Phylogeny and Evolution of Ontogeny of the Family Oxytomidae Ichikawa, 1958 (Mollusca: Bivalvia)

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Abstract—We described ontogenies and reconstructed morphogeneses of hinges in some supraspecific taxa of the bivalve family Oxytomidae Ichikawa, 1958 from the Mesozoic of Russia. The phylogeny of the family is reconstructed using evolutionary and cladistic methods. The appearance of the endemic genus *Arctotis* Bodylevsky, 1960 in the epicontinental seas of Siberia can be explained in terms of gradual transformations of the ligament and byssal apparatus in the Northern Siberian members of *Praemeleagrinella* Lutikov et Shurygin, 2009 and *Praearctotis* Lutikov et Shurygin, 2009.

Key words: bivalves, Oxytomidae, taxonomy, ontogeny, phylogeny, Mesozoic.

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INTRODUCTION

Bivalves of the family Oxytomidae Ichikawa, 1958 (superfamily Pectinoidea Rafinesque, 1815) are widespread in the Jurassic and Cretaceous of Russia, North America, Europe, Asia, Australia, and New Zealand and are commonly used in biostratigraphy. Long-term studies of the Mesozoic members of this group from Russia and the analysis of numerous publications show that there is a general agreement between most authors in the interpretation of the species-group taxa, while the taxonomies of the genus-group taxa differ. There is no agreement about generic and subgeneric assignment of many species, primarily because of insufficient knowledge of the morphology and function of hinge structures.

This study is aimed at (1) reconstructing the phylogeny of the genus-group taxa in the family Oxytomidae, mainly based on the characters of the hinge and byssal complexes of the north Siberian Jurassic–Cretaceous members of the family and (2) evaluation of characteristics allowing separation and systematization of the genus-group taxa.

The systematization of taxa in paleontology is often based on phylogenetic reconstructions and to a large extent depends on the methodological approach to these reconstructions (*Sovremennaya...*, 1988). The cladistic method suggests that taxa are grouped according to the increase of the coefficients of similarity in unweighted characters and that a phylogram is based on the principle of parsimony, without considering chronoclines (Krassilov, 1977; Eldredge, Cracraft, 1980; *Sovremennaya...*, 1988). The evolutionary approach, despite being rather subjective, considers an assembly of morphological criteria, divergence rates and qualitative differences among taxa. In the evolutionary approach, the ranks of taxa are based on the perceived degree of divergence from the common ancestor, often ascribing differing ranks to sister groups (Calow, 1986). In this paper an attempt is made to use both methods and compare the results.

MATERIAL AND METHODS

This paper is based on the material from the original and museum collections of Oxytomidae (Appendix 1). We considered only those taxa that possess the diagnostic set of characters of the family Oxitomidae as defined by the current classification (Cox and Newell, 1969). To reconstruct the evolution of the family we examined eight supraspecific taxonomic groups. To avoid confusion due to nomenclatural ranks, these groups were considered as equivalent supraspecific taxa without a rank (Appendix 2). Originally, the assignment of the species to supraspecific groups was made by taking into account all previously known and

two new supraspecific taxa (Lutikov and Shurygin, 2009). We used exemplars of type species or species from the type regions to define a set of supraspecific characters. When it was not possible to examine the types, we used published original descriptions of type species. Individual variability was assessed in samples from fossil populations.

Methodology of Studies of Morphogenesis

Because there is no agreement about the choice of characters determining the hinge mechanisms of oxytomids, we partly used the terminology used for buchiids, as the best developed for bivalves with a pterioid hinge (Zakharov, 1981). The terminology of oxytomid morphology is discussed in detail in our previous paper (Lutikov and Shurgin, 2009), in which we recognized several types and subtypes of ontogenetic changes of the ligament pit (resilifer). The morphogenesis of the hinge structures was studied using the comparison of homologous components in all oxytomids examined. We used Remane's homology criteria (Severtsov, 1987). The studies of the hinge were two-staged. At the first stage, we recognized an archetype, a set of non-specialized ancestral (plesiomorphic) characters, for the supposed initial form at the level of the genus-group taxa. We accepted the morphology of the species *Eumorphotis (Asoella) confertoradiata* Tokuyama, 1959 (Aviculopectinidae Meek et Hayden, 1864) from the Lower Norian of Japan as a hypothetical ancestral form. We considered characters with relative symmetry as nonspecialized a priori. The umbo of the archetype occupied a central position; the wide-angled resilifer was delineated by the ligament grooves diverging from the axis of symmetry; trans-ligament fields were of approximately the same size. Further specialization within the family proceeded towards the distortion of symmetry. At the second stage, the components of the hypothetical archetype were compared with the corresponding homologous components of the oxytomid shells. Growth variability was assessed primarily in adult specimens by the analysis of growth lines. In some cases the interpretation of the changes in the ligament and byssal character complexes were obtained from the examination of specimens of different sizes from the same sample of borehole core or samples from the same bed.

Recognition of Characters and Morphological Trends

Based on the studies of the Pectinoidea, Shurygin and Lutikov (1991), we chose 11 characters of the outer and inner shell surfaces for the supraspecific classification (Appendix 2). The characters were evaluated according to the previously developed gradational system (Lutikov and Shurygin, 2009). Based on the characters recognized, a matrix of 11 characters (Appendix 3) for seven representatives of supraspecific

taxa was created using the program NDE v.0.5.0 (Page, 2001). Of these, six characters were binary, whereas four had three states, and one character had four states. The coding at the species level was mainly based on the type species. To estimate the taxonomic weight of the morphological characters within the family Oxytomidae, for the 11 chosen characters, we recognized subgroups corresponding to individual states of characters for the cladistic analysis (see below). We recognized 27 subgroups of oxytomids (Fig. 1a). After the initial calculation of coefficients of similarity (Fig. 1b) in eight supraspecific groups, seven were accepted as valid. Groups chosen with identical characters were considered synonymous. For the cladistic study, morphological trends of the chosen characters were examined within major phyletic lineages. For the evolutionary method, the phylogenetic reconstruction was made after the analysis of the chronoclines and recognition of trends. Taking into account the trend toward quantitative changes of some characters in chronological lineages (chronoclines), genus-groups taxa were recognized. For this, the taxonomic weight of some characters (e.g., the resilifer obliquity, the angle of the ligamental plate, the presence or absence of the denticle) was reduced for parallel phylogenetic lineages.

METHODS

Phylogenetic Analysis

The phylogenetic analysis was performed using two methods. For the evolutionary method, the phylogenetic reconstructions and the presumed taxonomic ranks were based on the morphological analysis. The nodes of divergence were determined from a relative taxonomic value of characters based on their stability in the supraspecific groups included in the analysis. The order of character transformations was assumed to follow the succession of the historical development of the taxon. The extrapolation of phylogenetic conclusions was done in two stages: (1) from characters to a historical succession of ontogenies and (2) from a morphological trend in a historical succession of ontogenies to a taxon of a corresponding rank.

For the cladistic analysis, the morphological character matrix was analyzed under the parsimony as an optimality criterion using Winnona, (version 2.0; Goloboff, 1999), without preliminary character weighting or ordering. The stratigraphically earliest genus *Oxytoma* was used as an outgroup. The character data matrices were managed using WINCLADA v.1.00.08 (Nixon, 1999–2002). The phylogeny at the level of the supraspecific groups considered was reconstructed based on combining the results of the cladistic analysis with stratigraphic data.
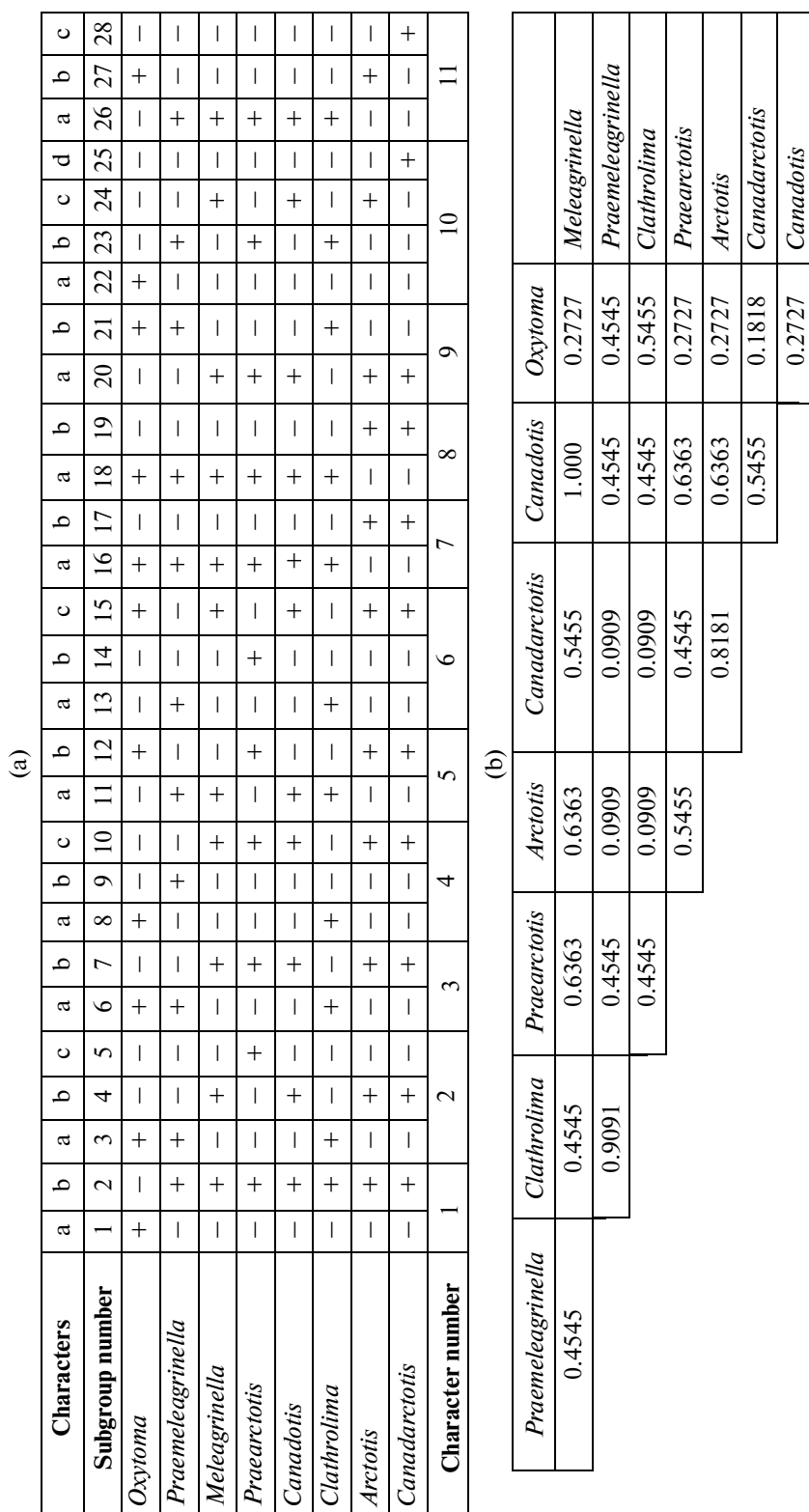
(a)

Characters	a	b	a	b	c	a	b	a	b	c	a	b	a	b	c	a	b	a	b	a	b	a	b	c	d	a	b	c
Subgroup number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
Oxytoma	+	–	+	–	–	+	–	+	–	–	–	+	–	–	+	+	–	+	–	–	+	+	–	–	–	–	+	–
Praemeleagrinella	–	+	+	–	–	+	–	–	+	–	+	–	+	–	–	+	–	+	–	–	+	–	+	–	–	+	–	–
Meleagrinella	–	+	–	+	–	–	+	–	–	+	+	–	–	–	+	+	–	+	–	+	–	–	–	+	–	+	–	–
Praearctotis	–	+	–	–	+	–	+	–	–	+	–	+	–	+	–	+	–	+	–	+	–	–	+	–	–	+	–	–
Canadotis	–	+	–	+	–	–	+	–	–	+	+	–	–	–	+	+	–	+	–	+	–	–	–	+	–	+	–	–
Clathrolima	–	+	+	–	–	+	–	+	–	–	+	–	+	–	–	+	–	+	–	–	+	–	+	–	–	+	–	–
Arctotis	–	+	–	+	–	–	+	–	–	+	–	+	–	–	+	–	+	–	+	+	–	–	–	+	–	–	+	–
Canadarctotis	–	+	–	+	–	–	+	–	–	+	–	+	–	–	+	–	+	–	+	+	–	–	–	–	+	–	–	+
Character number	1		2			3		4			5		6			7		8		9		10				11		

(b)

	Praemeleagrinella	Clathrolima	Praearctotis	Arctotis	Canadarctotis	Canadotis	Oxytoma	
	0.4545	0.4545	0.6363	0.6363	0.5455	1.000	0.2727	Meleagrinella
		0.9091	0.4545	0.0909	0.0909	0.4545	0.4545	Praemeleagrinella
			0.4545	0.0909	0.0909	0.4545	0.5455	Clathrolima
				0.5455	0.4545	0.6363	0.2727	Praearctotis
					0.8181	0.6363	0.2727	Arctotis
						0.5455	0.1818	Canadarctotis
							0.2727	Canadotis

Fig. 1. (a) Distribution of character states (see Appendix 2) among the supraspecific taxa of the family Oxytomidae Ichikawa, 1958; (b) matrix of coefficient of similarity of supraspecific groups in the family.

RESULTS AND DISCUSSION

Taxonomic Evaluation of Characters

Coefficients of similarity between different taxon pairs within Oxytomidae were calculated from the ratio of the total number of matches?to the total number of characters in eight supraspecific groups (Fig. 1b). In this analysis, *Canadotis* and *Meleagrinella* matched completely (1.000). With 11 characters being identical, both supraspecific groups were considered synonyms. Further analysis involved a senior synonym—*Meleagrinella*. The type of resilifer had the largest weight (i.e., the highest phenotypic stability and the lowest degree of homoplasy). Based on the resilifer morphology, we recognized two most genetically distant lineages that synchronously evolved in the Jurassic and the Cretaceous periods: oxytomids with a rectangular resilifer and those with a widely angled resilifer. Based on the morphology of the resilifer, the outgroup *"Oxytoma"* and "all remaining supraspecific groups" were assigned to parallel right grades originating from different ancestral taxa. The shell sculpture and the morphology of the byssal notch were on the second level of taxonomic significance. Two sculpture types have been recognized: the *"Meleagrinella*-type" (as in the type species of the genus *Meleagrinella*, where the radial ribs are irregularly differentiated in one–two orders) and the *"Arctotis*-type" (as in the type species of the genus *Arctotis*-type" ith a widely-nior synonym, where the ribs are regularly differentiated into three–four orders according to their degree of development). Based on sculpture, two genetically distant lineages evolved in the Middle Jurassic and the Cretaceous: *"Meleagrinella"* and *"Arctotis"*. Similarities in shell sculpture in the lineages *"Oxytoma"* and *"Arctotis–Canadarctotis"* are here considered convergent.

Two groups of oxytomids were recognized based on the type of the byssal notch: a group with an open byssal notch—*"Oxytoma, Meleagrinella, Praemeleagrinella, Clathrolima, Praearctotis"* and a group with a closed (overgrown) in adults byssal notch—*"Arctotis–Canadarctotis"*. All other characters have the same taxonomic weight.

The Individual Ontogenetic Variability of the Ligament and Byssal Character Complexes

The resilifers of *Praemeleagrinella*, *Meleagrinella* (provisionally), *Clathrolima*, *Praearctotis* and *Arctotis* are elongated and triangular at the juvenile stage. In *Praemeleagrinella* and *Clathrolima*, the early adult stage is characterized by the change of the resilifer's shape, the development of the ligamental ridge on the anterior side of the hinge, and the derease in the angle between the anterior and posterior ligamental grooves.

The valves of *Praemeleagrinella subolifex* from the Hettangian–Sinemurian of Central Siberia, judging by the growth lines, at the juvenile stage, have a con-siderably more elongated rectangular resilifer than the adult shells (Plate I, Fig. 1c). The lateral edges of the pit diverge from the prodissoconch to form an angle of ca. 120°. The anterior ligamental groove at the juvenile stage is two thirds of the length of the posterior ligament groove and forms an angle of ca. 140° with the external edge of the ligament plate. At the adult stage, the anterior ligament groove changes its position on the ligament plate, nearly forming a right angle with the lower edge of the ligament plate (Plate I, Figs. 1a, 1b). This feature was observed in specimens from various facies in the Nordvick (Anabar Bay) and Lena-Anabar (Kyra-Khos-Teryuteekh River, Olenek River Basin) regions.

Shells of *Praemeleagrinella sparsicosta* are less than 20 mm high from the Early Pliensbachian of the Vilyui Syncline and have a more rectangular resilifer compared to that of the adults (Plate I, Fig. 2b). In adult shells (ca. 25 mm high), the anterior ligament groove, as in *Praemeleagrinella subolifex*, is curved to form almost a right angle with the lower margin of the ligament chronocline (Plate I, Fig. 2a).

In *Praemeleagrinella tiungensis*, from the Early Pliensbachian of the Anabar River and Tyung River basins, the direction of resilifer growth from the juvenile to the adult stage is different from that in other Hettangian–Pliensbachian species. At the adult stage, the anterior ligament groove is curved towards the anterior margin of the shell to form an obtuse angle with the lower margin of the ligament plate (Plate I, Fig. 3).

In adolescent specimens of *Clathrolima doneziana*, from the Bajocian of the Mangyshlak Peninsula, the shape of the resilifer approaches a right triangle (Plate I, Fig. 5b), as in adult specimens of *Praemeleagrinella sparsicosta* from the Pliensbachian. At the adult stage, the anterior ligament groove is curved anteriorly to form an obtuse angle with the lower margin of the ligament plate (Plate I, Fig. 5a). Similar trends in the resilifer's growth were observed in specimens from the Donets Region (village of Kovalevka), assigned by A.A. Borissiak (1909) to the *"Pseudomonotis"* echinata var. *doneziana*, and specimens from the Bajocian of Kazakhstan (Ural River), which were assigned by E. Ivanov (1915) to *"Pseudomonotis" doneziana*.

In two specimens of *Clathrolima subechinata* from Borissiak's collection, from the Callovian of the Vladimir Region (Dmitrievy Gory), which Borissiak assigned to *"Pseudomonotis" subechinata* (var. *echinata*), the resilifers of the left valves differ considerably in shape despite being of approximately the same size as the valves. The anterior ligament groove in specimen no. 28/311 forms almost a right angle with the external edge of the resilifer (Plate I, Fig. 4a), whereas in specimen no. 26/311, it is strongly oblique posteriorly relative to the hinge axis (Plate I, Fig. 4b). In specimen no. 28/311, the denticle is developed, whereas in specimen no. 26/311, a weakly developed bulge is present on the anterior side of the "pseudolig-

Plate I. Ligament area and resilifers in oxytomids.

Fig. 1. *Praemeleagrinella subolifex Polubotko*. (a) KR-119/44, left valve of an adult specimen, ×5.5, Kyra-Khos-Teryuteekh River, Outcrop 3, Bed 1, Hettangian−Sinemurian; (b) AG-60/67, left valve of an adult specimen, ×5.5, Anabar Bay, Outcrop 5, Bed 18, Hettangian−Sinemurian; (c) KR-120/43, right valve of an adult specimen (oblique resilifer), ×5, Kyra-Khos-Teryuteekh River, Outcrop 3, Bed 1, Hettangian−Sinemurian.

Fig. 2. *Praemeleagrinella sparsicosta* (Petrova). (a) − T-165/2, left valve of an adult specimen, ×2.6, Tyung River, Outcrop 9, Bed 4, Early Pliensbachian; (b) T-94/2, right valve of an adult specimen, ×2.4; Tyung River, Outcrop 4, Bed 8, Early Pliensbachian.

Fig. 3. *Praemeleagrinella tiungensis* (Petrova). AN-15/2, left valve of an adult specimen (oblique-expanding resilifer), ×3.8, Anabar River, Outcrop 3, Bed 1, Early Pliensbachian.

Fig. 4. *Clarthrolima subechinata* (Lahusen).

Type specimens: (a) 28/311, left valve of an adult specimen with a developed denticle, ×6.5; (b) 26/311, left valve of an adult specimen with an undeveloped denticle, ×6.5 (after Borissiak, 1909, Plate 2, Figs. 14, 15)); (c) 33/311, right valve of an adolescent specimen (oblique resilifer), ×6.2, Vladimir Region, Middle Callovian.

Fig. 5. *Clarthrolima doneziana* (Borissiak). (a) MK-142/3, right valve of an adult specimen (oblique-expanding resilifer), ×5.3; (b) MK-142/2, right valve of an adolescent specimen (oblique resilifer), ×6.2, Mangyshlak Peninsula, Bajocian.

Fig. 6. *Clarthrolima braamburiensis* (Phillips). (a) MK-152/2, left valve of an adult specimen with a developed denticle, ×4.6; (b) MK-152/4, left valve of an adult specimen with an undeveloped denticle, ×4.6, Mangyshlak Peninsula, Middle Callovian.

Fig. 7. *Clarthrolima subovalis* Zakharov. (a) YUCH-4, left valve of an adolescent specimen, ×9; (b) YUCH-2, left valve of an adult specimen, ×4.5; (c) YUCH-1, right valve of an adult specimen (oblique-narrowing resilifer), ×10; (d) YUCH-2, right valve of an adolescent specimen (oblique resilifer), ×10; (e) YUCH-3, right valve of a juvenile specimen (elongate triangular resilifer), ×4.7, South Chulym Field, borehole 1, interval 1205.4−1213.4 m, Kimmeridgian-Volgian.

Fig. 8. *Meleagrinella curta* (Whitfield). Lectotype, view of the hinge of a left valve ×3.8, South Dakota, Black Hills, US, Upper Jurassic, Oxfordian (after Whitfield, 1880, Plate III, Fig. 22).

Fig. 9. *Praearctotis milovae* (Okuneva). (a) AG-103/1, left valve of a juvenile specimen (expanding resilifer), ×10; (b) AG-103/2, left valve of an adult specimen (inversely-narrowing resilifer), ×7.5, Anabar Bay, western bank, Outcrop 5, Bed 76, Lower Toarcian; (c) TX-1/1, right valve of an adult specimen (inversely-narrowing resilifer), ×7.9, Tengelyakh Field, line 1060, borehole 350, depth 31 m, Lower Toarcian.

Fig. 10. *Praearctotis marchaensis* (Petrova). (a) MX-111/2, left valve of an adult specimen wit ha reduced denticle, ×2.3; (b) MX-111/1, right valve of an adult specimen at the stage of differentiation of the resilifer (angular resilifer), Markha River, ×2.5, Outcrop 4, collected loosely near beds 2−4, Upper Toarcian.

Fig. 11. *Praearctotis vai* (Bodylevsky). AG-37/1, ×2.5, right valve of an adult specimen at the stage of differentiation of the resilifer (angular resilifer), Anabar Bay, Outcrop 4, Bed 18, Upper Toarcian.

Fig. 12. *Praearctotis viluiensis* Velikzhanina. (a) MN-216/1, left valve of an adult specimen, ×2.2; (b) MN-216/2, right valve of an adult specimen, ×2.3, Motorchuna River, Outcrop 4, Bed 2, Sample 216, Upper Toarcian; (c) TR-19/1, right valve of an adult specimen at the beginning of the formation of the ligament spoon-like pit (spoon-like resilifer), ×2.3, Eastern Taimyr, Outcrop 7, Bed 3, Upper Toarcian.

Fig. 13. *Arctotis tabagensis* (Petrova). (a) MD-2, left valve of an adolescent specimen (expanding resilifer), ×5, Molodo River, Outcrop 8, Bed 2, Lower Aalenian; (b) AG-116/1, right valve of an adult specimen at the final stage of the formation of a spoon-like resilifer, ×1.7, Anabar Bay, Outcrop 5, Bed 92, Upper Aalenian.

Fig. 14. *Arctotis sublaevis* (Bodylevsky). (a) AN-18/1-l, left valve of an adult specimen, ×1.5; (b) AN-18/1-p, right valve of an adult specimen, ×1.4, Anabar River, Outcrop 3, Bed 8, Lower Bajocian.

Fig. 15. *Canadarctotis intermedia* Bodylevsky. (a) KM-2, left valve of an adult specimen, ×4.4; (b) KM-1, right valve of an adult specimen, ×3.1, Kamennaya River, Eastern Taimyr, Volgian.

Fig. 16. *Canadarctotis anabarensis* (Petrova). (a) BK-2, left valve of an adult specimen, Boyarka River, ×1.6, Upper Berriasian; (b) type specimen, 643/5393, right valve of an adult specimen, ×1.5, Lyungdyul River, Valanginian.

Fig. 17. *Oxytoma jacksoni* (Pompeckj). (a) TX-1/1, right valve of an adult specimen, ×1.8, Tengelyakh Field, line 870, borehole 505, depth 9 m, Upper Toarcian−Lower Aalenian; (b) AG-115/1, right valve of a juvenile specimen (rectangular resilifer), ×6.3, Anabar Bay, Outcrop 5, Bed 90, Lower Aalenian.

amental plate." The right valve of adolescent specimen no. 33/311 has a right triangular resilifer (Plate I, Fig. 4c). A similarly shaped pit was observed on the left valves of *Clathrolima braamburiensis* from the Callovian of the Mangyshlak Peninsula (Plate I, Figs. 6a, 6b). This individual variability may be explained by the different onset times of the development of hinge elements in the ontogeny within the population. Apparently, valves lacking the denticle belonged to specimens with accelerated development. Accretion of the pseudoligamental plate could have proceeded due to the identical material and could shift the point of the intersection of the anterior ligament groove with the external edge of the resilifer toward the posterior shell margin. The degree of obliqueness of the anterior groove of the resilifer in adults with the denticle is almost the same as in the adolescent Bajocian specimens. On the other hand, the accelerative forms from the Callovian show more strongly oblique resilifers, similar to those in adolescent specimens of the Kimmeridgian species.

In *Clathrolima subovalis* from the Kimmeridgian of the Chulymo−Enisei watershed, the juvenile specimens (ca. 5 mm high) have an elongated triangular resilifer (Plate I, Fig. 7e). The pit has a right trianglular outline in adolescent specimens (Plate I, Fig. 7d) and is strongly oblique in adults (Plate I, Fig. 7c). In adolescent and adult specimens of *Clathrolima subovalis*,

Plate I
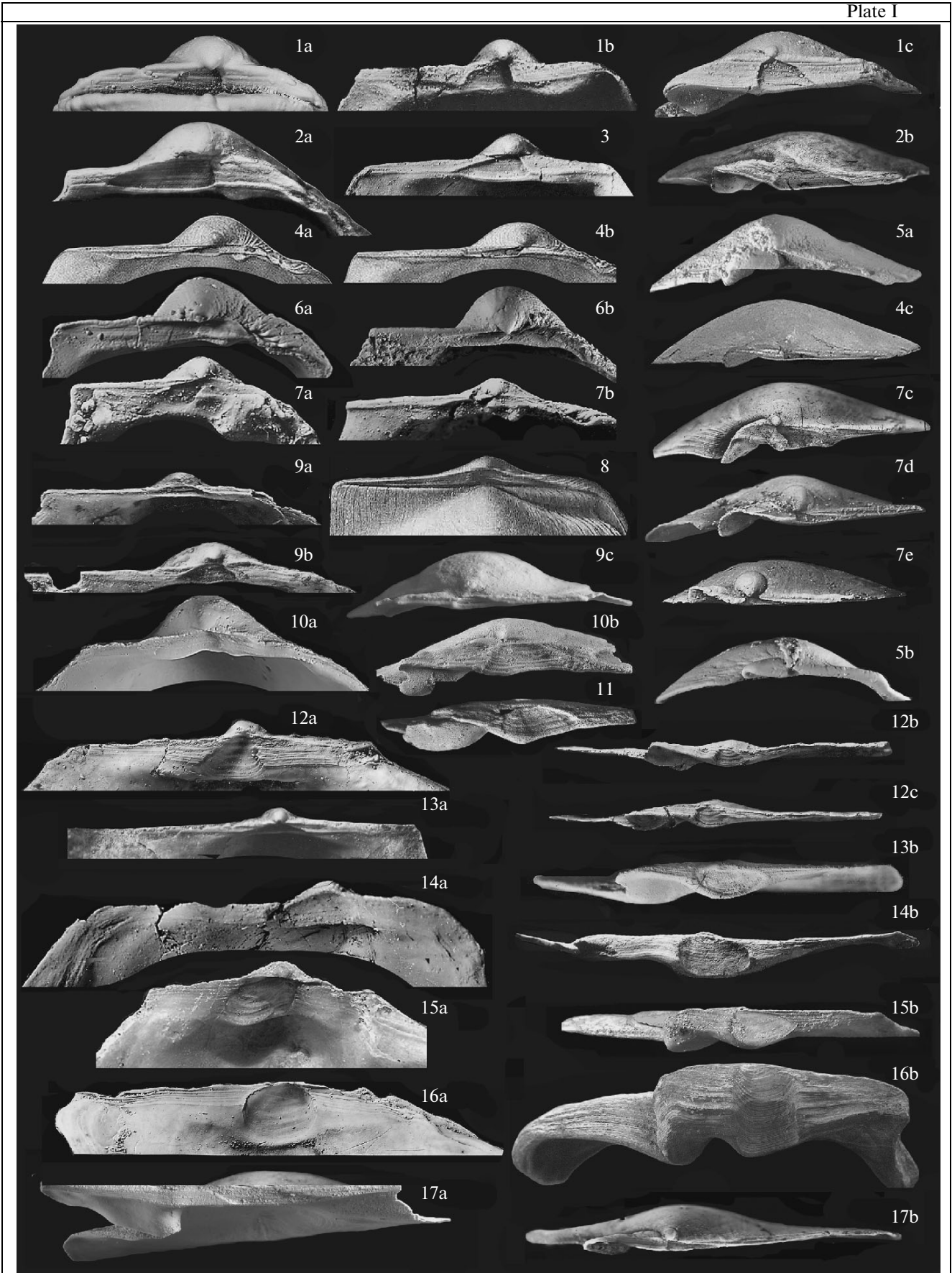
the initially elongated triangular shape of the resilifer is not retained in ontogeny (Plate I, Figs. 7a–7d). The holotype of this species from the Kimmeridgian of northern Central Siberia has a similar structure to the resilifer (Zakharov, 1966).

Adult forms of the type species *Meleagrinella curta* (Whitfield, 1880) from the Oxfordian of the US (South Dakota, Black Hills) have a wide resilifer (Plate I, Fig. 8). The anterior ligamental groove is curved toward the anterior shell margin, which makes a fundamental difference between the American specimens, and the aforementioned European and Siberian ones.

The resilifer in adolescent shells of *Praearctotis milovae* has a symmetrical outline. The grooves of the resilifer (in specimens of about 5 mm) form an angle of about 140° and diverge from the prodissoconch toward the anterior and posterior shell margins (Plate I, Fig. 9a). The anterior ligament groove forms an angle of about 160° with the external margin of the ligamental plate. In adult specimens, the lower part of the anterior ligamental groove is curved towards the lower margin of the ligamental plate (Plate I, Figs. 9b, 9c). The juvenile stage could not be observed. Supposedly, the shape of the resilifer in juveniles is asymmetrical and broadly triangular, as in *Meleagrinella*.

In *Praearctotis marchaensis*, beginning from the adolescent stage, the resilifer of the right valve has an angular outer edge. In adult specimens, from the upper part of the Toarcian section on the Markha River, the resilifer is heterogenous and has a flattened region near the posterior ligament groove and recessed ligamental plate, adjacent to the anterior ligament groove (Plate I, Fig. 10b). A similar differentiation of the resilifer was observed in specimens from the Nordvik Region (Anabar Bay), the type locality of *Praearctotis vai* (Plate I, Fig. 11). A recessed region in the anterior half of the resilifer was observed in two geographical populations referred by B.I. Bodylevskii and G.T. Petrova (*Atlas...*, 1947) to different species *Praearctotis vai* and *P. marchaensis*. Apparently this morphological phene was a prototype of the spoon-like resilifer of *Arctotis*. Adult specimens of both species have an inversely-narrowing resilifer.

Adult specimens of *Praearctotis viluiensis* from the Lower Toarcian of the Zhigan (Motorchuna River) and Eastern Taimyr regions, compared to *Praearctotis marchaensis*, have a ligamental plate more strongly inclined to the plane of the commissure in the left valve (Plate I, Fig. 12a). The resilifer of the right valve is shallow, very narrow, and regularly concave, with a rounded external edge. It is 1/4–1/5 of the width of the ligament chronocline (Plate I, Figs. 12b, 12c).

Juveniles of *Arctotis tabagensis* have an elongated triangular, symmetrical resilifer. The anterior ligament groove is the same size as the posterior groove and forms an angle of approximately160° to the external edge of the ligamental plate. In adolescent specimens of this species, the resilifer is expanded and the ante-rior ligament groove is curved anteriorly (Plate I, Fig. 13a). At this stage in the ontogeny of the ligament block (in specimens about 10 mm in size), a ligamental ridge develops on the anterior side of the pseudoligamental plate of the right valve, separating the resilifer from the transligamental field. A spoon-like resilifer appears in adolescents of Aalenian *Arctotis*. Ligament grooves of the right valve at the adult stage (in the lower region of the ligament chronocline) are curved downwards to form almost a right angle with the external edge of the ligament chronocline (Plate I, Fig. 13b). The spoon-like resilifer is wider and more strongly concave compared to *Praearctotis viluiensis*. The width of the resilifer of the right valve is 1/3 of the length of the ligamental plate.

The resilifer in *Arctotis sublaevis*, beginning from the adolescent stage, has a spoon-like shape. The ligament grooves of the right valves of adult specimens from the Bajocian of the Anabar River at the final stage are more curved toward the axis of symmetry of the shell than in the Aalenian specimens (Plate1, Fig. 14b).

The resilifers in *Canadarctotis intermedia* in adolescent specimens (specimens ca. 10 mm high) are asymmetrical in outline. The pseudoligamental plate left valves at the adult stage in these is shorter than in *Arctotis sublaevis* (Plate I, Fig. 15a). In the right valves at the adult stage, the anterior ligament groove is less strongly curved than in *Arctotis sublaevis* (Plate I, Fig. 15b).

The ligamental plates of the left valves in *Canadarctotis anabarensis* are more oblique in relation to the plane of the commissure compared to *Canadarctotis intermedia*. The pseudoligamental plate at the adult stage in *Canadarctotis anabarensis* is very short and is almost fused with the inner surface of the valve (Plate I, Fig. 16a). In the right valves at the adult stage, the ligament and pseudoligamental plates are very wide (Plate I, Fig. 15b).

The presence of the denticle is a relatively stable characteristic in *Praemeleagrinella* and *Clathrolima* (Plate1, Figs. 1b, 2a, 6a, 7a, 7b). In *Praemeleagrinella tiungensis*, the denticle has the shape of a weak semiellipsoid bulge (Plate I, Fig. 3). In *Clathrolima subechinata*, from the collection of Borissiak, one specimen does not have a pronounced denticle (Plate I, Fig. 4b). We observed varieties lacking a denticle in *Clathrolima braamburiensis* (Plate I, Fig. 6b) in the sample from the Middle Callovian of the Mangyshlak Peninsula. The denticle is present in all left valves of *Clathrolima subovalis* studied.

In representatives of the Toarcian group of *Praearctotis*, as in *Praemeleagrinella tiungensis*, the denticle has the shape of a weakly developed semiellipsoidal bulge on the anterior part of the pseudoligamental plate (Plate I, Figs. 9b, 10a, 12a). In the Middle Jurassic *Arctotis* and Kimmeridgian-Valanginian *Canadarctotis*, the denticle is completely absent (Plate I,

Figs. 13a, 14a, 15a, 16a). In Jurassic and Cretaceous oxytomids, the denticle is absent.

In *Praearctotis milovae*, at the juvenile stage, the byssal auricle is quadrangular, and rhomboidal in outline. Later, in ontogeny, in adolescents, the auricle did not grow onto the lower edge, whereas in juveniles the edge was elongated anteriorly. At the adult stage, the auricle was shaped like an upside down trapezoid with a shortened base. The byssal notch in adult shells is short (Plate II, Figs. 2a, 2b). Juvenile shells of *Praearctotis marchaensis* and *P. viluiensis* have a trapezoidal byssal auricle. In adult specimens, the auricle in ontogeny is initially shaped like an upside down trapezoid, and later becomes subtriangular, with a gently curved lower margin and a small notch on the anterior-lower edge (Plate II, Figs. 3a, 3b). In Aalenian and Bajocian species of *Arctotis*, the adolescent shells have a subtriangular byssal auricle with a gently curved lower edge and a deep byssal notch (Plate II, Fig. 4b). At the adult stage, the lower margin of the auricle merges with the anterior-upper shell margin (Plate II, Figs. 4a, 5a, 5b).

Morphogenesis of the Ligamental Characteristic Complex

The interpretation of the morphogenesis of the ligament block in *Meleagrinella* and *Arctotis* was based on the comparison of the ontogenetic changes of the resilifer, the relative position and relative width of the ligamental plates, and the degree of the curvature of the pseudoligamental plate of the left valve. The morphogenesis of the resilifer in the direction from *Praemeleagrinella* to the *Arctotis* was towards the development of the complex organ, i.e., a spoon-shaped ligamental plate. In the long-term course of the transformation, during most of the Toarcian, species with transitional states of generic characteristics evolved: *Praearctotis milovae* and *P. viluiensis*. The morphogenesis of the resilifer in the direction from the *Praemeleagrinella* to species of *Clathrolima* proceeded in the direction towards an increase in obliqueness of the resilifer. The morphogenesis of the resilifer proceeded toward the expanding of the resilifer from the *Praemeleagrinella* to the *Meleagrinella*.

The resilifer in all oxytomids is a part of the ligamental character complex and retains its triangular shape. The variability of the relative position of the ligament grooves is the main character, based on which the trend of morphogenesis within the family is identified. The resilifer in a supposed ancestral taxon *Eumorphotis (Asoella) confertoradiata*, is equilaterally triangular in outline (Tokuyama, 1959). The morphogenesis of the ligamental plate of the right valve in *Arctotis* proceeded toward the decrease of the relative length. The hinge line of the right valve in Toarcian *Prearctotis* is 0.80−0.75 of the shell length (Plate I, Figs. 9a, 10a, 11, 12b, 12c), in the Aalenian−Bajocian *Arctotis*, it is is 0.74−0.65 of the shell length (Plate I,

Figs. 13b, 14b). In *Canadarctotis intermedia* from the Volgian of Eastern Taimyr (Plate I, Fig. 15b) and in *C. anabarensis* from the Early Valanginian Lena-Anabar Region (Plate I, Fig. 16b), the hinge line of the right valve is 0.64−0.45 of the shell length. In juveniles of *Oxytoma jacksoni* from the Aalenian of the Anabar Bay, the resilifer is rectangular (Plate I, Fig. 17b). In adults of *O. jacksoni* from the Toarcian−Aalenian of the Tenkelyakh Field, the resilifer is strongly oblique (Plate I, Fig. 17a).

Morphogenesis of the Byssal Characteristic Complex

The interpretation of the morphogenesis of the byssal characteristic complex of *Meleagrinella* and *Arctotis* was based on the comparison of the ontogenies of the byssal auricle, byssal groove, and byssal notch. The morphogenesis of the byssal complex from *Praemeleagrinella* to *Clathrolima* proceeded from the change in the outline of the byssal auricle from trapezoid to rhomboid. The *Hettangian−Sinemurian Praemeleagrinella subolifex* have a quadrangular trapezoid byssal auricle, a wide byssal groove, and a deep byssal notch. The anterior margin of the auricle forms an acute angle with the hinge line (Plate I, Fig. 1b). In the Late Pliensbachian *P. sparsicosta*, the anterior margin of the auricle almost forms a right angle with the hingeline (Plate I, Fig. 2b; Plate II, Fig. 1b). In the Bajocian−Kimmeridgian *Clathrolima doneziana* (Plate I, Fig. 5a), Callovian *C. subechinata* (Plate I, Fig. 4c), and Kimmeridgian *C. subovalis* (Plate I, Fig. 7c), the anterior margin of the auricle forms an obtuse angle with the hingeline. The byssal auricle in the lineage *Praemeleagrinella subolifex* (Plate I, Fig. 1c)−*Meleagrinella curta* (Plate I, Fig. 8) changes its outline from a trapezoid with a wide base to a subquadratic without a byssal notch. The denticle disappeared.

The byssal complex of the right valve of the *Arctotis* had changed in a direction correlated with adaptive morphogenesis. The byssal groove changed from *Praemeleagrinella* to *Arctotis* from an open type in the Hettangian species to an overgrown type in the Bajocian species. The shape of the byssal auricle changed from subquadrate to subtriangular (Fig. 2d). In the chronocline of the outline of the byssal auricle in the morphological lineage *Praemeleagrinella tiungensis−Praearctotis milovae−Praearctotis marchaensis* there is a transition from subquadrate to trapezoid auricle with a shortened base and finally to subtriangular. In *Praearctotis marchaensis*, the plane of the auricle is curved in relation to the shell plane and is orientated almost in parallel to the ligamental plate of the right valve (Plate II, Figs. 3a, 3b). The appearance in *Praearctotis* in the Late Toarcian of the recurved auricle determined the direction of morphogenesis toward the formation of the overgrown auricle in the Aalenian species.

In the Volgian *Canadarctotis intermedia*, the byssal auricle is shortened in relation to the anterior margin of the valve, has a triangular shape, and has a notch on
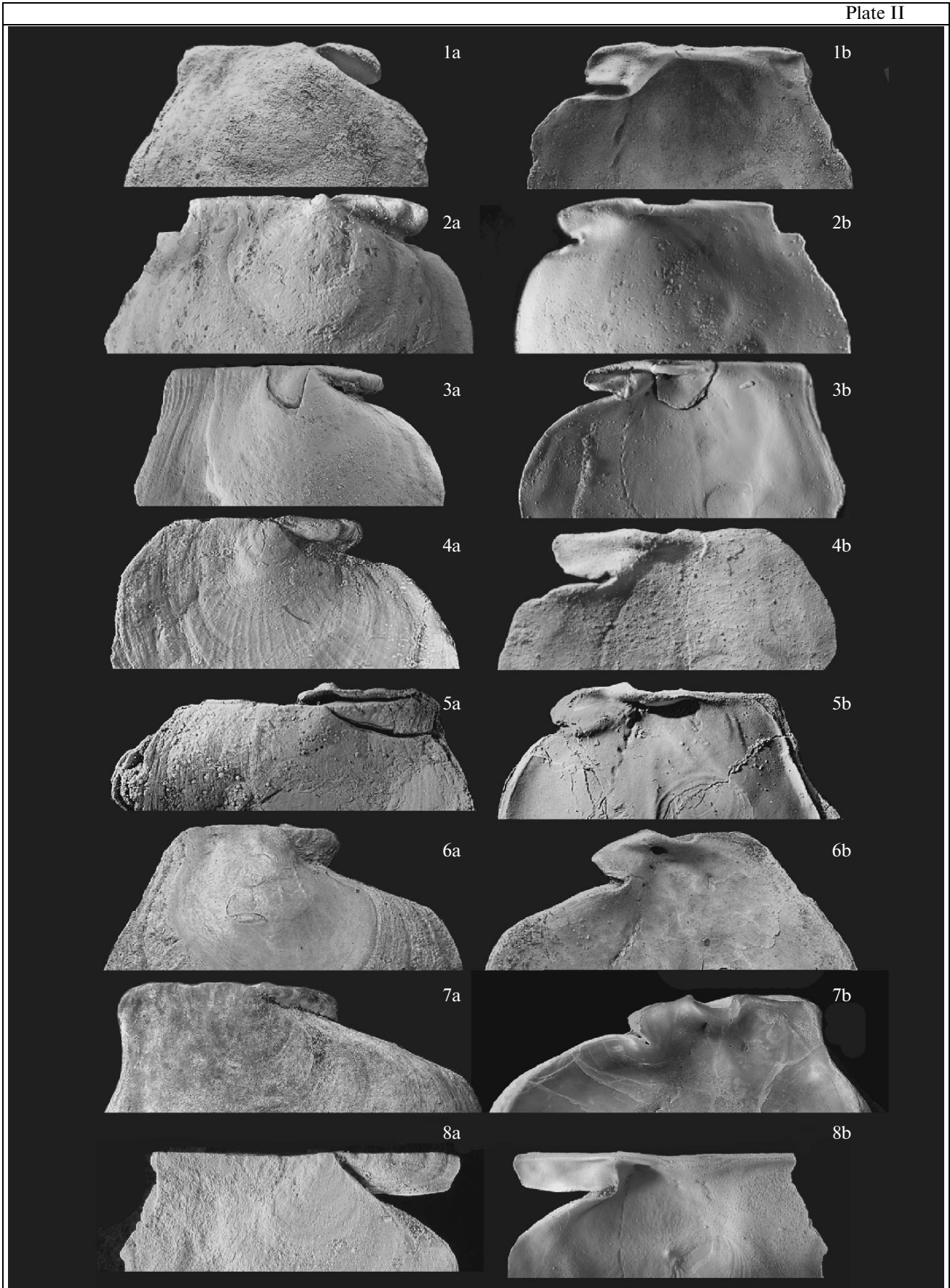
Plate II

Plate II. Auricles of right valves of oxytomids at the adult stage outside (a) and inside (b).

Fig. 1. *Praemeleagrinella sparsicosta* (Petrova). T-94/2, rhomboid byssal auricle, ×2.9, Tyung River, Outcrop 4, Bed 8, Early Pliensbachian.

Fig. 2. *Praearctotis milovae* (Okuneva). TX-1/2, trapezoid byssal auricle, ×9, Tengelyakh Field, line 1060, borehole 350, depth 31 m, Lower Toarcian.

Fig. 3. *Praearctotis marchaensis* (Petrova). TX-35/2, subtriangular recurved byssal auricle, ×3.5, Tengelyakh Field, line 1080, borehole 350, depth 35 m, Upper Toarcian.

Fig. 4. *Arctotis tabagensis* (Petrova). (a) AG-116/2, subtriangular byssal auricle with an overgrown byssal groove, ×1.5; (b) AG-116/2, subtriangular byssal auricle with a deep byssal notch (adolescent specimen), ×4.7, Anabar Bay, Outcrop 5, Bed 92, Upper Aalenian.

Fig. 5. *Arctotis sublaevis* (Bodylevsky). (a) AN-18/2, ×1; (b) AN-18/1-p, ×0.9, subtriangular byssal auricle with a completely overgrown byssal groove, Anabar River, Outcrop 3, Bed 8, Lower Bajocian.

Fig. 6. *Canadarctotis intermedia* Bodylevsky. KM-1, triangular byssal auricle with an open byssal groove, ×3, Kamennaya River, Eastern Taimyr, Outcrop 121, Bed 4, Volgian.

Fig. 7. *Canadarctotis anabarensis* (Petrova). Type specimen, 643/5393, triangular byssal auricle with an overgrown byssal groove, ×1.5, Lyungdyul River, Valanginian.

Fig. 8. *Oxytoma jacksoni* (Pompeckj). TX-1/1, subtriangular byssal auricle with a wide byssal notch, ×1.4, Tengelyakh Field, line 870, borehole 505, depth 9 m, Upper Toarcian−Lower Aalenian.

the lower margin. The byssal groove is shortened compared to the Middle Jurassic taxa and is orientated at an angle to the hinge line (Plate II, Figs. 6a, 6b). In the Valanginian *Canadarctotis anabarensis*, the byssal auricle is fused with the anterodorsal valve margin in adolescence. The inclination of the byssal notch increases compared to the Volgian taxa (Plate II, Figs. 7a, 7b).

In adults of *Oxytoma jacksoni* from the Toarcian-Aalenian of the Tenkelyakh Field, the byssal auricle is subtriangular, with a deep byssal notch (Plate II, Figs. 8a, 8b). The morphogenesis of the byssal block of *Oxytoma* was not studied.

Methods of Phylogenetic Reconstruction

The hypothetical evolutionary phylogeny of the family was based on chronoclines of independent characters. At the first state of divergence, in the Triassic, the genus *Oxytoma* and all other groups were assigned to different phylogenetic groups according to their resilifer. At the second stage of divergence, two other phylogenetic subgroups were established based on the shape of the auricle: with a subquadrangular byssal auricle—*Praemeleagrinella*, *Meleagrinella*, *Clathrolima*, and a subtriangular byssal auricle—*Praearctotis*, *Arctotis*, and *Canadarctotis*. At the third stage of divergence, in the Bajocian, a lateral linage *Meleagrinella* branched off the main lineage *Praemeleagrinella*, *Clathrolima* due to the loss of the denticle (Fig. 3a).

The cladistic analysis resulted in a single completely resolved tree, corresponding to the optimal distribution of transformations of morphological character states (length = 20; homoplasy indexes: CI = 0.85, RI = 0.82) (Fig. 2a). A clade *Praemeleagrina/Clathrolima* was recognized close to the base of the tree based on the presence of the denticle in species of both genera. Its sister group includes all the remaining taxa, united by three characteristics: a resilifer expanding in ontogeny, by its elongate triangular shape and the curvature of the pseudoligamental plate. *Praearctotis* was the basal taxon in this clade; whereas, other taxa had a shortened ligamental plate (extremely diminished in *Canadarctotis*, the latest taxon). The clade *Arctotis/Canadarctotis* was supported by an overgrown byssal groove and radial riblets differentiated in three−four orders. In general terms, the succession of branching of the oxytomid tree corresponded to the order of the first appearances of the genera in the geological record.

Summarizing the above data, a partly reconstructed phylogeny of this family is proposed (Fig. 3). The oxytomid phylogeny reconstructions based on the evolutionary and cladistic methods are largely the same. The position of *Meleagrinella* was fundamentally different: in the first case it was derived from *Praemeleagrinella* (Fig. 3a), whereas in the second case it derived from *Praearctotis* (Fig. 3b).

The phylogeny of the early evolutionary stages, suggesting a polyphyletic origin of oxytomids from taxa in the family Aviculopectinidae, was previously proposed by Ichikawa (1958). Our data do not presently reveal the phylogenetic relationships of the genera under study with other oxytomid taxa (*Avicularca*, *Cyrtorostra*, *Maccoyella*, *Pseudavicula*).

Evolution of Ontogenies

According to the evolutionary reconstruction, the chronocline of the subspecies of ontogenetic changes of the resilifer in the morphological lineage *Asoella confertoradiata−Praemeleagrinella subolifex−Praemeleagrinella sparsicosta* was reflected in the ontogeny of the resilifer of the Late Pliensbachian species *Praemeleagrinella sparsicosta*. The resilifer changed from symmetrical to elongated triangular and weakly oblique pits in the transition from juveniles to adults.

An alternative interpretation according to the cladistic reconstruction suggested an additional intermediate stage—the transformation of the symmetrical resilifer of *Aosella* into the rectangular pit of oxytomas.
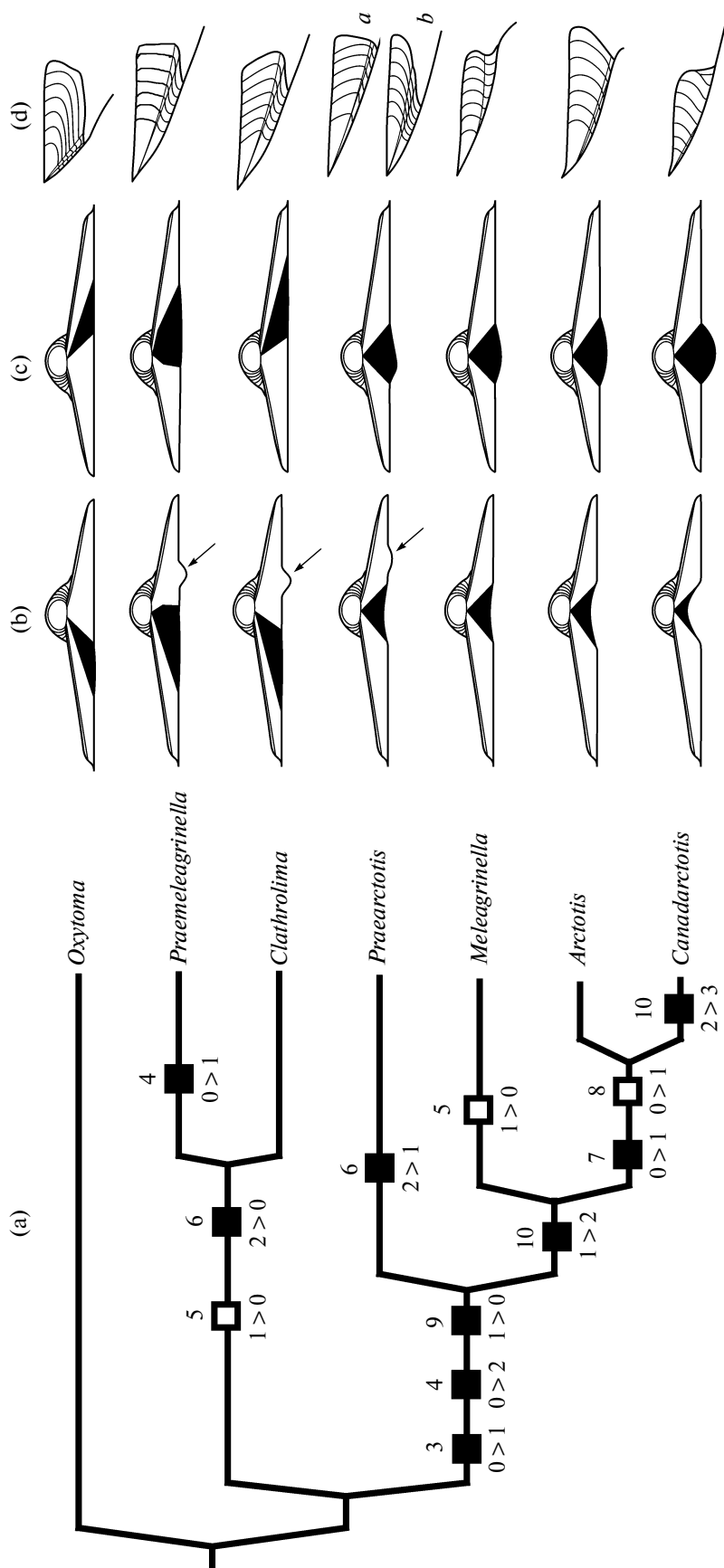
Fig. 2. Hypothetical relationships of the supraspecific taxa of the family Oxytomidae, based on cladistic analysis and corresponding distribution of character states of the ligamental and byssal complexes.

(a) the cladogram with apomorphic characters marked. Black squares show unequivocally optimized non-homoplastic characters, white squares show homoplastic characters. Figures above squares indicate character numbers (as listed in Appendices 2 and 3), figures below squares—transformations of character states; (b) left valve hinge; (c) right valve hinge; (d) byssal complex of the right valve. Black color in Figs. 2b and 2c indicates the shape of the resilifer. Arrow shows the denticle, (*a*) shape of the auricle in the earliest *Praearctotis*, (*b*) shape of the auricle in the latest *Praearctotis*.
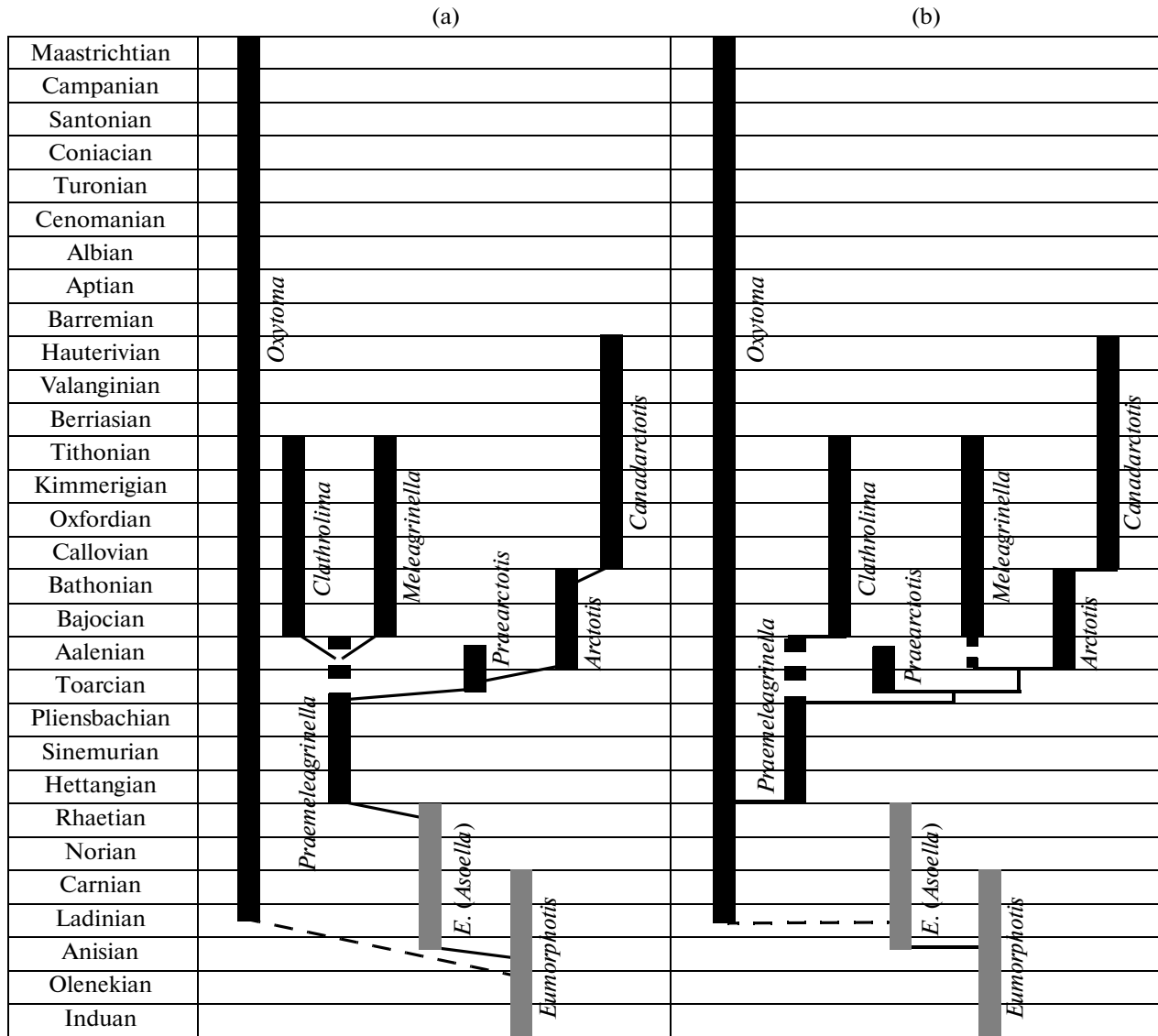
Fig. 3. Alternative reconstructions of phylogeny in the family Oxytomidae based on evolutionary (a) and cladistic (b) methods. Wide vertical lines show stratigraphic ranges of supraspecific groups studied (supposed ancestral oxytomids, members of the family Aviculopectinidae, are shown in gray), narrow lines indicate genetic links.

Both reconstructions showed a tendency towards asymmetrical resilifers.

The chronocline of subspecies in the lineage *Praemeleagrinella sparsicosta—Clathrolima subechinata—Clathrolima subovalis* was reflected in the ontogeny of the resilifer of the latest of the known *Clathrolima* species—the Kimmeridgian species *subovalis* (Plate I, Figs. 7c, 7d, 7e). The shape of the resilifer in the transition from juveniles to adults gradually changed with elongated triangular to weakly oblique and to strongly oblique. The group *Clathrolima* replaced *Praemeleagrinella*, without distorting the principal direction of the morphogenesis. In the chronocline of both groups, a directed increase of the shell size is observed. Shell

increase also occurred in the species *Praemeleagrinella* from Hettangian to the Late Pliensbachian, and in the *Clathrolima* species, from the Aalenian to the Kimmeridgian. The unresolved phylogenetic position of the *Meleagrinella* does not allow an unequivocal interpretation of the evolution of ontogeny in this group, which could have evolved in parallel with the *Praemeleagrinella* from the *Asoella*. However, no specimens of the *Meleagrinella* lacking a denticle have so far been recorded from the Lower Jurassic. Hinge structures of the *Meleagrinella* have not yet been recorded from the Lower Lias of Europe and Canada. The chronocline of ontogenetic changes of the resilifer in the morphological lineage *Praemeleagrinella subolifex—Meleagrinella*

curta, reconstructed based on the evolutionary method, represented a succession of forms from an oblique-narrowing to an oblique-expanding shape.

The cladistic analysis suggested a succession of the transformation of the resilifer at the adult stage from weakly oblique in the *Praemeleagrinella* to elongated triangular in the *Praearctotis*. The resilifer morphology of the latter was subsequently inherited by the species of *Meleagrinella*.

Among the diversity of shells of the *Arctotis*, two major adaptive types can be recognized: with an open byssal groove and with an overgrown byssal groove, suggesting considerably different ethological adaptations. Groups of species showing morphological trends in the ligamental and byssal complexes with relatively constant characters in definite time intervals, gradually replaced each other historically. The *Praearctotis* group united the Toarcian specimens with a resilifer of an expanding type. The ontogenetic chronocline of the resilifer in the morphological lineage *Praemeleagrinella tiungensis—Praearctotis milovae—Praearctotis marchaensis* represented a succession from a weakly oblique shape (with an expanding subtype) of the resilifer to an expanding shape (with a secondarily expanding subtype) to an expanding type (with an inversely narrowing subtype). The *Arctotis* group included the Late Toarcian—Bathonian species of *Arctotis*, which displays a larger inclination of the ligamental plate of the left valve in relation to the plane of the commissure. The byssal complex showed a semitriangular outline of the byssal auricle and an overgrown byssal notch in adults. The *Arctotis* Group included Oxfordian—Valanginian forms of *Canadarctotis*, juveniles of which did not maintain the resilifer of their ancestors. The byssal complex showed a smaller ligament area and shortened byssal auricle, more strongly oblique than the ligament groove in relation to the hinge line of the right valve, than in the second group. All these three groups were related by forms with intermediate states of various elements of the ligament and byssal blocks.

The ligament area, constituting part of the ligamental complex, maintained its triangular shape in the entire family, changing its inclination in relation to the plane of the commissure. An increase in the inclination of the ligamental plate of the left valve and the accentuation of the curvature of the outer side of the pseudoligamental plate in the right valve in the Pliensbachian—Toarcian *Meleagrinella* resulted in a change in the position of various parts of the hinge. The change of the position of the components of the ligament complex in relation to other parts of the shell led to the appearance of a new meron of *Meleagrinella* in the Aalenian and of a new genus-group taxon *Arctotis*. A group of Toarcian species with a ligament block suggesting an intermediate position between the Aalenian *Arctotis* and Pliensbachian *Praemeleagrinella* is assigned by us to the subgenus *Praearctotis*. Based on

the presence of a bulge on the pseudoligamental plate of the left valve, resembling the denticle of *Meleagrinella*, the Late Toarcian *Praearctotis marchaensis* (Plate I, Fig. 10a) and *Praearctotis viliuensis* (Plate I, Fig. 12a) are considered as transitional forms from *Praemeleagrinella* to *Arctotis*.

CONCLUSIONS

A comparative study of individual and age-related variability in members of the family Oxytomidae resulted in two versions of phylogenetic reconstructions for the *Meleagrinella* and *Arctotis*, based, respectively, on cladistic and evolutionary methods. The characteristics allowing delimitation of supraspecific taxa in the spatial-temporal continuum are defined.

(1). The evolutionary reconstruction of the phylogeny generally corresponds to the cladistic-based reconstruction. The main difference is the position of the supraspecific taxon *Meleagrinella* s. str., descending either from *Praemeleagrinella* (according to the evolutionary analysis, see Fig. 3a), or from *Praearctotis* (as suggested by the cladistic method, see Fig. 3b). Additional examination of hinge structures in specimens of Aalenian oxytomids, may allow us to resolve this uncertainty.

(2) Novel phenes are characteristics that allow delimitation of supraspecific taxa. The formation of the supraspecific taxon is completed by integration of several phenes at the origin of novel morphological structures providing new adaptations.

The formation of genus-group taxa of oxytomids occurred through the appearance of new phenes in many individuals across large territories. For instance, the angular subtype of the ligamental plate was a prototype of the spoon-like resilifer in the genus *Arctotis* and evolved in various populations in a group of *Praearctotis* species synchronously across the territory of the Vilyui (temperate) and Nordvik (northern temperate) epicontinental seas.

New accelerative forms appearing in populations can potentially provide a mechanism for the formation of a new phene. The change in the time of appearance and rate of the development of organs in descendants of oxytomids compared to their ancestors (heterochrony) is the basis of the systemstics of the genera *Meleagrinella* and *Arctotis*. The presence of accelerative forms with resilifers, with a new pattern of ontogenetic changes in the Hettangian and Callovian populations, defined the direction of the *Meleagrinella* phylogeny.

The formation of a new genus-group taxon of oxytomids was not accompanied by a sharp change in the adaptive type. The transitional period from one adaptive equilibrium to another was relatively long and was not characterized by a high rate of evolutionary transformation. Changes in adaptive types in the genus *Arctotis* from species with a solely byssal attachment to

those with an "anchor" attachment in adults continued from the Toarciana to the Bajociana (ca. 11.4 Ma).

ACKNOWLEDGMENTS

APPENDIX 1

LIST OF ALL SPECIMENS STUDIED

Repositories of studied specimens: F.N. Chernyshev TsNIGR Museum, St. Petersburg (TsNIGR), collection of I.V. Polubutko, All-Russia Research Geological Institute, St. Petersburg (VSEGEI), Paleontological and Stratigraphic Museum of Mining University, St. Petersburg (GU), Museum of all-Russia Petroleum Research Exploration Institute, St. Petersburg (VNIGRI), The Museum of the Institute of Petroleum Geology and Geophysics, Siberian Branch, Russian Academy of Sciences, Novosibirsk (INGiG SO Russian Academy of Sciences (RAS) (TsSGM)) and the collection of B.N. Shurygin, Novosibirsk (INGiG SO RAS). Specimens with no repository indicated were collected by O.A. Lutikov and are housed in the Siberian Research Institute of Geology, Geophysics and Mineral Resources, Novosibirsk (SNIIGGiMS).

Specimens studied were collected from the following regions: northern Central Siberia (Eastern Taimyr, Nordvik Peninsula, Anabar Bay, Nordvik Field); rivers Anabar, Lyungdyul, Levaya Boyarka, Boyarka, Kyra-Khos-Teryuteekh, Molodo, Motorchuna, Lena (near the village of Zhigansk); center of Central Siberia (rivers Vilyui, Tyung, Markha; Tengelyakh Field, Lena River near the Kangalakh Rock), Transbaikalia (Gazimur River), northeastern Siberia (Kedon and Astronomicheskaya rivers), Western Siberia (South Chulym Field), Central Russia (Vladimir Region), Far East (Bochara, Serbikan Rivers).

Praemeleagrinella subolifex Polubotko, 1968, type species: holotype no. 51-4g/R-64/2, type specimen 51-4g/R-64/1, Northeastern Siberia, Kedon River, Hettangian, collection I.V. Polubotko (VSEGEI); specimens from the adjacent area: KR-120/43, KR-119/44, Kyra-Khos-Teryuteekh River, Hettangian−Sinemurian; AG-60/67, Anabar Bay, Hettangian−Sinemurian.

Praemeleagrinella tiungensis (Petrova, 1947): holotype no. 446/5393, type specimens 438-451, Tyung River, Upper Pliensbachian, TsNIGR; specimen from the type chronocline AN-15/2, Anabar River, Upper Pliensbachian, from the collection of G.T. Petrova.

Praemeleagrinella sparsicosta (Petrova, 1947): holotype no. 689/5393, Tyung River, Early Pliensbachian, TsNIGR; specimens from the type chronocline: T-94/2, T-165/2, Tyung River, Upper Pliensbachian.

Praearctotis marchaensis (Petrova, 1947), type species: holotype no. 574/5393, type specimens 573/5393, 575/5393, Markha River, Upper Toarcian, TsNIGR; specimens from the type chronocline: MX-111/1, MX-111/2, Markha River, Upper Toarcian; specimen from the type chronocline TX-35/2, Tengelyakh Field, line 1080, borehole 350, depth 35 m, Upper Toarcian; specimens from the type chronocline AG-37/1, Anabar Bay, Upper Toarcian.

Praearctotis milovae (Okuneva, 2002): holotype no. 47/12919, type specimens 44-46/12919, Gazimur River Basin, Upper Toarcian, TsNIGR; specimens from an adjacent area: TX-1/2, TX-1/3, TX-1/4, Tengelyakh Field, line 1060, borehole 350, depth 31 m, Lower−Upper Toarcian; AG-103/4, Anabar Bay, Lower−Upper Toarcian; specimens from an adjacent area AK-77/1, Astronomicheskaya River (Kolyma Rive Basin), Lower−Upper Toarcian.

Praearctotis vai Bodylevsky, 1947: holotype no. 7/306, type specimen 8/306, Nordvik Peninsula, Yuryung-Tumus Cape, Upper Toarcian, GU, collection of B.I. Bodylevsky; specimen from the type chronocline AG-37/1, Anabar Bay, Outcrop 4, Bed 18, Upper Toarcian.

Praearctotis viluiensis Velikzhanina, 1966: holotype after Velikzhanina (1966, Plate III, Fig. 1), Vilyui River, Upper Toarcian−Lower Aalenian, VNIGRI; specimens from an adjacent area: MH-216/1, MH-216/2, Motorchuna River, Upper Toarcian; TR-19/1, Eastern Taimyr (Tsvetkova Cape), Upper Toarcian; specimen from a distant chronocline 6/3826, Nalchik Region, Chegem, Upper Toarcian, TsNIGR, collection V.F. Ptchelintseva.

Arctotis lenaensis (Lahuzen, 1886), type species: holotype no. 5/10942, type specimen 5/10942, Lena River, (near the village of Zhigansk), Bathonian, TsNIGR; type specimen 5/216, GU, Lena River, (near the village of Zhigansk), Bathonian, collection of I.I. Lahuzen.

Arctotis tabagensis (Petrova, 1953): holotype no. 602/5393, type specimens: 603/5393, Lena River, Kangalakh Rock, Aalenian, TsNIGR, collection G.T. Petrova; specimens from the type chronocline: MD-1, MD-2, Molodo River, Lower Aalenian; AG-116/1, AG-116/2, Anabar Bay, Upper Aalenian.

Arctotis sublaevis (Bodylevsky, 1958): holotype no. 123/238, Nordvik Field, borehole 1-R, depth 92.5 m, Bajocian, GU; specimens from the type chronocline: AN-18/1, 18/2, 18/3, Anabar River, Lower Bajocian.

Clathrolima lalmenti Cossmann, 1908, type species: lectotype figured by Cossmann (1908, Plate II, Fig. 8, text-figure), Bathonian, France.

Clathrolima doneziana (Borissiak, 1909): holotype no. 24/311, Ukraine, Donets Region, village of Kovalevka, Bajocian, TsNIGR; specimens from an adjacent area: MK-142/3, MK-142/2, Mangyshlak Peninsula, Bajocian, VNIGRI, collection of Yu.S. Repin.

Clathrolima braamburiensis (Phillips, 1829): holotype not established, specimens from the type chronocline figured by Duff (1978, p. 58−61), UK, Callovian; specimens from a distant chronocline: MK-152/2, MK-152/4, Mangyshlak Peninsula, Middle Callovian, VNIGRI, collection Yu.S. Repin.

Clathrolima subovalis (Zakharov, 1966): holotype no. 150/4135, Levaya Boyarka River, Lower Kimmeridgian, TSSGM; specimens from an adjacent area: YUCH-1, YUCH-2, YUCH-3, YUCH-4, South-Chulym Field, borehole 1, interval 1205.4−1213.4 m, Volgian−Kimmeridgian.

Clathrolima subechinata (Lahusen, 1883): holotype not re, specimens from the type chronocline: 26/311, 28/311, 33/311, Vladimir Region (Dmitrievy Gory), Middle Callovian, TsNIGR, collection Borissiak.

Meleagrinella curta (Whitfield, 1880), type species: holotype not established, type specimens figured by Whitfield (1880, Plate III, Fig. 22), South Dakota, Black Hills, USA, Oxfordian.

Canadarctotis anabarensis (Petrova, 1953), type species: holotype no. 642/5393, type specimens 641/5393−643/5393, Lyungdyul River (Anabar River Basin), Valanginian, TsNIGR, collection of G.T. Petrova (Ptchelintseva); specimens from the type chronocline: BK-1, BK-2, Boyarka River, Upper Berriasian, INGiG, collection of B.N. Shurygin.

Canadarctotis simkini (Voronetz, 1938): holotype no. 157/5622, Russian Far East, Bochara River, Upper Jurassic, Oxfordian, TsNIGR, collection of N.S. Voronets; specimen from the type chronocline 67/9295, Russian Far East, Serbikan River, Oxfordian, TsNIGR, collection of G.T. Petrova (Ptchelintseva).

Canadarctotis intermedia Bodylevsky, 1960: holotype no. 5/234, Eastern Taimyr, Kamennaya River, Lower Volgian Regional Stage, GU; specimens from the type chronocline: KM-1, KM-2, Eastern Taimyr, Kamennaya River, Lower Volgian Regional Stage, INGiG, collection of B.N. Shurygin.

Oxytoma jacksoni (Pompeckj, 1899): holotype not established, type specimens figured by Pompeckj (1898, Plate I, Figs. 13−14, 16); specimens from an adjacent area: TX-1/1, Tengelyakh Field, line 870, borehole 505, depth 9 m, Sample 1, Upper Toarcian−Lower Aalenian; AG-115/1, Anabar Bay, Outcrop 5, Bed 90, Sample 115, Lower Aalenian.

APPENDIX 2

MORPHOLOGICAL CHARACTERISTICS AND THEIR TAXONOMIC DISTRIBUTION

Characteristic 1. Type of the resilifer: 0, rectangular (*Oxytoma*); 1, elongated triangular (*Praemeleagrinella*, *Clathrolima*, *Meleagrinella*, *Praearctotis*, *Arctotis*, *Canadarctotis*, *Canadotis*).

Character 2. Subtype of the resilifer: 0, upright (*Oxytoma*, *Praemeleagrinella*, *Clathrolima*); 1, spoon-like (*Arctotis*, *Canadarctotis*, *Meleagrinella*, *Canadotis*); 2, angular (*Praearctotis*).

Characteristic 3. Ontogenetic trend of the resilifer: 0, oblique (*Oxytoma*, *Praemeleagrinella*, *Clathrolima*); 1, expanding (*Praearctotis*, *Arctotis*, *Canadarctotis*, *Canadotis*, *Meleagrinella*).

Characteristic 4. Shape of the resilifer in adults: 0, strongly oblique (*Clathrolima*, *Oxytoma*); 1, weakly oblique (*Praemeleagrinella*); 2, elongated triangular (*Praearctotis*, *Arctotis*, *Canadarctotis*, *Canadotis*, *Meleagrinella*).

Characteristic 5. Shape of the byssal auricle: 0, subquadrangular (*Praemeleagrinella*, *Meleagrinella*, *Clathrolima*, *Canadotis*); 1, subtriangular (*Oxytoma*, *Praearctotis*, *Arctotis*, *Canadarctotis*).

Characteristic 6. Presence of a denticle: 0, present (*Praemeleagrinella*, *Clathrolima*); 1, partly reduced (*Praearctotis*); 2, absent (*Oxytoma*, *Arctotis*, *Canadarctotis*, *Meleagrinella*, *Canadotis*).

Characteristic 7. Byssal notch: 0, open (*Oxytoma*, *Praemeleagrinella*, *Praearctotis*, *Clathrolima*, *Meleagrinella*, *Canadotis*); 1, overgrown (*Arctotis*, *Canadarctotis*).

Characteristic 8. Left valve ornamentation: 0, radial ribs differentiated into 1−2 orders (*Praemeleagrinella*, *Clathrolima*, *Praearctotis*, *Meleagrinella*, *Canadotis*); 1, radial ribs differentiated into 3−4 orders (*Oxytoma*, *Arctotis*, *Canadarctotis*).

Characteristic 9. Shape of the pseudoligamental plate of the left valve: 0, curved (*Praearctotis*, *Arctotis*, *Canadarctotis*, *Meleagrinella*, *Canadotis*); 1, upright (*Oxytoma*, *Praemeleagrinella*, *Clathrolima*).

Characteristic 10. Relative length of the ligamental plate: 0, very long (*Oxytoma*); 1, long (*Praemeleagrinella*, *Clathrolima*, *Praearctotis*); 2, short (*Arctotis*, *Meleagrinella*, *Canadotis*); 3, very short (*Canadarctotis*).

Characteristic 11. Relative convexity of right and left valves: 0, biconvex (*Praemeleagrinella*, *Clathrolima*, *Praearctotis*, *Canadotis*); 1, flattened-convex (*Oxytoma*, *Arctotis*); 2, concave-convex (*Canadarctotis*).

APPENDIX 3

MATRIX OF THE CHARACTER STATES USED IN CLADISTIC ANALYSIS

Oxytoma	0	0	0	0	1	2	0	1	1	0	1
Praemeleagrinella	1	0	0	1	0	0	0	0	1	1	0
Meleagrinella	1	1	1	2	0	2	0	0	0	2	0
Praearctotis	1	2	1	2	1	1	0	0	0	1	0
Canadotis	1	1	1	2	0	2	0	0	0	2	0
Clathrolima	1	0	0	0	0	0	0	0	1	1	0
Arctotis	1	1	1	2	1	2	1	1	0	2	1
Canadarctotis	1	1	1	2	1	2	1	1	0	3	2

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