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Early Cretaceous Trigoniids of the Crimea

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Abstract—This study is the first of a series of works on trigoniids (Class Bivalvia) from the Lower Cretaceous of the Crimea. It contains systematic descriptions of nine genera and 15 species and subspecies of trigoniids from the Berriasian, Valanginian, Hauterivian, and Albian of the southwestern and central Crimea. The morphology and microstructure of the shells of juvenile and young individuals of three species are discussed. The stratigraphic sections containing trigoniids are briefly described. Three species assemblages (Berriasian, Valanginian–Hauterivian, and Albian) are recognized.

Key words: Bivalves, trigoniids, Lower Cretaceous, stratigraphic significance, Crimea.

CONTENTS

INTRODUCTION

The Early Cretaceous stage in the evolution of the family Trigoniidae (Class Bivalvia) is very important. In the Early Cretaceous, 13 genera and four subfamilies emerged, the group reached considerable taxonomic diversity, developed a large number of new shell morphotypes, and became geographically widespread (cosmopolitan). These features suggest the progressive evolution of the family at that time. Subsequently, the evolution of trigoniids experienced a stage of stabilization (Late Cretaceous) and a stage of regression (Cenozoic). At present, it is a relict group.

Many occurrences of taxonomically rich Early Cretaceous trigoniid assemblages are found in the Tethyan and Peri-Tethyan regions of northern Eurasia. They are known from the Crimea, Caucasus, Central Asia, and western Kazakhstan. Trigoniids from these regions are described in many publications, mainly papers, or chapters in monographs, but there are only few major overviews of this group. The monograph by Saveliev (1958) *Lower Cretaceous Trigoniids of Mangyshlak and Western Turkmenistan* remains the best taxonomic study of this group. Saveliev (1960b) also wrote a chapter on trigoniids in *Fundamentals of Paleontology*. No large systematic study of trigoniids has appeared in Russian literature since. Several authors described a few species, or assemblages of species, characteristic of some stages in various regions. All trigoniid genera established prior to the 1960s are redescribed in *Treatise on Invertebrate Paleontology* (1969).

Large collections of trigoniids from the Jurassic, Lower and Upper Cretaceous of the Crimea, the northern Caucasus, and Central Asia are housed in the Paleontological Department of Moscow State University. Many of them are collected by myself. These collections could be the basis for several regional monographs. This study is one in this series.

The study of the Crimean material revealed new data on the shell morphology and taxonomy of this group, as well as on the stratigraphic position of trigoniid species and subspecies, which certainly should be taken into account by paleontological stratigraphic work in the Crimea. The scanning electron microscope (SEM) investigation of the morphology and microstructure of juvenile and young shells of Early Valanginian trigoniids has never been done before.

In the past 46 years, the author several times resumed his studies of trigoniids of the Crimea, as the new material accumulated. Three collections described are housed in the Earth Science Museum of Moscow University (MZ MGU), including no. 10 (Yanin, 1958), no. 39 (Yanin, 1979a), and no. 57 (Muromtseva and Yanin, 1960). New material collected after 1979, which was a basis for this study is housed in the Department of Monographic Collections of the Paleontological Institute of the Russian Academy of Sciences (PIN, no. 4925).

CHAPTER I. STRATIGRAPHY

This chapter contains brief descriptions of beds yielding trigoniids and a discussion of their stratigraphic significance. More complete stratigraphic studies of the Lower Cretaceous in the Crimea can be found in monographs by Drushchits (1960), Yanin and Vishnevskii (1989), and in recent papers by Baraboshkin and Mikhailova (1994), Baraboshkin (1997a, 1997b), Baraboshkin and Yanin (1997), Bogdanova *et al.* (1981), and Yanin and Baraboshkin (2000).

Because of the recent refinement of the stratigraphic scheme of the Lower Cretaceous of the Crimea, the geochronology of some trigoniid species described or recorded from this region has changed. All changes from previous identifications of genera and species are contained in Chapter II. 2. Emended stratigraphic positions of species are given in the descriptions of the sections. The biostratigraphic scheme for the Lower Cretaceous of the Crimean Fore-Mountains is in Table 1.

I. 1. Trigoniid Occurrences in the Lower Cretaceous of the Crimea

Trigoniids are most frequently found in the Berriasian, Valanginian, and Hauterivian beds of the southwestern and central Crimea, and, more rarely, in the Upper Albian of the southwestern regions and Barremian of the central regions of the Crimean Peninsula (the latter are redeposited). Occasionally, they are found in the Albian of the Crimean Plain. In the eastern Crimea, trigoniids are not found, because the Lower Cretaceous deposits there are usually represented by deep water clayey and marly facies. The major sections and outcrops containing trigoniids are described below.

The stratigraphic position of beds and members in the sections is shown by indices. The descriptions of sections in the text contain only the names of trigoniid species and lists of groups from the faunal assemblage of the respective bed. In some cases, the ammonite species are listed to provide a better correlation with the ammonoid geochronology. The sections are described and numbered in accordance with their geographic position in the southwestern and central Crimea (from west to east) (Fig. 1).

Vicinity of the Town of Balaklava

Trigoniids are recorded for the first time from this area. The material was collected by myself in 1989 and by E.Yu. Baraboshkin in 2002 from sandstone nodules in a member of flyschoid interbedding clays and marls dated Middle Albian (*dentata* Zone) (Outcrop no. 1). Upward in the section, the sandstone is overlain by Upper Albian clay containing *Aucellina gryphaeoides* (Sow.). The member outcrops in the eastern wall of the limestone quarry in the northwestern suburb of the town of Balaklava. Beds contain the trigoniid species *Rutitrigonia balaklavensis.*

Basin of the Chernaya River

Trigoniids are found in the series of sandstones interbedded with siltstones and clay dated Lower Berriasian (village of Kuchki) and in the Middle Albian sandstone (village of Verkhnee Chernorech'e).

The village of Verkhnee Chernorech'e (Outcrop no. 2). The casts of *Pterotrigonia taurica* and shells of *Rutitrigonia balaklavensis* are found in the vicinity of the village in sandstone that also contains many plant remains. The same sandstones (total thickness, ca. 50 m) overlying the eroded surface of the Tithonian limestones contained the Middle Albian ammonite *Hoplites dentatus* (Sow.).

The village of Kuchki (Section no. 3). The section studied by myself in 1959 contained *Pterotrigonia caudata* and *Rutitrigonia longa.* These trigoniids were reported by Yanin and Smirnova (1981). The section on the left bank of Kuchkinskii Creek (tributary to the Chernaya River), 1 km south of the village of Kuchki contains (Fig. 2):

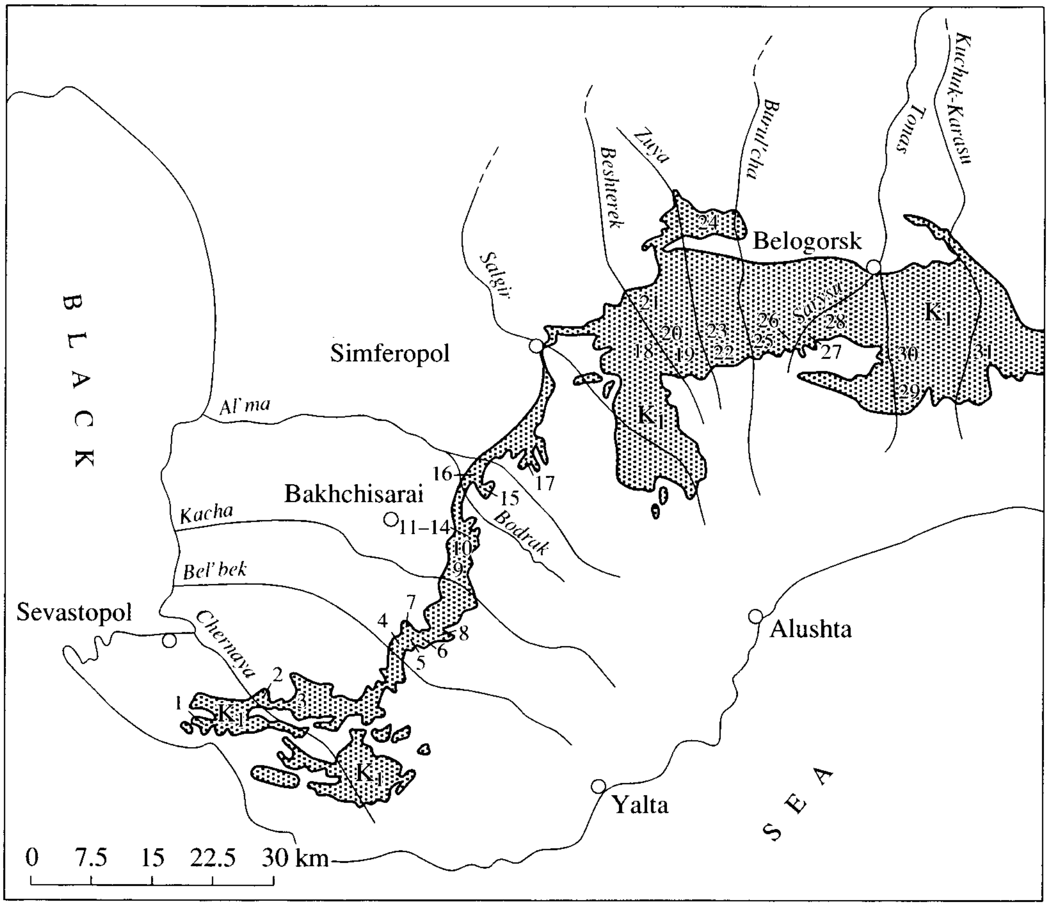


Fig. 1. Trigoniid localities in the Lower Cretaceous beds of the Crimean Fore-Mountains: (*1*) vicinity of the town of Balaklava; (*2–3*) basin of the Chernaya River: (*2*) village of Verkhnee Chernorech'e, (*3*) vicinity of the village of Kuchki; (*4–8*) basin of the Bel'bek River: (*4–6*) vicinity of the village of Golubinka: (*4*) Kabanii Gully, (*5*) Sbrosovyi Gully, (*6*) Bezymyannyi Gully; (*7*) vicinity of the village of Kuibyshevo; (*8*) vicinity of the village of Solnechnosel'e; (*9–10*): basin of the Kacha River: (*9*) village of Verkhorech'e, (*10*) Kayas-Dzhilga Ravine; (*11–15*): basin of the Bodrak River: (*11*) Nikolaev Yar Gully, (*12*) Dlinnaya Mountain, (*13*) village of Prokhladnoe, (*14*) Patil' Mountain, (*15*) Pervomaiskii Quarry, (*16*) vicinity of the village of Trudolyubovka; (*17*) basin of the Al'ma River, vicinity of the village of Konstantinovka; (*18*) basin of the Malyi Salgir River, village of Ivanovka; (*19–21*): basin of the Beshterek River: (*19*) village of Solov'evka, (*20*) village of Lesnosel'e, (*21*) village of Mazanka; (*22–23*): basin of the Zuya River: (*22*) vicinity of the village of Krasnogorskoe, (*23*) Balanovskoe Water Reservoir; (*24*) Zuya–Burul'cha interfluve, Zuiskii Quarry and Kunich Mountain; (*25*) basin of the Burul'cha River, village of Mezhgor'e; (*26–28*) basin of the Sarysu River: (*26*) vicinity of the village of Blagodatnoe, (*27*) village of Chernokamenka, (*28*) village of Novoklenovo; (*29–30*) basin of the Tonas River: (*29*) village of Krasnoselovka, (*30*) vicinity of the village of Golovanovka; (*31*) basin of the Kuchuk-Karasu River, village of Gorlinka; (K_1) exposures of the Lower Cretaceous beds.

K_1Ber_1. Underlying beds (>20 m) are composed of platy, micritic and bioclastic limestone forming the steep wall of a narrow canyon.

K_1Ber_1. Bed 1 (10 m). Rhythmic alternation of loose layers and compact plates of sandstone and limestone (especially in the lower part) with abundant plant remains. One of the small outcrops shows clayey sandstone overlying the uneven surface of the limestone. The rocks of this bed are well exposed on the lower slope of the valley, across the road leading to the east from the village to the Manester Gully, whereas the lower part of the bed was observed in a field used as a peach orchard (in this section, a spongy horizon is exposed). The bed contains sponges, solitary and colonial corals, bivalves (including *Rutitrigonia longa*), ammonites, belemnites, echinoids, crinoids, bryozoans, and brachiopods.

Bed 2 (6 m). Sandy clay and siltstone with rare intercalations of compact sandstone. Fossils include belemnites, echinoids, crinoids, and brachiopods.

Bed 3 (11 m). Alternation of loose and compact sandstone, containing small sideritic nodules. At the base of the bed, the rock forms a bench (1 m) of compact calcareous sandstone with oncolites and holes of decapods. Fossils include bivalves (including *Rutitrigonia longa*), ammonites, echinoids, crinoids, and brachiopods.

K_1Ber_2. Overlying beds (>20 m) are compact, platy sandstones with quartz pebbles and algal nodules.

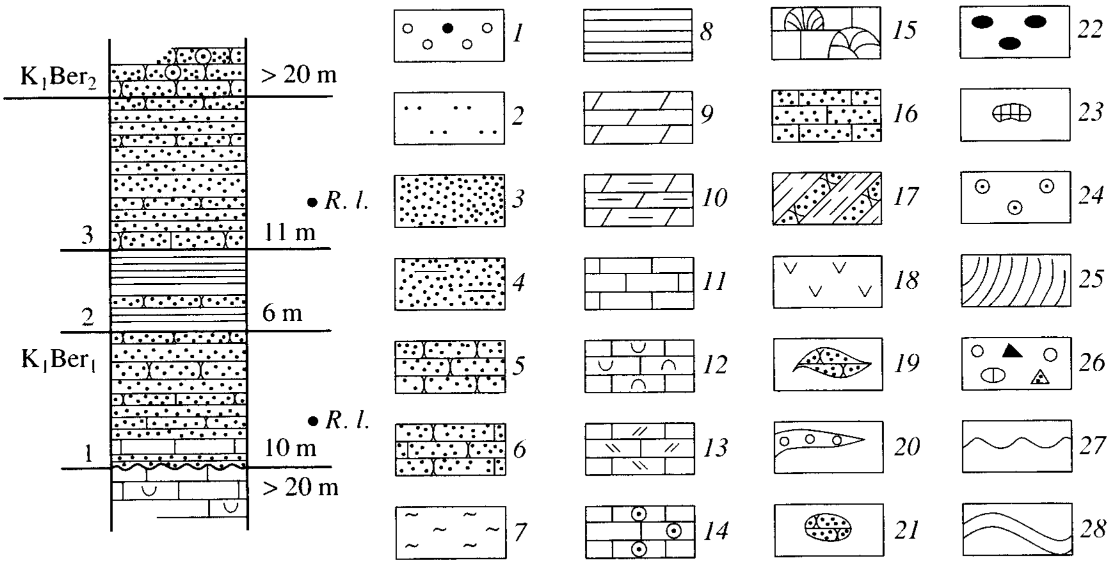


Fig. 2. Section no. 3 in the vicinity of the village of Kuchki. Explanations: (*1*) conglomerate; (*2*) gravelite; (*3–6*) sandstone: (*3*) loose and weakly cemented, (*4*) slightly clayey, (*5*) compactly cemented, and (*6*) strongly calcareous; (*7*) siltstone; (*8*) clay; (*9*) marl, (*10*) clayey marl; (*11–16*) limestone: (*11*) micritic, (*12*) bioclastic, (*13*) detrital, (*14*) oncolitic, (*15*) bioherm, and (*16*) sandy; (*17*) rocks of the Tavria Formation; (*18*) rocks of the Karadag Formation; (*19*) sandstone lenses; (*20*) pebble rock lenses; (*21*) sandstone nodules; (*22*) siderite concretions; (*23*) nodules of sponges; (*24*) oncolites; (*25*) cross-bedding; (*26*) pebbles of various composition; (*27*) surface of unconformity; (*28*) reduced thickness in the section; abbreviations of the trigoniid species and subspecies names: (*I. s.*) *Iotrigonia scapha*, (*L. b.*) *Linotrigonia bel'bekensis*, (*L. in.*) *Litschkovitrigonia inguschensis*, (*L. or.*) *Linotrigonia ornata*, (*M. l.*) *Myophorella loewinsonlessingi*, (*O. m.*) *Orthotrigonia mordvilkoae*, (*P. c.*) *Pterotrigonia caudata*, (*P. t.*) *Pterotrigonia taurica*, (*Q. n. o.*) *Quadratotrigonia nodosa orbignyana*, (*R. l.*) *Rutitrigonia longa*, (*T. c.*) *Trigonia carinata carinata*, (*T. c. c.*) *Trigonia carinata crimica*; abbreviations of the ammonite zones (Z.): (*E. t.*) *Eleniceras tauricum*, (*H. t.*) *Himantoceras trinodosum*, (*K. o.*) *Kilianella otopeta*, (*L. l.*) *Leopoldia leopoldina*, (*L. n.*) *Lyticoceras nodosoplicatum*, (*S. v.*) *Saynoceras verrucosum*, (*T. c.*) *Teschenites callidiscus*, and (*Th. p.*) *Thurmanniceras pertransiens*; (Bd.) beds with (*M. m.*) *Malbosiceras malbosi*; stratigraphic units: (J_1tv) Lower Jurassic, Tavria Formation; (J_2k) Middle Jurassic, Karadag Formation; (K_1) Lower Cretaceous: (*Ber*) Berriasian, (Vlg) Valanginian, (*Hau*) Hauterivian, (*Brm*) Barremian; (K_2Cen) Upper Cretaceous, Cenomanian; (*Ng*) Neogene; (1, 2) lower and upper substages.

Basin of the Bel'bek River

Karakash (1907) was the first to record trigoniids in the Lower Cretaceous exposed in the basin of the Bel'bek River. He found *"Trigonia"* sp. in the Neocomian (now Lower Berriasian) "dark gray loosely cemented sandstone" on the northern slope of the gully joining the valley of the Bel'bek River from the east, near a post marking the boundary between the Simferopol and Yalta districts (Karakash, 1907, p. 350). Fifty years later, I collected and identified *"Trigonia" loewinsonlessingi*, *"T." caudata*, and *"T." longa* from the same bed in the same gully (Yanin, 1957; Drushchits and Yanin, 1958). The species *"T." caudata* was also cited by Drushchits and Yanin (1958) from the brownish yellow sandstone exposed in the Sbrosovyi Gully between the upper (quartz) Valanginian conglomerates (presently dated Upper Berriasian) and the Lower Hauterivian clay with aptychi.

In 1958, I described for the first time *Myophorella loewinsonlessingi* from the "loosely-cemented sandstone" [alternating Lower Valanginian (presently Lower Berriasian) rocks]. I redescribed the same species in 1960, and in the same paper described *Rutitrigonia longa*. Later, I systematically redescribed the previously known species (Yanin, 1979a) *Myophorella loewinsonlessingi, Rutitrigonia longa*, and *Pterotrigonia caudata* from the vicinity of the village of Golubinka and described the new species *Linotrigonia* (*Oistotrigonia*) *belbekensis* (village of Golubinka) and *Myophorella* (*Orthotrigonia*) *mordvilkoae* from the village of Solnechnosel'e. Bogdanova *et al.* (1997) redescribed these species and figured the specimens, housed in the Museum of the St. Petersburg Mining Institute. All these specimens come from the Lower Berriasian series of rock alternation in the Kabanii Gully.

Identifications of some of the above species from this area are cited in stratigraphic papers, including Drushchits (1960) [*Pterotrigonia caudata* from the sandstone (8–10 m) containing ferruginous quartz pebbles (Sbrosovyi Gully; Lower Hauterivian)]; Kravtsov and Shalimov (1978) [*Myophorella loewinsonlessingi* from the Berriasian (conglomerates at the base of the series of rock alternation in the Orekhovyi Gully), *Myophorella loewinsonlessingi, Rutitrigonia longa*, and *Pterotrigonia caudata* from upper part of the Berriasian (alternating rocks in the Kabanii Gully), and *Pterotrigonia caudata* from the so-called pudding sandstone (Valanginian) in the Sbrosovyi Gully]; Yanin and Smirnova (1981) (*Myophorella loewinsonlessingi*, *Rutitrigonia longa*, *Pterotrigonia caudata*, and *Linotrigonia belbekensis* from the Berriasian of the Kabanii Gully, and *Pterotrigonia caudata*, *Rutitrigonia longa*, and *"Vaugonia" mordvilkoae* from the Berriasian near the village of Solnechnosel'e); Plotnikova *et al.* (1984) (*Myophorella loewinsonlessingi* from the Berriasian, most likely from the Kabanii Gully); Yanin and Vishnevskii (1989) [*Myophorella loewinsonlessingi* from the Upper Berriasian (Members II and III, as designated in the paper cited, in the Kabanii Gully)]; Yanin and Baraboshkin (2000) (*Myophorella loewinsonlessingi*, *M. mordvilkoae*, *Rutitrigonia longa*, *Pterotrigonia caudata*, and *Linotrigonia belbekensis* from the member of the Lower Berriasian sandstone and oncolitic limestone in the Kabanii Gully and *Pterotrigonia caudata* and *Linotrigonia belbekensis* from conglomerates at the base of the alternating rock series in the Bezymyannyi Gully on the slope of Konglomeratovaya Mountain.

Trigoniids from the Berriasian (six species) occurring the Kabanii, Bezymyannyi, and Orekhovyi gullies in the vicinity of the village of Golubinka and the village of Solnechnosel'e (village of Gornoe) are the most diverse. Only one occurrence of the Valanginian *Pterotrigonia caudata* is known from the Sbrosovyi Gully.

Kabanii Gully (Section no. 4). Outcrops in the right slope of the gully, 250 m from the road from Kuibyshevo to Sokolinoe, near the traffic sign 15/57 (Figs. 3, 4). For a detailed description of the section, see Yanin and Baraboshkin (2000).

Fig. 3. Outcrop of the Lower Berriasian (siltstones, sandstones, and limestones) in the right slope of the Kabanii Gully, 250 m from the road from Kuibyshevo to Sokolinoe (traffic sign 15/57 km).

K_1Ber_1. Underlying deposits. Lower polymictic conglomerates (40 m).

K_1Ber_1. Bed 1 (14.5 m). Alternating compact, strongly calcareous and loosely cemented clayey dark gray, fine-grained mainly quartz sandstones and siltstones, with abundant oncolites in the upper part of the bed. Some sandstone layers, especially compact, contain abundant fossils, mostly shells and casts of mollusks. In some horizons, they form coquinas and, sometimes, shell pavements, suggesting a shallow-water sedimentary environment with high turbulence (waves).

Trigoniids are found in the lower and middle parts of this member and are represented by both shells and casts. There are far more isolated valves than complete shells with closed valves. Shells in the live position are not found. The valves are variously preserved. Only occasional valves show traces of erosion. Some valves possess well-preserved ornamentation (transverse hatching on the costae and nodes and spines on the keels and costae). The member contains a rich invertebrate assemblage (foraminifers, solitary scleractinia, gastropods, and bivalves). Bivalves are represented by 37 species, five of which are trigoniids (*Myophorella loewinsonlessingi*, *Orthotrigonia mordvilkoae*, *Rutitrigonia longa*, *Pterotrigonia caudata*, and *Linotrigonia belbekensis*); they are accompanied by the ammonites *Dalmasiceras crassicostatum* (Djan.), *Ptychophylloceras semisulcatum* (d'Orb.), *Prototrigonites tauricus* Kulj.-Vor.; belemnites, brachiopods, crinoids, etc.

K_1Ber_2. Bed 2 (10.3 m). Alternating brownish gray, fine-oncolitic and detrital platy limestones and strongly calcareous sandstones forming lenticular interbeds. Fossils include foraminifers, corals, gastropods, and bivalves (16 species, including *Myophorella loewinsonlessingi* and *Orthotrigonia mordvilkoae*, which are found in sandstone interbeds and are rarer than in Bed 1), belemnites, crinoids, echinoids, etc.

Bed 3 (6 m). Brownish gray, oncolitic, thickly platy limestones. Their top is eroded and forms a hardground. Fossils include foraminifers, bivalves, and brachiopods.

Bed 4 (4.7 m). Yellowish gray unevenly cemented sandstones, sometimes with abundant small quartz pebbles. The lower half contains two plates of oncolitic limestones. The basal part of the plates contains a horizon with well-rounded pebbles of coral skeletons and bivalve shells. The pebbles overlie the eroded surface of the limestones of Bed 3. The basal horizon contains solitary corals and bivalves (11 species, including *Myophorella loewinsonlessingi*, *Orthotrigonia mordvilkoae*, *Linotrigonia belbekensis*, *Rutitrigonia longa*), brachiopods, etc.

K_1Ber_2. Overlying beds of oncolitic and detrital thickly bedded limestones (over 10 m).

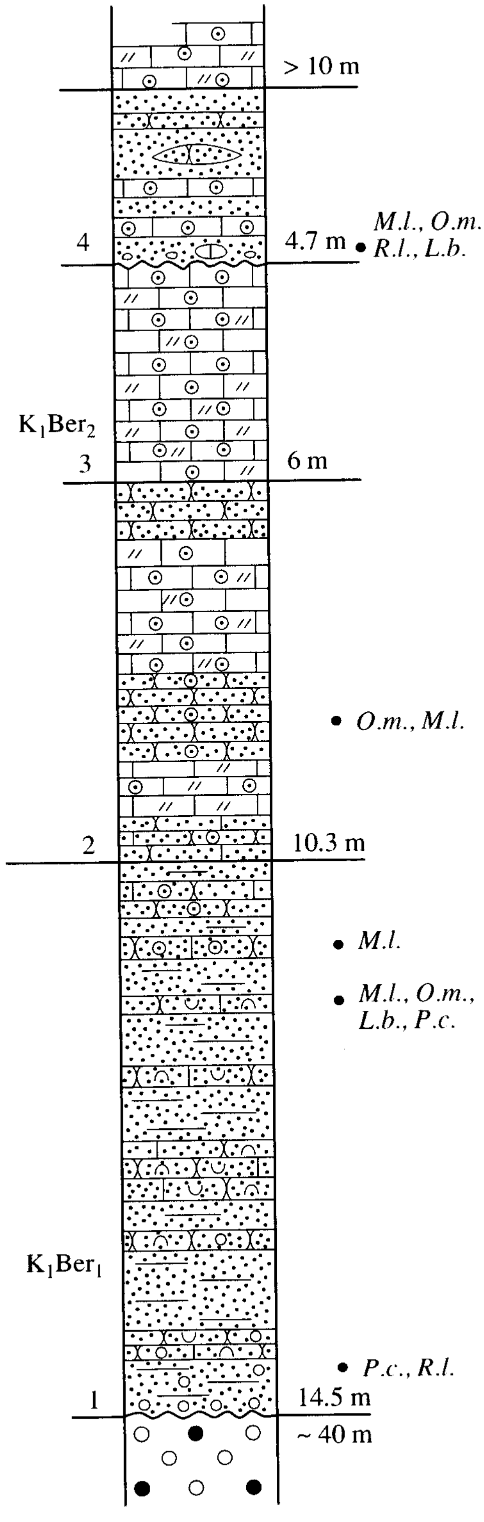


Fig. 4. Section no. 4 in the Kabanii Gully (see explanations for Fig. 2).

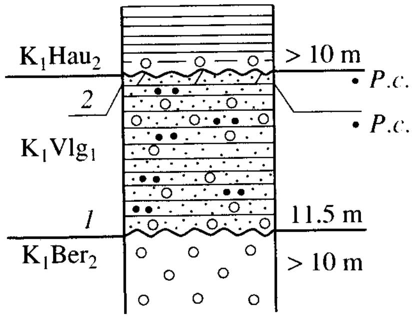


Fig. 5. Section no. 5 in the Sbrosovyi Gully (see explanation for Fig. 2).

S b r o s o v y i G u l l y (Section no. 5). The outcrop is on the southwestern slope of Konglomeratovaya Mountain, northeast of the village of Golubinka, in the lowermost slide block in the graben zone (Fig. 5). For a more complete description of this outcrop, see Baraboshkin and Yanin (1997), Arkadiev (1997), Yanin and Baraboshkin (2000).

K$_1$Ber$_2$. Underlying beds of the upper conglomerate series (over 10 m).

K$_1$Vlg$_1$. Bed 1 (11.5 m). Alternating thick plates and weakly cemented grayish brown, calcareous sandstones with abundant quartz pebbles and limonitic gravelite (so-called puddings). In the middle and upper parts of the bed, the sandstone is enriched by oolites of limonite and hydrogoethite and rare oncolites. At the base of the bed, sandstones contain larger and more abundant pebbles, and occasionally become conglomerates overlying the strongly eroded quartz conglomerates. Fossils include solitary corals, gastropods, bivalves (including *Pterotrigonia caudata*), brachiopods, etc.

Bed 2 (0.5 m). Strongly marly, weakly cemented sandstone, containing rare oncolites and rare small gravel. The bed is a condensation horizon. Fossils include solitary corals, gastropods, bivalves (including *Pterotrigonia caudata*), the ammonites *Neolissoceras grasianum* (d'Orb.), *Thurmanniceras* cf. *pertransiens* (Sayn.), *Kilianella roubaudiana* (d'Orb.), nautiloids, belemnites, brachiopods, echinoids, and crinoids. Based on the ammonite occurrences in the marly sandstone, this bed is referred to the Lower Valanginian (Beds with *roubaudiana*). The sandstones of beds 1 and 2 correlate with the equivalent rocks in the basin of the Kacha River at the base of the section, where they are referred to the *Kilianella otopeta* and *Thurmanniceras pertransiens* zones (Baraboshkin and Yanin, 1997; Yanin and Baraboshkin, 2000).

K$_1$Hau$_2$. Overlying beds of clay with the aptychus *Lamellaptychus angulicostatus* (Pict. et Lor.).

B e z y m y a n n y i G u l l y (Section no. 6). Trigoniids are only found in the base of the Lower Berriasian alternating rock series. I studied this outcrop in 1956 and 1963.

K$_1$Ber$_1$. Underlying beds (ca. 40 m) of polymictic (lower) conglomerates.

K_1Ber_1. Bed 1 (0.7 m). Pebble rock in loosely cemented clayey sandstone, transiting into densely packed conglomerates on the uneven surface of the underlying polymictic conglomerates.

Bed 2 (0.2 m). A plate of strongly calcareous compact conglomerate.

Bed 3 (0.6 m). Pebble rock with a clayey-sandy matrix, gradually becoming densely cemented conglomerate. Bivalves include *Pterotrigonia caudata* and *Linotrigonia belbekensis*. Trigoniids are represented by isolated valves and fragments, buried among the pebbles.

Bed 4 (0.2–0.5 m). A plate of dense sandstone. Bivalves include *Pterotrigonia caudata*.

K_1Ber_1. Overlying beds (>5 m). Alternating sandy clay, siltstone, and sandstone beds (the continuation of the alternating rock series).

T a m i s h' G r o v e (Outcrop no. 7). This outcrop is located on the right bank of Lagernyi Creek to the north of the former field station of Leningrad Mining Institute. This outcrop contains an alternating series of sandstone, siltstone, and clayey layers similar to that described above in the Kabanii Gully. The series overlies the lower polymictic Lower Berriasian conglomerates and is overlain with unconformity by the Cenomanian glauconite sandstones yielding a basal pebble layer (Yanin and Vishnevskii, 1989). Of trigoniids, *Rutitrigonia longa* is the most abundant, while *Myophorella loewinsonlessingi* occurs more rarely. Both species are represented by isolated valves, with their convex side oriented upwards (to form a shell pavement) (Pl. 7, fig. 9). The samples were collected by myself over several years beginning from 1956.

Village of S o l n e c h n o s e l'e (Section no. 8). The section is to the north of the village (on some maps, the village is called "Gornoe village"), on the slope of a limestone crest. The section is described here for the first time (Fig. 6) based on my studies of 1956, 1959, 1962, and 1975.

K_1Ber_1. Underlying beds, lower polymictic conglomerates (>10 m).

K_1Ber_1. Bed 1(18 m). Rhythmic alternation of compact layers of brownish gray strongly sandy, oncolite-detrital limestones, compact plates of yellowish gray, variously calcareous sandstones and interbeds of yellow, weakly cemented, variously grained sandstones. Sandstone interbeds are dominant in the lower part of the bed. Toward the top, the carbonate content increases. The thickness of the plates ranges from 0.2 to 0.55 m, and the sandstone interbeds are 0.2 to 1 m thick. At the base of the bed (lower 2–3 m), there are two plates (0.25 and 0.35 m thick) of small-pebbled conglomerates. The upper plate contains abundant bivalvian shells, including trigoniids. This plate is underlain and overlain by weakly cemented clayey sandstones with abundant quartz pebbles. Fossils are mainly found in compact layers and include sponges, solitary corals, serpulids, bivalves (including *Trigonia carinata crimica, Orthotrigonia mordvilkoae, Rutitrigonia longa,*

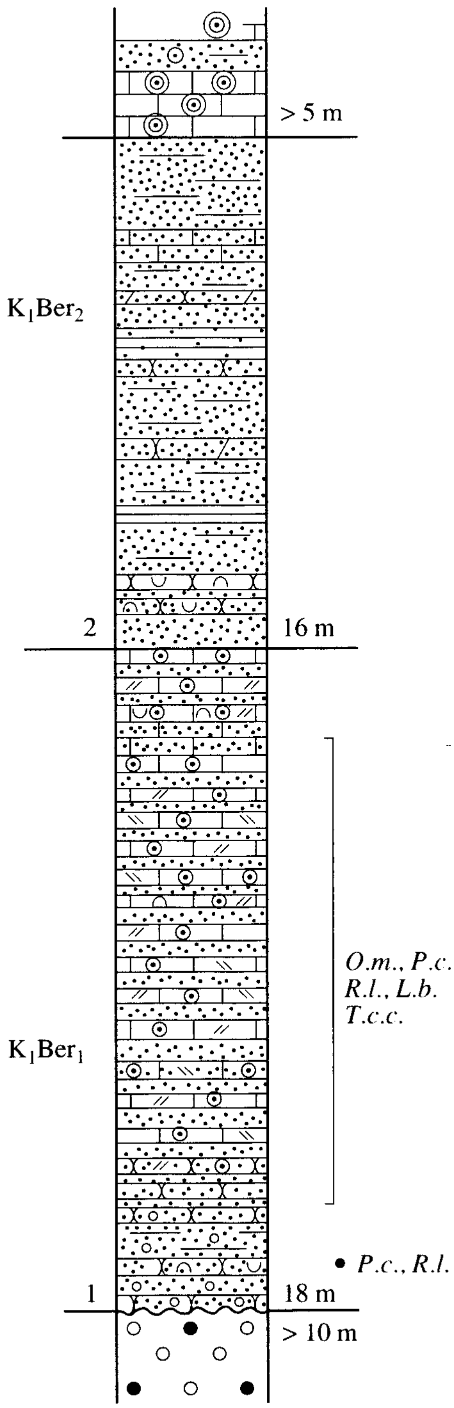


Fig. 6. Section no. 8 in the vicinity of the village of Solnechnosel'e (see explanations for Fig. 2).

Pterotrigonia caudata, Linotrigonia belbekensis), gastropods, ammonites *Kilianiceras janini* Drush., belemnites, brachiopods, echinoids, etc.

K_1Ber_2. Bed 2 (16 m). Irregular alternation of plates (0.1–0.8 m) of gray, bedded, fine-grained compact, calcareous, in the middle part, marly, sandstones containing many carbonaceous plant remains and interlayers

Fig. 7. Outcrop of the Valanginian and Hauterivian on the southeastern slope of Belaya Mountain and the eastern slope of Rezanaya Mountain (basin of the Kacha River, vicinity of the village of Verkhorech'e).

(0.8–3.5 m) of dark gray, clayey, fine-grained, bedded, loosely cemented sandstone. An interbed of silty clay occurs in the middle part of the bed of clayey sandstone. Fossils include corals, serpulids, bivalves, gastropods, ammonites, nautiloids, belemnites, brachiopods, and echinoids. Trigoniids are not found in this bed, probably because of the high clay content.

K_1Ber_2. The overlain deposits are represented by gray, compact, platy limestones (0.3–0.5 m) with large oncolites (0.5–1 cm) and interlayers (up to 5 m) of loosely cemented sandstones with abundant oncolites.

Beds 1–2 correlate with the respective beds in the Kabanii Gully. The trigoniid occurrences in this section were reported for the first time by myself in 1981.

Basin of the Kacha River

Eichwald (1865) was the first to report *"Trigonia" caudata* from the "ferruginous limestones of the village of Biasala" in his *Lethaea Rossica.* He described (but did not figure) the species based on a single, incompletely preserved specimen. Later, Karakash (1907) redescribed this species (also without illustration) based on a specimen from Eichwald's collection. Karakash (1907, p. 334) believed that *"T." caudata* comes from "the Valanginian and partly Hauterivian conglomerates of Biasala."

Species identifications of trigoniids from the Kacha section are cited in stratigraphic papers: Drushchits (1956) and Eristavi (1957) recorded *Trigonia carinata* from the Hauterivian; Yanin and Vishnevskii (1989) recorded the same species from the lower part of the Upper Hauterivian, Member X; Lychagin (1969) recorded the same species from the "lower and middle part of the series of Hauterivian sandstones, occurring 3 m above gravelites and conglomerates in the section of Mountain Rezanaya (a precise position of the occurrence is not mentioned; only a total thickness of 40 m is indicated for the series) (see also Lichagin *et al.*, 1971; Aliev *et al.*, 1985; Drushchits *et al.*, 1986). It is noteworthy that not a single specimen has been figured from this section, although trigoniids were first reported here over 130 years ago, and have been collected by many geologists since.

E.Yu. Baraboshkin restudied ammonites from the Kacha section and showed that the large part of the so-called Hauterivian beds are in fact Valanginian. Therefore, all known trigoniid occurrences from the section of Mountain Rezanaya are now dated Valanginian. Determinations of ammonites from the sections below are provided by Baraboshkin *et al.* (1997, 2000).

The village of Verkhorech'e (Section no. 9). The lower part of the section is well exposed at the base of the southeast slope of Belaya Mountain, while the upper part is exposed on the slopes and the top of Rezanaya Mountain (Fig. 7). A detailed description of the section was given by Yanin and Vishnevskii (1989) and Baraboshkin and Yanin (2000). I have been studying this section over many years beginning from 1956 (Fig. 8).

J_1tv. Underlying beds are Tavria shale.

K_1Vlg_1. Bed 1 (1 m). Basal conglomerates and so-called pudding sandstones exposed to the right of the field road from Nauchnyi to Verkhorech'e before its steep descent to the valley of the Kacha River. Fossils include solitary corals, gastropods, bivalves (including *Pterotrigonia caudata*), ammonites *Kilianella otopeta* (Thieul.), *K. roubaudiana* (d'Orb.), echinoids, etc.

Bed 2 (3 m). Irregular alternation of the plates of compact and loosely cemented sandstones and thin interbeds of silty clay. The rocks contain abundant ferruginous oolites and rare quartz pebbles. Fossils include solitary corals, gastropods, bivalves, ammonites *Thurmanniceras pertansiens* Sayn, nautiloids, belemnites, brachiopods, echinoids, etc.

K_1Vlg_2. Bed 3 (4.5 m). Alternation of plates of compact, strongly calcareous and loosely cemented sandstones, containing abundant ferruginous oolites. Fossils include gastropods, bivalves, ammonites *Neolissoceras subgrasianum* Drush., echinoids, etc.

Bed 4 (6 m). Alternation of calcareous sandstone, siltstones, and silty clay, with numerous marcasitic and phosphoritic nodules. Fossils include gastropods, bivalves, ammonites *Himantoceras* cf. *trinodosum* Thieul., *Neolissoceras grasianum* (d'Orb.), nautiloids, belemnites, brachiopods, echinoids, etc.

Bed 5 (16 m). Alternation of sandstones, siltstones, and silty clays containing marcasitic and phosphoritic nodules. Fossils include gastropods, bivalves (including *Trigonia carinata carinata*), ammonites *Teschenites neocomiensiformis* (Hohen.), *Neolissoceras subgrasianum* Drush., brachiopods, echinoids, etc.

Bed 6 (17 m). Alternation of compact and loosely cemented sandstones, siltstones, and silty clays containing rare marcasite nodules. Fossils include bivalves (including *Trigonia carinata carinata*), ammonites *Eleniceras tauricum* (Eichw.), *E. spiniger* (Koen.), nautiloids, brachiopods, etc.

K_1Hau_1. Overlying beds are composed of rhythmic alternation of compact, strongly calcareous, and weakly cemented sandstones that form the upper part of the slope and the top of Rezanaya Mountain.

Right bank of the Kayas-Dzhilga Ravine (Section no. 10) is on the southeast slope of the mountain (altitude mark, 638.8 m) situated to the southwest of the top of Sel'bukhra Mountain. I described this section in 1975–1979 along the trench of the gas pipe from Bakhchisarai to Yalta (Fig. 9).

J_1tv. Underlying beds are Tavria shale.

K_1Vlg_{1-2}. Bed 1 (10 m). Alternation of plates of compact, strongly calcareous sandstones and lesser plates of weakly cemented gray and brownish yellow sandstones. Compact varieties contain many ferruginous oolites. The basal part contains a basal conglomerate of quartz pebbles and Tavria Formation overlying the heavily eroded surface of the underlying beds. Fossils include gastropods, bivalves, and nautiloids.

K_1Vlg_2. Bed 2 (22 m). Alternation of plates of compact sandstones and lesser plates (in the uppermost part) of weakly cemented, mainly yellowish brown sandstones (the alternation of plates in the figure does not reflect their actual position, because the succession

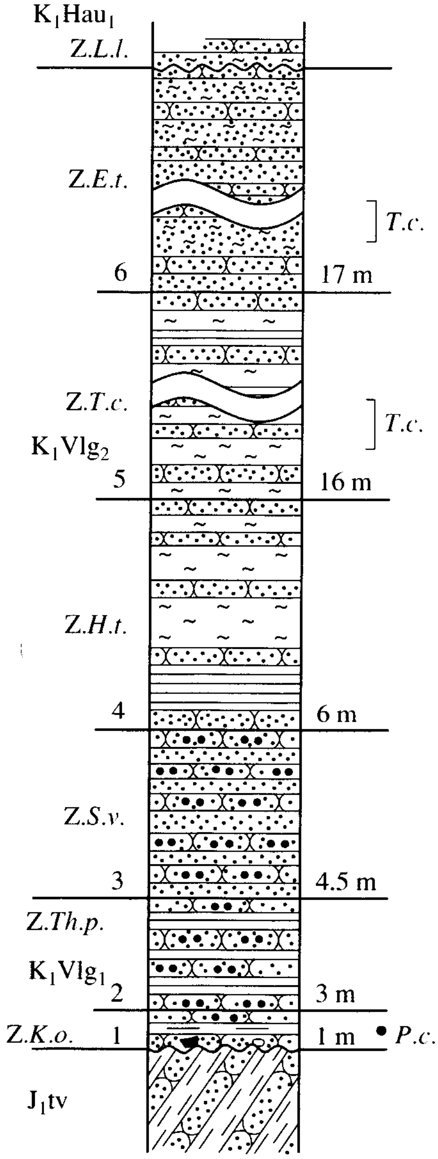


Fig. 8. Section no. 9 in the vicinity of the village of Verkhorech'e (see explanations for Fig. 2).

was partly reconstructed based on refuse rock on the sides of the trench). Some parts of this member contained thin interbeds of silty clay. Fossils include bivalves (including *Trigonia carinata carinata*), ammonites *Eleniceras nicolovi* Bresk., brachiopods, echinoids, nautiloids, etc.

K_1Hau_2. Overlying beds are "cephalopod" oolitic limestones.

Basin of the Bodrak River

Eristavi (1957) was the first to record Early Cretaceous trigoniids from this region in his stratigraphic paper. He indicated *Trigonia carinata* from the yellow loose Hauterivian sandstone on the eastern slope of

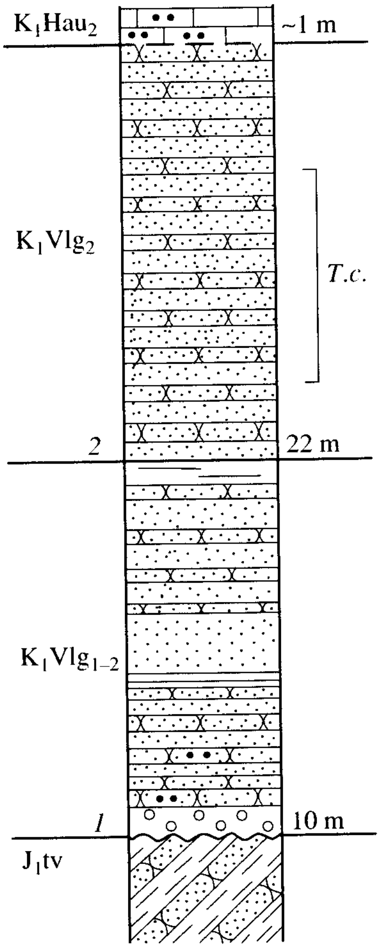


Fig. 9. Section no. 10 in the Kayas-Dzhilga Ravine, on the southeastern slope of summit 638.8 m (right tributary of the Kacha River) (see explanations for Fig. 2).

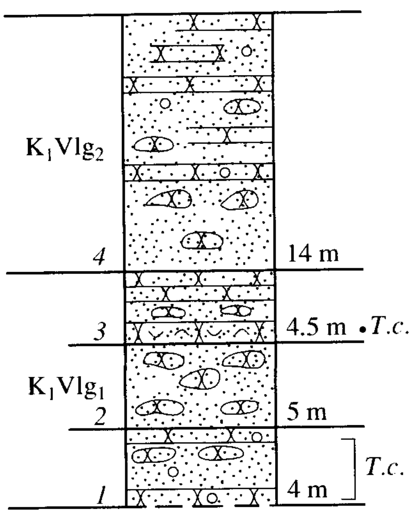


Fig. 10. Section no. 11 in the right bank of the Nikolaev Yar Gully (see explanations for Fig. 2).

Prisyazhnaya Mountain. I made the first identifications of trigoniids in 1957, and the first descriptions in 1958. The trigoniids came from the Hauterivian sandstones of Prisyazhnaya Mountain (*Trigonia carinata*), Dlinnaya Mountain (*Pterotrigonia caudata*), and the village of Trudolyubovka (*Quadratotrigonia nodosa*). In 1960, I redescribed the species *Trigonia carinata* from Prisyazhnaya Mountain. In 1964, I noted trigoniid occurrences for the first time in the Upper Albian near the village of Prokhladnoe. I found a single cast of the left valve in the polymictic coarse-grained sandstone (up to 1 m) of the Mangush Series exposed in the village of Prokhladnoe (Outcrop no. 13) on the path in the middle part of the slope, above the "lower fountain" in the left bank of small gully joining to Mangush Creek opposite the south slope of Sheludivaya Mountain. I erroneously identified this cast as *Linotrigonia* ex gr. *spinosa* (Yanin, 1964). In this paper, this specimen is redescribed under the name *Linotrigonia* sp. Based on ammonites found in the Mangush sandstones (*Hysteroceras varicosum* (Sow.), *Epihoplites gibbosus* Spath, etc.) the host rocks are referred to the Upper Albian (Drushchits, 1960; Yanin, 1964). A complete description of the Mangush Series section was given by Yanin and Vishnevskii (1989).

I previously reported the occurrence of redeposited *Trigonia carinata* and *Rutitrigonia longa* in the Upper Albian series of bullion conglomerates occurring on the top and western slopes of Prisyazhnaya Mountain (Yanin, 1964; Chernov and Yanin, 1975). Trigoniids were redeposited in sandstones that formed boulders and blocks of various sizes and in disintegrated state. In the latter case, the rock matrix filling the cavities of the shells was also sandstone. Most likely this was the product of abrasion of the rocky cliffs of the Mangush ingressive gulf formed by the compact Valanginian sandstone. Similar sandstones with *Trigonia carinata carinata* are exposed in the neighboring sections (Nikolaev Yar Gully; Kayas-Dzhilga Ravine; Sheludivaya, Dlinnaya, and Patil' mountains).

Most trigoniids from the basin of the Bodrak River come from the Lower Valanginian and Lower Hauterivian. Altogether six trigoniid species have been identified from the beds of this age in this region. At present, the geochronology of trigoniids is partly emended, and their identifications were included in some stratigraphic paper (Eristavi, 1957; Yanin and Vishnevskii, 1989; Baraboshkin and Yanin, 1997; Baraboshkin, 1997) (see Section II. 2).

N i k o l a e v Y a r G u l l y (Section no. 11). I described this section in 1979 from outcrops on terraces covered by forestry on the right slope of the gully, 400 m southeast of the top of Prisyazhnaya Mountain (Fig. 10).

J_1tv. Underlying beds are Tavria Shale (boundary is turf-covered).

K_1Vlg_1. Bed 1 (4 m). A member of weakly cemented sandstones, containing plates and nodules of compact,

Fig. 11. Rocky cliff on the southern slope of Dlinnaya Mountain.

strongly calcareous sandstones. Fossils include bivalves (including *Trigonia carinata carinata*).

Bed 2 (5 m). Weakly cemented sandstones with nodules of compact strongly calcareous sandstone.

Bed 3 (4.5 m). Alternation of compact plates and plates of loosely cemented sandstones containing sandy nodules, with a plate of shellstone at the base. Fossils include bivalves (including *Trigonia carinata carinata*), belemnites, ammonites, nautiloids, echinoids, etc.

K_1Vlg_2 (provisionally). Bed 4 (14 m). Alternation of plates of compact, strongly calcareous sandstones and loosely cemented sandstones containing rare sandy nodules. Fossils include bivalves, ammonites, brachiopods, echinoids, etc. Overlying beds were not preserved.

Dlinnaya Mountain (Section no. 12). Outcrops are on the steep southwestern slope and on the eastern termination of the mountain (Fig. 11). For a detailed description of the section, see Baraboshkin and Yanin (1997) and Baraboshkin (1997). Trigoniids from this section are described herein for the first time. I studied this section regularly from 1956 onwards (Fig. 12).

J_1tv. Underlying beds are Tavria Shale.

K_1Vlg_1. Bed 1 (1.5–2.5 m) is a member of the lens-shaped alternation of compact strongly calcareous, dolomitized and loosely cemented, obliquely bedded, polymictic sandstones. Fossils include solitary corals (cyclolites), gastropods, bivalves (including *Pterotrigonia caudata, Rutitrigonia longa, Quadratotrigonia nodosa orbignyana*), ammonites *Kilianella otopeta* (Thieul.), *Neolissoceras grasianum* (d'Orb.), belemnites *Duvalia lata* Bl., brachiopods, echinoids, etc.

Bed 2 (ca. 10 m). Rhythmic alternation of compact plates of calcareous sandstones and loosely cemented, obliquely bedded sandstones. Fossils include gastropods, echinoids, ammonites *Thurmanniceras pertransiens* Sayn, and bivalves.

K_1Hau_1. Bed 3 (4.5 m). Alternation of plates of compact calcareous sandstones, occasionally shellstones and plates of loosely cemented sandstones (the member is poorly exposed). Shellstones form the top of the mountain. No contact with the rocks of Bed 2 has been observed. Fossils include colonial corals, gastropods, bivalves (including *Trigonia carinata carinata, Quadratotrigonia nodosa orbignyana, Linotrigonia ornata*), nautiloids, ammonites, etc. Because of the abundant trigoniids, this bed can be referred to as the "Trigoniid Beds."

Patil' Mountain (Section no. 14). Rocky exposures on the southeastern side of the plateau, near the altitude sign 412.8 m. I studied this section regularly from 1956 onwards (Fig. 13).

J_1tv. Underlying beds are Tavria Shale.

K_1Vlg_1. Bed 1 (5 m). A member of compact plates and loosely cemented sandstones, usually detrital, sometimes with rare quartz pebbles. At the base of the member, there is a basal conglomerate horizon (0.9 m)

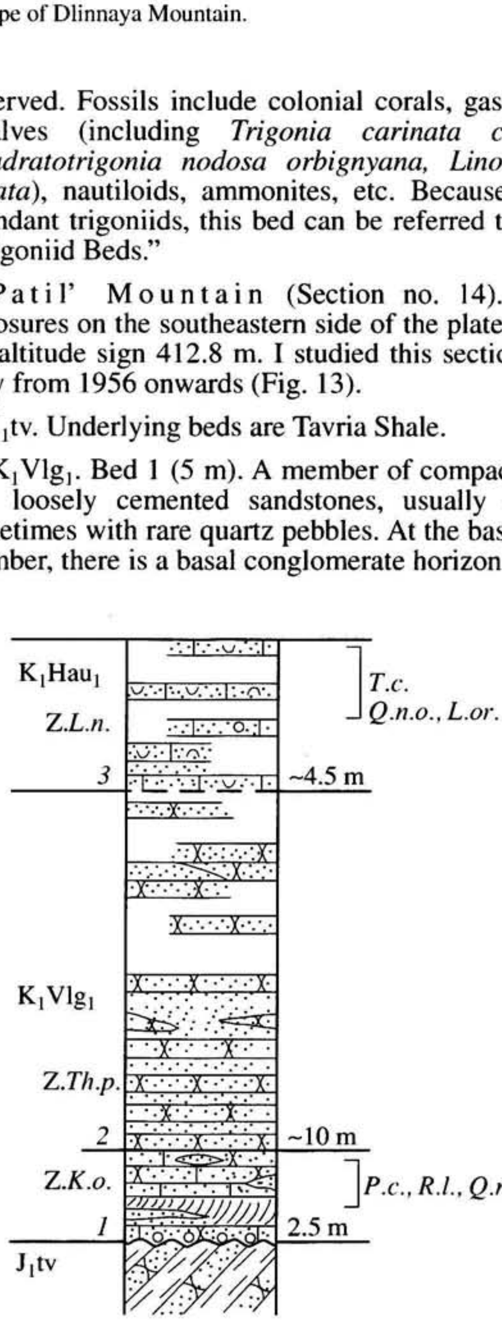


Fig. 12. Section no. 12 on the southwestern slope of Dlinnaya Mountain (see explanations for Fig. 2).

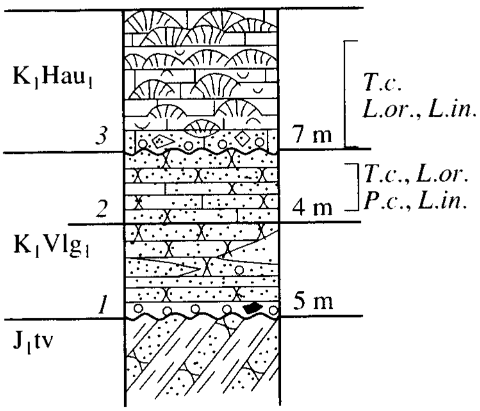


Fig. 13. Section no. 14 on the southeastern side of Patil' Mountain, near geodesic mark 412.8 m (see explanations for Fig. 2).

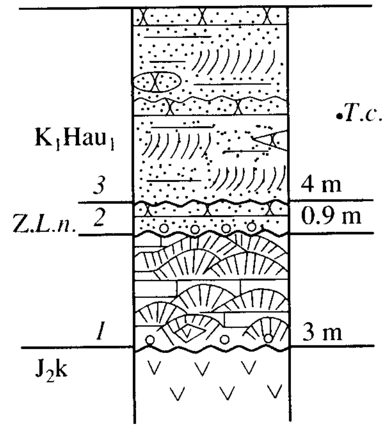


Fig. 14. Section no. 15 on the northern wall of the Pervomaiskii Quarry (right bank of the Bodrak River, upper reaches of the Papas-bair Gully) (see explanations for Fig. 2).

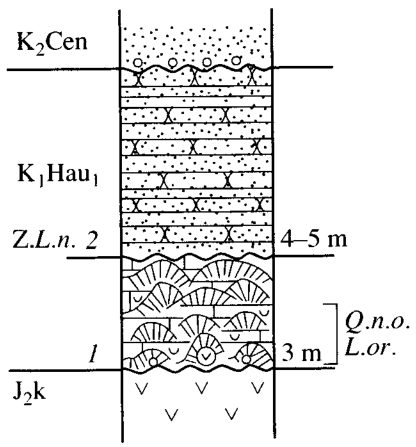


Fig. 15. Section no. 16 in the northeastern vicinity of the village of Trudolyubovka (near the "Forester's House") (see explanations for Fig. 2).

from the pebbles of quartz, sandstones, and siltstones of the underlying layer. Fossils include solitary corals, gastropods, bivalves, echinoids, etc.

Bed 2 (4 m). Compact, strongly calcareous, thickly bedded sandstones, in places transiting into sandy dolomitized limestones and cavernous shellstones. Fossils include solitary corals, gastropods, bivalves (including *Trigonia carinata carinata, Pterotrigonia caudata, Litschkovitrigonia inguschensis, Linotrigonia ornata*).

K$_1$Hau$_1$. Bed 3 (7 m). Biogenic, mostly coral limestones, in places bioclastic and detrital. Coral limestone interbeds are lens-shaped, composed of colonies (up to 0.3 × 0.3 m) of various scleractinians. The interspaces between the colonies are filled with bedded limestone matrix. A basal part of the member consists of conglomerate with pebbles of quartz and underlying Lower Valanginian sandstones. Colonial corals, gastropods, bivalves (including *Litschkovitrigonia inguschensis, Linotrigonia ornata, Trigonia carinata carinata*). The limestones of Bed 3 form the surface of the plateau.

Pervomaiskii Quarry (Section no. 15). The beds were described on the northern wall of the quarry in 1990 (Fig. 14). The quarry is in the upper reaches of the Papas-bair Gully.

J$_2$k. Underlying beds are gabbro-diabases of the Karadag Formation.

K$_1$Hau$_1$. Bed 1 (up to 3 m). Coral and bioclastic sandstones forming a biostrome of variable thickness. It is formed by large (0.3 × 1 m) massive colonies of scleractinians. The basal part of the bed is formed by pebbles of underlying rocks. Fossils include gastropods, bivalves, corals, brachiopods, echinoids, etc.

Bed 2 (0.9 m). Alternation of plates of compact, strongly calcareous sandstones (two distinct plates formed cyclolite banks) and plates of weakly cemented clayey sandstones, with pebbles and bullions formed from limestones of Bed 1. Fossils include solitary corals [abundant *Cunnolites intumescens* (Trd.)].

Bed 3 (4 m). A member of mainly weakly cemented and loose sandstones, obliquely bedded sands, with rare compact plates and lenses of strongly calcareous sandstones. Fossils include solitary corals *Cunnolites intumescens* (Trd.), bivalves (including *Trigonia carinata carinata*), ammonites *Spiticeras rotula* (Sow.), and aptychi.

Village of Trudolyubovka (Section no. 16). The outcrop is located in the northern vicinity of the village and represents a limestone rocky cliff to the east of Forester's Hut. I studied this outcrop for many years from 1956 onwards (Fig. 15).

J$_2$k. Underlying beds are volcanic rocks of the Karadag Formation.

K$_1$Hau$_1$. Bed 1 (3 m). Coral and bioclastic and detrital limestones forming the biostrome. The body of the biostrome is formed by massive colonies of corals of varying size. The interspaces between the colonies are filled with bedded limestones, in some places with abundant shells. The base of the bed is formed by pebbles and large bullions of underlying rocks. Fossils include colonial and solitary corals (scleractinians), gastropods, bivalves (including *Quadratotrigonia nodosa orbignyana, Linotrigonia ornata*), brachiopods, and echinoids.

Bed 2 (4–5 m). A member of frequent alternation of plates of compact, strongly calcareous sandstones and interbeds of weakly cemented sandstones. Fossils include gastropods and bivalves.

K_2Cen. Overlying beds formed by weakly cemented glauconite sandstones exposed at the base of the eastern slope of Kizil-Chigir Mountain, opposite the forester's hut.

Basin of the A l'm a R i v e r

Early Cretaceous trigoniids are reported for the first time from this district. They are found in a small sand quarry 1 km southeast of the village of K o n s t a n t i n o v k a (Section no. 17), on the right bank of a small gully oriented east–west and terminating near the southeast vicinity of the village of Partizany. I studied this section in 1987 and 1989 (Fig. 16). The underlying beds are not exposed.

K_1Hau_1. Bed 1 (ca. 2 m). A member of weakly cemented sandstones with interbeds and lenses of compact sandstones.

Bed 2 (ca. 4 m). Alternation of plates of compact, very calcareous sandstones, in places sandy limestones and interbeds of weakly cemented sandstones, in places sands with sandy nodules. Fossils include corals, serpulids (in places forming serpulite), bivalves (including *Litschkovitrigonia inguschensis, Trigonia carinata carinata, Pterotrigonia caudata*, and *Linotrigonia ornata*). The overlying beds are not preserved.

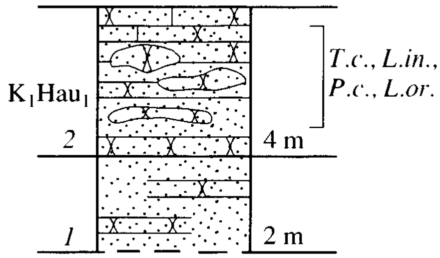


Fig. 16. Section no. 17 in the vicinity of the village of Konstantinovka (1 km southeast of the village) (see explanations for Fig. 2).

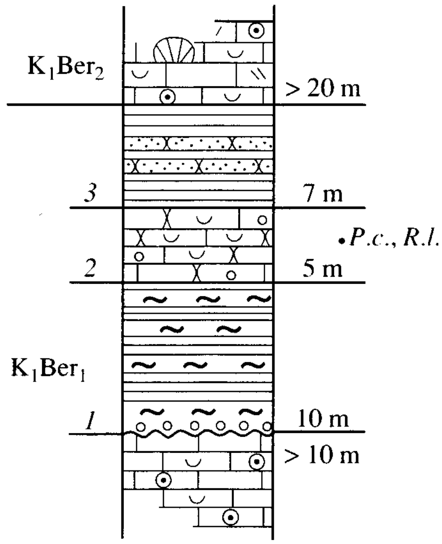


Fig. 17. Section no. 18 in the vicinity of the village of Ivanovka (see explanations for Fig. 2).

Basin of the M a l y i S a l g i r R i v e r

The trigoniids *Rutitrigonia longa* and *Pterotrigonia caudata* are for the first time reported in this paper. They come from the Lower Berriasian alternating rock series exposed in the gully in the northern vicinity of the village of I v a n o v k a (Section no. 18, Fig. 17). The section was described by me in 1975.

K_1Ber_1. Underlying beds (>10 m) are formed of bioclastic limestones composed mostly of algae and gastropods.

K_1Ber_1. Bed 1 (10 m). Very sandy clay and siltstone. A horizon of pebbles lies at the base, on the eroded surface of the underlying limestones.

Bed 2 (5 m). Lens-shaped alternation of very calcareous sandstones and sandy and bioclastic limestones, in places shellstones. Rocks contain abundant pebbles of varying composition. Fossils include solitary corals, gastropods, bivalves (including *Pterotrigonia caudata* and *Rutitrigonia longa*). Among trigoniids, the shells of *Rutitrigonia longa* are most abundant, occasionally forming shellstones. All valves are isolated, with their convex side mainly orientated upward (so-called shell pavement). Occasionally, the shells are inserted inside each other. All this suggests a shallow-water burial environment.

Bed 3 (7 m). Alternation of very silty clays and sandstones.

K_1Ber_2. Overlying beds (>20 m) are detrital, bioclastic limestones with horizons of coral bioherms.

Basin of the B e s h t e r e k R i v e r

The first records of trigoniids in the Lower Cretaceous deposits of the basin of the Beshterek River were published in 1958–1960. These included *Pterotrigonia caudata* described by myself without illustration in 1958 from the Lower Valanginian sandstones; *Pterotrigonia caudata* and *Rutitrigonia longa* were described from the same beds by me in 1979 (not figured). Later, three more species were found (*Iotrigonia scapha, Myophorella loewinsonlessingi*, and *Trigonia carinata*). These species were also recorded in stratigraphic

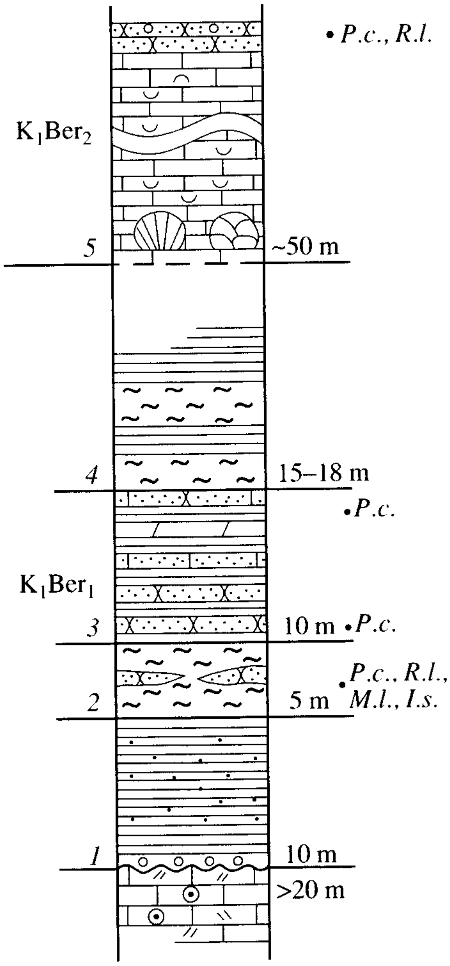


Fig. 18. Section no. 19 in the vicinity of the village of Solov'evka (see explanations for Fig. 2).

papers. Drushchits and Yanin (1959) reported *Pterotrigonia caudata* and *Rutitrigonia longa* in the "Hauterivian" sandstones overlying the series of the "Solov'evskie Limestones." The same species were listed by Lychagin (1969) as species characteristic of the "lower horizons of the Mazanka Formation," the age of which was determined by Lychagin as Early Hauterivian. Lysenko and Yanin (1979) reported *Rutitrigonia longa* from sandstones exposed in the vicinity of the village of Lesnosel'e, which directly overly the "Lower Valanginian" bioclastic limestones exposed near the village of Solov'evka. The same authors indicated *Pterotrigonia caudata* and *Rutitrigonia* longa from the Lower Hauterivian sandy nodules occurring at the base of a small quarry near the Motor Tractor Station (village of Mazanka) and *Trigonia carinata* from sandstones directly overlying Mazanka Sands near the northern vicinity of the village. Yanin and Smirnova (1981) reported *Myophorella loewinsonlessingi* and *Pterotrigonia caudata* from the Berriasian sandstones.

Most trigoniids in this region are found in the Lower Berriasian alternating rock series exposed in the vicinity of the villages of Solov'evka and Lesnosel'e. The section in the Beshterek River was studied by me in 1959–1968 and together with N.I. Lysenko in 1974–1976 in the right bank of the river valley. The deposits are found over a distance of 10 km from south to north and contain many dislocations, which are responsible for the stepped structure of the section. Previously, these dislocations have not been correctly recognized. As a result, the sequence of members in the section was estimated incorrectly, while their thickness was overestimated (Drushchits, 1960). The considerable length of outcrops in a north–south direction allow the tracing of facial transitions in members over long distances. For the most complete description of this section, see Lysenko and Yanin (1979).

Vicinity of the village of S o l o v'e v k a (Section no. 19, Fig. 18).

K_1Ber_1. Underlying beds (>20 m) are composed of bioclastic (rudist and gastropod) oolitic–detrital limestones. The beds are well-exposed 1.5 km to the south of the village of Solov'evka.

K_1Ber_1. Bed 1 (10 m). Silty clays, very sandy in the upper part. A pebble horizon lies at the base of the bed. The size of the limestone pebbles ranges from 2 to 8 cm in diameter.

Bed 2 (5 m). Siltstones with a lens-shaped interbed of sandstone. Fossils from this bed were collected in the village and 0.5–1 km to the south of the village (at present, most localities are either built on, or covered by forest). Fossils include solitary corals, bivalves (including *Myophorella loewinsonlessingi, Pterotrigonia caudata, Rutitrigonia longa*, and *Iotrigonia scapha*), ammonites *Euthymiceras euthymi* (Pict.), *Ptychophylloceras semisulcatum* (d'Orb.), *Dalmasiceras dalmasi* (Pict.), *D. crassicostatum* Djan., nautiloids, belemnites *Duvalia lata* Bl., etc.

Bed 3 (10 m). Alternation of clay, siltstone, sandstone, sandy limestone, and marl. Fossils include sponges, solitary and colonial corals, gastropods, bivalves (including *Pterotrigonia caudata*), ammonites *Euthymiceras euthymi* (Pict.), *Ptychophylloceras semisulcatum* (d'Orb.), *Protetragonites tauricus* Kulj.-Vor., and belemnites *Duvalia lata* Bl. and *Conobelus conicus* Bl.

Bed 4 (15–18 m). Alternation of siltstones and sandy clays (the upper part of the bed is not exposed).

K_1Ber_2. Bed 5 (ca. 50 m). Bioclastic, mainly gastropod (nerineiid) limestones, in their lower part (near the spring) with horizons of coral bioherms. Sandstones with quartz pebbles and conglomerates lie at the top of the bed. Sandstones contain corals, bivalves (including *Pterotrigonia caudata* and *Rutitrigonia longa*), brachiopods, etc. Overlying beds are not preserved.

V i c i n i t y of the village of L e s n o s e l'e (Outcrop no. 20). These deposits were studied in the right bank of the Beshterek River opposite the village of Lesnosel'e and the Yagodnyi collective farm. The section is mostly composed of terrigenous rocks, which correspond to the synchronous limestone series terminating the Berriasian section further to the south, near the village of Solov'evka (Section no. 19, Bed 5). This section is mainly composed of members of obliquely laminated sands, sandstones, pebble rocks, conglomerates with interbeds of marl in their upper part, and coral-algal bioherms in their middle part. Rare *Rutitrigonia longa* and *Pterotrigonia caudata* occur in compact sandstones with quartz pebbles. In the same beds with trigoniids, there were ammonites *Fauriella boissieri* (Pict.) and *Haploceras elimatum* (Opp.) based on which the entire terrigenous series under study is referred here to the Upper Berriasian. Previously, this series was dated Lower Hauterivian (Drushchits, 1960), or Lower Valanginian (Lysenko and Yanin, 1979). The latter authors considered this series to be the lower part of the Mazanka Formation.

V i l l a g e o f M a z a n k a (Section no. 21). Trigoniids are found in the right and left banks of the valley of the Beshterek River in two horizons of Valanginian sandstones (Fig. 19).

K_1Ber_2. Underlying beds (>20 m) are composed of obliquely laminated sands and sandstones with interbeds of marly limestones, exposed in the vicinity of the village cemetery.

K_1Vlg_1. Bed 1 (ca. 15 m). Alternation of interbeds of loose sands and plates of compact sandstones with quartz pebbles and large nodules (0.5 × 2 m) of very calcareous sandstones. Rocks are exposed along the eastern road from the center of the village along the northern fence of the Motor Tractor Station. The boundary with the underlying beds was not observed. Fossils include solitary corals, gastropods, bivalves (including *Pterotrigonia caudata* and *Rutitrigonia longa*), ammonites, and belemnites.

Bed 2 (35–40 m). Loose, weakly cemented, obliquely laminated, mostly quartz sands and sandstones with lenses and interbeds of quartz pebble rock. The rocks are exposed in the quarries on the both banks of the river close to the village center. The only fossils are burrows of small crustaceans *Ophiomorpha*.

Bed 3 (8–10 m). In the basal part, sands alternate with sandstones containing sandy nodules. In the upper part, the section is composed of clays with interlayers and lenses of sand and gravel. The rocks outcrop in the northern vicinity of the village in the lower part of the south slope of the cuesta composed of nummulitic limestones. Fossils include solitary corals and bivalves, including *Trigonia carinata carinata*. One specimen of the latter species was found in 1974 on the left bank of the Beshterek River, on the ledge of the nummulitic cuesta. It comes from a sandstone fragment (0.2 × 0.2 m) lying in the bullion horizon (0.3 m) in the middle part of the sandstone member (total thickness of ca. 0.5 m) exposed in the trench near the base of the slope. The trench was excavated in 1974. A sandstone fragment with *Trigonia carinata carinata* is originally Lower Valanginian and is redeposited in the Upper Valanginian bullion horizon. The same fragment also contains solitary corals (cyclolites), characteristic of the Lower Valanginian. This bullion horizon was not found in the right bank of the valley.

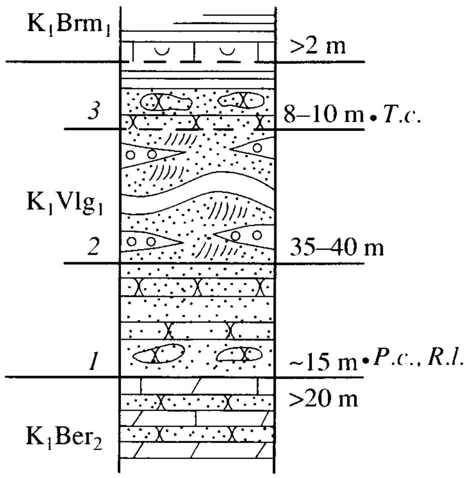


Fig. 19. Section no. 21 in the vicinity of the village of Mazanka (see explanations for Fig. 2).

K_1Brm_1. Overlying beds are brownish red, oolitic limestones with ammonites *Phyllopachyceras infundibulum* (d'Orb.) and numerous brachiopods. An immediate contact with the clays of Bed 3 was not observed.

Basin of the Z u y a R i v e r

One trigoniid species, *Pterotrigonia caudata*, was described for the first time by myself (but not figured) from the Berriasian in 1958 and later redescribed in 1979. I also established that, in the basin of the Zuya River, trigoniids come from two horizons: Lower Berriasian (*Myophorella loewinsonlessingi, Pterotrigonia caudata*, and *Rutitrigonia longa*) and Lower Valanginian (*Rutitrigonia longa*). They are found in several members of Section no. 22 on the right bank of the river valley and Section no. 23 near the Balanovskoe Reservoir.

Section no. 22 (Fig. 20) is stretched on the line from the village of K r a s n o g o r s k o e–town of Z u y a–village of L i t v i n e n k o v o. The section is extended along a long line from south to the north. I studied this section in 1954, 1955, 1959, and 1975. The lower part of the section (Beds 1–4) is exposed to the south of the village of Krasnogorskoe, near Tau-Kipchak cave.

K_1Ber_1. Bed 1 (ca. 30 m). Alternation of plates of loose and compact sandstones, conglomerates, and rare plates of limestones. The upper 10 m are not exposed. Fossils include gastropods, bivalves (including *Pterotrigonia caudata*), brachiopods, echinoids, etc. mostly from the lower 15 m.

K_1Ber_2. Bed 2 (15 m). Bioherm limestones (coral–algal) and bioclastic, oncolitic in the lower part. Fossils

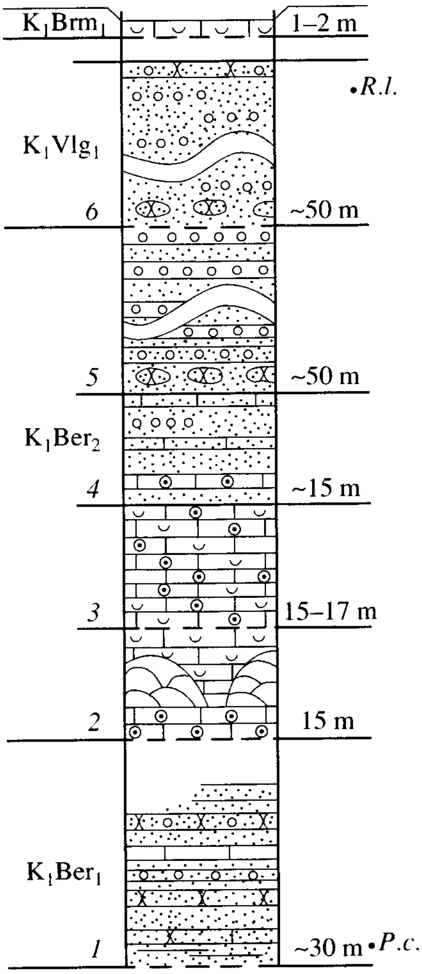


Fig. 20. Section no. 22 along the right bank of the Zuya River along the line from the village of Krasnogorskoe to the town of Zuya to the village of Litvinenkovo (see explanations for Fig. 2).

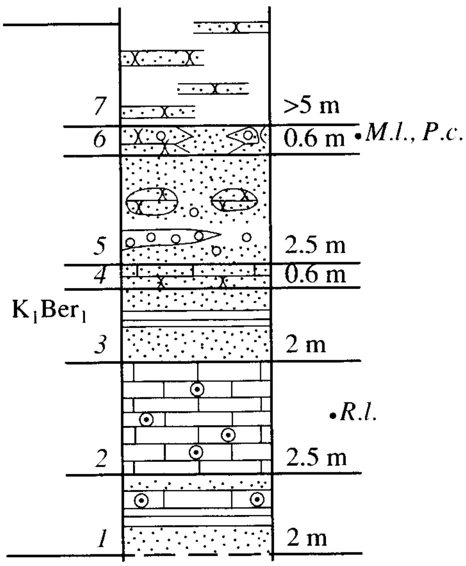


Fig. 21. Section no. 23 in the vicinity of the Balanovskoe Water Reservoir (valley of the Zuya River) (see explanations for Fig. 2).

include colonial corals, gastropods, bivalves, and brachiopods.

Bed 3 (15–17 m). Bioclastic and large-sized oncolitic limestones with abundant gastropods and rudists. Fossils include colonial corals, gastropods, bivalves, brachiopods.

Bed 4 (ca. 15 m). Alternation of interbeds of loosely cemented and very calcareous sandstone plates, lenses and pebble horizons, and oncolitic limestones in the lower part. Fossils include gastropods, bivalves, and brachiopods.

Bed 5 (ca. 50 m). The thickness is estimated tentatively because the bed is dislocated by transverse faults. The bed consists of alternation of layers of conglomerates and of loosely cemented sandstones. The basal part of the bed contains horizons of large pillow-shaped nodules of very calcareous sandstones, which are exposed in the central street of the village of Krasnogorskoe. In the middle part of the bed, there is a horizon with solitary corals. Fossils include corals, gastropods, bivalves, belemnites, and echinoids.

K_1Vlg_1. Bed 6 (ca. 50 m). Loose sands, conglomerates, pebbles, with a horizon of pillow-shaped nodules of strongly calcareous sandstones, and a plate of sandstone with quartz pebbles at the top. This plate is exposed in the southern vicinity of the town of Zuya. Fossils include gastropods, bivalves (including *Rutitrigonia longa*), and belemnites. Bed 6 is provisionally dated Early Valanginian, based on correlation with beds 2–3 in the section near the village of Mazanka.

K_1Brm_1. Overlying beds are brownish red, nodular limestones with abundant brachiopods. The relationship with the rocks of Bed 6 is unclear, because no intermediate strata were found for a great distance (they are overlain by the Albian and Cenomanian clays and marls). These limestones are poorly outcropped to the north of the town of Zuya, near the southern vicinity of the village of Litvinenkovo.

B a l a n o v s k o e R e s e r v o i r (Section no. 23). The trigoniids *Myophorella loewinsonlessingi* and *Pterotrigonia caudata* from the Berriasian of this region were reported for the first time by Yanin and Smirnova (1981). The section was described by me in 1978 near the southern termination of the dam of the reservoir, which is situated 2.5 km south of the village of Balanovo (Fig. 21).

K_1Ber_1. Bed 1 (2 m). Alternation of loose sandstones, clay and plates of firmly cemented calcareous sandstones and limestones.

Bed 2 (2.5 m). Platy limestones, sandy in the lower part, in places oncolitic, with numerous holes of decapods. Fossils include bivalves (e.g., *Rutitrigonia longa*).

Bed 3 (2 m). Strongly clayey sandstones, in the middle part, with a lens (0.5 m) of sandy clay.

Bed 4 (0.6 m). Compact, strongly calcareous sandstones, in places transiting into nodular limestones.

Bed 5 (2.5 m). A member of clayey sandstones, with lenses (up to 0.3 m) of quartz pebble rocks at the base, and with large (0.6 × 1.0 m) sandy nodules in the middle part, with abundant faunal remains.

Bed 6 (0.6 m). Sandstones with lens-shaped nodules of thinly bedded sandstones ("plitnyaki"), with white quartz pebbles and numerous bivalves, including *Myophorella loewinsonlessingi* and *Pterotrigonia caudata*. Similar flags are also found in the clay quarry above the reservoir.

Bed 7 (>5 m). Clay and loose sandstones on the forested slope. Fossils include solitary corals, collected loose. The overlain beds are eroded away.

Interfluve between the Zuya and Burul'cha Rivers

Three trigoniid species (*Trigonia carinata, Quadratotrigonia orbignyana*, and *Rutitrigonia longa*) were reported for the first time in a stratigraphic paper by Lysenko and Yanin (1979). These trigoniids were found in the sandstones of the Mazanka Formation in the Zuiskii Quarry located on the interfluve between the Zuya and Burul'cha rivers, 0.5 km south of Kunich Mountain and on its southern slope.

Collecting in 1975 and 1987–1990 provided me with exceptionally diverse and well-preserved material. Juvenile shells were found among the adult and young shells. A more complete trigoniid assemblage from this section (*Trigonia carinata, Quadratotrigonia nodosa orbignyana, Litschkovitrigonia* sp., *Linotrigonia ornata*, and *Rutitrigonia longa*) can be found in a recent paper by Baraboshkin and Yanin (1997). All these species are redescribed in the present study.

Sands and pebble rocks of the Zuiskii Quarry are referred to the Mazanka Formation, which was dated Hauterivian (Lychagin, 1957; Muratov, 1960; Yanin, 1979b); Late Hauterivian–Early Barremian (Muratov, 1973), Late Hauterivian (Drushchits, 1960; Plotnikova *et al.*, 1984), Early Hauterivian (Drushchits *et al.*, 1986); Late Berriasian–Early Hauterivian (Lysenko and Yanin, 1979—for the entire terrigenous Lower Cretaceous series of the central part of the Crimean Fore-Mountains). Recently, Baraboshkin reexamined ammonites from the sandy series of the Zuya Formation and concluded a Valanginian age of the Mazanka Formation in this region (Baraboshkin and Yanin, 1997).

In the section considered, I found trigoniids in the lens-shaped sandstone interbeds at two levels (in the middle and upper parts). It is possible that they may also be found at other levels, because this series is generally built of lenses. For a detailed description of the section see Baraboshkin and Yanin (1997).

Zuiskii Quarry–Kunich Mountain (section no. 24, Fig. 22). K_1Vlg_1. Bed 1 (30–40 m). A member of alternating obliquely laminated sandstones, gravelites, and conglomerates, mostly consisting of quartz. Generally, the member is composed of

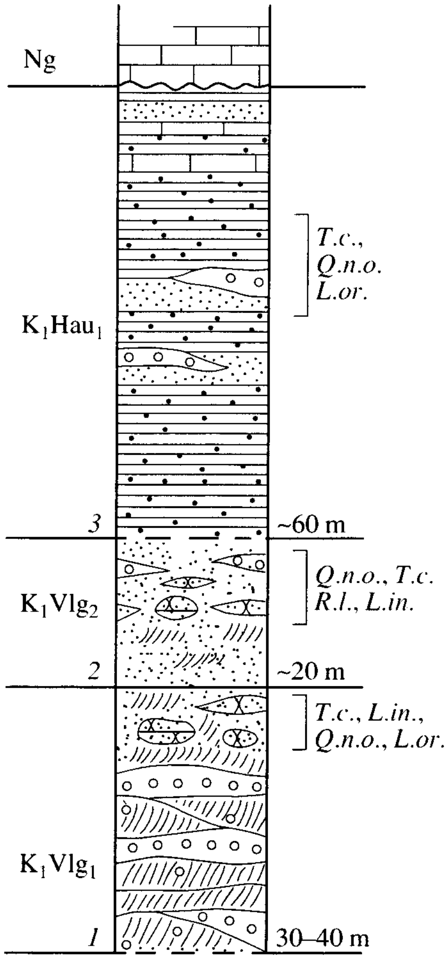


Fig. 22. Section no. 24 on the Zuya–Burul'cha interfluve (Zuiskii Quarry–Kunich Mountain) (see explanations for Fig. 2).

lenses. The top parts of some lenses show erosion cuts up to 1 m deep. The obliquely laminated sandstones in places contain numerous holes of decapods (ichnogenus *Ophiomorpha*). The upper part of the member contains horizons of nodules and lens-shaped interbeds of strongly calcareous sandstones with abundant faunal remains. Fossils include gastropods and bivalves (including *Trigonia carinata carinata, Litschkovitrigonia inguschensis, Quadratotrigonia nodosa orbignyana*, and *Linotrigonia ornata*).

K_1Vlg_2. Bed 2 (ca. 20 m). A member of alternating interbeds of obliquely laminated sands, pebble rock, and flags of firmly cemented sandstones, frequently transiting into horizons of nodules. The obliquely laminated sandstones contain numerous holes of *Ophiomorpha*. Nodules contain abundant fossils, mostly bivalves, among which we observed *Trigonia carinata carinata, Quadratotrigonia nodosa orbignyana, Litschkovitrigonia inguschensis*, and *Rutitrigonia longa*. Ammonites from this bed include *Neolissoceras grasianum* (d'Orb.) and *Neocomites flucticulus* Thieul.

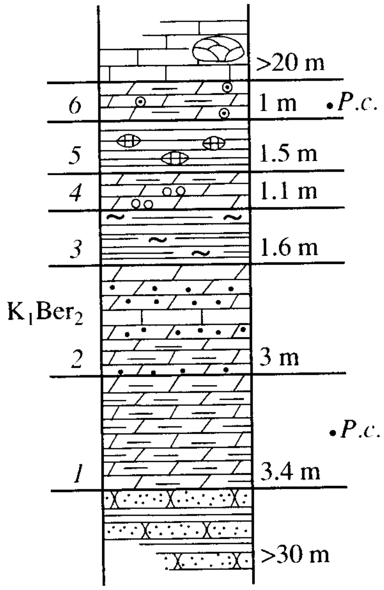


Fig. 23. Section no. 25 in the vicinity of the village of Mezhgor'e (see explanations for Fig. 2).

suggesting a Late Valanginian age of this member (Baraboshkin and Yanin, 1997).

K_1Hau_1. Bed 3 (ca. 60 m; the section continues on the southern slope of Kunich Mountain; the description is superficial). Clay interbedding with sandstones, lenses of pebble rock and of conglomerates. The upper part of the bed (sandstones, gravelites, and conglomerates) contains gastropods and bivalves, including *Trigonia carinata carinata, Linotrigonia ornata, Quadratotrigonia nodosa orbignyana*. The ammonite *Spitidiscus rotula* (Sow.) found in this bed above the surface of the sand quarry (ca. 40 m) indicates the Early Hauterivian age of Bed 3 (Baraboshkin and Yanin, 1997).

Ng. Overlying beds at the top of Kunich Mountain are Sarmatian limestones.

Basin of the Burul'cha River

Trigoniids from this section are described here for the first time. The section was described by myself in 1986 on the southern slope of Baksan Mountain, below the rock cliff above the village of Mezhgor'e (Section no. 25, Fig. 23).

K_1Ber_2. Underlying beds are sandstones interbedded with clay.

K_1Ber_2. Bed 1 (3.4 m). Gray, strongly clayey marl, in places with abundant fine shell detritus, indistinctly bedded. Fossils include bivalves (e.g., *Pterotrigonia caudata*) and nautiloids.

Bed 2 (3 m). Marl, clayey in the lower part and sandy in the upper part. In the middle part contains a layer of marly limestone. Fossils include gastropods, bivalves, and echinoids.

Bed 3 (1.6 m). Bluish gray clay and siltstone.

Bed 4 (1.1 m). Gray marl, oncolitic at the base and in the middle, and clayey at the top.

Bed 5 (1.5 m). Bluish gray, silty, very calcareous clay, containing nodules of algae. Fossils include sponges and bivalves.

Bed 6 (1 m). Oncolitic, in places, clayey marl. Fossils include bivalves, including *Pterotrigonia caudata*, and brachiopods.

K_1Ber_2. Overlying beds are thickly bedded, bioclastic limestones, transiting toward the top into the massive biohermic (coral–algal) limestones, which form the top and cliff of the mountain.

Basin of the Sarysu River

G.F. Veber was the first to find trigoniids in the Lower Cretaceous in this region. T.A. Mordvilko identified a shell found by Veber in the vicinity of the village of Novoklenovo as a new species, *Trigonia gertrudae*. This name was written on the label, but the species was neither described, nor figured. I included this species in the abstract of my report on the Lower Cretaceous of the Crimea (Yanin, 1957). Because the name "*gertrudae*" was an unpublished name, I named this species *Myophorella (Orthotrigonia) mordvilkoae* (in honor of T.A. Mordvilko, who recognized the new species in the material collected by G.F. Veber), and dated the specimen as Berriasian (Yanin 1979a). In the same paper, I reported another species (*Pterotrigonia (Pterotrigonia) caudata* in the basin of the Sarysu River, but did not figure the specimens. Yanin and Smirnova (1981) in their stratigraphic paper reported both species (*P. caudata* and *M. (O.) mordvilkoae*) from the Upper Berriasian of this region (the latter species was assigned to a different genus *Vaugonia*). Despite subsequent fossil collecting over many years in the Lower Cretaceous beds of the basin of the Sarysu River, no other trigoniid species have been found.

Most trigoniids in this region come from the Lower Berriasian shallow-water limestones and siltstones exposed in the vicinity of the villages of Blagodatnoe, Novoklenovo, and Chernokamenka.

Village of Blagodatnoe (Section no. 26). Outcrop is 300 m southwest of the village, in the left bank of the Tyus-Saigin Gully, near the water wells in the gully bed. The section is described by myself in 1968 (Fig. 24).

K_1Ber_1. Underlying beds (> 30 m) are gray, micritic, in places very clayey, platy limestones.

K_1Ber_1. Bed 1 (5.8 m). Calcareous sandstones interbedding with sandy limestones and silty clays. The base of the bed is formed by a horizon with pebbles and bullions (from 2 to 12 cm) of compact limestones from the underlying bed. Fossils include solitary corals (the first horizon with *Montlivaltia* sp.), bivalves (including *Pterotrigonia caudata*), the ammonites *Malbosiceras malbosi* (Pict.) and *Ptychophylloceras semisulcatum* (d'Orb.), nautiloids, and belemnites.

Bed 2 (ca. 6 m). Gray, carbonate clay, in places very silty, with a layer of a weakly cemented sandstone with abundant solitary corals (second horizon with *Montlivaltia* sp.), in places coquina. Fossils include solitary corals, gastropods, bivalve (including *Pterotrigonia caudata*), ammonites [*Malbosiceras malbosi* Pict., *Subthurmannia boissieri* (Pict.), *Protetragonites tauricus* Kulj.-Vor., and *Ptychophylloceras semisulcatum* (d'Orb.)], belemnites, brachiopods, etc. Beds 1–2 are referred to Beds with *Malbosiceras malbosi.*

K_1Ber_2. After a small gap, the overlying beds are traced to the west, on the slope of the meridional range (Quaternary terrace extending up to the village of Balki). These beds are over 20 m thick and are composed of clay with sideritic nodules, in the middle part, with numerous layers of sandstone and oyster shell rocks.

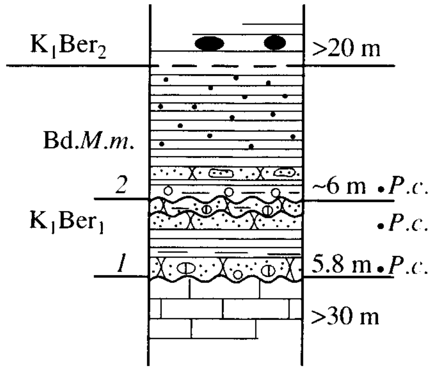


Fig. 24. Section no. 26 in the vicinity of the village of Blagodatnoe (Tyus-Saigin Gully, right tributary of the Sarysu River) (see explanations for Fig. 2).

V i c i n i t y   o f   t h e   v i l l a g e   o f   C h e r n o k a m e n k a (Section no. 27). A Lower Berriasian series of alternating rocks is exposed in the southeastern vicinity of the village. The section is described by myself in 1968 and 1978 (Fig. 25).

K_1Ber_1. Underlying beds (over 20 m) of gray, micritic, compact, bedded limestones, which form the right bank of the Enisarai Gully.

K_1Ber_1. Bed 1 (0.6 m). Gray, compact limestones, with ferruginous nodules and plant remains. Fossils include gastropods, bivalves, and echinoids.

Bed 2 (3 m). Dark gray, slightly sandy clay with small nodules. Fossils include bivalves.

Bed 3 (2 m). Compact clay interbedded with loosely cemented sandstones. Fossils include gastropods, bivalves, and echinoids.

Bed 4 (1 m). Bedded, finely clastic limestones, in places oncolitic, transiting into strongly calcareous sandstones containing plant remains. Fossils include solitary corals, gastropods, bivalves (including *Pterotrigonia caudata*), nautiloids, aptychi, echinoids, etc.

Bed 5 (3.3 m). Strongly sandy clay, with a sandstone plate (0.15 m) in the middle. Fossils include corals, bivalves, ammonites, etc.

Bed 6 (0.25 m). Marly sandstones, with abundant fossils (first faunal horizon). Fossils include solitary corals, gastropods, bivalves, and ammonites *Ptychophylloceras* sp.

Bed 7 (3 m). Bluish gray, sandy clay. Fossils include solitary corals.

Bed 8 (1 m). Marly sandstones forming two compact plates separated by an interbed of loosely cemented sandstone. Compact layers contain abundant fossils (second faunal horizon). Fossils include solitary corals, gastropods, bivalves (including *Orthotrigonia mordvilkoae*), ammonites, belemnites, and brachiopods.

Bed 9 (ca. 5 m). Strongly sandy clay, with a layer (0.15 m) of compact calcareous sandstone in the middle. Fossils include solitary corals, gastropods, bivalves, ammonites, and brachiopods. The overlying beds are eroded away.

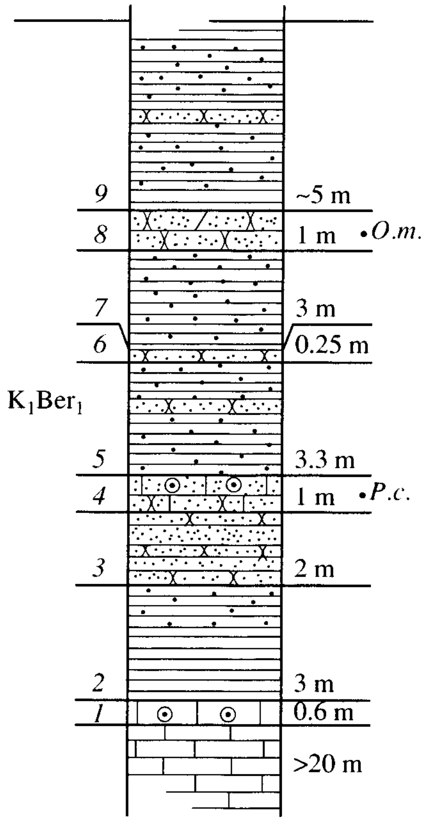


Fig. 25. Section no. 27 in the vicinity of the village of Chernokamenka (see explanations for Fig. 2).

V i c i n i t y   o f   t h e   v i l l a g e   o f   N o v o k l e n o v o (Section no. 28). The outcrops are near the eastern vicinity of the village, in a broad valley, which becomes a gully behind the horse farm. The section was studied by myself in 1968 and 1978 (Fig. 26).

K_1Ber_1. Underlying beds (>20 m) are gray micritic, in places detrital limestones, with layers of calcareous clay.

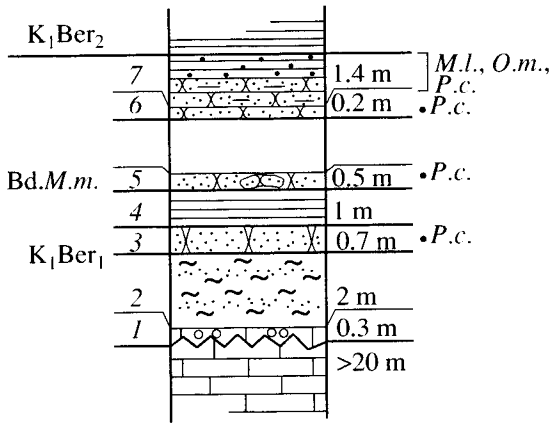


Fig. 26. Section no. 28 in the vicinity of the village of Novoklenovo (see explanations for Fig. 2).

K_1Ber_1. Bed 1 (0.3 m). Finely oncolitic, sandy limestones that form a distinct plate. The contact with the underlying limestones is along the tectonic dislocation. Fossils include solitary corals, bivalves, and ammonites.

Bed 2 (2 m). Bluish sandy siltstones, in places sandstones, with rare quartz pebbles. Fossils include bivalves, ammonites *Protetragonites rotundus* Drush., *Haploceras* sp.

Bed 3 (0.7 m). Fine-grained, calcareous sandstones forming a distinct plate. Fossils include solitary corals, gastropods, bivalves (including *Pterotrigonia caudata*), ammonites, brachiopods, and echinoids.

Bed 4 (1 m). Strongly aleuritic clay.

Bed 5 (0.5 m). Weakly cemented sandstones, with nodules (up to 0.3 m) of strongly calcareous sandstones, in places coquinas. Fossils include solitary and colonial corals, bivalves (including *Pterotrigonia caudata*), ammonites, and echinoids.

Bed 6 (0.2 m) (after a gap of 1–2 m). Marly, stained sandstones. Fossils include gastropods, bivalves (including *Pterotrigonia caudata*), and ammonites *Malbosiceras malbosi* (Pict.).

Bed 7 (1.4 m). Sandstones and siltstones, strongly clayey in the lower part (0.9 m) and silty clay in the upper part (0.5 m). Fossils include solitary corals, gastropods, bivalves (including *Myophorella loewinsonlessingi, Orthotrigonia mordvilkoae, Pterotrigonia caudata*), ammonites, and brachiopods. The bed extends along a wide gully toward the village.

K_1Ber_2. Overlying beds are composed of clay with sideritic nodules.

Basin of the Tonas River

Description and illustrations of one trigoniid species from this region (*Iotrigonia scapha*) were published for the first time by myself in 1958. A specimen belonging to this species was sent for identification by mapping geologists. According to their data, this specimen was found in the Hauterivian–Barremian series of conglomerates in the vicinity of the village of Golovanovka (Outcrop no. 30). Because no new specimens have been found in this section, its stratigraphic position is uncertain. Most likely, this specimen was recovered from a sandstone bullion redeposited in the Barremian conglomerates. This conclusion is based on the similarity of this occurrence and the occurrence of Valanginian trigoniids in the neighboring, more easterly section on the Kuchuk-Karasu River (see below).

In 1987, we found one trigoniid specimen at a lower level, i.e., in the member of Lower Berriasian flyschoid series of clay and breccia-like limestone in the vicinity of the village of Krasnoselovka (Outcrop no. 29), which are exposed on the right bank of the Trekh Trub Gully above the road from Krasnoselovka to Privetnoe. I assigned this specimen to *Myophorella tonasensis*.

Basin of the Kuchuk-Karasu River

In this region, five trigoniid species were found for the first time in the vicinity of the village of Gorlinka in 1955 and 1956. Out of these, I described and figured only two species, *Pterotrigonia caudata* and *Quadratotrigonia nodosa* (Yanin, 1958). Apart from these two species, Drushchits (1960, p. 63) reported (based on my identifications) *Litschkovitrigonia "subdaedalea."* All these trigoniids come from the bullions of Valanginian sandstones, redeposited in the conglomerate-bullion Barremian series, exposed in the southern vicinity of the village of Gorlinka.

Village of Gorlinka (Outcrop no. 31). Here, bullions of strongly calcareous sandstones up to 0.8 × 1.0 × 1.2 m in size lie in the member of bullion conglomerates along the bullions of Upper Jurassic limestone, Paleozoic shale, and abundant pebbles of quartz and dark colored rock.

The Barremian age of the bullion conglomerate series containing the above bullions is based on the belemnites *Mesohibolites uhligi* Schw. (Drushchits, 1960) found *in situ* in the matrix of the overlying beds. Previously, Yanin (1958) and Drushchits (1960) suggested that sandstones forming bullions and containing trigoniids are Hauterivian. Unfortunately, no ammonoids have been found in these bullions. The correlation with the section of the Lower and Upper Valanginian studied on the Zuya–Burul'cha interfluve (Zuiskii Sand Quarry, Section no. 24), which contains the same species assemblage of trigoniids, suggests that sandstones in bullions in the vicinity of the village of Gorlinka are Valanginian.

In 1959, 1963, and 1964, I collected additional well-preserved trigoniids from the same bullions. Six species are described from this locality (*Trigonia carinata carinata, Quadratotrigonia nodosa orbignyana, Litschkovitrigonia inguschensis* [this species was identified earlier (Drushchits, 1960, p. 63) as *L. subdaedalea*], *Linotrigonia ornata, Rutitrigonia longa,*

Table 1. Biostratigraphic scheme of the Lower Cretaceous beds of the Crimean Fore-Mountains (after Baraboshkin, 1997a, with additions on the Albian)

Stage	Substage	Zone	Frequency of trigoniid occurrences	Numbers of sections and outcrops	
Albian	U	*Stoliczkaia dispar*			
		Mortoniceras inflatum			
		Hysteroceras varicosum			
		Hysteroceras orbignyi	si	13	
	M	*Hoplites dentatus*	si	1, 2	
	L	no trigoniids found in situ			
Aptian					
Barremian					
Hauterivian	U				
	L	*Lyticoceras nodosoplicatum*	f	12, 15, 16, 17	
		"Crioceratites" loryi			
		Leopoldia leopoldina	f	14, 15	
Valanginian	U	*Eleniceras tauricum*	r	9, 10	24
		Teschenites callidiscus	r	9, 10	
		Himantoceras trinodosum			
		Saynoceras verrucosum			
	L	*"Busnardoites" campylotus*			
		Thurmanniceras pertransiens			
		Kilianella otopeta	f	5, 11, 12, 14, 21, 22, 24	
Berriasian	U	*Fauriella boissieri*	si	4, 19, 20, 25	
	L	*Eumthymiceras euthymi–Dalmasiceras dalmasi*	vf	3, 4, 6–8, 18, 19, 22, 23, 26–28	
		Berriasella privasensis			
		Pseudosubplanites ponticus	si	29	

Note: (vf) very frequently (in more than ten sections of the southwestern and central Crimea); (f) frequently (in 5–9 sections in the same regions); (r) rare (in 2–4 sections of the southwestern Crimea); and (si) singular occurrence (in one section); (U) Upper, (M) Middle, and (L) lower substages.

and *Pterotrigonia caudata*). Trigoniids from the sandstone bullions are represented by valves in various states of preservation. In places, they, together with other bivalves, form coquinas. The valves are occasionally inserted inside one another, which indicates burial in a very shallow, turbulent environment. The valves are not oriented in the same direction. In places, the sandstones contain quartz pebbles.

I. 2. Stratigraphic Significance of Trigoniids Studied

As noted above, most occurrences of trigoniids are found in the shallow water, mainly terrigenous (sandstones and siltstones) and carbonate (sandy and oncolitic limestones) beds. More rarely, they are found in sandstone or sideritic nodules contained in clay and in bioclastic limestones that fill the gaps between the coral colonies. Thus, the distribution of trigoniids is clearly controlled by facies.

Trigoniids found *in situ* are known from virtually all major sections of the southwestern and central Crimea, from the Chernaya River to the Tonas River. Three levels with characteristic species assemblages are recognized in their stratigraphic distribution.

The highest taxonomic diversity of trigoniids is established in the Berriasian, Valanginian, and Hauterivian beds of the Crimean Fore-Mountains. In the Barremian, they are only found redeposited. In the Aptian, mainly clayey beds of the Crimean Fore-Mountains, they have not been found. Trigoniids are very rarely found in the Upper Aptian. They are occasionally

Table 2. Distribution of trigoniids in the Berriasian of the Crimean Fore-Mountains

Species and subspecies	Chernaya River	Bel'bek River	Malyi Salgir River	Beshterek River	Zuya River	Burul'cha River	Sarysu River	Tonas River
Trigonia carinata crimica		Ber_1						
Myophorella loewinsonlessingi		Ber_{1-2}		Ber_1	Ber_1		Ber_1	
Myophorella tonasensis								Ber_1
Orthotrigonia mordvilkoae		Ber_{1-2}					Ber_1	
Iotrigonia scapha				Ber_1				
Rutitrigonia longa	Ber_1	Ber_{1-2}	Ber_1	Ber_{1-2}	Ber_1			
Pterotrigonia caudata		Ber_1	Ber_1	Ber_{1-2}	Ber_1	Ber_2	Ber_1	
Linotrigonia belbekensis		Ber_{1-2}						

Table 3. Distribution of trigoniids in the Valanginian of the Crimean Fore-Mountains

Species and subspecies	Bel'bek River	Kacha River	Bodrak River	Beshterek River	Zuya River	Zuya–Burul'cha interfluve
Trigonia carinata carinata		Vlg_2	Vlg_1	Vlg_{1-2}		Vlg_{1-2}
Litschkovitrigonia inguschensis			Vlg_1			Vlg_{1-2}
Quadratotrigonia nodosa orbignyana			Vlg_1			Vlg_{1-2}
Rutitrigonia longa			Vlg_1	Vlg_1	Vlg_1	Vlg_2
Pterotrigonia caudata	Vlg_1	Vlg_1	Vlg_1	Vlg_1		Vlg_1
Linotrigonia ornata			Vlg_1			Vlg_1

found in the Aptian and Albian clayey facies of the Crimean Plain. Below, the species assemblages of trigoniids are discussed according to their stratigraphic positions in the stages (Table 1).

Berriasian

Trigoniids are particularly frequently found in the Lower Berriasian virtually everywhere where Berriasian beds are exposed (Chernaya, Bel'bek, Malyi Salgir, Beshterek, Zuya, Burul'cha, Sarysu, and Tonas rivers). In some sections, trigoniids are also found from the Upper Berriasian (Table 2).

L o w e r B e r r i a s i a n. The majority of the Lower Berriasian trigoniids are found in the so-called series of alternating rocks, which usually include irregular alternations of sandstones, siltstones, clays, and more rarely limestones (sections nos. 3, 4, 6–8, 18, 19, 22, 23, 26–28). This rock series in the sections studied overlies the Lower Berriasian limestones (Chernaya River, village of Kuchki; Malyi Salgir River, village of Ivanovka; Beshterek River, villages of Solov'evka and Lesnosel'e; Sarysu River; villages of Blagodatnoe, Chernokamenka, and Novoklenovo), or conglomerates (Bel'bek River, villages of Golubinka and Solnechnosel'e). The above list of regions shows that the Lower Berriasian trigoniids mostly occur in the shallow-water beds of the southwestern and central Crimea. Only once was a trigoniid shell was found in a flyschoid series of clays and limestones exposed in the valley of the Tonas River (Outcrop no. 29).

The following species assemblage is recognized in the Lower Berriasian: *Trigonia carinata crimica, Myophorella loewinsonlessingi, M. tonasensis, Orthotrigonia mordvilkoae, Iotrigonia scapha, Rutitrigonia longa, Pterotrigonia caudata*, and *Linotrigonia belbekensis*. Of these, *T. carinata crimica, M. tonasensis*, and *I. scapha* are restricted to the Lower Berriasian. Other species continue into the Upper Berriasian, or even into the Valanginian.

U p p e r B e r r i a s i a n. Trigoniids are rarely found in the Upper Berriasian (in some layers and in four sections only [nos. 14, 19, 20, and 25]), because that interval included mostly clayey, marly, or carbonate facies. The sedimentary environment was unfavorable for these animals. The Upper Berriasian beds contain *Myophorella loewinsonlessingi, Orthotrigonia mordvilkoae, Rutitrigonia longa, Linotrigonia belbekensis*, and *Pterotrigonia caudata*.

Valanginian

The Valanginian trigoniids are found in six regions (Table 3). They are always found in sandstones. In some cases, together with other bivalves, they form platy or lenticular coquinas. They are also frequently found in sandstone nodules.

L o w e r V a l a n g i n i a n. The Lower Valanginian trigoniids are especially frequently found in the basins of the Bodrak River (sections nos. 12 and 14), Beshterek (no. 21), and on the Zuya–Burul'cha interfluve (Section no. 24). The highest taxonomic diversity is recorded for the Bodrak River basin and the Zuya–Burul'cha interfluve.

The Lower Valanginian beds contain the following species assemblage: *Trigonia carinata carinata, Litschkovitrigonia inguschensis, Quadratotrigonia nodosa orbignyana, Rutitrigonia longa, Pterotrigonia caudata*, and *Linotrigonia (Oistotrigonia) ornata*. Such taxa as *T. carinata carinata, L. inguschensis, Q. nodosa orbignyana*, and *L. (O.) ornata* first appear in the Lower Valanginian. The remaining two species are transitional, because they are also known in the Berriasian.

U p p e r V a l a n g i n i a n. The Upper Valanginian trigoniids are only found in two regions, in the basin of the Kacha River (sections nos. 9 and 10) and on the Zuya–Burul'cha interfluve (no. 24). Because of the distribution of sandy facies similar to those in the Lower Valanginian, the trigoniid species assemblage is also identical to the Lower Valanginian. The Upper Valanginian contains the following species: *Trigonia carinata carinata, Quadratotrigonia nodosa orbignyana, Rutitrigonia longa*, and *Litschkovitrigonia inguschensis*.

Hauterivian

In the Hauterivian, trigoniids occur much less frequently than in the Berriasian and Valanginian. They are also found in sandy facies in the region of the Bodrak River (sections nos. 12, 14, 15), Al'ma River (Section no. 17), and on the Zuya–Burul'cha interfluve (no. 24). In only one section (no. 16), are they found in bioclastic limestones and coquinas among the coral colonies in the body of a biostrome. In all the above sections, trigoniids are found in the Lower Hauterivian beds. The Hauterivian assemblage includes *Trigonia carinata carinata, Litschkovitrigonia inguschensis, Quadratotrigonia nodosa orbignyana, Pterotrigonia caudata*, and *Linotrigonia (Oistotrigonia) ornata* (Table 4). All these trigoniids are also found in the Valanginian, while the species *P. caudata* appeared even earlier, i.e., in the Lower Berriasian.

Barremian

In the Barremian, trigoniids are only found in the central Crimea, in the vicinity of the villages of Golovanovka (no. 30) and Gorlinka (no. 31). In these localities, they are found redeposited in the bullions of Valanginian sandstones in the Barremian series of bullion-block conglomerate. These blocks contain *Trigonia carinata carinata, Litschkovitrigonia inguschensis, Quadratotrigonia nodosa orbignyana, Iotrigonia scapha, Rutitrigonia longa, Pterotrigonia caudata*, and *Linotrigonia (Oistotrigonia) ornata*.

Table 4. Distribution of trigoniids in the Hauterivian of the Crimean Fore-Mountains

Species and subspecies	Bodrak River	Al'ma River	Zuya–Burul'cha interfluve
Trigonia carinata carinata	Hau_1	Hau_1	Hau_1
Litschkovitrigonia inguschensis	Hau_1	Hau_1	
Quadratotrigonia nodosa orbignyana	Hau_1		Hau_1
Pterotrigonia caudata		Hau_1	
Linotrigonia ornata	Hau_1	Hau_1	Hau_1

Albian

Trigoniids are very rarely found in the Albian and occur both *in situ*, and redeposited. The *in situ* occurrences include *Linotrigonia (Oistotrigonia)* sp. (Upper Albian, village of Prokhladnoe, no. 13), *Pterotrigonia taurica*, and *Rutitrigonia balaklavensis* (Middle Albian, vicinity of the town of Balaklava, Outcrop no. 1; village of Verkhnee Chernorech'e, Outcrop no. 2) (Table 1). Leshchukh (1987) described two incomplete casts of *Linotrigonia* aff. *spinosa* (Park.) from the Lower Albian clay found in borehole no. 11 (Oktyabr'skaya Square) in the central regions of the Crimean Plain. The specimens studied are housed in the department of monographic collections of the Institute of Geology and Geochemistry of Fossil Fuels, Academy of Sciences of Ukraine (collection no. 27). Unfortunately, I was unable to study them.

Sandstones and conglomerates of the Mangush series (Upper Albian) composing the top and the western slope of Prisyazhnaya Mountain often contain large specimens of *Trigonia carinata carinata* and, more rarely, small shells of *Pterotrigonia caudata* redeposited as isolated shell fragments in the slabs of Lower Valanginian sandstones.

* * *

The analysis of the stratigraphic distribution of trigoniids in the Lower Cretaceous of the Crimean Fore-Mountains allows the recognition of three clear levels with characteristic species assemblages (Table 5): (1) Berriasian (*Trigonia carinata crimica, Myophorella loewinsonlessingi, M. tonasensis, Iotrigonia scapha, Orthotrigonia mordvilkoae*, and *Linotrigonia belbekensis*), (2) Lower Valanginian–Lower Hauterivian (*Trigonia carinata carinata, Litschkovitrigonia inguschensis, Quadratotrigonia nodosa orbignyana*, and *Linotrigonia (Oistotrigonia) ornata*), and (3) Albian (*Rutitrigonia balaklavensis, Pterotrigonia taurica*, and *Linotrigonia* sp.). Trigoniids found at these three levels are included in the more general associations of bivalves, which are used as characteristic assemblages

Table 5. Stratigraphic distribution of trigoniids in the Lower Cretaceous of the Crimean Fore-Mountains

Stage	Substage	Species assemblage	*Trigonia carinata crimica*	*Myophorella tonasensis*	*Iotrigonia scapha*	*Myophorella loewinsonlessingi*	*Orthotrigonia mordvilkoae*	*Linotrigonia (Oistotrigonia) belbekensis*	*Rutitrigonia longa*	*Pterotrigonia caudata*	*Trigonia carinata carinata*	*Litschkovitrigonia inguschensis*	*Q.(Quadratotrigonia) nodosa orbignyana*	*Linotrigonia (Oistotrigonia) ornata*	*Rutitrigonia balaklavensis*	*Pterotrigonia taurica*	*Linotrigonia (Oistotrigonia)* sp.
Alb	U	3	redeposited trigoniids														
	M																
	L																
Apt			trigoniids are not found														
Brm			redeposited trigoniids														
Hau	U																
	L	2															
Vlg	U																
	L																
Ber	U	1															
	L																

in correlating sections and for the facial and paleogeographic analysis.

CHAPTER II. SYSTEMATIC PALEONTOLOGY

II. 1. History of Studies of the Early Cretaceous Trigoniids of the Crimea

The first description of a member of the Trigoniidae ("*Trigonia*" *caudata*) was given by Eichwald (1865), without illustration, and is based on a single specimen from the Neocomian conglomerates from the vicinity of the village of Biasala (Kacha River). The same specimen was redescribed (but also not figured) by Karakash (1907). Unfortunately, the descriptions of Eichwald and Karakash cannot be included in the synonymy list because of the absence of illustrations, unclear diagnoses, and incomplete stratigraphic dating.

Due to the intensive collecting of the fossil fauna of the Lower Cretaceous of the Crimea that took place in the 1950s, a representative assemblage of trigoniids has been collected. This assemblage was described and figured for the first time by myself in 1958 and included five species (*Trigonia carinata, Myophorella loewinsonlessingi, Quadratotrigonia nodosa, Iotrigonia scapha*, and *Pterotrigonia caudata*). The taxonomy followed the new system of the family Trigoniidae proposed by Saveliev (1958). I included these species and *Rutitrigonia longa* in the *Atlas of the Lower Cretaceous Fauna of the Northern Caucasus and Crimea* (Yanin, 1960). Thus, 90 years passed between the first record of trigoniids in the Lower Cretaceous of the Crimea and their first illustrations. Later, I described the better studied Berriasian trigoniids *Myophorella (Myophorella) loewinsonlessingi, M. (Orthotrigonia) mordvilkoae, Rutitrigonia longa, Pterotrigonia (Pterotrigonia) caudata*, and *Linotrigonia (Oistotrigonia) belbekensis* (Yanin, 1979a) and new Crimean forms from the Berriasian (*Trigonia carinata crimica* and *Myophorella tonasensis*) and Albian (*Rutitrigonia balaklavensis* and *Pterotrigonia taurica*) (Yanin, 2004).

Leshchukh (1987) discussed two trigoniid species (with no precise specific assignment) from the Aptian and Albian deposits from the borehole in the Crimean Plain. In the recently published *Atlas of the Cretaceous Fauna of the Southwestern Crimea*, Bogdanova *et al.* (1997) redescribed three previously known genera and four trigoniid species (*M. loewinsonlessingi, M. mordvilkoae, P. caudata*, and *L.* cf. *belbekensis*).

Thus, by the end of the 20th century, a general systematic composition of trigoniids and their occurrences in the Berriasian, Valanginian, Hauterivian, Aptian, and Albian beds of the Crimea were clarified, and descriptions and illustrations of the above species were published. The identifications of the species that I studied and described were used by many Lower Cretaceous workers in their stratigraphic publications. All these identifications are discussed in Section II. 2, where they are systematically revised with reference to relevant papers in which these identifications were cited. Since during almost 50 years, the stratigraphic position of many beds containing trigoniids has changed, the reference to each paper contains a reference to the age of beds, in which trigoniids were found.

To date, 15 species and subspecies of trigoniids have been established in the Lower Cretaceous of the southwestern and central Crimea. The descriptions of sections in these regions (Section I.1) provide an updated position for described species in accordance with the accepted stratigraphic scheme (Table 1).

II. 2. Revision of the Previous Identifications of Trigoniids from the Lower Cretaceous of the Crimean Fore-Mountains

Linotrigonia belbekensis sp. nov. (Yanin, 1957, p. 129; nomen nudum, Lower Valanginian) = *L. (Oistotrigonia) belbekensis* Yanin (Yanin, 1979a, p. 29, pl. 2, figs. 11, 12, Berriasian) = *L. belbekensis* (Yanin and Smirnova, 1981, p. 83; Upper Berriasian; Bogdanova *et al.*, 1997, p. 84, pl. 19, fig. 7, Berriasian; Yanin and Baraboshkin, 2000, p. 71, Lower Berriasian) [here, *L. (O.) belbekensis*, upper part of the Lower Berriasian and lower part of the Upper Berriasian].

Linotrigonia ornata (d'Orb.) (Yanin, 1958, p. 129, Hauterivian; Baraboshkin and Yanin, 1997, p. 21, Upper Valanginian) [here, *L. (Oistotrigonia) ornata*, Lower Valanginian–Lower Hauterivian (*in situ*) and Barremian (redeposited)].

Litschkovitrigonia inguschensis (Renng.) (Yanin, 1958, p. 131, Hauterivian) [here, *L. inguschensis*, Lower Valanginian–Lower Hauterivian].

Quadratotrigonia orbignyana (Lyc.) (Lysenko and Yanin, 1979, p. 78, Lower Hauterivian; Drushchits *et al.*, 1986, p. 131, Lower Hauterivian; Baraboshkin and Yanin, 1997, p. 21, Upper Valanginian) [here, *Q. (Q.) nodosa orbignyana*, Lower Valanginian–Lower Hauterivian (*in situ*) and Barremian (redeposited)].

Trigonia carinata Ag. (Drushchits, 1956, p. 57, Upper Hauterivian; Yanin, 1957, p. 152, Hauterivian; Eristavi, 1957, pp. 10, 13, Lower Hauterivian; Yanin, 1958, p. 131, pl. 1, fig. 1, Hauterivian; Drushchits, 1960, p. 62, Upper Hauterivian and redeposited slabs of Hauterivian sandstones in the Barremian conglomerates; Yanin, 1960, p. 205, pl. 19, fig. 2, Hauterivian; Lichagin *et al.*, 1971, pp. 167, 168, Hauterivian; Lysenko and Yanin, 1979, p. 78, Lower Hauterivian; Aliev *et al.*, 1985, p. 18, Lower Hauterivian; Drushchits *et al.*, 1986, p. 131, Lower Hauterivian; Yanin and Vishnevskii, 1989, p. 94, Lower Hauterivian; Baraboshkin and Yanin, 1997, p. 21, Upper Valanginian; Baraboshkin, 1997, p. 44, Lower Hauterivian [here, *T. carinata carinata*, Lower Valanginian–Lower Hauterivian (*in situ*), Barremian and Upper Albian (redeposited)].

Trigonia caudata Ag. (Yanin, 1957, p. 152, Valanginian–Hauterivian; Drushchits and Yanin, 1958, p. 173, Lower Valanginian; Lichagin *et al.*, 1971, p. 167, Hauterivian) = *Pterotrigonia caudata*; Yanin, 1958, p. 131, pl. 1, figs. 6–8, Valanginian–Hauterivian; Drushchits, 1960, p. 60, Lower Hauterivian; Yanin, 1960, p. 208, pl.22, fig. 1, Lower Valanginian–Hauterivian; Kravtsov and Shalimov, 1978, p. 44, Berriasian and p. 47, Valanginian; Lysenko and Yanin, 1979, p. 75, Upper Berriasian, p. 77, Lower Hauterivian; Yanin and Smirnova, 1981, p. 83, Upper Berriasian; Kravtsov *et al.*, 1983, p. 22, pl. 11, fig. 8, Berriasian; Yanin and Vishnevskii, 1989, p. 95, Lower Hauterivian; Bogdanova *et al.*, 1997, p. 83, pl. 19, fig. 8, Berriasian–Hauterivian; Baraboshkin and Yanin, 1997, pp. 9, 18, Lower Valanginian; Yanin and Baraboshkin, 2000, p. 71, Lower Berriasian) = *Pterotrigonia (Pterotrigonia) caudata* (Yanin, 1979a, p. 27, pl. 2, figs. 7–10, Berriasian–Lower Hauterivian) [here, *P. caudata*, upper part of the Lower Berriasian–Lower Hauterivian (*in situ*), Barremian and Upper Albian (redeposited)].

Trigonia gertrudae Mordv. (Yanin, 1957, p. 152, my identification was based on a specimen from the collection made for the *Catalogue of Lower Cretaceous Bivalves from the Southern USSR* by T.A. Mordvilko. This name was written by T.A. Mordvilko on the label. She assigned this specimen to a new species, but did not publish it. I named this specimen after T.A. Mordvilko *Myophorella mordvilkoae* Yanin (Yanin, 1979a, p. 25, pl. 2, figs. 2, 3, Upper Berriasian) [here, *Orthotrigonia mordvilkoae*, upper part of the Lower Berriasian and lower part of the Upper Berriasian].

Trigonia loewinsonlessingi Renng. (Yanin, 1957, p. 152, Lower Valanginian; Drushchits and Yanin, 1958, p. 173, Lower Valanginian) = *Myophorella loewinsonlessingi* (Yanin, 1958, p. 132, pl. 1, fig. 2, Lower Valanginian; Drushchits, 1960, p. 58, Lower Valanginian; Yanin, 1960, p. 205, pl. 19, fig. 3, Lower Valanginian; Kravtsov and Shalimov, 1978, p. 43, Berriasian; Lysenko and Yanin, 1979, p. 75, Upper Berriasian; Yanin and Smirnova, 1981, p. 83, Upper Berriasian; Kravtsov *et al.*, 1983, p. 22, pl. 11, fig. 7, Berriasian; Plotnikova *et al.*, 1984, p. 62, Berriasian; Yanin and Vishnevskii, 1989, pp. 83, 87, Upper Berriasian; Bogdanova *et al.*, 1997, p. 82, pl. 19, figs. 4, 5, Berriasian; Yanin and Baraboshkin, 2000, p. 71, Lower Berriasian, p. 72, Upper Berriasian) = *M. (M.) loewinsonlessingi* (Yanin, 1979a, p. 24, pl. 2, fig. 1, Berriasian) [here, *M. loewinsonlessingi*, upper part of the Lower Berriasian and lower part of the Upper Berriasian].

Trigonia longa Ag. (Yanin, 1957, p. 152, Valanginian–Hauterivian; Drushchits and Yanin, 1958, p. 173, Lower Valanginian and p. 174, Lower Hauterivian) = *Rutitrigonia longa* (Yanin, 1958, p. 129, Valanginian–Hauterivian; Drushchits, 1960, p. 60, Lower Hauterivian; Yanin, 1960, p. 208, pl. 21, fig. 1, Lower Valanginian; Lichagin *et al.*, 1971, p. 166, Hauterivian; Kravtsov and Shalimov, 1978, p. 44, Berriasian; Yanin, 1979a, p. 26, pl. 2, figs. 4–6, Berriasian–Lower Hauterivian; Lysenko and Yanin, 1979, p. 75, Upper Berriasian, and pp. 77, 78, Lower Hauterivian; Yanin and

Smirnova, 1981, p. 83, Upper Berriasian; Kravtsov *et al.*, 1983, p. 22, pl. 11, fig. 6, Berriasian; Baraboshkin and Yanin, 1997, p. 21, Upper Valanginian; Yanin and Baraboshkin, 2000, p. 71, Lower Berriasian, p. 72, Upper Berriasian) [here, *R. longa,* upper part of the Lower Berriasian–Upper Valanginian (*in situ*) and Barremian (redeposited)].

Trigonia cf. *mangyschlakenis* Lupp. (Yanin, 1957, p. 152, Hauterivian) [here, *Quadratotrigonia nodosa orbignyana* (Lyc.), Lower Valanginian–Lower Hauterivian *in situ* and Barremian (redeposited)].

Trigonia mordvilkoae sp. nov. (Yanin, 1957, p. 152, nomen nudum, Lower Valanginian; Yanin, 1958, p. 129, nomen nudum, Lower Valanginian) = *Myophorella (Orthotrigonia) mordvilkoae* Yanin (Yanin, 1979a, p. 25, pl. 2, figs. 2, 3, Berriasian) = *M. mordvilkoae* (Bogdanova *et. al.*, 1997, p. 83, pl. 19, fig. 6, Berriasian; Yanin and Baraboshkin, 2000, p. 71, Lower Berriasian, p. 72, Upper Berriasian [here, *Orthotrigonia mordvilkoae*, upper part of the Lower Berriasian and lower part of the Upper Berriasian].

Trigonia nodosa Sow. (Yanin, 1957, p. 152, Hauterivian) = *Quadratotrigonia nodosa* (Yanin, 1958, p. 133, pl. 1, figs. 3, 4, Hauterivian; Drushchits, 1960, p. 63, Barremian (redeposited); Yanin, 1960, p. 206, pl. 20, fig. 1, Hauterivian, and also from the redeposited slabs of Hauterivian sandstone in the Barremian conglomerates; Lichagin *et al.*, 1971, p. 166, Hauterivian; Yanin and Smirnova, 1981, p. 95, Lower Hauterivian [here, *Q. nodosa orbignyana* (Lyc.), Lower Valanginian–Lower Hauterivian (*in situ*) and Barremian (redeposited)].

Trigonia scapha Ag. (Yanin, 1957, p. 152, Hauterivian) = *Iotrigonia scapha* (Yanin, 1958, p. 134, pl. 1, fig. 5, Hauterivian; Yanin, 1960, p. 207, pl. 21, fig. 2, Hauterivian [here, *I. scapha*, upper part of the Lower Berriasian (*in situ*) and Barremian (redeposited)].

Trigonia ex gr. *spinosa* Park. (Yanin, 1957, p. 152, Upper Albian) = *Linotrigonia* ex gr. *spinosa* (Yanin, 1958, p. 131, Upper Albian; Yanin, 1964, p. 116, Upper Albian) = *L. spinosa* (Yanin, 1960, p. 210, Upper Albian) [here, *Linotrigonia (Oistotrigonia)* sp., lower zone of the Upper Albian].

Trigonia cf. *subdaedalea* Renng. (Yanin, 1957, p. 152, Hauterivian) = *Trigonia subdaedalea* (Lychagin, 1969, p. 168, Barremian) = *Litschkovitrigonia subdaedalea* (Drushchits, 1960, p. 63; Yanin, 1960, p. 206, Hauterivian (*in situ*), and also redeposited in the Barremian conglomerates) [here, *L. inguschensis*, Lower Valanginian–Lower Hauterivian (*in situ*) and Barremian (redeposited)].

Trigonia subornata sp. nov. (Yanin, 1957, p. 152, nomen nudum, Hauterivian) = *Linotrigonia ornata* (d'Orb.) (Yanin, 1958, p. 129, Hauterivian [here, *L. (Oistotrigonia) ornata*, Lower Valanginian–Lower Hauterivian (*in situ*) and Barremian (redeposited)].

Vaugonia mordvilkoae (Yanin) (Yanin and Smirnova, 1981, p. 83, Upper Berriasian) = *Myophorella (Orthotrigonia) mordvilkoae* (Yanin, 1979a, p. 25, pl. 2, figs. 2, 3; Berriasian) [here, *Orthotrigonia mordvilkoae*, upper part of the Lower Berriasian and lower part of the Upper Berriasian].

II. 3. Material, Methods, Terminology

M a t e r i a l. The collection studied comes from the Berriasian, Valanginian, Hauterivian, and Albian stages of the southwestern and central Crimea. Trigoniids are also found in the Barremian (redeposited). The major collections were made by the author in the 1956–1990. In various years, trigoniids were collected by V.V. Drushchits, T.N. Gorbatchik, T.N. Smirnova, E.I. Kuzmicheva, M.A. Golovinova, and other workers, and also by postgraduates and students of the Paleontological Department of Moscow State University. The long-term field work in the Crimea was conducted by the Lower Cretaceous Expedition Team headed by V.V. Drushchits (from 1953 to 1968) and myself (from 1970 to 1990). Some specimens were sent for identification by colleagues from different geological institutions, including V.M. Tseisler (Moscow Geological Prospecting University), V.N. Aleksandrova (*Krymgaznefterazvedka*), A.A. Shalya [All-Russia Scientific Research Institute of Natural Gases and Gas Technologies (VNIIGaz)], N.I. Lysenko (Simferopol University), E.Yu. Baraboshkin (Department of Regional Geology and History of Earth of the Geological Faculty of Moscow State University), and others. In addition, I studied the collections housed in the Bogdanov's Geological Museum of the Crimean Station (village of Prokhladnoe, Bakhchisarai District).

The trigoniid collection studied includes 190 specimens. The majority are well preserved and are represented by complete shells and isolated valves with a complete shell layer and ornamentation. The localities usually contain specimens at various growth stages. The occurrence of trigoniids in the sandstone lens in the series of Mazanka sands and pebble rocks exposed in the Zuiskii Quarry (Belogorskii District) is unique in this respect. The locality contains five species represented by individuals of various sizes: from juveniles (to several millimeters) to adults (several centimeters). All these represent a continuous series from a single sample, i.e., a paleopopulation buried *in situ*.

The major collections of trigoniids were made in the basins of the Chernaya River (village of Verkhnee Chernorech'e; Middle Albian), Bel'bek River (vicinity of the village of Kuibyshevo, villages of Golubinka and Solnechnosel'e; Berriasian), Kacha River (village of Verkhorech'e, Kayas-Dzhilga Gully; Valanginian), Bodrak River (Prisyazhnaya Mountain, villages of Prokhladnoe, Trudolyubovka, etc.; Valanginian, Hauterivian, and Albian), Malyi Salgir River (village of

Ivanovka; Berriasian), Beshterek River (villages of Solov'evka, Lesnosel'e, and Mazanka; Berriasian and Valanginian), Zuya River (Balanovskoe Water Reservoir, village of Krasnogor'e; Berriasian), Zuya–Burul'cha interfluve (Zuya Quarry, Kunich Mountain; Valanginian, Hauterivian), Tonas River (village of Golovanovka), and Kuchuk-Karasu River (village of Gorlinka; trigoniids in slabs of Valanginian sandstones redeposited in the Barremian conglomerates); vicinity of the town of Balaklava, Albian. The locality map is shown in Fig. 1.

The spatial and stratigraphic distribution of trigoniids is very uneven. Their major occurrences are found in the sandstone-siltstone beds of the Lower Berriasian, Valanginian, Lower Hauterivian, and Upper Albian. Thus, the distribution of trigoniids was controlled by the distribution of shallow water, usually medium- and coarse-grained sediments. As noted above, the majority of specimens come from the southwestern and central Crimea (Table 1). No trigoniids are found in the eastern Crimea, where the contemporary beds are represented by fine clayey, often flyschoid beds, and, on the other hand, by very coarse pebble-bullion horizons. Apparently, the environment was very unfavorable for trigoniids. Trigoniids are very rarely found in the Crimean Plain, where the Lower Cretaceous is mainly represented by clayey facies. However, trigoniids are found in Aptian and Albian siltstone and sandstone beds.

In the Berriasian, Valanginian, and Hauterivian sections of the Crimean Fore-Mountains, trigoniids often constitute the major part of the coquinas formed by the shells of bivalves, gastropods, brachiopods, and ammonites. Such a type of burial is especially clearly represented in the Lower Berriasian in the basin of the Bel'bek River (village of Golubinka: Kabanii Gully), in the Valanginian of the basin of the Bodrak River (mountains Dlinnaya and Patil'), and Zuya–Burul'cha interfluve (Zuiskii Quarry) (see description of relevant sections). Some data on the distribution and frequency of occurrence of trigoniids in the sections of the Lower Cretaceous of the Crimea are in Table 1. The total number and preservation of shells of each species are included in the systematic descriptions in the section Material.

Methods. In studying the trigoniid collection, I used the commonly accepted method for study of bivalves (Korobkov, 1954; Nevesskaja, 1960; Saveliev, 1958, 1960a, 1960b, etc.). The identification of the trigoniid species was preceded by a general preparation of the external and internal surface of the shell, especially the ornamentation and dental apparatus. Photographs were taken in various years using various photographic equipment, and various photographic printing materials. The macrophotographs were taken by the photographers N.L. Sadovenko (LAFOKI), G.P. Petukhova (Moscow State University), and A.V. Mazin (Paleontological Institute, Russian Academy of Sciences). The

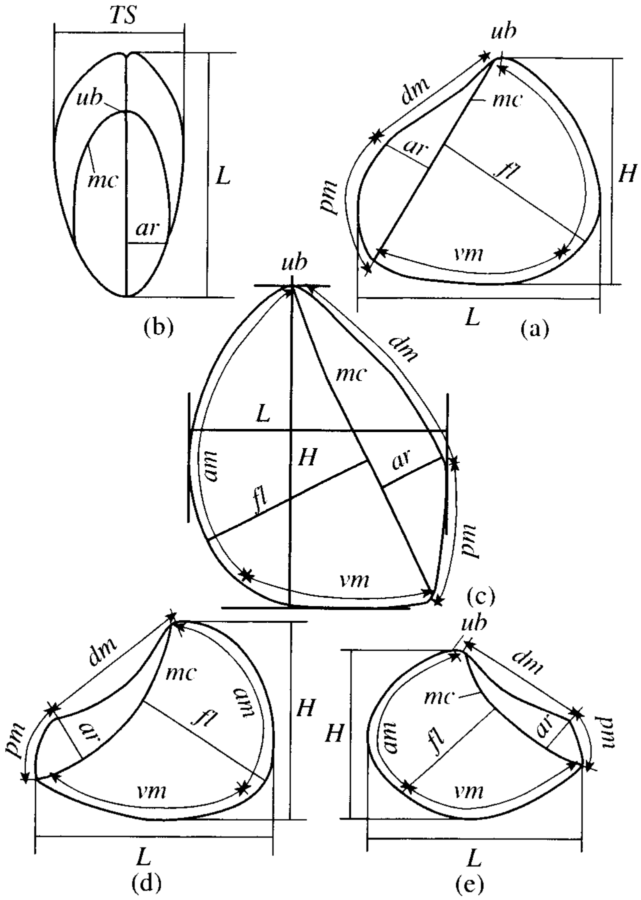


Fig. 27. Measurements and terminology of trigoniid shells: (a, b) *Orthotrigonia mordvilkoae*, shell: (a) external view, (b) upper view, from the umbo, ×1 (Pl. 5, fig. 4); (c) *Trigonia carinata carinata*, left valve, external view, ×1 (specimen MZ MGU, no. 1/10); (d) *Linotrigonia ornata*, right valve, external view, ×2 (Pl. 11, fig. 1); (e) *Rutitrigonia longa*, left valve, external view, ×1.5 (Pl. 8, fig. 9). Explanations: (*am*) anterior margin, (*ar*) area, (*dm*) dorsal margin, (*fl*) flank, (*H*) height, (*L*) length, (*mc*) marginal carina, (*pm*) posterior margin, (*TS*) thickness of a complete shell, (*ub*) umbo, and (*vm*) ventral margin.

drawings were made by the authors from enlarged photographs, and subsequently reduced. The SEM photographs of juveniles of three trigoniid species were obtained using the Cam Scan in the Laboratory of Electronic Photography of the Paleontological Institute of the Russian Academy of Sciences (operator L.T. Protasevich).

Terminology. When describing trigoniid taxa, I used the terminology proposed by Saveliev (1958, 1960a, 1960b) with slight modifications. All major morphological elements of the shell and hinges used in the descriptions of the genera and species are shown in Figs. 27–31. The structure of juveniles is shown in Figs. 32–33.

The following measurements are used in the section Dimensions for shells and isolated valves (Fig. 27):

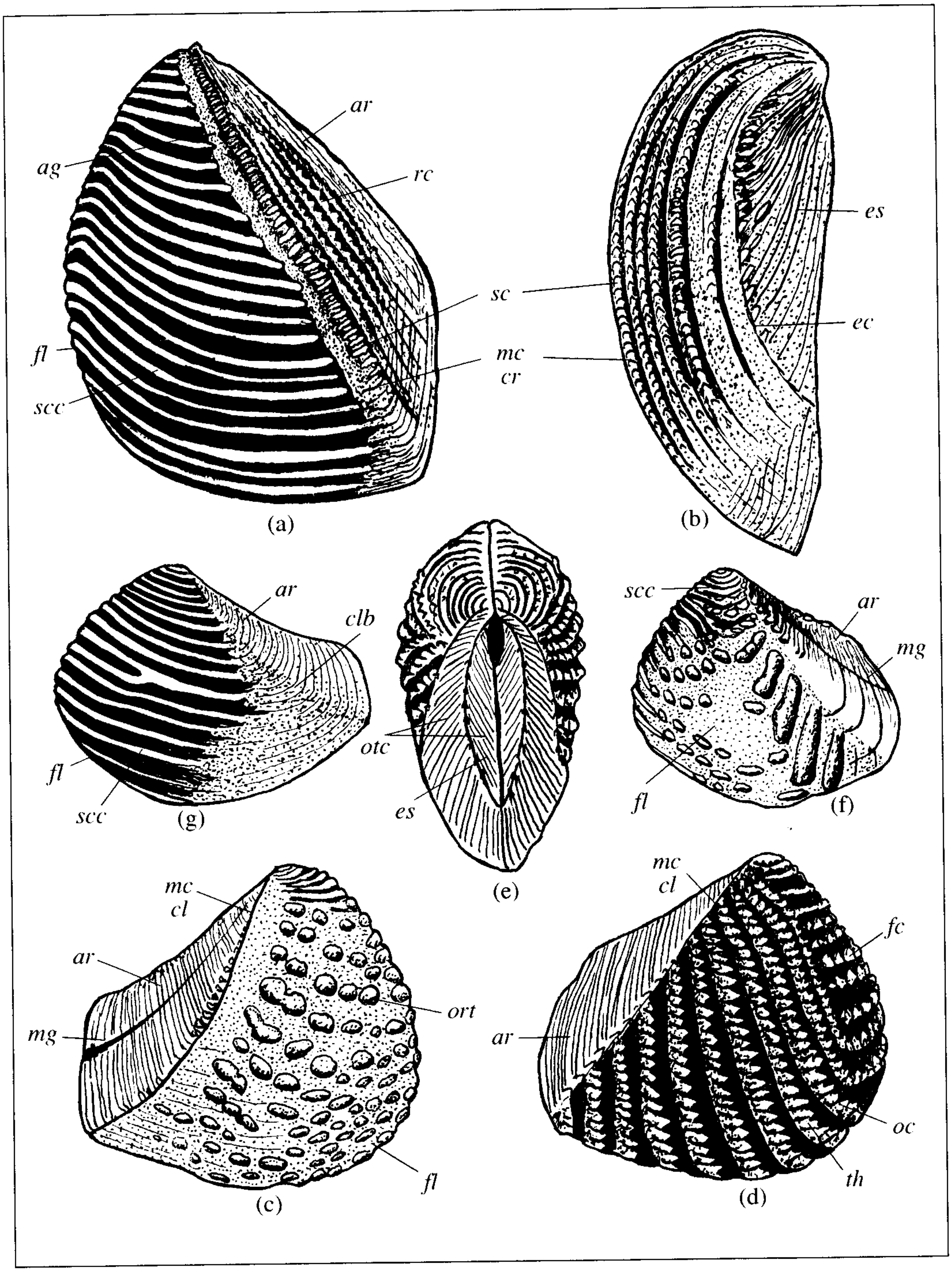


Fig. 28. External shell morphology in the genera *Trigonia, Myophorella, Orthotrigonia, Iotrigonia*, and *Rutitrigonia*: (a, b) *Trigonia carinata carinata*, left valve, ×1; (a) external view, (b) area view (Yanin, 1958, pl. 1, fig. 1); (c) *Myophorella loewinsonlessingi*, right valve, external view, ×1.5 (Pl. 4, fig. 1a); (d, e) *Orthotrigonia mordvilkoae*, shell, ×1.5: (d) external view, right valve, (e) upper (umbonal) view (Pl. 5, fig. 4); (f) *Iotrigonia scapha*, left valve, external view, × 1.5 (Pl. 7, fig. 8a); and (g) *Rutitrigonia longa*, left valve, external view, × 1.5 (Pl. 8, fig. 9). Explanations: (*ag*) antecarinal groove on the flank, (*ar*) area, (*clb*) carina-like bend, (*cl*) linear, thin, and smooth carina possessing small tubercles and terminations of the costae, (*cr*) ridgelike carina, (*ec*) escutcheon carina (between the area and escutcheon), (*es*) escutcheon, (*fc*) frontal costae near the anterior margin of the valve, (*fl*) flank, (*mc*) marginal carina (between the flank and area), (*mg*) median groove on the area, (*oc*) oblique costae on the flank, (*ort*) oblique rows of tubercles on the flank, (*otc*) obliquely transverse costellae on the area and escutcheon, (*rc*) radial costae on the area, (*sc*) scales on the costae and carinae, (*scc*) subconcentric costae on the flank, and (*th*) hatching on the posterior slopes of the costae on the flank.

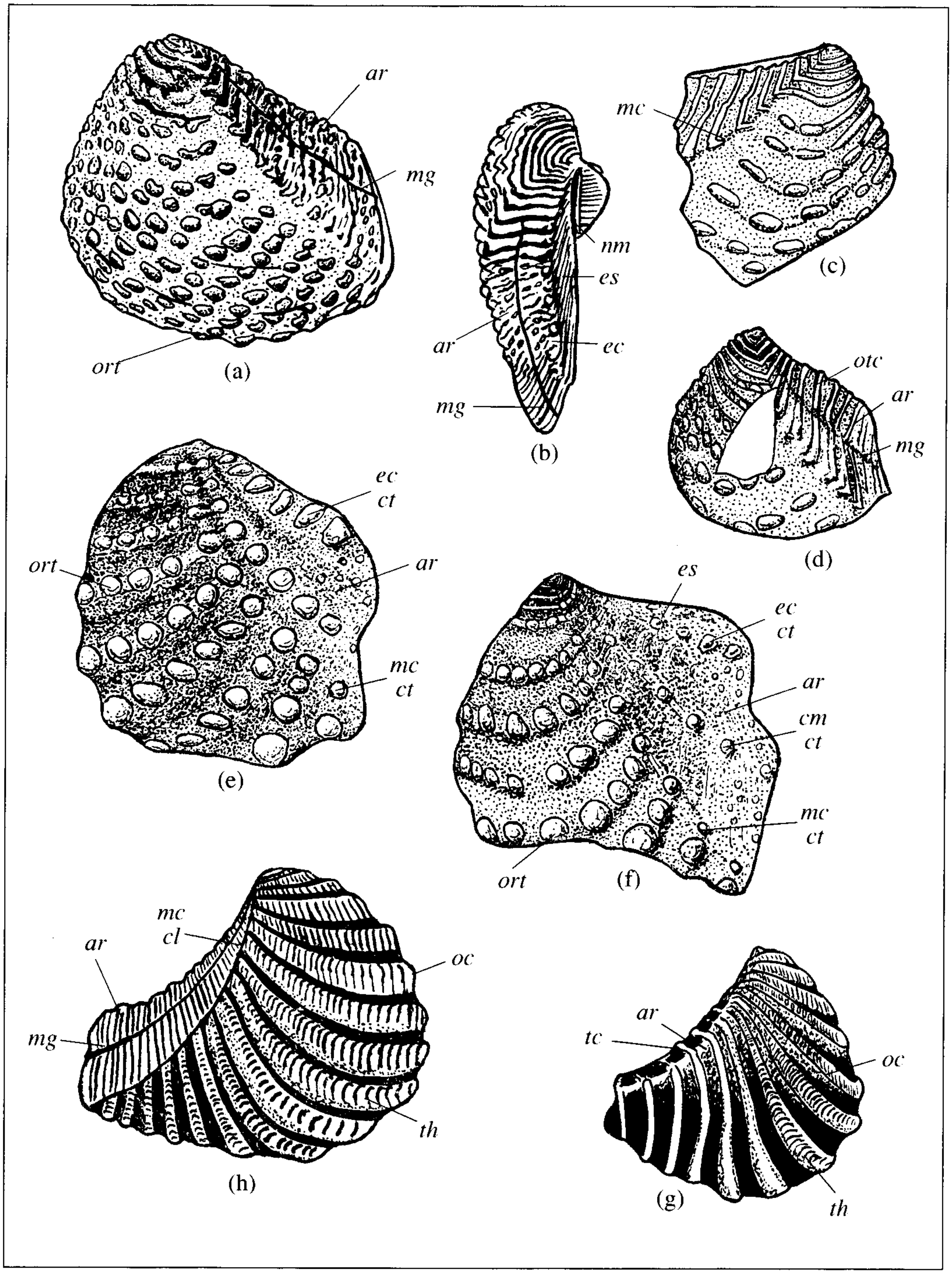


Fig. 29. External morphology of the shells of the genera *Litschkovitrigonia, Quadratotrigonia, Pterotrigonia*, and *Linotrigonia*: (a–d) *Litschkovitrigonia inguschensis*: (a, b) left valve, ×1.5: (a) external view, (b) area and escutcheon view (Pl. 5, figs. 7a, 7b); (c) fragment of the right valve of the young shell, external view, ×2 (Pl. 6, fig. 3); (d) left valve of a young shell, external view, ×2 (Pl. 6, fig. 5); (e, f) *Quadratotrigonia nodosa orbignyana*: (e) fragment of the left valve of a young shell, external view, ×2.5 (Yanin, 1958, pl. 1, fig. 3); (f) fragment of the left valve of a young shell, external view, ×2 (Pl. 6, fig. 9a); (g) *Pterotrigonia caudata*, right valve, external view, ×1.5 (Pl. 9, fig. 10); (h) *Linotrigonia ornata*, right valve of a young shell, external view, ×3 (Pl. 11, fig. 1). Explanations: (*ar*) area, (*cm*) median carina on the area, (*ct*) tuberculate carina (row of isolated tubercles), (*nm*) nymph, (*tc*) transverse costellae on the area and escutcheon; for other explanations, see Fig. 28.

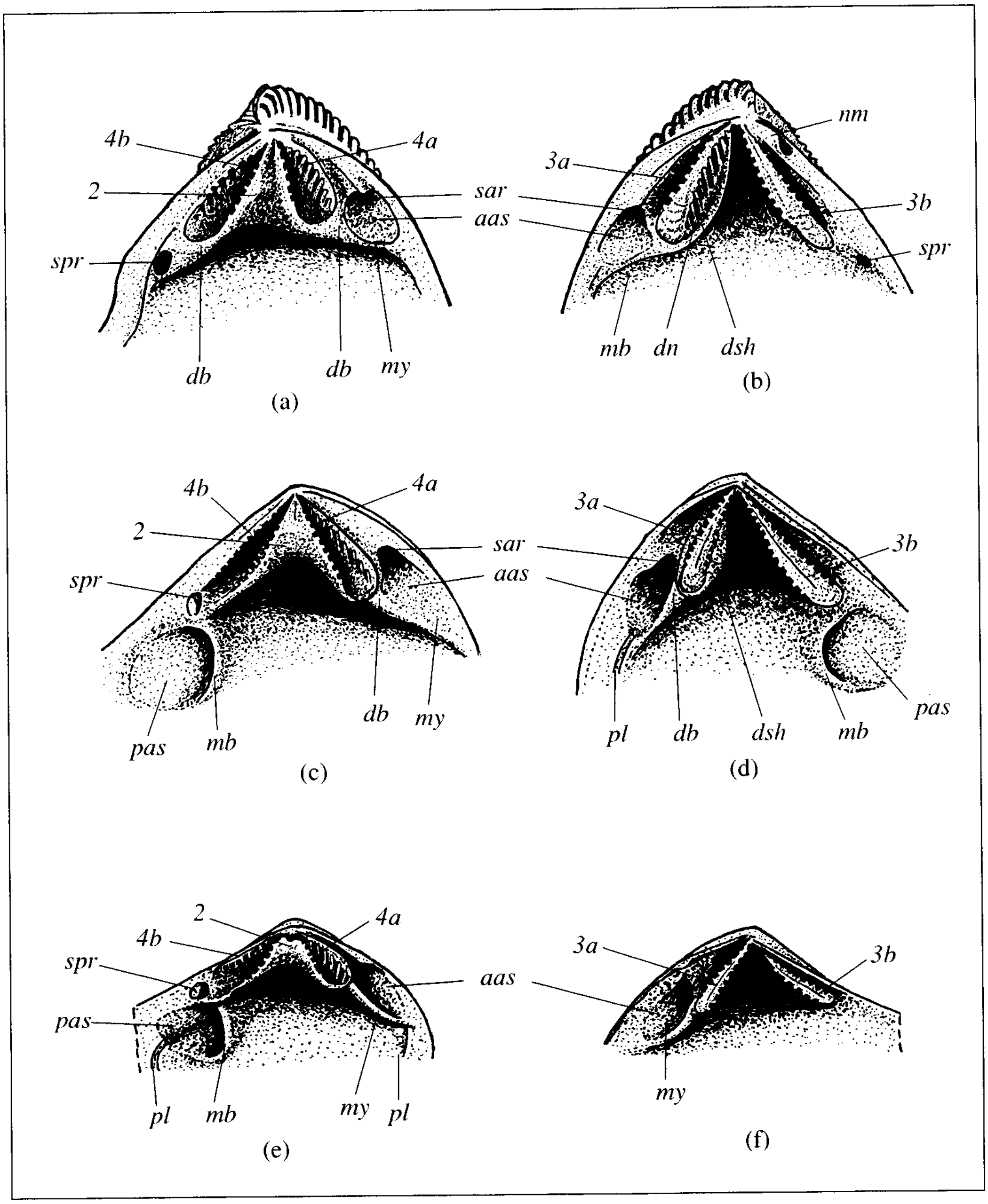


Fig. 30. Shell interior in the genera *Trigonia, Myophorella*, and *Rutitrigonia*: (a, b) *Trigonia carinata carinata*, ×1: (a) left valve (Pl. 3, fig. 1b); (b) right valve (Pl. 2, fig. 2b); (c, d) *Myophorella loewinsonlessingi*, ×2: (c) left valve (Pl. 4, fig. 3), (d) right valve (Pl. 4, fig. 2c); (e, f) *Rutitrigonia longa*, × 2: (e) left valve (Pl. 8, fig. 11c); (f) right valve (Pl. 8, fig. 6). The preserved structures on the valves are show only. Explanations: (*aas*) anterior adductor scar, (*db*) dental buttress, (*dn*) dental notches, (*dsh*) dental shelf, (*mb*) myophorous buttress (around the anterior and ventral sides of the posterior adductor scar), (*my*) myophore (support of the anterior adductor scar on both valves, continuation of the anterior dental buttress), (*nm*) nymph, (*pas*) posterior adductor scar, (*pl*) pallial line, (*sar*) anterior pedal retractor scar, and (*spr*) posterior pedal retractor scar; (*2*) median tooth on the left valve, (*3a, 3b*) anterior and posterior branches of tooth 3 on the right valve, (*4a, 4b*) anterior and posterior branches of tooth 4 on the left valve.

(L) length (distance between the anterior and posterior margins);

(H) height (distance between the lower and upper margins along the vertical to the line of length);

(T) thickness (distance between the point of the maximum convexity of the valve to the plane of commissure);

(H/L) degree of elongation (ratio of the valve height to its length);

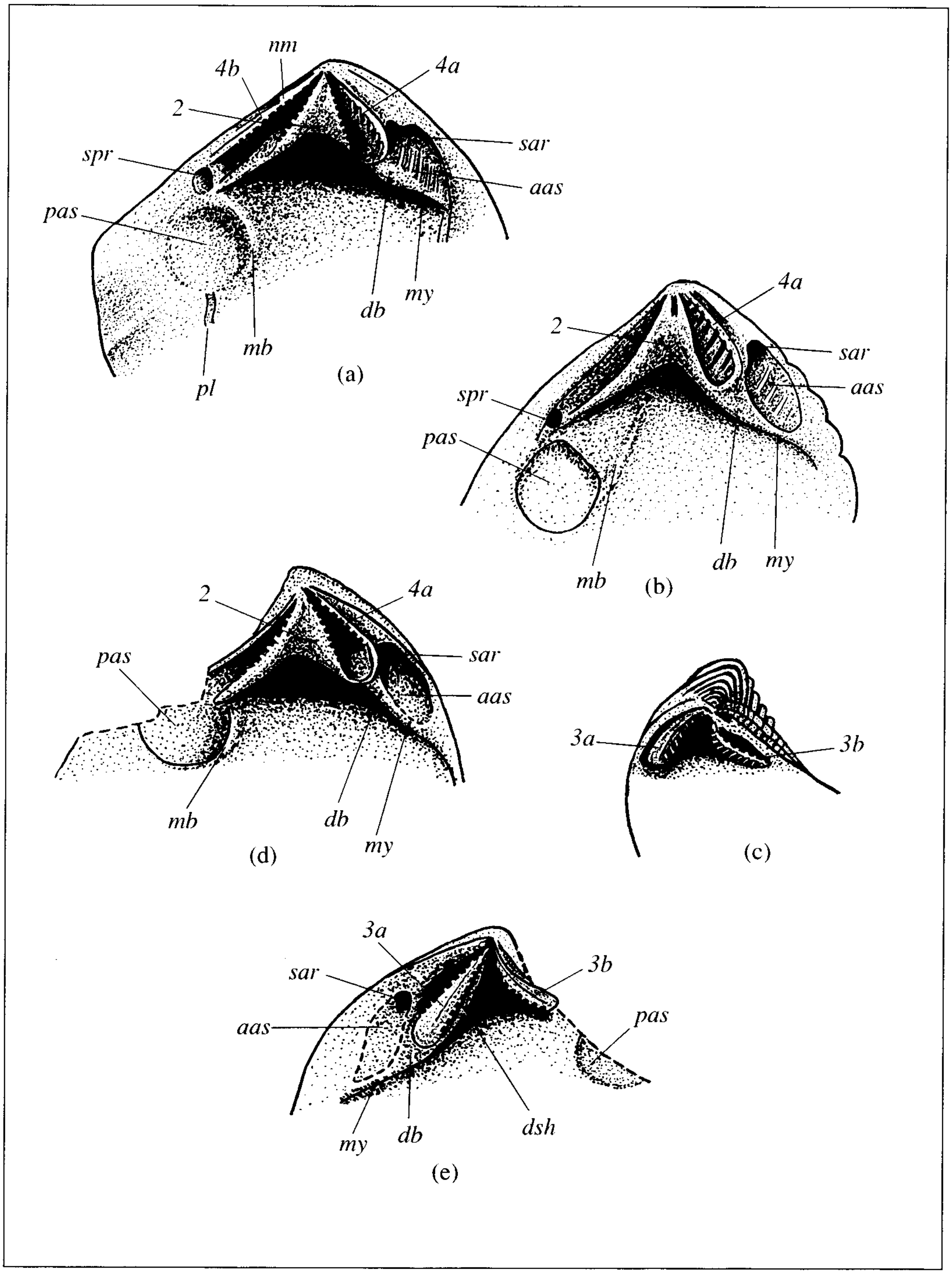


Fig. 31. Shell interior in the genera *Litschkovitrigonia, Quadratotrigonia, Pterotrigonia*, and *Linotrigonia*: (a) *Litschkovitrigonia inguschensis*, left valve, ×2 (Pl. 5, fig. 7c); (b) *Quadratotrigonia nodosa orbignyana*, left valve, ×1 (Pl. 6, fig. 10); (c) *Pterotrigonia caudata*, right valve, ×2 (Pl. 9, fig. 14); (d, e) *Linotrigonia belbekensis*, ×2: (d) left valve (Pl. 10, fig. 8b); (e) right valve (Pl. 10, figs. 4, posterior adductor scar and tooth 3b are partly broken off). The preserved structures of the valves are shown only. For explanations see Fig. 30.

(T/L) degree of convexity (ratio of the valve thickness to its length);
(FL) maximum width of the flank;
(AR) maximum width of the area;
(AR/FL) ratio of the area width to the flank width;

Abbreviations used in the section Material: (LV) left valve, (RV) right valve, (BS) bivalved shell.

In the species descriptions the following scale is used to indicate the relative size of the shell and valves

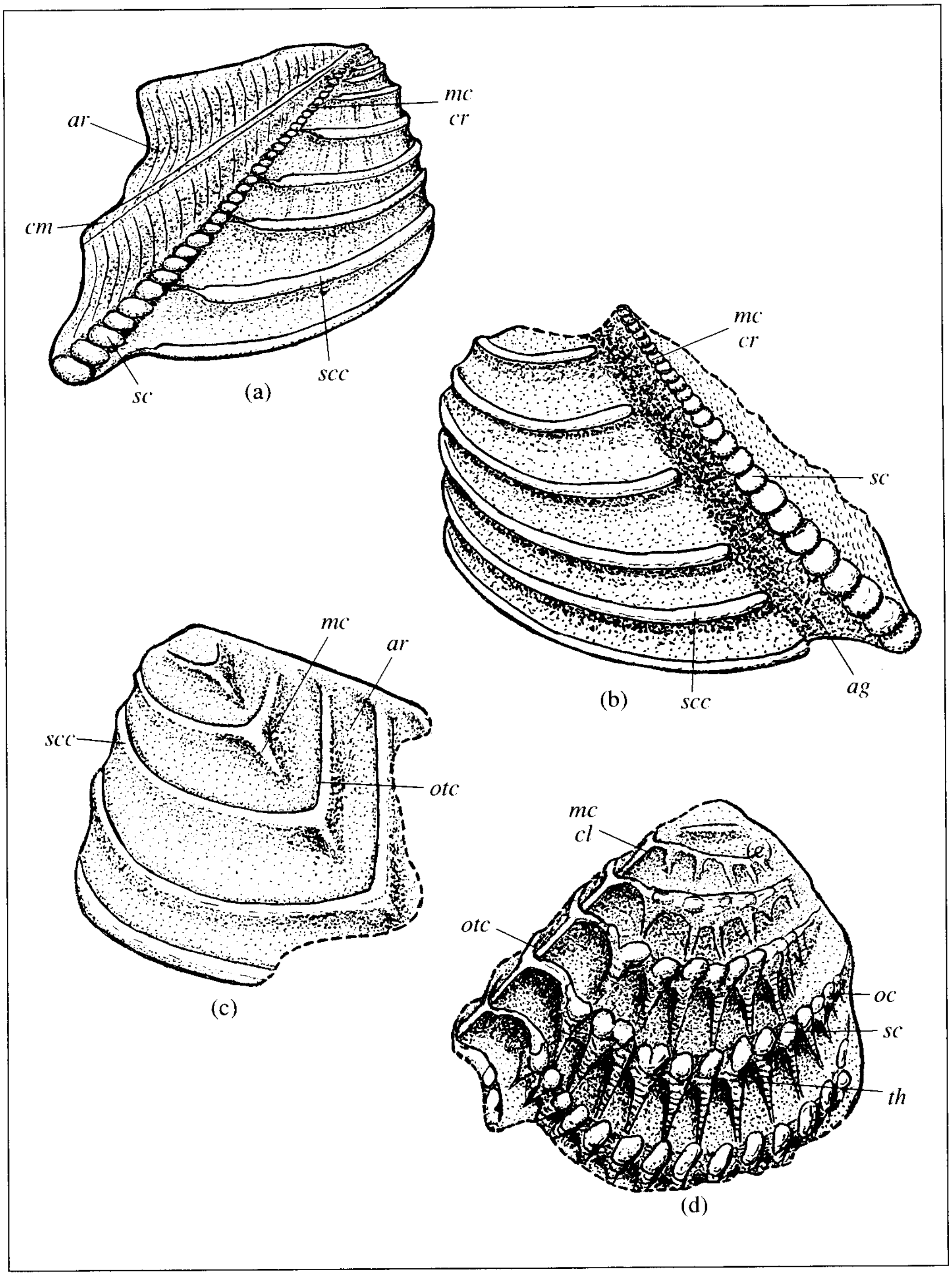


Fig. 32. Structure of the external surface of juvenile shells in the genera *Trigonia, Litschkovitrigonia*, and *Linotrigonia*: (a, b) *Trigonia carinata carinata*: (a) complete shell, view from right valve, ×11 (Pl. 12, fig. 1a); (b) left valve, broken umbo and dorsal margin, external view, ×12 (Pl. 14, fig. 1a); (c) *Litschkovitrigonia inguschensis*, fragment of the left valve, external view, ×16 (Pl. 11, fig. 10); (d) *Linotrigonia* (*Oistotrigonia*) *ornata*, fragment of the right valve of the juvenile shell, external view, ×24 (Pl. 11, fig. 9). Explanations: (*ag*) antecarinal groove, (*cl*) linear carina, (*cm*) median carina, (*cr*) ridgelike carina, (*mc*) marginal carina, (*oc*) oblique costae on the flank, (*otc*) obliquely transverse costellae on the area, (*sc*) scales on the costae and carinae, (*scc*) subconcentric costae on the flank, and (*th*) hatching on the posterior slopes of oblique costae.

(based on the maximum shell length of adults): small, up to 25 mm; medium-sized, from 25 to 60 mm; and large, over 60 mm.

In describing the taxa, the author used the instructions adopted by the *Paleontologicheskii Zhurnal* (Moscow).

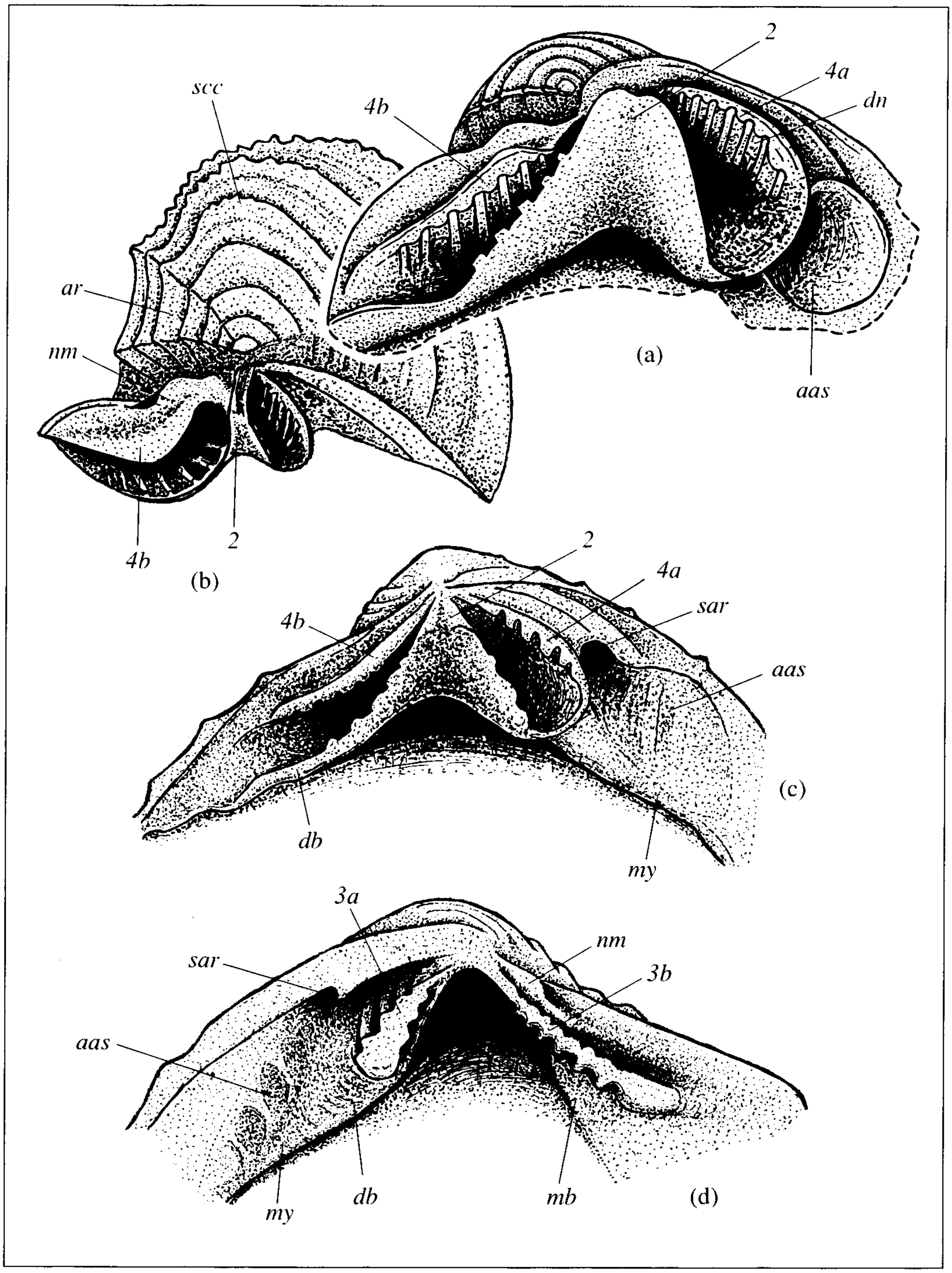


Fig. 33. Hinge of juvenile shells in the genera *Pterotrigonia* and *Linotrigonia*: (a, b) *Pterotrigonia caudata*, left valve (Pl. 15, fig. 1): (a) internal view, ×17; (b) umbonal view (the plane of commissure is parallel to the axis of view), ×14; (c, d) *Linotrigonia (Oistotrigonia) ornata*: (c) left valve, ×17 (Pl. 16, fig. 2); (d) right valve, ×30 (Pl. 16, fig. 1c). The preserved structures of the umbonal region of the valves are shown only. Explanations: (*aas*) anterior adductor scar, (*ar*) area, (*db*) dental buttress, (*dn*) dental notches, (*mb*) myophorous buttress, (*my*) myophore, (*nm*) nymph, (*sar*) anterior retractor scar, and (*scc*) subconcentric costae in the umbonal regions; for explanations of teeth, see Fig. 30.

II. 4. Systematic Descriptions

The taxonomy in this section follows Nevesskaja *et al.* (1971) for taxa above the family level, and Saveliev (1958, 1960b), with some amendments, for families, subfamilies, and genera. Amendments include the erection of the new subfamily Linotrigoniinae, and the treatment of the subgenus *Orthotrigonia* as a genus.

Order Actinodontida Douvillé, 1912

Suborder Trigoniina Dall, 1889

Superfamily Trigonioidea Lamarck, 1819

Family Trigoniidae Lamarck, 1819

Subfamily Trigoniinae Lamarck, 1819

Genus *Trigonia* Bruguière, 1789

Trigonia: Bruguière, 1789, p. 14; Lamarck, 1835, p. 512 (pars); Agassiz, 1840, p. 40 (pars); D'Orbigny, 1843–1847, p. 128 (pars); Pictet and Campiche, 1864–1867, p. 359 (pars); Lycett, 1872–1879, p. 179 (pars); Lichkov, 1913, p. 5 (pars); Cossmann, 1912, p. 59 (pars); Crickmay, 1932, p. 445; Mordvilko, 1949, p. 127 (pars); Saveliev, 1958, p. 86; 1960b, p. 95; Yanin, 1958, p. 131; 1960, p. 205; 2004, p. 26; Nakano, 1961, p. 82; Cox, 1969b, p. N478; Bogdanova, 1988, p. 153.

Type species. *Venus sulcata* Hermann, 1781; Lower Jurassic; France (Alsace, Hundershofen). Designated by Crickmay (1932, p. 445).

Diagnosis. Shell from subtriangular to semioval, with a sharp, high opisthogyre umbo. Flank with numerous smooth subconcentric costae; area with radial, usually denticulated, costae. Three carinae present. Marginal and escutcheon carinae usually massive, ridge-shaped, with transverse scales; median carina often indistinguishable from costae. Left valve with antecarinal groove. Escutcheon flattened, smooth, or with oblique–transverse growth wrinkles. Hinge high-triangular.

Species composition. Three species of this genus are established in the Early Cretaceous: *T. carinata* Agassiz, 1840, *T. corbierensis* Petter-Receveur, 1955, and *T. heva* Dollfuss, 1862.

Comparison. This genus is distinguished from *Frenguelliella* Leanza, 1942 (Lias–Late Cretaceous) by the more triangular shell outline, higher and pointed umbos, the presence of the median carina, and radial ribbing on the area (in *Frenguelliella*, the area possesses transverse costae), and by the absence of ornamentation in the antecarinal groove on the left valve. *Trigonia* differs from *Pleurotrigonia* Hoepen, 1929 from the Albian of the southeastern Africa in the higher shells, triangular in outline, in the more numerous, regular, and thin subconcentric costae on the flank (in *Pleurotrigonia*, costae are numerous, irregular, and coarse), in the more sharp, scaly marginal carina, more regular radial costae on the area, usually developed along its entire length (in *Pleurotrigonia*, costae are only present near the umbo).

Remarks. In contrast to Cox (1969b, p. N478), I consider *Frenguelliella* and *Pleurotrigonia* to be genera in their own right, rather than subgenera of *Trigonia*.

Occurrence. Triassic–Cenomanian. Cosmopolitan.

Trigonia carinata Agassiz, 1840

Trigonia carinata: Agassiz, 1840, p. 45, pl. 7, figs. 7–10; D'Orbigny, 1843–1847, p. 132, pl. 286, figs. 1–3; Lycett, 1872–1879, p. 179, pl. 35, figs. 3–6; Collot, 1899, p. 227, text-figs. 1 and 2; Karakash, 1897, p. 65, pl. 3, fig. 3; Stremoukhov, 1899, p. 185, text-figs. 1–3; Wollemann, 1900, p. 86, pl. 4, figs. 6 and 7; Mordvilko, 1949, p. 131, pl. 23, figs. 1a–1c; Yanin, 1958, p. 131, pl. 1, fig. 1; 1960, p. 205, pl. 19, figs. 1 and 2; Bogdanova, 1988, p. 153, pl. 30, figs. 1–3.

Trigonia harpa: Deshayes in Leymerie, 1842, p. 8, pl. 9, fig. 7; Matheron, 1842, p. 166, pl. 22, figs. 1 and 2.

Lectotype. Specimen represented by the mold, figured by Agassiz (1840, pl. 7, fig. 10); Switzerland, vicinity of the town of Neuchâtel, village of Hauterive; Lower Cretaceous, Hauterivian. Designated by Saveliev (1958, p. 198).

Description. The shell is subtriangular in outline, moderately high, with prominent, acute umbos, strongly shifted to the anterior margin. The flank has numerous subconcentric smooth costae. The area has a few radial costae, which are usually denticulated. Three carinae are well developed, in particular, the marginal and escutcheon carinae. These carinae are ridge-shaped and possesses coarse scales. The median carina is either distinct, or is similar to the costae. The left valve has an antecarinal groove. The right valve usually lacks this groove, or it is present at young stages.

Composition. Four Early Cretaceous subspecies: *T. c. carinata* Agassiz, 1840; *T. c. caspia* Saveliev, 1958; *T. c. argentinica* Saveliev, 1958; and *T. c. crimica* Yanin, 2004.

Comparison. This species is distinguished from *T. corbierensis* by the narrower area (AR/FL ranges from 0.5 to 0.8, while in *T. corbierensis*, it is 0.9, i.e., AR is almost equal to FL), by the presence of a more distinct median costa (median carina) and additional radial costae on the area (judging from the illustrations of *T. corbierensis* in the paper cited, only a coarse median carina is developed, whereas radial costae are absent).

This species differs from *T. heva* in the more numerous subconcentric costae in the flank (from 16 to 30 in adults, while, according to Petter-Receveur (1955, p. 10), who studied Dolfuss's original material, *T. heva* has only nine of these costae.

Remarks. Saveliev (1958, p. 198) was the first to propose that the "species *Trigonia carinata* Ag. was represented by three subspecies in the Neocomian:" (1) *typica* or *europaeica* (occurring within the Mediterranean Zoogeographic Province, especially in Western Europe, but also found in the Caucasus); (2) *caspia* (Mangyshlak); and (3) *argentinica* (Australian Zoogeographic Realm)." I agree with Saveliev's proposal and describe another subspecies, *crimica*, in addition to the three above.

Occurrence. Berriasian–Aptian: Berriasian–Hauterivian of the Crimea and Mangyshlak; Hauterivian–Barremian of the northern Caucasus; Upper Valanginian–Aptian of Western Europe; Valanginian–Hauterivian of Argentina.

Trigonia carinata carinata Agassiz, 1840

Plate 1, figs. 1–3; Plate 2, figs 1–3; Plate 3, figs. 1–3; Plate 12, fig. 1; Plate 13, fig. 1; Plate 14, fig. 1

Trigonia carinata typica: Saveliev, 1958, p. 198.

Trigonia carinata europaeica: Saveliev, 1958, p. 198.

L e c t o t y p e. Specimen represented by the mold of the shell, figured by Agassiz (1840, pl. 7, fig. 10); Switzerland, vicinity of Neuchatel, village of Hauterive; Lower Cretaceous, Hauterivian. Designated by Saveliev (1958, p. 198).

D e s c r i p t i o n (Figs. 27c, 28a, 28b, 30a, 30b, 32a, 32b). The shell ranges from medium-sized to large, obliquely triangular, very high (the height always exceeds the length). The umbo is strongly protruding, opisthogyre, narrow or wide, and slightly shifted anteriorly. The umbonal angle ranges from 80° to 90°. The anterior margin is long, weakly and evenly convex. It meets the weakly convex ventral margin along a strong curvature. The dorsal margin is relatively short and weakly convex. The posterior margin is short, obliquely truncated, weakly convex, forms a gentle curvature when passing into the dorsal margin. It forms an obtuse angle (100°–105°) when meeting the ventral margin. The shell margins are smooth from inside.

The flank is wide, with 16–35 costae (depending of the size of the shell). The costae are smooth, weakly asymmetric, rounded, of even thickness along their entire length, and subconcentric. The costae are mostly single, but are occasionally branching in various parts of the flank. Near the anterior margin, the costae form a distinct curvature and approach it at a right angle, although not reaching the very edge of the flank, which remains smooth. They radiate from the marginal carina at varying angles (in the umbonal region, at 40°–50°; in the mid-valve, at 50°–60°; and near the posterior margin, at 60°–70°). On the right valve of adult shells, the costae closely approach the marginal carina and are abruptly interrupted (their terminations never enter the carina). The left valve possesses a pronounced, smooth, flattened, or weakly concave antecarinal groove (Pl. 1, figs. 1a, 3c; Pl. 2, fig. 1b; Pl. 3, figs. 1a, 2a) between the sharp terminations of the costae and the marginal carina. This groove is especially prominent at the early and middle growth stages (in these cases, the groove is wide, i.e., its width is equal or greater than the nearby intercostal spaces) (Pl. 14, fig. 1a; Fig. 32b). In large shells, the groove usually disappears (it may be obscured by the termination of the costae that are adjacent to the carina in the proximity of the posterior margin of the valve). The costae in the flank are spread evenly, becoming slightly more convergent near the ventral margin in large specimens. They are usually singular, weakly curved, more rarely stepped-curved, or bifurcating (Pl. 2, fig. 2a). The intercostal spaces are wide (equal or exceeding the costa width), smooth, flattened, or weakly concave.

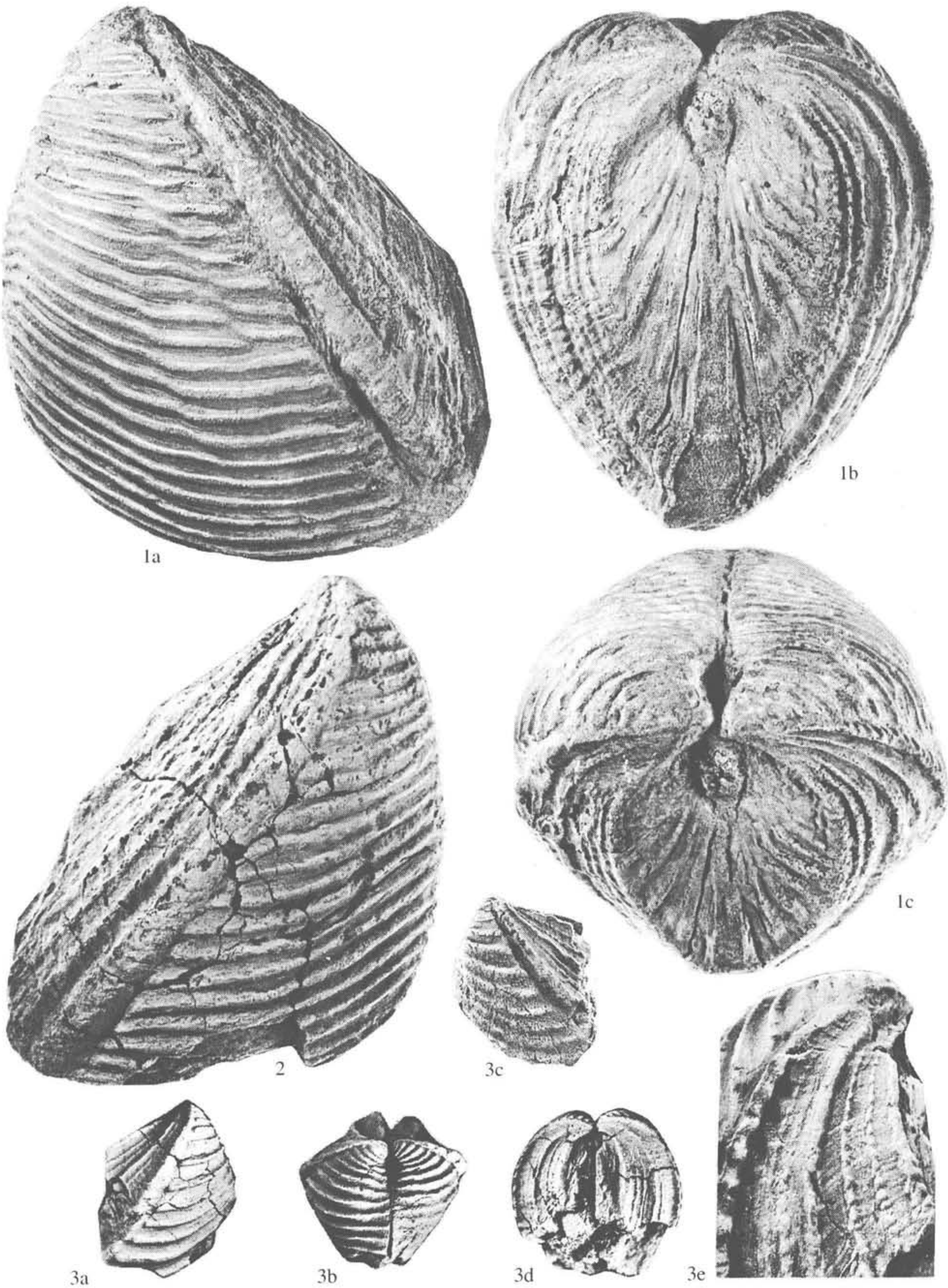
The area is relatively narrow (half the width of the flank), flattened at the young and middle growth stages and weakly concave in adults. It is covered by sparsely spaced radial costae, varying in number from five (Pl. 2, fig. 1a) to nine (Pl. 2, fig. 2a). The costae possess sharp scales, which are especially well developed at the young growth stages (Pl. 1, fig. 3e). In large shells, the costae of the area usually weaken toward the posterior margin and, sometimes, completely disappear in its proximity (in this case, the area is only covered by coarse wrinkles of growth, with a median carina barely discernible among them). The intercostal spaces are flattened or concave. Their width is equal or greater than that of the costae. The median groove is pronounced and concave. In adults, it becomes shallower and is seen only through the curvature of the growth wrinkles toward the posterior margin. The escutcheon is wide and flattened, with coarse growth wrinkles, possessing small nodes in the umbonal region. The nymph is very short, in the shape of a thickened ridge.

The marginal carina is sharply pronounced, ridgelike, with numerous coarse scales. The number of scales is larger than those on the costae in the flank. In large shells, the scales become smoother toward the posterior margin, while the carina becomes more rounded. The escutcheon carina is also sharp, especially in the umbonal region, but becomes smoother near the posterior margin. The scales on this carina are somewhat larger than on the costae of the area. The median carina is distinct, ridgelike, differing from the radial costae only in the slightly greater height and width. It is usually discernible up to the posterior margin. At that point, the posterior margin has its greatest convexity.

The hinge area is high and triangular. Hinge: on the left valve (Pl. 3, fig. 1b), tooth 2 is robust, almost in the shape of an isosceles triangle (length = width = 14 mm), with a straight upper termination and a median groove along the entire tooth. The lateral sides of the tooth possess coarse transverse notches (nine on the anterior side and ten on the posterior side); the dental angle is 50°; tooth 4a (length 13 mm) is robust and ridgelike, with seven notches on the posterior side; tooth 4b (length 13 mm) is hardly developed, merging with the shell margin. It possesses nine notches. The dental buttress is short, robust, ridgelike, ventrally bounding the socket for tooth 3b. On the right valve (Pl. 2, fig. 2b), tooth 3a (20 mm long, 6 mm wide) is slightly convex toward the anterior margin, with nine notches on the anterior side and 11 on the posterior side; with a dental shelf at its base; tooth 3b (28 long, 2 mm wide) is almost straight, only slightly curved near the umbo, with notches on the anterior and posterior sides; the dental angle 3a–3b is 80° (along their external sides) and 50° along their inner sides.

The anterior adductor scar on the left (Pl. 3, fig. 1b) and right valves (Pl. 2, fig. 2b) is rounded, deepened in its upper part, and bounded ventrally by a massive myophore buttress. The posterior adductor scar on the left valve (specimen PIN, no. 4925/15) is large (19 mm long, 16 mm wide), irregularly rounded in outline (from the anterior, ventral, and posterior sides, it is smoothly rounded and is bordered by the myophore buttress, while in the upper part, it is almost straight and very deep). The scar surface possesses longitudinal wrinkles. The anterior retractor scar on either valve is

Plate 1



deep, lying above the anterior adductor scar. The posterior retractor scar on the right valve (Pl. 2, fig. 2b) is in the shape of a deep, rounded depression, 3 mm in diameter, superficial, while on the left valve (Pl. 3, fig. 1b), the scar is deep, oval in outline, 2 × 3 mm in size, bounded ventrally by a rounded ridge.

The pallial line was observed on the mold of the left valve (Pl. 3, fig. 3). It is clearly seen, beginning from the middle of the base of the posterior adductor scar; then, it is curved in parallel to the posterior and ventral margins, at a considerable distance from them. The pallial sinus is absent. The siphonal ridge is weakly developed and occurs only near the posterior margin. The siphonal gape is very weak (in large shells, the width of the gape is 2 mm for the exhalant siphon and 1 mm for the inhalant siphon). The remaining elements of the internal structure were not observed.

Dimensions in mm and ratios:

Specimen PIN, no.	L	H	T	H/L	T/L	FL	AR	AR/FL
4925/14 (LV)	60	75	30	1.25	0.50	48	25	0.52
4925/9 (RV)	70	92	34	1.31	0.48	52	34	0.65
4925/11 (BS)	77	95	70	1.20	0.90	53	30	0.56
4925/8 (BS)	77	97	68	1.25	0.88	60	30	0.50

Comparison. The subspecies described is most similar to *T. carinata argentinica*, differing from it: (1) in the lower and wider shell, always subtriangular in outline (H/L in the Crimean *T. c. carinata* ranges from 1.2 to 1.31, while in *T. carinata argentinica*, it is 1.5, i.e., the valve height is 1.5 greater than the length); (2) in the more obtuse angles between the marginal carina and subconcentric costae of flank radiating from it (the angle in the Crimean subspecies is 40°–70°, whereas in *T. carinata argentinica*, it is 20°–30°), and (3) in the absence of radial ribbing on the escutcheon.

Remarks. Saveliev (1958, p. 198) proposed the subspecies *typica* (or *europaeica*) for the variety of *T. carinata* that occurs most widely in the Lower Cretaceous of Western Europe and Caucasus. He compared this subspecies with other subspecies (*caspia* and *argentinica*). I think that it is necessary to replace the names *typica* and *europaeica* by *T. carinata carinata*, because the same nomenclature type (lectotype) was proposed for the species and subspecies (*International Code...*, 2000, art. 47.2, 72.8).

Taphonomy and paleoecology. All shells and valves of this subspecies are found in terrigenous rocks (from the equigrained sandstone to gravelite). Isolated valves and their fragments are dominant; sometimes, they form coquinas (Patil' and Dlinnaya mountains, Zuiskii Sand Quarry). All this indicates a highly dynamic environment of their habitats and shell burial. It is possible that those complete shells with intact valves and preserved fossilized ligament (Pl. 1, fig. 1b; Pl. 2, fig. 1c) were buried when they were still alive. In this case, it is not possible that the shells were washed out of the sediment.

The ethology of *T. carinata* is widely discussed in the literature. It was discussed in detail by Saveliev (1958). Three hypotheses are proposed to explain their lifestyle: (1) They were attached to the bottom by the byssus. Lycett (1872–1879) noted a byssal gape in some shells from the Lower Cretaceous of southern England; (2) they "did not bury themselves in the mud, but moved along the bottom; some could occasionally be attached by byssal threads to objects on the bottom" (Saveliev, 1958, p. 29); or (3) byssus was absent in this species (Collot, 1899). Cox (1969b) indicated that all trigoniids are nonbyssal bivalves.

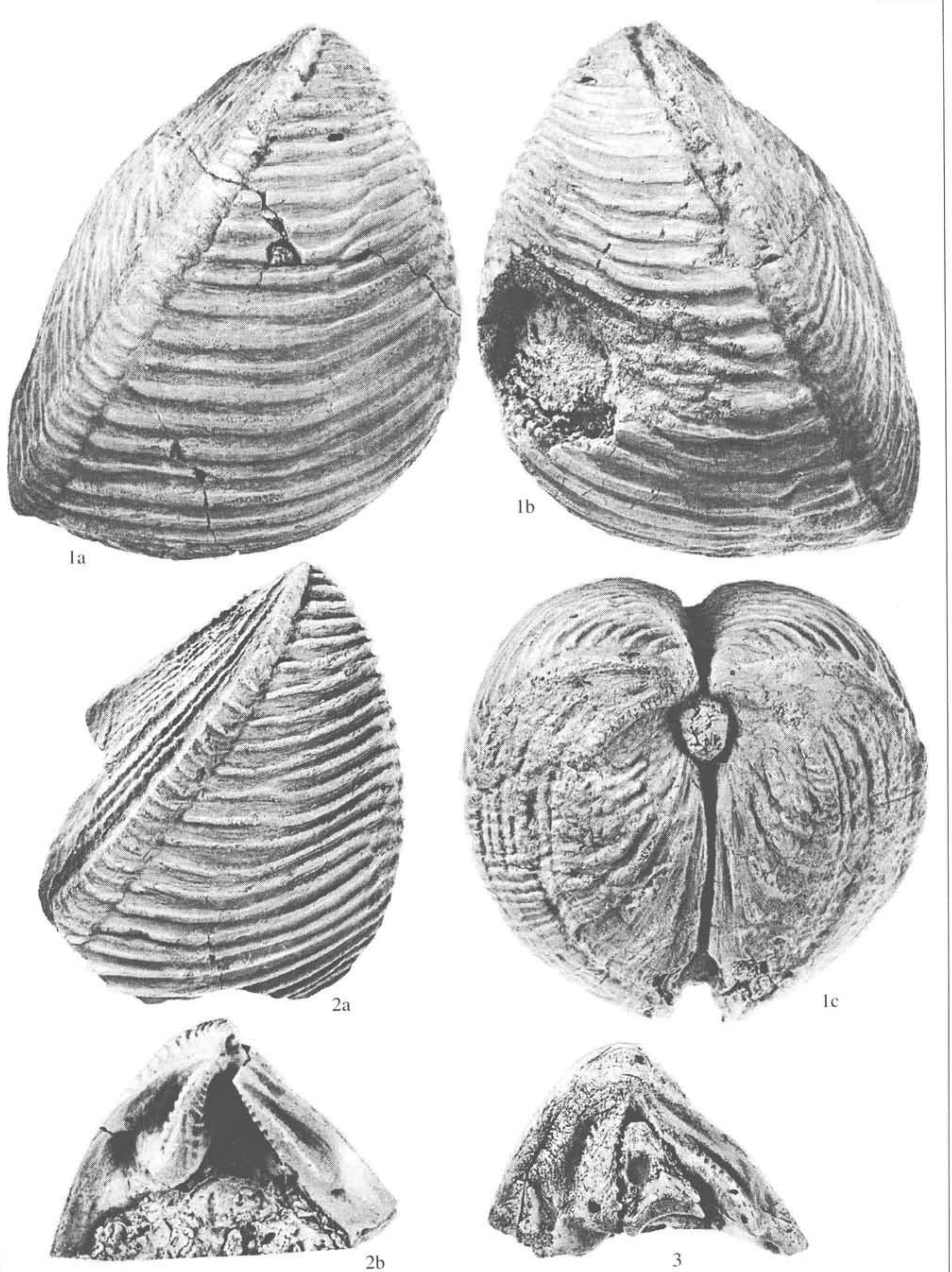
The Crimean specimens of *T. carinata* lack any features of a byssal notch on the anterior margin of the valve. Two complete specimens with intact valves (Pl. 1, fig. 1; Pl. 2, fig. 1) show two completely preserved pseudomorphoses of the ligament, which probably suggests that these shells were in the sediment at the moment of death. The presence of two siphonal gapes, while the pallial sinus is missing, may suggest the development of short inhalant and exhalant siphons. Therefore, it is possible that the animals were permanently in the subsurface layer of sediment during their life, contacting the bottom water layer with their short siphons. This is also supported by indirect evidence, i.e., on complete shells, attached epibionts occur only on the area, or in the carina region near the posterior margin. It is possible that the shell (area and carinae) was partly level with the sediment surface. Stanley (1977) reached similar conclusion, when discussing a complete shell of the Jurassic *T. papillata* (Ag.), which is morphologically similar to *T. carinata*. The escutch-

Explanation of Plate 1

All figures are of natural size, except of several specimens.

Figs. 1–3. *Trigonia carinata carinata* Agassiz: (1) PIN, no. 4925/8, complete shell: (1a) external view, left valve, (1b) escutcheon view, (1c) upper view (umbonal view); southwestern Crimea; basin of the Kacha River, Kayas-Dzhilga Gully, eastern slope of Sel'bukhra Mountain (southern summit); excess rocks from the trench for the gas pipe line Bakhchisarai–Yalta; Upper Valanginian (Section no. 10, Bed 2), coll. by B.T. Yanin in 1975; (2) PIN, no. 4925/9, right valve, external view; central Crimean, Beshterek River Valley, left bank, northern vicinity of the village of Mazanka, trench opposite the "nummulite cuesta"; from a block of the Lower Valanginian sandstone, redeposited in a member of the Upper Valanginian rubbly conglomerate (Section no. 21, Bed 3); coll. by B.T. Yanin in 1974; (3) PIN, no. 4925/10, a complete young shell with broken off ventral and posterior margins: (3a) external view, right valve, (3b) anterior view, (3c) external view, left valve, (3d) area and escutcheon view, and (3e) fragment of the area of the left valve with radial costae possessing sharp scales, ×3; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); coll. by B.T. Yanin in 1989.

Plate 2



eon of this shell had a fossilized ligament and a tube of a serpulid, which did not cross the marginal carina. At the same time, the surface of the flank of the shell lacks any traces of encrusting organisms. In his reconstruction of the life position of the shell, Stanley (1977, text-fig. 5) oriented it horizontally in the sediment, so that the marginal carina is in parallel to the surface of the sediment. The area, escutcheon, and posterior (siphonal) margin are slightly protruding above the ground.

The lateral surfaces of isolated valves of the Crimean *T. carinata carinata* often show encrusting epibionts and traces of borings (Pl. 3, fig. 2a), which may support the horizontal life position of these valves on the bottom, which were turned convex side up by the waves after their death.

O c c u r r e n c e. Valanginian–Aptian: Lower Valanginian–Lower Hauterivian of the Crimea: basin of the Kacha River (Upper Valanginian: village of Verkhorech'e, Kayas-Dzhilga Gully); basin of the Bodrak River (Lower Valanginian: Nikolaev Yar Gully, Patil' Mountain; Lower Hauterivian: Dlinnaya and Patil' mountains; Pervomaiskii Quarry, village of Trudolyubovka); basin of the Al'ma River (Lower Hauterivian: village of Konstantinovka); basin of the Beshterek River (Lower Valanginian: village of Mazanka); Zuya–Burul'cha interfluve (Lower and Upper Valanginian: Zuiskii Quarry; Lower Hauterivian: Kunich Mountain). The shells are also found redeposited in the Barremian (Kuchuk-Karasu River: village of Gorlinka) and in the Upper Albian (Bodrak River: Prisyazhnaya Mountain); Hauterivian–Lower Barremian of the northern Caucasus; Hauterivian of Mangyshlak and Kopet Dagh; Valanginian–Aptian of France; Hauterivian of Germany; Hauterivian–Aptian of Switzerland and Spain; Barremian–Aptian of southern England; Aptian of Bulgaria and North Africa.

M a t e r i a l. Twenty-two specimens: five complete shells, three LV, three RV, six fragments of valves, and five molds.

***Trigonia carinata crimica* Yanin, 2004**

Plate 3, figs. 4a–4c

Trigonia carinata crimica: Yanin, 2004, p. 26, pl. 3, fig. 1.

H o l o t y p e. PIN, no. 4925/1, right valve; southwestern Crimea, basin of the Bel'bek River, vicinity of the village Solnechnosel'e, the base of the limestone range to the north of the village; Lower Berriasian (*dalmasi* Zone). The holotype is designated by monotypy.

D e s c r i p t i o n. The shell is medium-sized, subtriangular, high (height is equal to length), weakly inequilateral, moderately convex. The umbo is strongly protruding, narrow. Its apex is sharply curved backwards. The umbonal angle is 90°. The anterior margin is long and moderately convex, evenly rounded. It continues into a weakly convex ventral margin through a sharp curvature. The dorsal margin is short and straight. The posterior margin is short, obliquely truncated, and forms an obtuse angle with the dorsal margin. The margins are smooth from inside.

The flank possesses 29 weakly asymmetrical, smooth, ridgelike, rounded, subconcentric costae. All costae reach the anterior margin or the anteroventral margin and approach the marginal carina at an acute angle without forming the antecarinal groove. The costae evenly cover the entire flank. In the middle part of the flank, they are the coarsest and the most widely spaced, whereas near the ventral margin, they are thinner and more densely spaced. The intercostal spaces are smooth, concave, as wide as the costae, but in the middle part of the flank, the spaces are wider than the costae.

The area is relatively narrow (half the width of the flank), with a flattened external surface and concave inner surface. It possesses nine almost identical thin, linear, finely denticulated radial costae, which have no superimposed obliquely transverse fold, and reaching the posterior margin of the shell without weakening. The median groove is distinctly pronounced. The escutcheon is relatively wide and is almost half the width of the area. It is flattened, with a straight dorsal margin, anteriorly, with small, thin, punctures arranged along the growth lines.

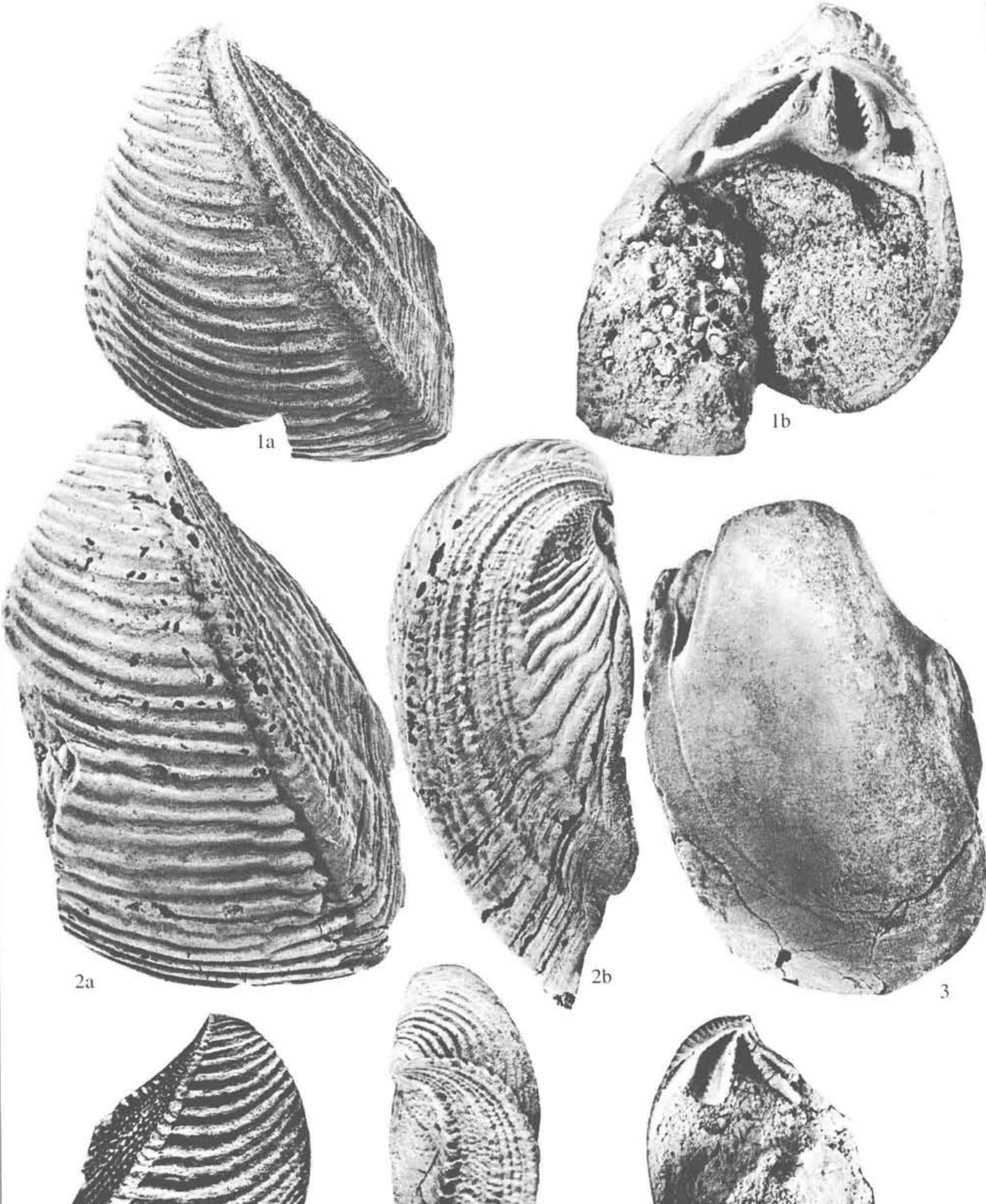
The marginal and escutcheon carinae are sharply pronounced, in a shape of strong high crests possessing coarse transverse scales. On the marginal carina, the scales are arranged perpendicular to the costae and intercostal spaces. The carinae do not become weaker toward the posterior margin.

The hinge plate is highly triangular. Hinge: tooth 3a is narrow, elongated, descending from the umbo along the line, almost parallel to the line of the shell maximum convexity; tooth 3b is even narrower and longer; near the umbo, it is fused with the valve margin, although in the middle and distal parts, it is distinctly separated from the dorsal margin of the valve by a narrow socket for tooth 4b. Dental notches on its anterior and posterior surfaces are well developed. The dental

E x p l a n a t i o n o f P l a t e 2

Figs. 1–3. *Trigonia carinata carinata* Agassiz: (1) PIN, no. 4925/11: (1a) complete shell, external view, right valve, (1b) external view, left valve, and (1c) upper view, umbos; southwestern Crimea, basin of the Kacha River, Kayas-Dzhilga Gully, eastern slope of Sel'bukhra Mountain (southern summit), excess rocks from the trench for the gas pipe line Bakhchisarai -Yalta; Upper Valanginian (Section no. 10, Bed 2); coll. by B.T. Yanin in 1975; (2) PIN, no. 4925/12, right valve: (2a) external view, (2b) internal view; central Crimea, Zuya–Burul'cha interfluve, Zuiski Sand Quarry; eastern wall; Lower Valanginian, Section no. 24, Bed 1); coll. by B.T. Yanin in 1987; (3) PIN, no. 4925/13, fragment of the right valve (umbonal region) from inside (the occlusion of teeth 3a, 2, and 3b is well seen); the same locality.

Plate 3



angle of 3a–3b is 50°. Other elements of the shell interior were not observed.

D i m e n s i o n s of the holotype in mm and ratios: L, ca. 50; H, ca. 52; H/L, ca. 1.0; T, 17; T/L, 0.34; FL, 30; AR, ca. 17; AR/FL, ca. 0.5.

C o m p a r i s o n. The subspecies described is distinguished from *T. carinata carinata* from the Barremian–Aptian of England by the smaller shell size, considerably larger number of costae on the flank (29 instead of 13–15 in *T. carinata carinata* at the same shell height, by the lesser shell convexity (T/L = 0.34 instead of 0.44–0.47), by the less acute angle between the costae in the flank and the marginal carina in the middle of the valve, and by that the costae of the area do not get weaker near the posterior margin. It differs from the Crimean specimens of *T. carinata carinata* in the same way as from the English specimens and, in addition, in that all costae in the area reach the posterior margin of the shell.

This subspecies is distinguished from *T. carinata caspia* from the Berriasian of Mangyshlak by the higher shell (H/L = 1.05 instead of 0.83–0.86 in *T. c. caspia*); by the presence of a sharp curvature between the anterior and ventral margins (in *T. c. caspia*, it is gradual), by the more acute umbonal angle (60° instead of 70–75° in *T. c. caspia*), by the absence of coarse obliquely transverse ribbing on the area near the posterior margin of the valve (the costae remain linear and clearly separated from each other up to the very end), by the straight scales on the marginal carina (in *T. c. caspia*, they descend at an acute angle to the umbo, see Saveliev, 1958, pl. 1, figs. 1a, 3a).

O c c u r r e n c e. Lower Berriasian of the southwestern Crimea.

M a t e r i a l. Holotype.

Subfamily Myophorellinae Kobayashi, 1954 (= Vaugoniinae Kobayashi, 1954)

Genus *Myophorella* Bayle, 1878

Myophorella: Bayle, 1878, pl. 120, Crickmay, 1932, p. 458; Kobayashi and Tamura, 1955, p. 91; Saveliev, 1958, p. 94; 1960a, p. 62; 1960b, p. 96; Yanin, 1958, p. 132; 1960, p. 205; 1979a, p. 24; 2004, p. 27; Piryatinsky, 1962, p. 146; Bogdanova, 1966, p. 110; 1988, p. 154; Bogdanova *et al.*, 1997, p. 82; Cox, 1969b, p. N483; Cooper, 1979, p. 21; Kelly, 1984, p. 82.

Trigonia: Renngarten, 1926, p. 72 (pars); Mordvilko, 1949, p. 127 (pars).

T y p e s p e c i e s. *M. nodulosa* Bayle, 1878, explanation to pl. 120; Upper Jurassic, Oxfordian; northern France. Subsequently designated by Crickmay (1932).

D i a g n o s i s. Shell from triangular-oval to oval-elongated, moderately convex. Flank with regular oblique costae or oblique rows of tubercles always reaching marginal carina. Area narrow, flattened, usually smooth, more rarely, with ornamentation. Median groove always distinct and linear. Marginal carina always well pronounced, ridgelike or obtusely rounded, often with tubercles. Escutcheon carina distinct, usually sharp, smooth, or with tubercles. Occasionally, area has median carina, usually smooth, sometimes with small tubercles. Escutcheon narrow, flattened, or weakly convex, and smooth. Umbo protruding, strongly shifted anteriorly, opisthogyre. Hinge plate wide. Hinge highly triangular. Apex of tooth 2 straight. Dorsal and ventral shell margins smooth from inside.

S p e c i e s c o m p o s i t i o n. Four species in the Lower Cretaceous of northern Eurasia: *M. ingens* (Lycett, 1872–1879), *M. loewinsonlessingi* (Renngarten, 1926), *M. rawsoni* Kelly, 1984, and *M. tonasensis* Yanin, 2004.

C o m p a r i s o n. This genus is distinguished from *Vaugonia* Crickmay, 1930 by the presence of the V-shaped bend of the costae on the flank. It differs from *Orthotrigonia* Cox, 1952 in the more strongly curved, often regularly arched oblique costae and in the absence of bifurcation near the anteroventral margin of the flank, and in the absence of short auxiliary costellae or rows of tubercles on the flank.

O c c u r r e n c e. Lower Jurassic–Lower Cretaceous. Cosmopolitan.

Myophorella loewinsonlessingi (Renngarten, 1926)

Plate 4, figs. 1–10

Trigonia loewinson-lessingi: Renngarten, 1926, p. 74, pl. 8, fig. 1; Mordvilko, 1949, p. 127, pl. 23, fig. 3.

Myophorella loewinsonlessingi: Yanin, 1958, p. 132, pl. 1, fig. 2; 1960, p. 205, pl. 19, figs. 3 and 4; Bogdanova, 1966, p. 110; 1988, p. 154, pl. 30, figs. 4 and 5; pl. 31, figs. 1 and 2; Bogdanova *et al.*, 1997, p. 82, pl. 19, figs. 4 and 5.

Myophorella (Myophorella) loewinsonlessingi: Saveliev 1958, p. 199, pl. 2, figs. 2–4; pl. 3, fig. 2; Yanin, 1979a, p. 24, pl. 2, fig. 1.

Myophorella (Myophorella) invittulina: Saveliev, 1958, p. 205, pl. 3, fig. 3; pl. 4, figs. 1 and 2.

Myophorella invittulina: Bogdanova, 1988, p. 155, pl. 31, figs. 4 and 5.

E x p l a n a t i o n o f P l a t e 3

Figs. 1–3. *Trigonia carinata carinata* Agassiz: (1) PIN, no. 4925/14, left valve: (1a) external view, (1b) internal view; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); coll. by B.T. Yanin in 1987; (2) PIN, no. 4925/15, left valve with a broken off anteroventral margin: (2a) external view, (2b) area and escutcheon view, the same locality and collector; (3) PIN, no. 4925/16, mold of the left valve, external view; southwestern Crimea, basin of the Bodrak River, village of Prokhladnoe, Patil' Mountain, region of the pumping station; Lower Valanginian (Section no. 14, Bed 2); coll. by P.E. Morozov in 1986.

Fig. 4. *Trigonia carinata crimica* Yanin: holotype PIN, no. 4925/1, right valve: (4a) external view, (4b) umbonal view, ×1.5; (4c) internal view; southwestern Crimea; basin of the Bel'bek River, village of Solnechnosel'e; Lower Berriasian, alternating rock series (Section no. 8, Bed 1); coll. by B.T. Yanin in 1962.

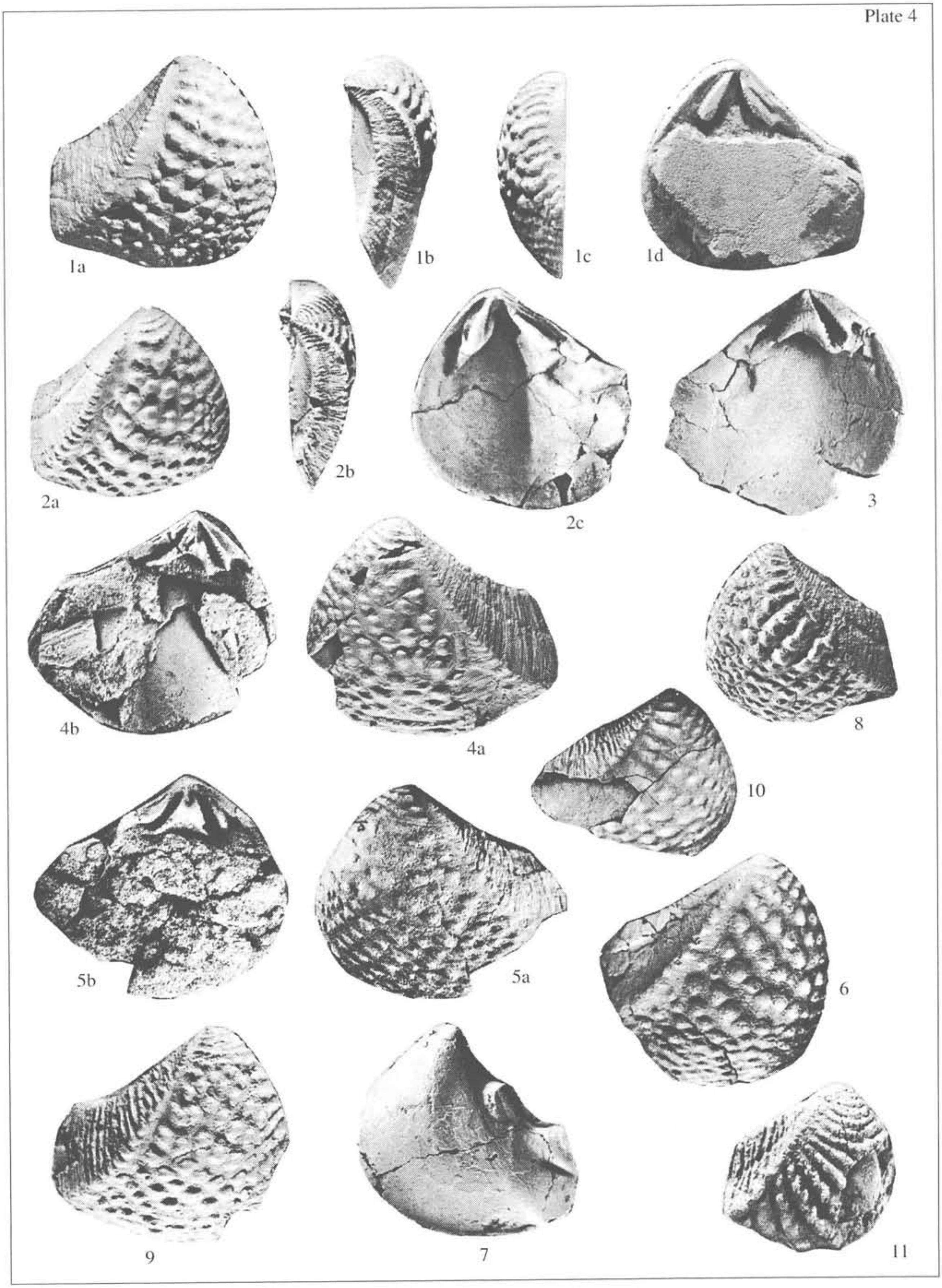


Plate 4
1a
1b
1c
1d
2a
2b
2c
3
4b
4a
8
10
5b
5a
6
9
7
11

Holotype. TsNIGR Museum, no. 334/56; external mold of the right valve; northern Caucasus, Assa River; Lower Cretaceous, Berriasian (the author of the species indicated the Lower Valanginian). The holotype is designated by monotypy.

Description (Figs. 28c, 30c, 30d). The shell is medium-sized, rounded triangular in outline, moderately and evenly convex, strongly inequilateral (wide in the anterior part and sharply tapering in the posterior part). The umbo is strongly protruding, opisthogyre, shifted anteriorly. The umbonal angle is 95°–100°. The anterior margin is strongly convex, gradually continuing into the weakly rounded ventral margin. The dorsal margin is long, straight, or widely concave, and forms a distinct angle of 145°–150° with the posterior margin. The posterior margin is short, very weakly convex, obliquely truncated, and forms an angle of 110°–120° with the ventral margin. The shell margins are smooth from inside.

The flank is wide, with 12–16 oblique rows of rounded and oval tubercles. The most regular arrangement of tubercles is observed only in the mid-flank. Toward the anterior and ventral margin of the valve, the regular arrangement is disturbed by the appearance of additional short rows of smaller tubercles, or the arrangement of tubercles becomes irregular. Close to the ventral margin of the valve, the tubercles are usually elliptical, extended along the growth lines. Near the anterior margin, the rows of tubercles are replaced by short nodular costellae, which become considerably thinner in the upper part of the margin and eventually disappear, leaving a narrow, smooth frontal strip (Pl. 4, fig. 1c). In the umbonal region, five to seven continuous, smooth (nontuberculate) asymmetrical subconcentric costellae are present instead of rows of tubercles (Pl. 4, figs. 2a, 2b, 4a, 8). The rows of tubercles and umbonal costae approach the marginal carina at a right angle. A smooth, antecarinal strip (narrow or wide) is usually present between the last tubercles and the marginal carina on both valves (Pl. 4, figs. 1a, 2a, 4a, 9, 10). In some valves, this strip is virtually undeveloped, or it is very narrow (Pl. 4, fig. 9), and in this case, some tubercles are located very close to the marginal carina, or disappear altogether (Pl. 4, fig. 8).

The area is narrow (half the width of the flank), flattened, with numerous thin transverse costae, which are often similar to wrinkles of growth. On the median groove, the costae are usually interrupted. In some specimens, the area possesses only growth lines near the posterior margin (Pl. 4, fig. 4a). The median groove is sharply pronounced and is filiform. The escutcheon is smooth, narrow, strongly deepened along the escutcheon carina, but flattened and slightly elevated along the dorsal margin. The nymph is short and lamellar.

The marginal and escutcheon carinae are sharp, ridgelike, with tubercles. The number and size of the tubercles vary within a wide range. The median carina is absent.

The hinge plate is moderately high and triangular. Hinge: on the left valve (Pl. 4, figs. 3, 4b, 5), tooth 2 (9 mm long, 9 mm wide) is in the shape of an equilateral triangle, with the upper termination weakly inclined posteriorly; the anterior surface of the tooth is flat, the posterior surface is weakly concave; its apex is straight and rounded; the dental angle is 50°; tooth 4a (8 mm long) is robust, ridgelike, high; its apex is well separated from the anterior margin; tooth 4b (10 mm long) is thin, lamellar, weakly separated from the dorsal margin; the dental buttress is short, ridgelike. On the right valve (Pl. 4, fig. 1d) tooth 3a (9 mm long, 2 mm thick) is robust, straight, with a dental shelf on the internal surface; tooth 3b (11 mm long, 2.5 mm thick) is weakly curved; the dental angle 3a–3b is 55°.

The anterior adductor scar is elongated oval in outline (5 mm long, 2 mm wide), extended almost in parallel to the anterior valve margin. The anterior retractor scar has the appearance of a narrow (less than 1 mm), but deep depression. It is not separated from the anterior adductor scar.

The posterior adductor scar (Pl. 4, figs. 2c, 3, 7) is subquadrate in outline, with a flattened surface (6 mm in both length and width). It is strongly deepened and marked by a distinct myophorous buttress on the anterior and anteroventral sides, but it is not delineated on the upper and posterior sides. The posterior retractor scar

Explanation of Plate 4

Figs. 1–10. *Myophorella loewinsonlessingi* (Renngarten): (1) MZ MGU, no. 2/10, right valve: (1a) external view, (1b) upper view, (1c) anterior view, (1d) internal view; southwestern Crimea, Bel'bek River, vicinity of the village of Golubinka, Kabanii Gully; Lower Berriasian, alternating rock series, *dalmasi* Zone (Section no. 4, Bed 1); coll. by B.T. Yanin in 1956; (2) MZ MGU, no. 39/1, right valve: (2a) external view, (2b) upper view, (2c) internal view (slightly magnified); the same locality; (3) PIN, no. 4925/17, left valve, internal view, the same locality; (4) PIN, no. 4925/18, left valve: (4a) external view, (4b) internal view; the same locality; (5) PIN, no. 4925/19, left valve with a broken off posterodorsal margin: (5a) external view, (5b) internal view; the same locality; (6) PIN, no. 4925/20, right valve with a broken off posterior margin, external view; the same locality; coll. by B.T. Yanin in 1975; (7) PIN, no. 4925/21, mold of the left valve, external view; the same locality; coll. by B.T. Yanin in 1956; (8) PIN, no. 4925/22, left valve, external view; basin of the Bel'bek River, vicinity of the village of Kuibyshevo, Tamish' Grove; Lower Berriasian, alternating rock series, *dalmasi* Zone (Outcrop no. 7); coll. by B.T. Yanin in 1957; (9) PIN, no. 4925/23, right valve with a broken off anteroventral margin, external view; the same locality; (10) PIN, no. 4925/24, right valve with a broken off ventral margin, external view; central Crimea, basin of the Sarysu River, right bank of the valley between the villages of Blagodatnoe and Chernokamenka; Lower Berriasian; found loosely; coll. by V.V. Drushchits in 1957.

Fig. 11. *Myophorella tonasensis* Yanin: holotype PIN, no. 4925/2, right valve, external view, ×2; central Crimea, Tonas River, vicinity of the village of Krasnoselovka; Lower Berriasian, flyschoid series; coll. by B.T. Yanin in 1987.

is distinct, has the appearance of a narrow (1 mm), but deep depression, surfaced, and lies below the termination of tooth 4b. The pedal elevator scar is clearly pronounced, has the appearance of a narrow (ca. 1 mm), but deep depression, which lies immediately below the umbo.

The pallial line (mold of the left valve: Pl. 4, fig. 7) is seen from the middle point of the lower side of the anterior adductor scar to the posterior side of the posterior adductor scar, near which it makes a slight curvature to inside. This curvature corresponds to the position of the exhalant siphon. The pallial sinus is absent. The siphonal ridge is well developed; it divides the posterior margin into two unequal parts. Its position corresponds to that of the median groove on the area. The siphonal gape is small.

D i m e n s i o n s in mm and ratios:

Specimen no.	L	H	T	H/L	T/L	FL	AR	AR/FL
PIN, no. 4925/22 (LV)	36	33	11	0.91	0.30	25	12	0.48
MZ MGU, no. 39/1 (RV)	38	34	10	0.89	0.26	–	–	–
PIN, no. 4925/18 (LV)	46	40	12	0.86	0.26	28	14	0.50
PIN, no. 4925/19 (LV)	47	42	11	0.89	0.23	31	13	0.41

C o m p a r i s o n. The species described is distinguished from *M. rawsoni* from the Berriasian and Valanginian of England, which is similar in shell shape, ornamentation and in the presence of the antecarinal strip, by the less regular rows of tubercles on the flank, the presence of additional rows of tubercles and the irregular arrangement of tubercles in the proximity of the ventral margin, by the more strongly truncated (almost straight) posterior margin, by the absence of the median carina, and by the coarser ornamentation on the area. It is distinguished from the less similar *M. ingens* from the Valanginian and Hauterivian of England by the more strongly triangular shell outline, less regular rows of tubercles, and by the absence of continuous costae near the ventral margin on the flank, by the more densely spaced and larger tubercles on the marginal carina, by the presence of several subconcentric costae in the umbonal area, and by the absence of the median carina on the area. Many of above characters easily distinguish the species described from *M. juddiana* (Lycett, 1872–1879) from the Kimmeridgian of England.

R e m a r k s. When describing a new species, Rengarten did not specify the presence of a smooth antecarinal strip on the holotype. Saveliev (1958, p. 204) noticed this, but remarked that the presence of the "antecarinal strip" is one of the major definitive characters of *M. loewinsonlessingi.*

The study of the Crimean specimens of this species, which all come from the same horizon, has shown that the antecarinal strip is not always pronounced in some of them. It may be obscured by the tubercles, which closely approach the carina (Pl. 4, fig. 8), or may become so narrow that the antecarinal strip cannot be considered to be a good identification criterion for this species. Therefore, the species *M. invittulina*, established by Saveliev (1958, p. 205), is here synonymized with *M. loewinsonlessingi*, to which it is very similar in shell shape and ornamentation. When describing *M. invittulina*, Saveliev (1958, p. 206) indicated that, "in rare cases, a narrow, irregular space is observed in front of the marginal carina (its width is variable, but does not exceed the width of a large tubercle). Tubercles in some places do not enter this space (Saveliev, 1958, pl. 4, fig. 2a). However, because this space is not deepened, it does not have a clear boundary with the tubercles of the flank and does not expand regularly downward, it cannot be considered to be a real antecarinal strip." Careful examination of shells of two species (*M. loewinsonlessingi* and *M. invittulina*) figured by Saveliev clearly displayed the considerable variability of the width of the antecarinal strip in *M. loewinsonlessingi.* It may be quite wide (pl. 3, fig. 2a), or narrow (pl. 2, figs. 2a, 4a). In *M. invittulina*, the upper tubercles in the oblique rows on the flank do not always approach the marginal carina, and a smooth space of variable size is left between the tubercles and the carina, which is similar to an antecarinal strip (pl. 3, fig. 3a; pl. 4, fig. 2a). Discussing the validity of the two species, it is also necessary to take into account that most specimens of both species collected by V.I. Dragunov in 1951 and described by Saveliev (1958) come from the same horizon (Lower Valanginian, presently Berriasian) of the same locality (Southern Mangyshlak Anticline, Karasyaz' Well). Their co-occurrence in the Berriasian sandstones (Bed 2: *Neocosmoceras–Septaliphoria semenovi* Regional Zone) on the Karasyaz'–Taspas Anticline near the Karasyaz' 2 Well was also indicated by Lobacheva *et al.* (1988).

Based on the above discussion, I conclude that a strong intraspecific variability is present in *M. loewinsonlessingi*, which is manifested not only in the presence or absence of the antecarinal strip, but also in the degree of the tubercle development on the carinae, in the regularity of the rows of tubercles in the flank, and in the character of the development of the coarse oblique ribbing in the area.

T a p h o n o m y a n d p a l e o e c o l o g y. All specimens of *M. leowinsonlessingi* described in this paper mostly come from the Lower Berriasian fine-grained sandstones and siltstones and are represented by isolated valves and their fragments. In some outcrops in the basin of the Bel'bek River, the shells are found in coquina (alternating series), which indicated a high-energy environment. The presence of siphonal ridge on the valves and the absence of the pallial sinus suggest that this species had short siphons, which allowed shallow burrowing into the loose sandy or silty sediment. Fursich (1977) studied benthic marine communities of England and Normandy and concluded that *Myophorella included* "shallowly burrowing" forms. The reconstruction of "*Myophorella community*" by this author (Fursich, 1977, text-fig. 10) shows the shell of this genus near the surface of the sediment, while its obliquely truncated siphonal margin is parallel to the water–sediment boundary. The same subsurface position of the *Myophorella* shells is shown in the reconstructions of Oschmann (1988, text-figs. 8, 10, 12, 15) for the benthic communities of the Late Jurassic sea in southern England. These reconstructions show the position of shell slightly different from that proposed by Fursich (only the upper posterior angle touches the sediment surface, while the siphons are shown completely in the sediment).

Occurrence. Berriasian–Valanginian: Lower and Upper Berriasian of the southwestern Crimea [basin of the Bel'bek River: village of Kuibyshevo (Tamish' Gully), village of Golubinka (Kabanii Gully)], and central Crimea (Beshterek River, village of Solov'evka; Sarysu River, village of Novoklenovo); Lower Berriasian of the northern Caucasus and Dagestan; Berriasian and Valanginian of Mangyshlak and Kopet Dagh.

Material. Twenty-one specimens: eight LV, nine RV, and four molds.

Myophorella tonasensis Yanin, 2004

Plate 4, fig. 11

Myophorella tonasensis: Yanin, 2004, p. 27, pl. 3, fig. 2.

Holotype. PIN, no. 4925/2, right valve; Central Crimea, Tonas River, vicinity of the village of Krasnoselovka, Lower Cretaceous, Lower Berriasian, flyschoid series. The holotype is designated by monotypy.

Description. The shell is small (possibly a young individual), subquadrate in outline, high, weakly and evenly convex, moderately inequilateral. The umbo is prominent, approaching the anterior margin, and straight. The umbonal angle is 100°. The anterior margin is evenly convex, gradually continuing into the almost straight ventral margin. The dorsal margin is short and straight and forms a distinct obtuse angle of 140° with the posterior margin. The posterior margin is straight, obliquely truncated and forms a right angle with the ventral margin.

The flank is wide, with 13 oblique costae extending immediately from the marginal carina. In the anterior half of the flank, they follow a regular arch and run anteriorad and downward from the carina, and eventually reach the anteroventral margin of the valve. All costae have thin transverse scales. In the posterior half of the flank, the costae are coarse, extending from the carina toward the ventral margin, reaching it with their tips. These costae possess large obliquely transverse scales.

The area is almost as wide as the flank, flattened, with coarse, transverse, smooth costellae resembling the wrinkles of growth. The median groove is distinct, linear and possesses costae. The escutcheon is narrow, flattened, with short thin transverse costellae.

The marginal and escutcheon carinae are sharp, ridgelike, with sparsely spaced, coarse tubercles, especially in their posterior parts. The median carina is absent. The inner structure was not observed.

Dimensions of the holotype in mm and ratios: L, 15; H, 14; T, 5; H/L, 0.93; T/L, 0.33; FL, 10; AR, 4; AR/FL, 0.40.

Comparison. This species is distinguished from *M. loewinsonlessingi* by: (1) the shorter and higher shell (H/L = 0.93; most specimens of *M. loewinsonlessingi* have a more elongated shape); (2) the character of ribbing of the flank, i.e., the presence of regular denticulated costae (instead of the rows of rounded tubercles). *Myophorella tonasensis* differs from *M. formosa* (Lycett, 1872–1879) from the Middle Jurassic of England, similar in the character of ribbing, in the coarser denticulated costae in the flank, and in the presence of larger, coarser tubercles on the costae.

Remarks. *Myophorella tonasensis* is similar to *Orthotrigonia mordvilkoae* (Pl. 5, figs. 1–6) in the shape of the area and carinae, although differing in the subquadrate shape of the shell (instead of triangular in *Orthotrigonia mordvilkoae*) and in the character of ribbing in the flank, i.e., in the more regular, evenly curved costae in the middle of the flank and in the absence of additional costae near the anterior margin of the valve.

Taphonomy and paleoecology. The valve of *Myophorella tonasensis* was found on the surface of a thin plate of clastic limestone, containing well-rounded grains of limestone of gravel size and shell debris, including the fragments of echinoderm skeletons and oyster valves, with serpulids attached to them. The shell was oriented with its convexity upward in relation to the bedding plane. It was buried in the wave zone.

The presence of a thin median groove on the area indicates the development of the siphonal ridge separating, like in all trigoniids, the inhalant and exhalant siphons. The absence of a well-developed siphonal gape suggests the development of weak siphons. Therefore, it is possible that this apparently young individual could only burrow at a shallow depth in the sediment.

Occurrence. See holotype.

Material. Holotype.

Genus _Orthotrigonia_ Cox, 1952

Myophorella (Orthotrigonia): Cox, 1952, p. 56; Saveliev, 1958, p. 95; 1960b, p. 96; Piryatinsky, 1962, p. 148; Yanin, 1979a, p. 25.

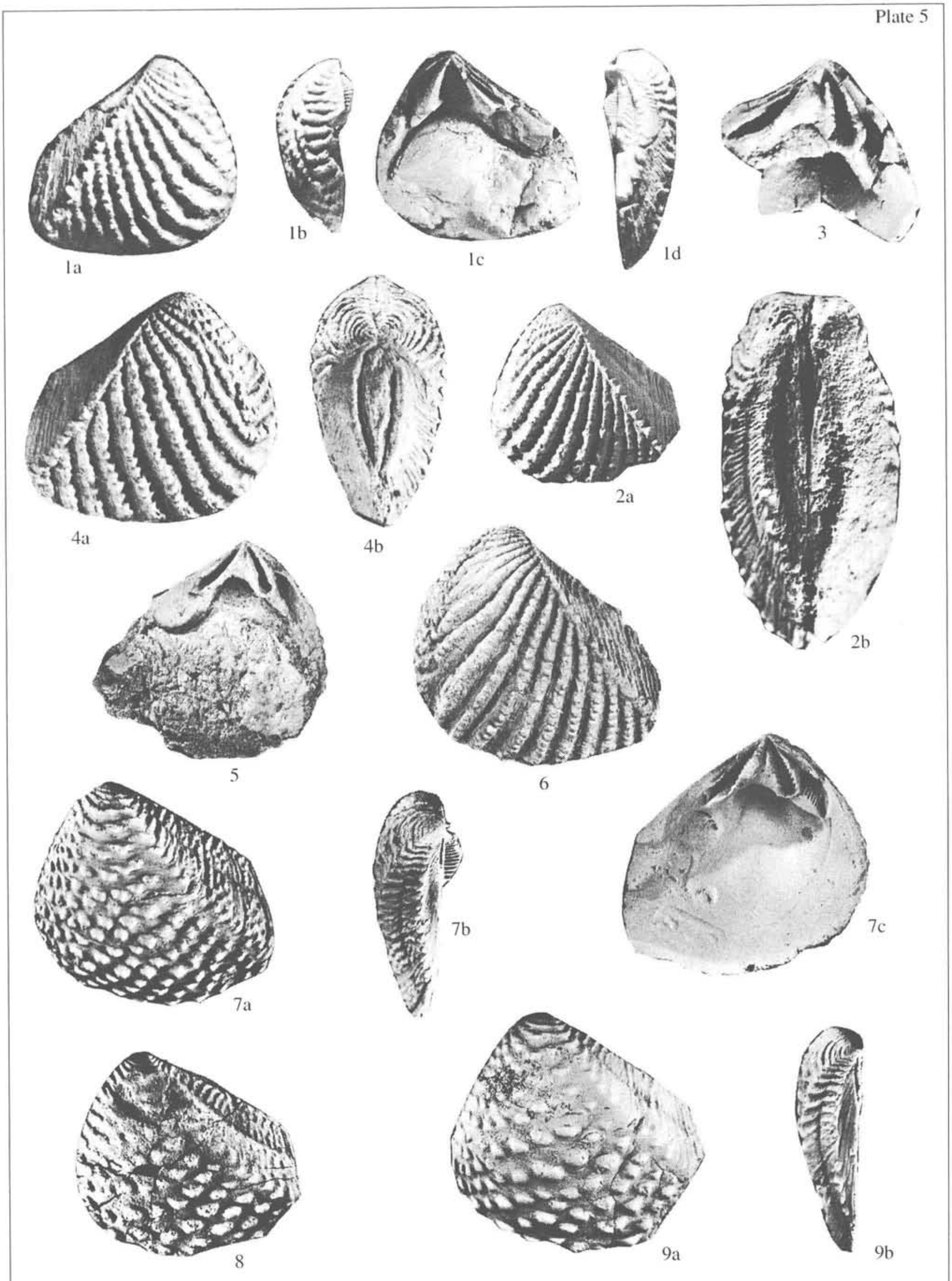
Orthotrigonia: Kobayashi and Mori, 1955, p. 86.

Vaugonia (Orthotrigonia): Cox, 1969b, p. N488.

Type species. *Trigonia duplicata* J. Sowerby, 1819; Middle Jurassic of England. Designated by Cox (1952, p. 56).

Diagnosis. Shell subtriangular, moderately convex. Flank with finely tuberculate, narrow, densely spaced costa: straight in lateral and posterior zones of flank, subconcentric in umbonal zone, sharply curved anteriorad, sometimes radiating in fan shape near the anterior margin and bifurcating near the ventral margin.

Plate 5



Anterior margin occasionally with frontal costellae. Area narrow, flattened, with thin obliquely transverse costellae. Median groove developed to different extent. Marginal carina always pronounced, ridgelike, with small pointed tubercles. Escutcheon carina also prominent, usually having small tubercles. Escutcheon narrow, flattened, or weakly concave. Umbo protruding, opisthogyre, displaced close to anterior margin. Hinge plate wide; hinge high-triangular, almost symmetrical. Apex of tooth 2 straight. Ventral margin smooth from inside or weakly denticulated by terminations of costae in flank.

Species composition. Six Jurassic species are known from Eurasia: *O. bathonica* (Lycett, 1872–1879), *O. duplicata* (Sowerby, 1819), *O. gemmata* (Lycett, 1872–1879), *O. recticosta* (Lycett, 1872–1879), established in England, *O. midareta* Kobayashi et Mori, 1955 and *O. corrugata* Kobayashi et Mori, 1955 from northern Japan; and the sole species *O. mordvilkoae* Yanin, 1979 known from the Berriasian of the Crimea.

Comparison. This genus is distinguished from *Myophorella* Bayle, 1878 by the presence of narrow, finely tuberculate, straight costae on the lateral and posterior parts of the flank (in *Myophorella*, this flank in covered with regular oblique rows of tubercles), by the development of short auxiliary (frontal) costae, often radiating in a fan shape near the anterior margin of the shell, and often by the bifurcation of the costae in the ventral margin of the shell. It differs from *Vaugonia* Crickmay, 1930 in the straight rows of finely tuberculate costae in the flank and in the absence of the V-shaped bend of costae in the middle of the flank.

Occurrence. Lower Jurassic (Lower Lias)–Lower Cretaceous (Berriasian). Cosmopolitan in the Jurassic.

***Orthotrigonia mordvilkoae* (Yanin, 1979)**

Plate 5, figs. 1–6

Myophorella (Orthotrigonia) mordvilkoae: Yanin, 1979a, p. 25, pl. 2, figs. 2 and 3.

Myophorella mordvilkoae: Bogdanova *et al.*, 1997, p. 83, pl. 19, fig. 6.

Holotype. MZ MGU, no. 39/2, right valve (Yanin, 1979a, pl. 2, fig. 2); central Crimea, Sarysu River, village of Novoklenovo; Lower Cretaceous, Lower Berriasian.

Description (Figs. 27a, 27b; 28d). The shell is medium-sized, irregularly triangular in outline, inequilateral: wide in the anterior part and sharply tapering in the posterior part. The umbonal angle is 90°–100°. The anterior and ventral margins are evenly rounded. The dorsal margin is weakly concave, almost straight, oblique. It forms a distinct angle of 145°–155° with the posterior margin. The posterior margin is short, very weakly convex, obliquely truncated, and forms an angle of 90°–100° with the ventral margin. The shell margins are smooth from inside, sometimes, weakly denticulated.

The flank has 20–23 narrow, finely nodular, symmetrical costae. The costae are straight on the lateral and posterior parts of the flank and weakly curved near the anteroventral margin of the valve. The costae closely approach the marginal carina. On the anterior margin, the costae are sharply bent anteriorly, and one or two short auxiliary frontal costae usually appear in each space between the main costae (Pl. 5, figs. 1b, 4a; Fig. 28d). They are often arranged in a fanlike pattern. Sometimes, near the anteroventral margin of the valve, the main costae become weaker, whereas the tubercles on them diminish. In the umbonal region, the costae of the flank are subconcentric, without auxiliary frontal costae. The intercostal spaces on the flank are smooth, deep, narrow, equal in width to the costae, or, in places (near the anteroventral margin), somewhat wider than the latter.

The area is 0.4 as wide as the flank, flattened, with distinct, numerous, thin, smooth obliquely transverse costae, which often resemble wrinkles of growth (the costae continue across the median groove). The median groove is distinct, filiform. The escutcheon is narrow, weakly concave, with thin obliquely transverse costellae (seen in well-preserved specimens). The nymph is relatively long and lamellar. The marginal and escutcheon carinae are sharp, ridgelike, with pointed tubercles. The median carina is absent.

The hinge plate is moderately wide and triangular. Hinge: on the left valve (Pl. 5, figs. 3, 5), tooth 2 (9 mm long, 8 mm wide) is in a shape of an equilateral triangle, with an almost straight upper termination; its anterior

Explanation of Plate 5

Figs. 1–6. *Orthotrigonia mordvilkoae* Yanin: (1) holotype MZ MGU, no. 39/2, right valve: (1a) external view, (1b) anterior view, (1c) internal view, (1d) area view; central Crimea, Sarysu River, vicinity of the village of Novoklenovo; Lower Berriasian, alternation rock series, beds with *Malbosiceras malbosi* (Section no. 28, Bed 7); coll. by V.V. Drushchits in 1955; (2) PIN, no. 4925/25, shell: (2a) external view, left valve, (2b) area view, ×2; the same locality; coll. by V.V. Drushchits in 1955; (3) PIN, no. 4925/26, fragment of the left valve (umbonal region), internal view, ×1.5; the same locality; coll. by V.V. Drushchits in 1955; (4) MZ MGU, no. 39/3, shell: (4a) external view, right valve, (4b) upper view; southwestern Crimea, basin of the Bel'bek River, vicinity of the village of Solnechnosel'e (Section no. 8, Bed 1); Lower Berriasian, alternating rock series, *dalmasi* Zone; coll. by B.T. Yanin in 1956; (5) PIN, no. 4925/27, left valve, internal view; the same locality; coll. by Popov in 1960; (6) PIN, no. 4925/28, left valve, external view; the same locality; coll. by B.T. Yanin in 1962.

Figs. 7–9. *Litschkovitrigonia inguschensis* (Renngarten); (7) PIN, no. 4925/29, left valve: (7a) external view, (7b) area view, and (7c) internal view; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry; Lower Valanginian (Section no. 24, Bed 1); coll. by B.T. Yanin in 1987; (8) PIN, no. 4925/30, left valve; the same locality; coll. by B.T. Yanin in 1989; (9) PIN, no. 4925/31, left valve with a broken off posteroventral margin: (9a) external view, (9b) area view; the same locality; coll. by B.T. Yanin in 1987.

surface is flat, while the posterior surface is very weakly concave; the apex is straight, rounded, subdivided by a deep groove shifted to the anterior surface; it subdivides the apex of the tooth into two unequal parts: narrow anterior part corresponding to the ridge of the anterior surface, and a wider, more robust, and more rounded posterior part; the dental angle is 45°; tooth 4a (7 mm long) is robust, ridgelike, high; its apex is well separated from the anterior margin of the valve; tooth 4b (7 mm long) is thin, lamellar, well delineated from the nymph; the dental buttress is short, ridgelike; on the right valve (Pl. 5, fig. 1c), tooth 3a (14 mm long) is robust, almost straight, with an upper termination only weakly curved backwards. This termination is merged with the termination of the umbo; a concave dental shelf supporting the ridge of the anterior surface of tooth 2 is developed on the internal side. Tooth 3b (13 mm long) is weakly concave; the dental angle of 3a–3b ranges from 40° to 60° because of the curvature of the posterior tooth.

The anterior adductor scar is elongated oval in outline (6 mm long, 2 mm wide), extending almost in parallel to the anterior margin of the valve. The scar of the anterior retractor has a shape of a narrow, deep depression that is not separated from the anterior scar.

The posterior adductor scar (Pl. 5, figs. 1c, 5) is subquadrate in outline, relatively large (6 mm long, 7 mm wide), strongly depressed and surrounded from all sides by an adductor buttress. Remaining elements of the internal structure have not been observed.

D i m e n s i o n s in mm and ratios:

Specimen no.	L	H	T	H/L	T/L	FL	AR	AR/FL
PIN, no. 4925/25 (BS)	34	32	8	0.90	0.20	24	9	0.37
MZ MGU, no. 39/2, holotype(RV)	35	33	10	0.94	0.28	27	–	–
PIN, no. 4925/27(LV)	37	36	10	0.97	0.27	27	12	0.44
MZ MGU, no. 39/3 (BS)	45	42	13	0.93	0.20	30	12	0.44

C o m p a r i s o n. This species is particularly similar to *O. duplicata* from the Bajocian of England (in the size, subtriangular outline, and the presence of thin narrowly denticulated straight costae on the flank), but is distinguished from it by the less intensely bifurcating costae in the flank near the anterior margin of the valve and by the presence of more regular, short auxiliary frontal costae near the anterior margin. It differs from *O. midareta* from the Middle Jurassic of northern Japan in the more regular arrangement of costae in the flank, in the development of the shorter and more regular frontal costae near the anterior margin, in the presence of the obliquely transverse costellae on the escutcheon, and in the absence of the median carina in the area.

R e m a r k s. Because of the presence of the V-shaped bend of the costae in the umbonal region on the shell of "*T*". *duplicata* Sow., figured by Lycett (1872–1879, pl. 1, fig. 8) and Cox (1969b), this species was assigned to the genus *Vaugonia* Crickmay, 1930 and was designated by Cox (1952, p. 56) as the type species of the subgenus *Orthotrigonia* of the genus *Vaugonia*. The examination of the drawing from the holotype of "*T.*" *duplicata* (Sowerby, 1819, pl. 237, fig. 4) and other specimens of this species figured by Lycett (1872–1879) has shown that the V-shaped bend of the costae in the flank is not typical of this species, but a rather rare event; therefore, it cannot be considered to be the main diagnostic feature in the determination of the generic or subgeneric affinity of this species. Both the holotype and some other shells described by Lycett show regular subconcentric costae in the umbonal region (Lycett, 1872–1879, pl. 1, fig. 9).

The Crimean specimens of *O. mordvilkoae* described in the present paper also show subconcentric costae in the umbonal region. The presence of the narrow, straight, non V-shaped, frequently bifurcating costae in the flank is an important character, based on which representatives of *Orthotrigonia* are easily distinguished from the genus *Vaugonia*. Therefore, I agree with the opinion of Kobayashi and Mori (1955) of the independent status of the genus *Orthotrigonia*. Previously, I assigned the species described to the subgenus *Orthotrigonia* of the genus *Myophorella* (Yanin, 1979a).

T a p h o n o m y a n d p a l e o e c o l o g y. The majority of specimens of the species described come from the compact beds of the coarse, strongly sandy and oncolitic Lower Berriasian limestones overlying the series of polymictic (lower) conglomerates in the vicinity of the village of Solnechnosel'e. Less frequently, this species is found in carbonate, strongly marly Lower Berriasian sandstones and siltstones on the Sarysu River, in the vicinity of the village of Novoklenovo. Thus, this species is more strongly facially controlled compared to other species from the subfamily Myophorellinae. The collection mostly contains isolated valves and their fragments. Very few complete valves are found. Shells with two intact valves are extremely scarce.

Because the rock is very compact, the shell interior in the siphonal region could not be exposed. Therefore, the presence of the siphonal ridge separating the inhalant and exhalant siphons may be indirectly suggested by the presence of a well-developed groove on the area. It is possible that these mollusks were shallow burrowers similar to *M. loewinsonlessingi*, to which they are morphologically similar (in shell shape, oblique posterior margin, median groove).

O c c u r r e n c e. Lower and Upper Berriasian of the southwestern Crimea (basin of the Bel'bek River, village of Solnechnosel'e) and Lower Berriasian of the central Crimea (Sarysu River, village of Novoklenovo).

M a t e r i a l. Fourteen specimens, including two complete shells, eight LV, and four RV.

Subfamily Quadratotrigoniinae Saveliev, 1958

Genus *Litschkovitrigonia* Saveliev, 1958

Litschkovitrigonia: Saveliev, 1958, p. 97; 1960b, p. 96; Yanin, 1960, p. 206; Prozorovsky, 1961, p. 136; 1962, p. 144; Piryatinsky *et al.*, 1962, p. 51; Bogdanova, 1988, p. 155.

Steinmanella (Litschkovitrigonia): Cox, 1969b, p. N487.

Trigonia: Renngarten, 1926, p. 72 (pars); Mordvilko, 1949, p. 127 (pars).

Type species. *Trigonia ingens* Litschkov, 1912, p. 111 (= *Trigonia litschkovi* Mordvilko, 1953, non *T. ingens* Lycett, 1872–1879); Lower Cretaceous, Lower Hauterivian of Mangyshlak. Designated by Saveliev (1958, p. 97).

Diagnosis. Shell oval or subtriangular, moderately convex, with umbo strongly shifted to anterior margin. Flank usually with regular oblique rows of large rounded tubercles. Few subconcentric or V-shaped costae present only in umbonal region. Near anterior margin, rows of tubercles often continue into thin, smooth, or weakly tuberculate frontal costae, usually curved upwards. Near ventral margin, rows of tubercles often become less regular and replaced by irregularly arranged oval or ellipsoid tubercles. Some representatives with narrow antecarinal strip. Area narrow, flattened; in umbonal region, with obliquely transverse costellae. Remaining surface of area with small tubercles irregularly spaced or arranged along growth lines, or smooth, especially in large individuals. Upper part of area narrower than lower part. Marginal and escutcheon carinae distinct, usually with tubercles, less frequently, smooth, in shape of rounded flexures, especially in adults. Median carina absent. Median groove distinct, narrow, and filiform. Escutcheon narrow, flattened, or concave, usually smooth, less frequently with small tubercles. Hinge plate wide. Hinge highly triangular, almost symmetrical, apex of tooth 2 straight and rounded. Ventral margin of shell smooth from inside.

Species composition. The Lower Cretaceous of northern Eurasia contains eight species: *L. litschkovi* (Mordvilko, 1953), *L. inguschensis* (Renngarten, 1926), *L. media* Saveliev, 1958, *L. minor* (Litschkov, 1912), *L. multituberculata* (Litschkov, 1912), *L. ovata* (Litschkov, 1912), *L. subdaedalea* (Renngarten, 1926), and *L. tenuituberculata* Saveliev, 1958.

Comparison. This genus is distinguished from *Quadratotrigonia* Dietrich, 1933 by the less subquadrate outline, narrower area, and by the proportions of its zones (the upper part is narrower than the lower part, while in *Quadratotrigonia*, the proportions are reversed), and by the absence of the median carina in the area.

Remarks. *Litschkovitrigonia* is similar to the genus *Myophorella* (subfamily Myophorellinae, see above) in the general shell outline, the presence of oblique rows of tubercles on the flank, narrow and flattened area, and the proportions of its zones (the upper part is narrower than the lower part), distinct, often tuberculate carinae, narrow escutcheon, and other characters. However, *Litschkovitrigonia* is distinguished from *Myophorella* by the absence of tuberculate costae in the flank (they are present in some *Myophorella* in places of the tubercles), by the absence of the median carina in the area (it is present in some *Myophorella*), usually by the presence of small tubercles in the area and on the escutcheon (in *Myophorella*, the escutcheon never has tubercles).

Occurrence. Lower Valanginian–Lower Aptian of the eastern regions of the Alpine Belt; Lower Valanginian–Lower Hauterivian of the Crimea.

Litschkovitrigonia inguschensis (Renngarten, 1926)

Plate 5, figs. 7–9; Plate 6, figs. 1–8; Plate 11, fig. 10

Trigonia inguschensis: Renngarten, 1926, p. 73, pl.7, figs. 6 and 7; Mordvilko, 1949, p. 128, pl. 21, fig. 7; pl. 23, fig. 4.

Litschkovitrigonia inguschensis alta: Prozorovsky, 1961, p. 137, pl. 11, fig. 4; pl. 12, fig. 2; pl. 13, fig. 2.

Litschkovitrigonia subdaedalea: Yanin, 1960, p. 206, pl. 20, fig. 5 (non fig. 4).

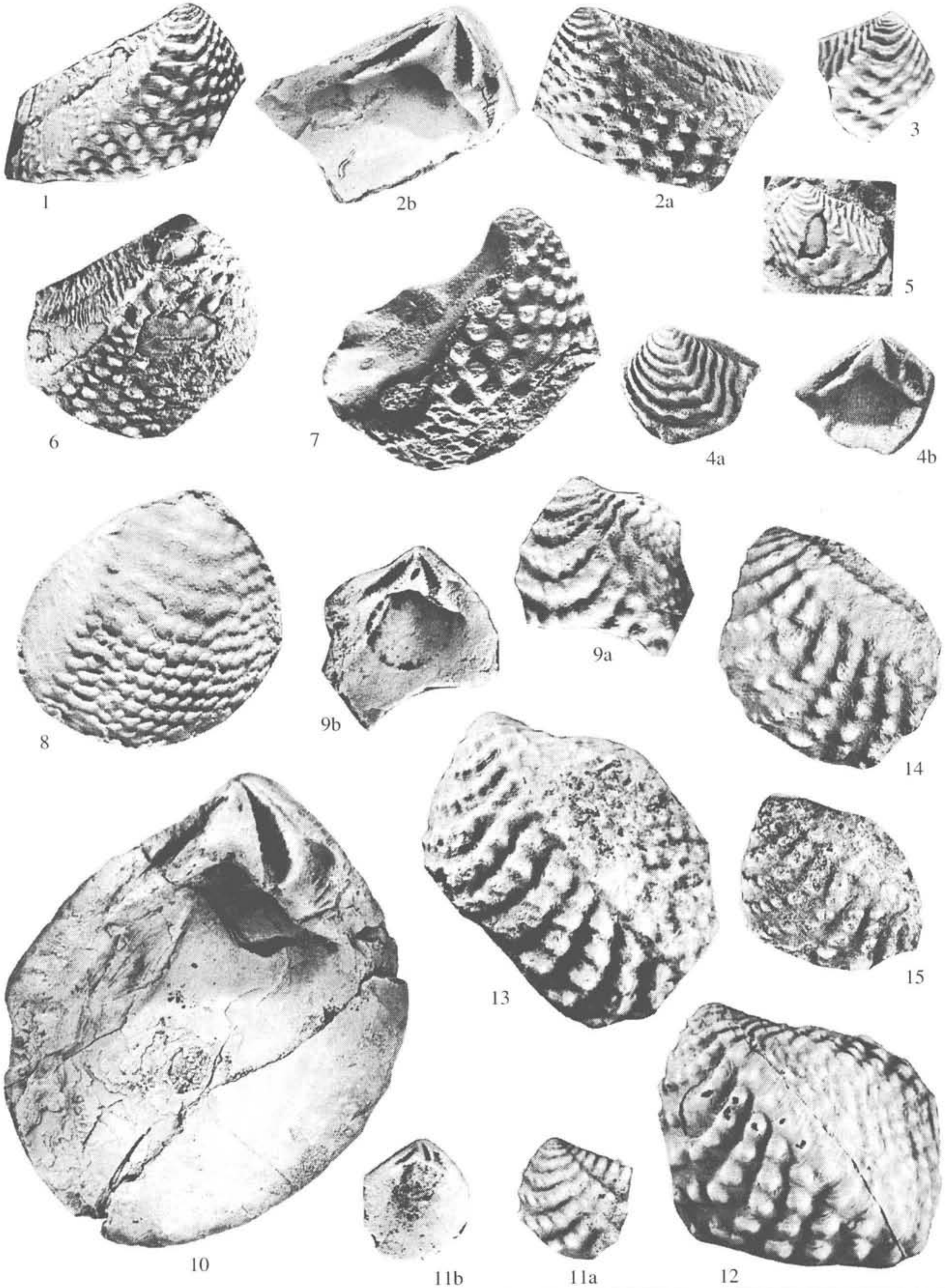
Lectotype. TsNIGR Museum, specimen no. 53/334, right valve (Renngarten, 1926, pl. 7, fig. 6); Lower Cretaceous, Barremian; northern Caucasus, Assa River. Designated herein.

Description (Figs. 29a–29d; 31a, 32c). The shell is medium-sized, from semi-oval to subtriangular in outline, inequilateral. The umbonal angle is 95°–100°. The anterior and ventral margins are gently rounded. The dorsal margin is long and straight along the entire length. It forms a distinct angle of 140°–145° with the posterior margin. The posterior margin is short, very weakly convex, oblique. It forms a obtusely rounded curvature of 110°–120° with the ventral margin. The shell margins are smooth from inside.

The flank possesses numerous (from nine to 15–17) regular, oblique rows of rounded tubercles, excluding the umbonal region, where subconcentric costae are observed instead of rows of tubercles (up to five–six costae). The costae are replace on the lateral side of the flank by two or three V-shaped tuberculate costae (Pl. 5, fig. 7a; Pl. 6, figs. 1, 2a, 3). Near the anterior margin, the rows of tubercles continue into short thinly denticulated, or smooth frontal costae, with terminations curved upwards (Pl. 6, figs. 1, 3). Occasionally present auxiliary frontal costae approach the anterior margin, although a narrow smooth band remains near the umbo of adult shells. Near the ventral margin, and, occasionally, on the lateral side of the flank, the rows of tubercles become less regular (Pl. 5, figs. 7a, 9a). For instance, the rows can bend, additional short rows may appear, or the tubercles become ellipsoid, arranged along the growth lines. Sometimes, tubercles are very small and densely spaced, and their rows are also closely spaced (Pl. 6, fig. 8). The spaces between the rows in most shells are distinct, smooth, flattened, or weakly concave. The antecarinal strip is usually well developed, smooth, only occasionally with small irregular tubercles near its termination.

The area is narrow (half the width of the flank), flat, or slightly concave along the median groove. In the umbonal region, the area possesses obliquely transverse costellae. The remaining surface has very small tubercles irregularly arranged or forming obliquely transverse rows along the growth lines (Pl. 5, fig. 7a);

Plate 6



less frequently, with thin folds in the posterior part (wrinkles of growth) (Pl. 6, fig. 6). The median groove is filiform, deep, subdividing the flank into two unequal parts (the upper is always narrower than the lower). The escutcheon is narrow, flat, or weakly concave along the escutcheon carina. It usually has small, irregularly arranged tubercles; less frequently, it is smooth (Pl. 5, figs. 7b, 9b). The nymph is short and lamellar.

The marginal and escutcheon carinae are always well pronounced, with rounded or pointed tubercles. The tubercles on the carinae in some individuals decrease in size toward the posterior margin, become smoother and eventually disappear. As a result, the carinae may have the appearance of smooth, obtusely rounded angulations (Pl. 5, fig. 9a).

The hinge plate is highly triangular. Hinge: on the left valve, tooth 2 (Pl. 5, fig. 7c; Fig. 31a: 10 mm long, 8 mm wide; Pl. 6, fig. 2b: 10 mm long, 9 mm wide) is in the shape of an almost equilateral triangle, in which the anterior surface is flat, while the posterior surface is very weakly concave and slightly longer than the anterior surface; the apex of the tooth is straight and rounded; its upper slope has a groove that subdivides the tooth into two almost equal parts; the dental angle is 50°; tooth 4a (9 and 10 mm long in the above specimens, respectively) is robust, crestlike, and high; its ridge is well delineated from the anterior margin of the valve; tooth 4b (10 and 12 mm long, respectively) is lamellar, weakly separated from the nymph. The dental buttress is very short and ridgelike. The hinge of the right valve is partly preserved in several shell fragments. Its structure may be interpreted based on deep dental socket for 3a and 3b on the left valve. A narrow dental shelf is present in the socket for 3a from inside.

The anterior adductor scar is well preserved only on the left valves (Pl. 5, fig. 7c; Fig. 31a; Pl. 6, fig. 2b). It shows a myophore and surface zones. The myophore zone is wide, elongated oval in outline, flattened, with coarse, obliquely transverse bifurcating wrinkles, which increase the attachment area of the adductors. At the base, it is bordered by a robust myophorous buttress (Fig. 31a). The surface part of the scar lies immediately on the shell wall. It is smooth, with a straight lower side (corresponding to the plane of the myophore) and the arched upper side. The surface of this part of the scar is weakly concave. The shine of the inner shell layer distinguishes this zone from the remaining part of the valve. The anterior retractor scar has the appearance of a deep, narrow, horseshoe-shaped depression, with a convexity directed toward the anterior margin and occurring between the lower termination of tooth 4a and the anterior margin. It is separated from the anterior adductor scar by a short ridge.

The posterior adductor scar (Pl. 5, fig. 7c; Fig. 31a; Pl. 6, fig. 2b) is large, rounded, with a slightly elongated posterior side. It is superficial, smooth, or with weak longitudinal wrinkles. The anterior side of the scar is strongly deepened, with an even slope, and bordered by the myophorous buttress from the front and from below. The scar of the posterior retractor on the left valve (Pl. 5, fig. 7c; Fig. 31a; Pl. 6, fig. 2b) is distinct, has the appearance of an oval depression, which is deepened anteriorly and is superficial posteriorly, and separated from the posterior adductor scar by a smooth narrow ridge. The pedal elevator scar (prepared only on the left valve) has an appearance of a deep depression lying in the umbonal recess and bordered anteriorly by the myophorous buttress.

The pallial line was only observed on the left valve (Pl. 5, fig. 7c). It is at a considerable distance from the ventral margin of the valve, has no sinus, although it has a small concave zone near the posterior adductor

Explanation of Plate 6

Figs. 1–8. *Litschkovitrigonia inguschensis* (Renngarten); (1) PIN, no. 4925/32, right valve with a broken off ventral margin, external view; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); coll. by B.T. Yanin in 1987; (2) PIN, no. 4925/33, left valve with broken off posterior and ventral margins: (2a) lateral view; (2b) internal view; the same locality; coll. by B.T. Yanin in 1989; (3) PIN, no. 4925/34, fragment of the right valve of a young individual, external view; the same locality; coll. by B.T. Yanin in 1987; (4) PIN, no. 4925/35, × 2; left valve of a young individual: (4a) external view; (4b) internal view; coll. by B.T. Yanin in 1989; (5) PIN, no. 4925/36, left valve of a young individual, external view; central Crimea, Kuchuk-Karasu River, village of Gorlinka; found redeposited in the block of Valanginian sandstone in the series of Barremian conglomerates (Outcrop no. 31); coll. by B.T. Yanin in 1959; (6) PIN, no. 4925/37, right valve, external view; central Crimea, Beshterek River, collective farm Yagodnyi; Upper Berriasian, *boissieri* Zone (Outcrop no. 20); coll. by B.T. Yanin in 1962; (7) PIN, no. 4925/38; right valve with partly preserved shell, external view; southwestern Crimean, basin of the Bodrak River, vicinity of the village of Prokhladnoe, summit of Dlinnaya Mountain; Lower Hauterivian (Section 12, Bed 3); coll. by B.T. Yanin in 1990; (8) PIN, no. 4925/39, plaster cast of the right valve (the umbo was not preserved), external view; village of Prokhladnoe, Patil' Mountain; Lower Hauterivian (Section no. 14, Bed 3); coll. by B.T. Yanin in 1956.

Figs. 9–15. *Quadratotrigonia nodosa orbignyana* (Lycett): (9) PIN, no. 4925/40; left valve of a young individual with broken off ventral and posterior margins: (9a) external view, (9b) internal view; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1), coll. by B.T. Yanin in 1987; (10) PIN, no. 4925/41, left valve, internal view, the same locality; (11) PIN, no. 4925/42, left valve of a young individual: (11a) external view, (11b) internal view; the same locality; coll. by B.T. Yanin in 1990; (12) PIN, no. 4925/43, left valve with broken off anterior and ventral margins, external view; the same locality, coll. by B.T. Yanin in 1989; (13) PIN, no. 4925/44, left valve with a broken off ventral margin, external view; central Crimea, Kuchuk-Karasu River, village of Gorlinka; from a block of Valanginian sandstone redeposited in the Barremian conglomerates (Outcrop no. 31); coll. by B.T. Yanin in 1963; (14) PIN, no. 4925/45, left valve with a broken off posterior margin, external view; southwestern Crimea, basin of the Bodrak River, vicinity of the village Prokhladnoe, summit of Dlinnaya Mountain; Lower Hauterivian (Section no. 12); coll. by B.T. Yanin in 1982; (15) PIN, no. 4925/46, left valve with a broken off dorsoposterior margin; external view, the same locality.

scar. It extends from the lower termination of the superficial part of the anterior adductor scar. The siphonal ridge (well-preserved in specimen PIN, no. 4925/29; Pl. 5, fig. 7c; Fig. 31a) is relatively short, smooth, rounded, wide in the anterior part and narrow in the posterior part. It extends from the posteroinferior side of the posterior adductor scar. The siphonal incisions (notches) are well developed. Of these, the lower notch (corresponding to the inhalant siphon) is wider. These depressions correspond to two weak siphonal gapes on the posterior margin of the shell.

D i m e n s i o n s in mm and ratios:

Specimen PIN, no.	L	H	T	H/L	T/L	FL	AR	AR/FL
4925/36 (LV)	20	17	4	0.85	0.20	12	6	0.50
4925/30 (LV)	40	37	9	0.92	0.22	25	12	0.48
4925/29 (LV)	44	41	12	0.93	0.27	29	12	0.44
4925/37(RV)	45	42	~14	0.93	0.31	27	13	0.40

V a r i a b i l i t y. The Crimean representatives of this species have variable shell proportions in individuals of different age (with age the height and convexity of the shell increase). The ornamentation of the anterior and posterior parts of the flank also varies. In some specimens, the auxiliary rows of tubercles and even irregularly arranged tubercles are observed together with regular rows of tubercles in the flank (Pl. 5, figs. 7a, 9b). Small tubercles may be present on the entire surface of the posterior part of the flank, or only in its middle part (in this case, the posterior half of the flank remains smooth, or covered by the wrinkles of growth). The degree of expression of tubercles on the carinae may also vary (they may range from large to very small) and be developed along the entire carina, or only before its middle (in this case, the posterior part of the carina has no tubercles).

In contrast, in one specimen, the rows of tubercles and tubercles themselves are more closely spaced near the lower and posterior parts of the flank (Pl. 6, fig. 8). This specimen is so different from typical representatives of *L. inguschensis* that it is possible that it represents a separate morph, i.e., *L. inguschensis* morpha *stenotuberculata* (densely tuberculate). There is not enough data to establish a new species, because this morph is represented by a single poorly preserved specimen (incomplete external mold). Moreover, it was found together with typical forms of *L. inguschensis* (on Patil' Mountain).

C o m p a r i s o n. The specimens of *L. inguschensis* from the Crimea are most closely similar to *L. media* from the Lower Hauterivian of Mangyshlak and differ from it in the less elongated shell and the straight dorsal margin. *L. inguschensis* is distinguished from *L. subdaedalea* from the Barremian of the northern Caucasus by the smaller shell (two-thirds to half of the shell size of *L. subdaedalea*), less elongated shell (H/L = 0.89–0.93 instead of 0.80 in the typical specimen: see Renngarten, 1926, pl. 3), and by the smaller tubercles in the flank and on the carinae.

R e m a r k s. Crimean specimens of *L. inguschensis* are somewhat different from the typical Caucasian representatives described by Renngarten (1926, pl. 7, figs. 6, 7). They are smaller, with more densely spaced rows of small tubercles in the flank, with smaller and more closely spaced tubercles on the carinae, while some specimens are different in that the tubercles in the posterior half of the carinae are absent altogether.

T a p h o n o m y a n d p a l e o e c o l o g y. The shells of the species described are found mostly in the Valanginian sandstones exposed in the basins of the Bodrak and Zuya rivers. Isolated specimens were found in the finely pebbled conglomerates and coquinas in the basins of the Zuya and Kuchuk-Karasu rivers. In the latter region, they occur in the redeposited blocks of sandstones and conglomerates. In places (Patil' Mountain), they are found in coquinas. All specimens collected are represented by isolated valves and their fragments. In some localities (Patil' Mountain), they are found mostly as impressions of valves, which resulted from the dissolving of the valve walls. Some specimens from the lenses of weakly cemented sandstones with pebbles found in the series of Mazanka sands and pebble-stones in the Zuiskii Quarry are excellently preserved. Some shells from this locality allow close examination of the entire shell interior (see Section II. 5).

Because of the presence of the siphonal ridge and a small gape on the posterior margin, it is possible to suggest that the mollusks burrowed shallowly in the loose sandy sediment. This loose coarse sediment was reworked by the waves, and as a result shells were washed out of it either during life or postmortem, and their valves were separated. The valves were subsequently broken and rounded, which can be inferred from their fragmentary preservation (Pl. 6, figs. 1–4).

O c c u r r e n c e. Valanginian–Barremian: Lower Valanginian–Lower Hauterivian of the southwestern Crimea (basin of the Bodrak River: Patil' Mountain, Dlinnaya Mountain; basin of the Al'ma River: village of Konstantinovka) and of the central Crimea (Zuya-Burul'cha interfluve: Zuiskii Quarry); the species also occurs in the basin of the Kuchik-Karasu River: village of Gorlinka (redeposited in the Barremian); and in the Hauterivian–Barremian of the northern Caucasus.

M a t e r i a l. Eighteen specimens: five LV, four RV, six valve fragments, and three imprints.

Genus *Quadratotrigonia* Dietrich, 1933

Quadratotrigonia: Dietrich, 1933, p. 331; Saveliev, 1958, p. 102; 1960b, p. 96; Yanin, 1958, p. 133; 1960, p. 206.

Trigonia: Renngarten, 1926, p. 72 (pars); Mordvilko, 1949, p. 127 (pars).

T y p e s p e c i e s. *Trigonia nodosa* J. Sowerby, 1829; Lower Cretaceous, Lower Aptian of England. Designated by Saveliev (1958, p. 102).

Diagnosis. Shell subquadrate, subtriangular, or oval-rectangular, moderately, or strongly convex. Flank with oblique, usually regular rows of large tubercles. Only umbonal region of shell with a few subconcentric tuberculate costae. Area wide or narrow, weakly convex, sometime flattened, with obliquely transverse rows of small tubercles, more rarely, with sparsely spaced and irregularly arranged tubercles or with coarse obliquely transverse folds, or wrinkles of growth. Sometimes, area smooth in adults. Marginal, median, and escutcheon carinae always well developed, having appearance of rows of tubercles. Escutcheon convex, with transverse rows of small tubercles or with irregularly arranged large tubercles, less frequently, smooth. Umbo protruding in varied extent, opisthogyre, shifted to anterior margin. Hinge plate wide; hinge highly triangular, almost symmetrical. Apex of tooth 2 straight and rounded. Ventral shell margin smooth from inside.

Composition. The Lower Cretaceous of Eurasia contains two subgenera, *Quadratotrigonia* Dietrich, 1933 and *Leptotrigonia* Saveliev, 1958.

Comparison. This genus is distinguished from other genera known from the Cretaceous of Eurasia by the following features. It is distinguished from *Litschkovitrigonia* Saveliev, 1958 by the presence of the median carina and a relatively wider area. It differs from *Korobkovitrigonia* Saveliev, 1958 by the presence of the median carina and large tubercles on the marginal and escutcheon carinae, by the more regular oblique rows of tubercles, and, usually, by the absence of the V-shaped bend of the costae in the umbonal region. It is distinguished from *Asiatotrigonia* Cox, 1952 by the mainly subquadrate shell outline, lesser shift of the umbo forward, by the presence of regular oblique rows of tubercles in the flank; by the absence of thin radial ribbing in the flank, by the presence of the median carina, sharp tuberculate marginal and escutcheon carinae (in *Asiatotrigonia*, they are virtually undeveloped).

Occurrence. Lower–Upper Cretaceous. Cosmopolitan.

Subgenus *Quadratotrigonia* Dietrich, 1933

Quadratotrigonia (Quadratotrigonia): Saveliev, 1958, p. 103; 1960b, p. 96.

Yaadia (Quadratotrigonia): Cox, 1969b, p. N488.

Type species. *Trigonia nodosa* J. Sowerby, 1829; Lower Cretaceous, Lower Aptian, green sandstone; England.

Diagnosis. Shell from subquadrate to semi-oval. Flank usually with oblique rows of tubercles, excluding umbonal region. Area wide. Escutcheon usually with tubercles.

Species composition. Six species are known from the Cretaceous of Eurasia: *Q. (Q.) daedalea* (Parkinson, 1811), *Q. (Q.) mangyschlakensis* (Luppov, 1932), *Q. (Q.) nodosa* (Sowerby, 1829), *Q. (Q.) padernensis* (Petter-Reserveur, 1955), *Q. (Q.) quadrata* (Agassiz, 1840), and *Q. (Q.) spectabilis* (Sowerby, 1829).

Comparison. This subgenus is distinguished from *Leptotrigonia* by the subquadrate or semi-oval shell outline (in *Leptotrigonia*, the shell is subtriangular), by the umbos more strongly shifted forward (in *Leptotrigonia*, the umbos are almost central), by the less oblique dorsal and posterior margins (in *Leptotrigonia*, the dorsal margin is strongly oblique giving the shell a triangular outline), by the absence of regular obliquely transverse costellae in the area, and by the presence of ornamentation on the escutcheon (in *Leptotrigonia*, it is often smooth).

Occurrence. Valanginian–Cenomanian. Cosmopolitan.

Quadratotrigonia (Quadratotrigonia) nodosa (J. Sowerby, 1829)

Trigonia nodosa: J. Sowerby, 1829, p. 7, pl. 507, fig. 1; Pictet and Renevier, 1855–1858, p. 94; pl. 12, fig. 2; Lycett, 1872–1879, p. 106, pl. 25, figs. 1 and 2; pl. 37, figs. 5 and, 6; Wollemann, 1900, p. 90, pl. 4, fig. 8; Woods, 1900, p. 78; Gillet, 1920, p. 153, pl. 7, figs. 1 and 2; Luppov, 1932, p. 191, pl. 1, fig. 5.

Trigonia nodosa var. *orbignyana*: Lycett, 1872–1879, p. 107, pl. 24, figs. 1–3; Gillet, 1921, p. 11, pl. 2, fig. 5; Renngarten, 1926, p. 72, pl. 7, figs. 4 and 5.

Trigonia nodosa var. *karakaschi*: Mordvilko, 1932, p. 39, pl. 3, figs. 1 and 2; pl. 4, fig. 1; pl. 5, fig. 3; 1949, p. 129, pl. 24, fig. 1.

Quadratotrigonia nodosa: Yanin, 1958, p. 133, pl. 1, figs. 3 and 4; 1960, p. 206, pl. 20, figs. 1–3.

Quadratotrigonia (Quadratotrigonia) nodosa: Saveliev, 1958, p. 253, pl. 23, figs. 1 and 2; 1960b, p. 96, pl. 20, fig. 7.

Quadratotrigonia (Quadratotrigonia) nodosa nodosa: Dimitrova, 1974, p. 99, pl. 47, figs. 3 and 4.

Quadratotrigonia (Quadratotrigonia) nodosa var. *orbignyana*: Saveliev, 1958, p. 257, pl. 25, fig. 1.

Quadratotrigonia (Quadratotrigonia) nodosa orbignyana: Dimitrova, 1974, p. 100, pl. 47, fig. 6.

Yaadia (Quadratotrigonia) nodosa: Cox, 1969b, p. N488, text-fig. D 74.3.

Trigonia rudis: D'Orbigny, 1843–1847, p. 137, pl. 289, figs. 1 and 2 (non figs. 3, 4).

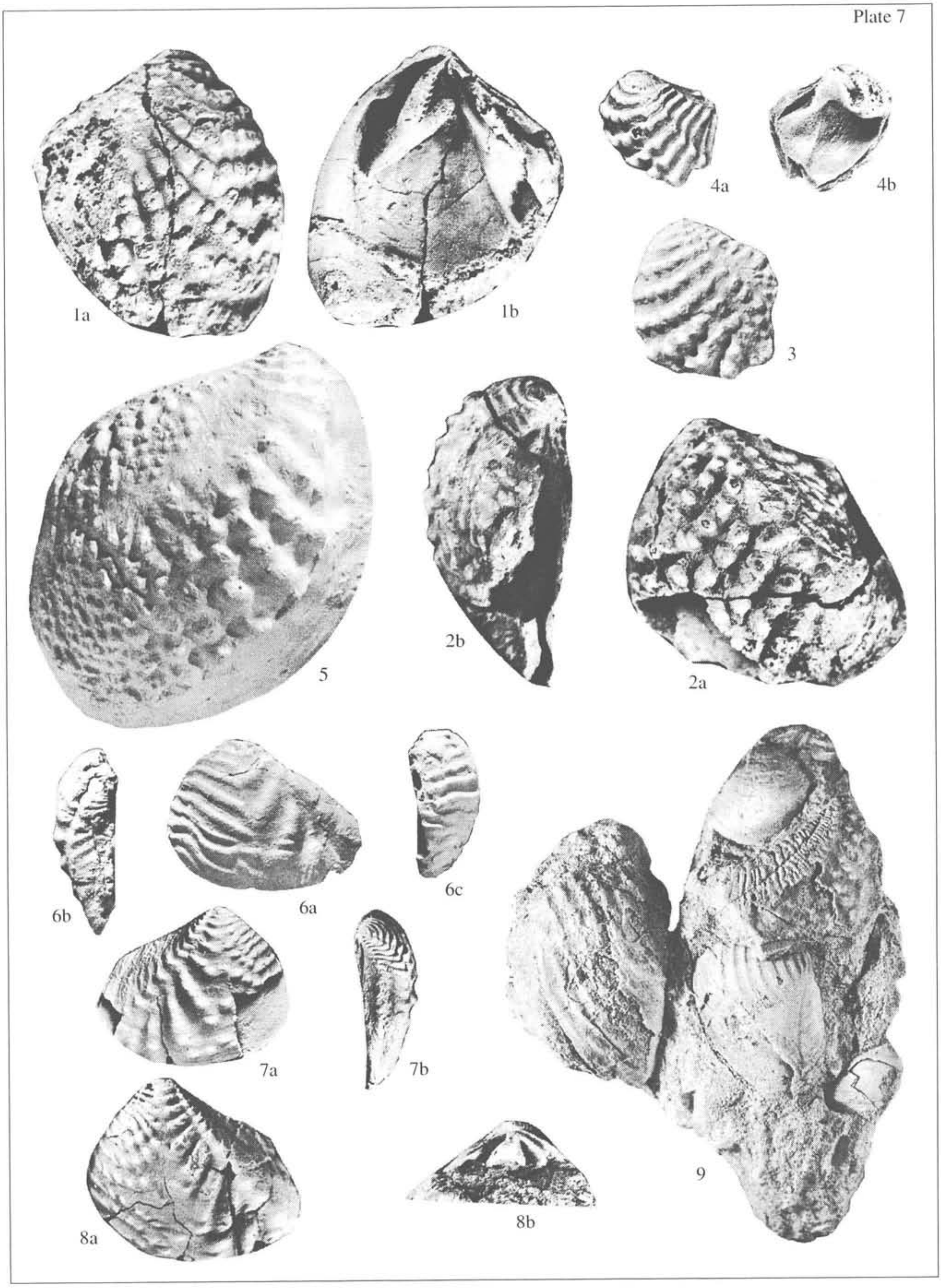
Trigonia daedalea: Parkinson, 1811, p. 176, pl. 12, fig. 6; Pictet and Renevier, 1855–1858, p. 92, pl. 12, fig. 1.

Neotype. Specimen figured by Lycett (1872–1879, pl. 25, fig. 2), right valve; southern England, Tilby; Lower Cretaceous, Upper Barremian. Designated by Saveliev (1958, p. 254) because Lycett (1872–1879, p. 110) and Woods (1900, p. 79) noted that the holotype figured by Sowerby (1829, pl. 507, fig. 1) was lost.

Description. The shell outline varies from subquadrate to semi-oval. The flank has oblique, sparsely spaced, regularly curved rows of large rounded tubercles. The area is broad, flattened, or weakly concave, with small tubercles, arranged irregularly, or in obliquely transverse rows. Three well-developed carinae possess isolated tubercles. The escutcheon is narrow, weakly convex, with coarse tubercles arranged irregularly, or in oblique rows.

Composition. Three subspecies are known from the Cretaceous of Eurasia: *Q. (Q.) nodosa nodosa* (Sowerby, 1829), *Q. (Q.) nodosa orbignyana* (Lycett, 1872–1879), and *Q. (Q.) nodosa karakaschi* (Modvilko, 1932).

Plate 7



Comparison. This species is distinguished from *Q. (Q.) daedalea* from the Albian–Cenomanian of Western Europe by the more sparsely spaced oblique rows of larger tubercles in the flank, by the sharper marginal, median, and escutcheon carinae possessing large isolated tubercles, usually by the absence of the V-shaped bend in the rows of tubercles in the umbonal region in the flank. It differs from *Q. (Q.) quadrata* from the Cenomanian of France in the presence of three carinae in adults, more sparsely spaced rows of tubercles in the flank, seen at all growth stages, in the absence, or, less frequently, weak development of the V-shaped bend in the rows of tubercles in the umbonal region of the flank. It is different from *Q. (Q.) mangyschlakensis* from the Lower Hauterivian of Mangyshlak in the less convex valves (the convexity of valves is usually 0.2–0.4, whereas in *Q. (Q.) mangyschlakensis*, according to Luppov, it is 0.8), in the subquadrate outline (in *Q. (Q.) mangyschlakensis*, the shell is oval), in the more strongly curved rows of tubercles in the flank (in *Q. (Q.) mangyschlakensis*, the rows in the posterior zone of the flank almost vertically extend from the marginal carina in relation to the ventral margin). It is distinguished from *Q. (Q.) padernensis* from the Middle Albian of France by the less strongly curved rows of tubercles in the flank, more prominent carinae in adults, and by the absence or weak development of the V-shaped bend of the tuberculate costae in the umbonal zone of the flank.

Occurrence. Lower Valanginian–Middle Cenomanian. Cosmopolitan.

Quadratotrigonia (Quadratotrigonia) nodosa orbignyana (Lycett, 1872–1879)

Plate 6, figs. 9–15; Plate 7, figs. 1–5

Trigonia nodosa var. *orbignyana*: Lycett, 1872–1879, p. 107, pl. 24; figs. 1–3; Gillet, 1921, p. 11, pl. 1, fig. 5; Renngarten, 1926, p. 72, pl. 7, figs. 4 and 5.

Quadratotrigonia (Quadratotrigonia) nodosa var. *orbignyana*: Saveliev, 1958, p. 257, pl. 25, fig. 1.

Quadratotrigonia (Quadratotrigonia) nodosa orbignyana: Dimitrova, 1974, p. 100, pl. 47, fig. 6.

Quadratotrigonia nodosa: Yanin, 1958, p. 133, pl. 1, figs. 3 and 4; 1960, p. 206, pl. 20, figs. 1–3.

Lectotype. Specimen figured by Lycett (1872–1879, pl. 24, figs. 1, 2); Lower Cretaceous, Neocomian; southern England. Designated by Saveliev (1958, p. 257).

Description (Figs. 29e, 29f, 31b). The shell is medium-sized or large, usually moderately convex, inequilateral. The umbo is weakly protruding, strongly shifted anteriorly, opisthogyre. The umbonal angle is approximately 100°. The anterior and ventral margins are evenly rounded. The dorsal margin is weakly concave near the umbo and weakly convex in the remaining part. It forms a distinct obtusely rounded bend with the posterior margin in subquadrate shells. The posterior margin is long, always convex, weakly oblique, forming a broadly rounded bend with the ventral margin. The shell margins are smooth from inside.

The flank possesses 10–13 regular oblique rows of large rounded tubercles. The tubercles in a row are usually separated from each other, but their bases are often merged to form tuberculate costae. This is always observed in the umbonal zone of the flank, although in some specimens, tuberculate costae occupy the entire flank. At a young stage, three to five first costae (in the umbonal zone) are smooth, lacking tubercles (Pl. 6, fig. 11a). Close to the ventral margin and, less frequently, near the anterior margin, tubercles may become elliptical, or intercalating rows of tubercles or tuberculate costae may appear (Pl. 7, fig. 1a). Spaces between the rows and intercostal spaces are smooth, usually weakly concave, equal in width to tubercles or costae in the corresponding part of the flank.

The area is wide (0.6–1.0 of the flank width), weakly concave, or flattened, in the umbonal region,

Explanation of Plate 7

Figs. 1–5. *Quadratotrigonia nodosa orbignyana* (Lycett): (1) PIN, no. 4925/47, right valve with broken off ventral and posterior margins: (1a) external view, (1b) internal view; central Crimea, Kuchuk-Karasu River, village of Gorlinka; from a block of Valanginian sandstone, redeposited in the series of Barremian conglomerates (Outcrop no. 31); coll. by B.T. Yanin in 1959; (2) PIN, no. 4925/48, left valve with broken off ventral and posterodorsal margins: (2a) external view, (2b) area view; the same locality; (3) MZ MGU, no. 3/10, left valve of a young individual with a broken off posterior margin, external view; the same locality; (4) PIN, no. 4925/49, fragment of the umbonal part of the left valve: (4a) external view, (4b) internal side; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); coll. by B.T. Yanin in 1987; (5) MZ MGU, no. 4/10, plaster cast of the external imprint of the right valve, external view; southwestern Crimea, Bodrak River, northern vicinity of the village of Trudolyubovka; coral biostrome near the "House of Forester"; Lower Hauterivian (Section no. 16, Bed 1); coll. by V.V. Drushchits in 1955.

Figs. 6–8. *Iotrigonia scapha* (Agassiz): (6) MZ MGU, no. 5/10, left valve: (6a) external view, (6b) upper view, umbonal view, (6c) anterior view; central Crimea, basin of the Tonas River, 2 km east of the village of Golovanovka (a precise stratigraphic position of this specimen is not established; it most likely comes from a block of Valanginian sandstone redeposited in the series of Barremian conglomerates similar to that in the village of Gorlinka on the nearby Kuchuk-Karasu River); coll. by mapping geologists in 1957, (7) PIN, no. 4925/50, right valve with a broken off anteroventral margin: (7a) external view, (7b) area view; central Crimea, Beshterek River, southern vicinity of the village of Solov'evka; Lower Berriasian, alternating rock series, *dalmasi* Zone (Section 19, Bed 2); coll. by B.T. Yanin in 1963; (8) PIN, no. 4925/51, left valve: (8a) external view, (8b) umbonal region, internal view, ×1.5; the same locality.

Fig. 9. Fragment of coquina composed of isolated valves of *Rutitrigonia longa* (Agassiz) and *Myophorella loewinsonlessingi* (Renngarten): PIN, no. 4925/52, view of the top of the Bed (shell pavement); southwestern Crimea, basin of the Bel'bek River, Tamish' Grove (east of the village of Kuibyshevo); Lower Berriasian, alternating rock series (Outcrop no. 7); coll. by B.T. Yanin in 1957.

with obliquely transverse costellae, on the remaining surface, with small tubercles, usually forming obliquely transverse rows parallel to growth lines (this is especially noticeable near the posterior margin of the area in well-preserved specimens: Pl. 6, fig. 12). The median groove has an appearance of a weakly concave, or flattened depression.

The marginal, median, and escutcheon carinae are always well developed in a shape of rows of rounded tubercles (Figs. 29e, 29f). The median carina subdivides the area into two unequal parts, of which the upper part is always somewhat wider than the lower. The number of tubercles on the carinae corresponds to the number of tubercles or tuberculate costae in the flank (this correspondence is observed approximately until the middle of the area). Near the posterior end of the carinae, the tubercles may decrease in size, become smoother, or disappear. The escutcheon is wide, concave in the umbonal region, and convex in the middle and posterior regions, with obliquely transverse rows of small tubercles (Pl. 6, fig. 12), or with irregularly arranged tubercles. The nymph is long and lamellar.

The hinge plate is wide and highly triangular. Hinge: on the left valve, tooth 2 (Pl. 6, fig. 11b: 2.5 mm long, 3 mm wide; Pl. 6, fig. 9b: 7 mm long, 5 mm wide; Pl. 6, fig. 10; Fig. 31b: 15 mm long, 13 mm wide) has a shape of almost equilateral triangle, in which the anterior surface is flat, while the posterior surface is very weakly convex and always somewhat longer than the anterior surface. The apex of the tooth is straight, rounded, its upper slope has a groove, which subdivides the tooth into two almost equal parts. The dental angle is 45°–48°. Tooth 4a (the above specimens are 3, 5, 8, and 17 mm long, respectively) is robust, ridgelike, high. Its apex is clearly detached from the anterior margin of the shell. Tooth 4b is robust, weakly separated from the nymph, thinly lamellar in a young specimen (Pl. 6, fig. 11b). The dental buttress is short and ridgelike. The hinge on the right valve is partially preserved in only one specimen (Pl. 7, fig. 1b): tooth 3a (15 mm long) is robust, almost straight, with the upper termination only weakly curved backwards and contacting the umbo. A dental shelf is located below the tooth on the internal inside. The dental shelf is wide and flattened in the lower part and narrow and concave in the upper part. Tooth 3b (only its lower end is preserved; 21 mm long) is separated by a socket from the dorsal margin of the valve. A narrow, flattened dental shelf is on its inner side.

The anterior adductor scar is elongated oval in outline, flattened, extended almost parallel to the anterior margin of the valve, up to 15 mm long (in large individuals), with coarse transverse, asymmetric, often bifurcating wrinkles, which enhanced the muscle attachment. Basally, it is bordered by a massive myophorous buttress (Fig. 31b). The anterior retractor scar (well-preserved in the left valve of specimen PIN, no. 4925/43) in the shape of a narrow horseshoe-like pit that is convex toward the anterior margin and lies between the lower termination of tooth 4a and the anterior margin of the valve. This scar is separated from the anterior adductor scar by a short ridgelike septum only in the anterodorsal part of the valve. The bottom of the retractor scar is uneven and nodular.

The posterior adductor scar (well-preserved only in specimen PIN, no. 4925/43) is large (17 mm long, 15 mm wide), semicircular, superficial, with weak, closely spaced longitudinal folds. The anterior side of the scar is considerably deepened, with a small constriction in the middle. The scar is bordered basally by a ridgelike myophorous buttress, dipping under the dental buttress of tooth 2. The posterior retractor scar (well-preserved in specimen PIN, no. 4925/43) is relatively large (4 mm wide), in a shape of an oval depression, with its long axis positioned perpendicular to the dorsal margin of the valve. It lies on the continuation of the socket for tooth 3b. It is strongly deepened anteriorly and surfaced posteriorly and separated from the posterior adductor scar by a narrow smooth elevation. The posterior retractor scar (preserved in specimen PIN, no. 4925/47: Pl. 7, fig. 1b) has a shape of an oval depression up to 3 mm deep. It lies immediately below the lower termination of tooth 3b and is separated from the posterior adductor scar by a narrow smooth elevation. The pedal elevator scar (observed only in the left valve: specimen PIN, no. 4925/40: Pl. 6, fig. 9b and no. 4925/43: Pl. 6, fig. 12) in a shape of deep depression lying in the umbonal recess and bordered anteriorly by a massive myophorous buttress.

The pallial line (observed only in specimen PIN, no. 4925/47: Pl. 7, fig. 1b) lacks a sinus. It is at a considerable distance from the ventral margin of the valve and extends immediately from the lower termination of the anterior adductor scar and reached approximately the middle of the posterior adductor scar, from which it is separated by a myophorous buttress.

D i m e n s i o n s in mm and ratios:

Specimen PIN, no.	L	H	T	H/L	T/L	FL	AR	AR/FL
4925/42 (LV)	~20	20	6	1.0	0.30	11	10	0.90
4925/46 (LV)	39	38	12	0.9	0.30	22	–	–
4925/48 (LV)	56	56	23	1.0	0.41	40	~31	~0.77
4925/41 (LV)	70	76	20	1.0	0.20	45	28	0.62

V a r i a b i l i t y. The Crimean representatives of *Q. (Q.) nodosa orbignyana* show high degree of variability. All shell parameters vary to some extent. These include: (1) the position of the umbo varies from the moderately shifted anteriorly (Pl. 6, fig. 12) to almost terminal (Pl. 6, fig. 14); (2) the degree of convexity varies from moderately convex (majority of specimens) to strongly convex (T/L–0.41: Pl. 7, fig. 1); (3) the relative width of the area decreases with age in relation to the width of the flank (see *Dimension*); (4) the degree of obliquity of the posterior margin increases with age (in young shells, it is almost parallel to the anterior margin, while the angle between the dorsal and posterior margins is almost straight); (5) character of ribbing in different specimens, even from the same locality, varies from regular rows of tubercles (Pl. 6, fig. 12) to tuberculate costae (Pl. 6, fig. 13). All this makes identification of subspecies very difficult. For this reason, many researchers have recognized varieties within the species *Q. (Q.) nodosa* (see synonymy of this species). Dhondt and Dieni (1988, p. 44) also noted a large individual ("ecophenotypical") variability of this species.

C o m p a r i s o n. This subspecies is different from *Q. (Q.) nodosa nodosa* from the Aptian of Western Europe in its umbo less shifted anteriorly, more oblique posterior margin (because of which the angle between the posterior margin and dorsal margin is more obtuse), in the presence of obliquely transverse rows of small tubercles between the carinae in the area (in *Q. (Q.) nodosa nodosa*, the tubercles are arranged irregularly), and in the stepped structure of the area associated with the strong development of the median groove (in *Q. (Q.) nodosa nodosa*, the area is flattened and even). It is distinguished from *Q. (Q.) nodosa karakaschi* from the Middle–Upper Aptian of the northern Caucasus by the more angular outline, more pronounced large tubercles on the marginal carina, by the presence of obliquely transverse rows of tubercles covering almost the entire area at the intermediate growth stage (in *Q. (Q.) nodosa karakaschi*, the rows of tubercles or tuberculate costae are present mostly in the umbonal region of the area, while the zone near the posterior margin always possesses only growth wrinkles), and by the strongly concave area due to the development of a deep median groove.

R e m a r k s. Our collection contains a single specimen (PIN, no. 4925/48: Pl. 7, fig. 2), which has a somewhat more convex shell (T/L = 0.41) than other specimens studied (0.20–0.30). If this character alone is taken into account, this specimen could have been assigned to *Q. (Q.) nodosa mangyschlakensis*. However, other morphological features of this specimen are within the range of the variability of *Q. (Q.) nodosa orbignyana*. Furthermore, the locality near the village of Gorlinka on the Kuchuk-Karasu River (central Crimea), from which the above specimen was recovered, yielded other shells, which were normally convex. As it is mentioned in the section *Variability*, *Q. (Q.) nodosa orbignyana* has a high degree of individual variability, including the convexity.

T a p h o n o m y   a n d   p a l e o e c o l o g y. Shells of this subspecies come mainly from the Valanginian sandstones occurring in the basins of the Bodrak, Beshterek, and Zuya rivers. Some specimens were found in the blocks of sandstone and finely pebble conglomerates (basin of the Kuchuk-Karasu River) in the redeposited state. In places (Dlinnaya and Patil' mountains), these shells are found in coquinas. All specimens collected are isolated valves and their fragments. The localities on Patil' Mountain and in the vicinity of the village of Trudolyubovka contain mostly imprints. The valves of the individuals of different age are especially well preserved in the lenses of sandstones–coquinas in the Zuiskii Quarry.

Because the collection does not contain shells allowing the study of the complete internal structure of the posterior part of valves (siphonal ridge in particular), we can only speculate on the lifestyle of this species. The absence of the pallial sinus suggests that mollusks were shallow burrowers. It is likely that their ecology was similar to that of the morphologically similar trigoniids. Saveliev's (1958, p. 29) hypothesis that *Quadratotrigonia* "certainly did not burrow, but moved on the sea bottom", and that "in some periods of life, some of them possibly attached by byssus to objects on the bottom" cannot be either denied nor supported, because the collection does not contain the shells with intact two valves, and the presence or absence of a byssal gape in these shells remains unclear. The byssal gape was observed by Saveliev (1958, pl. 25, fig. 1b) in one shell of *Q. (Q.) nodosa* var. *orbignyana* from the Lower Aptian of western Turkmenistan, based on which he assigned this species to byssal mollusks. I am somewhat doubtful about this conclusion.

O c c u r r e n c e. Valanginian–Aptian: Lower Valanginian–Lower Hauterivian of the southwestern Crimea (basin of the Bodrak River: Patil' and Dlinnaya mountains, village of Trudolyubovka), and central Crimea [Beshterek River, village of Mazanka; Zuya–Burul'cha interfluve: Zuiskii Quarry; also found on the Kuchuk-Karasu River (village of Gorlinka) in the redeposited state]; Hauterivian–Barremian of the northern Caucasus; Lower Aptian of western Turkmenistan; Valanginian–Aptian of France; Hauterivian of Germany and Sardinia; Upper Barremian–Aptian of southern England; Hauterivian–Aptian of Switzerland; Aptian of Spain and Bulgaria.

M a t e r i a l. Twenty-two specimens: nine LV, five RV, five fragments of valves, and three imprints.

Subfamily Iotrigoniinae Saveliev, 1958

Genus *Iotrigonia* Hoepen, 1929

Iotrigonia: Hoepen, 1929, p. 6; Crickmay, 1932, p. 17; Saveliev, 1958, p. 108; 1960b, p. 97; Yanin, 1958, p. 134; 1960, p. 207; Cox, 1969b, p. N481; Bogdanova, 1983, p. 86.

T y p e   s p e c i e s. *Iotrigonia crassitesta* Hoepen, 1929; Lower Cretaceous; southwestern Africa, Zululand.

D i a g n o s i s. Shell elongated oval, oval-triangular, boat-shaped, or pear-shaped, often with extended rostriform posterior margin. Flank with two systems of costae: thin concentric costae in anterior region and thickened oblique and straight costae in posterior region of flank. Both systems of costae meet at acute angle in mid-flank, forming V-shaped pattern. Costae often replaced by rows of tubercles. Area narrow, flattened, smooth, except for umbonal region. Marginal and escutcheon carinae well developed, with tubercles, occasionally replaced by rounded carina-like bends.

Median groove variously developed. Escutcheon narrow to wide, flattened or weakly concave. Umbo moderately high, triangular, weakly or moderately shifted anteriorly, with thin ornamentation. Hinge plate broadly triangular. Teeth moderately divergent. Apex of tooth 2 straight.

Species composition. The Lower Cretaceous of Eurasia contains *Iotrigonia abichi* (Anthula, 1899), *I. jakshysaurensis* (Luppov, 1932), *I. naltschikensis* (Mordvilko, 1949), *I. robinaldina* (d'Orbigny, 1843–1847), and *I. scapha* (Agassiz, 1840).

Comparison. Only one genus is known from the subfamily.

Occurrence. Upper Jurassic–Upper Cretaceous. Cosmopolitan.

Iotrigonia scapha (Agassiz, 1840)

Plate 7, figs. 6–8

Trigonia scapha: Agassiz, 1840, p. 15, pl. 7, figs. 17–20; Pictet and Campishe, 1864–1867, p. 367, pl. 128, figs. 6 and 7; Woods, 1900, p. 73; Litchkov, 1912, p. 104, pl. 12, fig. 2 (non fig. 1); Mordvilko, 1949, p. 128, pl. 22, fig. 1.

Trigonia (Clavotrigonia) scapha: Gerasimov, 1955, p. 54, pl. 3, figs. 4 and 5.

Iotrigonia scapha: Yanin, 1958, p. 134, pl. 1, fig. 5; 1960, p. 207, pl. 21, figs. 2 and 3; Bogdanova, 1983, p. 86, pl. 16, fig. 11; pl. 19, figs. 7 and 8.

Iotrigonia scapha transcaspia: Saveliev, 1958, p. 269, pl. 29, figs. 1–6.

Lectotype. Specimen figured by Agassiz (1840, pl. 7, fig. 20); mold of a left valve, with partially preserved costae; Lower Cretaceous, Neocomian; Switzerland, vicinity of Neuchâtel. Designated by Saveliev (1958, p. 273).

Description (Fig. 28f). The shell is medium-sized, oval-triangular in outline, inequilateral, slightly extended posteriorly, moderately convex. The umbo is triangular, with the umbo slightly opisthogyre. The anterior margin is strongly convex. It continues into the weakly convex ventral margin along a steep but stepless curve. The posterior margin is obliquely truncated, meeting the ventral margin at a sharply rounded bend. The dorsal margin is short and straight. It forms a distinct obtuse angle with the posterior margin. The valve margins are smooth from the inside.

The flank is usually completely covered by costae and tubercles. The umbonal region possesses several continuous, smooth, even, asymmetrical subconcentric costae. On the umbo, the costae are weakly curved in a V-shaped manner, while at the mid-flank, they are bent more strongly to form an acute angle between the anterior and posterior branches. Approximately in the dorsal third of the flank, the costae are interrupted, which led to two series of ornamentation, antecarinal and subconcentric. The antecarinal costae, extending downwards from the marginal carina, are short, smooth, sparsely spaced, coarse, in places inflated, separated by wide concave intercostal spaces. They have large rounded tubercles near the ventral margin and are sometimes separated from the marginal carina by a narrow antecarinal strip. The subconcentric costae in the anterior part of the flank are only seen on the anterior margin (frontal costae). They are short, smooth, rounded, symmetrical. These costae become weaker near the margin, which they do not reach, forming a smooth marginal strip, which is especially distinct in the umbonal region. In the anteroventral part of the flank, the costae are replaced by oblique or subconcentric rows of small, smooth, elongated oval tubercles, which are occasionally fused together. Generally, the series of subconcentric and the series of oblique anterocarinal elements of ornamentation meet in the mid-flank to form a V-shaped pattern (Fig. 28f). The posterior part of the field is covered only by the antecarinal costae and tubercles occurring on their continuation.

The area is narrow, flattened, smooth in the middle and posterior parts, but with obliquely transverse costellae near the umbo. Their number is usually the same as the number of antecarinal costae of the flank. The median groove is pronounced, in the shape of a weakly concave narrow depression.

The marginal and escutcheon carinae are well developed, straight, or weakly curved. They possess small, sparsely spaced tubercles. In the umbonal region, there are corresponding meeting points of the costae of the flanks and of the area. The escutcheon is narrow and flattened. The nymph is massive and ridgelike.

The hinge plate is relatively wide and low. Hinge: on the left valve (Pl. 7, fig. 8b), tooth 2 is high, narrowly split, with a straight apex (its length and width 7 mm); the dental angle is 50°; tooth 4a is in the shape of a well-delineated sharp ridge (6 mm long); tooth 4b is in the shape of a weakly delineated long ridge (9 mm long). Other elements of the shell interior were not observed.

Dimensions in mm and ratios:

Specimen PIN, no.	L	H	T	H/L	T/L	FL	AR	AR/FL
4925/50 (RV)	35	28	10	0.80	0.28	24	10	0.41
4925/51 (LV)	39	33	10	0.84	0.25	25	11	0.44

Comparison. This species is distinguished from *I. jakshysaurensis* from the Lower Cretaceous of Mangyshlak by the absence of inflation in the anterior part of the shell, lesser height, more weakly curved carinae, which often possess small tubercles (in *I. jakshysaurensis*, the carina-like bends are always smooth), presence of the subconcentric costae, or rows of tubercles in the anterior part of the flank (in *I. jakshysaurensis*, a considerable part of the flank is smooth at adults stage). It differs from *I. naltschikensis* from the Barremian of the northern Caucasus in the smaller size, tapering posterior margin, frequent development of subconcentric costae in the flank (in *I. naltschikensis*, the flank usually possesses rows of tubercles), more pronounced carinae possessing small tubercles (in

I. naltschikensis, the carina-like bends are wider, more strongly rounded, and smooth).

Remarks. The Crimean specimens of *I. scapha* are distinguished from the typical French (Pictet and Campiche, 1864–1867) and Mangyshlak (Saveliev, 1958) specimens by the shorter shell, subtriangular in outline, and less expressed V-shaped pattern of ribbing on the flank. They are also different from the Mangyshlak specimens in the absence of the rostriform extension of the posterior margin, presence of small tubercles on the carinae, and also in the absence of regular subconcentric costae in the anterior part of the flank (tubercles are usually developed in this region).

Taphonomy and paleoecology. The material studied comes from the shallow-water fine-grained sandstones with abundant shell debris and rare quartz pebbles. All valves are isolated. All this indicates a high energy environment in the place of burial of the shell remains. It is possible that *I. scapha*, like other mollusks similar in shell shape and ornamentation, was a burrower. The presence of a median groove indicates the presence of siphonal ridge separating the inhalant and exhalant siphons. The short shell and the absence of the pallial sinus suggest that these mollusks were shallow burrowers.

Occurrence. Berriasian–Hauterivian: upper part of the Lower Berriasian of central Crimea (Beshterek River: village of Solov'evka), and on the Tonas River (village of Golovanovka) redeposited in the Barremian conglomerates; Berriasian of the Russian Platform (Ryazan Region); Hauterivian of the northern Caucasus and Mangyshlak; Valanginian–Hauterivian of Switzerland.

Material. Five specimens: two LV and three RV.

Subfamily Rutitrigoniinae Hoepen, 1929

Genus *Rutitrigonia* Hoepen, 1929

Rutitrigonia: Hoepen, 1929, p. 31; Crickmay, 1932, p. 443; Saveliev, 1958, p. 115; 1960b, p. 97; Yanin, 1960, p. 208; 1979a, p. 26; 2004, p. 28; Cox, 1969b, p. N487.

Type species. *R. peregrina* Hoepen, 1929; Lower Cretaceous; South Africa, Zululand.

Diagnosis. Shell elongated oval. Flank with regular, rounded, smooth, nontuberculate, even along entire length, subconcentric costae. Costae usually disappearing near carina-like bend. Area narrow, weakly convex and smooth, excluding umbonal region. Marginal and escutcheon carina-like bends smooth, developed to various extents. Median groove narrow, filiform. Escutcheon narrow, smooth, flattened, or weakly concave. Umbo low, wide, shifted anteriorly, always with fine ornamentation. Hinge plate narrow, elongated. Teeth widely divergent. Apex of tooth 2 strongly curved upwards. Shell margins smooth inside.

Species composition. The Cretaceous of Eurasia contains *R. balaklavensis* Yanin, 2004; *R. coquandiana* (d'Orbigny, 1843–1847), *R. costatissima* Petter-Receveur, 1955, *R. eccentrica* (Parkinson, 1811), *R. laeviscula* (Lycett, 1872–1879), *R. longa* (Agassiz, 1840), *R. sanctaecrucis* (Pictet et Campiche, 1864–1867).

Comparison. Only one genus is known from this subfamily.

Remarks. In my opinion, the subspecies *R. longa costatissima* described by Petter-Receveur (1955) from the Albian of southern France is morphologically very distinct from the typical *R. longa* (see below). In addition, it is found stratigraphically higher. Therefore, I suggest that it represents a separate species *R. costatissima*.

Occurrence. Upper Jurassic (Kimmeridgian)–Upper Cretaceous. Cosmopolitan.

Rutitrigonia longa (Agassiz, 1840)

Plate 7, fig. 9; Plate 8, figs. 1–12

Trigonia longa: Agassiz, 1840, p. 47, pl. 8, fig. 1; D'Orbigny, 1843–1847, p. 130, pl. 285, figs. 1–6; Pictet and Renevier, 1855–1858, p. 102, pl. 14, fig. 3; Cossmann, 1916, p. 411, pl. 15, figs. 12–14.

Megatrigonia (Rutitrogonia) longa: Cox, 1952, p. 55.

Rutitrigonia longa: Yanin, 1960, p. 208, pl. 21, fig. 1; 1979a, p. 26, pl. 2, figs. 4–6.

Trogonia lajoyei: Deshayes in Leymerie, 1842, p. 7, pl. 8, fig. 4.

Holotype. Specimen figured by Agassiz (1840, pl. 8, fig. 1; mold of the right valve); Lower Cretaceous, "Neocomian"; Switzerland, vicinity of Neuchâtel. Designated by monotypy.

Description (Figs. 27e, 28g, 30e, 30f). The shell is medium-sized, oval-elongated in outline, inequilateral, slightly extended posteriorly, moderately convex. The umbo is low and wide. The umbo hangs over the dorsal margin, almost fusing with it. The umbonal angle is approximately 105°. The anterior margin is strongly and evenly convex, continuing into the weakly convex ventral margin along a steep curve. The posterior margin is weakly convex and obtusely rounded. The dorsal margin is long, weakly concave or, less frequently, straight. The margins are smooth from inside.

The flank has 15–20 almost symmetrical, smooth ridgelike, rounded, subconcentric costae. All costae, except for the lowest ones, extend onto the anterior margin (Fig. 28g). Sometimes, near the anterior margin, the costae become sinuous. In the upper and middle parts of the anterior margin, the costae are almost perpendicular to this margin. Almost all costae reach the marginal carina-like bend; however, sometimes near the posterior margin, they become smoother, or disappear (Fig. 28g). The intercostal spaces are smooth, flattened, or weakly concave. They are as wide as the costae, or slightly wider.

The area is narrow (a third of the flank), weakly convex, sometimes flattened near the posterior margin, smooth in the middle and posteriorly, but always covered with small, thin obliquely transverse costellae in the umbonal region. Each costella is a continuation of a corresponding costa in the flank. The point where they meet on the marginal carina-like bend sometimes has a

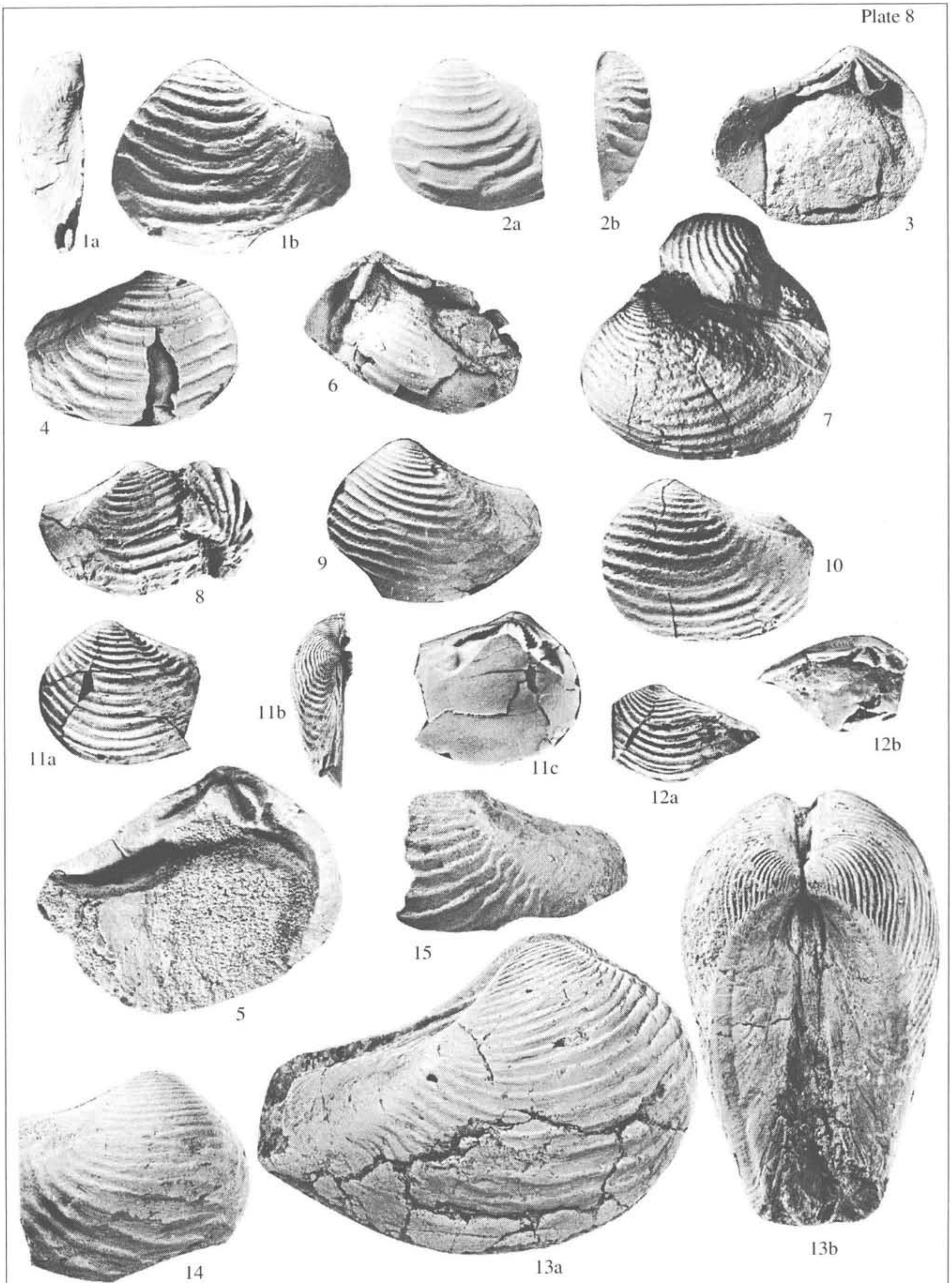


Plate 8
1a
1b
2a
2b
3
4
6
7
8
9
10
11a
11b
11c
12a
12b
5
15
13a
13b
14

chevron-like pattern, especially distinct in the umbonal region (Pl. 8, fig. 11b). The median groove is narrow, filiform, and often hardly noticeable. The escutcheon is narrow, weakly concave, and smooth or, less frequently, possesses terminations of the obliquely transverse costellae of the area, which enter it near the umbo. The nymph is distinct and ridgelike.

The marginal and escutcheon carina-like bends are weakly developed, especially in the posterior zone of the valves. Sometimes, they are only delineated by the change in ornamentation running across them, or by the disappearance of the ornamentation (Fig. 28g).

The hinge plate is narrow and elongate. Hinge: on the left valve, tooth 2 is low, widely split, with strongly elevated apex (the apex is often on a level with the dorsal margin). Tooth 2 is 5 mm long and 8 mm wide. The dental angle is 60° (Pl. 8, fig. 11c; Fig. 30e). Tooth 4a (5.5 mm long) is in the shape of a separated sharp ridge. Tooth 4b has an appearance of an elongated, often indistinct ridge. In poorly preserved specimens, the apex of the tooth is usually fused into the valve margin, and, in this case, it is only discernible by the dental notches. On the right valve (Pl. 8, fig. 6; Fig. 30f), tooth 3a (6 mm long) is almost straight. Its apex is almost completely fused with the umbo. Tooth 3b (8 mm long) is weakly curved, parallel to the dorsal margin. The dental angle 3a–3b is 80°. The distance between the tooth ends is 13 mm. The dental buttress on the left valve is robust, ridgelike, somewhat thickened posteriorly (Pl. 8, fig. 11c).

The anterior adductor scar is elongated oval in outline, almost parallel to the upper part of the anterior margin. It lies on the concave myophore, which is bordered basally by the myophorous buttress (Figs. 30e, 30f). The anterior retractor scar is deep, located in a socket, immediately below 4a on the left valve and anteriorly of the termination of 3a on the right valve.

The posterior adductor scars are superficial on both valves, larger than the anterior adductor scars. They lie immediately next to the dental buttress, anteriorly deepened in the shell wall. The upper side of the scars is straight, parallel to the dorsal margin of the valve. It forms distinct angle with the anterior and posterior sides of the scars. The lower side of the scar is rounded (Fig. 30e). The posterior retractor scar is shallow, in the shape of an oval depression, lying near the termination of the thickened dental buttress. It is separated from the posterior adductor scar by a distinct elevation, which is a continuation of the dental buttress. The remaining elements of the shell interior were not observed.

Dimensions in mm and ratios:

Specimen no.	L	H	T	H/L	T/L	FL	AR	AR/FL
PIN, no. 4925/58 (LV)	38	28	9	0.73	0.23	22	11	0.50
PIN, no. 4925/59 (LV)	37	28	10	0.75	0.27	24	10	0.40
PIN, no. 4925/53 (RV)	39	28	10	0.71	0.23	25	9	0.36
MZ MGU, no. 39/5 (LV)	42	32	10	0.76	0.23	–	–	–
MZ MGU, no. 39/6 (LV)	43	35	13	0.91	0.30	32	10	0.31

Comparison. This species is distinguished from *R. sanctaecrucis* from the Valanginian of Switzerland by the more sparsely spaced, coarser subconcentric costae in the flank, which approach the anterior margin at a right angle (in *R. sanctaecrucis,* these costae are almost concentric), by the absence of costae near the posterior margin in the flank and area. It differs from *R. eccentrica* from the Aptian of southern England in the more strongly elongated shell, more sparsely spaced, coarser costae covering the entire flank, in the presence of the distinct escutcheon carina-like bend. It is different from *R. laeviscula* from the Aptian of southern England in the presence of obliquely transverse costellae on the area in the umbonal region, and in that the subconcentric costellae of the flank almost always reach the marginal carina-like bend (in *R. laeviscula*, the posterior part of the flank is smooth). It is distinguished from *R. coquandiana* from the Cenoma-

Explanation of Plate 8

Figs. 1–12. *Rutitrigonia longa* (Agassiz): (1) MZ MGU, no. 39/6, left valve with a broken off posteroventral margin: (1a) upper (umbonal) view, (1b) external view; southwestern Crimea, Bel'bek River, Kabanii Gully; Lower Berriasian, alternating rock series, *dalmasi* Zone (Section no. 4, Bed 1); coll. by B.T. Yanin in 1959; (2) MZ MGU, no. 39/4, left valve with a broken off posterior margin; (2a) external view, (2b) anterior view; the same locality; (3) MZ MGU, no. 39/5, left valve, internal view; the same locality; (4) PIN, no. 4925/53, right valve, external view; the same locality; (5) PIN, no. 4925/54, left valve, internal view, ×2; (6) PIN, no. 4925/55, right valve, internal view; basin of the Bel'bek River, Tamish Grove (east of the village of Kuibyshevo) (Outcrop no. 7), the same age; (7) PIN, no. 4925/56, two left valves, external view, ×1.5; southwestern Crimea, Malyi Salgir River, village of Ivanovka; Lower Berriasian, alternating rock series (Section no. 18, Bed 2); coll. by B.T. Yanin in 1975; (8) PIN, no. 4925/57, right valve, external view (the anterior part of this valve is cemented together with the left valve of *Pterotrigonia caudata* (Agassiz); the same locality; (9) PIN, no. 4925/58, left valve with a broken off anteroventral margin, external view; the same locality; (10) PIN, no. 4925/59, left valve, external view; the same locality; (11) PIN, no. 4925/60, left valve with a broken off posterior margin: (11a) external view, (11b) upper (umbonal) view, (11c) internal view; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); coll. by B.T. Yanin in 1989; (12) PIN, no. 4925/61, fragment of a deformed left valve; (12a) external view, (12b) internal view; the same locality; coll. by B.T. Yanin in 1987.

Figs. 13–15. *Rutitrigonia balaklavensis* Yanin: (13) holotype, PIN, no. 4925/3, complete shell: (13a) external view, right valve, (13b) area view; southwestern Crimea, northern vicinity of the town of Balaklava, limestone quarry, eastern wall, clay with nodules; Middle Albian, *dentatus* Zone (Outcrop no. 1); collected by E.Yu. Baraboshkin in 1997; (14) PIN, no. 4925/4, right valve, with broken off posterior margin, external view; Chernaya River, village of Verkhnee Chernorech'e; Middle Albian, *dentatus* Zone; collected by V.M. Tseisler in 1957; (15) PIN, no. 4925/5; fragmentary left valve, external view; the same locality.

nian of France by the broader, obtusely rounded posterior margin of the shell (in *R. coquandiana*, it is acute), and by the absence of the auxiliary costae in the intercostal spaces on the flank.

R e m a r k s. The Crimean specimens of *R. longa* are different from the typical Western European adult shells of this species in their somewhat shorter shell, more pronounced area, which is bounded on two sides by carina-like bends, in the more sparsely spaced, coarser costae on the flank. Agassiz (1840, p. 47), who described *R. longa* based on a single specimen (mold) noted that "no ornamentation is seen in it." D'Orbigny later disputed Agassiz's assignment of this species to the group of Laevigatae (smooth trigoniids) and noted that the illustration of the mold in Agassiz's paper (1840, pl. 8, fig. 1) "shows that there is some indication of costae" (d'Orbigny, 1843–1847, p. 131). When describing this species, he noted "noticeable coarse longitudinal costae not parallel to growth striae" (d'Orbigny, 1843–1847, p. 130).

T a p h o n o m y a n d p a l e o e c o l o g y. The degree of ribbing in the umbonal region of the area depends primarily on the preservation of the shell. In leached and rounded shells, this ribbing completely disappears. In most cases, the valves of the Crimean *R. longa* are found isolated. This is apparently due to the re-washing of shells from the sediment. The separation of the valves in this case happened quickly, because the hinge in the valves is strongly elongated parallel to the dorsal margin, and the apex of tooth 2 is strongly curved upwards, which made the separation of the valves easier. Specimens PIN, no. 4925/52 (Pl. 7, fig. 9) and no. 4925/56 (Pl. 8, fig. 7) show shell pavements formed by the isolated valves with long axes oriented horizontally. This suggests high-energy wave turbulence in the place of the valve burial.

At the same time, the collection contains specimen PIN, no. 4925/55 with two intact, although weakly displaced valves. This may indicate that after death, the mollusk was completely covered by the sediment. The siphons in these animals were short, because the shell lacked a posterior gape and a pallial sinus, facts suggesting that they were shallow burrowers. The posterior end of the shell was on a level with the sediment surface. The occurrences of *R. longa* with closed valves are also known from the Neocomian of southern France (d'Orbigny, 1843–1847, pl. 285, figs. 1–6) and the Aptian of Switzerland (Pictet and Renevier, 1855–1858, pl. 14, fig. 3).

O c c u r r e n c e. Berriasian–Aptian: upper part of the Lower Berriasian in the southwestern Crimea (basin of the Bel'bek River: village of Golubinka, Tamish' Grove; basin of the Malyi Salgir: village of Ivanovka) and the Lower Valanginian of the central Crimea (Zuya–Burul'cha interfluve: Zuiskii Quarry); in the central Crimea (Kuchuk-Karasu River: village of Gorlinka, the shells of this species were found in the redeposited state in the Barremian conglomerates); Berriasian of the northern Caucasus; Valanginian–Hauterivian of Armenia; Valanginian–Aptian of France and Switzerland; Aptian of Spain; Lower Cretaceous of South America.

M a t e r i a l. Sixteen specimens: 14 LV and two RV.

Rutitrogonia balaklavensis Yanin, 2004

Plate 8, figs. 13–15

Rutitrigonia balaklavensis: Yanin, 2004, p. 28, pl. 3, figs. 3–5.

H o l o t y p e. PIN, no. 4925/3, complete shell (Yanin, 2004, pl. 3, fig. 3); southwestern Crimea, vicinity of the town of Balaklava; Middle Albian, *dentatus* Zone.

D e s c r i p t i o n. The shell is medium-sized, elongated oval in outline, inequilateral, strongly extended posteriorly, and moderately convex. The umbo is low and wide. The umbo hangs over the dorsal margin, almost merging with it. The umbonal angle is 110°. The anterior margin is evenly convex, gently continues into the weakly convex ventral margin. The dorsal margin is long and weakly concave. The posterior margin is obtusely rounded. The margins are smooth from inside.

The flank has 25–34 slightly asymmetrical, smooth, ridgelike, rounded subconcentric costae. In the umbonal region, all costae reach the anterior margin, retaining their regular linear shape. In the middle of the flank and especially near the ventroanterior margin, the costae usually become zigzagging, sometimes becoming stepped (Pl. 8, fig. 14) and are strongly smoothened. The lowest costae often terminate near the anteroventral and even ventral margin (Pl. 8, fig. 13a). All costae come close to the marginal carina-like bend. In the umbonal region, they approach at an acute angle; in the middle part, at a right angle, often becoming characteristically curved with their convex side forward (PL. 8, fig. 15). Near the posterior margin, costae do not become smoothened and do not disappear. The intercostal spaces are smooth, flattened, or weakly concave. Their width is equal to that of the costae in the umbonal region and wider than those in the remaining part of the flank.

The area is narrow (a third of the flank), weakly convex, posteriorly flattened, entirely smooth, except in the umbonal region. The median groove is well developed, narrow, and filiform. The escutcheon is narrow, weakly concave, and smooth. The marginal and escutcheon carinae are weakly pronounced, especially posteriorly. Other elements of the shell exterior and interior were not observed.

D i m e n s i o n of the holotype (PIN, no. 4925/3 in mm and ratios: L > 50; H, 37; FL, 34; AR, 10; AR/FL, 0.3.

C o m p a r i s o n. The species described is most similar in the shell outline and size to *R. laeviscula* and *R. eccentrica* from the Aptian of England. It differs from the former in the more elongated shell, presence of costae in the entire flank (in *R. laeviscula*, costae become smoothened and disappear near the posterior margin and the marginal carina-like bend), in the presence of the stepped curvature of some costae near the anteroventral margin. It is distinguished from *R. eccentrica* by the smooth area (in *R. eccentrica*, the area is covered by transverse costellae, which are continuations of the costae of the flank), and by the stepped–curved costae near the anteroventral margin.

The species described is different from *R. longa* in the larger size, presence of the stepped curvature of some costae in the flank, presence of the peculiar sharp curvature of some costae on the flank near the marginal carina-like bend.

R. balaklavensis is very similar in its shell exterior and size to *R. costatissima* from the Albian of southern France, but differs in the presence of the stepped curvature of the costae on the flank near the anteroventral margin of the shell and in the curvature of some costae in the middle part of the flank when they approach the marginal carina-like bend.

O c c u r r e n c e. Middle Albian of the southwestern Crimea (vicinity of the town of Balaklava; basin of the Chernaya River: village of Verkhnee Chernorech'e).

M a t e r i a l. Three specimens: apart from the holotype, one RV with a broken off posterior margin and one fragment of LV with ornamentation preserved on the flank.

Subfamily Pterotrigoniinae Hoepen, 1929

Genus *Pterotrigonia* Hoepen, 1929

Pterotrigonia: Hoepen, 1929, p. 9; Crickmay, 1932, p. 444; Saveliev, 1958, p. 116; 1960b, p. 97; Yanin, 1958, p. 134; 1979a, p. 27; 2004, p. 29; Casey, 1961, p. 577; Nakano and Numano, 1961, p. 90; Cox, 1969b, p. N487; Bogdanova *et al.*, 1997, p. 83.

Trigonia: Renngarten, 1926, p. 72 (pars); Mordvilko, 1949, p. 127 (pars).

T y p e s p e c i e s. *P. cristata* Hoepen, 1929; Middle Cretaceous; South Africa, Zululand.

D i a g n o s i s. Shell from winglike to pearlike and crescent-shaped in outline, strongly expanded and inflated anteriorly, and narrowed, flattened, and rostriform posteriorly, with high, pointed, and prominently opisthogyre umbo. Flank with oblique costae, smooth, or tuberculate, often sharply widened in mid-flank. In some specimens, oblique costae near anteroventral margin replaced by subconcentric costae. Area very narrow, smooth, or with obliquely transverse costellae, in shape of two ridgelike strips separated from one another by median groove. True carinae absent. Hinge plate narrow, high, obliquely triangular. Hinge asymmetric: teeth 2 and 3b strongly curved backwards. Siphonal gape often well developed. Shell margins notched from inside by terminations of costae.

S p e c i e s c o m p o s i t i o n. The Lower Cretaceous of Eurasia contains *P. aliformis* (Parkinson, 1811), *P. caudata* (Agassiz, 1840), *P. cubanica* Saveliev, 1958, *P. druzczici* Yanin, 2004, *P. etheridgei* (Lycett, 1872–1879), *P. gokderensis* Saveliev, 1958, *P. hemilunaris* Saveliev, 1958, *P. klytschevae* Saveliev, 1958, *P. mantelli* Casey, 1961, *P. piriformis* (Mordvilko, 1932), *P. scabricola* (Lycett, 1872–1879), *P subaliformis* Saveliev, 1958, *P. subpiriformis* Saveliev, 1958, *P. tatianae* Saveliev, 1958, *P. taurica* Yanin, 2004, and *P. vectiana* (Lycett, 1872–1879).

C o m p a r i s o n. This genus is distinguished from *Scabrotrigonia* Dietrich, 1933 by the degree of inflation and elongation of the shell, which is more convex, often inflated anteriorly and very narrow and elongated, usually rostriform posteriorly. It is also different in the structure of the area, which has the appearance of two usually smooth convex strips (in *Scabrotrigonia*, the area is not developed, being replaced by a deep median groove, with costae running across this groove along its entire length).

O c c u r r e n c e. Lower and Upper Cretaceous. Cosmopolitan.

Pterotrigonia caudata (Agassiz, 1840)

Plate 9, figs. 1–14; Plate 15, fig. 1

Trigonia caudata: Agassiz, 1840, p. 32, pl. 7, figs. 11–13; D'Orbigny, 1843–1847, p. 133, pl. 287, figs. 1–6; Pictet and Renevier, 1855–1858, p. 97, pl. 13, fig. 1; Lycett, 1872–1879, p. 129, pl. 26, figs. 5–7; Karakash, 1897, p. 68, pl. 3, fig. 6; Woods, 1900, p. 81; Gillet, 1921, p. 9, pl. 1, figs. 1 and 2; Mordvilko, 1949, p. 130, pl. 24, figs. 4 and 5.

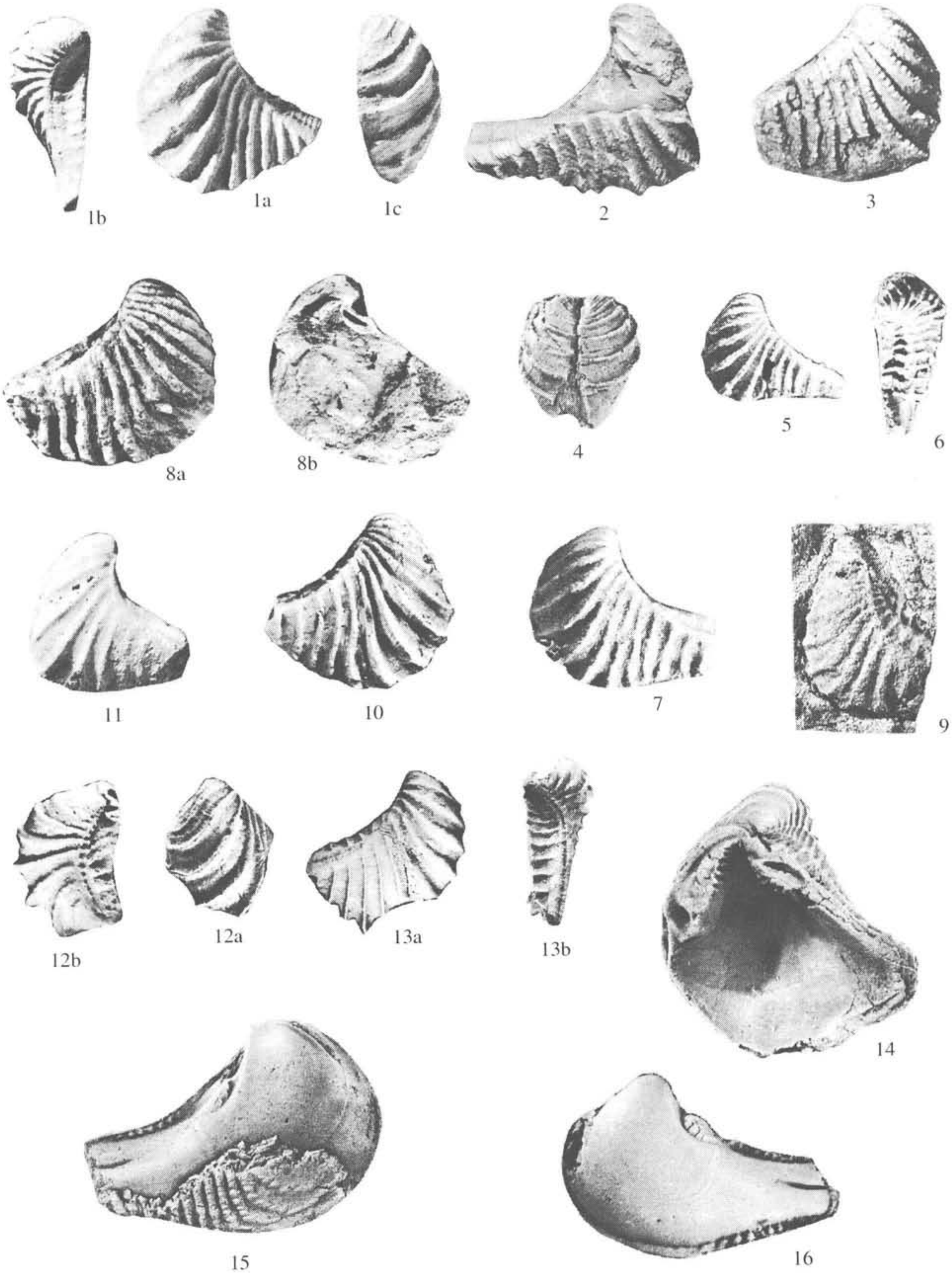
Pterotrigonia caudata: Saveliev, 1958, p. 323, pl. 39, figs. 4–8; Yanin, 1958, p. 134, pl. 1, figs. 6–8; 1960, p. 208, pl. 22, fig. 1–3; 1979a, p. 27, pl. 2, figs. 7–10; Prozorovsky, 1961, p. 139, pl. 14, figs. 3 and 4; Cox, 1969b, p. N487, text-fig. D73.6; Bogdanova *et al.*, 1997, p. 83, pl. 19, fig. 8.

L e c t o t y p e. Specimen figured by Agassiz (1840, pl. 7, figs. 11, 12, 13, mold of a shell); Switzerland, vicinity of Neuchâtel; Lower Cretaceous, "Neocomian." Designated by Saveliev (1958, p. 323).

D e s c r i p t i o n (Figs. 29g; 31c, 33a, 33b). The shell is medium-sized, winglike, strongly inequilateral, high and strongly convex, sometimes inflated in the anterior third, approximately along the line of its height, and strongly narrowed, rostriform posteriorly. The umbo is very high, usually narrow, opisthogyre, less frequently, straight, strongly shifted anteriorly. The umbonal angle is 76°–80°. The anterior margin is strongly convex, gently continuing into the ventral margin. The ventral margin is convex anteriorly and straight posteriorly. The dorsal margin is long and concave. The posterior margin is short, convex, with a siphonal gape. The shell margins are notched from inside.

The flank is very wide, with 17–20 oblique costae that are narrow, high, acute, ridgelike, weakly denticulated, sometimes with oblique hatching on the posterior slopes (the last two characters are only observable in well-preserved specimens). The costae become thicker (without abrupt inflation) towards the anterior and ventral margins. In the anterior part of the flank, the costae have equal slopes or, less frequently, they are weakly asymmetric. In the posterior part, they are always symmetric, thinner, straight, and usually smooth (Fig. 29g). When the valves are closed, the terminations of the cos-

Plate 9



tae on the flanks on both valves do not coincide on the anterior margin. The intercostal spaces are wide (two or three times wider than the costae), flattened, often (in well-preserved specimens) with low, wide, smooth median longitudinal elevations.

The area is very narrow, in a shape of two strongly curved parallel ridgelike elevations separated by a narrow, filiform median groove. These elevations are usually covered by sparsely spaced, thin, sharp, smooth transverse costellae, especially in the umbonal region (Fig. 29g). The escutcheon is long, concave, with obliquely transverse costellae, which are very long, smooth, and, less frequently, thinly dentate. The terminations of the costellae on the escutcheon form notches on the dorsal margin of the valve. The nymph is in the shape of a very short ridge.

The hinge plate is short and subtriangular. The dental apparatus was only examined in young specimens. The hinge of the left valve is well preserved in two specimens. In specimen PIN, no. 4925/85 (Fig. 33a; pl. 15, fig. 1), which is a fragment of the umbonal region of a young shell, tooth 2 is obliquely triangular, weakly split basally, with the upper termination weakly curved backwards. Its width is 2 mm. Each surface has seven notches. Tooth 4a (2 mm long) is weakly separated from the anterior margin and is parallel to it, with eight notches. Tooth 4b (2 mm long) has a crest well separated from the dorsal margin of the valve and possesses over five notches. Teeth 4a and 4b are positioned asymmetrically in relation to the vertical surface of tooth 2. The upper end of tooth 4b is strongly descended in comparison with the similar end of tooth 4a, which agrees with the strongly opisthogyre umbo of this valve. The socket for tooth 3a is wide (1 mm), while the socket for tooth 3b is narrow (slitlike) and elongated. The other specimen of the left valve (Pl. 9, fig. 12) has obliquely triangular tooth 2, with the upper part strongly curved backwards. Its width is 3 mm. Six notches are seen on the anterior surface of this tooth (the posterior surface is not preserved). Tooth 4a is ridgelike, weakly delineated from the anterior margin of the valve and possesses ten notches. Tooth 4b is completely decayed. On the right valve (Pl. 9, fig. 8b), teeth 3a (length 4 mm) and 3b (5 mm long) are thin, ridgelike, in the upper part, strongly curved backward and slightly dipping under the umbo. Tooth 3a is more weakly curved. Tooth 3b is arched (it was not possible to prepare the notches on the teeth). The socket for tooth 4a is narrow and almost straight, while the socket for tooth 4b is narrow, deep, curved almost parallel to the dorsal margin of the valve.

The anterior adductor scar was observed in specimen PIN, no. 4925/85 (Pl. 15, fig. 1) and no. 4925/66 (Pl. 9, fig. 12), but its surface in both cases was strongly decayed, resulting in the deep cavities bordered by the myophorous buttresses. The anterior retractor scar on the left valve (the same specimen) has an appearance of a shallow rounded depression.

The posterior adductor scar on the right valve (specimen PIN, no. 4925/67) is irregularly oval in outline, superficial, flattened, lies at a distance from the termination of the dental buttress, basally bordered by a distinct rounded myophorous buttress. The scar is 6 mm long and 5 mm wide. The posterior retractor scar is superficial, has an appearance of a shallow rounded depression, and is distinctly separated from the margin of the posterior adductor scar. The pallial line on the right valve extends from the posterior side of the posterior adductor scar, lacking a sinus. It is weakly and broadly convex towards the posterior margin, from which it is separated by a very wide strip. The siphonal ridge is only slightly developed near the broken posterior margin. It begins near the posteroventral side of the posterior adductor scar and has an appearance of a wide

Explanation of Plate 9

Figs. 1–14. *Pterotrigonia caudata* (Agassiz): (1) MZ MGU, no. 6/10, left valve: (1a) external view, (1b) escutcheon view, and (1c) anterior view; central Crimea, Kuchuk-Karasu River, village of Gorlinka; from a block of Valanginian sandstone, redeposited in the series of Barremian conglomerates (Outcrop no. 31); collected by B.T. Yanin in 1958; (2) MZ MGU, no. 7/10, right valve, external view; the same locality; (3) MZ MGU, no. 39/8, right valve with broken off posterior margin, external view; southwestern Crimea, Bel'bek River, vicinity of the village of Golubinka, Kabanii Gully; Lower Berriasian, alternating rock series, *dalmasi* Zone (Section no. 4, Bed 1); collected by B.T. Yanin in 1959; (4) PIN, no. 4925/62, complete shell, anterior view; the same locality; (5) MZ MGU, no. 39/7, left valve, external view; the same locality; (6) MZ MGU, no. 39/9, right valve, escutcheon view; the same locality; (7) MZ MGU, no. 39/10, mold of the left valve, external view; the same locality; (8) PIN, no. 4925/63, right valve: (8a) external view and (8b) internal view; central Crimea, Burul'cha River, village of Mezhgor'e, southern slope of Baksan Mountain; Upper Berriasian (marl member under bioherms) (Section no. 25, Bed 6); collected by B.T. Yanin in 1959; (9) PIN, no. 4925/64, mold of the left valve of a young individual, external view, ×2; Sarysu River, vicinity of the village of Blagodatnoe; Lower Berriasian, alternating rock series, *dalmasi* Zone (Section no. 26, Bed 1); (10) PIN, no. 4925/65, right valve, external view; southwestern Crimea, Malyi Salgir River, village of Ivanovka; Lower Berriasian, alternating rock series (Section no. 18, Bed 2); collected by B.T. Yanin in 1975; (11) MZ MGU, no. 8/10, mold of the left valve, external view; Bodrak River Basin, village of Prokhladnoe, Patil' Mountain; Lower Valanginian (Section no. 14, Bed 2); collected by students; (12) PIN, no. 4925/66, fragmentary anterior part of the left valve: (12a) external view and (12b) escutcheon view; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); collected by B.T. Yanin in 1989; (13) PIN, no. 4925/67, right valve with broken off anterior margin: (13a) external view and (13b) escutcheon view; the same locality; (14) PIN, no. 4925/68, right valve with broken off anterior, lower, and posterior margins, internal view, ×2; the same locality.

Figs. 15 and 16. *Pterotrigonia taurica* Yanin: (15) holotype, PIN, no. 4925/6, mold of the right valve with remains of the shell layer, external view; southwestern Crimea, Chernaya River, village of Verkhnee Chernorech'e; Middle Albian, *dentatus* Zone (Outcrop no. 2); collected by V.M. Tseisler in 1957; (16) PIN, no. 4925/7, mold of the left valve, external view; the same locality.

elevation. It lies immediately below the median groove of the area, between the two siphonal depressions. Other elements of the shell interior were not observed.

Dimensions in mm and ratios:

Specimen no.	L	H	T	H/L	T/L
MZ MGU, no. 39/7 (LV)	24	19	7	0.79	0.29
PIN, no. 4925/65 (RV)	~35	31	12	~0.88	~0.34
PIN, no. 4925/63 (RV)	~37	31	11	~0.82	~0.29
MZ MGU, no. 7/10 (RV)	43	33	20	0.70	0.50

Comparison. This species is distinguished from *P. aliformis* from the Aptian of southern England by its higher and sharper umbos, more strongly curved backwards, by the absence of strong inflations and bends of costae in the flank, by the narrower area, completely covered by transverse costellae. It differs from *P. etheridgei* from the Barremian of southern England in the smaller size of adult specimens, the lower and blunter umbos, the absence of a smooth strip on the posterior half of the flank between the upper terminations of the costae and area (in *P. caudata*, the costae tightly approach the area along the entire flank), occasionally, in the presence of small tubercles and oblique hatching on the oblique costae of the flank, and in the presence of transverse costellae on the area (in *P. etheridgei*, the area is smooth). It is distinguished from *P. scabricola* from the Aptian of southern England by the smaller size of adult shells, lower and less opisthogyre umbos, and by the narrower area, which usually has thin transverse costellae.

Variability. The degree of the shell elongation (rostriform appearance) ranges from 0.70 to 0.88.

Taphonomy and paleoecology. Most specimens studied are isolated valves. Many of these have a well-preserved shell with ornamentation. Fewer specimens are molds. The shell matrix in this case may be leached in the process of weathering (especially typically occurring in the Lower Valanginian sandy dolomites of Patil' Mountain). Almost all shells and mold of this species come from sandstones and siltstones, less frequently, from coquinas. Specimens from the Valanginian loosely cemented sands exposed in the Zuiskii Quarry are especially well preserved. In this locality, the specimens are only represented by isolated valves and their fragments that were mechanically reworked, but retained shell layers and ornamentation. These sands contained adult specimens and one young specimen (Pl. 15, fig. 1) with an excellently preserved hinge.

The presence of the siphonal gape in representatives of this species at the end of the posterior margin and the presence of the separating siphonal ridge suggest the presence of well-developed siphons. They were not very long, because the pallial line lacks any traces of a pallial sinus. Similar features are described from other specimens of this species found by different authors in various localities and at different stratigraphic levels (e.g., Lycett 1872–1879, pl. 26, fig. 6, a complete shell with a distinct siphonal gape). It is possible that individuals of *P. caudata* were shallow burrowers in the subsurface layers of sandy grounds. The terminations of their short siphons were on the surface of the ground. The inflated anterior part of the shell, often frontally flattened, helped anchoring in the sediment, while the elongated posterior (rostriform, or caudal) part of the shell supported siphons in the vertical position. The life position of *P. caudata* was similar to that reconstructed by Stanley (1977, p. 881, text-fig. 5) for the morphologically similar genus *Scabrotrigonia.*

Occurrence. Berriasian–Aptian: Lower Berriasian–Lower Hauterivian of the southwestern Crimea (basin of the Bel'bek River: village of Golubinka; Bodrak River: village of Prokhladnoe; Malyi Salgir River: village of Ivanovka) and of the central Crimea [Burul'cha River: village of Mezhgor'e; Sarysu River: village of Blagodatnoe; Zuya–Burul'cha interfluve: Zuiskii Quarry; Kuchuk-Karasu River: village of Gorlinka (redeposited in the block of Valanginian sandstone in the series of Barremian conglomerates)]; Lower Berriasian–Barremian of the northern Caucasus; Berriasian–Lower Aptian of Mangyshlak; Valanginian–Aptian of western Turkmenistan; Hauterivian–Barremian of Tajikistan; Valanginian–Aptian of France and Switzerland; Hauterivian of Germany; Hauterivian–Aptian of Tunisia and Morocco; Barremian of southern England; Barremian–Aptian of Bulgaria; Aptian of Spain; Neocomian of Portugal.

Material. Twenty-three specimens: one complete shell, three LV, five RV, and 14 molds, fragments, and imprints.

Pterotrigonia taurica Yanin, 2004

Plate 9, figs. 15 and 16

Pterotrigonia taurica: Yanin, 2004, p. 29, pl. 3, figs. 6 and 7.

Holotype. PIN, no. 4925/6; mold of the right valve (Yanin, 2004, pl. 3, fig. 6); southwestern Crimea, Chernaya River, village of Verkhnee Chernorech'e; Lower Cretaceous, Middle Albian (*dentatus* Zone).

Description. The shell is medium-sized, winglike in outline, and weakly convex. The umbonal angle is 80°. The anterior margin is strongly and evenly convex, gradually continuing into the straight ventral margin. The dorsal margin is long and weakly concave. The posterior margin is short and truncated. The dorsal and ventral margins are notched from inside.

The flank is very wide, covered with costae (preserved incompletely). The posterior half of the flank of adult shells has up to 10 or 11 costae. All costae are narrow, ridgelike, finely notched, straight, perpendicular to the ventral margin and forming notches on it. Five oblique costae are preserved in the mid-flank of the holotype. The costae gradually widen toward the ventral margin and are notched by small transverse scales. The costae extend downward from the area, but before reaching the ventral margin they gently turn forward, where they are parallel to the anteroventral margin of the valve (Pl. 9, fig. 15). The costae do not extend beyond this margin, which remains smooth (Pl. 9, fig. 16, mold). The tracing of the two preserved lower costae toward the anterior margin shows that they approach it obliquely. Thus, the shell has two types of ribbing (oblique and subconcentric). The intercostal spaces are smooth. In the posterior region, they are similar in width to the costae, while in the middle part, they are either equal to, or slightly wider than, the costae.

The area (judging from the molds of the left and right valves) is very narrow. It has the appearance of two ridgelike strips on the shell separated from one another by a deep median groove, especially distinct near the posterior margin (typical marginal and escutcheon carinae are absent). The escutcheon is wide and concave. The ornamentation on the area and escutcheon is not preserved, but, judging from the notched dorsal margin, it is possible to suggest that the escutcheon had thin transverse costellae (at least in its posterior half).

The anterior adductor scar is elongated oval and superficial. Its axis is almost parallel to the anterior margin of the valve. The posterior adductor scar is subquadrate in outline, deepened anteriorly and superficial posteriorly. It has differently oriented wrinkles.

The pallial line (Pl. 9, fig. 16) is at a large distance from the valve margins. It is gently curved anteriorly and approaches the lower side of the anterior adductor scar along a broad curve. Other elements of the shell exterior and interior were not observed due to an incomplete preservation of specimens.

D i m e n s i o n s in mm and ratios:

Specimen PIN, no.	L	H	T	H/L	T/L
Holotype, 4925/6 (RV)	~45	34	9	~0.70	~0.20
4925/7 (LV)	50	39	9	0.66	0.18

C o m p a r i s o n. The species described is distinguished from most species of the genus *Pterotrigonia* by two distinct features: (1) the presence of subconcentric costae on the flank and (2) the absence of notches on the inner surface of the anteroventral margin of the valves (in many *Pterotrigonia* species, these margins are notched by the terminations of oblique costae, which approach them straight, or at an angle).

This species differs from *P. piriformis* from the Upper Aptian of the northern Caucasus, which has a smooth anteroventral margin and a smooth anterior part of the flank, in the weak and regular convexity of the valves, more elongated shell, lesser shell height, and in the presence of subconcentric costae on the flank.

P. taurica shows the greatest similarity in the general shell shape and ribbing of the flank to *P. chivensis* (Arkh.) (Arkhangelsky, 1916, pl. 4, figs. 6, 8, 10; 1952, pl. 4, figs. 6, 8, 10) from the Cenomanian of western Turkmenistan. However, it is distinguished by the presence of subconcentric costae in the anteroventral part of the flank, which are immediately approach the ventral margin (in *P. chivensis*, the anteroventral part of the flank is smooth, because the costae disappear in this region), and by a more coarse dentation of oblique costae.

R e m a r k s. Although our collection contains only four specimens (molds of isolated valves) (only one specimen has a zone where ornamentation is preserved on the flank), I find it possible to establish a new species based on the characters, which make it very different from other species of *Pterotrigonia* (see above). A more complete characterization of the new species will require material of better preservation from the locality in the vicinity of the village of Verkhnee Chernorech'e.

T a p h o n o m y a n d p a l e o e c o l o g y. All specimens come from the coarse-grained sandstones containing abundant shell and plant debris, which indicates the coastal, highly dynamical environment of the molluskan habitat and burial. Because of the strong recrystallization of the shell layers, shells were easily broken while being separated from the densely cemented rock.

A deep siphonal groove on the molds, a strongly extended rostriform posterior end of the shell, and a considerable distance (almost up to mid-valve) of the pallial line from the posterior margin indicate the presence of a relatively long siphon, allowing relatively deep burrowing. In its life position, the shell was most likely oriented vertically.

O c c u r r e n c e. See Holotype.

M a t e r i a l. Four molds: two LV and two RV; out of these, two with a broken posterior margin; only the holotype has partly preserved ornamentation.

Subfamily Linotrigoniinae Yanin, subfam. nov.

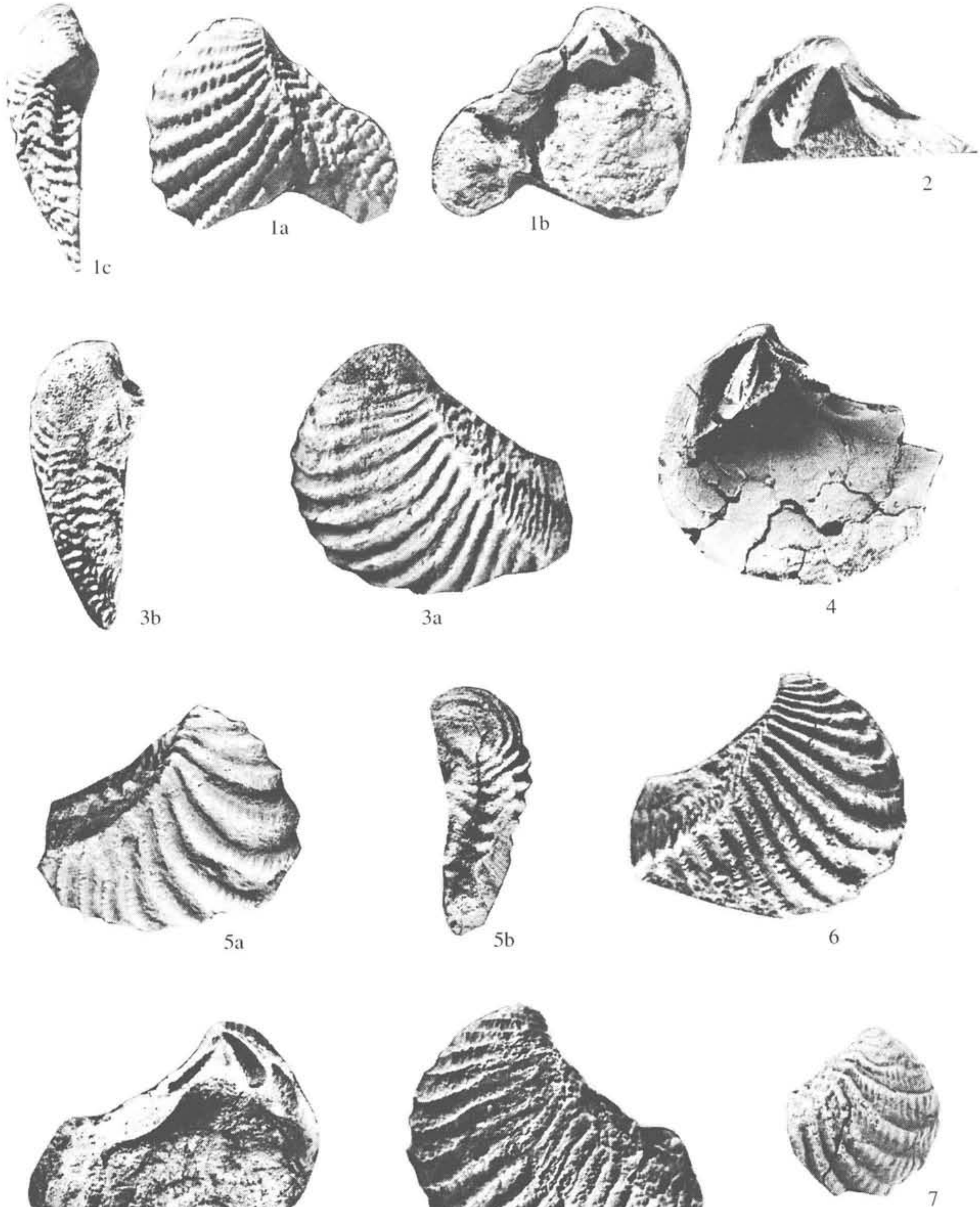
T y p e g e n u s. *Linotrigonia* Hoepen, 1929.

D i a g n o s i s. Shell from subtriangular to oval in outline, sometimes, with extended posterior margin. Flank with tuberculate and scaly, less frequently, smooth oblique costae. Posterior slopes of scaly costae often possess hatching. Area wide, flattened, or weakly convex, usually, with obliquely transverse, finely tuberculate, scaly costellae, sometimes, smooth near posterior margin. Marginal and escutcheon carinae well developed, usually linear, less frequently ridgelike. In most representatives, costae of flank and area usually correspond to each other and their terminations on marginal carina forming angular, chevronlike pattern. Escutcheon carina crossed by transverse costellae of area, or smooth and ridgelike. Escutcheon concave or weakly convex, usually with obliquely transverse costellae, oriented with their convexity upwards. Costellae present on entire escutcheon, or only in umbonal region.

C o m p o s i t i o n. One genus *Linotrigonia* Hoepen, 1929.

C o m p a r i s o n. Some representatives are similar to members of the subfamily Pterotrigoniinae in the shell outline and ribbing of the flank (the genus *Linotrigonia* was previously assigned to the Pterotrigonii-

Plate 10



nae) (Saveliev, 1958, 1960b, etc.). However, they are different from Pterotrigoniinae in the presence of a relatively wide, flattened or weakly convex area (in the Pterotrigoniinae, the area has a shape of two ridgelike strips), in the presence of distinct, normally linear marginal and escutcheon carinae, in the usually shorter and not winglike shell (in the Pterotrigoniinae, the shell is usually winglike, with a rostriform posterior margin), in the more evenly thickened costae on the flank, without abrupt inflations, in the presence of costae on the entire area and escutcheon in most representatives (in the Pterotrigoniinae, the area in adults is usually smooth), in the presence of a chevron pattern on the marginal carina at the points of meeting of the costae of the flank and area in most representatives.

Occurrence. Upper Jurassic–Upper Cretaceous.

Genus *Linotrigonia* Hoepen, 1929

Linotrigonia: Hoepen, 1929, p. 15; Crickmay, 1932, p. 445; Saveliev, 1958, p. 117; 1960b, p. 98; Yanin, 1958, p. 29; Cox, 1969b, p. N483; Leshchukh, 1987, p. 86; Bogdanova *et al.*, 1997, p. 83.

Trigonia: Renngarten, 1926, p. 72 (pars); Mordvilko, 1949, p. 127 (pars).

Type species. *L. linifera* Hoepen, 1929; Cretaceous; southern Africa, Zululand.

Diagnosis. See the diagnosis for the subfamily.

Composition. Two subgenera, *Linotrigonia* Hoepen, 1929 and *Oistotrigonia* Cox, 1952.

Comparison. The subfamily is monotypic.

Occurrence. Upper Jurassic–Upper Cretaceous. Cosmopolitan.

Subgenus *Oistotrigonia* Cox, 1952

Linotrigonia (Oistotrigonia): Cox, 1952, p. 60; 1969b, p. N483; Saveliev, 1958, p. 118; 1960b, p. 98; Yanin, 1979a, p. 29.

Oistotrigonia: Kobayashi and Tamura, 1955, p. 101.

Linotrigonia: Yanin, 1960, p. 209; Leshchukh, 1987, p. 86; Bogdanova *et al.*, 1997, p. 83.

Type species. *Trigonia spinosa* Parkinson, 1811; Lower Cretaceous; Upper Aptian of southern England. Subsequently designated by Cox (1952).

Diagnosis. Shell triangular–oval, oval, or semicircular, short, moderately, or weakly convex. Flank has densely spaced regular oblique costae possessing small tubercles, spines, or scales. Costae usually have oblique hatching on their posterior slopes. Area wide, usually flattened, with obliquely transverse costellae on its entire surface, less frequently, smooth in posterior part. Median groove distinct, narrow, and linear. Marginal carina sharp, always with ornamentation (costae of flanks and area meet to form chevronlike pattern). Escutcheon weakly convex, flattened, or weakly concave, always with obliquely transverse costellae. Umbo ranging from low to moderately protruding, opisthogyre, shifted to anterior margin. Shell margins notched from inside by terminations of costae.

Species composition. The Cretaceous of Eurasia contains *L. (O.) alekseitschiki* Saveliev, 1958, *L. (O.) archiaciana* (d'Orbigny, 1843–1847), *L. (O.) belbekensis* Yanin, 1979, *L. (O.) convexa* Saveliev, 1958, *L. (O.) crenulata* (Lamarck, 1801), *L. (O) crenulifera* (Lycett, 1872–1879), *L. (O.) divaricata* (d'Orbigny, 1843–1847), *L. (O.) dragunovi* Saveliev, 1858, *L. (O.) immutata* Saveliev, 1958, *L. (O.) ornata* (d'Orbigny, 1843–1847), *L. (O.) rectaespinosa* Saveliev, 1958, *L. (O.) spinosa* (Parkinson, 1811), *L. (O.) tamalakensis* Saveliev, 1958, *L. (O.) tenuispinosa* Saveliev, 1958, *L. (O.) upwarensis* (Lycett, 1872–1879), and *L. (O.) vicaryana* (Lycett, 1872–1879).

Comparison. This subgenus is distinguished from the subgenus *Linotrigonia* by the more closely spaced, usually, finely tuberculate, spiny, or scaly oblique costae of the flank, usually possessing oblique hatching (in *Linotrigonia*, these costae may be smooth, or tuberculate, and lack hatching), by the presence of obliquely transverse costellae on the area, or in its major surface (in *Linotrigonia* sensu stricto, the costellae of the area may disappear in adults).

Occurrence. Upper Jurassic (Kimmeridgian of Japan)–Lower and Upper Cretaceous. Cosmopolitan.

Linotrigonia (Oistotrigonia) belbekensis Yanin, 1979

Plate 10, figs. 1–8

Linotrigonia (Oistotrigonia) belbekensis: Yanin, 1979a, p. 29, pl. 2, figs. 11 and 12.

Linotrigonia (Oistotrigonia) cf. *belbekensis:* Bogdanova *et al.*, 1997, p. 84, pl. 19, fig. 7.

Holotype. MZ MGU, no. 39/11, left valve (Yanin, 1979a, pl. 2, fig. 11); southwestern Crimea, Bel'bek River, vicinity of the village of Golubinka (Kabanii Gully); Lower Cretaceous, Lower Berriasian.

Explanation of Plate 10

Figs. 1–8. *Linotrigonia (Oistotrigonia) belbekensis* Yanin: (1) holotype, MZ MGU, no. 39/11, left valve with broken off ventral margin: (1a) external view, (1b) internal view, and (1c) escutcheon view; southwestern Crimea, Bel'bek River, vicinity of the village of Golubinka, Kabanii Gully; Lower Berriasian, alternating rock series, *dalmasi* Zone (Section no. 4, Bed 1); collected by B.T. Yanin in 1956; (2) MZ MGU, no. 39/12, fragment of the umbonal region of the right valve, internal view; the same locality; (3) PIN, no. 4925/69, left valve: (3a) external view and (3b) area and escutcheon view; the same locality; (4) PIN, no. 4925/70, right valve, internal view; the same locality; (5) PIN, no. 4925/71, right valve: (5a) external view and (5b) escutcheon view; the same locality; (6) PIN, no. 4925/72, right valve, external view; Bel'bek River, vicinity of the village of Golubinka, Bezymyannyi Gully; Lower Berriasian, alternating rock series, *dalmasi* Zone (Section no. 6, Bed 3); collected by B.T. Yanin in 1963; (7) PIN, no. 4925/73, right valve with broken off lower and posterior margins, external view; the same locality; (8) PIN, no. 4925/74, left valve: (8a) external view and (8b) internal view; Bel'bek River Basin, vicinity of the village of Solnechnosel'e; Lower Berriasian, alternating rock series (Section no. 8, Bed 1); collected by V.V. Drushchits in 1957.

D e s c r i p t i o n (Figs. 31d, 31e). The shell is medium-sized, from irregularly triangular to suboval in outline, moderately convex, strongly inequilateral: wide anteriorly and sharply tapering posteriorly. The umbo is strongly protruding, opisthogyre, approaching the anterior margin. The umbonal angle is 75°–80°. The anterior margin is strongly convex, gradually continues into the ventral margin. The dorsal margin is long, widely concave, forming an obtuse angle with the posterior margin. The posterior margin is very short, very slightly convex, and obliquely truncated. The dorsal and ventral margins are notched from inside by the terminations of the costae.

The flank is wide, with 20–25 costae. The costae are low, broadly rounded, regular, evenly thickening toward the valve margins. In the anterior part of the flank, the costae are oblique and asymmetric, gently curved forward. Near the anterior margin, they are curved upward and approach the very margin at an acute or right angle. In the umbonal region and in the mid-flank, the costae are notched by large scales. On the posterior slopes of the costae, the scales continue into coarse oblique hatching. In the posterior part of the flank, the costae are straight, symmetrical, narrower, notched by small, densely spaced scales, and lack hatching.

The area is relatively narrow (0.42 of the flank width), flattened. Its surface is entirely covered by coarsely dentate obliquely transverse costellae. The ribbing pattern may vary in different zones of the area. In the anterior part of the area, the costellae are convex toward the umbo and are weakly dentate. In the posterior part of the area, they have a geniculate bend. The costellae extend from the marginal carinae obliquely forward, then, they are curved at an obtuse angle toward the posterior margin, become weaker at the line of the median groove, then, are sharply curved obliquely forward, and eventually curved again near the escutcheon carina. In some specimens, costellae are replaced by elongated coarse rounded ridges parallel to the growth lines in the anterior half of the area. The median groove is distinct, deepened near the posterior margin and possesses costae. The escutcheon is narrow, concave, with finely notched obliquely transverse costellae, which are directed obliquely forward and correspond in number to the costellae of the area. The nymph is robust and lamellar. The marginal and escutcheon carinae are sharp, ridgelike. Sharp tubercles are formed at the place where costae meet.

The hinge plate is moderately wide, triangular. Hinge: on the left valve (Pl. 10, fig. 8b; Fig. 31d), tooth 2 (8 mm long and 10 mm wide) is obliquely triangular, with the upper part inclined backwards. The slopes of the tooth are unequal. The anterior slope has a larger surface, whereas its upper margin is positioned immediately below the umbo. The posterior slope is more gently sloping. Its upper margin is separated from the umbo by a smooth strip. The apex of the tooth is straight and rounded. The dental angle is 55°. Tooth 4a (10 mm long) is robust, ridgelike. Its apex is well separated from the anterior margin. Tooth 4b (10 mm long) is thin, lamellar, not separated from the upper margin of the valve. The dental buttress is short, robust, ridgelike. On the right valve (Pl. 10, fig. 4; Fig. 31e), tooth 3a (14 mm long and 3 mm wide) is robust, ridgelike, almost straight, with the upper part slightly turned backwards. Its end touches the umbo. Tooth 3b (13 mm long) is arched toward the posterior margin. Its upper end does not touch the umbo.

The anterior adductor scar is elongated oval in outline. Its long axis is almost parallel to the valve margin. Basally, it is bordered by a robust myophorous buttress (Fig. 31d). The anterior retractor scar is in a deep depression, lying between the lower end of tooth 4a and the valve margin, and is not separated from the anterior adductor scar, although being located higher than it.

The posterior adductor scar is irregularly oval in outline. Its long axis is almost parallel to the dorsal margin of the valve. Basally and anteriorly, the scar is rimmed by a rounded myophorous buttress. Its anterior part is less sharp and is merged with the termination of the dental buttress (Fig. 31d). The posterior retractor scar is small, lies in a rounded depression near the termination of the dental buttress and does not touch the adductor scar. The siphonal gape is well pronounced. Other elements of shell interior were not observed.

D i m e n s i o n s in mm and ratios:

Specimen no.	L	H	T	H/L	T/L	FL	AR	AR/FL
PIN, no. 4925/71 (RV)	45	39	11	0.86	0.24	29	13	0.44
PIN, no. 4925/72 (RV)	45	40	14	0.88	0.31	28	12	0.42
PIN, no. 4925/69 (LV)	45	42	13	0.93	0.28	30	15	0.50
Holotype MZ MGU, no. 39/11 (LV)	49	34	10	0.80	0.25	–	–	–
PIN, no. 4925/74 (LV)	49	43	14	0.86	0.28	30	13	0.43
MZ MGU, no. 39/12 (RV)	53	51	17	0.96	0.42	–	–	–

V a r i a b i l i t y. The scales and hatching on the costae of the flank are variously developed. The ribbing of the area varies from simple obliquely transverse and complex geniculate costae to obliquely transverse rows of strongly elongated tubercles.

C o m p a r i s o n. This species is most similar in its shell shape, proportions of the flank, and ornamentation to *L. (O.) crenulifera* from the Cenomanian of southern England, being distinguished by the lower and less strongly opisthogyre umbo, the presence of tubercles on the carinae, the presence of hatching on the costae of the flank, by the coarser ribbing on the area (in *L. (O.) crenulifera*, the costae are thinly lamellar). It is different from *L. (O.) crenulata* from the Cenomanian of France in the wider, regularly arched costae in the anterior and middle parts of the flank, in the sharper and more coarsely dentated carinae, in the presence of coarse costae on the entire surface of the area, and in the less strongly inclined posterior margin. It differs from *L. (O.) immutata* from the Upper Albian of Mangyshlak in the lower and less strongly opisthogyre umbo, in the more sparsely spaced and coarser costae on the flank, which have fewer and coarser scales and hatching, in the coarser, often tuberculate carinae, coarser and less regular, often knee-shaped costellae on the area (in *L. (O.) immutata*, these costellae are finely scaly and more regularly and evenly curved along a broad curvature), in the obliquely triangular asymmetrical tooth 2 and more arched tooth 3b, the upper part of which does not reach the umbo, more oval outline of the posterior adductor scar (in *L. (O.) immutata*, it is angular, especially on its posteroventral side). It is distinguished from *L. (O.) ornata* from the Valanginian–Hauterivian of the Crimea and the Valanginian–Aptian of Western Europe by the larger shell, knee-shaped bent and coarser costae on the are, which begin from the marginal carina, then extend forward (in *L. (O.) ornata*, the costae extend backwards from the marginal carina, producing a chevron-shaped pattern).

R e m a r k s. In specimen PIN, no. 4925/74 (Pl. 10, fig. 8b), tooth 2 has a deep median groove running along its entire length. It remained unclear whether this feature is a species-specific character, or it is a product of poor preservation.

T a p h o n o m y a n d p a l e o e c o l o g y. Out of 20 specimens in the collection, only one is a complete shell with displaced valves (specimen PIN, no. 4925/71). The remaining representatives are isolated valves and their fragments. Some valves possess traces of rounding and erosion, due to which the costae on the flank in these specimens often lack scales or hatching, whereas the posterior half of the area remains smooth. All specimens come from coarse-grained, gravelite, strongly calcareous sandstones and oncolitic limestones. It is possible that the individuals of this species preferably inhabited the coarse-grained, well washed ground lacking clay material. The presence of the siphonal gape and a well-developed siphonal groove on the area indicates that the animals were submerged in the sediment. Judging from the presence of a short siphonal ridge on the inner side of the valves and the absence of the mantle sinus, the animals were shallow burrowers.

O c c u r r e n c e. The upper part of the Lower and lower part of the Upper Berriasian (mainly the *dalmasi* Zone) of the southwestern Crimea (basin of the Bel'bek River: village of Golubinka, Kabanii Gully, Bezymyannyi Gully; village of Solnechnosel'e).

M a t e r i a l. Twenty specimens: one complete shell, six LV, six RV, and seven mold and fragments.

Linotrigonia (Oistotrigonia) ornata **(D'Orbigny, 1843–1847)**

Plate 11, figs. 1–7; Plate 15, fig. 2; Plate 16, figs. 1 and 2; Plate 17, fig. 1

Trigonia ornata: D'Orbigny, 1843–1847, p. 136, pl. 288, figs. 5–7; Pictet and Renevier, 1854–1858, p. 96, pl. 12, fig. 4; Lycett, 1872–1879, p. 139, pl. 24, figs. 6 and 7; Woods, 1900, p. 85, pl. 19, fig. 13; Gillet, 1921, p. 10, pl. 1, figs. 3 and 4; Renngarten, 1926, p. 75.

Trigonia ornata var. *urgonensis*: Cossmann, 1916, p. 412, pl. 15, fig. 15.

Linotrigonia (Oistotrigonia) ornata: Saveliev, 1958, p. 366; Yanin, 1958, p. 129.

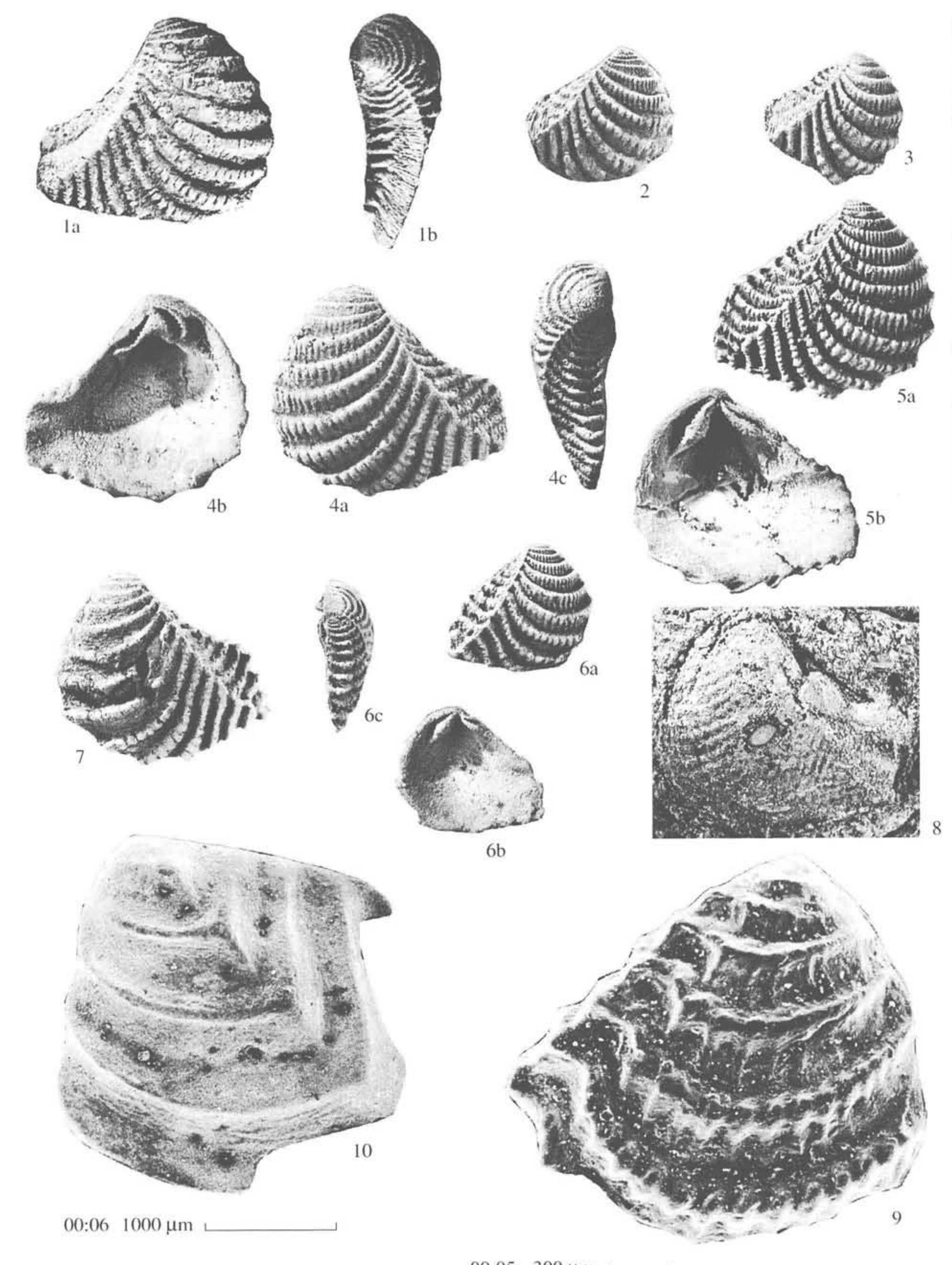
L e c t o t y p e. *Trigonia ornata* d'Orbigny, 1843–1847 (pl. 288, figs. 5, 6, complete shell); Lower Cretaceous, Valanginian; France. Designated here.

D e s c r i p t i o n (Figs. 27d, 29h, 31d, 31e, 32d). The shell is small, from suboval to semilunar in outline, extended and tapering posteriorly, moderately convex, strongly inequilateral, wide anteriorly and narrow posteriorly. The umbo is strongly prominent, opisthogyre, shifted anteriorly. The umbonal angle is approximately 90°. The anterior margin is strongly convex, gradually continuing into the ventral margin. The dorsal margin is straight or concave to a various extent, forms a distinct angle of 120°–140° with the posterior margin. The posterior margin is short, oblique, forms an angle of 100° with the ventral margin. The dorsal and ventral margins are notched from inside by the terminations of the costae.

The flank is wide, with 15–18 costae (depending on the individual age). The costae are low, rounded ridge-like, regularly and evenly widening towards the valve margins (Fig. 29h). In the anterior part of the flank, the costae are oblique, asymmetric, evenly bent forward and downward. They reach the anterior margin at a right angle, becoming slightly thinner near it. At the same place, some shells have short smooth auxiliary frontal costellae. In the umbonal region and in the mid-flank, the costae are dentate with coarse scales, which continue into oblique hatching on the posterior slopes of the costae. In the posterior zone of the flank, the costae are straight, symmetrical, narrower, and dentate with small, closely spaced scales and usually lacking hatching. These scales here become more rounded, resembling very small spines. The intercostal spaces on the flank are concave or weakly flattened, with a variable width in different parts of the flank.

The area is approximately half the width of the flank, flattened, with the surface entirely covered by scaly, regularly arched backwards, obliquely transverse costellae. The costae of the area are similar to the costae of the flank in the presence of scales and hatching. The number of costae on the area is the same as in the flank, but their terminations do not always coincide. In the umbonal region and in the middle of the marginal carina, their terminations meet, whereas further posteriorad they do not coincide (see Section II. 5). The median groove is linear, distinct, in some specimens, its presence is emphasized by a weak decrease in the height of the obliquely transverse costellae along the entire area. The escutcheon is narrow (approximately half the width of the area), concave, with thinly scaled obliquely transverse costellae directed obliquely forward and corresponding in number to the costellae of the area. The nymph is short and lamellar.

Plate 11



The marginal carina is sharp, thin, linear, emphasized by the terminations of the costae on the flanks, which form a chevronlike pattern on it. The escutcheon carina has an appearance of a noticeable bend. The costellae of the area and escutcheon do not become weaker and do not discontinue on the carina, but form a regularly curved arch, with its convexity directed posteriorly.

The hinge plate is narrow and triangular. Hinge: on the left valve (Pl. 11, fig. 4b), tooth 2 (3.5 mm wide) is triangular, straight, sometimes weakly curved posteriorly. Its apex is straight, rounded, merging into the umbo. The dental angle is 55°. Tooth 4a (4 mm long) is robust, ridgelike, well-separated from the anterior margin. Tooth 4b (4 mm long) is thin, lamellar, clearly separated from the upper margin of the valve. On the right valve (Pl. 11, fig. 5b), tooth 3a (5 mm long) is robust, ridgelike, almost straight. Tooth 3b (5 mm long) is curved posteriorly. Its upper end touches the umbo. The dental angle 3a–3b is 55°. The structure of the dental apparatus in the juvenile shells is shown in Pl. 15, figs. 1 and 2; Pl. 16, figs. 1 and 2; Figs. 33c and 33d.

The anterior adductor scar in both valves is elongated oval, with an acute lower side. The anterior retractor scar lies in a deep depression, which is located higher than the level of the adductor scar between the lower termination of tooth 4a and the anterior margin of the valve. The posterior adductor scar on either valve is relatively wide, subquadrate in outline, superficial, only slightly deepened anteriorly, with a weakly pronounced myophorous buttress bordering the scar anteriorly and basally. The posterior retractor scar is small, lies in a small, rounded depression. In the left valve, it lies near the end of the dental buttress and is separated from the adductor scar by a sharp, short, and narrow thickening. In the right valve, it is superficial, lies on the continuation of the lower surface and is separated from the adductor scar by a narrow strip. The pedal elevator scar lies in a deep narrow depression in the umbonal recess. The structure of the muscle and pedal scars in the juvenile shells is shown in Pl. 15, fig. 2; Pl. 16, figs. 1 and 2; Figs. 33c and 33d.

The pallial line lacks a sinus. It begins from the posterior side of the posterior adductor scar. The strip between the pallial line and the valve margins is very wide. The siphonal ridge is weak, broadly rounded, short, begins from the middle of the posterior adductor scar. The siphonal gape is weakly developed.

D i m e n s i o n s in mm and ratios:

Specimen PIN, no.	L	H	T	H/L	T/L	FL	AR	AR/FL
4925/88 (LV)	10	9	3	0.90	0.30	7	2.5	0.35
4925/77 (RV)	11	10	3	0.90	0.27	7.5	3	0.40
4925/80 (RV)	12	10	3.5	0.83	0.28	8.8	3.5	0.43
4925/81 (LV)	18	16	5	0.88	0.27	12	6	0.50
4925/78 (LV)	19	17.5	6	0.92	0.31	13	5	0.38
4925/79 (RV)	19	18	6	0.94	0.31	13	6	0.46
4925/75 (RV)	21	19	7	0.90	0.30	15	6	0.40

C o m p a r i s o n. This species is similar to *L. (O.) divaricata* from the Valanginian of France in its general shell shape, tapering and extension of the posterior margin, and ornamentation, being distinguished by the presence of scales and hatching along the entire length of the oblique costae in the flank (in *L. (O.) divaricata*, the scales are absent on the costae near the anterior and ventral margins, while the frontal part of the shell possesses only smooth oblique costae), and by the presence of the scaly obliquely transverse costellae on the area (in *L. (O.) divaricata*, a large part of the area lacks costellae). It differs from the similar *L. (O.) coihuicoensis* from the Barremian–Aptian of Argentina in the less convex shell (in *L. (O.) coihuicoensis*, T almost equals H), in the presence of well-developed oblique hatching on the costae of the flank, in the different type of ribbing on the area and on the escutcheon (in *L. (O.) ornata*, the obliquely transverse costellae on the area deviate from the marginal carina obliquely posteriorad and along a broad curve, which is arched posteriorad,

Explanation of Plate 11

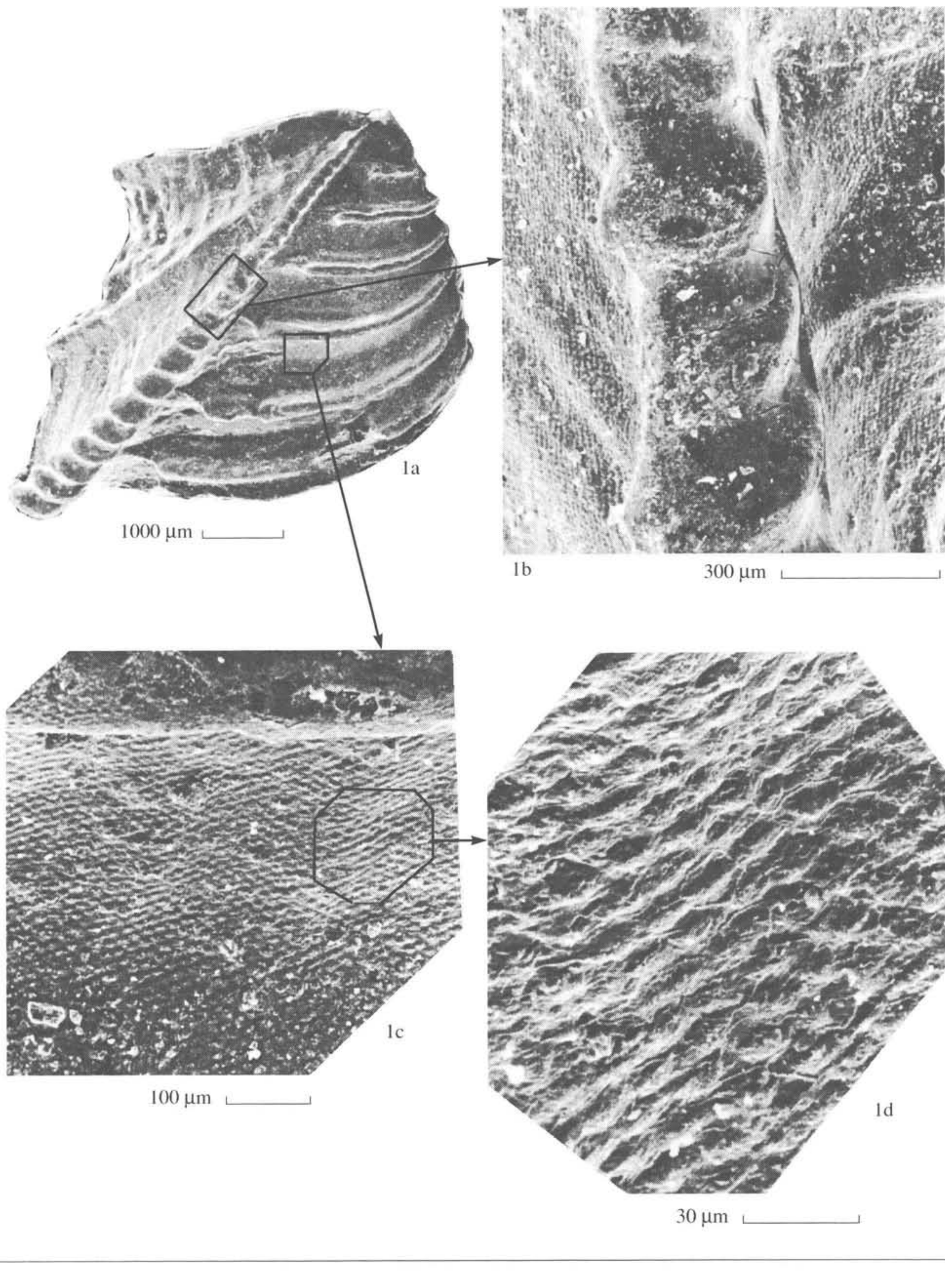
Figs. 1–7. *Linotrigonia (Oistotrigonia) ornata* (d'Orbigny): (1) PIN, no. 4925/75, right valve, ×2: (1a) external view and (1b) area and escutcheon view; central Crimea, Kuchuk-Karasu River, vicinity of the village of Gorlinka; from a block of Valanginian sandstone, redeposited in the series of Barremian conglomerates (Outcrop no. 31); collected by B.T. Yanin in 1959; (2) PIN, no. 4925/76, right valve, external view, ×2; the same locality; (3) PIN, no. 4925/77, right valve, external view, ×2; the same locality; (4) PIN, no. 4925/78, left valve, ×2: (4a) external view, (4b) internal view, and (4c) area view; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); collected by B.T. Yanin in 1989; (5) PIN, no. 4925/79, right valve, ×2: (5a) external view and (5b) internal view; the same locality; (6) PIN, no. 4925/80, right valve, ×2: (6a) external view, (6b) internal view, and (6c) area view; the same locality; (7) PIN, no. 4925/81, left valve, external view, ×2; southwestern Crimea, River Bodrak Basin, village of Prokhladnoe, Patil' Mountain; Lower Hauterivian (Section no. 9); collected by B.T. Yanin in 1955.

Fig. 8. *Linotrigonia (Oistotrigonia)* sp., PIN, no. 4925/82, mold of the left valve, external view; southwestern Crimea, River Bodrak Basin, village of Prokhladnoe, left slope of Mangush Gully; Upper Albian, Mangush Beds, *orbignyi* Zone (Outcrop no. 13); collected by B.T. Yanin in 1955.

Fig. 9. *Linotrigonia (Oistotrigonia) ornata* (d'Orbigny): PIN, no. 4925/89, umbonal region of the right valve of a juvenile, external view (photograph by CamScan, ×24); central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); collected by B.T. Yanin in 1987.

Fig. 10. *Litschkovitrigonia inguschensis* (Renngarten): PIN, no. 4925/90, umbonal region of the left valve of a juvenile, external view (photograph by CamScan, ×20); central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24); collected by B.T. Yanin in 1987.

Plate 12



then gradually continue onto the escutcheon, while in *L. (O.) coihuicoensis*, the costellae of the area extend from the marginal carina obliquely anteriorad and are curved on the escutcheon carina to form a chevron-shaped pattern). It is also distinguished from *L. (O.) coihuicoensis* by a more weakly developed median groove on the area.

L. (O.) ornata differs from *L. (O.) archiaciana* from the Albian of France, *L. (O.) vicaryana* and *L. (O.) upwarensis* from the Aptian of southern England, *L. (O.) tamalakensis* and *L. (O.) alekseitschiki* from the Albian of Mangyshlak, which are less similar in the shell shape and ribbing, in the more extended and tapering posteriorly shell, fewer costae in the flank, the presence of coarser scales on the costae, and in the relatively narrower area.

Remarks. The first record of *L. ornata* in the Lower Cretaceous of the Crimea belongs to Yanin (1958). Mordvilko (1953) recorded this species from the Lower Aptian of Mangyshlak (see Saveliev, 1958, p. 150). I also found this species in the Barremian of the northern Caucasus (basins of the Belaya and Gubs rivers) in the 1950s. Despite the wide distribution of this species in the Lower Cretaceous of the Alpine Belt of northern Eurasia, until recently it was not described in Russian journals.

Taphonomy and paleoecology. All specimens under study are variously preserved isolated valves and their fragments. Some valves show traces of rounding and leaching, as a result of which the costae on the flank and area have become smooth (lacking both hatching and scales), whereas the area itself appears smooth, which can lead to a taxonomic confusion. Many valves were found without the extended posterior margin, which is the most easily vulnerable in the process of mechanical reworking of the shells. All specimens come from the fine-grained and medium-grained sandstones. Some valves recovered from the loose Lower Valanginian sandstones in the Zuiskii Quarry are exceptionally well or even excellently preserved.

The weak gape and short siphonal ridge suggest the development of short siphons in this species. Apparently, these animals were shallow burrowers.

Occurrence. Valanginian–Aptian: Lower Valanginian–Lower Hauterivian of the southwestern Crimea (basin of the Bodrak River: Dlinnaya and Patil' mountains, village of Trudolyubovka; Al'ma River; village of Konstantininovka) and of the central Crimea (Zuya–Burul'cha interfluve: Zuiskii Quarry; also redeposited in the block of Valanginian sandstones in the series of Barremian conglomerates in the valley of the Kuchuk-Karasu River: village of Gorlinka); Valanginian–Aptian of France; Hauterivian of Germany; Hauterivian–Aptian of Switzerland; Barremian–Lower Aptian of southern England, Bulgaria, and Spain; Neocomian of Denmark (redeposited).

Material. Twenty-six specimens: seven LV, nine RV, and ten fragments and imprints.

Linotrigonia (Oistotrigonia) sp.

Plate 11, fig. 8

Description. The shell (based on an external mold of the left valve) is medium-sized, triangular–oval in outline, weakly extended posteriorly, and moderately convex. The umbo is high. The anterior margin is regularly convex, continuing along an even curve into a weakly convex ventral margin. The posterior margin is obliquely truncated, forming a sharply rounded bend at the transition to the ventral margin. The dorsal margin is short, weakly concave, forming an angle of 120° with the posterior margin.

The flank is completely covered with numerous (more than 28) thin costae with the traces of small scales and hatching. In the anterior half of the flank, the costae are oblique, and straight near the posterior margin. All costae reach the valve margin and continue onto the marginal carina.

The area is narrow (0.4 as wide as the flank), flattened (no ornamentation is preserved on the mold). The marginal carina is distinct and has an appearance of a sharp rounded bend. The median groove is hardly noticeable and very narrow. Other elements of shell morphology were not observed.

Dimensions in mm and ratios: specimen PIN, no. 4925/82: L, 39; H, 37; H/L, 0.9; FL, 26; AR, 10; AR/FL, 0.4.

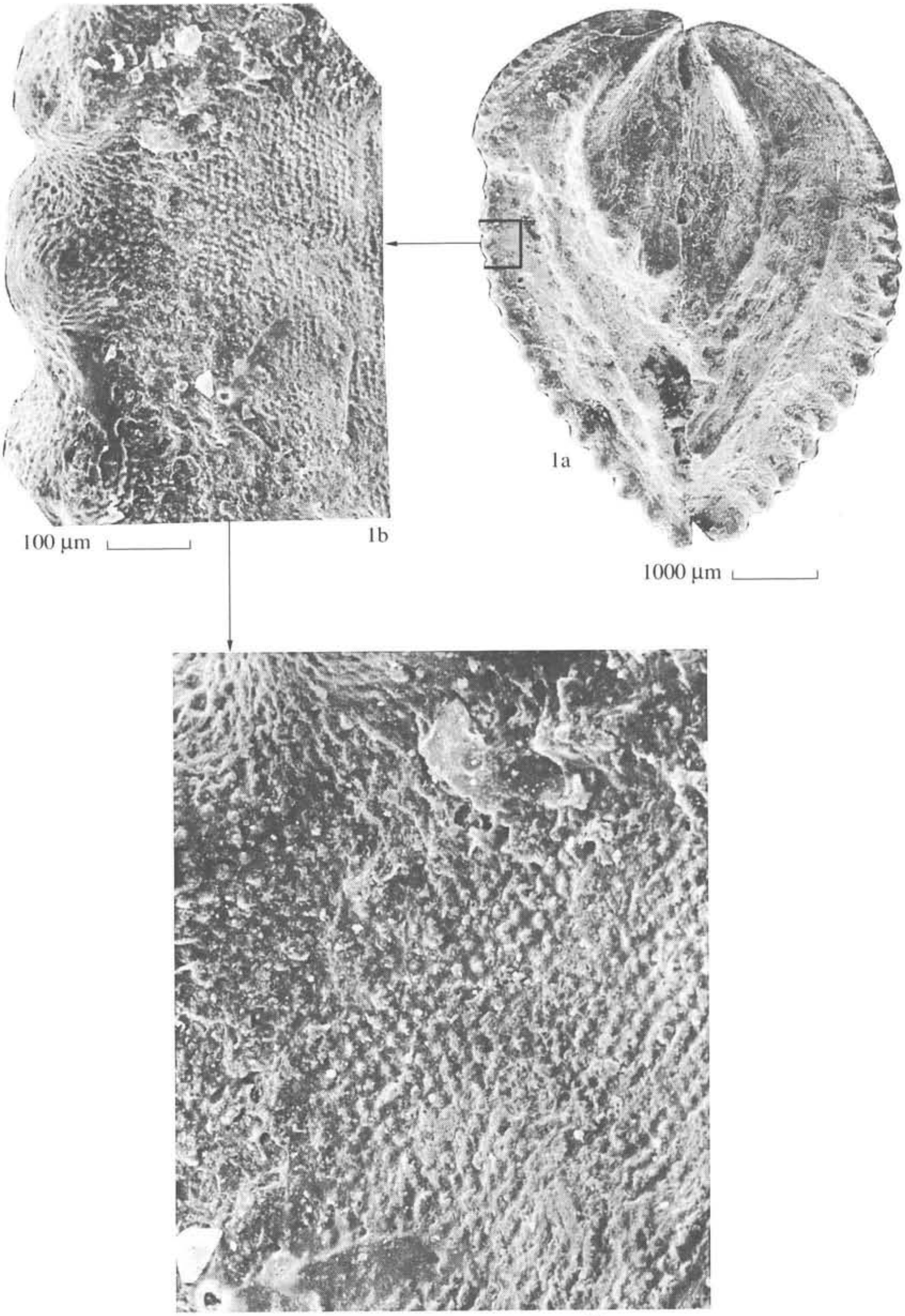
Comparison. This specimen is very similar to *L. (O.) immutata* from the Upper Albian of Mangyshlak (Saveliev, 1958, pl. 47, figs. 1–4) in the general shell outline, strongly oblique posterior margin, type of ribbing, presence of scales and hatching on the costae of the flank, and in the number of costae on the flank (in specimens of approximately the same size). However, a positive identification of this species is not possible because of the incomplete preservation of the Crimean specimen.

It is distinguished from the Aptian–Albian species *L. (O.) spinosa* by the more strongly extended and oblique posterior margin, greater number of costae on

Explanation of Plate 12

Fig. 1. *Trigonia carinata carinata* Agassiz: PIN, no. 4925/83, complete shell of a juvenile (photograph by CamScan): (1a) right valve, external view, ×14; (1b) magnified fragment of the marginal carina, with the flank on the right of it and area on the left; all elements with shagreen microstructure, ×90; (1c) magnified fragment in the central part of the flank, under the third costa (as counted from below); mineralized covering periostracum is well-preserved, through which prismatic structure of ostracum is clearly seen, ×150; and (1d) magnified fragment of fig. 1c, ×700; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); collected by B.T. Yanin in 1987.

Plate 13



the flank, and by the development of scales and hatching on the costae (in *L. (O.) spinosa*, costae on the flank possess sharp spines and lack hatching).

R e m a r k s. Despite the poor preservation of the specimen, representing an external mold of the left valve, I included this specimen in this study because the subgenus *Oistotrigonia* is very rarely found in the Albian of the Crimean Fore-Mountains.

O c c u r r e n c e. Upper Albian (sandstones of the Mangush series, *orbignyi* Zone) of the southwestern Crimea (basin of the Bodrak River: village of Prokhladnoe).

M a t e r i a l. One specimen (mold of the left valve).

II. 5. Juvenile Shells of Trigoniids

In most cases, paleontologists studying trigoniids deal with shells buried at adult or senescent ontogenetic stages. Such shells do not normally have remains of the earlier stages preserved (the umbos may be broken, rounded, or strongly eroded). Very rarely localities contain young and juvenile shells. The study of such shells is important for understanding the phylogenetic relationships between the closely related species and genera. Only a few papers published are concerned with this problem. These are the study of the Jurassic trigoniids of northwestern India (Kitchin, 1903), Jurassic trigoniids of southern Germany, and Cenozoic trigoniids of Australia (Lebküchner, 1932), Miocene and Recent trigoniids of Australia (Deschet, 1966), and others. Of Russian paleontologists, Saveliev (1958), who studied this problem, discusses growth stages of several trigoniid species based on the excellently preserved material from the Lower Cretaceous of Mangyshlak and western Turkmenistan.

All previous authors used schematic drawings to illustrate juvenile shells. In contrast, the present paper shows SEM photographs of juvenile shells and details of their structure (magnification up to 1100). The material studied is unique because for the first time for the region under consideration we obtained shells of different species which represented different growth stages.

Because all specimens do not show growth lines on juvenile and young shells, it was impossible to determine the stage of individual development in years. To identify the growth stage, we had to use sets of morphological criteria, which are species-specific. For two of the species studied (juveniles of which are present in the collection), three growth stages are recognized (juvenile, young, and adult). Juveniles and young shells are described below, according to their systematic position (see Section II. 3).

II. 5. 1. Morphology

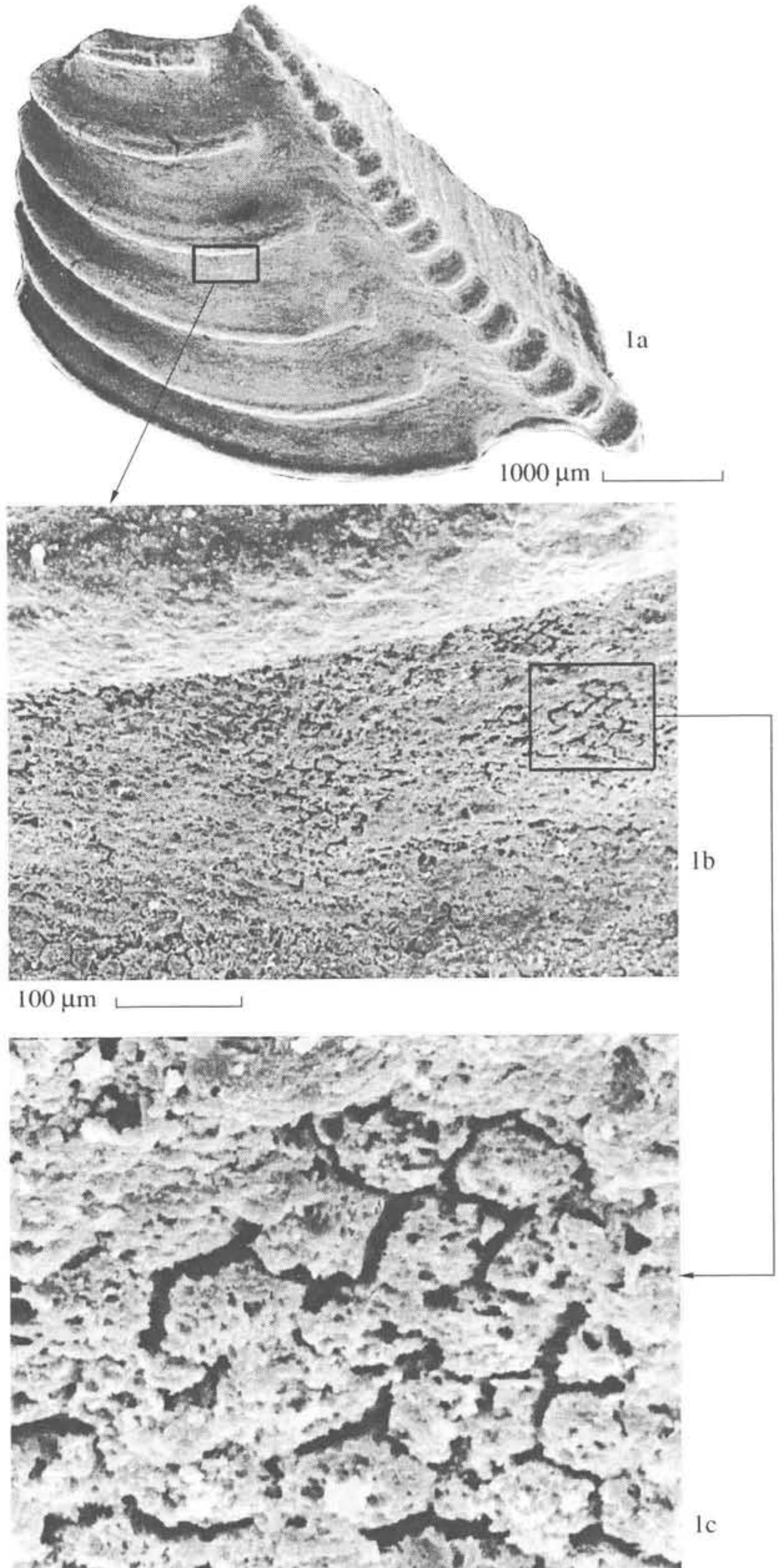
Trigonia carinata carinata. The collection contains two juvenile shells from the Lower Valanginian of the Zuiskii Quarry. Specimen PIN, no. 4925/83 (Pl. 12, figs. 1a–1d; Pl. 13, figs. 1a–1c; Fig. 32a) is a complete shell with intact valves: L = 6 mm, H = 5 mm, T = 5 mm; the marginal carina is 7 mm long, the escutcheon carina is 4 mm long; FL = 3 mm, AR = 2.5 mm, AR/FL = 0.83. The shell is subquadrate in outline, with an extended posteroventral angle of 60°. The posterior margin is obliquely truncated, with a sharply protruding termination of the median carina. The flanks are evenly convex, with nine subconcentric costae. The costae are very narrow, thin (up to 0.1–0.2 mm), weakly asymmetric. On the lateral side of the flank, the planes of the costae are somewhat tilted towards the ventral margin. When approaching the anterior margin, the plane of some costae is weakly inclined toward the umbo, or the costae remain symmetrical. The costae are smooth along their entire length. Near the anterior margin of the valves, the costae gradually decrease in height and become thinner and reach the margin, forming an acute angle with it. Near the marginal carina, the costae on the flank of the left valve are sharply interrupted (as if being cut off); as a result, a narrow, smooth, weakly concave antecarinal groove appears between their terminations and the carina. It is clearly visible beginning from the third costa, counting from the umbo. On the right valve, the costae become abruptly narrower near the marginal carina, but are not interrupted. They approach the base of the carina in the shape of thin, very low folds (the antercarinal groove is absent). The intercostal spaces on the flank are smooth and two or three times wider than the costae. The area is weakly concave, excluding the median longitudinal part that corresponds to the sharply expressed smooth median carina. The inner part of the area is somewhat wider than the outer part. Both its halves are smooth, only bearing the traces of growth following the outline of the posterior margin of the valve.

The marginal carina is high, narrow, and ridgelike, with numerous scales, with their long axes oriented subparallel to the costae on the flank. The scales are ellipsoid in outline, have rounded apices, and form notches on the carina. They are asymmetric, with their wider surfaces dipping toward the umbo. One intercostal space on the flank corresponds to two to three scales

Explanation of Plate 13

Fig. 1. *Trigonia carinata carinata* Agassiz: PIN, no. 4925/83, complete shell of a juvenile also represented in Pl. 11, fig. 1 (photograph by CamScan): (1a) shell, area view, ×14; (1b) magnified fragment near the marginal carina; area and carina with shagreen microstructure, ×130; (1c) magnified fragment of fig. 1b with well-preserved mineralized covering periostracum, ×280; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); collected by B.T. Yanin in 1987.

Plate 14



on the carina. The escutcheon is well developed, concave, smooth, up to 1 mm wide. The nymph is distinct.

Specimen PIN, no. 4925/84 (Pl. 14, fig. 1a; Fig. 32b) is an incomplete left valve (without the umbo and most of the area); L = 6 mm, FL = 4 mm. This shell has an antecarinal groove typical of *Trigonia* and clearly shows scales on the marginal carina. Other morphological structures are similar to those of specimen PIN, no. 4925/83.

The same locality contained another specimen (PIN, no. 4925/10) represented by a young shell, with an excellently preserved juvenile stage (Pl. 1, figs. 3a–3e). A shell with the first eight or nine costellae can be referred to the juvenile stage. It is distinguished from the subsequent young stage in that the costae of the flank gradually turn upwards near the anterior margin and obliquely approach the valve margin. The young stage of the shell growth begins from the ninth or tenth costae, which approach the anterior margin almost at a right angle. The space between the anterior side of the juvenile stage and the anterior margin of the valve remains smooth.

In addition, two first radial costellae possessing small sharp triangular scales appear on the inner part of the area at the beginning of the young stage of this specimen. These triangles have unequal slope. The anterior slope is gentle, dipping toward the umbo, whereas the posterior surface of the triangle is steep and terminated in a sharp spine corresponding to the meeting point of costae and growth lines (Pl. 1, fig. 3e). Soon, radial costellae also appear on the external half of the area. The specimen studied is approximately 30 mm long and has five costellae on the area [if the largest costa (median carina) is not taken into account]. The median carina has no scales preserved, but judging from the traces of their bases, they were also present on this structure.

In the young specimen studied, the anterior part of the escutcheon has weak thin longitudinal costellae with small spines, while the posterior part has obliquely transverse rows of tubercles. These rows have a different orientation in relation to the longitudinal costae in that they approach the dorsal margin of the valve obliquely from backwards. The nymph on both valves of the young specimen is well developed and has an appearance of short subtriangular ridges.

The subsequent adult growth stage of *T. carinata carinata* does not show significant changes in the structure of ribbing on the flank or area (they only increase in number). Three carinae become more strongly pronounced, but often may become smoother toward the posterior margin. The scales on the costae and carinae increase in side, and sometimes become smoother and disappear at the senile stage (see Section II. 4).

Specimen PIN, no. 4925/10 clearly shows the antecarinal groove beginning from the second or third costae of the flank on the left valve. It is not seen on the right valve of the juvenile stage (costae of the flank approach the marginal carina as in specimen PIN, no. 4925/83 (see above); however, beginning from the eighth or ninth costae, it appears and later widens up to 3 mm) (at shell length of 30 mm), and is almost identical to the antecarinal groove of the left valve. This is a unique specimen, because in all other specimens (large adult shells), the antecarinal groove is not developed on the right valve, but a distinct line between the carina and terminations of the costae on the flank is always seen.

Litschkovitrigonia inguschensis. The collection contains one juvenile specimen (PIN, no. 4925/90) (Pl. 11, fig. 10; Fig. 32c). The left valve has a posterior margin broken off; L = 4 mm, H = 4 mm, the marginal carina is approximately 4.5 mm long, FL = 2.5 mm, AR = 1.5 mm, AR/FL = 0.6. The valve is subquadrate in outline. The anterior and dorsal margins are straight. The angle between them is 90°. The posterior margin, judging from the orientation of the fourth costa on the area, is straight, obliquely truncated, forming an angle of 100° with the ventral margin. A sharp bend is observed between the anterior and ventral margins.

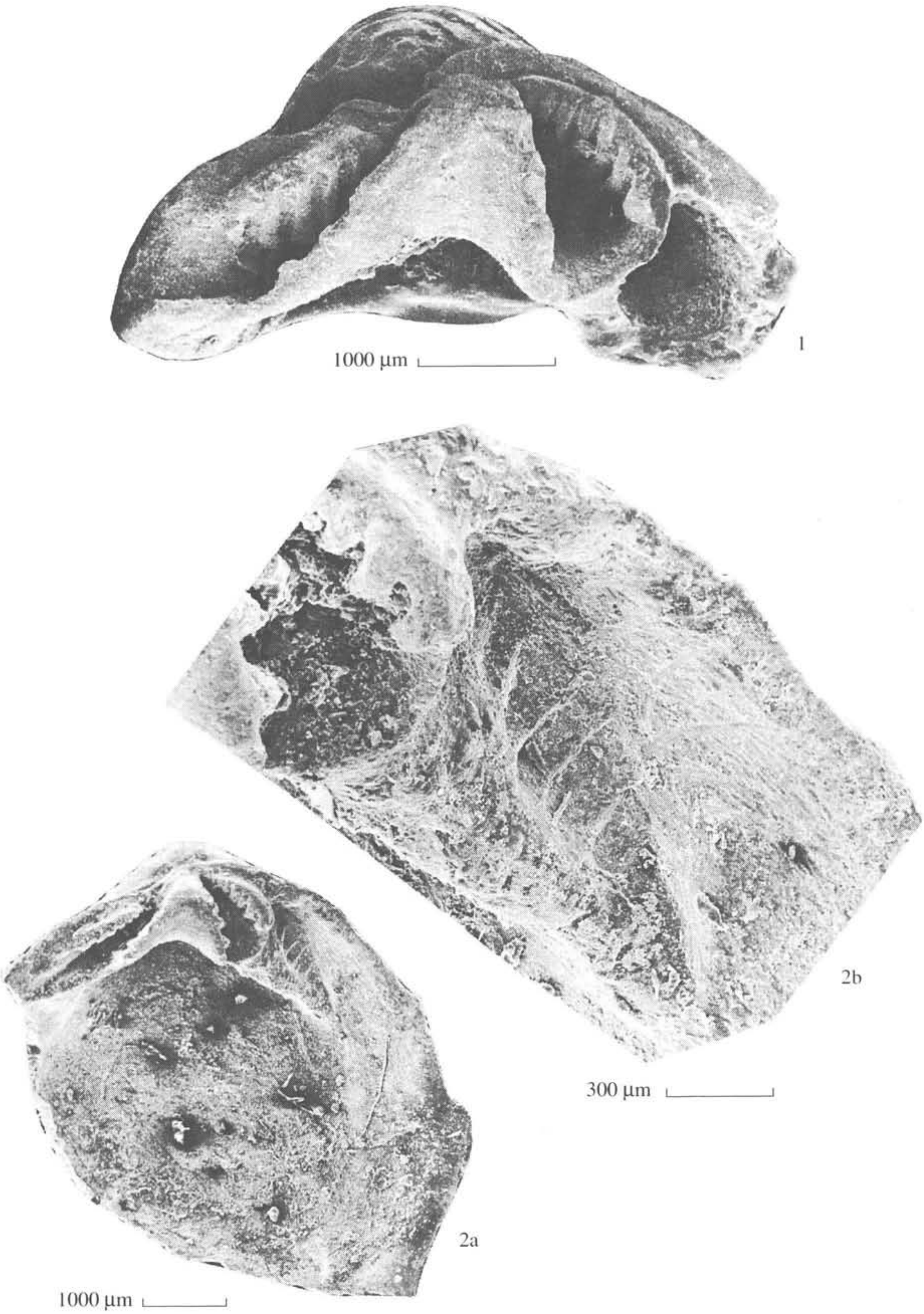
The flank is weakly and evenly convex, with five subconcentric costellae. They are high, with a smooth narrow (up to 0.1 mm) ridge. The upper surface of the costellae is slightly steeper than the lower surface. All costellae obliquely approach the anterior margin of the valve, becoming slightly thinner near it. Their outline is similar to that of concentric costae observed in most bivalves. The intercostal spaces are smooth and V-shaped.

The area is flattened, with four obliquely transverse costellae (the fifth costella is not preserved), similar to those on the flank. All costellae reach the dorsal margin. The costellae on the flank and area meet approximately in the center of the valve and form a distinct triangular (arrow-shaped) pattern. The acute angle of these triangles is directed towards the posteroventral margin of the valve. This is the initial stage of the development of the marginal carina. The intercostal spaces are smooth and weakly asymmetric. The escutcheon carina, escutcheon, and nymph are not developed in this specimen. The median groove on the area is not yet developed. The hinge apparatus is partially preserved. The shell shows distinct tooth 2 and a socket for tooth 3a.

Explanation of Plate 14

Fig. 1. *Trigonia carinata carinata* Agassiz: PIN, no. 4925/84, left valve of a juvenile with broken off umbo and dorsal margin (photograph by CamScan): (1a) external view, ×13; (1b) magnified fragment in the central part of the flank, under the fourth costa (as counted from below); partially preserved mineralized layer of the periostracum (shagreen microstructure) and underlying prismatic layer are visible, ×190; (1c) magnified fragment of fig. 1b, prismatic layer with mineralized walls of organic matrix is seen (dark grid), ×1100; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); collected by B.T. Yanin in 1987.

Plate 15



Tooth 2 does not show notches (perhaps, because of the incomplete preservation of the valve).

The juvenile stages of growth are also preserved in several young (Pl. 6, figs. 3–5) and adult shells (Pl. 5, figs. 7, 9; Pl. 6, figs. 1, 2). Because of this, three growth stages of this species may be recognized. These stages are characterized by the following features, sequentially replacing each other.

(1) Juvenile stage (first five or six costae): valves are subquadrate in outline; the costae on the flank are subconcentric, smooth, lacking tubercles. On the anterior margin of the valve, they are strongly curved toward the umbo. The costae on the flank and on the area are similar in structure and meet approximately in the center of the valve to form regular triangles. The median groove is not yet developed.

(2) Young stage (from seven or eight to 15 or 16 costae on the flank): valves acquire typical outline. The first tubercles appear on the subconcentric costae of the flank, which gradually increase in size and number during this stage; this leads to the replacement of the tuberculate costae by the rows of tubercles. The costae approach the anterior margin at an acute angle, which become smoother later. A smooth antecarinal strip is developed because of the descent of the terminations of the costae on the flank and subsequent deviation of the rows of tubercles from the marginal carina. The median groove is barely noticeable and forms the line where the costae on the area are bent. The escutcheon and nymph are clearly seen. The hinge is well developed. For instance, specimen PIN, no. 4925/35 (Pl. 6, fig. 4b; left valve, 10 mm long: the beginning of the young stage, because it has four costae with tubercles) has all typical elements of the hinge. The anterior surface of tooth 2 (its height is 3 mm) has ten notches, its posterior surface has 12, whereas the surface of tooth 4a has ten. Notches are very small, narrow, and almost straight near the umbo. Towards the lower terminations of the teeth, they become noticeably larger, wider, and are symmetrically curved, with their convexity facing downwards.

(3) Adult stage (after the 15th or 16th costae on the area). The shell is somewhat elongated. The flank possesses numerous rows of tubercles, less frequently, irregularly arranged tubercles. The antecarinal strip becomes narrower and disappears because tubercles appear on its continuation. The marginal and escutcheon carinae are well developed, possessing a single row of small tubercles each. The costae on the area are replaced by rows of small isolated tubercles, oriented parallel to the growth lines. The median groove is well developed. As the shell grows, all teeth become larger, and the number of notches on their surfaces increases. The notches are longest approximately in the middle of the tooth. Towards the lower end of the teeth, the notches become by a half or two-thirds shorter and are thicker compared to the notches in the middle part. In the adult shell (specimen PIN, no. 4925/29; Pl. 5, fig. 7c; left valve, 40 mm long), the anterior surface of tooth 2 has 15 notches (its height is 8 mm), its posterior surface has 13 notches, the surfaces of teeth 4a and 4b have 14 and 12 notches, respectively. Thus, there is no correspondence in the number of notches on the teeth of adults and young mollusks. Adult shells would have had more notches, possibly, 1.5 times their present number. The thin umbonal teeth disappear in the course of shell growth; they seem to be covered by new carbonate material because of the enlargement and thickening of the umbonal region of the valve. This is especially clearly seen in specimen PIN, no. 4925/29, on the posterior surface of tooth 2, where the anterior end of the massive ridgelike nymph adjoins and merges with the upper part of this surface. Below it, thin juvenile notches are not seen.

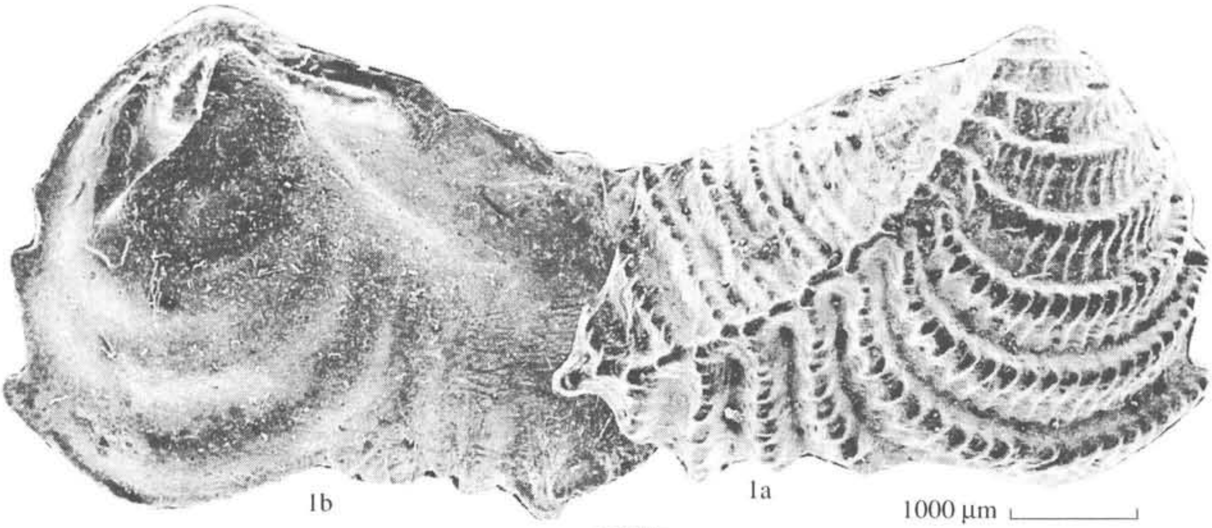
Linotrigonia (Oistotrigonia) ornata. The collection contain one juvenile (specimen PIN, no. 4925/89, Pl. 11, fig. 9; Fig. 32d) and three young individuals with well-preserved juvenile shells (PIN, no. 4925/86, Pl. 15, figs. 2a, 2b; no. 4925/87, Pl. 16, figs. 1a–1c; Fig. 33d; no. 4925/88, Pl. 16, fig. 2; Pl. 17, fig. 1a; Fig. 33c). The juvenile stage is well represented in specimen PIN, no. 4925/89 (right valve with partly broken off dorsal and posterior margins: L = 3 mm, H = 2.5 mm, FL = 2 mm). The valve is semicircular in outline. The anterior and ventral margins are evenly convex. The flank has seven or eight high, asymmetric, oblique costellae, with steep anterior and gentle posterior slopes. The first three or four costellae have a ridgelike top, in places with small tubercles, from which obliquely transverse hatching extends onto the posterior slopes. The subsequent costae possess numerous scales that have rounded ellipsoid apices, from which hatching extends obliquely downwards. This hatching continues up to the base of the subsequent costa. The hatching is dense and regular, but in the antecarinal region of the flank, the distance between the last hatching of the costae and the carina is 1.5–2 times wider than the

Explanation of Plate 15

Fig. 1. *Pterotrigonia caudata* (Agassiz): PIN, no. 4925/85, fragment of the umbonal region of the left valve of a juvenile, hinge and strongly deepened (because of leaching) anterior adductor and anterior retractor scars are visible (photograph by CamScan, ×18); central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); collected by B.T. Yanin in 1987.

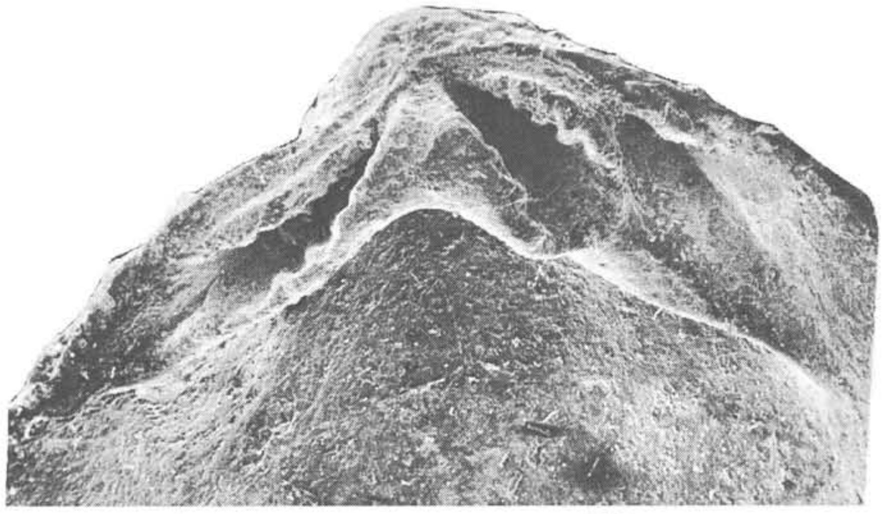
Fig. 2. *Linotrigonia (Oistotrigonia) ornata* (d'Orbigny): PIN, no. 4925/86, left valve of a juvenile with broken off ventral and posterior margins (photograph by CamScan): (2a) internal view, ×13, and (2b) magnified fragment of fig. 2a (lower part of teeth 2 and 4a and anterior adductor scar with distinct transverse wrinkles), ×46; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); collected by B.T. Yanin in 1987.

Plate 16



1b 1a 1000 μm

1c 300 μm



2 1000 μm

distance between the neighboring hatching. The costae of the flank and area are not interrupted on the marginal carina and are not displaced in relation to each other.

Hinge: only tooth 3a (0.5 mm long), with four or five hardly noticeable notches on each surface, and a deep socket for tooth 2 are well preserved. The dental buttress is distinct and continues into the myophorous buttress. The anterior adductor scar and the depression of the anterior retractor are morphologically indistinct. They were superficial and lay between the dental buttress and the myophorous buttress on one side and the anterior margin on the other. The posterior adductor scar is superficial, rounded in outline, and lacking the myophorous buttress.

The determination of subsequent stage in this species is difficult because the shell retains a general structural pattern of costae on the flank, area, and escutcheon. The only possible conclusion is that, at the beginning of the young stage, the costae discontinue on the marginal carina, while their terminations are shifted in relation to each other. As a result, the terminations of the costae do not meet on the carina, i.e., the terminations of the costae of the area lie opposite the intercostal spaces in the flank, and the costae of the area shifted anteriorly in relation to costae of the flank. This character corresponds to the appearance of the first straight costa in the posterior half of the flank, which extends from the marginal carina towards the ventral margin. In both juvenile and young shells, the costae of the escutcheon reach the anterior margin. As the shell grows, the costal terminations widen and notch the upper margin of the valve. This is especially clearly seen in adult shells.

It is almost impossible to determine the boundary between the young and adult stages. The terminations of the costae of the flank and of the area on the marginal carina still do not correspond. The number of straight costae on the flank gradually increases, with the number of costae reaching the posterior margin of the valve. In a 20-mm-long shell, the number of both type of costae is four or five.

The young shells of *L. (O.) ornata* show the structure of the hinge. It is especially well preserved in specimens PIN, nos. 4925/86 (Pl. 15, fig. 2a), 4925/87 (Pl. 16, figs. 1b, 1c; Fig. 33d), and 4925/88 (Pl. 16, fig. 2; Fig. 33c). In specimen PIN, no. 4925/87 (right valve of a young 7-mm-long individual), teeth 3a and 3b are ridgelike; 3a has six notches on both surfaces; 3b has eight notches on the anterior surface and six on the posterior surface.

As the shell grows, the teeth become larger, and the number of notches usually also increases. For instance, in specimen PIN, no. 4925/79 (right valve of the adult shell, with L = 18 mm), tooth 3a has ten notches on the anterior surface and eight on the posterior surface; tooth 3b has 12 notches on the anterior surface and nine on the posterior surface. However, this is not universally true; thus, in specimen PIN, no. 4925/88 (left valve of the young shell, with L = 10 mm), the anterior surface of tooth 2 has seven notches, and the posterior surface has ten, while the surface of 4b has seven notches. The left valve of a 20-mm-long adult (specimen PIN, no. 4925/78) has six notches on the anterior surface of tooth 2, eight notches on the posterior surface, and seven notches on tooth 4a. Thus, the number of notches remains almost the same in adults as in young stages (with the twofold increase of the valve length). This is most likely related to the disappearance of juvenile notches as the teeth grow, and primarily to the thickening of the teeth in the umbonal part of the shell.

II. 5. 2. Microstructure

In the adult shells of trigoniids in our collection, the shell matrix is completely recrystallized, and the primary microstructure is destroyed. Only a few publications describe the microstructure of fossil trigoniids (Bøggild, 1930; Lebküchner, 1932; Cox, 1969a; Taylor *et al.*, 1969). Three layers reported to have been present in their shell are known in the Recent *Neotrigonia margaritacea* Lam.: (1) the periostracum, the outer layer consisting of conchiolin in the living mollusk; (2) the ectostracum, the middle prismatic layer, located under the periostracum and composed of aragonite; and (3) the endostracum, the inner, nacreous layer covering the entire inner surface of the shell and also composed of aragonite. According to classification of Oberling (1964), the family Trigoniidae is assigned to the nacreous-prismatic group based on the shell microstructure.

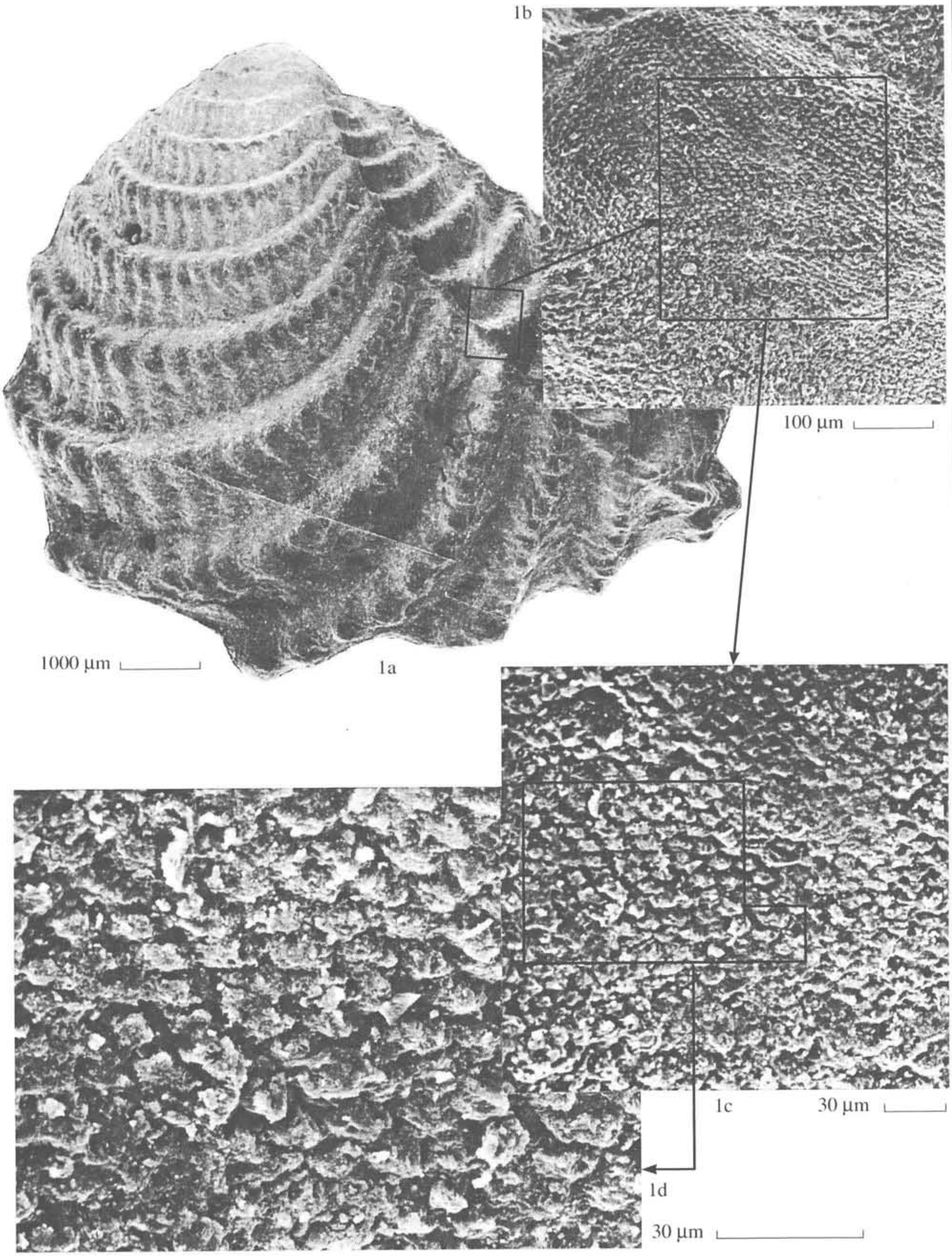
The SEM study of the surfaces of the excellently preserved juvenile and young shells of trigoniids from the Lower Valanginian of the Zuiskii Quarry showed the presence of two distinct layers, the peristracum and the ectostracum. We did not attempt to study the endostracum.

P e r i o s t r a c u m. In the Recent *N. margaritacea*, the periostracum is a very thin conchiolin film covering the prismatic layer that lies below. Conchiolin is also present in the ectostracum, where it forms thin walls between aragonite prisms (Deschet, 1966). A similar structure of the outer layer of the shells is also recorded in other groups of living bivalves (Nevesskaja, 1960; Chel'tsova, 1969; Cox, 1969a; Popov, 1977; etc.).

Explanation of Plate 16

Figs. 1 and 2. *Linotrigonia (Oistotrigonia) ornata* (d'Orbigny) (photograph by CamScan): (1) PIN, no. 4925/87, right valve of a juvenile: (1a) external view, ×14, and (1b) internal view, ×18, (1c) magnified fragment of fig. 1b, the hinge and anterior adductor scar are visible, ×30; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); collected by B.T. Yanin in 1987; (2) PIN, no. 4925/88, fragment of the left valve of a young individual (see Pl. 17, fig. 1a): the hinge, anterior adductor scar, and pedal imprint, ×17; the same locality.

Plate 17



Deschet (1966) described the microstructure of the surface of periostracum in *N. margaritacea.* He noted that the "study of the *Neotrigonia* shell surface using a binocular microscope shows honey-comb-shaped microornamentation, where each polygon has its own center of a small circle." The ornamentation of the surface of the periostracum is a reflection of the surface of the prismatic layer, on which it is compactly reflected (Deschet, 1966, pp. 70, 71). It is natural to suggest the presence of similar microornamentation of the periostracum in fossil trigoniids, if it could be fossilized.

Most experts agree that the periostracum (organic structure) is not preserved in fossils (Deschet, 1966; etc.). However, there are records in the literature of Jurassic trigoniids with very rare occurrences of the layer of external surface, covering the underlying prismatic layer and showing a peculiar microstructure. For instance, Lycett (1872–1879, p. 166; pl. 31, fig. 2a) indicated the presence of a granulated epidermal cover on the most part of the surface of the shell of *Trigonia (Lyriodon) monilifera* Ag. from the Kimmeridgian of southern England. These so-called granules were visible to the naked eye on the costae and in the intercostal spaces on the flank. At four times magnification, they showed a linear arrangement in the shape of pits that formed a reticulate pattern. A similar pattern was also observed by Lebküchner (1932) on the shell surface of the Jurassic *Clavotrigonia clavellata* Strand. He interpreted them as the sides of prisms, which were revealed on the outer surface as a result of the destruction of periostracum (Lebküchner, 1932, p. 11). According to him, he had previously thought that these were traces of dissolving.

We observed a similar "granulated epidermal" outer layer on the juvenile shells of *Trigonia carinata carinata.* It showed a characteristic microstructure represented by minute (fraction of a micron), rounded and elongated oval pits arranged in rows. Such a pattern is referred to as a shagreen microstructure. In specimen PIN, no. 4925/83 (Pl. 12, figs. 1a–1d), the shagreen layer evenly covers the entire shell surface, including the flank, area, and carinae. Plate 12, fig. 1d shows that it is composed of several thin layers, which are interrupted on the carinae between the pits because, in the central parts of the pits, these layers are strongly depressed. Plate 13, fig. 1b shows the shagreen layer embracing each side of each tubercle of the marginal carinae. Specimen PIN, no. 4925/84 (Pl. 14, figs. 1a–1c) shows that, in some places, the shagreen layer is not preserved. In these, places the upper terminations of the prisms of the underlying ectostracum appear as if recovered from under it (this is particularly clearly seen in Pl. 14, fig. 1b). Thus, it is concluded that the shagreen layer overlies the prismatic layer, and its pitted structure completely corresponds to the reticulate structure of the prismatic ectostracum. In places (Pl. 14, fig. 1b), the embracing layer has no pitted structure, i.e., the sides of the prisms of the ectostracum do not emerge from under it. This indicates the embracing (covering) nature of the shagreen layer.

As noted above, the cellular microstructure of the embracing layer is closely related to the microstructure of the underlying ectostracum. A complete correspondence of the pits in this layer to the prisms of ectostracum suggests that conchiolin walls of prisms were nothing other than continuation of conchiolin of periostracum into ectostracum, as it is established in modern bivalves, including *Neotrigonia* (Deschet, 1966, pl. 1, fig. 3).

The attempts to find an outer layer with a shagreen microstructure in the shells of young and adult individuals of Early Cretaceous trigoniids were not successful. This is probably attributable to the fact that (1) a very thin layer of periostracum was eroded off in the process of mechanical reworking of the shells in the turbulent wave zone, where coarse sandy sediment accumulated, and (2) during fossilization of the carbonate shell matrix, it was completely recrystallized, so that not only the organic membranes between the prisms were destroyed, but also the overlying conchiolin layer.

This suggests that, in fossil trigoniids, the periostracum was likely to be preserved in juveniles and young shells, which were quickly covered by sediment and were not mechanically reworked. In addition, the conchiolin layer should be quickly fossilized, i.e., replaced by minerals.

E c t o s t r a c u m. The presence of a prismatic layer in the shells of fossil trigoniids has been known for a long time (Bøggild, 1930; Lebküchner, 1932; etc.). Previously, it was discovered in the Jurassic *Clavotrigonia bronni* Ag., *C. clavella* Strand (presently *Myophorella*) and *Lyriodon interlaevigatum* Qu. (presently *Trigonia*). We also observed prismatic ectostracum in the Early Cretaceous trigoniids (genera *Trigonia* and *Linotrigonia*).

The juvenile shell of *T. carinata carinata* (specimen PIN, no. 4925/84) (left valve, less than 10 mm long; Pl. 14, figs. 1a–1c) shows that the sides of the prisms appear everywhere in places where the mineralized layer with shagreen microstructure, which previously covered them, was destroyed (see above). The SEM

Explanation of Plate 17

Fig. 1. *Linotrigonia (Oistotrigonia) ornata* (d'Orbigny): PIN, no. 4925/88, left valve of a young individual (photograph by CamScan): (1a) external view, ×13, (1b) magnified fragment of the area: fragment of the fourth costa and intercostal interval between the fourth and fifth costae (prismatic microstructure is clearly visible because the mineralized periostracum is not preserved), ×140; (1c) magnified fragment of fig. 1b, ×340; (1d) magnified fragment of fig. 1c (prismatic microstructure of the ostracum is clearly visible, dark grid is matrix between prisms), ×900; central Crimea, Zuya–Burul'cha interfluve, Zuiskii Sand Quarry, eastern wall; Lower Valanginian (Section no. 24, Bed 1); collected by B.T. Yanin in 1987.

photographs of various magnifications (up to × 1100) show that the sides of the prisms oriented perpendicular to the outer surface of the shell have irregularly polygonal sections and different sizes (Pl. 14, fig. 1c). A subdivision of one prism into two smaller prisms is also clearly seen. Each prism was surrounded by interprismatic conchiolin walls. In the photograph, they appear as dark lines, which emphasize the reticulate structure of the layer.

Specimen PIN, no. 4925/83 (Pl. 12, figs. 1a–1d; Pl. 13, figs. 1a–1c) shows that the prisms that are visible through the semitransparent conchiolin layer are developed over the entire shell surface. Everywhere they are oriented perpendicular to the outer surface of the valve. Naturally, the prisms on the carinae and costae are arranged in a fan-like manner.

In *L. (O.) ornata*, the prismatic structure is also seen over the entire shell surface. The sides of the prisms are exposed on the surface because the shagreen layer that covered them is not preserved. It is noteworthy that the prisms in the ectostracum of this species form a reticulum with smaller and less regular cells, which have thicker interprismatic walls (specimen PIN, no. 4925/88; Pl. 17, figs. 1a–1d).

According to the microstructure classification of the Bivalvia shells, the ectostracum microstructure of *T. carinata carinata* and *L. (O.) ornata* described here belong to the simple prismatic structure type.

CONCLUSIONS

Trigoniids are very widespread in the Lower Cretaceous of northern Eurasia. They are especially frequently found in the mountainous regions of the Alpine Belt (Crimea, Caucasus, central Asia), which belonged to the Mediterranean Paleozoogeographic Realm. The first trigoniids in these regions were recorded as early as the second half of the 19th century. Over the past 140 years, many short notes and paper with descriptions of some species have been published. Many species, along with other Bivalvia groups, were included in monographs and atlases of index fossils. However, only one monograph specifically dealing with trigoniids was published over this time (Saveliev, 1958). It was devoted to trigoniids of Mangyshlak and western Turkmenistan and is the most profound research ever published on this group.

(1) The present study is the first monograph on the Early Cretaceous trigoniids of the Crimea. It contains descriptions of nine genera and 15 species and subspecies from the Berriasian, Valanginian, Hauterivian, and Albian, including four taxa previously unknown from this region. This considerably expands the knowledge of the biodiversity of Bivalvia in the Cretaceous seas of southern regions of northern Eurasia.

(2) The discovery of juvenile and young shells of four species (*Linotrigonia ornata, Litschkovitrigonia inguschensis, Pterotrigonia caudata*, and *Trigonia carinata carinata*) in the Lower Valanginian sandstones of the Zuiskii Quarry in the central Crimea allowed SEM studies of the external shell morphology and shell microstructure, including the hinge and muscle scars. The results of this study are illustrated for the first time using SEM photographs.

(3) The juvenile and young shells of *T. carinata carinata* and *L. (O.) ornata* were shown to have fossilized layers, i.e., periostracum and ectostracum. A study of this type has never been performed before for the Crimean trigoniids. The results of the microstructure studies are unique because the shell matrix of fossil trigoniids is usually completely recrystallized during fossilization.

(4) The study of the stratigraphic distribution of trigoniids described allowed the recognition of three species assemblages in the Lower Cretaceous of the Crimean Fore-Mountains. These are (1) Berriasian (*Iotrigonia scapha, Linotrigonia belbekensis, Myophorella loewinsonlessingi, M. tonasensis, Orthotrigonia mordvilkoae*, and *Trigonia carinata crimica*); (2) Lower Valanginian–Lower Hauterivian (*Linotrigonia ornata, Litschkovitrigonia inguschensis, Quadratotrigonia nodosa orbignyana*, and *Trigonia carinata, carinata*); and (3) Albian (*Linotrigonia* sp., *Pterotrigonia taurica*, and *Rutitrigonia balaklavensis*) assemblages.

(5) The Lower Cretaceous sections are briefly described to indicate the precise position of the species and subspecies studied in the particular beds. An updated biostratigraphic scheme for the Lower Cretaceous of the Crimean Fore-Mountains with indication of ammonite zones will allow the correlation at the zonal level with the synchronous beds in the northern Caucasus, central Asia, and Western Europe, containing equivalent trigoniid assemblages.

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