Vol. 8: Lower and Middle Jurassic), Moscow–Leningrad: Gosgeolizdat, 1947 [in Russian].

Atlas triasovoi fauny i flory Severo-Vostoka SSSR (Atlas of Triassic Flora and Fauna of the Northeastern USSR), Moscow: Nedra, 1976 [in Russian].

Belousov, L.V., *Biologicheskii morfogenez* (Biological Morphogenesis), Moscow: Mosk. Gos. Univ, 1987 [in Russian].

Bodylevsky, V.I., A new Late Jurassic representative of Aviculopectinidae in Taimyr, in *Novye vidy drevnikh rastenii i bespozvonochnykh SSSR. Ch. 2* (New Species of Fossil Plants and Invertebrates of the USSR. Pt. 2), Moscow: Gosgeoltekhizdat, 1960, pp. 44–45.

Bodylevsky, V.I. and Glazunova, A.E., New Aalenian and Neocomian oksitomy from the Olenek River basin and the Russian Platform, in *Novye vidy drevnikh rastenii i bespozvonochnykh SSSR. Vyp. II. Ch. 1* (New Species of Fossil Plants and Invertebrates of the USSR. Vol. II, Pt. 1), Moscow: Nauka, 1968, pp. 183–186.

Bodylevskii, V.I. and Shul'gina, N.I., *Yurskie i melovye fauny nizov'ev Eniseya* (Jurassic and Cretaceus Faunas of the Lower Yenisei Region), Moscow: Gosgeoltekhizdat, 1958 [in Russian].

Borissiak, A.A., About *Pseudomonotis* (*Eumorphotis*) lenaensis Lah. (=Hinnites lenaensis Lah.), *Trudy Geol. Muzeya im. Petra Velikogo Imper. Akad. Nauk*, 1914, vol. VIII, pp. 141–153.

Borissiak, A.A., *Pelecypoda Yurskikh otlozhenii Evropeiskoi Rossii. Vyp. IV. Aviculidae* (Pelecypodes from Jurassic Deposits of European Russia. Vol. IV. Aviculidae), St. Petersburg: Izd. Geol. Kom., 1909, vol. 26.

Bronn, H.G., Verzeichnis der in dem Heidelberger Mineralien-Komptoir vorhandenen Konchylien-, Pflanzentheir und andern Versteinerungen, *Zeit. Mineral.*, 1829, vol. 1, pp. 72–80.

Bronn, H.G., *Lethaea Geognostica, oder Abbildungen und Beschreibungen der für die Gebirgs-Formationen bezeichnendsten Versteinerungen*, Stuttgart, 1837, vol. 1

Calow, P., *Evolutionary Principles*, Glasgow: Chapman and Hall, 1986.

Carter, J.G., Altaba, C.R., Anderson, L.C., Araujo, R., Biakov, A.S., Bogan, A.E., Campbell, D.C., Campbell, M., Chen, J., Cope, J.C.W., Delvene, G., Dijkstra, H.h., Fang, Z., Gardner, R.N., Gavrilova, V.A., Goncharova, I.A., Harries, P.J., Hartman, J.H., Hautmann, M., Hoeh, W.R., Hylleberg, J., Jiang, B., Johnston, P., Kirkendale, L., Kleemann, K., Koppka, J., Kříž, J., Machado, D., Malchus, N., Márquez-Aliaga, A., Masse, J.-P., McRoberts, C.A., Middelfart, P.U., Mitchell, S., Nevesskaja, L.A., Özer, S., Pojeta, J.Jr., Polubotko, I.V., Pons, J.M., Popov, S., Sánchez, T., Sartori, A.F., Scott, R.W., Sey, I.I., Signorelli, J.H., Silantiev, V.V., Skelton, P.W., Steuber, T., Waterhouse, J.B., Wingard, G.L., and Yancey, T., Synoptical Classification of the Bivalvia (Mollusca), *Paleontol. Contrib.*, 2011, Art. 4.

Caswell, B.A., Coe, A.L., and Cohen, A.S., New range data for marine invertebrate species across the early Toarcian (Early Jurassic) mass extinction, *J. Geol. Soc.*, 2009, vol. 166, no. 5, pp. 859–872.

Chen Jin-hua and Chen Chu-zhen, Jianchuania, A new genus of Bivalvia from the Upper Triassic in Yunnan, *Acta Polaeontol. Sinica*, 1980, vol. 19, no. 1, pp. 57–59.

Conrad, T.A., Description of new fossil shells of the United States, *J. Acad. Nat. Sci. Phil.*, 1853. Pt. 3, 2nd ser., vol. 2, pp. 273–274.

Cossman, M., Description de quelques Pélécypodes jurassiques recueillis en France, in *Association Française pour l'Avancement des Sciences. Congrès de Reims*, 1908, pp. 292–305.

Cox, L.R., Notes on Jurassic Lamellibranchia. VII. On the identity of Echinois Marwick with Melleagrinella Whitfield, *Proc. Malacalog. Soc. London*, 1941, vol. 24, pp. 133–135.

Cox, L.R., New genera and subgenera of Mesozoic bivalvia, *Palaeontology*, 1961, vol. 4, no. 4, pp. 592–598.

Crame, J.A., New Late Jurassic oxytomid bivalves from the Antarctic Peninsula region, *British Antarctic Surv. Bull.*, 1985, no. 69, pp. 35–55.

Crame, J.A., Pirrie, D., Crampton, J.P., and Duante, A.M., Stratigraphy and regional significance of the Upper Jurassic–Lower Cretaceous Byers Group, Livingston Island, Antarctica, *J. Geol. Soc. London*, 1993, vol. 50, pp. 1075–1087.

Dagys, A.S. and Kurushin, N.I., Triassic brachiopods and bivalves in the north of Central Siberia, in *Tr. IGiG SO AN SSSR. Vyp. 633* (Trans. Inst. Geol. Geophys. Sib. Fil. USSR Acad. Sci. Vol. 633), Moscow: Nauka, 1985.

Damborenea, S.E., Early Jurassic Bivalvia of Argentina. Part 2: Superfamilies Pteriacea, Buchiacea and part of Pectinacea, Palaeontogr. Abt. A, 1987, pp. 113–216.

Damborenea, S.E., Echevarria, J., and Ros-Franch, S., *Southern Hemisphere Palaeobiogeography of Triassic-Jurassic Marine Bivalves*, Dordrecht, Heidelberg, New York, London: Springer, 2013.

Darwin, Ch., *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, London, 1872.

Devyatov, V.P., Nikitenko B.L., and Shurygin B.N., Jurassic paleogeography of Siberia at the stages of major rearrangements, *News Paleontol. Stratigr. Suppl. Russ. Geol. Geophys.,* 2011, vol. 52, nos. 16–17, pp. 87–101.

Duff, K.L., *Bivalvia from the English Lower Oxford Clay (Middle Jurassic)*, London: Palaeontogr. Soc., 1978.

Dumortier, E., *Etudes Paleontologiques sur les Depots Jurassiques du Bassin du Rhone. Troisième Partie (Lias Moyen)*, Paris: F. Savy, 1869.

Frebold, H., Fauna, age and correlation of the Jurassic rocks of Prince Patrick Island, *Bull. Geol. Surv. Canada*, 1958, no. 41.

Goldfuss, G.A., Petrefacta Germaniae tam ea, quae in museo universitatis regiae Borussicae Friedericiae Wilhelminae Rhenanae servantur quam alia quaecunque in museis Hoeninghusiano Muensteriano aliisque extant, iconibus et descriptionibus illustrata, in *Abbildungen und Beschreibungen der Petrefacten Deutschlands und der Angränzenden Länder unter Mitwirkung des Herrn Grafen Georg zu Münster*, Dusseldorf, 1835, vol. 2, pp. 69–140.

Hall, J., Letter from Professor James Hall, of New York, containing observations on the geology and paleontology of the country traversed by the expedition, and notes upon some of the fossils collected on the route, in *Exploration and Survey of the Valley of the Great Salt Lake of Utah, Including a Reconnaissance of a New Route through the Rocky Mountains, by Howard Stansbury*, 1852, Appendix E, pp. 398–414.

Hayami, I., Lower Liassic lamellibranch fauna of the Higashinagano formation in west Japan, *J. Fac. Sci. Univ. Tokyo. Ser. 2*, 1959, vol. 12, Pt. 1, pp. 31–84.

Hayami, I., Pelecypods from the Liassic Yamaoku Formation in West Japan. Studies on the Liassic Pelecypods in Japan, in *Trans. Proc. Paleontol. Soc. Japan. New Ser. Palaeontol. Soc. Japan*, 1961, vol. 1961, no. 43, pp. 113–116.

Hesselbo, S.P. and Pienkowski, G., Stepwise atmospheric carbon-isotope excursion during the Toarcian oceanic anoxic event (Early Jurassic, Polish Basin), *Earth Planet. Sci. Lett.*, 2011, vol. 301, nos. 1–2, pp. 365–372.

Hodges, P., The Early Jurassic Bivalvia from the Hettangian and lower Sinemurian of south-west Britain. Part 4, *Monogr. Palaeontogr. Soc. London*, 2022, vol. 176, no. 662, pp. 145–330.

Hoffmann, K. and Martin, G., Die Zone des Dactylioceras tenuicostatum (Toarcien, Lias) in NW und SW-Deutschland, *Paläontol. Z., Stuttgart*, 1960, vol. 34, pp. 103–149.

Ichikawa, K., Zur Taxionomie und Phylogenie der Triadischen "Pteriidae" (Lamellibranchia). Mit besonderer Berucksichtigung der Gattungen Claraia, Eumorphotis, Oxytoma und Monotis, *Palaeontographica A*, 1958, vol. 111, nos. 5/6, pp. 131–212.

International Code of Zoological Nomenclature, London: Int. Trust for Zool. Nomenclature, Nat. Hist. Mus., 1999.

Ivanov, E., Note on *Pseudomonotis doneziana* Boriss. from the Jurassic of the Ural Region, *Tr. Geol. Kom.*, 1915, vol. 34, no. 2, pp. 271–288.

Jackson, R.T., Phylogeny of the Pelecypoda: the Aviculidae and their allies, *Boston Soc. Nat. Hist., Mem. Boston Soc. Nat. Hist.*, 1890, vol. 4, pp. 277–400.

Jeletzky, J.A. and Poulton, T.P., A new genus and subgenus and two new species of latest Jurassic oxytomid bivalves from Arctic Canada, *Can. J. Earth Sci.*, 1987, no. 24, pp. 711–722.

Kirina, T.I., Stratigraphy of Lower Jurassic deposits of western part of the Vilyui syneclise, in *Tr. VNIGRI. Vyp. 249* (Trans. All-Russ. Petrol. Res. Explor. Inst. Vol. 249), Leningrad: Nedra, 1966, pp. 18–71.

Kirina, T.I., Mesezhnikov, M.S., and Repin, Yu.S., About new local subdivisions in the Jurassic of Western Yakutia, in *Novye dannye po stratigrafii i faune yury i mela Sibiri* (New Data on Jurassic and Cretaceous Stratigraphy and Fauna of Siberia), Novosibirsk: Sib. Otd. Akad. Nauk SSSR, 1978, pp. 70–85.

Knyazev, V.G., Devyatov, V.P., and Shurygin, B.N., *Stratigrafiya i paleogeografiya rannei yury vostoka Sibirskoi platformy* (Lower Jurassic Stratigraphy and Paleogeography of the East Siberian Platform), Yakutsk: Yakutsk. Nauchn. Tsentr Sib. Otd. Ross. Akad. Nauk, 1991 [in Russian].

Knyazev, V.G., Kutygin, R.V., Devyatov, V.P., Nikitenko, B.L., and Shurygin, B.N., *Zonal'nyi standart toarskogo yarusa Severo-Vostoka Azii* (The Zonal Standard of the Toarcian Stage of the Northeastern Asia), Yakutsk: Izd. Sib. Otd. Ross. Akad. Nauk, 2003 [in Russian].

Korchinskaya, M.V., Early Norian Fauna of the Archipelago of Svalbard, in *Geologiya osadochnogo chekhla arkhipelaga Sval'bard* (Geology of the Sedimentary Cover of the Archipelago of Svalbard), Leningrad: Nauchno-Issled. Inst. Geol. Arktiki, 1980, pp. 30–43.

Koshelkina, Z.V., New Middle Jurassic *Arctotis* species of Northern Siberia, in *Novye vidy drevnikh rastenii i bespozvonochnykh SSSR. Ch. 2* (New Species of Fossil Plants and Invertebrates of the USSR. Pt. 2), Moscow: Gosgeoltekhizdat, 1960, pp. 46–47.

Koshelkina, Z.V., Stratigraphy and bivalves of the Jurassic deposits of the Vilyui Syneclise and Cis-Verkhoyansk Foredeep, in *Tr. SVKNII* (Trans. Shilo North-East Interdisciplinary Sci. Res. Inst. FEB RAS), 1963, vol. 5.

Krassilov, V.A., Evolutionary biology, Vol. 6, *Paleontol. Zh.*, 1976, no. 2, pp. 140–142.

Krassilov, V.A., *Evolyutsiya i biostratigrafiya* (Evolution and Biostratigraphy), Moscow: Nauka, 1977 [in Russian].

Krymgol'ts, G.Ya., *Materialy po stratigrafii morskoi yury r. Burei* (Materials on Stratigraphy of Marine Jurassic in the Bureya River Basin), Leningrad–Moscow: TsNIGRI, 1939 [in Russian].

Krymgol'ts, G.Ya., Petrova, G.T., and Pchelintsev, V.F., *Stratigrafiya i fauna morskikh mezozoiskikh otlozhenii Severnoi Sibiri* (Stratigraphy and Fauna of the Marine Mesozoic Deposits of North Siberia), Leningrad: Glavsevmorput', 1953 [in Russian].

Lahuzen, I., *Fauna from Jurassic deposits of the Ryazan Province*, *Tr. Geol. Kom.*, 1883, vol. 1.

Lahusen, I., Die Inoceramen—Schichten an dem Olenek und der Lena, *Mém. Acad. St.-Petérsb. VII Sér.*, 1886, vol. 33, no. 7, pp. 1–13.

Logan, A., A new species of Cyrtorostra (Bivalvia) from the Permian of the Canadian Arctic, *J. Paleontol.*, 1970, vol. 44, no. 5, pp. 867–871.

Lutikov, O.A., Biochronological scale of the Upper Toarcian–Lower Aalenian of Eastern Siberia by bivalve mollusks of the genus *Arctotis* Bodylevsky, 1960, *Stratigr. Geol. Correl.*, 2021, vol. 29, no. 6, pp. 680–709. https://doi.org/10.31857/S0869592X21060065

Lutikov, O.A., Stratigraphy of Toarcian deposits of Eastern Siberia and Northeastern Russia based on bivalve mollusks (family Oxytomidae Ichikawa, 1958), Part I. A brief outline of the development of views on the zonal stratigraphy of Northeast Asia, the history of studying oxytomides, materials and methods of fossil research, *Stratigr. Geol. Correl.*, 2024, vol. 32, no. 7 (in press).

Lutikov, O.A. and Arp, G., Revision of *Monotis substriata* (Münster, 1831) and new species of bivalve in the Lower Toarcian in northern Russia and southern Germany (family Oxytomidae Ichikawa, 1958), in *Yurskaya sistema Rossii: problemy stratigrafii i paleogeografii. Mater. VIII Vseross. Soveshch. s mezh. uchastiem. Onlain-konf., 7–10 sentyabrya 2020 g.* (Proc. VIII All-Russ. Online Conf. with Int. Participation "Jurassic System of Russia: Problems of Stratigraphy and Paleogeography" (Online-Conf., September 7–10, 2020)), Zakharov, V.A., Ed., Syktyvkar: Inst. Geol. Komi NTs Ural. Otd. Ross. Akad. Nauk, 2020, pp. 126–131.

Lutikov, O.A. and Arp, G., Taxonomy and biostratigraphic significance of bivalves of the genus *Meleagrinella* Whitfild, 1885, *Stratigr. Geol. Correl.*, 2023a, vol. 31, no. 1, pp. 1–33.

Lutikov, O.A. and Arp, G., A Boreal Toarcian biochronological zonation based on bivalve mollusks of the genus *Meleagrinella* Whitfield, 1885, *Stratigr. Geol. Correl.*, 2023b, vol. 31, no. 2, pp. 49–70.

Lutikov, O.A. and Shurygin, B.N., New data on the systematics of the Jurassic and Cretaceous bivalves of the family Oxytomidae Ichikawa, 1958, *News Paleontol. Stratigr.*, 2010, vol. 14, pp. 111–140.

Lutikov, O.A., Temkin, I.E., and Shurygin, B.N., Phylogeny and evolution of ontogeny of some representatives of the family Oxytomidae Ichikawa, 1958 (Mollusca: Bivalvia), in *Yurskaya sistema Rossii: problemy stratigrafii i paleogeografii. Tret'e Vseross. soveshch.* (Jurassic System of Russia: Problems of Stratigraphy and Paleogeography. Proc. 3rd All-Russ. Conf.), Saratov: Izd. Tsentr "Nauka", 2009, pp. 122–125.

Lutikov, O.A., Temkin, I.E., and Shurygin, B.N., Phylogeny and evolution of ontogeny of the family Oxytomidae Ichikawa, 1958 (Mollusca: Bivalvia), *Stratigr. Geol. Correl.*, 2010, vol. 18, no. 4, pp. 376–391.

Lutikov, O.A., Shurygin, B.N., Sapjanik, V.V., Aleinikov, A.N., and Alifirov, A.S., New data on stratigraphy of the Jurassic (Pliensbachian–Aalenian) sediments of the Cape Tsvetkov Region, Eastern Taimyr, *Stratigr. Geol. Correl.*, 2021, vol. 29, no. 6, pp. 655–679.
https://doi.org/10.31857/S0869592X22010033

Mayr, E., *Principles of Systematic Zoology*, New York: McGraw-Hill, 1969.

Martindale, R.C. and Aberhan, M., Response of macrobenthic communities to the Toarcian Oceanic Anoxic Event in northeastern Panthalassa (Ya Ha Tinda, Alberta, Canada), *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 2017, vol. 478, pp. 103–120.

Marwick, J., Some new genera of the Myalinidae and Peteriidae of New Zealand, *Trans. Proc. N. Z. R. Soc.*, 1935, pp. 295–303.

McLearn, F.H., New pelecypods from the Fernie Formation of the Albert Jurassic, *Trans. R. Soc. Canada. Ser. 3*, 1924, vol. 18, Pt. 4, pp. 39–61.

Meek, F.B. and Hayden, F.V., Descriptions of new organic remains from the Tertiary, Cretaceous, and Jurassic rocks of Nebraska, *Proc. Acad. Nat. Sci. Philadelphia*, 1860.

Meek, F.B. and Hayden, F.V., Palaeontology of the upper Missouri: Invertebrates, *Smithsonian Contributions to Knowledge*, 1864, vol. 14, no. 192, Art. 5 (172).

Meyen, S.V., Principles and methods of paleontological systematics, in *Sovremennaya paleontologiya. Metody, napravleniya, problemy, prakticheskoe prilozhenie: Spravochnoe posobie: V 2-kh tomakh* (Modern Paleontology: Methods, Directions, Problems, Practical Application. Reference Manual, in 2 vols.), Menner, V.V. and Makridin, V.P., Eds., Moscow: Nedra, 1988, vol. 1, pp. 447–466.

Meyen, S.V., *Vvedenie v teoriyu stratigrafii* (Introduction to the Theory of Stratigraphy), Moscow.: Nauka, 1989 [in Russian].

Mojsisovics, E., Arktische Triasfaunen, *Mem. Acad. Imp. Sci. St-Petersb. Ser. 7*, 1886, vol. 33, no. 6, pp. 1–154.

Morris, N.J., Knight, R.I., Little, C.S., and Atkinson, J.W., Mollusca—Bivalves. Fossils from the Lias of the Yorkshire Coast, *Palaeontol. Assoc. Field Guide to Fossils*, 2019, no. 15, pp. 105–157.

Morton, N., Mitta, V.V., and Underhill, J.R., Ammonite occurrences in North Sea cores: Implications for Jurassic Arctic–Mediterranean marine seaway connectivity, *Scottish J. Geol.*, 2020, vol. 56, no. 2, pp. 175–195.

Münster, G., Uber das geognostische Vorkommen einiger zu Monotis gehorenden Versteinerungen, *Jahrb. Mineral., Geognos., Geol. Petrefakt.*, Heidelberg, 1831, pp. 403–408.

Muscente, A.D., Martindale, R.C., Schiffbauer, J.D., Creighton, A.L.A., and Bogan, B.A., Taphonomy of the Lower Jurassic Konservat-Lagerstätte at Ya Ha Tinda (Alberta, Canada) and its significance for exceptional fossil preservation during oceanic anoxic events, *Palaios*, 2019, vol. 34, pp. 515–541.

Nevesskaya, L.A., Popov, S.V., Goncharova, I.A., Guzhov, A.V., Yanin, B.T., Polubotko, I.V., Biakov, A.S., and Gavrilova, V.A., Phanerozoic bivalves of Russia and adjacent countries, in *Tr. PIN RAN* (Trans. Paleontol. Inst. Russ. Acad. Sci.), 2013, vol. 294.

Newell, N.D., Classification of the bivalvia, *Am. Mus. Novitates*, 1965, no. 2206.

Newell, N.D. and Boyd, D.W., Pectinoid bivalves of the Permian–Triassic crisis, *Bull. Am. Mus. Nat. Hist.*, 1995, vol. 227, pp. 1–95.

Okuneva, T.M., Jurassic system. Lower and Middle Divisions. Marine Deposits and mollusks, in *Atlas fauny i flory paleozoya i mezozoya Zabaikal'ya* (Atlas of the Fauna and Flora of the Paleozoic–Mesozoic of Transbaikalia), Novosibirsk: Nauka, Sib. Izd. Firma Ross. Akad. Nauk, 2002, pp. 354–387.

Paraketsov, K.V. and Paraketsova, G.I., *Stratigrafiya i fauna verkhneyurskikh i nizhnemelovykh otlozhenii Severo-Vostoka SSSR* (Stratigraphy and Fauna of the Upper Jurassic and Lower Cretaceous Deposits of North-East of the USSR), Moscow: Nedra, 1989 [in Russian].

Pavlinov, I.Ya., *Vvedenie v sovremennuyu filogenetiku (kladogeneticheskii aspekt)* (Introduction to Contemporary Phylogenetics (A Cladogenetic Aspect)), Moscow: T-vo Nauchn. Izd. KMK, 2005 [in Russian].

Pavlinov, I.Ya., Two weighting concepts in taxonomy: character weighting and similarity weighting, *Russ. Ornitol. Zh.*, 2009, vol. 18, Express-iss. 497, pp. 1187–1204.

Pchelintsev, V.F., The late Liassic fauna of the Caucasus, in *Tr. Vsesoyuz. Geologo-razved. O-va*, 1933, vol. 253.

Pchelintseva, G.T., *Stratigrafiya i fauna plastinchatozhabernykh Zapadnogo Priokhot'ya* (Stratigraphy and Fauna of Lamellibranchs of the Western Okhotsk Region), Moscow–Leningrad: Izd. Akad. Nauk SSSR, 1962 [in Russian].

Phillips, J., *Illustrations to the Geology of Yorkshire, or a Description of the Strata and Organic Remains of the Yorkshire Coast: Accompanied by a Geological Map, Sections, and Plates of the Fossil Plants and Animals*, London, 1829.

Polevoi atlas yurskoi fauny i flory Severo-Vostoka SSSR (Field Atlas of the Jurassic Fauna and Flora of the Northeastern USSR), Efimova, A.F., Kinasov, V.P., and Paraketsov, K.V., Eds., Magadan: Magadan. Knizhn. Izd., 1968 [in Russian].

Pompeckj, J.F., The Jurassic fauna of Cape Flora, Franz Josef Land, in *The Norwegian North Polar Expedition 1893–1896, Scientific Results*, Nansen, F., Ed., London: Green & Co, 1900, vol. 1, pp. 1–148.

Pompeckj, J.F., Uber Aucellen und Aucellen-ahnliche Formen, *Neues Jahrb. Mineral., Geol., Palaontol. Stuttgart*, 1901, vol. XIV, pp. 319–368.

Quenstedt, F.A., *Der Jura*, Tubingen, 1858.

Rasnitsyn, A.P., The process of evolution and methodology of systematics, *Trudy Russ. Entomol. O-va*, 2002, vol. 73.

Rasnitsyn, A.P., Theoretical foundation of evolutionary biology, in *Vvedenie v paleoentomologiyu* (Introduction in Paleoentomology), Zherikhin, V.V., Ponomarenko, A.G., and Rasnitsyn A.P., Eds., Moscow: T-vo Nauchn. Izd. KMK, 2008.

Rogov, M.A. and Lutikov, O.A., *Dactylioceras–Meleagrinella (Clathrolima)* assemblage from the Agardhbukta (eastern coast of Western Spitsbergen): A first *in situ* Toarcian molluscan occurrence from Svalbard providing interregional correlation, *Norwegian J. Geol.*, 2022, vol. 102.

Rogov, M., Ershova, V., Vereshchagin, O., Vasileva, K., Mikhailova, K., and Krylov, A., Database of global glendonite and ikaite records throughout the Phanerozoic, *Earth System Science Data*, 2021, vol. 13, no. 2, pp. 343–356.

Röhl, H.-J., Hochauflösende palökölogische und sedimentologische Untersuchungen im Posidonienschiefer (Lias epsilon) von SW-Deutschland, *Tübinger Geowiss. Arbeiten*, 1998, vol. 47, pp. 1–170.

Rollier, L., *Fossiles Nouveaux ou peu Connus des Terrains Secondaires du Jura*, Paris, 1914.

Ros-Franch, S., Márquez-Aliaga, A., and Damborenea, S.E., Comprehensive database on Induan (Lower Triassic) to Sinemurian (Lower Jurassic) marine bivalve genera and their paleobiogeographic record, *Paleontol. Contrib.*, 2014, no. 8, pp. 1–219.

Ruzhentsev, V.E., Principles of systematics, system, and phylogeny of Paleozoic ammonoids, in *Tr. Paleontol. Inst. Akad. Nauk SSSR* (Trans. Paleontol. Inst. USSR Acad. Sci.), 1960, vol. 83.

Schmid-Röhl, A. and Röhl, H.J., Overgrowth on ammonite conchs: Environmental implications for the Lower Toarcian Posidonia Shale, *Palaeontology*, 2003, vol. 46, no. 2, pp. 339–352.

Sey, I.I. and Kalacheva, E.D., Biostratigraphy of Lower–Middle deposits of the Far East, *Tr. Vseross. Nauchno-Issled. Geol. Inst., Nov. Ser.*, 1980, vol. 285.

Severtsov, A.S., *Osnovy teorii evolyutsii* (Principles of Evolutionary Theory), Moscow: Mosk. Gos. Univ., 1987 [in Russian].

Simpson, G.G., *Principles of Animal Taxonomy*, New York: Columbia Univ. Press, 1961.

Smith, W., *Stratigraphical System of Organized Fossils, with Reference to the Specimens of the Original Geological Collection in the British Museum: Explaining Their State of Preservation and Their Use in Identifying the British Strata*, London: E. Williams, 1817.

Sokolov, D.N., Originals and paratypes of C.F. Rouillier and H.A. Trautschold in the collection of Fahrenkohl from the village of Gal'evo, *Tr. Muz. im. Petra Velikogo Imper. Akad. Nauk*, 1912, vol. 6, no. 4, pp. 97–119.

Stanley, S.M., Relation of shell form to life habits of the Bivalvia (Mollusca), *Geol. Soc. Am.*, 1970.

Stratigrafiya yurskoi sistemy severa SSSR (Stratigraphy of Jurassic System of the Northern USSR), Moscow: Nauka, 1976 [in Russian].

Szente, I., Some macrofossils, chiefly bivalves, from the Lower Jurassic black shale of the Mecsek Mts (Hungary), *Hantkeniana (Budapest)*, 2015, vol. 10, pp. 55–58.

Teichert, S. and Nützel, A., Early Jurassic anoxia triggered the evolution of the oldest holoplanktonic gastropod *Coelodiscus minutus* by means of heterochrony, *Acta Palaeontol. Pol.*, 2015, vol. 60, no. 2, pp. 269–276. https://doi.org/10.4202/app.00145.2014

Tokuyama, A., Late Triassic Pteriacea from the Atsu and Inline Series, West Japan, *Japanese J. Geol. Geogr.*, 1959, vol. 30.

Triasovaya fauna Severo-Vostoka Azii (Triassic Fauna of Northeastern Asia), Dagys, A.S., Dagys, A.A., Ermakova, S.P., et al., Novosibirsk: Nauka, Sibirskaya izd. firma RAN, 1996 [in Russian].

Turbina, A.S., Jurassic *Meleagrinella* species of Western Siberia and their biostratigraphic significance, in *Mater. po regional'noi geologii Sibiri* (Materials of Regional Geology of Siberia), Novosibirsk: Sib. Nauchno-Issled. Inst. Geol. Geofiz. Miner. Syr'ya, 1984, pp. 35–36.

Treatise on Invertebrate Paleontology. Pt. N. Mollusca 6, Bivalvia, Moore, R.C., Ed., N.Y.: Geol. Soc. Am., 1969, vol. 1–3.

Urlichs, M., Alter und Genese des Belemnitenschlachtfeldes im Toarcium von Franken, *Geologische Blatter fur Nordost-Bayern*, 1971, no. 21, pp. 65–83.

Velikzhanina, L.S., Representatives of the genera *Meleagrinella* and *Arctotis* from the Lower and Middle Jurassic of Western Yakytia, in *Geologiya i neftegazonosnost' Zapadnoi Yakutii. Tr. VNIGRI. Vyp. 249* (Geology and Oil Productivity of Western Yakutia. Trans. All-Russ. Petrol. Res. Explor. Inst.), Leningrad: Nedra, 1966, pp. 80–120.

Velikzhanina, L.S., *Oxytoma kirinae* Velikzhanina sp. nov., in *Novye vidy drevnikh rastenii i bespozvonochnykh SSSR* (New Species of Fossil Plants and Invertebrates of the USSR), Leningrad: Nedra, 1973, pp. 64–65.

Verma, H.M., *Upper Triassic Eumorphotis and Meleagrinella (Bivalvia) from British Columbia. Doctoral Dissertation*, 1968.

Voronets, I.S., Fauna of Upper Jurassic deposits of the Upper Kolyma Region, in *Materialy po izucheniyu Kolymo-Indigirskogo kraya. Geologiya i geomorfologiya* (Materials on the Study of the Kolyma–Indigirka Region. Geology and Geomorphology), Moscow: Ob"ed. Nauchno-Tekhn. Izd. NKTP SSSR, 1938, pp. 38–70.

Voronets, N.S., Mesozoic fauna of the Kharaulakh Ridge, *Trudy Arkt. Inst.*, 1936, vol. 37, pp. 7–36.

Waterhouse, J.B., Aspects of the evolutionary record for fossils of the Bivalve Subclass Pteriomorphia Beurlen, *Earthwise*, 2008, vol. 8.

Whitfield, R.P., *Preliminary Report on the Paleontology of the Black Hills, Containing Descriptions of New Species of Fossils from the Potsdam, Jurassic, and Cretaceous Formations of the Black Hills of Dakota. United States Geological and Geographical Survey Rocky Mts. Region*, Washington, 1877.

Whitfield, R.P., Paleontology of the Black Hills of Dakota, in *Report on the Geology and Resources of the Black Hills of Dakota*, Newton, H. and Jenney, W.P., Eds., Washington, 1880, pp. 325–468.

Whitfield, R.P., *Brachiopoda and Lamellibranchiata of the Raritan Clays and Greensand Marls of New Jersey*, New Jersey: Mon. U.S. Geol. Surv., 1885.

Wierzbowski, A., Kulicki, C., and Pugaczewska, H., Fauna and stratigraphy of the uppermost Triassic and the Toarcian and Aalenian deposits in the Sassenfjorden, Spitsbergen, *Acta Palaeontol. Pol.*, 1981, vol. 26, pp. 195–241.

Zakharov, V.A., *Pozdneyurskie i rannemelovye dvustvorchatye mollyuski severa Sibiri (otryad Anisomyaria) i usloviya sushchestvovaniya* (Late Jurassic and Early Cretaceous Bivalves of Northern Siberia (Order Anisomyaria) and Their Habitats), Moscow: Nauka, 1966 [in Russian].

Zakharov, V.A., *Bukhiidy i biostratigrafiya boreal'noi verkhnei yury i neokoma* (Buchiids and Biostratigraphy of the Boreal Upper Jurassic and Neocomian), Moscow: Nauka, 1981 [in Russian].

Zakharov, V.A. and Shurygin, B.N., *Biogeografiya, fatsii i stratigrafiya srednei yury Sovetskoi Arktiki (po dvustvorchatym mollyuskam)* (Biogeography, Facies and Stratigraphy of the Middle Jurassic of the Soviet Arctic (Based on Bivalves)), Novosibirsk: Nauka, 1978 [in Russian].

Zakharov, V.A., Shurygin, B.N., Kurushin, N.I., Meledina, S.V., and Nikitenko, B.L., A Mesozoic Ocean in the Arctic: Paleontological evidence, *Russ. Geol. Geophys.*, 2002, vol. 43, no. 2, pp. 143–170.

Zakharov, V.A., Meledina, S.V., and Shurygin, B.N., Paleobiochores of Jurassic boreal basins, *Russ. Geol. Geophys.*, 2003, vol. 44, no. 7, pp. 633–644.

Zavertyaev, B.P., *Kratkii slovar' selektsionno-geneticheskikh terminov v zhivotnovodstve* (A Short Dictionary of Breeding and Genetic Terms in Animal Breeding), Moscow: Rossel'khozizdat, 1983 [in Russian].

Zieten, C., *Die Versteinerungen Wurttemergs*, Stuttgart, 1830.