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Permian Terebratulids of Eurasia: Morphology, Systematics, and Phylogeny

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Abstract—The Permian terebratulids of Eurasia are revised. The taxonomic composition of the Permian terebratulids of the Russian Platform, Northern Caucasus, Transcaucasia, northern and southeastern Pamirs, and northern China (Inner Mongolia) is elucidated. Fifty-one species (13 described here as new), 21 genera (3 described here as new), 7 families, and 6 superfamilies are described. During the progress of the study, the author (Smirnova, 2004a, 2004b, 2006a, 2006b) and Smirnova and Grunt (2002, 2003a, 2003b) described for the first time 19 species, nine genera, two families, and one superfamily. Morphofunctional analysis reveals a great diversity of internal structures, of the time of their appearance in the ontogeny, and of their taxonomic significance. Ontogenetic study reveals phylogenetic relationships between the Permian and Meso-Cenozoic terebratulids, the presence of the superfamilies Terebratuloidea and Loboidothyroidea in the Permian, and a new type of brachidium ontogeny characterizing the superfamily Compositelasmatoidea. This book is intended for paleontologists and biologists interested in problems of taxonomy and phylogeny, and includes 5 plates, 80 figures, and 75 bibliographic references.

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Key words: Permian, terebratulids, Eurasia, morphology, systematics, phylogeny.

CONTENTS

INTRODUCTION

Permian terebratulids are poorly known in comparison with the other brachiopods of the same age. Well-pronounced homeomorphy of the shell exterior is one of the reasons for that; thus, taxa of almost all ranks are hard to distinguish. Only studies of the internal structures can help to solve this problem. Since the shells are mainly closed, the laborious and time consuming method of serial cross sectioning must be used. The Permian terebratulids have been unevenly studied in different regions of the world. The Australian and Texan terebratulids have been described in detail, including the internal structures. Some species of Permian terebratulids from western Europe, Northern Caucasia, and the Pamirs have been described and figures of the shell interior have been provided. The interior of the terebratulids from Transcaucasia and northern China is unknown. The absence of detailed descriptions of the internal structures of most Permian terebratulids hinders the study of their taxonomic diversity and the development of a single system for the classification of this group. This study elucidates the taxonomic composition of the terebratulids from the Russian Platform, Northern Caucasia, Transcaucasia, north and southeastern Pamirs, and northern China (Inner Mongolia). Fifty-one species (13 designated here), 21 genera (3 designated here), 6 superfamilies, and 7 families are described. This paper is devoted to the detailed study of terebratulid morphology, especially of the internal structure of all of the species described. Old taxa are revised, and a system of the classification and the position of Permian terebratulids in the phylum Brachiopoda are established. The direction of evolutionary changes in different groups and possible phylogenetic relationships with the Mesozoic terebratulids are revealed using ontogenetic studies.

MATERIALS AND METHODS

The collection of Permian terebratulids made over many years by T.A. Grunt, Paleontological Institute of the Russian Academy of Sciences (PIN), serves as a basis for the current study. In expeditions from 1965 to 2000 she collected copious material in the western Darvaz from the basins of the Gundara, Zidadara, and Charymdara rivers and Tangi-Gor Gorge (northern Pamirs, Tajikistan) (Fig. 1) (collection no. 4104, PIN).

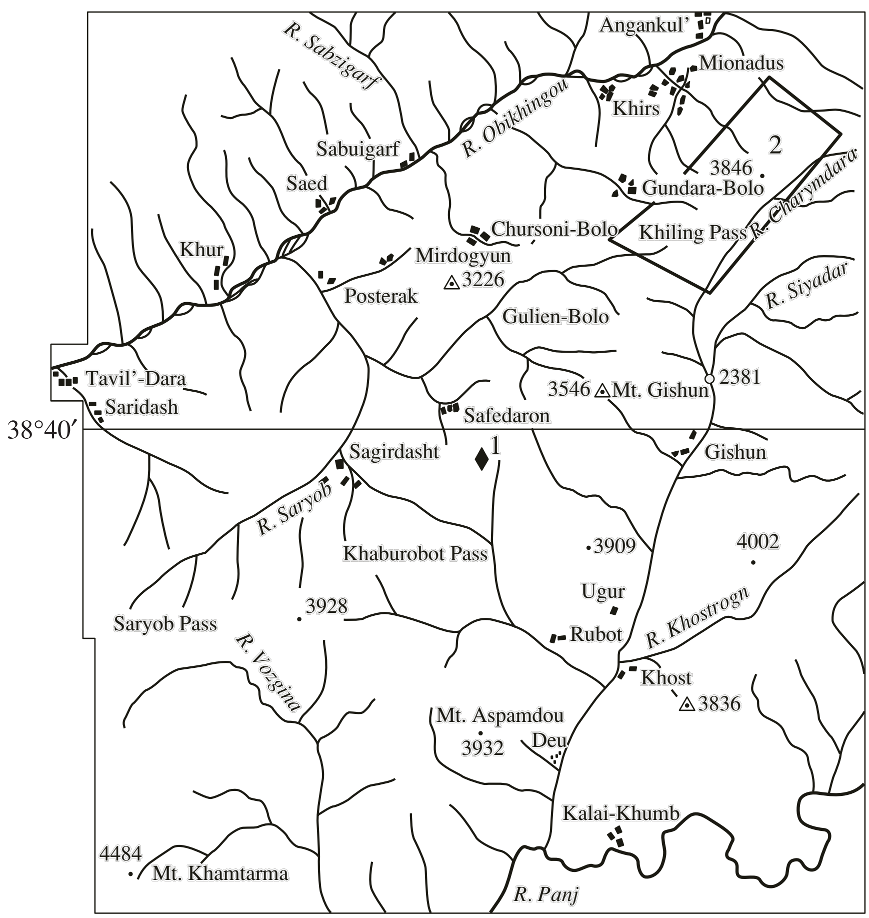


Fig. 1. Schematic map of the localities with Permian terebratulids in the southwestern Darvaz (compiled by Grunt in Smirnova and Grunt, 2002): (1) isolated limestone massif of the Safetdaron Formation south of the kishlak of Safetdaron; (2) Charymdara, Gundara, and Zidadara Rivers basins.

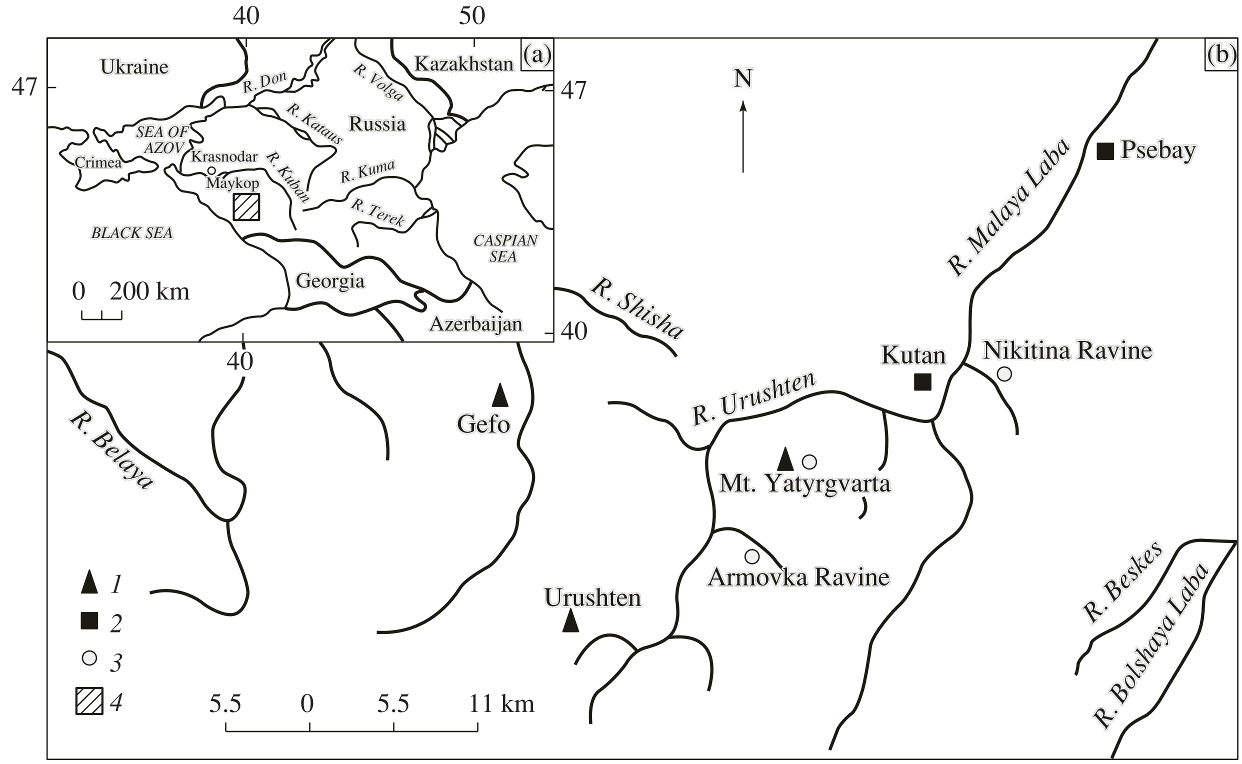


Fig. 2. (a) Schematic map of the location of the Permian deposits studied in Northern Caucasia; (b) Schematic map of the localities with the Permian terebratulids in Northern Caucasia (both figures by Kotlyar et al., 2004): (*1*) mountains, (*2*) populated settlements; (*3*) localities with terebratulids; (*4*) study area of Permian deposits.

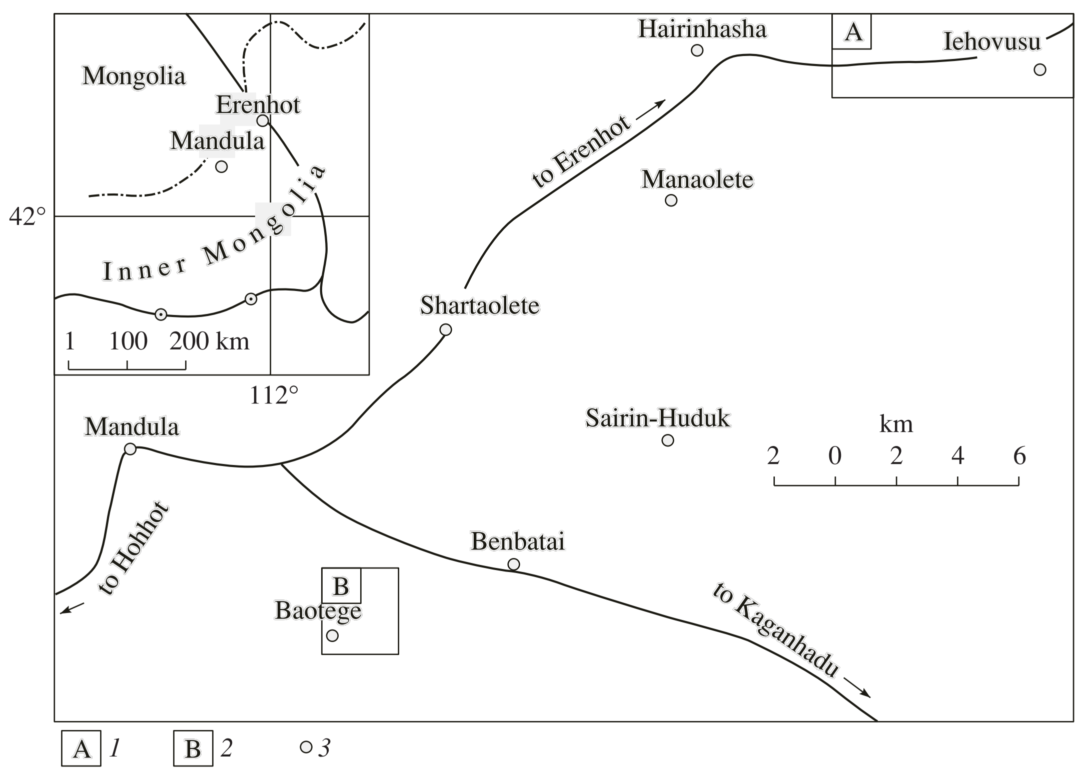


Fig. 3. Schematic map of the localities with Permian terebratulids in northern China (Inner Mongolia) (Leven et al., 2001): (*1*) Zhesi Hongor region; (*2*) Baotege region; (*3*) populated settlements.

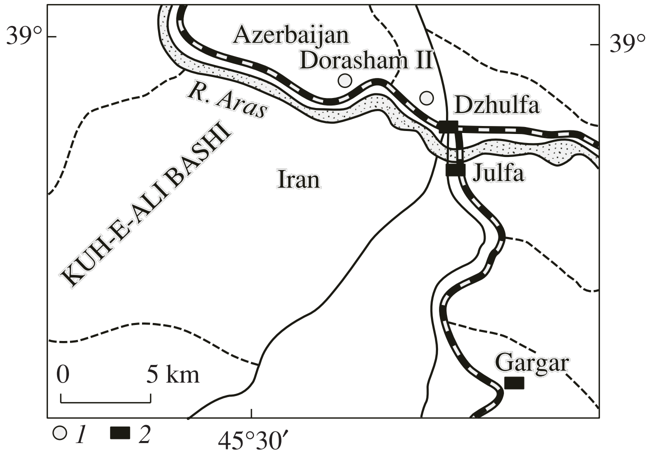


Fig. 4. Schematic map of the localities with Permian terebratulids in Transcaucasia (Shu-Zhong Shen et al., 2004): (*1*) localities with terebratulids; (*2*) populated settlements.

E.Ya. Leven (Geological Institute, Russian Academy of Sciences) and V.Yu. Dmitriev (PIN) presented material collected in the same regions. Grunt also presented collections from the Trans-Alay Range region, southeastern Pamirs, collected by Grunt and Dmitriev (collection no. 2228, PIN); from Northern Caucasia (Fig. 2), from the foothills of Mts. Yatyrgvarta and Sunduki, Malaya Laba River basin (collection no. 4918 PIN); from northern China (Inner Mongolia) (Fig. 3), valley of the Zhesi Hongor River (collection no. 5133, PIN). Some species from Licharew's collection housed in the Central Research Geological Prospecting Museum (TsNIGR Museum) (collection no. 4424) were restudied together with Grunt. Licharew described these species in an unpublished report in 1934. Grunt presented the collections of A.A. Shevyrev and T.G. Ilyina (PIN), made in 1960 in Transcaucasia (Fig. 4), near the villages of Dorosham-2 and Geranos, along the Aras River, and material collected by T.G. Sarycheva and A.N. Sokol'skaya in 1961 near the villages of Chanakhchi and Ogbin, Vedi River basin (collection no. 2073, PIN).

The collection of Lower Kazanian (Upper Permian) terebratulids from the Russian Platform (Fig. 5) (collection no. 4898, PIN) was presented by Grunt, A.A. Madison, A.V. Shatulin (PIN), N.K. Esaulova, V.P. Boltaeva (Kazan State University), N.V. Kalashnikov (Institute of Geology, Komi Scientific Center, Syktyvkar, Ural Division, Russian Academy of Sciences), and S.V. Moloshnikov (former doctoral student of the Department of Paleontology, Faculty of Geology, Moscow State University).

The brachiopods described in this monograph are restricted to the above collections, which include about 4000 specimens in a good and satisfactory state of preservation. The shell cavity is filled with fine terrigenous material or, more rarely, with quartz or calcite. Thus, the material is mainly appropriate for the study of the internal structure.

The main method of the study of Permian terebratulids is the serial cross sectioning at frequent intervals (no less than 0.05 mm). This method was introduced by Muir-Wood in 1934. Based on the sections we reconstructed the elements of internal skeleton, brachidium, and cardinalia, mainly for the forms with a brachidium differing from the standard triangular construction. Due to the bulk of material and presence of numerous shells of different ages, the development of the cardinalia and brachidium in some groups of Permian terebratulids was studied using cross sectioning. The youngest shells studied were 2.5 mm long. The differences in the cardinalia structure appear in genera at the earliest developmental stages, thus facilitating the determination of

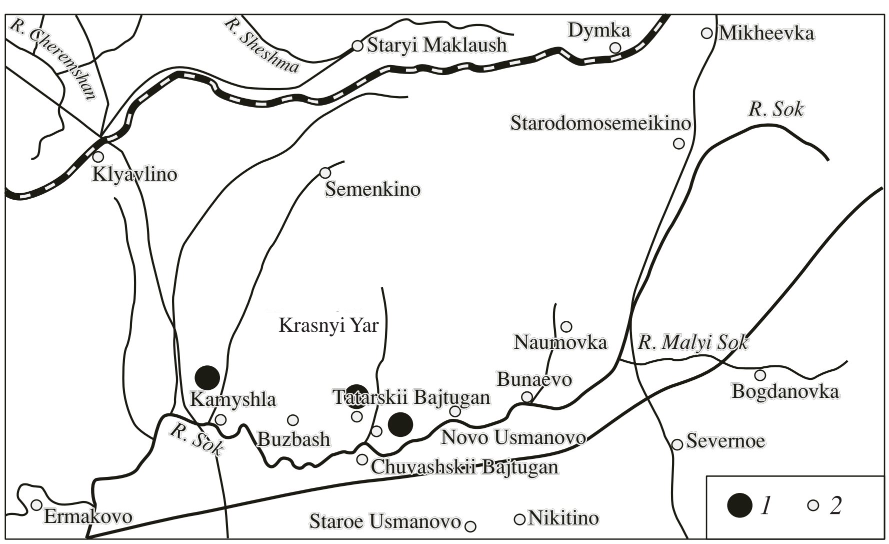


Fig. 5. Schematic map of the localities with terebratulids in the Lower Kazanian deposits of the Sok River basin, eastern Russian Platform (compiled by Esaulova in Smirnova et al., 2004): (*1*) localities with terebratulids; (*2*) populated settlements.

genera of young shells, and of the whole ontogenetic series. This is especially important because the shell exterior frequently shows the phenomenon of homeomorphy.

Open shells varying in length from 1 to 2 mm were studied using scanning electron microscopy (SEM), thus greatly adding to the data received from the sections, especially the details of the cardinalia structure. SEM photographs were produced on CAmSCAN-4 in PIN.

CHAPTER 1. A HISTORICAL REVIEW OF THE STUDY OF PERMIAN TEREBRATULIDS

At the end of 19th–beginning of 20th century, detailed monographic descriptions of large assemblages of Permian terebratulid species from Europe and Asia, mainly from the Russian Platform, Transcaucasia, Carnian Alps, Sicily, Pamirs, India, and Pakistan, were published. Within this interval several genera that include many of the identified species were described for the first time. Most of the papers are classic studies on which a several generations of scientists based their research. The informative illustrations of the type material make it possible to determine characteristic features of species and, to some extent, genera, although descriptions of the internal skeleton structure are rare or absent.

In one of the first papers on Permian terebratulids, Davidson (1862) established *Terebratula flemingii* Davidson, *T. biplicata* Brocchi var. *problematica* Davidson, *T. himalayensis* Davidson, and *T. subvesicularis* Davidson from the basin of the Indus River, near the town of Kalabagh, north Pakistan, the upper part of the Salt Range limestone. The latter two species were found to be widely distributed from Transcaucasia to northern China.

Abich (1878) studied Permian deposits in the Julfa Region (Transcaucasia) and established a new terebratulid species *Terebratula djoulfensis*, which is now assigned to *Notothyris*.

Waagen (1882–1887) described monographically Late Permian terebratulids from the *Productus* limestone (Pakistan), which is now referred to the Murgabian and Midian stages. Waagen designated new genera *Notothyris*, *Dielasmina*, and *Hemiptychina*. The terebratulid assemblage consists of four genera and 24 species, of which 19 are new. There are ten *Dielasma* species, of which eight are new. One new species belongs to *Dielasmina*, five species belong to *Hemiptychina*, four of them are new; eight species belong to *Notothyris*, six of them are new. The internal structure was studied in the open shells of *Dielasma acutangulum* Waagen, *D. breviplicatum* Waagen, *Hemiptychina himalayensis* Davidson, and *Notothyris subvesicularis* Davidson. This monograph is still considered to be the most comprehensive study that shows in detail the morphology of the large assemblage of the Late Permian terebratulids of Pakistan.

Netschajew (1894) was one of the first to investigate the Permian terebratulids of the Russian Platform. He identified *Dielasma elongata* (Schlotheim, 1816) in Kazanian deposits from the Sok River basin and described the new species *D. angusta* from the Vyatka River basin. In 1911, he described a large assemblage of Late Permian terebratulids of the genus *Dielasma*, which he found in many regions of the eastern Russian Platform. The exteriors of five previously known species were described in detail, and four new species, *D. nikitini*, *D. rara*, *D. jakowlewi*, and *D. elliptica* were established. Two more species were mentioned as *Dielasma* sp. His study remains important. Specialists on the Permian of the Russian Platform usually begin with Netschajew's papers.

Gemmellaro (1899) devoted his monograph to the rich assemblage of Late Permian terebratulids from the Sosio reef limestones in Sicily, limestones corresponding to the uppermost Kubergandian–lowermost Murgabian stages. The terebratulids are represented by the genus *Heterelasmina* with four new species, and the new genus *Rostranteris* with ten new species. The shell interior with details of the brachidium was described and figured for *Rostranteris sinuatum, R. guttula*, and *R. salomonense.*

Schellwien (1900) studied Early Permian terebratulids from the Carnian Alps. He described *Notothyris* with two species, *Terebratula* (*Dielasma*) with one species, *T.* (*Hemiptychina*) with four species (three new), and *Cryptocanthia* with one species. Schellwien was one of the first to apply the method of longitudinal sections to the reconstruction of the brachidium for *Notothyris ovalis* Gemmellaro, *N. exilis* Gemmellaro, *Hemiptychina carniolica* Schellwien, *H. dieneri* Gemmellaro, *H. tschernyschewi* Schellwien, and *H. pseudoelongata* Schellwien.

Tschernyschew published the monograph *Upper Carboniferous Brachiopods of the Urals and Timan* (1902). He studied Early Permian (Asselian) terebratulids from the *Schwagerina* limestones of the Southern and Middle Urals, outskirts of the town of Sterlitamak, and the basins of the Ufa, Ai, Sylva, and Yuryuzan' rivers. A few species were found in the same horizon in Timan. In total 24 species belonging to the genera *Dielasma*, *Hemiptychina*, *Notothyris*, *Aulacothyris*, and *Waldheimia* were described. Nine species were new. The shell interior was studied using longitudinal sectioning. The brachidium was reconstructed for *Dielasma supracarbonicum* Tschernyschew, *D. juresanense* Tschernyschew, *Hemiptychina orientalis* Tschernyschew, *H.* aff. *pygmae* Gemmellaro, and *Notothyris nucleus* Kutorga. The species described were figured in six plates. In 1914, Tschernyschew published a paper on the fauna from the Upper Paleozoic deposits of the Darvaz based on the material collected in 1904–1906 by Ya.S. Edel'shtein during an expedition to the Darvaz. Fifteen species are described, six of them new. The generic assemblage consists of *Dielasma*, *Dielasmina*, *Hemiptychina*, *Notothyris*, and *Aulacothyris*. Twelve species were found in the Safetdaron Formation (Lower Permian) of the Tangi-Gor Gorge, near the kishlak (village) of Safedaron. *Hemiptychina (Beecheria) pseudoelongata* Schellwien, 1900, was found in the Gundara Formation (Upper Permian) of the Gundara River basin. *Dielasma elongata* Schlotheim, 1816 and a new species *Heterelasmina darvasica* were described from the Obikhingou River basin, from deposits that are now referred to the Djulfian Stage. Netschajew prepared Tschernyschew's unfinished manuscript for publication and made essential refinements to the specific characters and the distribution of the species. The paper is illustrated with excellent images of the fauna clearly showing specific characters. The collection described by Tschernyschew is stored in the TsNIGR Museum (coll. no. 340), St. Petersburg.

Diener (1915) described Late Permian terebratulids from the districts of Kinnaur and Spiti (India). The species composition of the assemblage consists of *Hemiptychina himalayensis* Davidson, 1862, *Dielasma latouchei* Diener, 1897, *D. biplex* Waagen, 1882, and *D. acutangulum* Waagen, 1882. Diener noted the resemblance between the species composition of the assemblages of Permian terebratulids in India and northern China.

The earliest paper of Licharew (1913) is devoted to the Permian terebratulids discovered in the outskirts of the town of Kirillov in Novgorod Province. He described four species of *Dielasma,* of which *D. sandyriwense* and *D. kirillowense* were new.

In the 1930s, the study of the Permian terebratulids covered new areas: fundamental papers on Northern Caucasia and northern China were published. The number of recognized genera increased considerably, new species were intensively described, and previously described terebratulid taxa were revised. Licharew (1934) continued the study of Permian terebratulids from the Darvaz that had been started by Tschernyschew in 1914. Licharew described 25 new species and several varieties, mainly from the Safetdaron Formation (Lower Permian), near the kishlak of Safedaron, and from the Gundara Formation (Upper Permian) of the Obikhingou River basin. Since there were only a few specimens of each species, Licharew was not able to study the internal structure. However, he found that some slightly damaged shells of some *Dielasma* species had no dental plates and thus referred them to *Hemiptychina*. Seven species were conditionally assigned to *Dielasma*. Eleven species were described with new subspecies, three of the latter were later published as species. *H. cuboides* Licharew in Smirnova, 2001 and Licharew's species *H. juresanensiformis* Licharew, *H. latesinuata* Licharew, and *H. planoventrum* Licharew were prepared for publication and published by Grunt and Smirnova (2002). Five species were described within *Notothyris*, one of which was new. In 1934, Licharew established a new genus, *Pseudoharttina*. Licharew's study of terebratulids from the Darvaz has not all been published, and is currently stored as a report in the geological funds of the Karpinsky All-Russia Research Institute of Geology, no. 11127. The collection is stored in the TsNIGR Museum (coll. no. 4424), St. Petersburg. In the 1930s, Licharew studied brachiopods from Northern Caucasia. By serial cross sectioning, he soundly established new taxa: the genus *Gefonia* and subgenus *Notothyris* (*Notothyrina*), which were published in the 1936 issue of *Problems of Paleontology* (Licharew, 1936). In the section "Permian System" of the *Atlas of the Index Forms of the Fossil Faunas of the USSR* Licharew (1939) described six species belonging to the genera *Dielasma*, *Hemiptychina*, and *Notothyris*.

Grabau (1931) described terebratulids in detail in the summary of the results of the Central Asian Expedition to northern China (Inner Mongolia). Most of the specimens were collected in the limestones of the Zhesi Hongor Formation of the Zhesi Hongor Region, which corresponds to the Murgabian Stage. He established the new endemic genera *Morrisina*, *Mongolina*, and *Jisuina* without studying the internal structure. *Jisuina* is represented by a single incompletely preserved specimen; thus, it was impossible to study the shell interior. *Morrisina* and *Mongolina* were restudied by Stehli (1962) and Smirnova and Grunt (2000) in order to reveal their internal structure and validity. The main value of Grabau's paper is the detailed description of the entire diversity of terebratulids from the Murgabian of northern China. He studied eight *Dielasma* species, two *Hemiptychina* species, one *Beecheria* species, two *Morrisina* species, one *Mongolina*, one *Jisuina* species, and five *Notothyris*. In total, twenty species were described.

In the 1950s, along with new genera and species, new families were established and the type material of the previously prescribed genera was revised at a new level. Internal structures were also studied. Licharew (1956) described the new genus *Labaia*, and the new monotypic family Heterelasminidae for the genus *Heterelasmina* Licharew, 1939 and the new species *H. schucherti*.

Stehli (1956) is the founder of the single system of classification of the Paleozoic terebratulids. He systematically studied the Permian terebratulids and revised the type material that had been previously published. Stehli studied the internal structure of the type species of the genera *Dielasma* King, 1850 and *Beecheria* Hall et Clarke, 1893 and established precise diagnoses for both genera. This was important because these genera have well-pronounced homeomorphy and cannot be distinguished based on external features.

The 1960s–1980s were the most productive period in the study of Permian terebratulids. During this period many papers on various regions of the world were published: Australia, Thailand, Texas, Transcaucasia, Germany, Pamirs, Primorye, and Russian Platform. It was necessary to systematize the vast accumulated material and thus, fundamental summaries on brachiopods were published. In Russia it was *Fundamentals of Paleontology: Bryozoans, Brachiopods* (1960). In 1965, an international summary *Treatise on Invertebrate Paleontology: Part H. Brachiopoda* was published with combined data on all of the brachiopod groups of the world and with contributions of authors from many countries.

Stehli (1961) established the new genera *Gilledia*, *Fletcherina*, and *Yochelsonia* from the Permian of Australia. He used serial cross sectioning for the study of the internal structure in order to reconstruct the internal skeleton. In the same year he described new Permian genera, *Lowenstamia* from Texas; *Pakistania,* widespread in Oklahoma, Pakistan, and Sicily; and *Timorina* from Timor island. In 1962, he demonstrated that *Notothyris* and *Rostranteris* were separate genera, rejecting the view of those authors who believed *Rostranteris* to be a junior synonym of *Notothyris.* Stehli figured schematic sections of the type species of *Gefonia* Licharew, 1936 and *Pseudoharttina* Licharew, 1934. His system of the Paleozoic and, therefore, of the Permian terebratulids was reflected in *Treatise on Invertebrate Paleontology: Part H, Brachiopoda.* It was created almost half a century ago and up to now it is the key to the study of this group. Like any other pioneering study, his work has some inaccuracies. He considered *Heterelasmina* Licharew, 1956 to be a junior synonym of *Jisuina* Grabau, 1931, although he had no data on the shell interior of the latter, and included *Mongolina* Grabau, 1931 in *Rostranteris* Gemmellaro, 1899, without any explanation.

Licharew was the author of the section on Paleozoic terebratulids in *Fundamentals of Paleontology: Bryozoans, Brachiopods* (1960). There he established a new family, Notothyrididae, uniting terebratulids with a simple or complicated centronelliform loop and with a visceral foramen.

In his monograph on brachiopods of New Zealand, Waterhouse (1964) established new genera of Permian terebratulids, *Maorielasma* and *Marinurnula*, and referred them to the family Dielasmatidae. Both genera were found in the Kungurian–Tatarian deposits of the southern syncline of South Island, New Zealand.

Campbell (1965) published a monograph on a large assemblage of Permian terebratulids from Australia. He discovered many endemic genera and species. Using the method of serial cross sectioning, he established a new genus, *Hoskingia*, and determined the genera *Fletcherithyris* Stehli, 1961, *Yochelsonia* Stehli, 1961, *Gilledia* Stehli, 1961, *Maorielasma* Waterhouse, 1964, *Marinurnula* Waterhouse, 1964, *Hemiptychina* Waagen, 1882, *Jisuina* Grabau, 1931, *Pseudodielasma* Brill, 1940, and *Glossothyropsis* Girty, 1934. He studied the type material of *Gilledia*, refined its diagnosis, revealed the presence of dental plates, and thus established a new family Gillediidae, which was widespread in the Permian tropical seas. Campbell referred *Gilledia*, *Maorielasma*, *Marinurnula*, and *Hemiptychina* to this family.

Wan yi, Tin yigan, and Fan Dawei (1964, in Chinese) redescribed the species *Hemiptychina mongolica*, *H. morrisi*, *H. subdieneri*, *H. elegantula*, and *H. sparsiplicata* Waagen, 1882, which were originally described by Grabau (1931) from the Permian of northern China. All figures were taken from Grabau (1931).

Sarycheva, Sokol'skaya, and Grunt (1965) described six species of Permian terebratulids belonging to the genera *Notothyris* and *Dielasma* from the Permian of Julfa. *Notothyris ovalis* (Gemmellaro, 1899), *N. djoulfensis* (Abich, 1878), and *N. nucleus* (Kutorga, 1842) were shown to occur in the Djulfian deposits (Upper Permian). *Dielasma plica* (Kutorga, 1842), *D. elongata* (Schlotheim, 1816), and *D. mongolicum* (Grabau, 1931) were found in the Gnishik Horizon, Guadalupian Stage. The paper contains figures of *Notothyris* species.

Grigorjeva (1967) found *Beecheria* Hall et Clarke, 1893 in the Lower Kazanian of the Russian Platform. She noted that the majority of the species that were usually referred to *Dielasma* may belong to *Beecheria*. A new species, *B. netschajewi*, was studied using serial cross sections through the umbonal region, showing that it belongs to *Beecheria*. This was the first paper for half a century to give data on the Late Permian terebratulides of the Russian Platform.

Dagys (1972) contributed considerably to the study of onto- and phylogenetic relationships between the Late Permian and Triassic terebratulids. He revealed two main types of brachidium development: simple, without secondary elements, and complicated, with secondary elements in the loop growth. In Permian terebratulids, Dagys (1968) discovered the simple type of development in *Dielasma elongata* (Schlotheim, 1816) from the Zechstein of Thuringia. He revealed six successive ontogenetic stages, which he called a dielasmoid type of development with formation of a simple triangular loop. Dagys distinguished several phylogenetic lines characterizing large Mesocenozoic taxa with the complicated type of brachidium development. He studied the ontogeny of the Late Permian *Labaia* Licharew, 1956 and *Gefonia* Licharew, 1936 using the example of *L. muirwoodae* Licharew, 1956 and *G. cubanica* Licharew, 1936 from the Urushten deposits of Northern Caucasia. In the adult specimens, he found additional bands that were formed during the simple type of development and were not the ascending branches of the brachidium. Dagys (1974) suggested that possible ancestors of the Mesozoic terebratulids were Permian forms related to *Oligothyrina* Cooper, 1956 and *Pseudodielasma* Brill, 1940, an opinion shared by Koczyrkewicz (1976) and Smirnova (2001).

Grunt, in (Grunt and Dmitriev, 1973), was the first to describe the terebratulid assemblage of three families from the Permian of the southeastern Pamirs. The family Labaidae Licharew, 1956 was characterized by the genus *Labaia* Licharew, 1956 with a new species, *L. dmitrievi*. *Heterelasmina* Licharew, 1934 was described within the family Heterelasminidae Licharew, 1956 with two species, one of which, *H. pygmae*, was new. Grunt assigned the genera *Notothyris*, with one species, and *Rostranteris*, with the subgenus *Notothyrina* (one species), to the family Centronellidae Waagen, 1882. *Notothyris pseudojoulfensis* Licharew, sp. nov., *Heterelasmina lepton* (Gemmellaro, 1899), *H. pygmae* sp. nov., and *Rostranteris (Notothyrina) pontica* (Licharew, 1936) were described from the Djulfian Stage, Lower–Middle Takhtabulak Formation. *Labaia dmitrievi* characterizes the Kizyldzilga Horizon (Darvazian Stage) of the Pamirs. Grunt provided descriptions with series of cross and longitudinal sections and with photographs that fixed the principle structures of the shell interior from the sections. The taxonomic composition found in the Permian terebratulids from the southeastern Pamirs greatly added to the data on the distribution of this group and enabled correlation of communities of Permian terebratulids from different basins of the Paleoequatorial Superregion.

Grunt and Novikova (2002) examined the assemblage of Late Permian terebratulids from an exotic block of limestone of Kubergandian–Murgabian age near the Kichkhi-Burnu cliff, Marta River basin (Crimean Mountains). The terebratulids were represented by *Heterelasmina cuboides* Licharew in Smirnova, 2001; *H. nikitini* Gemmellaro, 1899; and *Rostranteris mongoliensis* (Grabau, 1931).

Brügge (1974) described a lectotype of *Dielasma elongata* (Schlotheim, 1816) from the type locality in Pöneck, Thuringia. Based on detailed sections, he was able to study the shell interior and refine the diagnosis of *Dielasma*. As the majority of Permian terebratulids were for a long time assigned to this genus, his study is indisputably significant. Using statistical methods, *D. elongata* was shown to be the only representative of *Dielasma* in the German Zechstein.

In their monograph on the Permian brachiopods from the Guadalupian of western Texas, Cooper and Grant (1976) described many taxa, of which two-thirds are orthides, rhynchonellides, and spiriferides and one-third are terebratulids. These authors suggested a new classification of terebratulids with two superfamilies, Cryptonellacea and Dielasmatacea. The families Cranaenidae, Cryptonellidae, and Notothyrididae were referred to Cryptonellacea. The Dielasmatacea included the families Dielasmatidae, Heterelasminidae, and a new family, Pseudodielasmatidae, which retained some features of Mesozoic terebratulids. Nineteen genera and more than 100 species were described, most of which were new (predominantly endemic) taxa. The numbers of species in the most widespread genera of Permian terebratulids are as follows: 27 *Dielasma species*, 14 *Heterelasmina species*, 11 *Pseudodielasma species*, 6 *Texarina species*, 3 *Timorina species*, and 3 *Notothyris species*. Representatives of all brachiopod orders are illustrated with 117 excellent plates, of which 34 show terebratulids. The photographs of the shell interior of all of the genera described are of great value. The smallest details of the cardinalia and brachidium are visible. The characterizations of many genera were revised, and the classification of Permian terebratulids was refined based on this monograph.

Koczyrkewicz (1976) was the first to introduce a new classification of the Permian terebratulids from the Chandalaz Horizon (Midian Stage) of southern Primorye. His system differs from that of Stehli (1965). Koczyrkewicz placed the family Heterelasminidae into the superfamily Terebratulacea based on the terebratuloid cardinalia in the genus *Heterelasmina* and in new heterelasminid genera, *Permicola* and *Amurothyris*. Koczyrkewicz (1984) was the first to find a Mesozoic representative of the family Angustothyrididae Dagys, 1972 and described a new genus, *Praeangustothyris*, with the species *P. faticana* Koczyrkewicz, in which the author discovered a young stage with characteristic features of the angustothyridid type of brachidium development. Koczyrkewicz described the dielasmatid genus *Hemiptychina* Waagen, 1882 and a new genus, *Latiflexa*, with four new species.

Grant (1976) discovered an assemblage of endemic Artinskian–Sakmarian terebratulid species in southern Thailand that included three new *Hemiptychina species*, two new *Notothyris species*, *Dielasma* sp., and *Gefonia* sp.

Yanagida and Nishikawa (1984) found Early Permian terebratulids in southeastern Japan. They described *Dielasma* sp. and a new *Chondronia species*.

Smirnova (1985) studied ontogenetic changes in the Late Permian *Notothyris pseudojoulfensis* Licharew in Grunt, 1973 and *Gefonia* sp. (=*Gefonia licharewi* sp. nov.) from the Djulfian deposits (Takhtabulak Formation) of the southeastern Pamirs. The visceral foramen was found to appear during the middle developmental stages as a result of overgrowth of the ventral tips of the crural bases. The cardinalia and brachidium were reconstructed for several ontogenetic stages of these species.

The beginning of the 21st century is marked by the examination of large collections from the southeastern Pamirs and the Russian Platform, the revision of previously collected material from these regions, the description of taxa using the serial cross sectioning method, the detailed examination of the internal structures, and the development of a system of classification of Permian terebratulids based on new data on morphology and ontogeny. The comparison of the taxonomic composition of Permian terebratulids from many regions of different climatic zones of the world revealed peculiarities of their paleozoogeographic zonation. In the new edition of *Treatise on Invertebrate Paleontology*, Vol. 5.: *Brachiopoda* (2006), a new system of the classification of Permian terebratulids was introduced in collaboration with Russian specialists, based on the latest advances.

Leven et al. (2001) determined the stratigraphic level from which Grabau (1931) collected terebratulids in northern China (Inner Mongolia). It was defined as Murgabian–Early Midian by the integrated study of various marine faunistic groups.

Smirnova (2001) established a new genus *Fredericksolasma* and a new species *Rostranteris ovaleformis* from the Gundara Formation (Upper Permian) of the southwestern Darvaz. She traced the development of the brachidium and cardinalia in *Heterelasmina cuboides* Licharew in Smirnova, 2001 and *Fredericksolasma lata* (Licharew, 1939). Terebratuloid and loboidothyridid types of brachidium development that are characteristic of the Mesozoic terebratulids were revealed. Thus, the appearance of the superfamilies Terebratuloidea and Loboidothyroidea in the Permian was established.

A series of papers (Smirnova and Grunt, 2002, 2003a, 2003b) continues the study of the Permian terebratulids from the southwestern Darvaz (northern Pamirs). For the first time, all the species from this region were studied using the method of serial cross sectioning, and thus the generic composition was revealed. Considerable taxonomic diversity was discovered following detailed study of the outer and internal structure. The superfamilies Centronelloidea Waagen, 1882 (with the family Notothyrididae Licharew, 1960), Gilledioidea Campbell, 1965 (with the family Gillediidae Campbell, 1965), Terebratuloidea Gray, 1840 (with the family Heterelasminidae Licharew, 1956), and Loboidothyroidea Makridin, 1964 (with the family Pseudodielasmatidae Cooper, 1976) were delimited. Eight genera and 22 species were described, of which six genera and 16 species were new.

Smirnova and Grunt (2005) analyzed the taxonomic composition of the Permian terebratulids in different regions of the world and revealed the peculiarities of the differentiation of this group depending on climatic conditions. Permian terebratulids were found to precisely characterize basins with different temperature conditions. Endemic biotas of boreal and tropical terebratulids at the species, generic, and family levels were distinguished. The greatest number of taxa was recorded in the Paleoequatorial Paleozoogeographic Superregion: 140 species belonging to 19 genera, 5 families, and 5 superfamilies. Twenty-four species, 8 genera, 3 families, and 2 superfamilies are known from the Boreal Superregion. The superfamilies and families were shown to characterize superregions, generic assemblages to characterize regions and subregions, and separate genera and species assemblages to characterize provinces. The main morphological distinctions of terebratulids from the Paleoequatorial Superregion are the absence of dental plates, the complicated brachidium, and the presence of the visceral foramen in a number of forms. The boreal terebratulids have dental plates, simple adult brachidium, and no forms with a visceral foramen.

Smirnova (2004a, 2004b, 2006a, 2006b) studied Early Kazanian (Late Permian) terebratulids from the eastern Russian Platform and revealed their rich taxonomic composition. She described 20 species, ten genera, three families, and two superfamilies. Sixteen species, eight genera, two families, and one superfamily were new. The species and genera cannot be determined using external features because of the well-pronounced homeomorphy. Since the specimens were well preserved and the shell cavity was filled with fine terrigenous material, the method of serial cross sectioning was successfully employed. Details of the internal structure were revealed and systematics of the boreal Late Permian terebratulids, differing from that of the terebratulids of the Paleoequatorial Superregion, was elaborated. The ontogenetic method was applied to *Compositelasma* Smirnova, 2006, *Gruntelasma* Smirnova, 2004, *Grigorjevaelasma* Smirnova, 2004, and *Campbellelasma* Smirnova, 2004. The complicated transformations of brachidium that are unknown in other terebratulids were revealed in all genera. Based on this type of development, the superfamily Compositelasmatoidea Smirnova, 2006 was established. The secondary elements that continued to develop in the Mesozoic were found in the ontogeny of the brachidium in the Permian.

From the papers above, two main stages in the history of the study of Permian terebratulids can be distinguished. The first stage covers the end of the 19th–first half of the 20th century. Then the fundamental regional studies with descriptions of large species assemblages were published. The second stage lasted from the second half of the 20th century to the beginning of the 21st century. During this period investigations were conducted with more sophisticated methods. Monographs and large summaries embracing all accumulated material of Permian terebratulids were published. Earlier established taxa were revised based on the detailed study of the shell interior. The investigations cover large areas in different climatic zones of the world.

CHAPTER 2. THE MORPHOGENESIS AND TAXONOMIC VALUE OF THE CARDINALIUM

The following designations are used in this chapter: (i.h.p.) inner hinge plate, (i.s.r.) inner socket ridges, (c.p.) crural plates, (c.b.) crural bases, (o.h.p.) outer hinge plate, and (s.) septum.

Study of the abundant material of Permian terebratulids has revealed great diversity of their internal structures, which are extremely important for taxonomy. The cardinalia and brachidium are of considerable importance for determining the taxonomic position of terebratulids. The cardinalia basically consists of inner

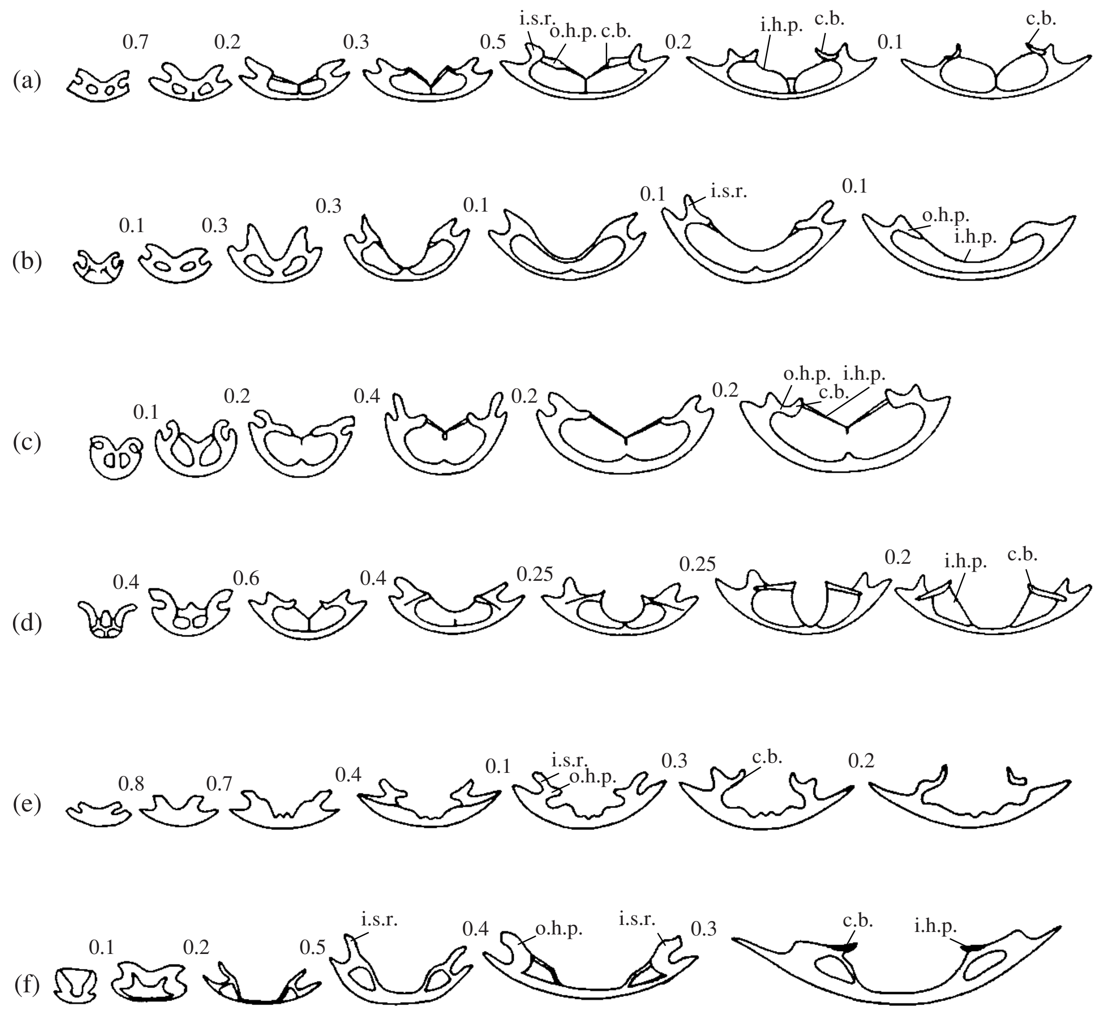


Fig. 6. Developmental changes of the outer hinge plate: (a) *Campbellelasma variiforme*, (b) *Gruntelasma bajtuganensis*, (c) *Grigorjevaelasma rossica*, (d) *Compositelasma evolutum*, (e) *Fredericksolasma lata*, and (f) *Hemiptychina sparsiplicata*; figures indicate distances between the sections in mm.

and outer hinge plates, crural plates, and septal elements in the dorsal valve and the dental plates and pedicle collar in the ventral valve. The cardinal process in the Permian terebratulids is unknown. Characteristic features may be evaluated taxonomically, and possible phylogenetic relationships between various terebratulid groups can be determined based on data on the appearance of different elements in ontogeny. There are almost no such studies involving Permian terebratulids.

Elements of the cardinalia in the dorsal valve are very important for diagnostics of taxa of different rank. The type of combination of hinge plates and septal elements, the degree of development and the shape of the outer and inner hinge plates, and the presence of crural plates are important in generic and partly in familial determination.

Outer hinge plates run from the inner socket ridges to the middle of the valve, and are usually subparallel to the dorsal valve. The presence or absence of the outer hinge plates is taken into account in the family diagnoses. The outer hinge plates may be absent as in tropical forms of the family Heterelasminidae, or be poorly developed as in the boreal family Beecheriidae (genera *Beecheria* and *Tapetulasma).* These families became extinct at the end of the Permian and were replaced by Mesozoic terebratulids in which the outer hinge plates were always developed and showed a wide range of morphological diversity. Some groups of Permian terebratulids have well-developed outer hinge plates that clearly differ in morphology. Examples are the genera of the family Compositelasmatidae *Campbellelasma* (Fig. 6a), *Gruntelasma* (Fig. 6b), *Grigorjevaelasma* (Fig. 6c), and *Compositelasma* (Fig. 6d), which have wide well-pronounced outer hinge plates, often with projecting crural bases. The genera *Fredericksolasma* (Fig. 6e) and *Levenolasma* belonging to the family Pseudodielasmatidae have almost horizontal outer hinge plates. The outer hinge plates of the genera

*Pyandzhelasma a*nd *Hemiptychina* (family Gillediidae) are steeply inclined (Fig. 6f).

The term **"inner hinge plates"** has various interpretations. In general, the inner hinge plates are the elements situated between the crural bases. This viewpoint was held by Thomson (1927) and Campbell (1965). Muir-Wood (1934) suggested the term "septalium" for Mesozoic terebratulids, while "inner hinge plates" were reserved for terebratulids similar to *Terebratula*. This terminology is still used by specialists on Mesozoic terebratulids. In Paleozoic terebratulids, the elements located between the crural bases are more variable than those of the Paleozoic terebratulids. Thus, different authors use different terms for individual modifications. Cloud (1942) called the septalium-like structures "crural grooves"; and the inner hinge plate (either entire or perforated by a visceral foramen), "inner hinge plate." In this paper, we follow Thomson and Campbell, whose views are consistent with ontogenetic data showing that the majority of structures may have a common origin. Inner hinge plates are considered to be morphologically different structures situated between the crural bases (except the crural plates). An inner hinge plate may be an entire plate or a plate perforated by a visceral foramen; or a free plate not resting on septal elements or the shell bottom; or a cup-shaped formation supported by a septum or by two separate plates resting on the shell bottom.

Two groups of Permian terebratulids are recognized, with and without an inner hinge plate. The first group includes all of the known representatives of the superfamily Loboidothyroidea, represented in our collection by *Fredericksolasma* (Fig. 6e) and *Levenolasma*, and the superfamily Terebratuloidea, which in our collection is represented by *Heterelasmina* (Fig. 7a) and *Gundarolasmina*, genera that lack inner hinge plates even at early developmental stages. Consequently, the absence of inner hinge plates may be used as a characteristic feature of the family. Most of the Permian terebratulids possess inner hinge plates and thus belong to the second group. This group comprises terebratulids with an inner hinge plate that was supported by septal structures at different developmental stages. Four subgroups were distinguished as a result of ontogenetic studies. The first group comprises terebratulids with an inner hinge plate supported by a septum at the earliest stages and consists of the family Notothyrididae. In adult *Rostranteris ovaleformis* (Fig. 7b) and *Notothyris pseudojoulfensis*, the inner hinge plate is free, hanging, not resting on a septum or on the shell bottom. In the 3.5-mm-long shell of *N. pseudojoulfensis* (Fig. 7c), the inner hinge plate is joined to the septum in the apical region. In a 4.2-mm-long shell, the plate becomes free. Smirnova (1985) studied the formation of a entire inner hinge plate in *Notothyris pseudojoulfensis* and *Gefonia* sp. from the Upper Permian of the northwestern Pamirs. Small (a few mm long) specimens have a separated inner hinge plate with well-developed dorsal and ventral tips of the crural bases. The dorsal tips reduce in the development; the ventral tips grow inward the valve and merge to form a single plate bordering the visceral foramen. This mode of formation of a single inner hinge plate is characteristic of the family Notothyrididae, but probably not of all terebratulids. The second group consists of the terebratulids with the inner hinge plates joining the septal structures at the early and middle developmental stages and later becoming free, hanging, or resting on the shell bottom. In *Gruntelasma bajtuganensis* (Fig. 6b) and *Grigorjevaelasma rossica* (Fig. 6c) of the family Beecheriidae, the inner hinge plate breaks free of the septum early in ontogeny and transforms into a slightly concave single plate hanging over the shell bottom. In the third group, the inner hinge plate experiences a short period of connection with a low septum and then divides into two parts that independently rest on the shell bottom. This form of cardinalia is widely spread in the boreal terebratulids of the family Compositelasmatidae such as *Compositelasma evolutum* (Fig. 6d) and the family Dielasmatidae such as *Dielasma subelongatum* sp. nov. (Fig. 7d) and *D. kirillowense* (Fig. 7e), and also in warm-water terebratulids of the family Gillediidae such as *Pyandzhelasma juresanensiformis* (Fig. 7f) and *Hemiptychina sparsiplicata* (Fig. 6f). The forth group combines terebratulids with the inner hinge plate supported by septal elements at all developmental stages. Such cardinalia is typical of the boreal *Calycelasma kalaschnikovi* (Fig. 7g) and *Sokelasma guttiformis* (Fig. 7h) from the family Beecheriidae. Characteristic features of each subgroup may be used in generic determination. Forms with the inner hinge plate connected with a septum may conditionally be considered as the ancestors of the majority of terebratulids. Different variants of the combination of these structures arose in evolution to form the diversity of cardinalia in the Permian terebratulids.

Crural plates are two plates that are perpendicular to the surface of the dorsal valve and remote from the inner socket ridges. The crural bases evolved from the crural plates. Various terms have been suggested for these structures. Stehli (1962) and Grunt and Dmitriev (1973) used the term "crural bases." Campbell (1965) called them "outer hinge plates." Koczyrkewicz (1976) named these structures "crural supports." We accept the term "crural plates," which was used by many specialists (Licharew, 1939, 1956, 1960; Stehli, 1965; Waterhouse and Piyasin, 1970).

Crural plates are characteristic of the boreal and warm-water Permian terebratulids. If inner hinge plates are developed, the crural plates may be supported by a septum in the boreal family Beecheriidae, e.g., *Beecheria kargaliensis* (Fig. 7i), with the crural plates separated from the inner socket ridges and, together with the inner hinge plates, bordering narrow cavities; or *Tapetulasma boltaevae* (Fig. 7j) with the crural plates connected with the inner hinge plates, which cover the bottom of the dorsal valve. A septum supporting the inner hinge plates was observed in the apical

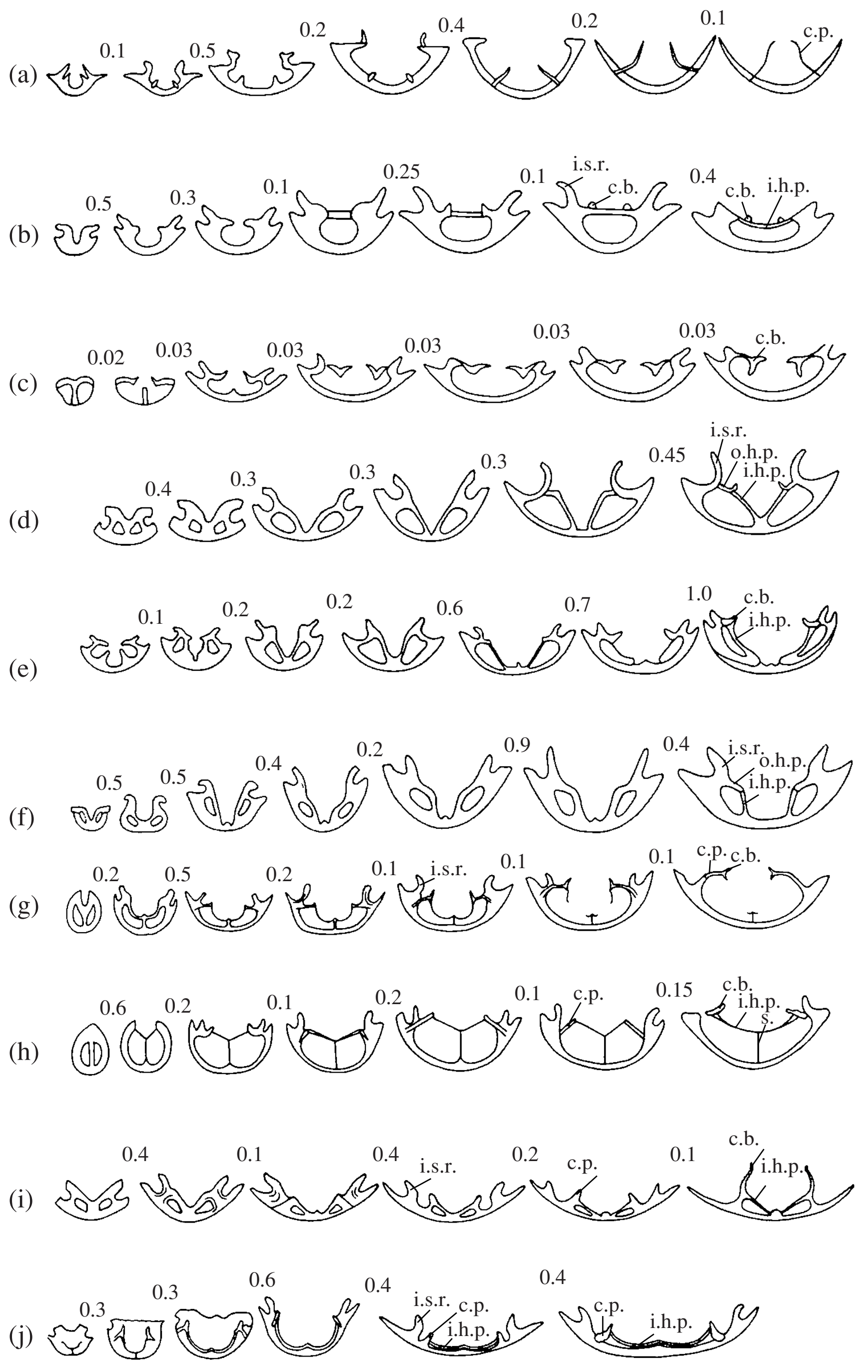


Fig. 7. Developmental changes of the inner hinge plate: (a) *Heterelasmina cuboides*, (b) *Rostranteris ovaleformis,* (c) *Notothyris pseudojoulfensis*, (d) *Dielasma subelongatum*, (e) *D. kirillowense*, (f) *Pyandzhelasma juresanensiformis*, (g) *Calycelasma kalaschnikovi*, (h) *Sokelasma guttiformis,* (i) *Beecheria kargaliensis*, and (j) *Tapetulasma boltaevae*; figures indicate distances between the sections in mm.

region of young shells of these species. In warm-water habitats, crural plates occur in the family Heterelasminidae, e.g., in *Heterelasmina cuboides* (Fig. 7a), in which the crural plates are free (not supported by the inner hinge plates). Crural plates arose repeatedly in the Paleozoic terebratulids: in the Devonian family Cranaenidae, Devonian–Permian Heterelasminidae, and Carboniferous–Permian Beecheriidae. In all of the above-mentioned families, the outer hinge plates are reduced. The presence of the crural plates and their combination with the inner hinge plates are the main characteristic features of the family rank. Koczyrkewicz (1976) believed that the crural plates arose independently in different lineages.

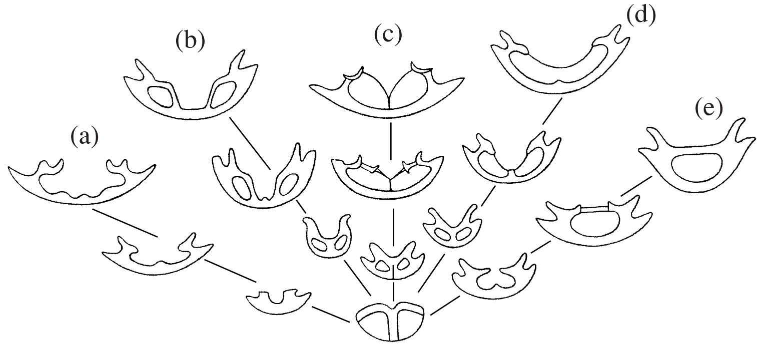


Fig. 8. Main types of the cardinalium development in superfamilies: (a) Terebratuloidea, (b) Dielasmatoidea, (c) and (d) Compositelasmatoidea, and (e) Centronelloidea.

Dagys (1974) suggested a scheme for the main lines in the development of the cardinalia in terebratuloid brachiopods. He believed that the oldest form of the hinge plate was a structure consisting of two plates. According to Dagys, it was the initial form of the cardinalia in all terebratulids, and it first of all gave rise to taxa with a single inner hinge plate perforated by a visceral foramen. In the ontogeny of *Notothyris pseudojoulfensis*, we discovered the presence of an inner hinge plate connected with a septum in a 3.5-mm-long shell. The septum is high and is clearly visible in two sections of this specimen (Fig. 7c). In shells of 4.2 mm or longer, the septum disappears and a divided inner hinge plate arises. This plate enlarges to form a single plate, which is perforated by a visceral foramen in the species studied. Thus, the earliest structure in the development of the cardinalia is the inner hinge plate connected with a septum, followed by a parted hinge plate. The study of the ontogeny of cardinalia in the Permian terebratulids with an inner hinge plate confirms this suggestion (Fig. 8). The connection of the inner hinge plates with the variously high septum were found to be the initial developmental stages in the superfamilies Centronelloidea, Dielasmatoidea, and Compositelasmatoidea. This stage may be of very short duration, as in Centronelloidea, or of longer duration, as in Dielasmatoidea and some Compositelasmatoidea (*Beecheria* from the family Beecheriidae), or it may persist throughout ontogeny, as in the family Compositelasmatidae (superfamily Compositelasmatoidea). In all of the above-mentioned superfamilies, the initial form of the cardinalia with inner hinge plates supported by a septum was detected at earlier developmental stages. Different morphological types of cardinalia, defining families and superfamilies, form at subsequent stages.

According to Dagys's scheme, the dielasmoid type of cardinalia with a parted inner hinge plate resting on the shell bottom was derived from the cardinalia with a solid hinge plate. In our observational data, the dielasmoid cardinalia goes through the stage of a hinge plate connected with the septum in the early developmental stages, i.e., the same initial stage as the other Permian terebratulids with an inner hinge plate. Consequently, the forms with a solid or perforated hinge plate that became extinct at the end of the Permian were probably a dead-end side branch and could hardly have given rise to new structures. Terebratulids lacking inner hinge plates are a special branch. They were widespread in the Mesozoic and arose in the Permian (superfamilies Terebratuloidea and Loboidothyroidea, personal data). Dagys was probably right in deriving them from the groups with the inner hinge plate supported by a septum. This stage may have been lost in tachygenesis.

In the ventral valve, the presence of **dental plates** is of much interest because in a number of cases this is a good diagnostic feature. The Permian terebratulids may be subdivided in two large groups according to the structure of the ventral valve. The group lacking dental plates comprises warm-water terebratulids from the Paleoequatorial Superregion and consists of the superfamilies Centronelloidea, Gilledioidea, Terebratuloidea, Loboidothyroidea, and Angustothyridoidea. The group comprising terebratulids with dental plates consists of the boreal superfamilies Dielasmatoidea and Compositolasmatoidea. Thus, the presence or absence of dental plates may characterize high-level taxa such as groups of superfamilies. In Permian terebratulids, we revealed five types of dental plates according to their orientation to the plane of symmetry. The first type consists of dental plates adjacent to the umbo wall (Fig. 9a). It is typical of small or middle-sized shells from the family Compositelasmatidae, especially *Compositelasma evolutum* and *Campbellelasma variiforme.* Ontogenetic studies may help in generic determination in the two above-mentioned genera. The second type consists of diverging dental plates (Fig. 9b), which are a characteristic feature of the family Compositelasmatidae, representatives of which often retain this feature for their whole life; e.g., *Grigorjevaelasma rossica* and *Calycelasma kalaschnikovi.* Adult specimens of many species from the family Dielasmatidae also have

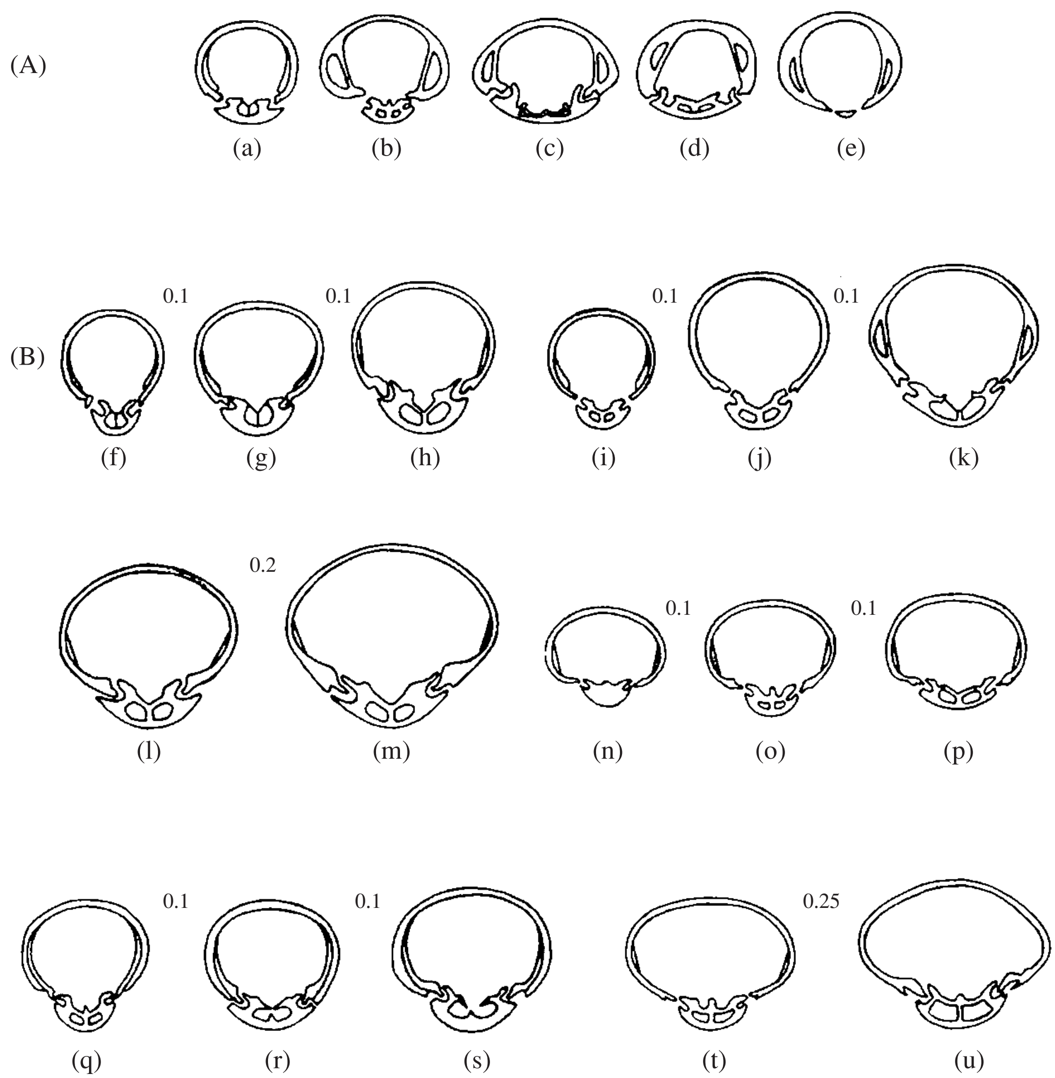


Fig. 9. (A) Types of dental plates: (a) adjacent to the umbo wall, (b) diverging, (c) subparallel, (d) converging, and (e) concave; (B) shape of dental plates at different developmental stages in *Compositelasma evolutum*, serial cross sections through the apical region of the umbo: (f)–(h) 4.2-mm-long shell; (i)–(k) 4.3-mm-long shell; (l) and (m) 6-mm-long shell; *Campbellelasma variiforme*: (n)–(p) 5-mm-long shell, (q)–(s) 6.1-mm-long shell; (t) and (u) 7.1-mm-long shell; figures indicate distances between the sections in mm.

diverging dental plates, e.g., *D. kirillowense, D. robustum, D. jakowlewi*, and all *Fletcherithyris* and *Yochelsonia* species.

Subparallel dental plates constitute the third type (Fig. 9c) and have been found in *Beecheria angusta*, *B. netschajewi*, and *Tapetulasma boltaevae* of the family Beecheriidae. This type may be regarded as a subsidiary diagnostic feature of the family Beecheriidae. The fourth type consists of converging dental plates (Fig. 9d). It has only been recorded in an adult shell of *Beecheria samarica.* The fifth type, which consists of dental plates that are concave toward the plane of symmetry, has been observed in an adult specimen of *Dielasma kirillowense* (Fig. 9e).

Ontogenetic study of the internal structure makes it possible to determine the time when the dental plates begin to develop in five species of the family Compositelasmatidae. The earliest appearance was detected in a 3.8-mm-long shell of *Gruntelasma bajtuganensis*, in which the dental plates are located close to the umbo wall but are not fused with it. At all developmental stages, the dental plates remain thin, diverging, and bordering narrow umbonal remains in the ontogeny of *Grigorjevaelasma rossica* and *Calycelasma kalaschnikovi.* Young specimens of *Compositelasma evolutum* with a 4.2-mm-long shell have dental plates pressed to the umbo wall or slightly diverging from it to form narrow slitlike umbonal cavities (Figs. 9f–9h). In a 4.3-mm-long specimen, the dental plates are tightly

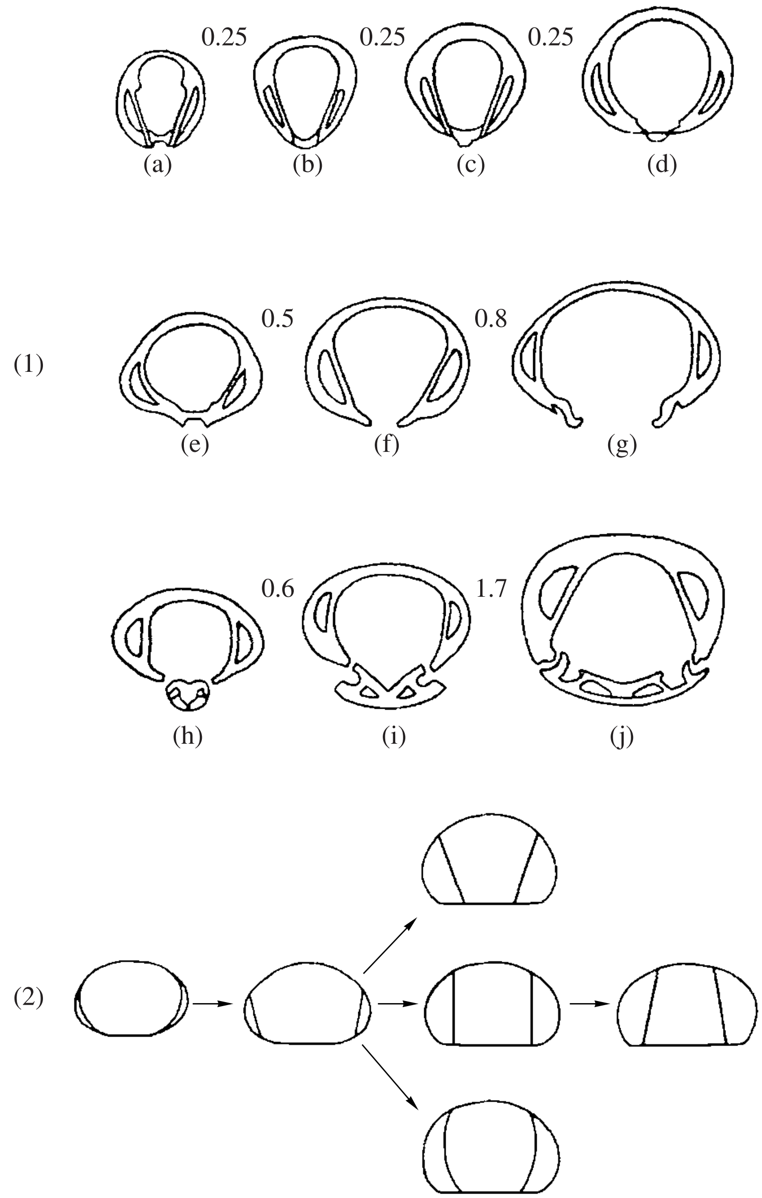


Fig. 10. (1) Developmental changes of the dental plates in a single specimen, serial cross sections through the apical region of the umbo: (a)–(d) *Dielasma kirillowense.* (e)–(g) *D. subelongata*; (h)–(j) *Beecheria samarica;* figures indicate distances between the sections in mm. (2) Scheme of the assumed relations between different types of dental plates.

pressed to the umbo wall in the apical region and deviate from it anteriorly (Figs. 9i–9k). In the shells longer than 6 mm and up to the adult stage, the dental plates are diverging and do not touch the umbo wall (Figs. 9l, 9m). The developmental changes of dental plates in ontogeny may be observed in *Campbellelasma variiforme.* In a 5-mm-long shell (Figs. 9n–9p) and in a 6.1-mm-long shell (Figs. 9q–9s), the dental plates are pressed to the umbo wall. In a 7-mm-long shell (Figs. 9t, 9u), they are separated from the umbo wall by narrow cavities and continue to diverge up to the adult stage. In this case, ontogenetic study may help to restrict generic determination to two genera, *Compositelasma* and *Campbellelasma*. Data on the ontogeny confirm the preservation of the developmental stages of the dental plates in one shell. Developmental changes in the form of dental plates can be observed in series of polished cross sections. Sometimes several types of dental plates are preserved in one specimen. In *Dielasma kirillowense* (Figs. 10.1a–10.1d), the dental plates are diverging near the apex of the umbo and became more convex anteriorly toward the lateral sides of the ventral valve. In *Dielasma subelongatum* (Figs. 10.1e–10.1g), the diverging dental plates are replaced by subparallel ones. In *Beecheria samarica* (Figs. 10.1h–10.1j), the

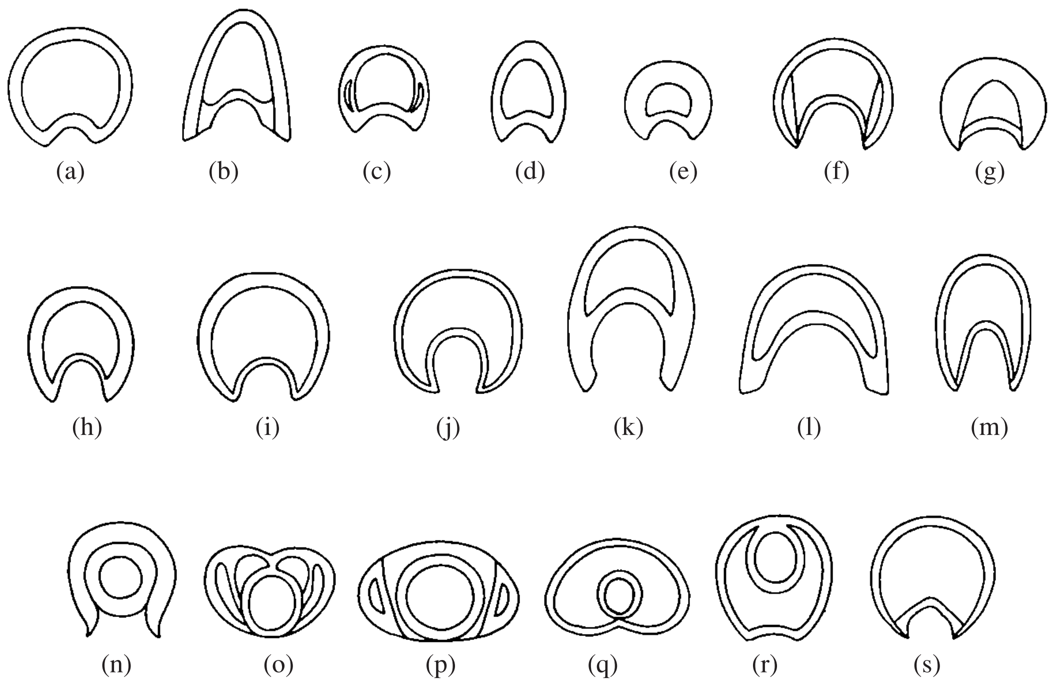


Fig. 11. Morphological diversity of the pedicle collar. Gently arched pedicle collar: (a) *Dielasma robustum*, (b) *D. kirillowense*, (c) *Hoskingia wandageensis*, (d) *Beecheria kargaliensis*, (e) *B. netschajewi*; average deep pedicle collar: (f) *Tapetulasma boltaevae,* (g) and (h) *Fredericksolasma lata*, (i) *F. darvasica*; deep pedicle collar: (j) *Pyandzhelasma juresanensiforme*, (k) and (l) *Hemiptychina sparsiplicata*, (m) *Gundarolasmina acutangulum*; ring-shaped pedicle collar: (n) *Dielasma jakowlewi*, (o) *Fletcherithyris reidi*, (p) *Beecheria samarica*, (q) *Calycelasma kalaschnikovi*, (r) *Hemiptychina mirabilis*; angular pedicle collar: (s) *Sokelasma esaulovae.*

dental plates change from subparallel to converging in the anterior half.

Ontogenetic study reveals the succession of different types of dental plates (Fig. 10.2). The oldest dental plates are possibly those adjoining the umbo wall. This type of dental plates were retained in the ontogeny of two genera, *Campbellelasma* and *Compositelasma*. In other cases, the plates possibly disappeared in tachygenesis. In cross sections of *Campbellelasma variiforme* (Figs. 9q–9u), pressed dental plates move aside from the umbo wall to form slitlike umbonal cavities that are bordered by thin, diverging dental plates. This type of dental plates were probably ancestral to the concave dental plates, e.g., *D. kirillowense* (Figs. 10.1a–10.1d), and to the subparallel dental plates, e.g., *Dielasma subelongatum* (Figs. 10.1e, 10.1g). Parallel dental plates possibly originated from converging dental plates, e.g., *Beecheria samarica* (Figs. 10.1h–10.1j).

Pedicle collar is developed in almost all of the species studied. It is morphologically highly variable. The comparative analysis is restricted to the anterior region of the pedicle collar. Series of sections with ontogenetic changes of structure are given separately. Five types of the pedicle collar are recognized: (1) gently-curved, arc-shaped, only slightly entering the umbonal penetrating cavity; (2) medium-deep, entering the umbonal cavity at less than half of its height; (3) deep, entering the umbonal cavity more that half of its height; (4) ring-shaped; and (5) angular. In every family several types of the pedicle collar are usually developed. All morphological types were revealed in the family Compositelasmatidae.

The gently-curved, arc-shaped pedicle collar is the simplest type of the structure. It is known in most of the families, but most commonly in Dielasmatidae, e.g., *Dielasma robustum* (Fig. 11a), *D. kirillowense* (Fig. 11b), and *Hoskingia wondageensis* (Fig. 11c), and in Beecheriidae, e.g., *Beecheria kargaliensis* (Fig. 11d) and *B. netschajewi* (Fig. 11e). The medium-deep pedicle collar is distinguished rather conventionally and sometimes there is hardly any difference from the deep pedicle collar. It is known in the family Beecheriidae, e.g., *Tapetulasma boltaevae* (Fig. 11f), and in *Fredericksolasma lata* (Figs. 11g, 11h) and *F. darvasica* (Fig. 11i) from the family Pseudodielasmatidae. For *F. lata* two serial sections are given; the first section (Fig. 11g) shows a gently-curved, arc-shaped pedicle collar, and the second section (Fig. 11h) shows a medium-deep pedicle collar. Most representatives of the family Gillediidae have a deep pedicle collar. It is well-developed in *Pyandzhelasma juresanensiforme* (Fig. 11j), *P. piriforme, Mongolina subdieneri* (Fig. 11k), *Hemiptychina sparsiplicata* (Fig. 11l), and *Gundarolasmina acutangulum* (Fig. 11m). In rare

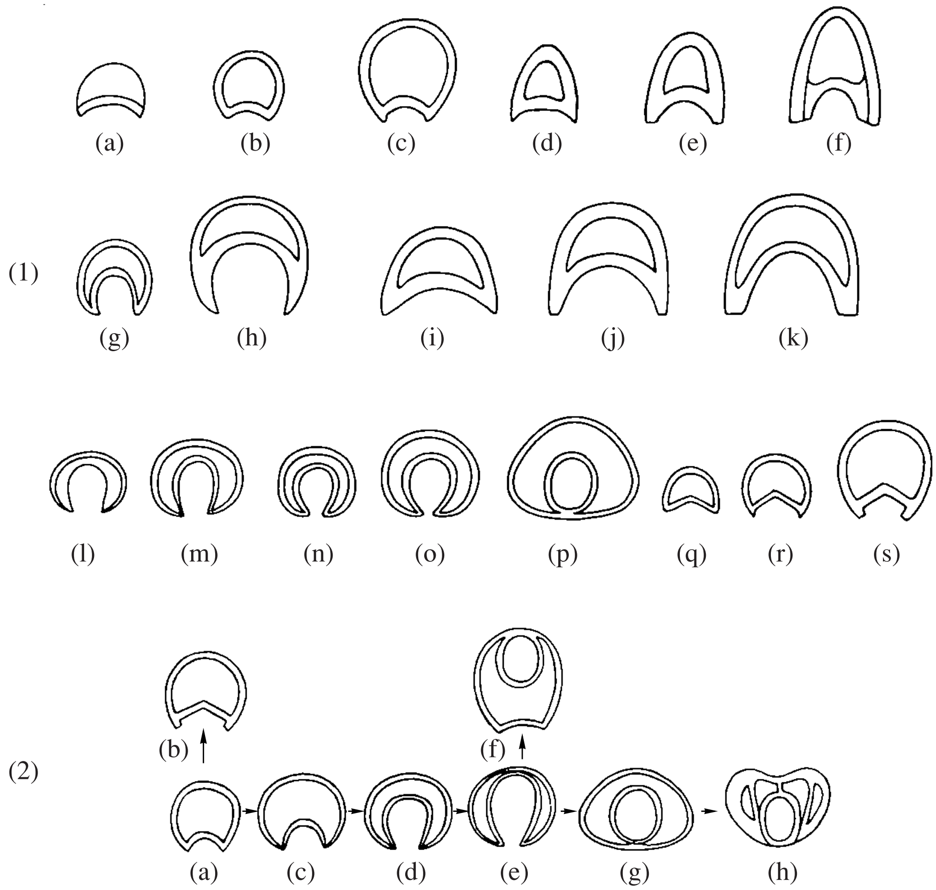


Fig. 12. (1) Pedicle collar remains gently arched in the development of *Gruntelasma bajtuganensis*: (a) 3.8-mm-long shell, and adult (b) 11.7-mm-long shell and (c) 15.1-mm-long shell; (d)–(f) pedicle collar remains gently arched in all sections through the adult shell of *Dielasma kirillowense*; pedicle collar remains deep in the 6.4-mm-long shell (g) and section through adult 14.5-mm-long shell (h) of *Grigorjevaelasma rossica*; shape of pedicle collar changes from gently arched (i) through average deep pedicle collar (j) to deep pedicle collar (k) in sections through one shell of *Hemiptychina sparsiplicata*; deep pedicle collar in 6-mm-long shell of *Calycelasma kalaschnikovi* (l) and (m) transforms through looplike pedicle collar in 7.2-mm-long shell (n) and (o) to ring-shaped in adult shells (p); angular pedicle collar preserves in 2.9-mm-long shell (q), 6.3-mm-long shell (r), and adult 15-mm-long shell (s) of *Compositelasma evolutum*; figures indicate distances between the sections in mm. (2) The assumed transformations of pedicle collar in Permian terebratulids: (a) gently arched, (b) angular, (c) medium deep, (d) deep, (e) looplike, (f) ring-shaped and adjacent to the outer wall of umbo, (g) ring-shaped and adjacent to the inner wall of umbo, (h) ring-shaped with a vertical vinculum, which fastens it to the outer wall of umbo.

instances this type of pedicle collar is developed in the family Compositelasmatidae. The ring-shaped pedicle collar was found in the families Dielasmatidae, Beecheriidae, Gillediidae, and Compositelasmatidae. It is developed mainly in massive shells with a strongly curved umbo. Such shells are supported over the substrate by a solid tube that entirely envelops the pedicle base. Several types of ring-shaped pedicle collar were revealed. The wide pedicle collar is closely adjacent to the umbo wall in *Dielasma jakowlewi* (Fig. 11n). In *Fletcherithyris reidi* (Fig. 11o), the ring-shaped pedicle collar is located between the dental plates, touches them, and fastens to the outer wall of the umbo with a short vertical vinculum. The ring-shaped pedicle collar may lean on the inner side of the umbonal cavity while not touching the dental plates and the outer wall of the umbo, as in *Beecheria samarica* (Fig. 11p). An adult specimen of *Calycelasma kalaschnikovi* (Fig. 11q) has a pedicle collar that also leans on the inner side of the umbo. The ring-shaped pedicle collar adjoins the outer wall of the umbo only in *Hemiptychina mirabilis* (Fig. 11r). The angular pedicle collar is only known in *Sokelasma esaulovae* (Fig. 11s) from the family Beecheriidae and in *Compositelasma evolutum* (Figs. 12.1q–12.1s) from the family Compositelasmatidae.

Study of the development stages in numerous shells revealed that the pedicle collar appears early in ontogeny. The smallest specimen with a pedicle collar is 2 mm long. The initial form is probably the gently-curved, arc-shaped pedicle collar. It may remain unchanged in ontogeny, as in *Gruntelasma bajtuganensis*.

In this species, the pedicle collar remains gently curved and arc-shaped in shells that are 3.8 mm long (Fig. 12.1a) 11.7 mm long (Fig. 12.1b) and in an adult 15.1-mm-long shell (Fig. 12.1c). In serial cross sections through the umbo of an adult shell of *Dielasma kirillowense* (Figs. 12.1d–12.1f), the pedicle collar remains shallow all over its length. The deep pedicle collar may also remain unchanged, as in two developmental stages of *Grigorjevaelasma rossica* in which a deep pedicle collar is observed in a 6.4-mm-long shell (Fig. 12.1g) and in an adult 14.5-mm-long specimen (Fig. 12.1h). The type of the pedicle collar may change in development. In the serial cross sections through the umbo of *Hemiptychina sparsiplicata*, the pedicle collar gradually transforms from the gently-curved, arc-shaped (Fig. 12.1i) to the medium-deep (Fig. 12.1j) and then to the deep pedicle collar (Fig. 12.1k). The transformation of the pedicle collar from the deep to the ring-shaped was traced in *Calycelasma kalaschnikovi.* In the first section of a 6-mm-long shell, the pedicle collar is shaped like a high arc and touches the outer wall of the umbo (Fig. 12.1l). In the next section, the pedicle collar moves from the outer wall of the umbo to become loop-shaped (Fig. 12.1m). The first section of a 7.2-mm-long shell again shows a loop-shaped pedicle collar typical of the previous stage (Fig. 12.1n). In the next section, the pedicle collar gradually moves off from the outer wall of the umbo (Fig. 12.1o). The last section shows the ring-shaped pedicle collar that is far removed from the outer wall of the umbo and rests on the inner surface of the umbo (Fig. 12.1p). The adult shells have the same form of the pedicle collar: the subsequent stages follow the form of the previous stages. The ring-shaped pedicle collar is a derivative of the deep pedicle collar: it results from the closure of the inner side of the latter. The ring-shaped pedicle collar could support the pedicle all around. Early developmental stages of the pedicle collar are fixed in ontogeny and may be traced in a single adult specimen during serial cross sectioning through the umbo. *Compositelasma evolutum* preserves the angular pedicle collar through all developmental stages, in the smallest 2.9-mm-long shells (Fig. 12.1q), at the middle stages in a 6.3-mm-long shell (Fig. 12.1r), and in adult 15-mm-long shells (Fig. 12.1s). It can be assumed that the pedicle basis was triangular in section. The angular pedicle collar was possibly derived from the gently-curved, arc-shaped pedicle collar, which resembles the former in shape.

Study of the developmental stages in the shells of different size and the observation of changes of the pedicle collar in the serial sections of adult shells preserving junior stages reveal the direction of the ontogenetic changes in this structure and the relations between different types of pedicle collar. The gently-curved, arc-shaped pedicle collar is an initial form that gave rise to the other types of this structure (Fig. 12.2a). The main direction is the deepening into the umbonal cavity to form the medium-deep (Fig. 12.2c) and then the deep pedicle collar (Fig. 12.2d). The deep pedicle collar gives rise to the loop-shaped variety (Fig. 12.2e) and several types of the ring-shaped pedicle collar (Figs. 12.2f–12.2h). The angular pedicle collar is a separate branch (Fig. 12.2b). The shape of the pedicle collar, varying from the gently-curved, arc-shaped to the deep and the ring-shaped, reflects the degree of the pedicle attachment and determines the angle that the shell makes with the substrate. The mass of the shell is also important. A more massive shell requires a larger area for pedicle support. This is obtained by the deepening of the pedicle collar. The shape of this structure is a good characteristic feature of a species rank. In a number of cases it may be used in generic diagnoses. *Pyandzhelasma* species have the deep collar, while *Fredericksolasma* species have the gently-curved, arc-shaped pedicle collar. The deep pedicle collar is developed in six species belonging to five genera of the family Gillediidae. In this family, the shape of the pedicle collar is a secondary taxonomic feature.

CHAPTER 3. THE MAIN ONTOGENETIC TRANSFORMATIONS OF THE BRACHIDIUM OF PERMIAN TEREBRATULIDS AND THEIR PHYLOGENETIC RELATIONSHIPS WITH MESOZOIC TEREBRATULIDS

The main difficulties in the study of the brachidium evolution in terebratulids result from the preservation of only one of several developmental stages in the shell and the formation of morphologically similar brachidium structures in adult stages of different phylogenetic branches. The ontogenetic study of this group yields the most reliable results, which may be useful in taxonomy and phylogenetic research. The study of the development of brachidium in Mesozoic and Cenozoic terebratulids started about 150 years ago, and a considerable body of data has been accumulated since that time. Early publications were Moore (1860), Friele (1877), Beecher (1893), Thomson (1927), Elliott (1950), etc. Russian specialists made an important contribution to the study of the ontogeny of modern (Konzhukova, 1948, 1957) and fossil (Kats, 1962; Antoshchenko, 1969, 1970; Smirnova, 1962, 1984; Dagys, 1968, 1972) terebratulids.

The development of Paleozoic terebratulids is less studied. The ontogeny of the Permian genus *Dielasma* was described in the earliest papers (Beecher et Schuchert, 1893; Watson, 1909). Stehli (1956) described the development of the brachidium in the Devonian *Cranaena*. Cooper and Grant (1976) studied ontogenetic changes in *Texarina, Heterelasma*, and *Glossothyropsis* from the Permian of Texas.

Two main types of the brachidium development were revealed (Beecher, 1893). In the simple type, the

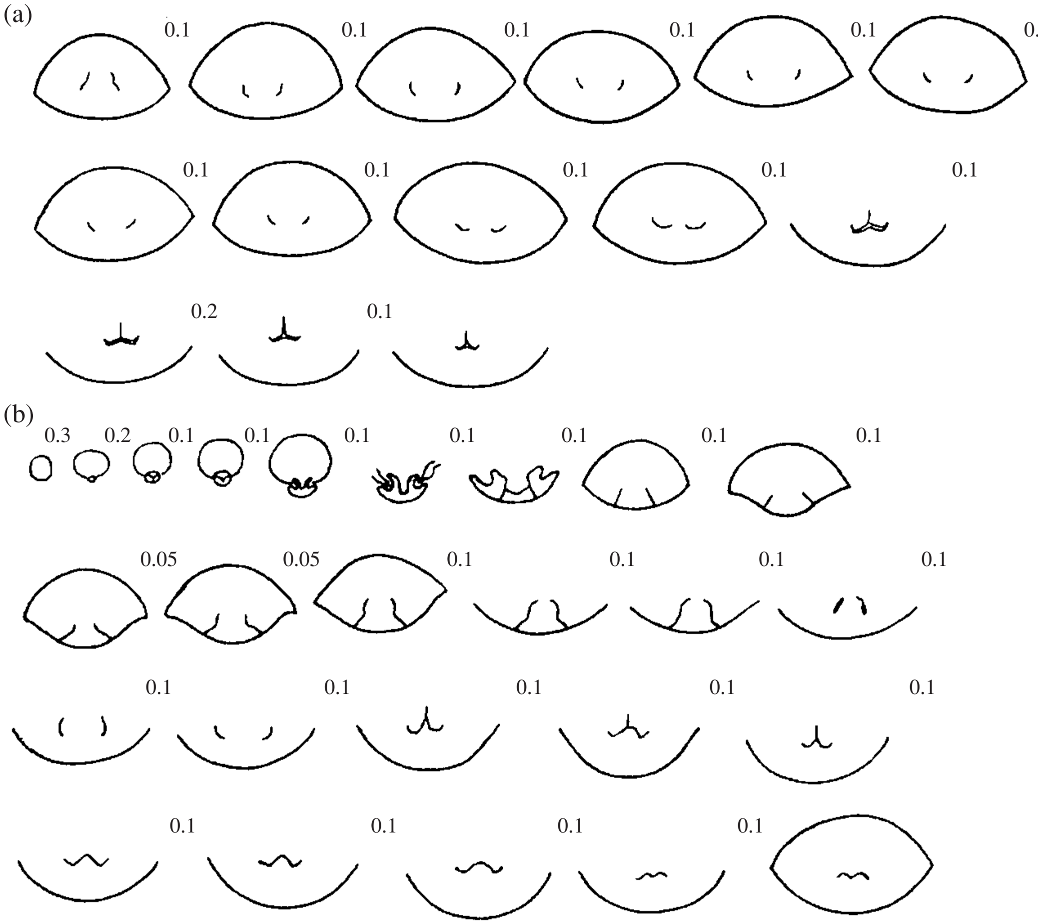


Fig. 13. *Heterelasmina cuboides* Smirnova, 2001; serial sections through the shell: (a) specimen PIN, no. 4104/15, 6.5-mm-long shell, (b) specimen PIN, no. 4104/16, 7.1-mm-long shell; figures indicate distances between the sections in mm.

brachidium grows away from the cardinalia and develops based on the centronelloid loop without secondary elements to form a short triangular loop at the adult stage. In this case the loop experiences no complicated transformations. This type of development, with a well-pronounced centronelloid stage is called dielasmoid for the Paleozoic terebratulids. The simple type of loop development, usually lacking a distinct centronelloid stage, which could be reduced in the accelerated development, is characteristic of Meso-Cenozoic terebratulids and is called terebratuloid (Dagys, 1968, 1972). The complicated development of brachidium is connected with the appearance of a vertical plate at the junction of the descending branches or on the dorsal septum. The secondary elements of the loop form in a variety of ways through several developmental stages based on transformations of the vertical plate. These transformations usually result in a complicated loop, which is commonly long. Dagys (1974) established the presence of zeilleroid, dallinoid, loboidothyridid, angustothyridid, and aulacothyroid types of brachidium development in the Mesozoic. He noted that the development of secondary elements of brachidium based on a vertical plate that appeared at the early developmental stages was restricted to the Mesozoic and Cenozoic. The modes of the formation of brachidium, which are characterized by different types of ontogeny, may serve as a basis for establishing families and superfamilies.

The first terebratulids with a complicated loop (*Cryptonella*) appeared in the Devonian. Cooper (1957) studied brachidium development in the Paleozoic terebratulids with a long loop (Carboniferous *Cryptacanthia*) and revealed the absence of secondary elements in ontogeny. Cooper and Grant (1976) described many ontogenetic stages for these two genera and stated that they developed in a *Cryptacanthia-like mode*, i.e., without participation of the vertical plate.

Dagys (1972) studied brachidium ontogeny in the Upper Permian *Labaia muirwoodae* Licharew and *Gefonia cubanica* Licharew from the Urushten Formation of northwestern Caucasia. He discovered a vertical plate that gave rise to complicated loops. Smirnova (1985) described the development of the brachidium in *Notothyris pseudojoulfensis* Licharew and *Gefoni*a sp. from the Upper Permian of the southeastern Pamirs.

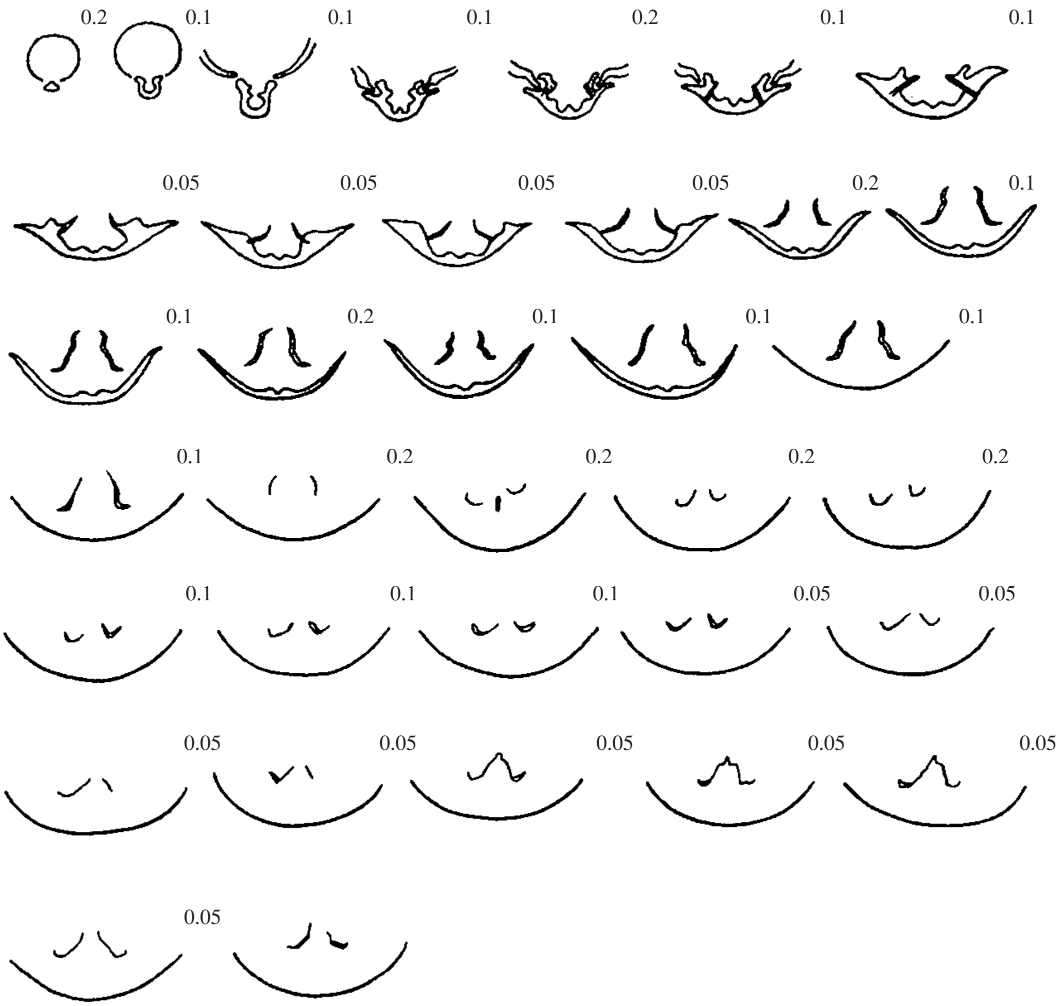


Fig. 14. *Heterelasmina cuboides* Smirnova, 2001, specimen PIN, no. 4101/17, serial sections through a 8.2-mm-long shell; figures indicate distances between the sections in mm.

She revealed the presence of a high vertical plate and described its transformations in successive developmental stages in *Notothyris pseudojoulfensis* and the formation of secondary elements of the loop based on the plate in *Gefonia* sp. Reconstructions of the development of the brachidium were made.

Complicated brachidium development with secondary elements developed on the basis of a vertical plate was revealed in the ontogenetic study of the Late Permian terebratulids from the northern Pamirs (southwestern Darvaz) and the Russian Platform. Grunt (1995) studied ontogeny in the families Notothyrididae, Heterelasminidae, and Pseudodielasmatidae from the southeastern Pamirs and southwestern Darvaz (Paleoequatorial Superregion) and the family Compositelasmatidae from the Russian Platform (Boreal Superregion). It was found that these areas, which belong to different paleozoogeographic regions, possess different types of ontogeny.

In the study of the ontogeny of *Heterelasmina cuboides* Licharew (which is closely related to the type species of the genus *Heterelasmina*, *H. dieneri*) from the Bolorian Stage of the Lower Permian of the southwestern Darvaz, the terebratuloid type of brachidium development was discovered (Smirnova, 2001). The following ontogenetic stages were revealed in the development of *Heterelasmina cuboides.* A 6.5-mm-long specimen (Fig. 13a) shows a stage close to the centronelloid but differs from the latter in the absence of a dorsally directed plate growing away from the junction of the descending branches with the vertical plate. A high vertical ventrally directed plate has been discovered. In a 7.1-mm-long shell (Fig. 13b), the vertical plate is partly split and a sharply curved transverse band of the loop with the remains of a vertical plate appears. A 8.2-mm-long specimen (Figs. 14, 16a) has differentiated descending branches and a transverse band with a pointed projection in the middle, which is a split of

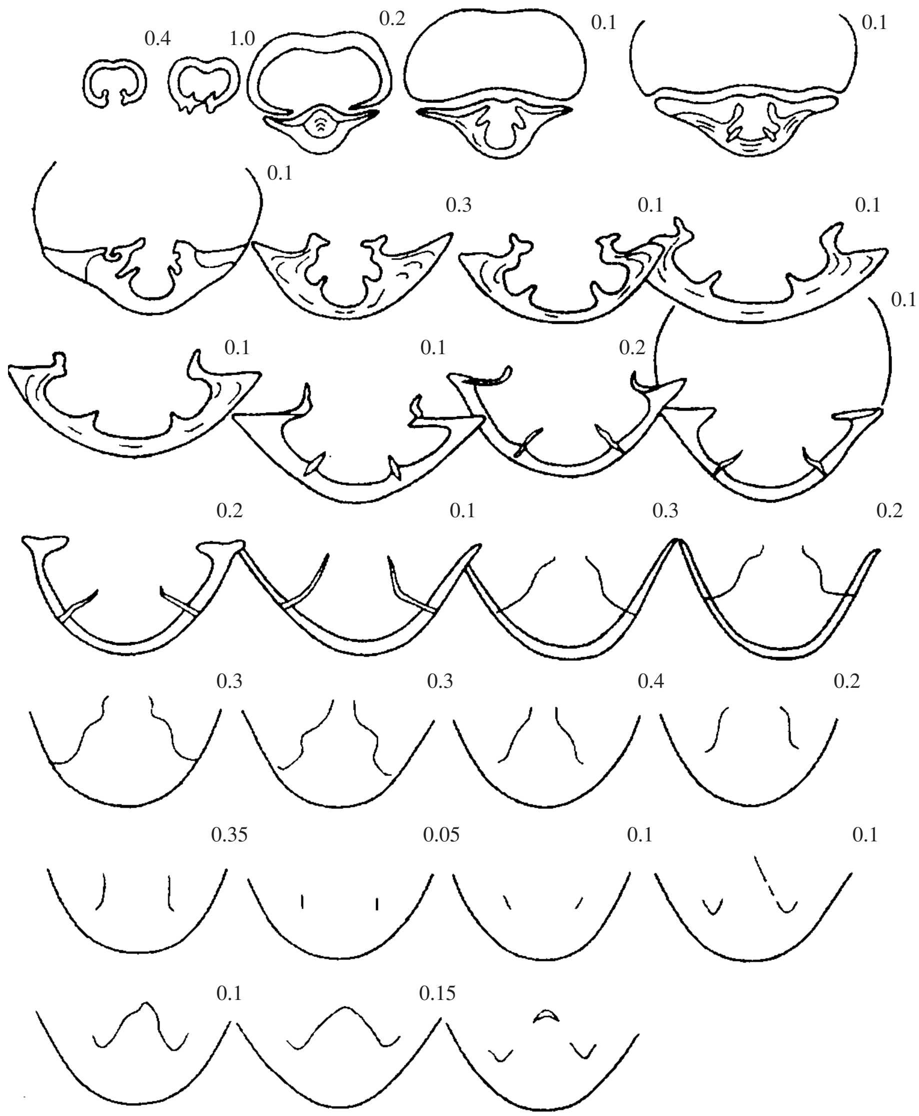


Fig. 15. *Heterelasmina cuboides* Smirnova, 2001, specimen PIN, no. 4104/18, serial sections through a 14.4-mm-long adult shell; figures indicate distances between the sections in mm.

the vertical plate. In adult shells longer than 14.4 mm (Figs. 15, 16b), the loop is about one-third of the dorsal valve length, triangular, and without evidence of a vertical plate.

In *Fredericksolasma lata* (Licharew) (family Pseudodielasmatidae) from the Gundara Formation (Upper Permian) of the southwestern Darvaz, a complicated loboidothyridid type of brachidium development was established (Smirnova, 2001). Two 3.8-mm-long specimens (Fig. 17a) have a centronelloid-like loop consisting of descending branches, with a ventrally directed vertical plate, with a small thickening at the top, at the junction of the branches. In a 4.5-mm-long shell (Fig. 17b), the thickening at the end of the vertical plate transforms into a small hood. In a 4.8-mm-long specimen (Fig. 18a), the hood enlarges to become irregular hexagonal, the vertical plate splits, and the descending branches diverge but remain connected with the hood. This stage may be compared with the campagiform stage. In a 5.5-mm-long shell (Fig. 18b), the dorsal wall of the hood, which connects the hood with the diverging branches of the loop, reduces. The branches diverge to form a free loop with a wide transverse band, which is the ventral wall of the hood. This is the early dictiothyridid stage. In a 9.7-mm-long shell (Fig. 19), the loop corresponds to the dictiothyridid stage. The hood loses the dorsal junction with the loop branches. The divergence of the descending loop branches increases. The loop flanks appear. An adult 14.5-mm-long shell (Fig. 20) has a short, narrow, triangular loop, which corresponds to the terebratuloid

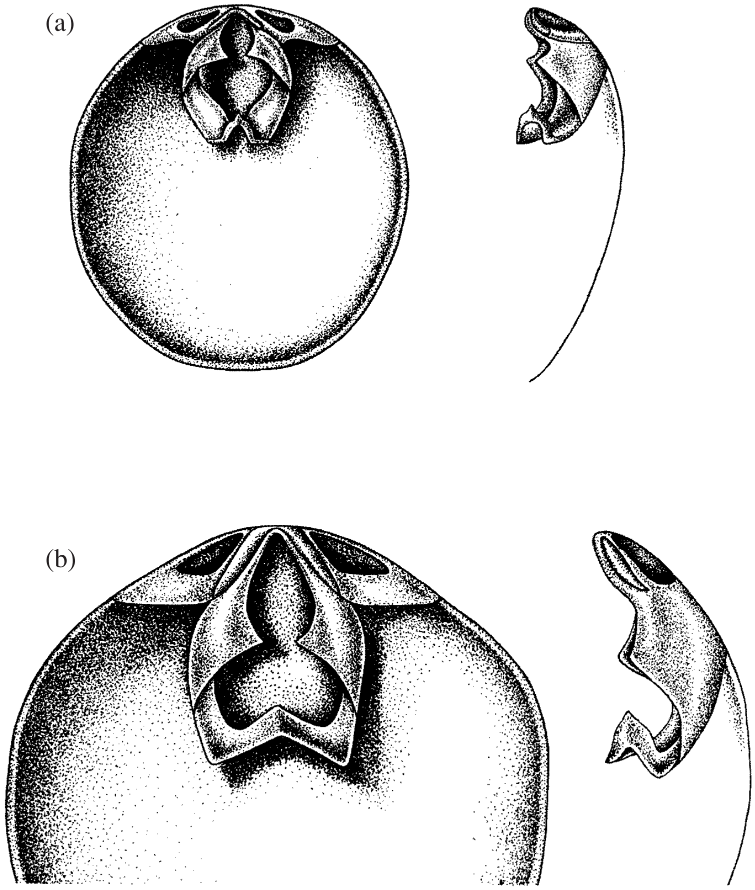


Fig. 16. *Heterelasmina cuboides* Smirnova, 2001, reconstruction of the internal structures in specimens with lengths (a) 8.2 mm and (b) 14.4 mm.

stage. The inner structure is reconstructed for four developmental stages of *Fredericksolasma lata* (Figs. 21a–21d).

In the Permian family Notothyrididae, secondary elements appear at early developmental stages; e.g., *Notothyris pseudojoulfensis* Licharew from the Upper Permian of the southeastern Pamirs (Smirnova, 1985). A 3.5-mm-long specimen lacks a visceral foramen. The crural bases have ventral and dorsal tips. The descending branches of the brachidium are wide and fuse to form a well-pronounced echmidium. The vertical plate is absent. A 4.2-mm-long specimen (Fig. 22) also lacks a visceral foramen. The descending branches are wide and steeply curved in the middle at the junction with the vertical plate. A 7.9-mm-long shell has a small well-pronounced visceral foramen. The foramen is bordered by the inner hinge plate, which is formed by the fusion of the ventral tips of the crural bases. The loop branches are short and are connected with a small vertical plate. The ventral tip of the plate bears a well-developed thickening, which is a primordium of the ascending plate. The loop branches are strongly curved anteriorly. A 9.7-mm-long shell has a visceral foramen. The loop branches are narrow and are connected with a high vertical plate. An ascending plate appears from the thickening in the anterior part of the vertical plate. The ascending plate differs notably from the vertical plate in the slight curvature and in the thickening at the base. An adult 11.3-mm-long specimen (Fig. 23) has a relatively large visceral foramen. The foramen is confined laterally by the crural bases, which are well pronounced in relief. The inner hinge plate is solid. The loop branches are narrow and are connected with a high vertical plate. The ascending plate is thin, narrow, located on the slightly thickened top of the vertical plate and envelopes the latter in the broadened base. Both plates are oriented differently; the ascending plate is slightly inclined to the vertical plate. The same structures were found in the adult *Rostranteris ovaleformis* Smirnova from the Gundara Formation (Upper Permian) of the southwestern Darvaz. The same deposits yielded shells of *Gefonia licharewi* (=*G.* sp.) of varying age. These shells allowed the postembryonic development of the brachidium to be studied. The smallest 3.8-mm-long specimen (Fig. 24) has a visceral foramen. The

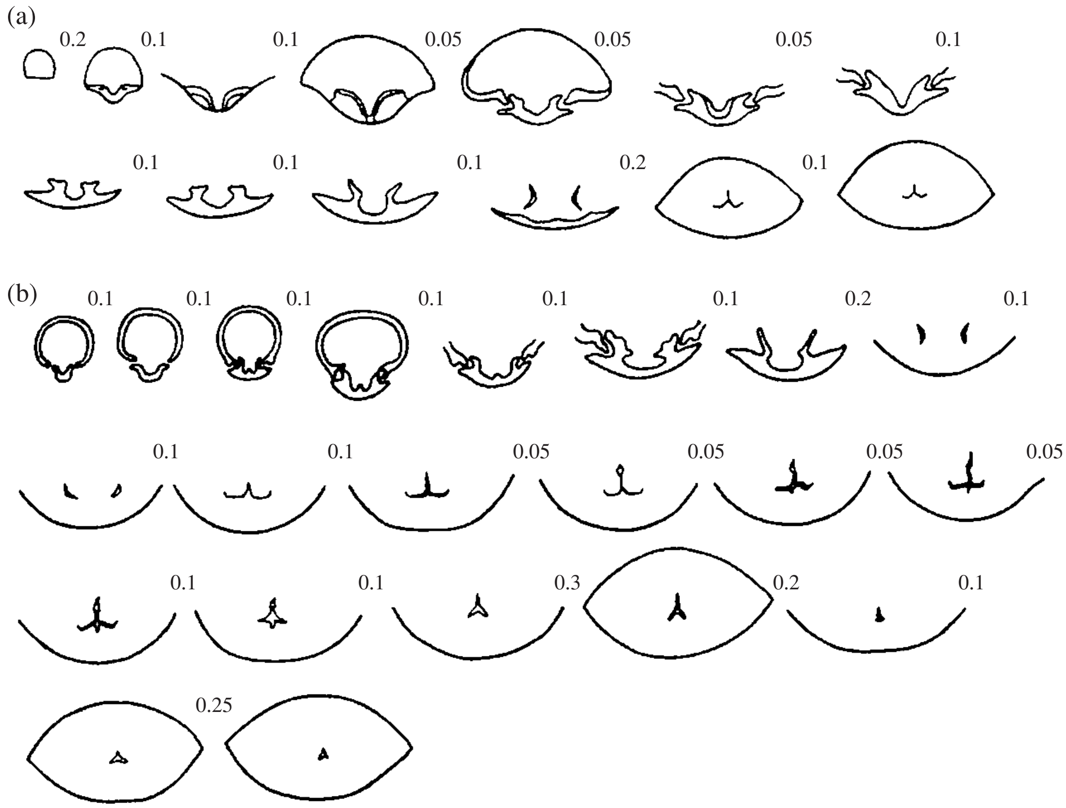


Fig. 17. *Fredericksolasma lata* (Licharew, 1939), serial sections through the shell: (a) specimen PIN, no. 4104/19, 3.8-mm-long shell, (b) specimen PIN, no. 4104/20, 4.5-mm-long shell; figures indicate distances between the sections in mm.

descending branches of the loop are wide and are connected at a considerable distance with a high vertical plate. The branches are angularly curved at the junction. The anterior part of the brachidium bears an ascending plate contacting the vertical plate without enveloping it. The ventral tip of the ascending plate is deeply split and forms wide ascending branches. In a 6-mm-long specimen, the ventral tips of the crural bases grow to touch each other and then fuse to form a single platform. The loop branches are connected with a high vertical plate. The ascending plate is well-pronounced and broadened at the base at the junction with the vertical plate. The ascending branches are widely diverged and connected with the ascending plate. In some sections, small spines are visible at the junction of the descending branches with the vertical plate. In a 7-mm-long shell, the vertical plate partly reduces and the ascending plate reduces completely. The hollow on the dorsal side of the descending branches enlarges up to the splitting of the vertical plate and to the diverging of the descending branches. A small thickening and slightly widened loop branches mark the location of the former vertical plate. The descending and ascending branches fuse in the anterior part of the brachidium. The tips of the ascending branches are slightly curved toward the umbo. Long small spines are developed. In the adult 11- to 12-mm-long shells (Fig. 25), the vertical plate is reduced to a spinelike projection at the fusion of the descending branches. The descending and ascending branches fuse in the middle of the brachidium length. The inner structures of *Notothyris pseudojoulfensis* and *Gefonia licharewi* are reconstructed at different developmental stages (Fig. 26).

Ontogenetic changes in the brachidium of the Late Permian terebratulids from the Russian Platform (Boreal Superregion) were studied for the first time. A special feature of their ontogeny is the presence of two vertical plates at early and middle developmental stages. The dielasmoid type of development, which is typical of Paleozoic terebratulids, is related with one plate. The other plate determines the angustothyridid type of development, known in Triassic terebratulids. Both plates are directed ventrally with respect to the junction of the loop branches with the plate. This type of development was observed in several genera and species of the Late Permian terebratulids from the superfamily Compositelasmatoidea and was referred to as the compositelasmoid type (Smirnova, 2006a). Ontogenetic changes of the brachidium of this type were previously unknown in terebratulids. The most detailed study of ontogeny was conducted for *Compos-*

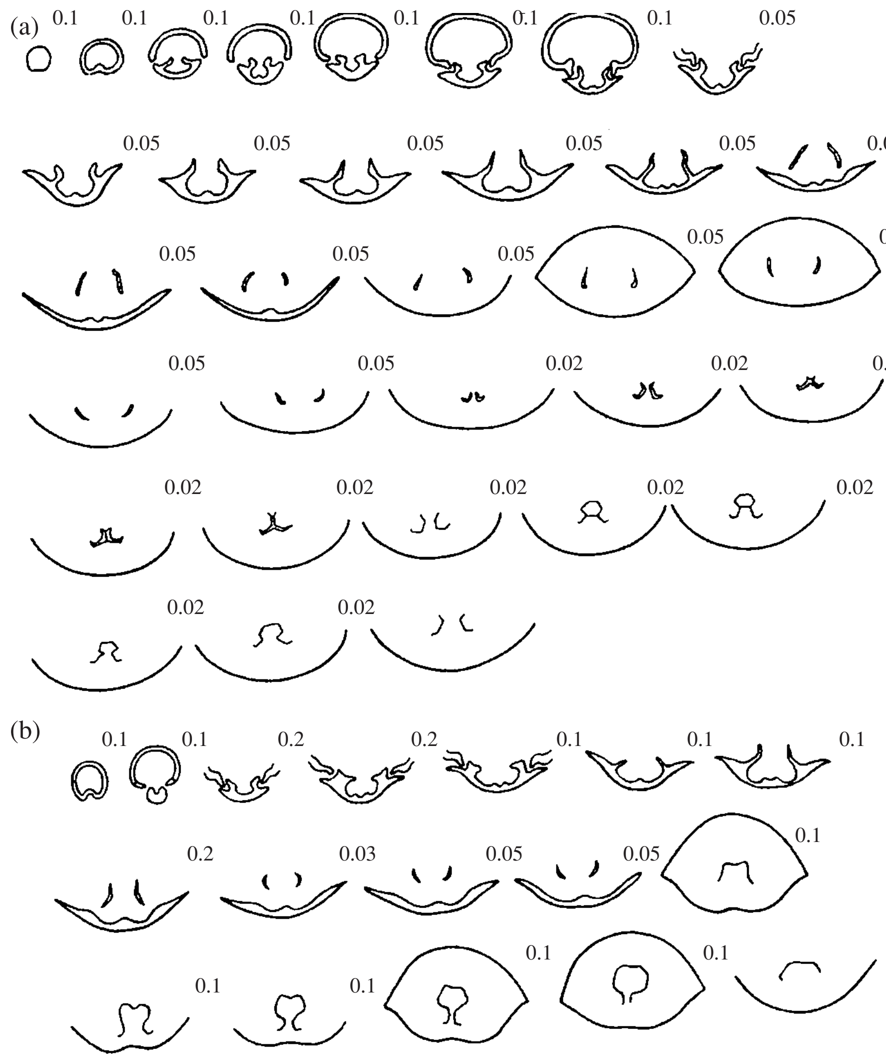


Fig. 18. *Fredericksolasma lata* (Licharew, 1939), serial sections through the shell: (a) specimen PIN, no. 4104/21, 4.8-mm-long shell, (b) specimen PIN, no. 4104/22, 5.5-mm-long shell; figures indicate distances between the sections in mm.

itelasma evolutum Smirnova. The 2.9-mm-long shell (Fig. 27) has two weakly differentiated vertical plates. The first vertical plate is supported by the fused brachidium branches with a distinct ventral bend at their junction. This is the early mutationelliform stage of the dielasmoid type of brachidium development. The second ventral vertical plate has a small thickening on the ventral tip that corresponds to the ascending elements. This stage is close to the late centronelloid stage. In the 3.2-mm-long and 4.2-mm-long shells (Fig. 28), both vertical plates are well-pronounced. The brachidium is deeply curved ventrally at the junction with the first ventral vertical plate—a mutationelliform stage. The second ventral vertical plate has a well-pronounced thickening on the ventral tip and a short dorsal tip projecting beyond the brachidium—a late centronelloid stage. The 5.3-mm-long shell (Fig. 29) has a well-pronounced first vertical plate connected with the brachidium branches, which are ventrally curved at the junction. This structure corresponds to the mutationelliform stage of the dielasmoid type of development. The second ventral vertical plate is split in the thickening (primordium of the ascending element) to form a hood–a campagiform stage of the angustothyridid type of development. The structures corresponding to both types of ontogeny are separated by a small distance. In the 6.2-mm-long shell (Fig. 30), the first vertical plate disappears. The hood on the second plate enlarges and the brachidium branches diverge. This stage corresponds to the dictiothyridid stage of the angustothyridid type of development. In the 7.4-mm-long shell (Fig. 31), the dorsal wall of the hood is reduced. The ventral wall of the hood forms the transverse band of the loop—a late dictiothyridid stage. Larger shells have an adult, almost triangular brachidium, which is characteristic of this species (Fig. 32). The developmental

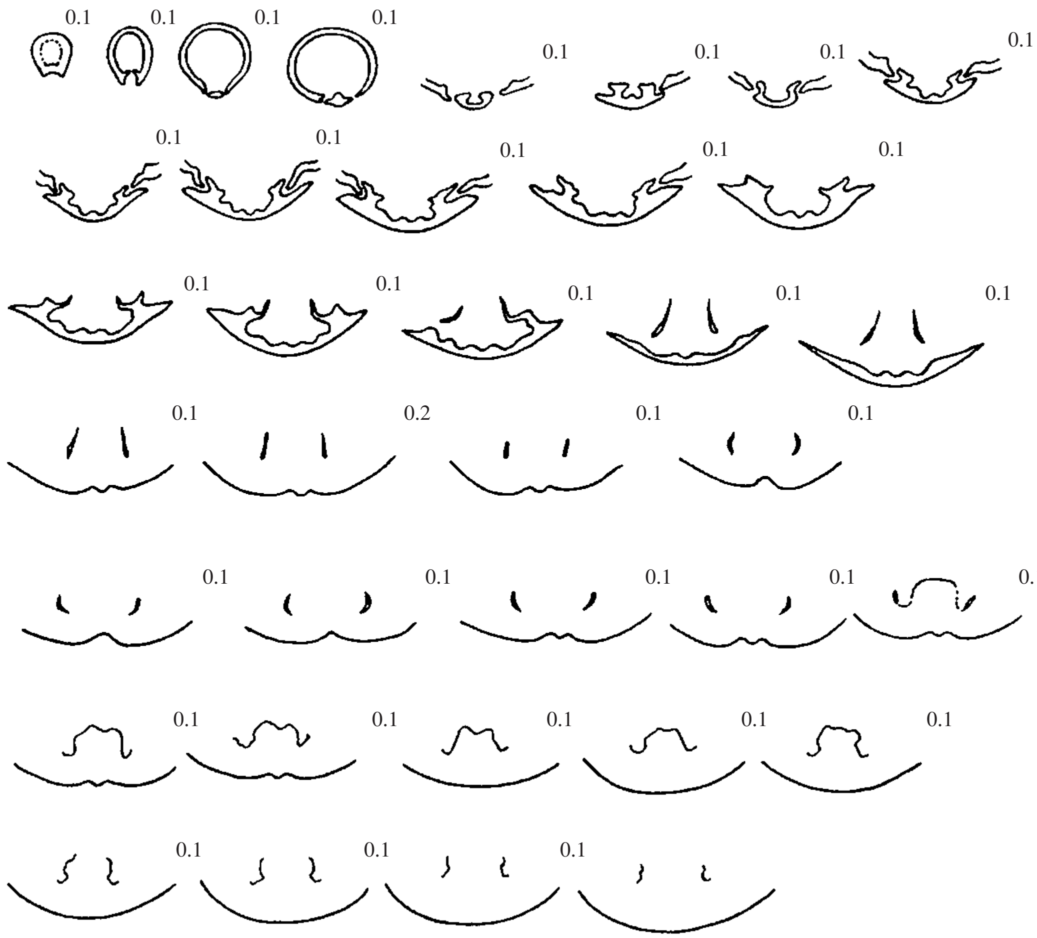


Fig. 19. *Fredericksolasma lata* (Licharew, 1939), specimen PIN, no. 4104/23, serial sections through a 9.7-mm-long shell; figures indicate distances between the sections in mm.

stages of *Compositelasma evolutum* are reconstructed in Fig. 33. In the study of the development of *Gruntelasma bajtuganensis* and *Grigorjevaelasma rossica* (Smirnova, 2006b), the same type of ontogeny was revealed. Based on this fact, the genera *Gruntelasma* and *Grigorjevaelasma* should be referred to the family Compositelasmatidae. The juvenile stages of these genera combine features of the dielasmoid and angustothyridid types of development. Features of the dielasmoid type of development disappear in the middle stage. Only elements of the angustothyridid type are present in the middle and adult stages. The adult triangular loop begins to form when the shell length reaches about one-third of the adult shell. *Campbellelasma* is characterized by the loss of the angustothyridid type of brachidium development during early stages, when the shell length is about one-third of the adult shell, and by the persistence of the dielasmoid type in the middle and adult stages. A 3.0-mm-long shell of *Campbellelasma variiforme* (Fig. 34) has short, laterally curved brachidium branches. The brachidium corresponds to the mutationelliform stage of the dielasmoid type of development. The high first ventral vertical plate is supported by the fused brachidium branches, which are strongly curved ventrally at the junction with the vertical plate. The brachidium length is about two-thirds of the dorsal valve length. The 4-mm-long shell (Fig. 35) shows a short but well-pronounced mutationelliform stage. The vertical plate is low. The ascending branches differentiate anteriorly and then join to form a horizontal platform. The second vertical plate forms in the middle of the platform to give rise to the development of the secondary elements of the brachidium. The brachidium length is about two-thirds of the dorsal valve length. In the 4.6-mm-long shell (Fig. 36), the mutationelliform stage is characterized by a vertical plate and brachidium branches that are fused and curved in the shape of a dome. The descending brachidium branches diverge anteriorly and then fuse to form a single platform with a horizontal surface in the middle. The second vertical plate forms in the middle of the platform near the anterior margin. In the 5-mm-long shell, the brachidium branches are narrow. The first vertical plate is connected with V-shaped, curved, fused descending

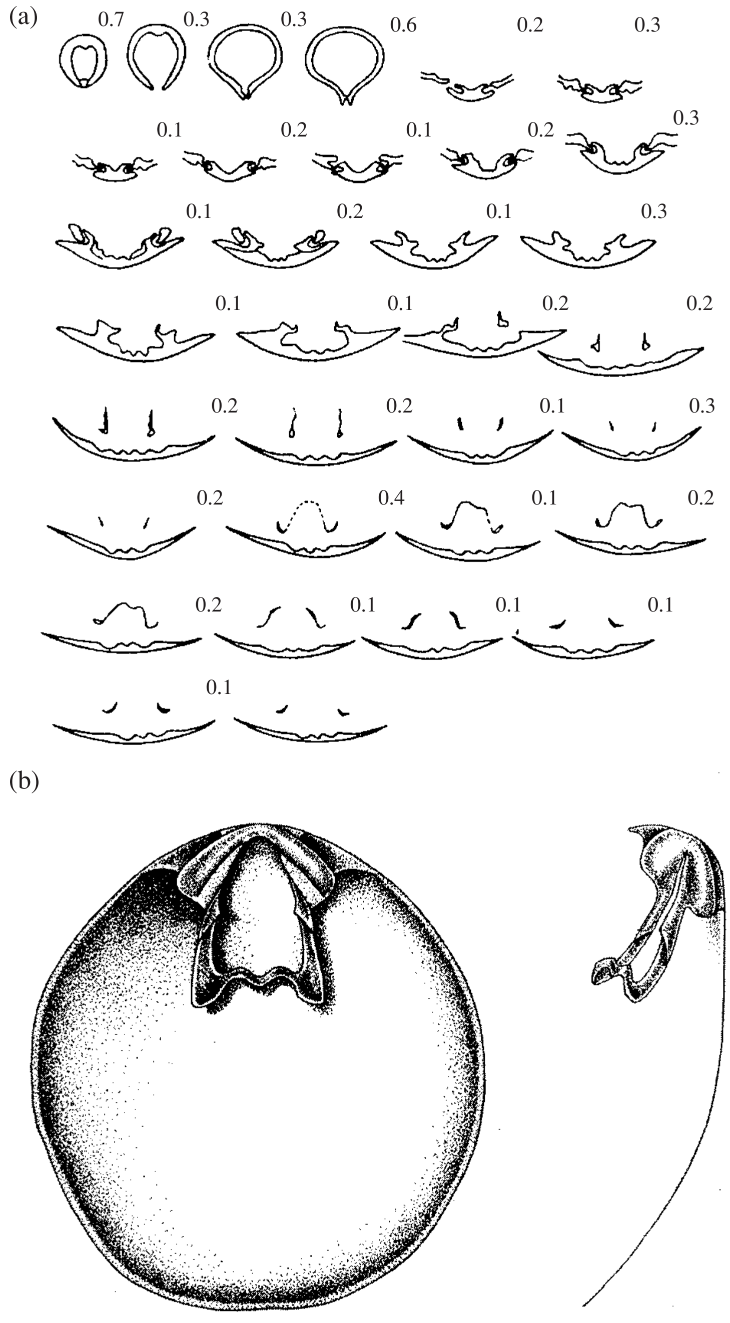


Fig. 20. *Fredericksolasma lata* (Licharew, 1939); (a) specimen PIN, no. 4104/24, serial sections through a 14.5-mm-long adult shell; figures indicate distances between the sections in mm; (b) reconstruction of the internal structures in 14.5-mm-long shell.

branches, that corresponds to the mutationelliform stage of the dielasmoid type of brachidium development. In the anterior part of the brachidium, the plate splits and the transverse band of the loop begins to form. The second vertical plate develops at early stages and disappears in the development of the dielasmoid type. A 6.1-mm-long shell (Fig. 37) has a narrow loop of dielasmoid type. The transverse band of the loop retains features of the mutationelliform stage. In cross section, it is V-shaped with horizontal lateral sides. The loop length is about one-half of the dorsal valve length. The internal structure of the young *Campbellelasma variiforme* is reconstructed in Fig. 38. The adult loop appears in the 12-mm-long shell, the internal structure

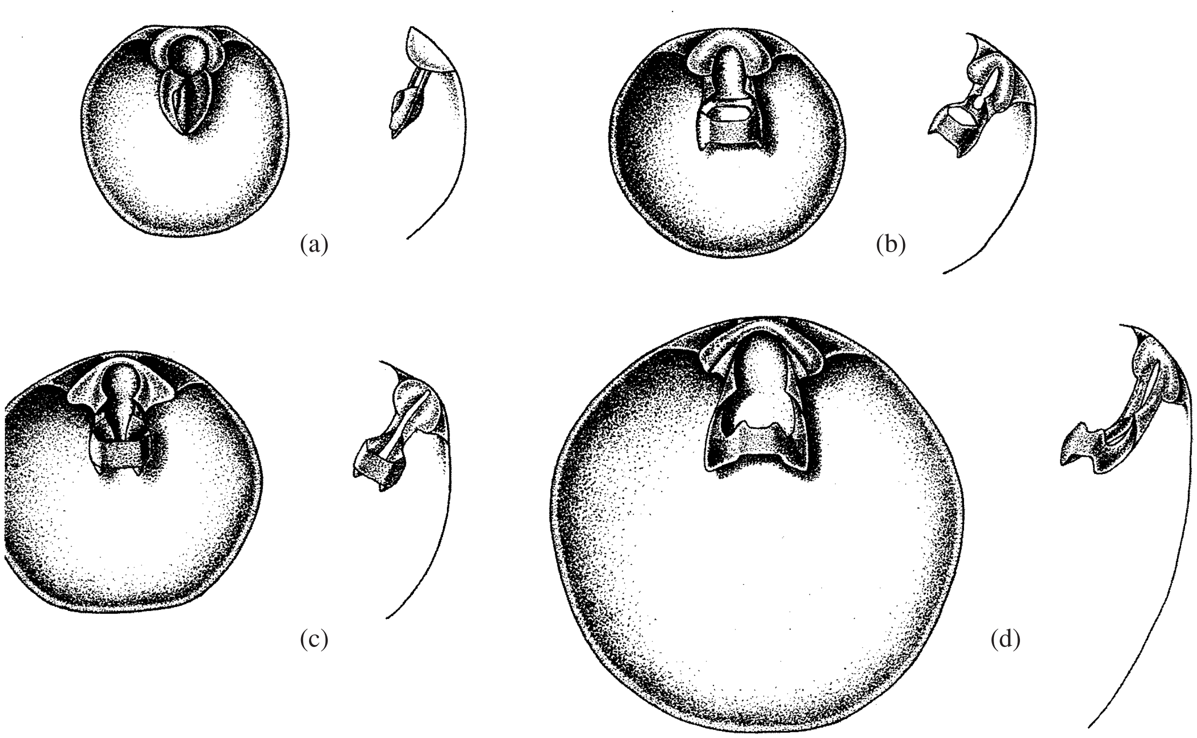


Fig. 21. *Fredericksolasma lata* (Licharew, 1939); reconstruction of the internal structures in specimens with lengths: (a) 4.5 mm, (b) 4.8 mm, (c) 5.5 mm, and (d) 9.7 mm.

is reconstructed in Fig. 57. The dielasmoid type of development was widespread in the Permian terebratulids and had long historical roots. In this species, it proved to be more vital and finally settled at the middle and adult stages. In all species considered above, the adult brachidium began to form when the shell length was about two-thirds of the adult shell length. In terebratulids, the loss of the early stages of the postembryonic development of brachidium as a result of tachygenesis was mentioned by Thomson (1927). Comparison of Dagys's (1968) data on the Triassic terebratulids suggests a considerable acceleration of the formation of an adult loop in geological history. In the Late Permian terebratulids, the ratio of the length of the shell in which the first occurrence of an adult loop has been recorded to that of an adult shell is about 0.7. In the Triassic terebratulids this coefficient is on average 0.3.

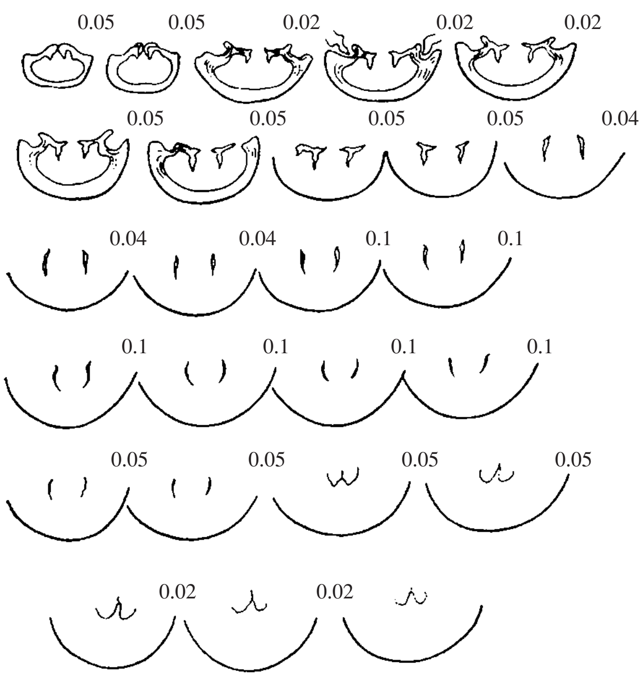


Fig. 22. *Notothyris pseudojoulfensis* Licharew in Grunt, 1973, specimen PIN, no. 139/727, serial sections through a 4.2-mm-long shell; figures indicate distances between the sections in mm.

Permian terebratulids are quite important in solving systematic and phylogenetic problems in the order Terebratulida. It is difficult to determine the phylogenetic relationship between the Paleozoic and Mesozoic terebratulids because the taxonomic composition of the Permian terebratulids, special features of their internal structure, and brachidium ontogeny are poorly known. Besides, all Permian families except Angustothyrididae became extinct at the Paleozoic–Mesozoic boundary. Cardinalia structures such as the perforated inner hinge plate associated with the visceral foramen, typical of the family Notothyrididae, and the crural plates resting on the bottom of the dorsal valve, characteristic of the family Heterelasminidae, disappeared at this boundary. They were replaced in the Triassic by terebratulids with a single or separated inner hinge

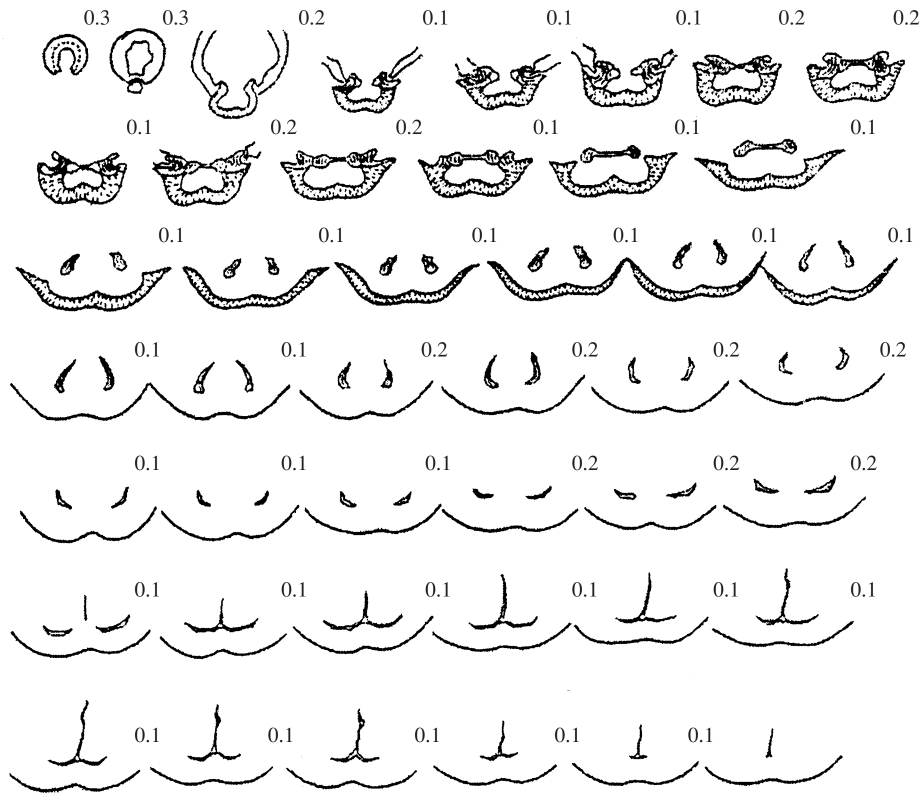


Fig. 23. *Notothyris pseudojoulfensis* Licharew in Grunt, 1973, specimen PIN, no. 139/715, serial sections through a 11.3-mm-long shell; figures indicate distances between the sections in mm.

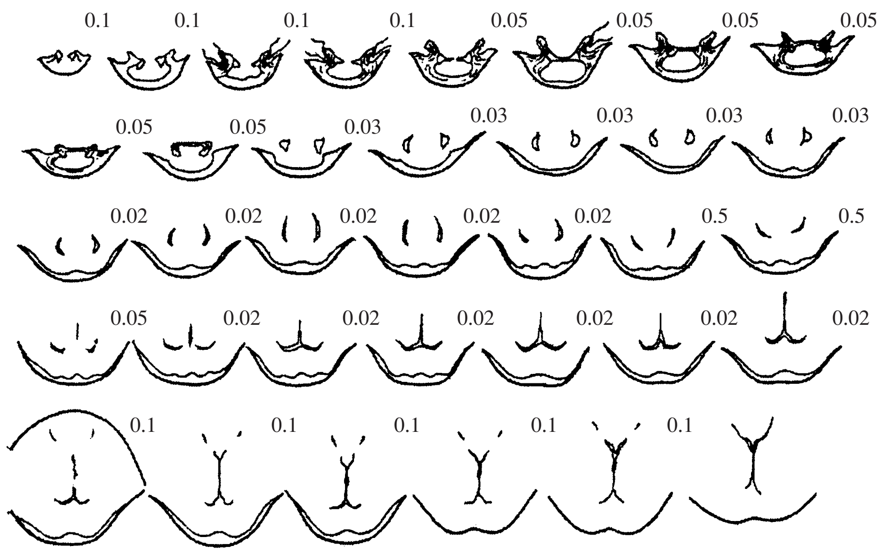


Fig. 24. *Gefonia* sp. (=*Gefonia licharewi* sp. nov.), specimen PIN, no. 139/756, serial sections through a 3.8-mm-long shell; figures indicate distances between the sections.

plate, well-developed outer hinge plates, and complicated types of brachidium development. Most of the structures that arose in the Triassic became characteristic features of the Mesozoic and Cenozoic terebratulids. The type of cardinalia is the main characteristic of families and its rapid change prevents the establishing of direct relationships between the Paleozoic and Mesozoic families of terebratulids. The other important internal structures are the lophophore supports, or brachidium, which is a loop of varying complexity.

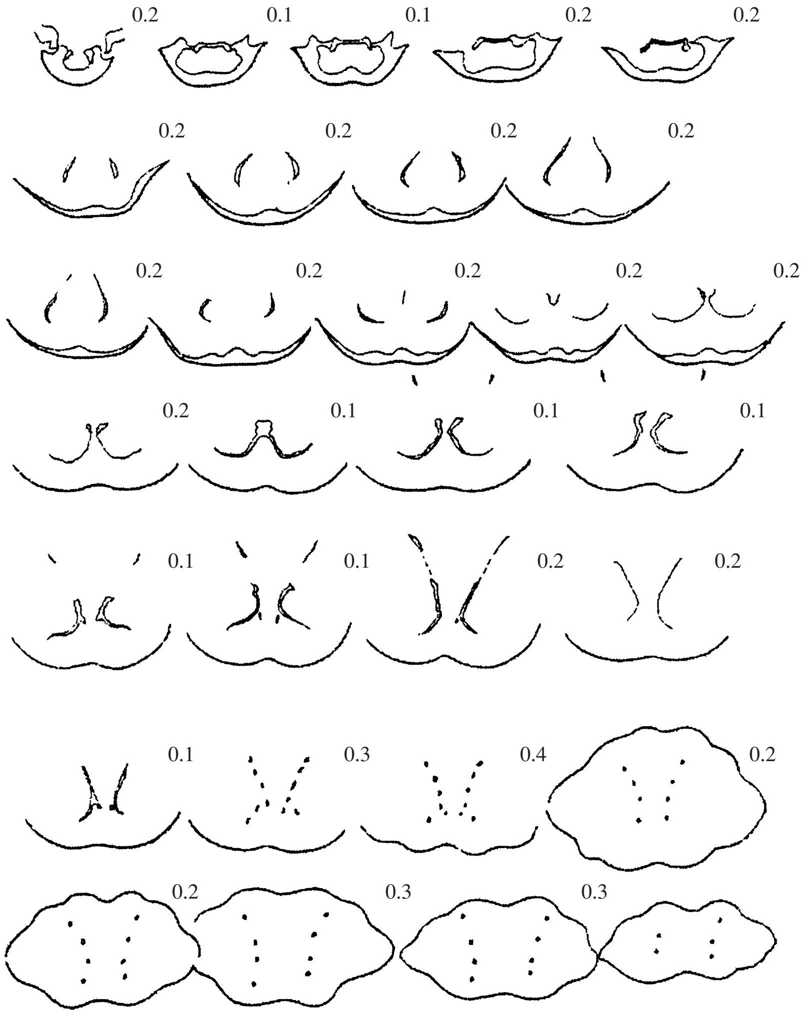


Fig. 25. *Gefonia* sp. (=*Gefonia licharewi* sp. nov.), specimen PIN, no. 139/701, serial sections through a 11.3-mm-long shell; figures indicate distances between the sections in mm.

In the study of the Late Permian terebratulids from the southwestern Darvaz, the presence of a vertical plate that may serve as a base for the development of various types of loop was discovered. The terebratuloid and loboidothyridid types of ontogeny, which are typical of the Mesozoic, were revealed. On this basis, the appearance of the Mesozoic superfamilies Terebratuloidea and Loboidothyroidea in the Permian was established.

The Permian family Heterelasminidae is of interest for interpreting the phylogenetic relationships between the Paleozoic and Mesozoic terebratulids. Until recently it was referred to the superfamily Dielasmatoidea. Based on our data on the ontogeny of *Heterelasmina*, we place this family into the Meso–Cenozoic superfamily Terebratuloidea. The developmental stages of *Heterelasmina cuboides* Licharew, which is related to the type species of the genus *Heterelasmina*, *H. dieneri*, were studied. In the 6.5-mm-long shell, the young loop of *H. cuboides* is close to the centronelloid stage: a vertical plate and descending branches have been identified. In the 8.2-mm-long specimen, a narrow ridge-shaped bend develops instead of the former vertical plate. In the larger specimens, the bend transforms into the transverse band of a simple triangular loop. This type of ontogeny is known for the Mesozoic and Cenozoic terebratulids. Dagys (1972) described it in the Late Triassic *Lobothyris kushlini* Dagys and Early Jurassic representatives of *Lobothyris*. Smirnova (1984) revealed the same type of the loop development in the Early Cretaceous *Nucleata* Quenstedt and *Weberithyris* Smirnova. It is also typical of the superfamily Terebratuloidea. It is known with certainty from the Late Triassic. It has now been found in the Permian. The absence of dental plates and the terebratuloid type of the loop development are special features of the superfamily

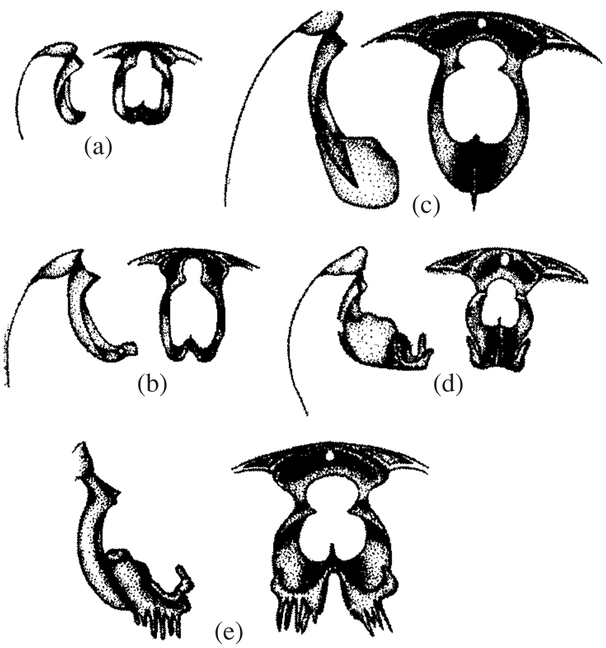


Fig. 26. Reconstruction of the internal structures of *Notothyris pseudojoulfensis* in specimens with lengths: (a) 4.2 mm, (b) 7.9 mm, (c) 11.3 mm; and of *Gefonia* sp. (=*Gefonia licharewi* sp. nov.) in specimens with lengths: (d) 3.8 mm and (e) 11.3 mm.

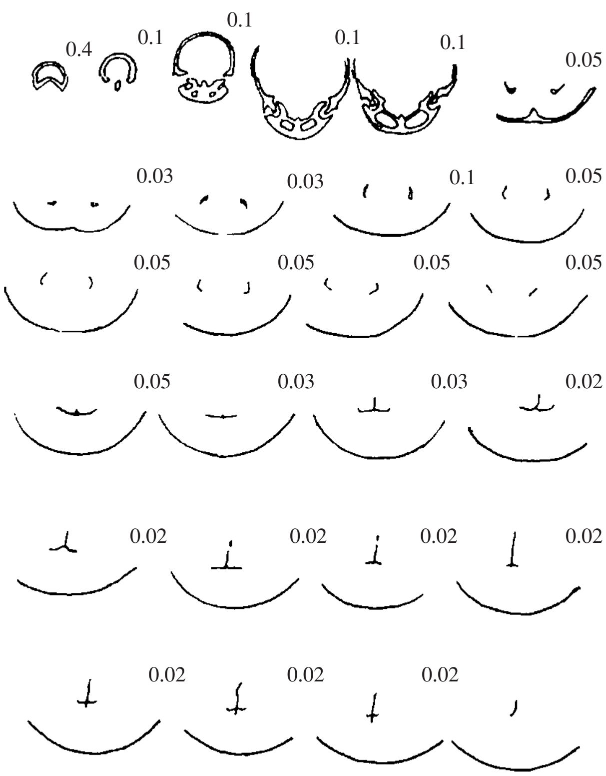


Fig. 27. *Compositelasma evolutum* Smirnova, 2006, specimen PIN, no. 4898/2397, serial sections through a 2.9-mm-long shell; figures indicate distances between the sections in mm.

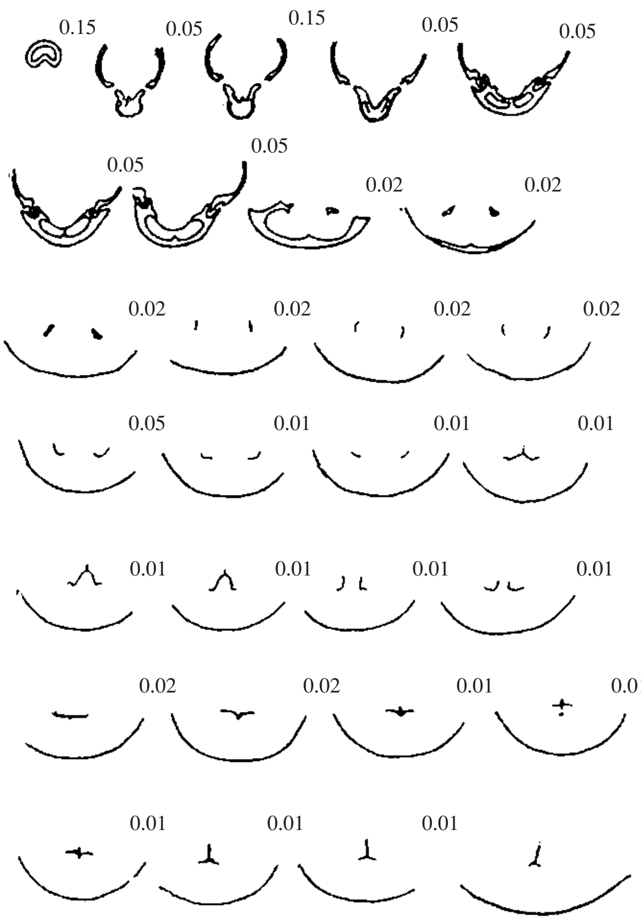


Fig. 28. *Compositelasma evolutum* Smirnova, 2006, specimen PIN, no. 4898/2398, serial sections through a 3.2-mm-long shell; figures indicate distances between the sections in mm.

Terebratuloidea. On this basis Heterelasminidae are referred to the superfamily Terebratuloidea. Thus, Koczyrkewicz (1976) was right in removing this family from the Dielasmatoidea and suggesting its possible placement in the superfamily Terebratuloidea.

Until recently the Permian family Pseudodielasmatidae was assigned to the superfamily Dielasmatoidea. Dagys (1968) studied the development of the loop in Dielasmatoidea in the type material *Dielasma elongata* Schlotheim from the Zechstein of Thuringia. He revealed the simple development of the loop without secondary elements. In the Late Permian pseudodielasmatids, the loop develops in a different way. We studied developmental stages in *Fredericksolasma lata* and revealed centronelloid, quasicampagiform, campagiform, early dictiothyridid, and terebratuloid stages of brachidium development. These stages are characteristic of the loboidothyridid type of loop development. The latter was established by Dagys (1968) for the Early Jurassic *Viligothyris* Dagys and Early Cretaceous

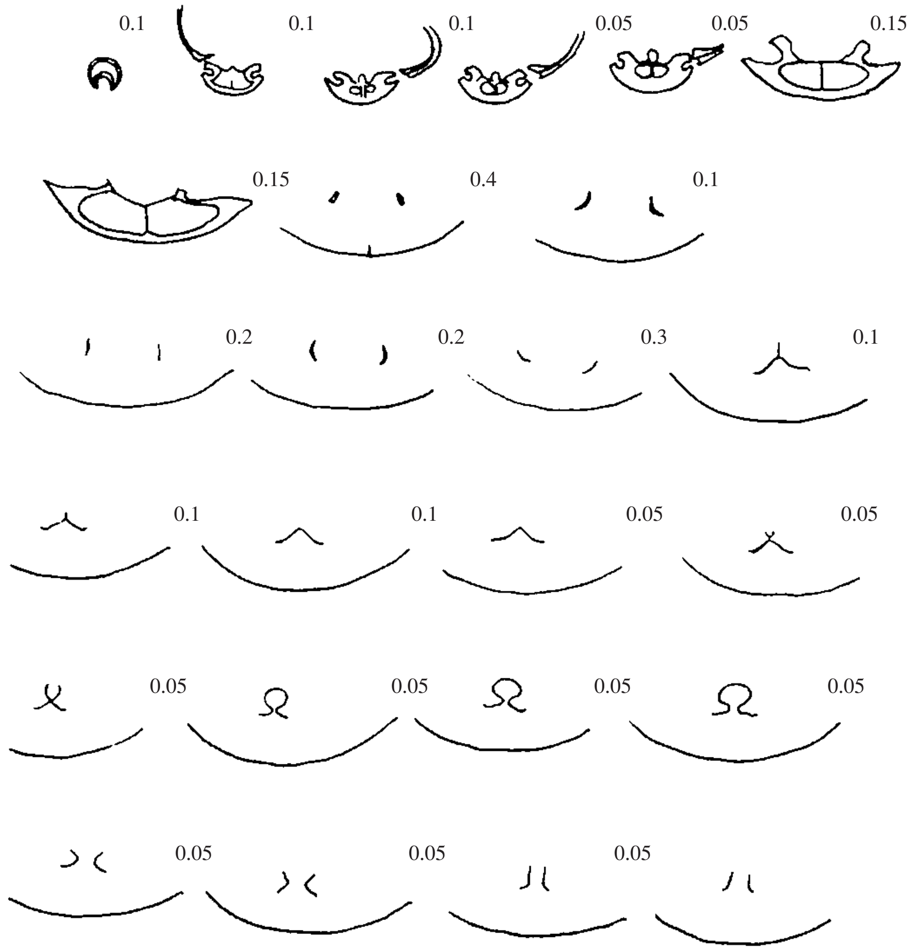


Fig. 29. *Compositelasma evolutum* Smirnova, 2006, specimen PIN, no. 4898/2400, serial sections through a 5.3-mm-long shell; figures indicate distances between the sections in mm.

Taimyrothyris Dagys. Smirnova (1984) revealed the same developmental stages in the Late Jurassic *Postepithyris* Makridin and Early Cretaceous *Dictyothyris* Douvillé. The structure of the cardinalia and the loboidothyridid type of brachidium development that have been studied in representatives of Pseudodielasmatidae show that these representatives belong to the superfamily Loboidothyroidea. This suggests that Permian Pseudodielasmatidae were the oldest known representatives of the superfamily Loboidothyroidea. They could have given rise to the Triassic family Loboidothyrididae, from which the Mesozoic families Dictyothyrididae and Boreiothyrididae descended (Fig. 39).

The Permian family Notothyrididae, which unites terebratulids with a primitive centronelloid loop, clearly demonstrates the appearance of the primordia of secondary elements of the loop. The ascending plate adjoining the vertical plate is distinctly seen in adult *Notothyris pseudojoulfensis* from the Upper Permian of the southeastern Pamirs. This stage corresponds to the early stages of the brachidium in many groups of Mesozoic and Cenozoic terebratulids with a complicated development of the loop. The basis for the formation of complicated loops, which developed in later terebratulids, certainly existed in the Late Permian. The vertical and ascending plates could have arisen earlier. The time of their origin and, thus, the time of arising of complicated developmental changes in the brachidium in terebratulids may be determined by ontogenetic study of the older groups.

Praeangustothyris Koczyrkewicz from the Late Permian of Primorye is conventionally assigned to the superfamily Dielasmatoidea. The young brachidium stages studied by the author are comparable with that of the Triassic Angustothyrididae Dagys, 1972. The assignment of *Praeangustothyris* to the family Angustothyrididae is confirmed by the similar structure of the cardinalia. Thus, the family Angustothyrididae existed from the Late Permian up to the Triassic inclusive. This family could be the ancestor of the Mesozoic

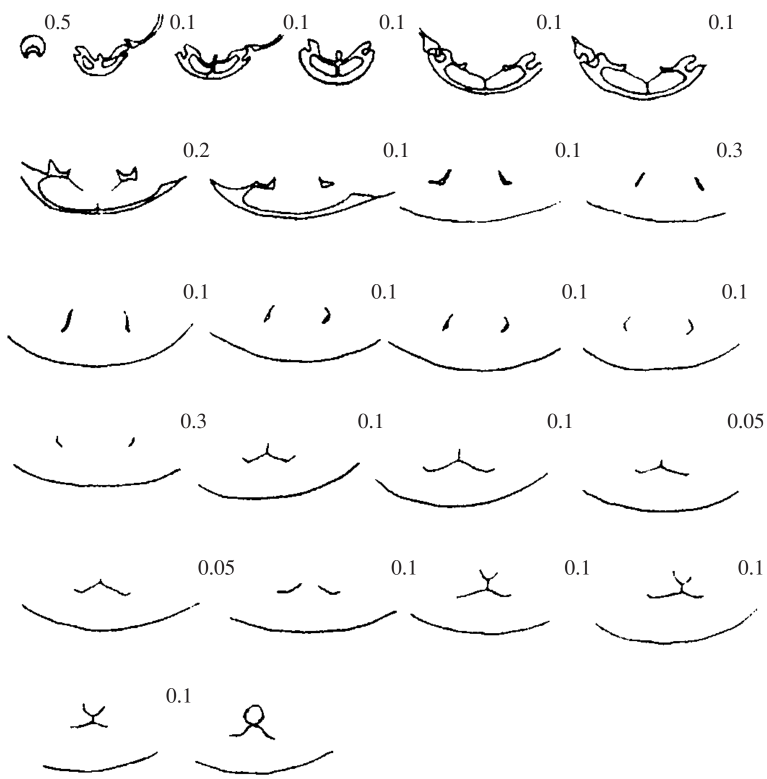


Fig. 30. *Compositelasma evolutum* Smirnova, 2006, specimen PIN, no. 4898/2401, serial sections through a 6.2-mm-long shell; figures indicate distances between the sections in mm.

terebratulids with a complicated brachidium development, such as the family Zeilleridae Rollier, 1915. The similar structure of the cardinalia, the developmental stages of the loop, and the temporal succession all confirm a possible relationship between these two families. Since Zeilleridae are the initial group of the abundant Meso-Cenozoic family Dallinidae, the role of Angustothyrididae in the phylogeny of the Mesozoic terebratulids becomes clear. Therefore, it is obvious that in the Paleoequatorial Superregion in the Late Permian there were groups ancestral to several large Mesozoic terebratulid taxa. They survived the global crisis at the Permian–Triassic boundary and gave rise to the Mesozoic superfamilies Terebratuloidea, Loboidothyroidea, and the family Angustothyrididae from the superfamily Dielasmatoidea. Thus, a partial continuity may be postulated between the Late Paleozoic and Mesozoic terebratulids at the superfamily level.

The superfamily Dielasmatoidea was widespread in the Permian boreal basins, and the dielasmoid type of brachidium development dominated. Although this superfamily is combined, the typical representatives of dielasmatoids existed up to the Late Triassic (Dagys, 1974). In this case, the continuity of the boreal taxa may be supposed. The appearance of the compositelasmoid type of development with two vertical plates in the Permian boreal basins can hardly be unambiguously explained. Most probably this type of development, which is based on the dielasmoid type and did not exist in the Permian, aimed to build a stronger, more complex skeleton. The study conducted gave evidence of the simultaneous arising of secondary elements on the base of the vertical plate in different groups of terebratulids and of the complex development of the brachidium in the Late Permian basins of the Paleoequatorial paleozoogeographic superregion (northern and southeastern Pamirs) and of the Boreal paleozoogeographic superregion (Russian Platform).

It is possible to assume that there was a certain evolutionary level at which some evolutionary potentials of terebratulids were achieved by increasing skeletal complexity at different ontogenetic stages. Possibly this was an early step towards the formation of a new, more advanced, type of brachidium development. In the Mesozoic such attempts resulted in the appearance of various kinds of brachidia, which characterize various families and superfamilies. It is difficult to determine at present whether any direct descendants of Permian boreal terebratulids exist in the Mesozoic.

It is more likely that there were branches that showed major tendencies in development, that were subsequently achieved by a number of large Mesozoic groups. In the analysis of data obtained from the onto-

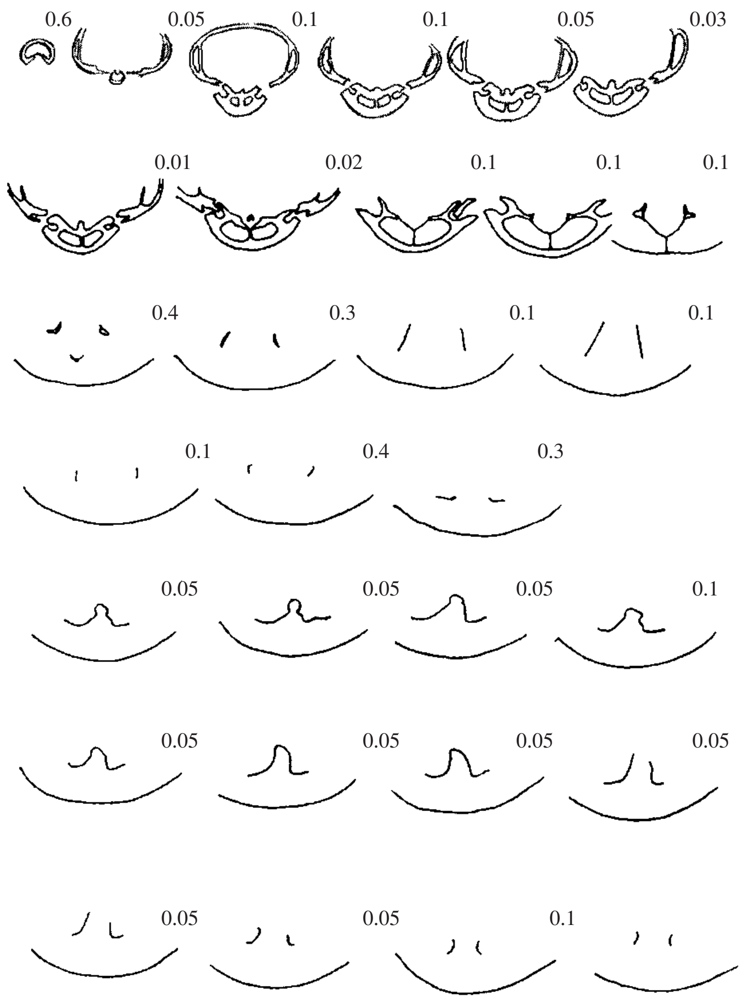


Fig. 31. *Compositelasma evolutum* Smirnova, 2006, specimen PIN, no. 4898/2402, serial sections through a 7.4-mm-long shell; figures indicate distances between the sections in mm.

genetic studies of the Late Permian terebratulids of the Russian Platform, the specificity of the evolutionary transformations in the Late Paleozoic terebratulids was revealed, a new type of loop development was established, the origin of the complicated brachidium transformations in the order Terebratulida was discovered, the time of origin of the initial structures of the loop, which are the basis of its complicated metamorphosis, was specified, and the Mesozoic elements in brachidium development were discovered.

CHAPTER 4. SYSTEMATIC PALEONTOLOGY

Order Terebratulida Waagen, 1883

D i a g n o s i s. Brachidium loop very complicated, the result of numerous transformations during ontogeny.

C o m p a r i s o n. The order differs from all other articulated brachiopod orders in the morphology and ontogeny of the brachidium.

C o m p o s i t i o n. Superfamilies Stringocephaloidea King, Cryptonelloidea Thomson, Cranaenoidea Cloud, Centronelloidea Waagen, Dielasmatoidea Schuchert, Terebratuloidea Gray, Gilledioidea Campbell, and Compositelasmatoidea Smirnova.

S u p e r f a m i l y Centronelloidea Waagen, 1882

Centronellidina: Stehli, 1965, H729.

D i a g n o s i s. Dental plates weakly developed or absent. Crural plates present or absent. Inner hinge plate entire or perforated. Brachidium at the centronelloid stage.

C o m p o s i t i o n. Families Centronellidae Waagen, 1882; Notothyrididae Licharew, 1960; Stringocephalidae King, 1850; and Mutationellidae Cloud, 1942.

Family Notothyrididae Licharew, 1960

Notothyrinae: Licharew et al., 1960, pp. 288, 289.

Notothyrididae: Stehli, 1965, H758; Cooper and Grant, 1976, p. 2848.

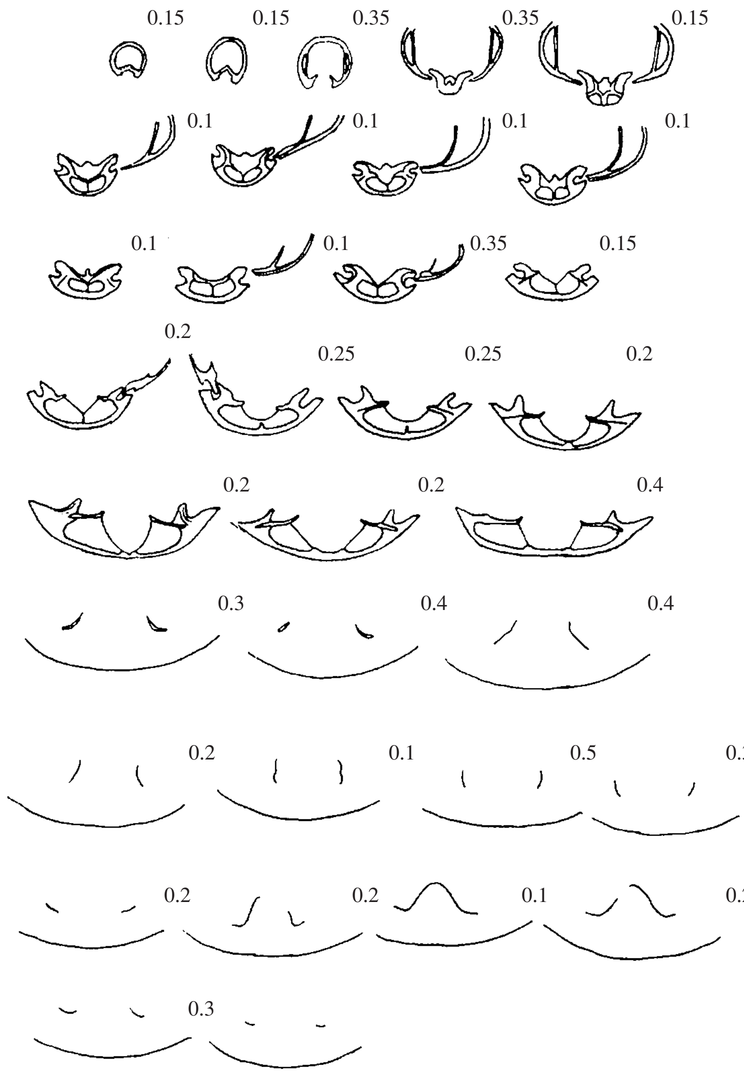


Fig. 32. *Compositelasma evolutum* Smirnova, 2006, specimen PIN, no. 4898/2403, serial sections through a 14-mm-long adult shell; figures indicate distances between the sections in mm.

D i a g n o s i s. Shell small, plicate, ribbed, or smooth. Visceral foramen present. Crural bases growing away from entire inner hinge plate. Loop consisting of short descending branches connected with high vertical plate. Additional loop branches may be developed.

C o m p o s i t i o n. *Notothyris* Waagen, 1882; *Notothyrina* Licharew, 1936; *Rostranteris* Gemmellaro, 1899; *Timorina* Stehli, 1961; *Gefonia* Licharew, 1936; *Chondronia* Cooper et Grant, 1976; and *Levinotothyris* Smirnova, gen. nov.

C o m p a r i s o n. This family differs from the family Stringocephalidae King, 1850 in the small shell, the absence of dental plates, and the entire inner hinge plate. It differs from Mutationellidae Cloud, 1942 in the absence of dental plates and in the radial ornamentation.

O c c u r r e n c e. Carboniferous–Permian; worldwide.

Genus *Notothyris* Waagen, 1882

Notothyris: Waagen, 1882, pp. 375–377; Tschernyschew, 1902, p. 463; Licharew, 1939, p. 120; Licharew et al., 1960, p. 288; Stehli, 1965, H758; Waterhouse, 1970, p. 160; Grunt, 1973, p. 156, 157; Cooper, 1976, pp. 2848–2849; Grant, 1976, p. 252.

T y p e s p e c i e s. *Notothyris subvesicularis* Davidson, 1862.

D i a g n o s i s. Shell rounded pentagonal, rounded triangular, or oval with low folds bordered in the anterior half by shallow sinuses in both valves. Posterior half usually smooth. Anterior commissure paraplicate or biplicate, complicated with ribs. Pedicle collar may be developed. Visceral foramen small. Outer and inner hinge plates present. Crural bases projecting on the dorsal side of the inner hinge plate. Loop centronelloid. Additional loop branches may be developed. Brachidium may bear small spines.

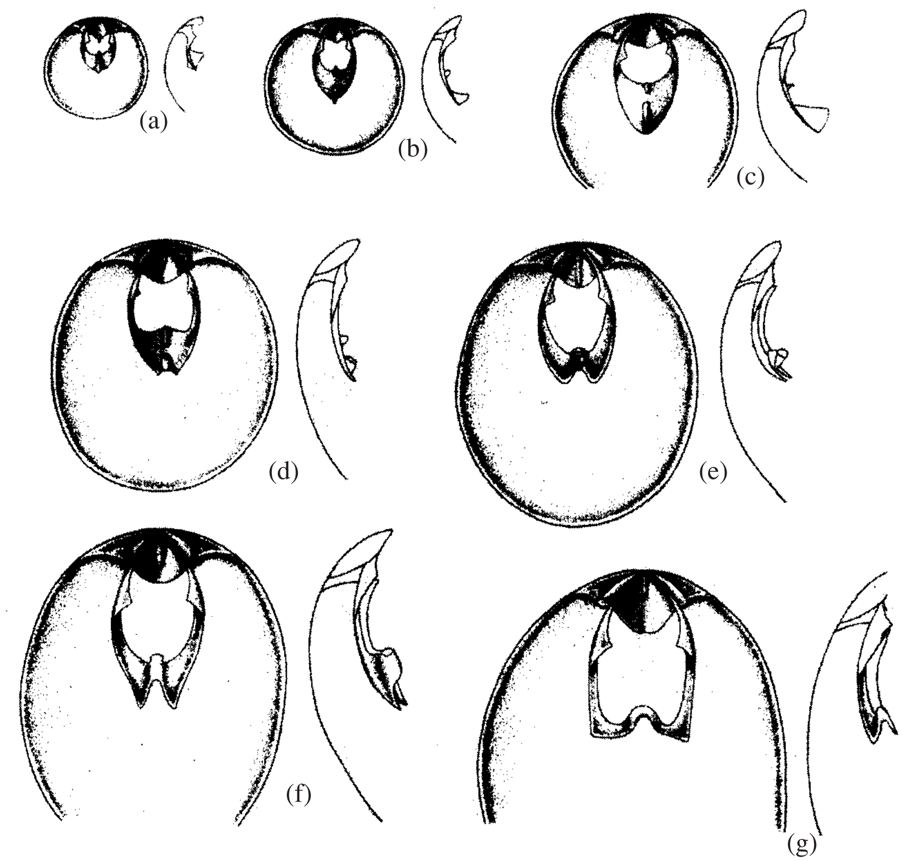


Fig. 33. *Compositelasma evolutum* Smirnova, 2006; reconstruction of the internal structures in specimens with lengths: (a) 2.9 mm, (b) 3.2 mm, (c) 4.2 mm, (d) 5.3 mm, (e) 6.2 mm, (f) 7.4 mm, and (g) 14 mm.

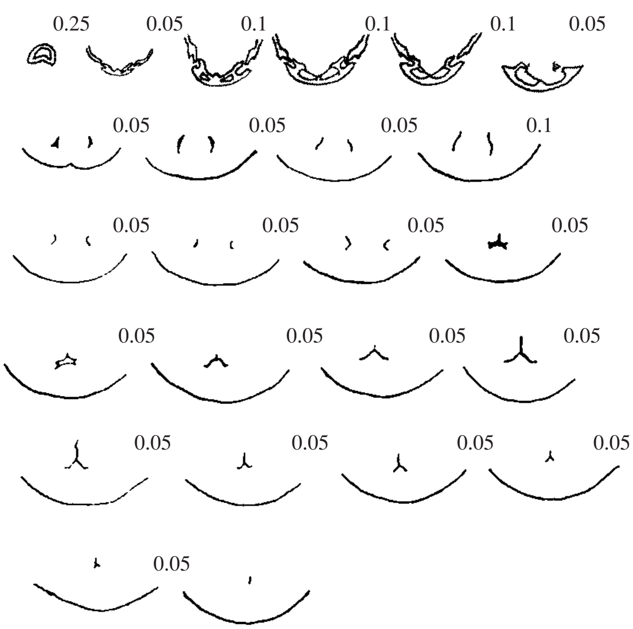


Fig. 34. *Campbellelasma variiforme* Smirnova, 2004, specimen PIN, no. 4898/1716, serial sections through a 3-mm-long shell; figures indicate distances between the sections in mm.

S p e c i e s c o m p o s i t i o n. Type species, *N. djoulfensis* (Abich, 1878) from the Djulfian Stage (Upper Permian) of Transcaucasia; *N. pseudodjoulfensis* Licharew in Grunt, 1973, from the Urushten Horizon (Djulfian Stage, Upper Permian) of Northern Caucasia; *N. warthi* Waagen, 1882, *N. lenticularis* Waagen, 1882, *N. minuta* Waagen, 1882, and *N. subvesicularis* Davidson, 1862 from the Murgabian and Midian stages (Upper Permian) of Pakistan; and *N. triplex* Cooper et Grant, 1976 from the Upper Permian of western Texas.

C o m p a r i s o n. This genus differs from the genus *Rostranteris* Gemmellaro, 1899 in the smooth posterior half of the shell and in the crural bases located on the dorsal side of the inner hinge plate. It differs from *Gefonia* in the deep sinuses on both valves, folds not so sharp, smooth posterior half of the shell, and centronelloid loop.

Notothyris djoulfensis (Abich, 1878)

Plate 1, fig. 1; Fig. 40

Terebratula djoulfensis: Abich, 1878, pp. 68 and 69, pl. 6, figs. 10a–10c.

Notothyris djoulfensis: Waagen, 1882, pp. 379–382, pl. 28, figs. 5 and 6.

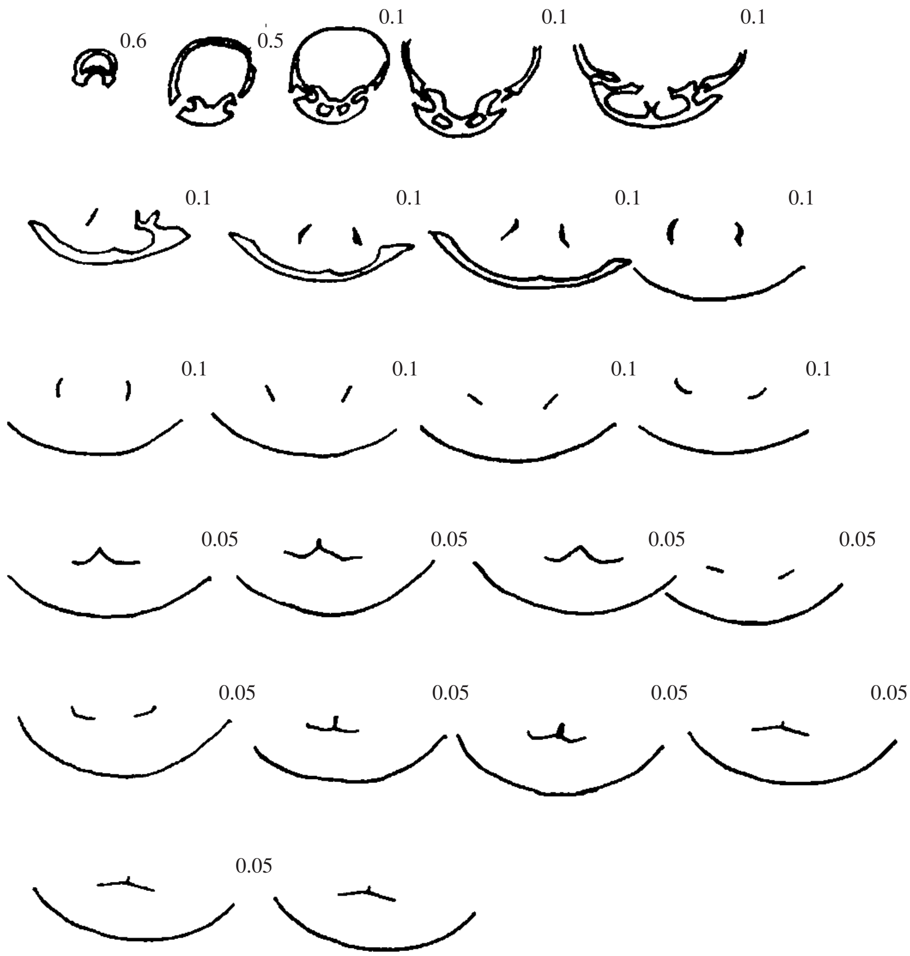


Fig. 35. *Campbellelasma variiforme* Smirnova, 2004, specimen PIN, no. 4898/1718, serial sections through a 4-mm-long shell; figures indicate distances between the sections in mm.

H o l o t y p e. St. Petersburg State University (LGU), no. 85/99; Upper Permian, Djulfian Stage; Transcaucasia, Julfa.

D e s c r i p t i o n. The shell is rounded pentagonal, more rarely oval, with more convex ventral valve and smooth umbonal region. The anterior third of the shell and even the anterior half in well-preserved shells are plicate. The dorsal valve bears four folds and the ventral valve bears three folds. Each valve bears four smooth, low lateral folds. The anterior commissure is low and W-shaped. The lateral commissures are arched and denticulate in the anterior half. The maximum width is in the middle or is slightly shifted to the anterior margin. The maximum thickness is in the middle. The ventral valve is strongly convex. The sulcus is shallow and runs up to the middle of the valve. One low fold is in the middle of the sulcus, and two higher folds bound the sulcus. The umbo is high, massive, and curved. The false area is high, concave, and bordered by rounded umbonal keels. The apical angle is 80°–83°. The foramen is large and labiate. The dorsal valve is flattened. The elevation is low and bears four folds. The two bordering folds are higher than the median folds.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
2073/1001	12.7	11.5	8.2	0.91	0.64
2073/1002	12.6	11.2	9.2	0.88	0.72
2073/1003	12.5	11.0	7.6	0.88	0.61
2073/1004	11.7	10.0	8.2	0.85	0.70
2073/1005	11.6	10.0	8.0	0.86	0.68

S h e l l i n t e r i o r. The pedicle collar is strongly curved. The teeth are narrow and enter the sockets obliquely. The inner and outer denticles are developed. The outer hinge plates are narrow. The visceral foramen is small. The inner hinge plate is wide and horizontal. The crural bases have equally developed ventral and dorsal tips. The crural processes are short. The descending loop branches are narrow, short, angular at the junc-

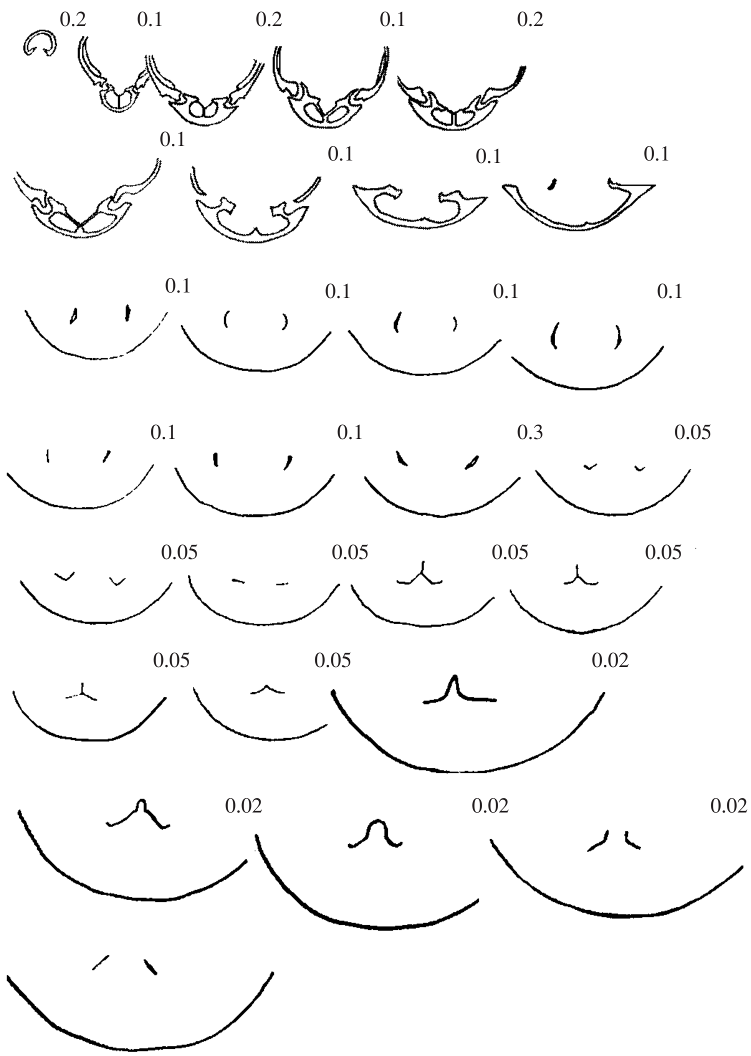


Fig. 36. *Campbellelasma variiforme* Smirnova, 2004, specimen PIN, no. 4898/1720, serial sections through a 4.6-mm-long shell; figures indicate distances between the sections in mm.

tion with the vertical plate, and bear short small spines. The vertical plate is high. The ascending plate joins the vertical plate and differs from the latter in the curved surface, small inclination to the vertical plate, and well-pronounced widening at the ventral end. The vertical plate projects beyond the brachidium. The loop length is about one-half of the dorsal valve length.

Comparison. This species differs from *N. pseudodjoulfensis* Licharew in Grunt, 1973 in having four folds on the ventral valve, shorter and lower folds, more flattened anterior margin, smooth umbonal region, and the dorsal valve flattened throughout its surface. It differs from *N. triplex* Grant, 1976 in the higher, curved umbo, more numerous folds, and denticulate commissures. From *N. subvesicularis* Davidson, 1862 it differs in the more convex valves, more numerous folds, and higher umbo.

Material. Twenty-six complete shells and nine shells with broken margins from Transcaucasia, village of Dorosham-2, Aras River.

Genus *Rostranteris* Gemmellaro, 1899

Rostranteris: Gemmellaro, 1899, p. 104; Licharew, 1960, pp. 288 and 289; Stehli, 1962, pp. 99 and 100; Stehli, 1965, H759; Grunt, 1973, p. 159.

Type species. *Dielasma adrianense* Gemmellaro, 1894.

Diagnosis. Shell small, with biconvex valves and high folds. Ventral valve bears two and dorsal valve bears three folds. Weakly developed lateral folds may occur on both valves. Anterior commissure from antiplicate to sulcate. Pedicle collar may be developed. Small visceral foramen may be present. Outer and inner hinge plates well-developed. Crural bases usually on the ventral side of the inner hinge plate. Brachidium at

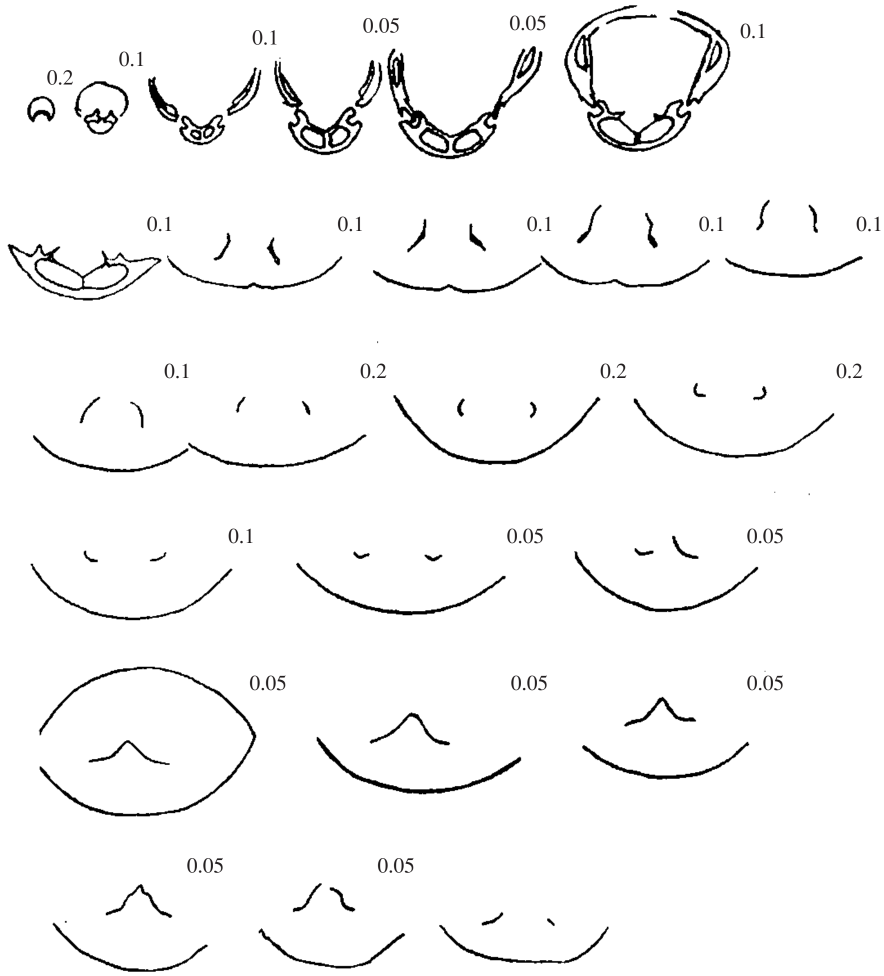


Fig. 37. *Campbellelasma variiforme* Smirnova, 2004, specimen PIN, no. 4898/1722, serial sections through a 6.1-mm-long shell; figures indicate distances between the sections in mm.

the centronelloid stage, with loop of varying length and high vertical plate.

Species composition. Type species, *R. mediterraneum* Gemmellaro, 1899; *R. pulchrum* Gemmellaro, 1899; *R. exile* Gemmellaro, 1899; *R. inflatum* Gemmellaro, 1899; *R. gibbosum* Gemmellaro, 1899; *R. sinuatum* Gemmellaro, 1899; *R. ovale* Gemmellaro, 1899; and *R. guttula* Gemmellaro, 1899 from the uppermost Kubergandian–lowermost Murgabian (Upper Permian) of Sicily and *R. bukharica* (Tschernyschew, 1914); *R. ovaleformis* Smirnova, 2001; *R. gemmellaroi* Smirnova et Grunt, 2002; and *R. charymdarensis* Smirnova et Grunt, 2002 from the Gundara Formation (Upper Permian) of the southwestern Darvaz.

Comparison. This genus differs from *Notothyris* Waagen, 1882 in the type of arrangement of the folds, strongly curved commissures, and in the crural bases located on the ventral side of the inner hinge plate. It differs from *Timorina* Stehli, 1961 in the pattern of folds on the shell and in the centronelloid loop.

Remarks. Some authors (Shellwien, 1900; Tschernyschew, 1902, 1914; Licharew, 1936, 1960) believed *Rostranteris* to be the junior synonym of *Notothyris*. Stehli (1962) reestablished *Rostranteris* as a separate genus. The historical background of the problem was described in detail by Grunt (Grunt and Dmitriev, 1973).

Rostranteris ovaleformis Smirnova, 2001

Plate 1, fig. 2

Rostranteris ovaleformis: Smirnova, 2001, pp. 33–35, text-figs. 1 and 2.

Holotype. PIN, no. 4104/1; Tajikistan, southwestern Darvaz, Gundara River; Upper Permian, Gundara Formation.

Description (Fig. 41). The shell is small and elongated, oval or rounded pentagonal, with a high, laterally compressed umbo. The anterior commissure is narrowly W-shaped. The maximum width is in the anterior third of the shell. The maximum thickness is in the middle. The hinge line is curved almost at a right angle.

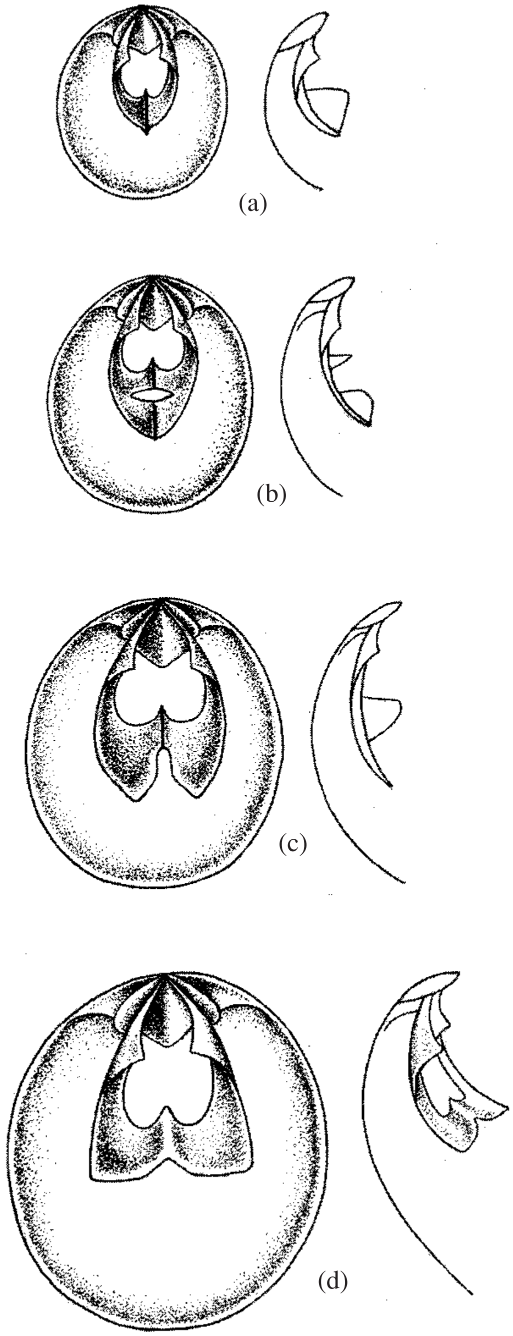


Fig. 38. *Campbellelasma variiforme* Smirnova, 2004; reconstruction of the internal structures in specimens with lengths: (a) 3 mm, (b) 4 mm, (c) 4.6, and (d) 6.1 mm.

The lateral commissures are sharply curved near the anterior margin. The anterior margin is plicosulcate and narrow. The ventral valve is considerably more convex than the dorsal valve. Two high, sharpened folds are separated by a deep sulcus and extend from the umbo up to the anterior margin. The lateral sides of the valve are steeply inclined to the commissural plane and bear low, rounded folds. The umbo is narrow and strongly curved. The umbonal keels are absent. The apical angle is 60°. The foramen is ovally elongate, labiate, and submesothyrid. The dorsal valve is moderately convex and slightly curved. It bears three low, leveled folds separated by shallow grooves. The folds start within one-third of the valve length from the umbo and extend up to the anterior margin.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
Holotype 4104/1	12.10	8.70	10.0	0.72	0.83
4104/2	13.2	10.0	–	0.76	–

S h e l l i n t e r i o r. The pedicle collar is low and arched. The outer denticle is present. The outer hinge plate consists of two horizontal plates. The inner tips of the outer hinge plate enlarge anteriorly and connect with each other to form a concave inner hinge plate, which borders the visceral foramen. The crural bases are shaped like ventrally projecting tubercles on the inner hinge plate. The crural processes are subparallel. The descending loop branches are long and angular at the junction with the high vertical plate. The ascending plate adjoins the vertical plate and differs from the latter in the curved outline. The loop length is about one-third of the dorsal valve length.

C o m p a r i s o n. This species differs from *R. ovale* Gemmellaro, 1899 in the higher umbo, sharper folds extending over the whole length of the ventral valve, weakly developed folds on the dorsal valve, and W-shaped anterior margin. It differs from *R. adrianense* Gemmellaro, 1899 in the ovally pentagonal outline of the shell, higher umbo, sharper folds, strongly convex valves, and plicosulcate anterior margin.

M a t e r i a l. Two complete shells, one ventral valve, and one specimen with a broken umbo; Gundara River, at height 3661 m.

Rostranteris gemmellaroi **Smirnova et Grunt, 2002**

Plate 1, fig. 3

Rostranteris gemmellaroi: Smirnova and Grunt, 2002, pp. 41–44, text-figs. 4a–4d.

H o l o t y p e. PIN, no. 4104/603; Tajikistan, southwestern Darvaz, Zidadara River; Upper Permian, Gundara Formation.

D e s c r i p t i o n. The shell is small, wide, with moderately convex valves, and rounded pentagonal to pyriform in outline. The folds on both valves are low and well-pronounced. The anterior margin is flattened, narrow, and plicosulcate. The maximum width is shifted slightly anteriorly. The maximum thickness is in the middle. The hinge line is long and slightly curved. The lateral commissures are straight. The anterior commissure is biplicate and undulate curved. The ventral valve is slightly more convex than the dorsal valve and bears two rounded folds that are weakly developed in

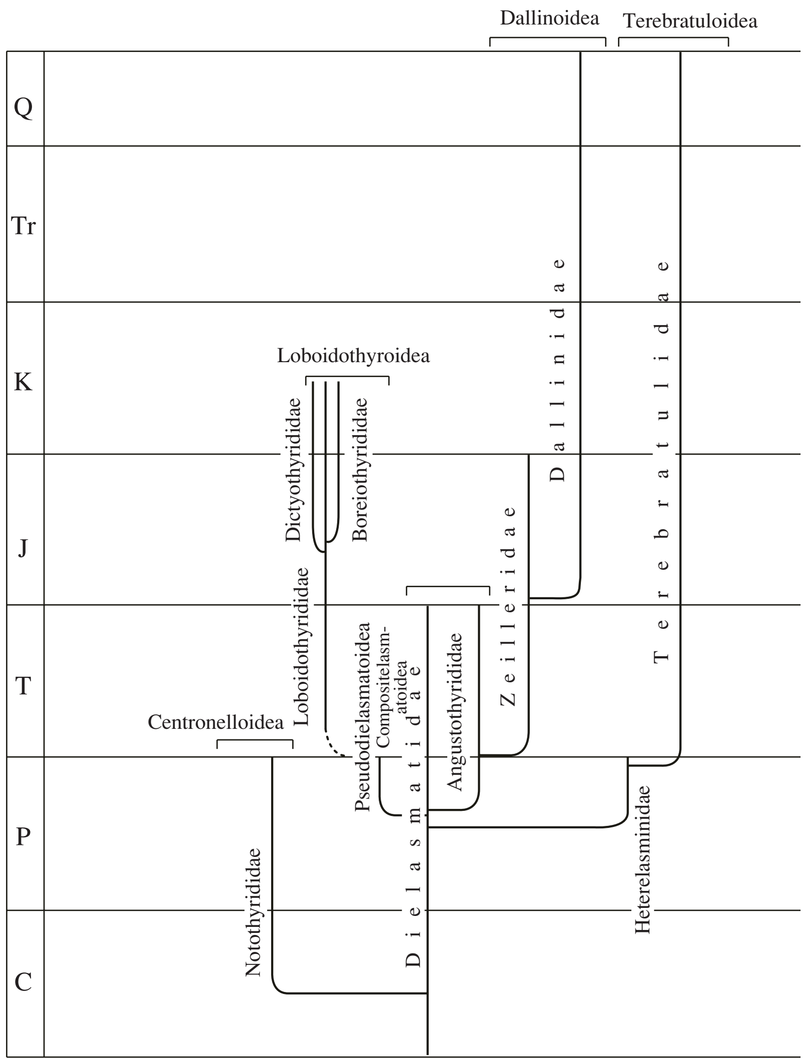


Fig. 39. The assumed phylogenetic relationship between the Permian and Mesozoic terebratulids.

the posterior half and better pronounced in the anterior half. A deep and narrow sulcus is located between the folds. The lateral sides of the valve are wide and flattened. The umbo is wide and curved. The umbonal keels are short and well-pronounced. The apical angle is 75°–81°. The foramen is small, oval, and submesothyrid. The dorsal valve is slightly convex. The flattened anterior half of the valve bears three low, rounded folds separated by two shallow sinuses.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
Holotype					
4104/603	13.0	11.3	7.0	0.87	0.54
4104/604	14.3	11.4	8.1	0.79	0.56
4104/605	13.8	11.6	7.4	0.84	0.54
4104/606	12.7	11.0	7.8	0.86	0.81

C o m p a r i s o n. This species differs from *R. bukharica* (Tschernyschew, 1914) in the larger shell, less convex valves, and less curved umbo. It differs from *R. ovaleformis* Smirnova, 2001 in the wider shell, less convex valves, larger apical angle, less curved hinge line, flattened anterior margin of the shell, and in the presence of low folds on both valves.

M a t e r i a l. Nine complete and ten damaged shells from the type locality.

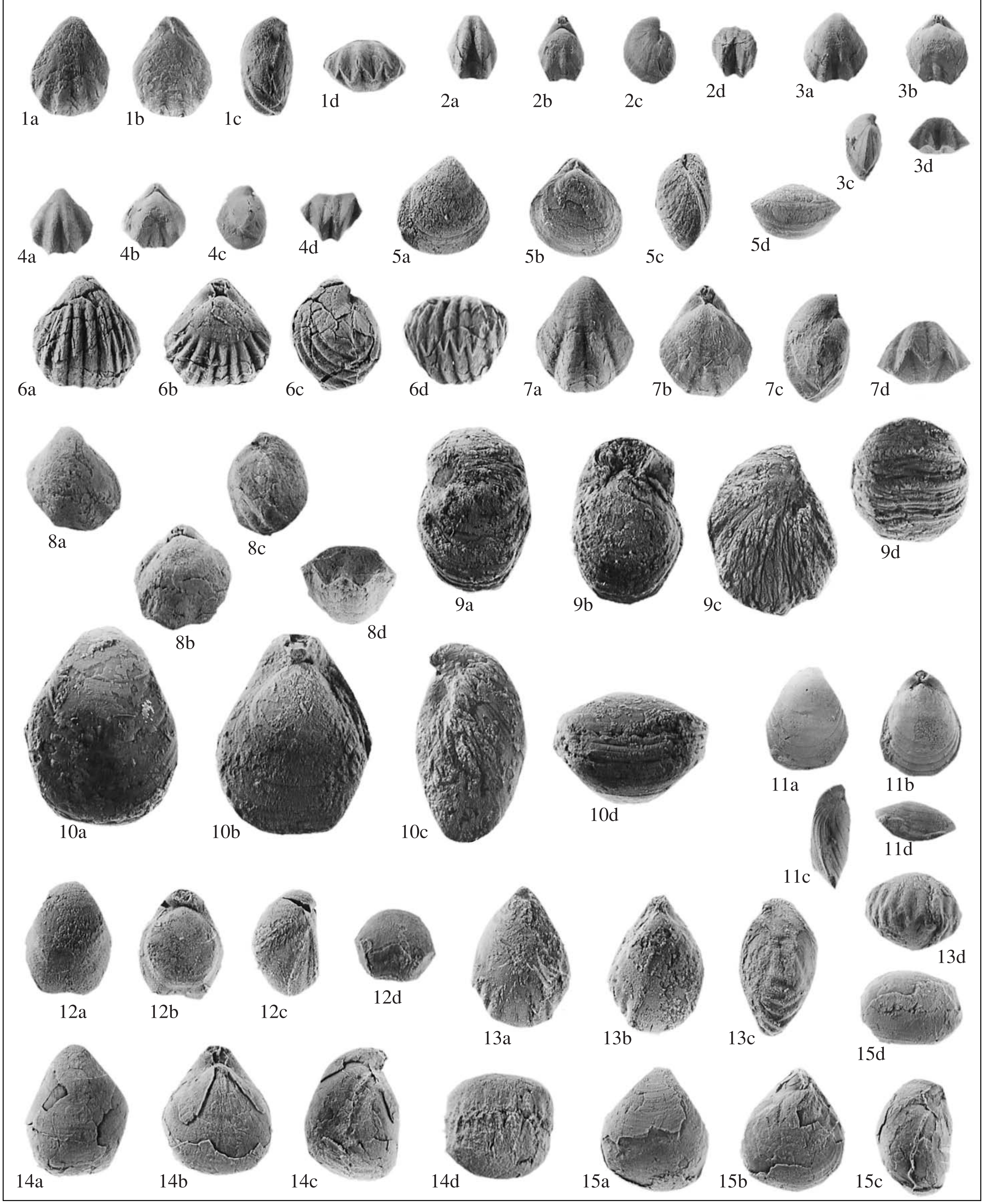
Rostranteris charymdarensis Smirnova et Grunt, 2002

Plate 1, fig. 4

Rostranteris charymdarensis: Smirnova and Grunt, 2002, p. 44, text-figs. 4e–4h.

H o l o t y p e. PIN, no. 4104/595; complete shell; Tajikistan, southwestern Darvaz, interfluve between the Charymdara and Zidadara rivers, at height 3837.4 m; Lower Permian, Safetdaron Formation.

Plate 1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Description (Fig. 42). The shell is small, rounded pentagonal, moderately biconvex, with a narrow umbo and wide lateral sides. The length and width are almost equal. High, sharpened folds are well-developed on both valves. The anterior margin is short and strongly curved. The maximum width and thickness are slightly shifted anteriorly from the middle of the shell. The hinge line is long and strongly curved. The lateral commissures are curved at a right angle in the anterior half of the shell. The anterior commissure is biplicate and plicosulcate. The ventral valve is considerably more convex than the dorsal valve. Two high folds start within one-third of the valve length from the umbo. They are divided by a narrow sulcus and separated from the lateral sides by shallow depressions. The lateral sides of the valve are wide and flattened. The umbo is narrow, high, and overhangs the dorsal valve. The umbonal keels are absent. The apical angle is 70°–78°. The foramen is small, labiate, and submesothyrid. The dorsal valve is strongly curved in the anterior half and flattened in the posterior half of the shell. The sulcus starts near the hinge line and rapidly broadens and deepens anteriorly. It is bordered by two high, rounded folds, which separate the sulcus from the wide, slightly concave, lateral surfaces. In the sulcus a well-pronounced fold runs from the middle of the valve up to the anterior margin.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
Holotype 4104/595	12.2	11.0	8.9	0.90	0.73
4104/596	12.2	11.1	8.8	0.91	0.72

Shell interior. The pedicle collar is absent. The outer hinge plate consists of two plates in the apical region. The plates are fused together anteriorly to form a slightly convex inner hinge plate bordering the visceral foramen. The crural bases have short ventral and longer dorsal tips. The loop branches are curved, subparallel posteriorly, and diverging anteriorly. The vertical plate is high, about one-half of the shell convexity. The ventral tip of the vertical plate bears a small thickening. The loop length is more than one-third of the dorsal valve length.

Comparison. This species differs from *R. sinuatum* Gemmellaro, 1899 in the higher umbo that is not adjacent to the dorsal valve, wider and rounded lateral sides of the shell, shorter and strongly curved anterior margin, and high folds on both valves. It differs from *R. bukharica* (Tschernyschew, 1914) in the wider shell, well-pronounced and sharpened folds on both valves, narrow and high umbo, and in the shape of the anterior margin.

Explanation of Plate 1

Fig. 1. *Notothyris joulfensis* (Abich, 1878); specimen PIN, no. 2073/1015, ×2: (1a) ventral valve, (1b) dorsal valve, (1c) lateral view, (1d) anterior margin; Djulfian Stage, Upper Permian, Transcaucasia.

Fig. 2. *Rostranteris ovaleformis* Smirnova, 2001; holotype PIN, no. 4104/1, ×1: (2a) ventral valve; (2b) dorsal valve; (2c) lateral view; (2d) anterior margin; Gundara Formation, Upper Permian; southwestern Darvaz.

Fig. 3. *Rostranteris gemmellaroi* Smirnova et Grunt, 2002; holotype PIN, no. 4104/603, ×1: (3a) ventral valve; (3b) dorsal valve; (3c) lateral view; (3d) anterior margin; Gundara Formation; southwestern Darvaz.

Fig. 4. *Rostranteris charymdarensis* Smirnova et Grunt, 2002; holotype PIN, no. 4104/595, ×1: (4a) ventral valve; (4b) dorsal valve; (4c) lateral view; (4d) anterior margin; Bolorian Stage, Safetdaron Formation, Upper Permian; southwestern Darvaz.

Fig. 5. *Levinotothyris rotunda* sp. nov.; holotype PIN, no. 2228/1001, ×1.5: (5a) ventral valve; (5b) dorsal valve; (5c) lateral view; (5d) anterior margin; Kyzyldzhilga Horizon, Upper Permian; southeastern Pamirs.

Fig. 6. *Gefonia licharewi* sp. nov.; holotype PIN, no. 2228/258, ×1.5: (6a) ventral valve; (6b) dorsal valve; (6c) lateral view; (6d) anterior margin; Djulfian Stage, Upper Permian; southeastern Pamirs.

Fig. 7. *Gefonia plicata* Licharew, 1936; specimen PIN, no. 4918/1501, ×1.5: (7a) ventral valve; (7b) dorsal valve; (7c) anterior margin; (7d) lateral view; Djulfian Stage, Upper Permian; Northern Caucasia.

Fig. 8. *Notothyrina pontica* Licharew, 1936; specimen PIN, no. 4918/1504, ×2: (8a) ventral valve; (8b) dorsal valve; (8c) lateral view; (8d) anterior margin; Djulfian Stage, Upper Permian; Northern Caucasia.

Fig. 9. *Dielasma robustum* Smirnova, 2004; holotype PIN, no. 4898/2351, ×2: (9a) ventral valve; (9b) dorsal valve; (9c) lateral view; (9d) anterior margin; Lower Kazanian Substage, Upper Permian; Russian Platform.

Fig. 10. *Dielasma kirillowense* Licharew, 1913; specimen PIN, no. 4898/2356, ×2: (10a) ventral valve; (10b) dorsal valve; (10c) lateral view; (10d) anterior margin; Lower Kazanian Substage, Upper Permian; Russian Platform.

Fig. 11. *Dielasma subelongatum* sp. nov.; holotype PIN, no. 4898/2544, ×1: (11a) ventral valve; (11b) dorsal valve; (11c) lateral view; (11d) anterior margin; Lower Kazanian Substage, Upper Permian; Russian Platform.

Fig. 12. *Hemiptychina kutorgi* sp. nov.; holotype PIN, no. 2073/1036, ×1: (12a) ventral valve; (12b) dorsal valve; (12c) lateral view; (12d) anterior margin; Guadalupian Stage, Upper Permian; Transcaucasia.

Fig. 13. *Hemiptychina hymalayensis* (Davidson, 1862); specimen PIN, no. 2073/1042, ×1.5: (13a) ventral valve; (13b) dorsal valve; (13c) lateral view; (13d) anterior margin; Guadalupian Stage, Upper Permian; Transcaucasia.

Fig. 14. *Hemiptychina morrisi* Grabau, 1931; specimen PIN, no. 5133/2, ×1.5: (14a) ventral valve; (14b) dorsal valve; (14c) lateral view; (14d) anterior margin; Murgabian Stage, Upper Permian; northern China (Inner Mongolia).

Fig. 15. *Hemiptychina sparsiplicata* Waagen, 1882; specimen PIN, no. 5133/19, ×1.5: (15a) ventral valve; (15b) dorsal valve; (15c) lateral view; (15d) anterior margin; Murgabian Stage, Upper Permian; northern China (Inner Mongolia).

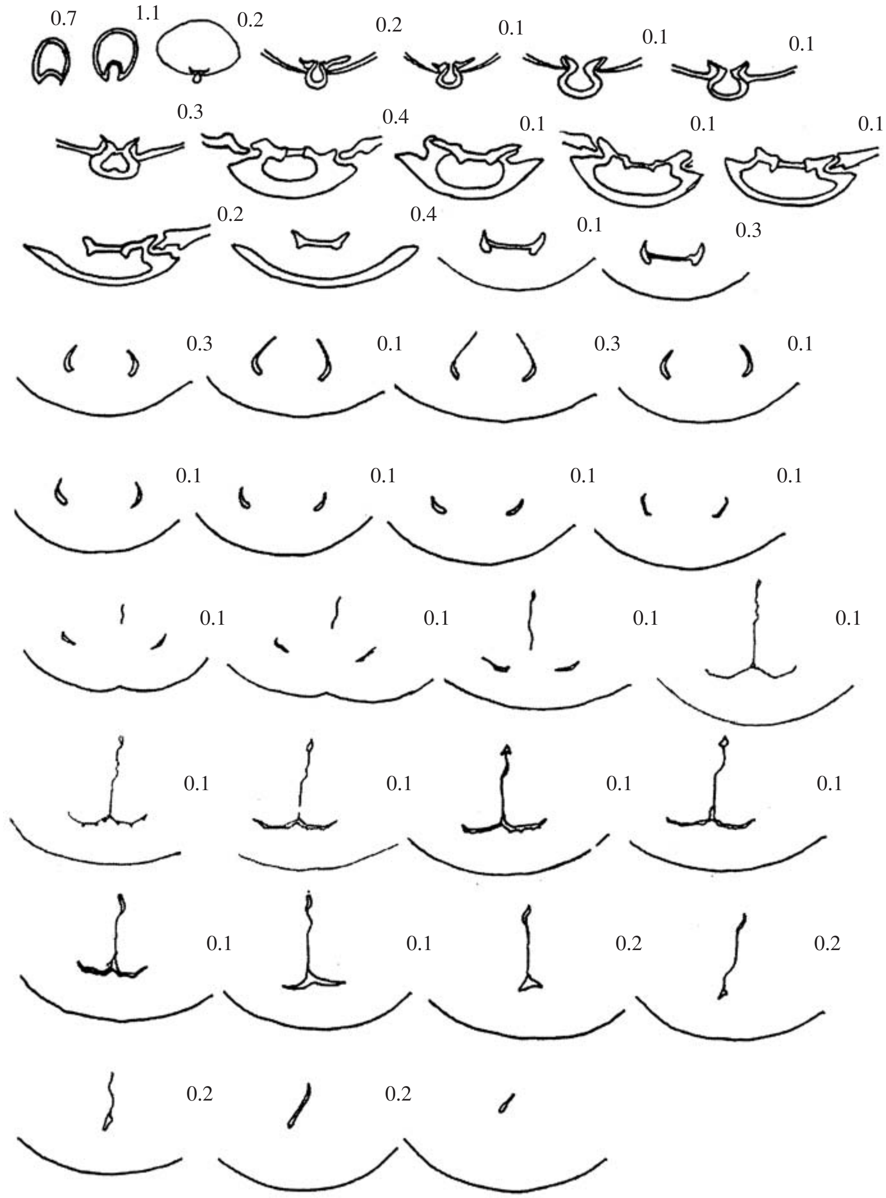


Fig. 40. *Notothyris djoulfensis* (Abich, 1878), specimen PIN, no. 2073/1006, serial cross sections; figures indicate distances between the sections in mm.

M a t e r i a l. Three complete and one damaged shell from the type locality.

Genus *Levinotothyris* Smirnova, gen. nov.

E t y m o l o g y. From the Latin *levi* (smooth) and generic name *Notothyris*.

T y p e s p e c i e s. *Levinotothyris rotunda* Smirnova, sp. nov.

D i a g n o s i s. Shell small, smooth or with small ventral sulcus near the anterior margin. Valves almost equiconvex. Anterior commissure widely arched or straight. Pedicle collar present. Visceral foramen spotlike. Outer hinge plates wide. Inner hinge plate thin. Crural bases located on ventral side of inner hinge plate. Free loop branches very short. Vertical plate high, long, and projecting beyond brachidium. Loop centronelloid. Loop length less than one-half of dorsal valve length.

S p e c i e s c o m p o s i t i o n. Type species, *L. dmitrievi* Grunt, 1973 from the Lower Kyzyldzhilga Subhorizon (Darvazian Stage, Upper Permian) of the southeastern Pamirs and *L. salomonense* Gemmellaro, 1899 from the uppermost Kubergandian–lowermost Murgabian (Upper Permian) of Sicily.

C o m p a r i s o n. The new genus differs from the genera *Notothyris* Waagen, 1882; *Rostranteris* Gemmellaro, 1899; and *Notothyrina* Licharew, 1936 in the

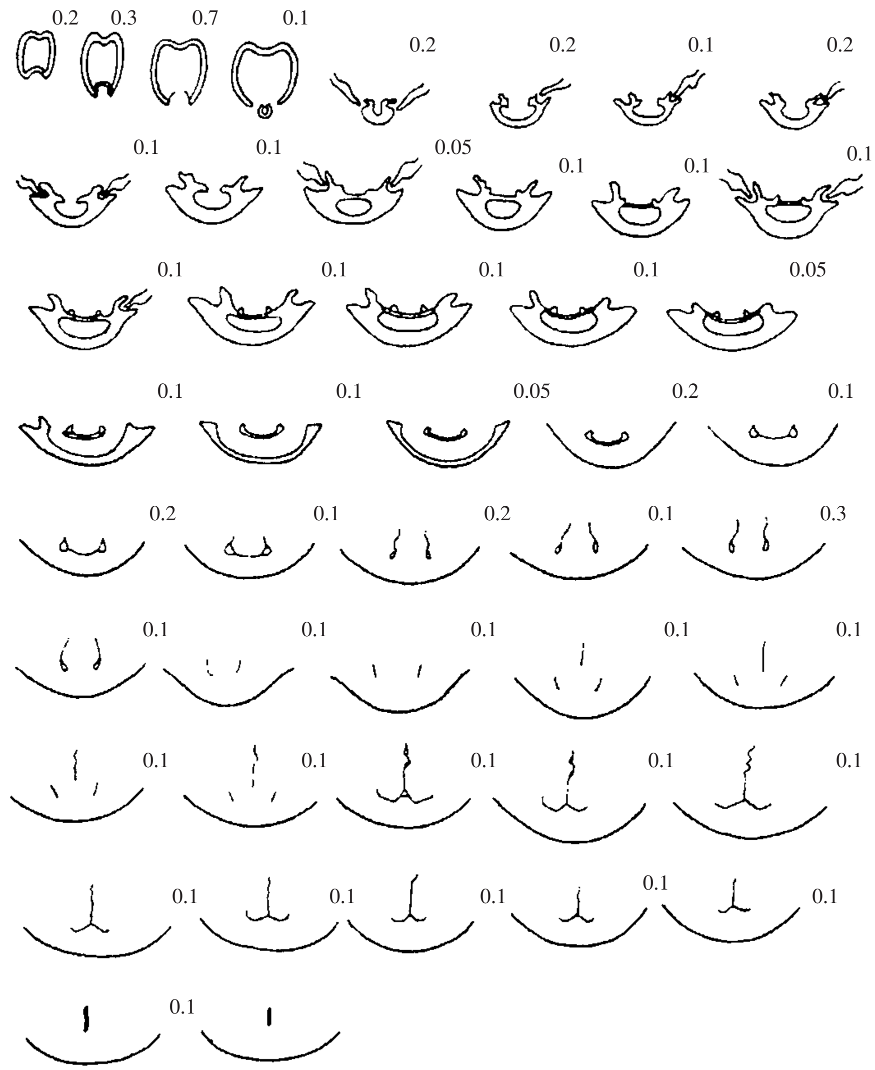


Fig. 41. *Rostranteris ovaleformis* Smirnova, 2001, specimen PIN, no. 4104/19, serial cross sections; figures indicate distances between the sections in mm.

smooth shell, straight or uniplicate anterior commissure, short loop, spotlike visceral foramen, and ventrally directed crural bases.

R e m a r k s. Gemmellaro (1899) assumed that *Rostranteris salomonense* Gemmellaro, 1899 should have been referred to another genus. It differs from *Rostranteris* in having one rounded fold on the ventral valve, a uniplicate anterior commissure, and a short loop. However, Gemmellaro had only one specimen and could not establish a new genus.

Levinotothyris rotunda Smirnova, sp. nov.

Plate 1, fig. 5

E t y m o l o g y. From the Latin *rotundus* (rounded).

H o l o t y p e. PIN, no. 2228/1001, complete shell; southeastern Pamirs, Mamazair River; Upper Permian, Kyzyldzhilga Horizon.

D e s c r i p t i o n (Fig. 43). The shell is small and rounded. The umbo is projecting. The width and length are almost equal. The anterior commissure is arched and uniplicate. The lateral commissures are straight. The hinge line is long and strongly curved. The maximum width is in the posterior third of the shell. The maximum thickness is in the middle. The lateral sides of the shell are slightly flattened. The ventral valve is widely arched in cross section. The shallow sulcus on the ventral valve is well-developed near the anterior margin, which projects slightly dorsally. The sulcus surface gradually transforms to the lateral sides of the valve. The umbo is high and pointed. The false area is high, concave, and bordered by the sharpened umbonal keels. The apical angle is 80°–90°. The dorsal valve is strongly convex in the posterior half and is flattened laterally and near the anterior margin, where a wide, flattened fold is present.

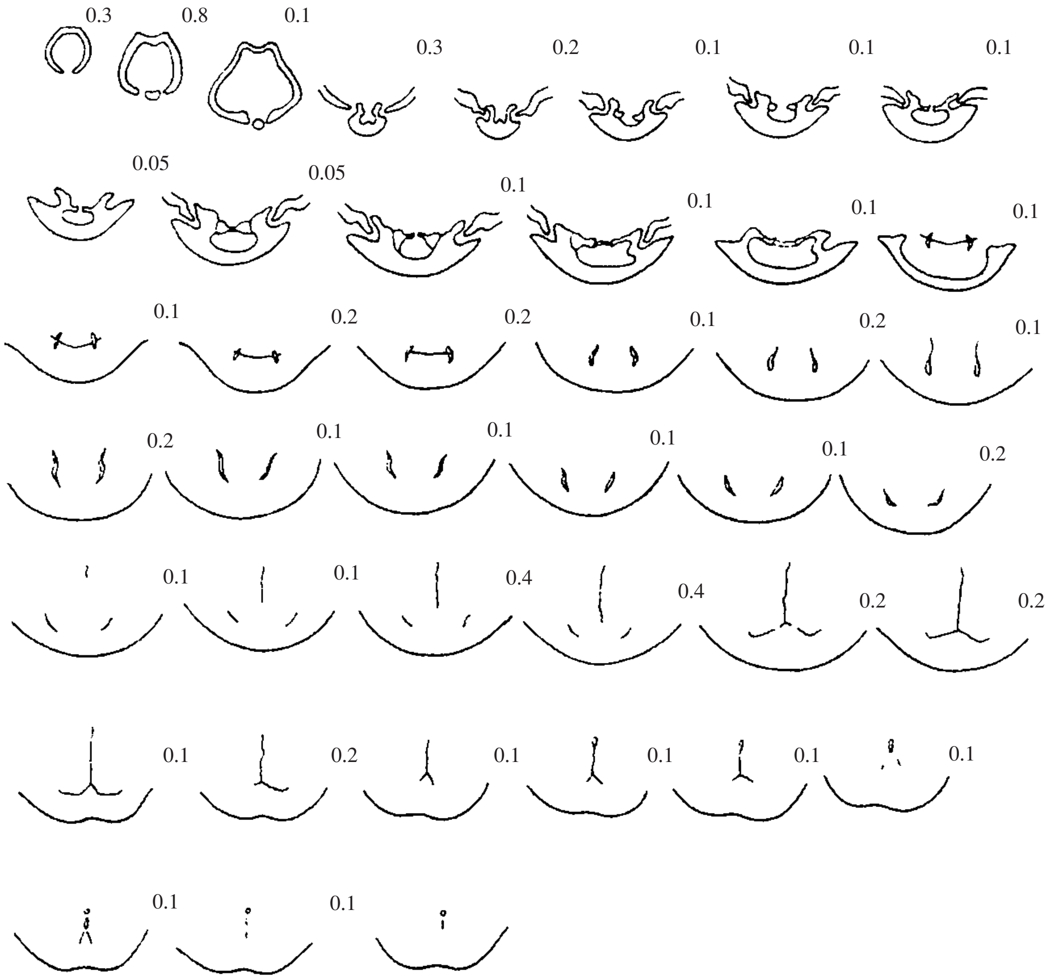


Fig. 42. *Rostranteris charymdarensis* Smirnova et Grunt, 2002, specimen PIN, no. 4104/607, serial cross sections; figures indicate distances between the sections in mm.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
Holotype					
2228/1001	12.0	11.3	7.0	0.94	0.58
2228/1002	11.6	11.4	6.0	0.98	0.51
2228/1003	10.0	10.0	4.5	1.0	0.45
2228/1004	8.9	9.2	4.8	1.03	0.54
2228/1005	8.5	7.5	4.5	0.88	0.53

S h e l l i n t e r i o r. The pedicle collar is narrow and arched. The teeth have not been preserved. The visceral foramen is small. The outer hinge plates are wide and almost horizontal. The inner hinge plate is narrow and concave. The loop branches fuse near the cardinalia. A high vertical plate with a weakly developed thickening at the top is located at the junction of the loop branches. The vertical plate projects beyond the loop and has an irregular anterior margin.

C o m p a r i s o n. The new species differs from *L. dmitrievi* in the wider shell, larger apical angle, uniplicate commissure, flattened margins of the shell, and in the presence of a shallow sulcus on the ventral valve.

O c c u r r e n c e. Upper Permian, Darvazian Stage, Lower Kyzyldzhilga Subhorizon; southeastern Pamirs.

M a t e r i a l. Thirteen well-preserved specimens from the Mamazair River basin, one well-preserved shell and five shells with broken margins from the outskirts of the village of Igrimiyuza.

Genus *Gefonia* Licharew, 1936

Gefonia: Licharew, 1936, p. 264; Stehli, 1965, H758 and H759; Grant, 1976, p. 254.

T y p e s p e c i e s. *Gefonia cubanica* Licharew, 1936.

D i a g n o s i s. Shell small, biconvex, rounded pentagonal or oval, and bi- or multiplicate. Both valves bear sulci bordered by folds. Small folds may be developed in sulci. Pedicle collar may be absent. Visceral

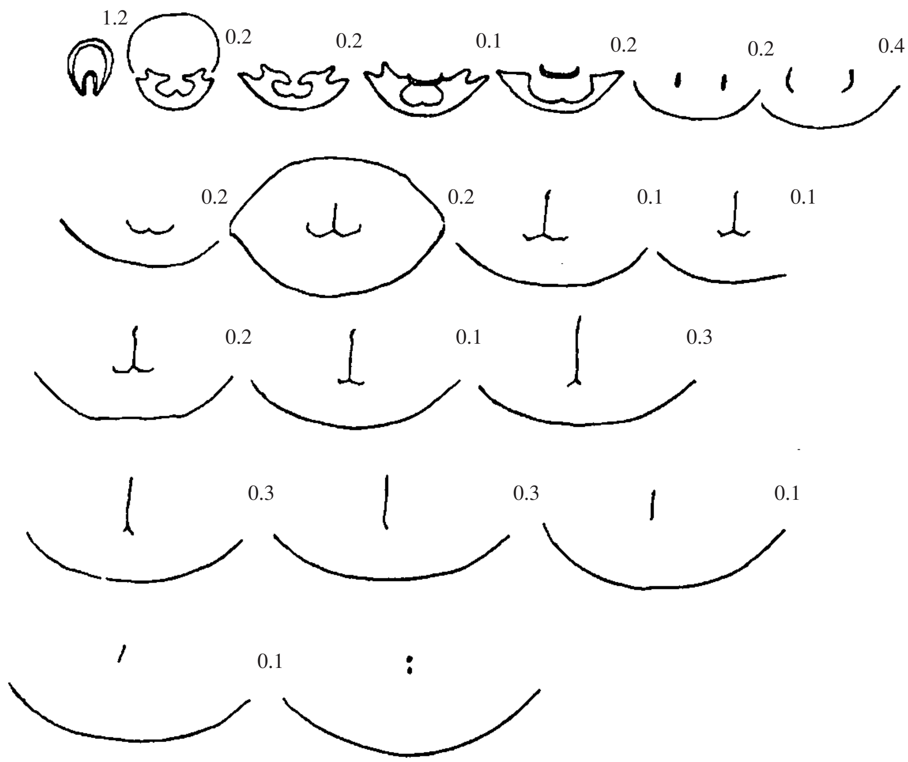


Fig. 43. *Levinotothyris rotunda* sp. nov., specimen PIN, no. 2228/1006, serial cross sections; figures indicate distances between the sections in mm.

foramen present. Inner hinge plate horizontal and free. Crural bases raised. Brachidium consisting of long and complicated loop. Descending branches connected in the middle by transverse plate, which is usually convex ventrally. Ends of long flanks directed posteriorly and form long bands. Anterior ends of the flanks bear small spines.

S p e c i e s c o m p o s i t i o n. Type species, *G. plicata* Licharew, 1936, and *G. levis* Licharew, 1936 from the Urushten Horizon (Djulfian Stage, Upper Permian) of Northern Caucasia; *G. licharewi* sp. nov. from the Takhtabulak Formation (Djulfian Stage, Upper Permian) of the southeastern Pamirs.

C o m p a r i s o n. This genus differs from *Notothyris* Waagen, 1882 and *Rostranteris* Gemmellaro, 1899 in the long, complicated loop.

Gefonia licharewi Smirnova, sp. nov.

Plate 1, fig. 6

E t y m o l o g y. In honor of the geologist B.K. Licharew.

H o l o t y p e. PIN, no. 2228/258, complete shell; southeastern Pamirs, village of Kuristyk; Upper Permian, Djulfian, Takhtabulak Formation.

D e s c r i p t i o n (Figs. 24, 25). The shell is small, wide, strongly convex, and rounded pentagonal. The folds are sharp, numerous, and start near the umbo. The length and which are almost equal. The anterior commissure is rectimarginate. The lateral commissures are almost straight. All commissures are denticulate. The maximum width and thickness are in the middle. The hinge line is long and strongly curved. The ventral valve is strongly convex lengthwise and transversally and bears 14 folds. The sulcus is poorly developed, flattened, located in the anterior third of the valve, and bears four high folds. The lateral sides bear five lower folds. The umbo is massive, obtuse, and strongly curved. The false area is high and flattened. The umbonal keels are weakly developed. The apical angle is 75°–80°. The foramen is small and submesothyrid. The dorsal valve is uniformly convex, slightly flattened in the anterior third, and bears 12 or 13 folds.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
Holotype 2228/258	13.2	12.8	11.0	0.97	0.83
2228/1019	13.1	12.6	9.8	0.96	0.75
2228/1020	12.1	11.8	10.0	0.98	0.83
2228/1021	7.0	6.8	5.1	0.97	0.73

S h e l l i n t e r i o r. The pedicle collar may be developed. The inner hinge plate is horizontal and borders the small visceral foramen. The outer hinge plate is narrow. The ventral and dorsal tips of the crural bases are equal. The crural processes are long. The descending loop branches are short and join at a small distance. The transverse band of the loop is poorly developed. The flanks of the loop are very long, curved posteriorly, and bear long small spines on the anterior end.

C o m p a r i s o n. The new species differs from *G. cubanica* Licharew, 1936 (type species) and *G. levis* Licharew, 1936 in the larger number of folds on both valves, strongly convex valves, denticulate commissures, and in the presence of sulci on both valves.

O c c u r r e n c e. Lower Permian, Bolorian Stage, Safetdaron Formation of the southwestern Darvaz; Djulfian Stage, Takhtabulak Formation of the southeastern Pamirs.

M a t e r i a l. Five shells from the village of Kuristyk, southeastern Pamirs, and two shells from the interfluve between the Charymdara and Zidadara rivers, southwestern Darvaz.

Gefonia plicata Licharew, 1936

Plate 1, fig. 7

Gefonia cubanica var. *plicata*: Licharew, 1936, p. 264, pl. 1, fig. 3.

H o l o t y p e. TsNIGR Museum, no. 1547/2139; Northern Caucasia, Nikitina ravine; Upper Permian, Djulfian, Urushten Horizon.

D e s c r i p t i o n. The shell is small, biplicate, and rounded pentagonal, with an elongated umbonal region. The anterior commissure is W-shaped. The lateral commissures are slightly arched. The ventral valve is more convex than the dorsal valve. The maximum width is in the middle or slightly shifted to the anterior margin. The maximum thickness is in the middle. The ventral valve is strongly convex in the umbonal region and widens anteriorly in the form of a roof. The sulcus is narrow, deep, and extends in the middle of the valve from the umbo up to the anterior margin. It is bordered by high, sharpened folds. The folds bear small hollows on the outside. The lateral sides are wide and flattened. The umbo is high and strongly curved. The false area is narrow. The umbonal keels are rounded. The apical angle is 67°–75°. The foramen is large and labiate. The dorsal valve is convex in the posterior half and flattened in the anterior half, where one middle and two lateral folds are present. The lateral folds are bordered outside by shallow depressions. The lateral sides of the dorsal valve are wide and rounded.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
4918/71	13.5	10.8	8.5	0.80	0.63
4918/62	13.5	11.5	8.5	0.86	0.63
4918/1501	14.0	12.0	9.2	0.85	0.65
4918/1502	13.0	11.2	9.0	0.86	0.69

C o m p a r i s o n. This species differs from *G. cubanica* Licharew, 1936 in the high and sharp folds, high umbo, less convex valves, and rounded lateral sides of the shell. It differs from *G. licharewi* sp. nov. in the biplicate shell, W-shaped anterior commissure, narrow and deep sulcus on the ventral valve, and narrower shell.

O c c u r r e n c e. Upper Permian, Djulfian Stage, Urushten Horizon; Northern Caucasia.

M a t e r i a l. Three complete shells and two shells with broken margins from Mt. Yatyrgvarta.

Genus *Notothyrina* Licharew, 1936

Notothyris (*Notothyrina*): Licharew, 1936, p. 271.

Rostranteris (*Notothyrina*): Stehli, 1965, H759.

T y p e s p e c i e s. *Notothyris* (Notothyrina) *pontica* Licharew, 1936.

D i a g n o s i s. Shell small and biplicate, from rounded triangular to rounded pentagonal. Ventral valve more convex than dorsal one. Pedicle collar and visceral foramen present. Crural bases located on the ventral side of the inner hinge plate. Inner hinge plate free. Outer hinge plate developed in the apical region. Loop long and triangular. Descending branches short. Flanks constitute most of the loop. Transverse band angular in outline and located in the middle of the loop.

S p e c i e s c o m p o s i t i o n. Type species, *N. levis* Licharew, 1936 from the Urushten Horizon, Djulfian Stage, Upper Permian of Northern Caucasia.

C o m p a r i s o n. This genus differs from *Gefonia* Licharew, 1936 in the structure of the loop, the absence of additional bands of the loop that are directed posteriorly, the shape of the transverse band, and the absence of small spines on the loop. It differs from the genus *Rostranteris* Gemmellaro, 1899, which is similar in exterior structure, in the complicated loop with long flanks and in the transverse band of the loop. From *Notothyris* Waagen, 1882 it differs in the biplicate shell, long triangular loop, and in the presence of flanks.

Notothyrina pontica Licharew, 1936

Plate 1, fig. 8

Notothyris (Notothyrina) pontica: Licharew, 1936, p. 271, pl. 1, fig. 4, text-fig. 3; Licharew et al., 1960, p. 289, pl. 68, fig. 5, text-figs. 441 and 442.

Rostranteris (Notothyrina) pontica: Grunt, 1973, pp. 160 and 161, pl. 13, fig. 9, pl. 16, figs. 3 and 4, text-figs. 59 and 60.

H o l o t y p e. TsNIGR Museum, no. 631/2139, complete shell; Northern Caucasia, Nikitina ravine, 1 km from the mouth of the Malaya Laba River; Upper Permian, Djulfian, Urushten Horizon.

D e s c r i p t i o n (Fig. 44). The shell is mostly rounded pentagonal with two folds on the ventral and three folds on the dorsal valve. The folds are well-pronounced in the anterior half of the shell. The valves are

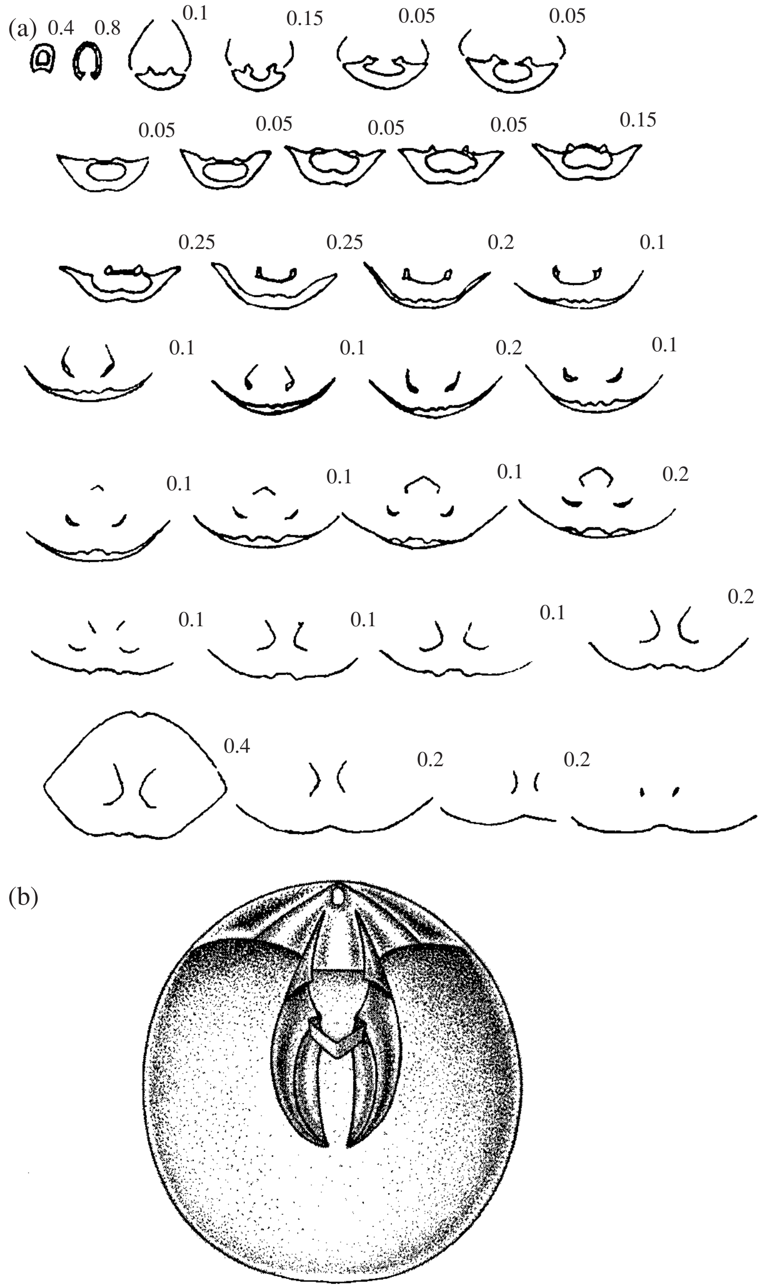


Fig. 44. *Notothyrina pontica* Licharew, 1936, specimen PIN, no. 4918/1508: (a) serial cross sections; figures indicate distances between the sections in mm; (b) reconstruction of the internal structures.

moderately to strongly convex. The anterior commissure is W-shaped. The lateral commissures are slightly arched. The hinge line is long and strongly curved. The maximum width is in the middle or in the anterior third of the shell. The maximum thickness is in the middle or in the posterior third of the shell. The ventral valve is considerably more convex than the dorsal one. The umbonal region is strongly convex. The umbo is high, narrow, and curved. The false area is short. The umbonal keels are smooth. The apical angle is 72°–77°. The foramen is large and apical. The dorsal valve is more convex in the posterior half.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
4918/1504	8.0	7.5	4.5	0.94	0.56
4918/1505	9.2	7.5	5.8	0.81	0.63
4918/1506	9.0	7.6	7.0	0.84	0.77
4918/1507	7.0	7.0	4.5	1.00	0.64

Shell interior. The pedicle collar is gently arched. The visceral foramen is small. The outer hinge plate is very narrow and convex. The inner hinge plate forms as a result of enlarging the inner tips of the outer hinge plate. The crural bases are shaped like tubercles and are located on the ventral side of the inner hinge plate. The descending branches are short, wide, and concave. The transverse plate of the loop is thin and triangular in section. The flanks of the loop are long, wide, and concave toward the lateral sides of the shell. The loop length is more than one-half of the dorsal valve length.

R e m a r k s. The specimens described were referred to *N. pontica* since they are identical in external appearance and occur at the same stratigraphic level as the holotype of *N. pontica*, only a few kilometers from the type locality.

O c c u r r e n c e. Upper Permian, Djulfian Stage, Urushten Horizon of Northern Caucasia and Transcaucasia; Djulfian Stage, Middle Takhtabulak Subformation of the southeastern Pamirs.

M a t e r i a l. Two specimens from Mt. Yatyrgvarta, Northern Caucasia, one specimen from the village of Dorosham-2, Transcaucasia; two well-preserved shells and two shells with broken margins near the village of Kutal', southeastern Pamirs.

S u p e r f a m i l y Dielasmatoidea Schuchert, 1913

D i a g n o s i s. Dental plates and inner hinge plates present. Crural plates absent. Loop short and triangular. Brachidium development simple, without secondary elements. Brachidium ontogeny with centronelloid, mutationelliform, and dielasmoid stages.

C o m p o s i t i o n. Dielasmatidae Schuchert, 1913.

Family Dielasmatidae Schuchert, 1913

Dielasmatidae: Campbell, 1965, p. 21; pars Stehli, 1965, H756; Licharew et al., 1960, p. 292.

D i a g n o s i s. Shell smooth or uniplicate. Dental plates always developed. Outer hinge plates well-pronounced. Inner hinge plates resting on the bottom of the dorsal valve or supported by septum, forming septalium. Crural bases connected with outer hinge plates. Loop triangular and short.

O c c u r r e n c e. Carboniferous–Triassic.

R e m a r k s. Until recently, the concept of the family Dielasmatidae was broad: terebratulids with and without dental plates were included. Campbell (1965) studied the internal structures of the type species of the genus *Dielasma*, *D. elongatum* Schlotheim, 1816. He suggested that terebratulids with dental plates and a simple triangular loop should be placed into the family Dielasmatidae. Campbell established the family Gillediidae for terebratulids with the same structure of the loop but lacking dental plates.

C o m p o s i t i o n. *Dielasma* King, 1859: *Fletcherithyris* Stehli, 1961; *Jochelsonia* Stehli, 1961; *Elasmata* Waterhouse, 1982; *Ectoposia* Cooper et Grant, 1976; *Plectelasma* Cooper et Grant, 1976; *Adygella* Dagys, 1959; and *Sulcatinella* Dagys, 1974.

Genus *Dielasma* King, 1859

Dielasma: King, 1859, p. 260; Licharew, 1913, pp. 25 and 26; 1939, p. 118; Netschajew, 1911, pp. 108 and 109; Stehli, 1956, p. 301; 1965, H756; Licharew et al., 1960, p. 292; Campbell, 1965, pp. 22–24; Brügge, 1974, pp. 185–189; Cooper et Grant, 1976, pp. 2860–2863; Grant, 1976, p. 244.

T y p e s p e c i e s. *Dielasma elongatum* Schlotheim, 1816.

D i a g n o s i s. Shell small to large. Ventral valve convex or flattened. Sulcus may be developed on the ventral valve. Umbo variously curved. Foramen labiate. Pedicle collar present. Lateral and anterior commissures widely arched. Dental plates variously long. Cardinal process absent. Outer hinge plates from narrow to wide. Inner hinge plates connected with the valve bottom separately and may be supported by the euseptoid or low septum to form wide septalium. Loop narrow and extends up to one-third or one-half of the dorsal valve length.

R e m a r k s. The holotype of *Terebratulites elongatus* Schlotheim, 1816 from limestone near Glücksbrunn (Thuringia) was housed in the Museum of Geology and Paleontology in Berlin and destroyed during World War II. A neotype was designated from the same horizon as the type species on the outskirts of the town of Pößneck (Thuringia). Externally it is quite similar to Schlotheim's type.

S p e c i e s c o m p o s i t i o n. Type species, *D. robustum* Smirnova, 2004 and *D. kirillowense* Licharew, 1913, from the Lower Kazanian Substage (Upper Permian) of the Kirov region, and *D. subelongatum* sp. nov. from the Lower Kazanian Substage (Upper Permian) of the Samara Region. Cooper and Grant (1976) described 31 species from the Guadalupian Stage (Upper Permian) of western Texas, of which the new species *D. adamanteum*, *D. compactum*, and *D. expansum* are widespread.

C o m p a r i s o n. This genus differs from *Fletcherithyris* Stehli, 1961 in the curved umbo, absence of a cardinal process, low dorsal septum, and wide septalium. It differs from *Yochelsonia* Stehli, 1961 in the type of valve curvature, curved umbo, longer dental plates, and in the presence of the ventral sulcus.

Dielasma robustum Smirnova, 2004

Plate 1, fig. 9

Dielasma robustum: Smirnova, 2004b, p. 28, pl. 4, figs. 3a–3d.

H o l o t y p e. PIN, no. 4898/2351, complete shell; eastern Russian Platform, Kirov Region, Chimbulatskii quarry; Upper Permian, Lower Kazanian.

D e s c r i p t i o n (Fig. 45). The shell is oval, with thick valves and coarse growth lines transforming into rugae in the anterior half. The valves are equiconvex and strongly inflated. The lateral surfaces are subparal-

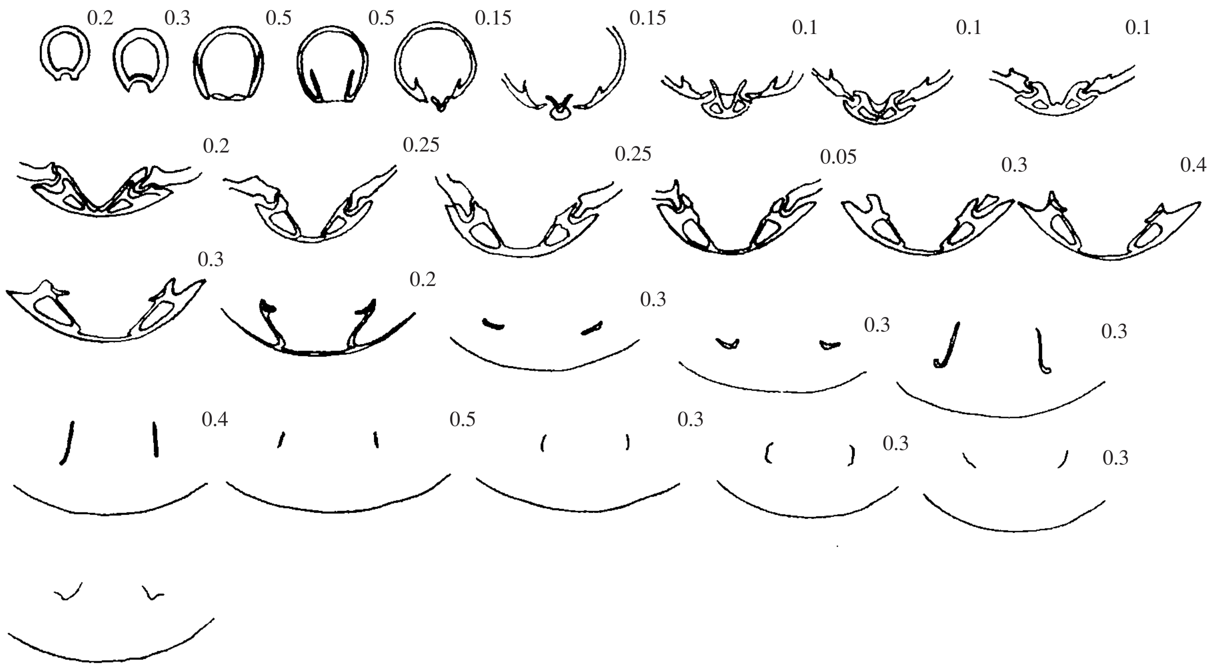


Fig. 45. *Dielasma robustum* Smirnova, 2004, specimen PIN, no. 4898/2352, serial cross sections; figures indicate distances between the sections in mm.

lel and almost perpendicular to the flattened middle region of the valves. The maximum width is in the middle. The maximum convexity is in the anterior third of the shell. The lateral commissures are almost straight. The anterior commissure is slightly arched. The ventral valve is strongly convex throughout the surface and is slightly flattened near the anterior margin. The umbo is wide and massive. The umbonal keels are rounded. The foramen is absent. The apical angle is 60°–65°. The false area is absent. The dorsal valve is flattened in the posterior half and strongly inflated in the anterior half. The angle of its bend between the anterior and posterior margins is about 100°.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
Holotype 4898/2351	14.5	10.2	11.5	0.70	0.79
4898/2352	15.9	12.7	11.8	0.80	0.74

S h e l l i n t e r i o r. The pedicle collar is gently arched. The dental plates are short and diverging. The teeth enter the sockets obliquely and bear outer and inner denticles. The outer hinge plates are horizontal. The inner hinge plates are supported by the euseptoid in the umbonal region and form a deep septalium. Anteriorly the septal plates rest on the valve bottom at a considerable distance from each other. The crural bases are parallel to the valve bottom and not raised over the outer hinge plate. The crural processes are narrow and subparallel. The descending branches of the loop are narrow. The transverse band of the loop has not been observed.

C o m p a r i s o n. This species differs from other *Dielasma* species in the strongly inflated valves, parallel inner surfaces, slightly curved commissures, and coarse growth lines. In addition, it differs from *D. kirillowense* Licharew, 1913 in the crural bases parallel to the valve bottom and inner hinge plates located far from each other. From *D. elongatum* Schlotheim, 1816 it differs in the short dental plates and inner hinge plates located far from each other.

M a t e r i a l. Two satisfactorily preserved specimens from the type locality.

Dielasma kirillowense **Licharew, 1913**

Plate 1, fig. 10

Dielasma kirillowense: Licharew, 1913, pp. 28 and 29, pl. 1, figs. 12 and 20; Smirnova, 2004b, pp. 28 and 29, pl. 4, figs. 4a–4d.

H o l o t y p e. TsNIGR Museum, no. 27/26, complete shell; eastern Russian Platform, Kirov Region, village of Sandyreva; Upper Permian, Lower Kazanian.

D e s c r i p t i o n (Figs. 7e, 46). The shell is oviform, with slightly straightened anterior margin. The valves are uniformly convex along the entire length. The ventral valve is slightly more convex than the dorsal. The lateral commissures are almost straight. The anterior commissure is straight or gently arched. The maximum width is in the anterior third of the shell. The maximum thickness is in the middle. The ventral valve is not plicate and may have a weakly developed hollow in the middle of the anterior margin. The umbo is high, massive, strongly curved, and overhanging the dorsal

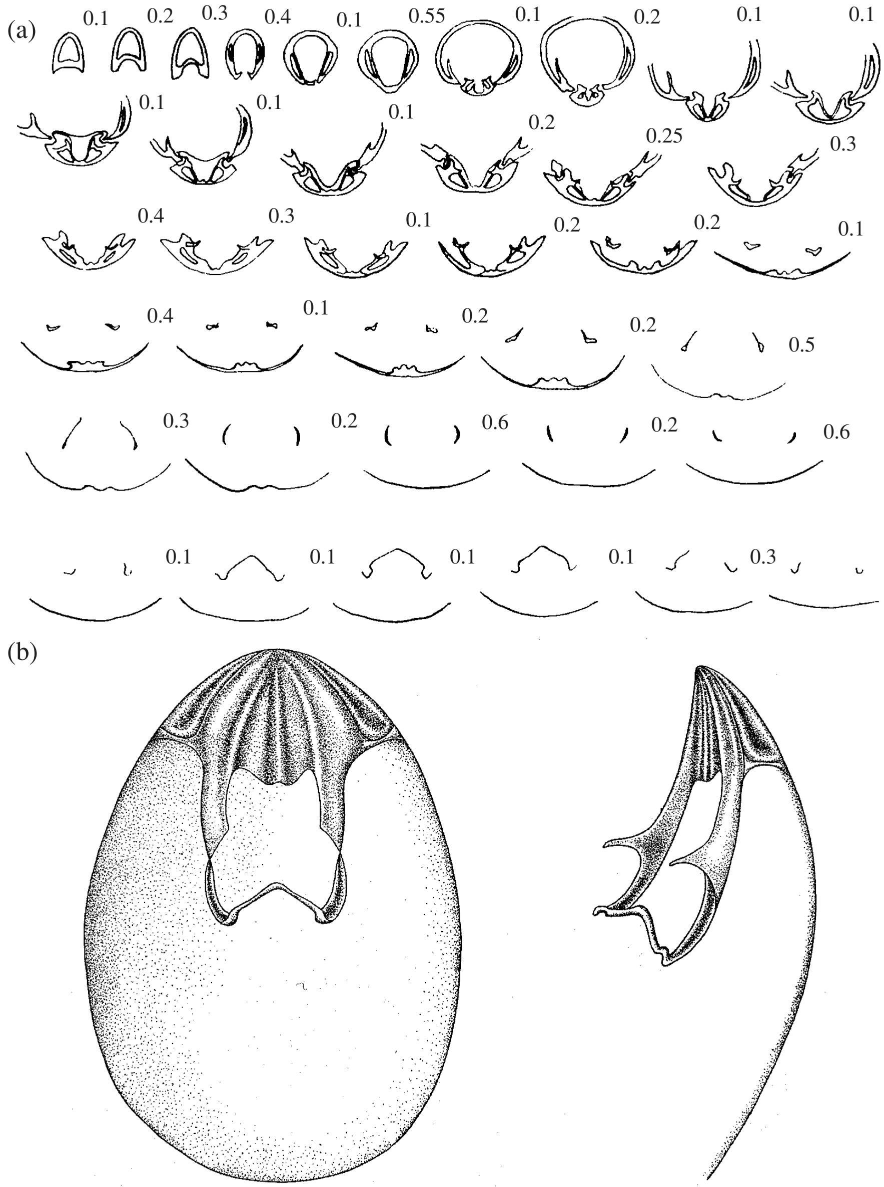


Fig. 46. *Dielasma kirillowense* Licharew, 1913, specimen PIN, no. 4898/2357: (a) serial cross sections; figures indicate distances between the sections in mm; (b) reconstruction of the internal structures.

valve. The false area is high and bordered by coarse, long, and smooth umbonal keels. The apical angle is 60°–66°. The foramen is large, umbonal, oval, and labiate. The dorsal valve is smooth, not plicate, and of equal curvature both transversely and longitudinally.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
4898/2353	20.5	15.2	11.4	0.74	0.55
4898/2354	19.5	13.6	10.9	0.69	0.56
4898/2355	18.8	13.8	12.0	0.73	0.64
4898/2356	18.0	13.2	9.2	0.73	0.51
4898/2357	17.6	14.0	10.3	0.79	0.58

Shell interior. The pedicle collar is gently arched. The dental plates are diverging and border narrow umbonal cavities. The teeth are hook-shaped, vertically enter the sockets, and bear inner and outer denticles. The outer hinge plates are narrow and concave. The inner hinge plates rest on the valve bottom alongside each other in the umbonal region. Anteriorly they rest on the bottom at a distance from each other without forming septalium. The crural bases are raised over the outer hinge plate. The crural processes are wide, with ventral tips inclined to the plane of symmetry. The loop branches are narrow and subparallel. The transverse band is angularly arched and curved in the middle at an angle of 90°–110°. The loop branches are concave at

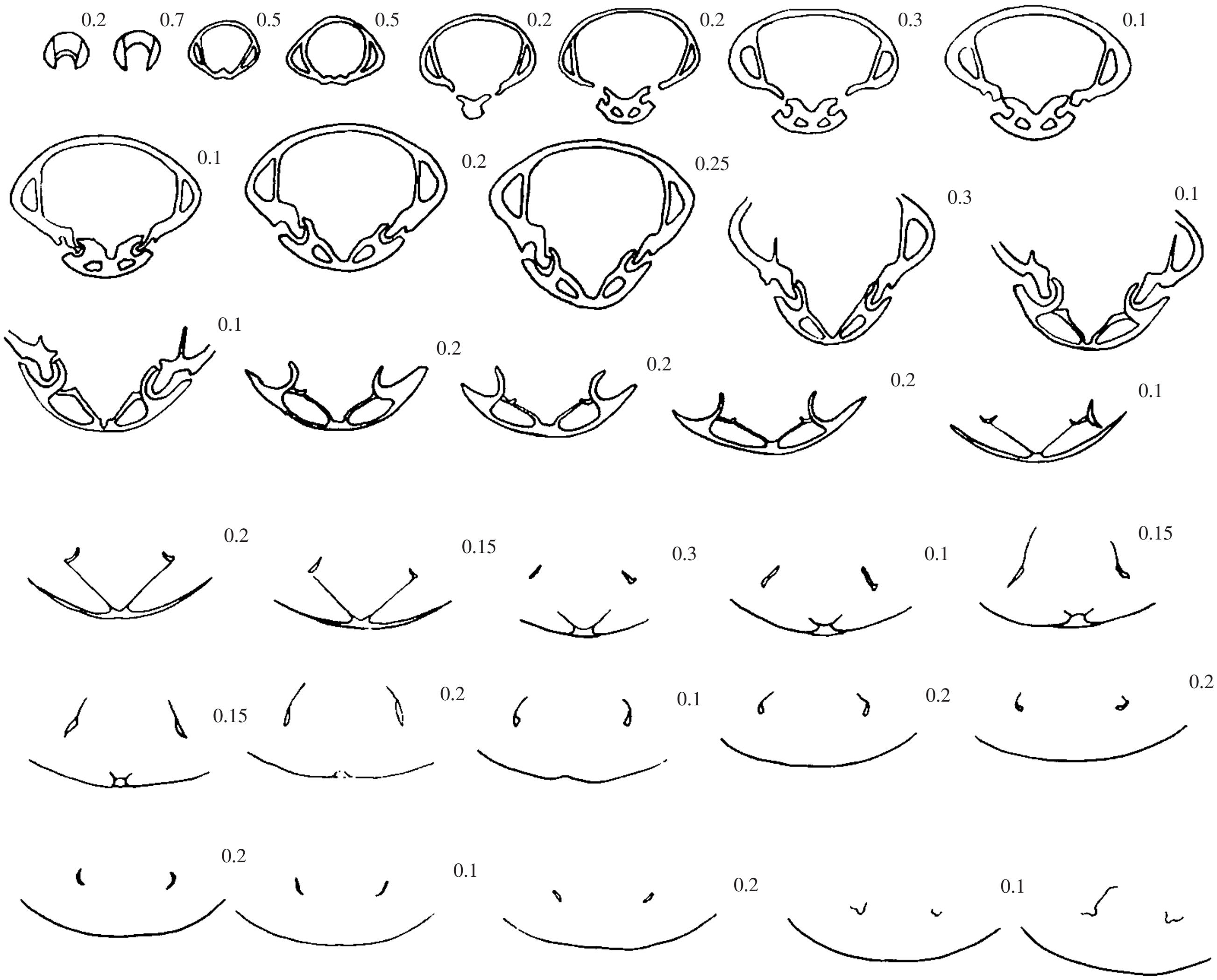


Fig. 47. *Dielasma subelongatum* sp. nov.; specimen PIN, no. 4898/2549, serial cross sections; figures indicate distances between the sections in mm.

the junction with the transverse band. The loop length is about one-half of the dorsal valve length.

C o m p a r i s o n. This species differs from *D. elongatum* Schlotheim, 1816 in the oviform shell, convex lateral sides, high and massive umbo, straight lateral commissures, and slightly curved anterior commissure.

O c c u r r e n c e. Upper Permian, Lower Kazanian Substage; eastern Russian Platform.

M a t e r i a l. Fifty specimens: ten well-preserved specimens from the Chimbulatskii quarry, Kirov Region, and 40 satisfactorily preserved specimens from the Sok River basin, Samara Region.

Dielasma subelongatum **Smirnova, sp. nov.**

Plate 1, fig. 11

Dielasma elongata: Netschajew, 1911, pp. 109–111, pl. 15, fig. 4.

E t y m o l o g y. From the resemblance to the related species *D. elongatum* Schlotheim, 1816.

H o l o t y p e. PIN, no. 4898/2544, complete shell; Samara Region, Sok River, village of Kamyshla; Upper Permian, Lower Kazanian, Bajtugan Beds.

D e s c r i p t i o n (Fig. 47). The shell is middle-sized, oval, with elongated umbo and flattened lateral and anterior margins. The ventral valve is more convex than the dorsal one. The anterior commissure is gently arched. The lateral commissures are widely arched. The hinge line is short and strongly curved. The maximum width is in the anterior third of the shell. The maximum thickness is in the middle. The ventral valve is smooth, with maximum thickness in the posterior half. The umbo is high and slightly curved. The foramen is large and labiate. The false area is low, narrow, and bordered by the smooth umbonal keels. The apical angle is 80°–85°. The dorsal valve is slightly convex in the middle, with flattened margins. A poorly pronounced elevation may be present in the anterior half.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
Holotype 4898/2544	21.5	16.2	8.6	0.75	0.40
4898/2545	21.0	15.0	8.4	0.71	0.40
4898/2546	21.1	17.0	8.5	0.81	0.40
4898/2547	22.8	17.5	9.1	0.76	0.40
4898/2548	23.2	17.5	9.7	0.75	0.42

S h e l l i n t e r i o r. The pedicle collar is strongly arched. The teeth are massive, enter the sockets obliquely, and widen at their ends. The outer denticle is well-developed. The dental plates are long, diverging in the apical region, and subparallel anteriorly. The outer hinge plates are developed only near the hinge line. The inner hinge plates are supported by a short septum in the apical region and form a septalium. Anteriorly they are supported by the euseptoid. The crural bases are concave and appear in the location of the outer hinge plates. Their tips are curved ventrally. The crural processes and loop branches are narrow. The transverse band of the loop is trapezoidal.

C o m p a r i s o n. The new species differs from *D. elongatum* Schlotheim, 1816 in the longer and larger shell, high umbo, flattened margins, long dental plates, and in the shape of the inner hinge plates. It differs from *D. kirillowense* Licharew, 1913 in the more convex ventral valve, low false area, short hinge line, slightly curved umbo, large apical angle, weakly developed outer hinge plates, shape of the inner hinge plates, and shape of the transverse band of the loop.

M a t e r i a l. Twenty satisfactorily preserved shells from the type locality.

S u p e r f a m i l y Gilledioidea Campbell, 1965

D i a g n o s i s. Dental plates absent. Inner hinge plates connected with the valve bottom or septum. Crural plates absent. Brachidium consists of a loop at the terebratuliform stage. Ontogeny of brachidium unknown.

O c c u r r e n c e. Permian.

C o m p o s i t i o n. Gillediidae Campbell, 1965

Family Gillediidae Campbell, 1965

Gillediidae: Campbell, 1965, pp. 69.

D i a g n o s i s. Shell middle-sized, biconvex, smooth, often finely plicate in the anterior half. Outer hinge plates narrow or absent. Inner hinge plates separately rest on the valve bottom or connected with septum to form a sessile septalium. Loop short.

O c c u r r e n c e. Permian.

C o m p o s i t i o n. *Gilledia* Stehli, 1961; *Maorielasma* Waterhouse, 1964; *Marinurnula* Waterhouse, 1964; *Mongolina* Grabau, 1931; *Lowenstamia* Stehli, 1961; *Camarelasma* Cooper et Grant, 1976; *Aneuthelasma* Cooper et Grant, 1976; *Hemiptychina* Waagen, 1882; and *Pyandzhelasma* Smirnova et Grunt, 2002.

Genus *Hemiptychina* Waagen, 1882

Hemiptychina: Waagen, 1882, pp. 361–364; Grabau, 1931, pp. 77 and 78; Licharew, 1939, p. 119; Licharew et al., 1960, p. 292; Stehli, 1965, H756; Grant, 1976, p. 245.

Morrisina: Grabau, 1931, p. 97.

T y p e s p e c i e s. *Terebratula himalayensis* Davidson, 1862.

D i a g n o s i s. Shell small, oval, biconvex, slightly to strongly convex. Dorsal valve flattened in the umbonal region. Umbo strongly curved. Foramen large. Anterior region of the shell bears numerous fine plications. Anterior and lateral commissures denticulate. Anterior margin usually perpendicular to the surfaces of both valves. Pedicle collar present. Inner hinge plates wide, resting separately on the bottom of the dorsal valve, or supported by short septum. Outer hinge plates poorly pronounced. Crural bases variously developed.

S p e c i e s c o m p o s i t i o n. Type species, *H. sublaevis* Waagen, 1882, *H. sparsiplicata* Waagen, 1882, *H. inflata* Waagen, 1882, and *H. crebriplicata* Waagen, 1882 from the Murgabian and Midian Stages of Pakistan; *H. morrisi* Grabau, 1931 from the Murgabian Stage of northern China (Inner Mongolia); and *H. kutorgi* sp. nov. from the Gnishik Horizon (Guadalupian Stage) of Transcaucasia.

C o m p a r i s o n. This genus differs from *Gilledia* Stehli, 1961 in the smaller shell, strongly curved umbo, fine plication of the shell, absence of a cardinal process, and wide inner hinge plates supported by a septum or resting on the bottom of the dorsal valve alongside each other. It differs from *Pyandzhelasma* Smirnova et Grunt, 2002 in the more convex valves, smaller shell, absence of a sulcus on the ventral valve, and wider umbo.

Hemiptychina kutorgi Smirnova, sp. nov.

Plate 1, fig. 12

Notothyris nucleolus: Sarycheva et al., 1965, p. 65, pl. 49, fig. 9.

E t y m o l o g y. In honor of S. Kutorga.

H o l o t y p e. PIN, no. 2073/1036, complete shell; Transcaucasia, Vedi River; Guadalupian, Gnishik Horizon.

D e s c r i p t i o n (Fig. 48). The shell is small or middle-sized and rounded, with strongly convex ventral valve and flattened dorsal valve. The lateral sides of the shell are convex and slightly flattened anteriorly. The anterior commissure is gently W-shaped. The lateral commissures are almost straight. The hinge line is long and strongly curved. The maximum width is in the middle. The maximum thickness is in the anterior third of the shell. The ventral valve is strongly convex, slightly flattened in the anterior half, and rounded quadrangular in cross section. The flattened surface is bordered by rounded low folds. The umbo is high, wide, and

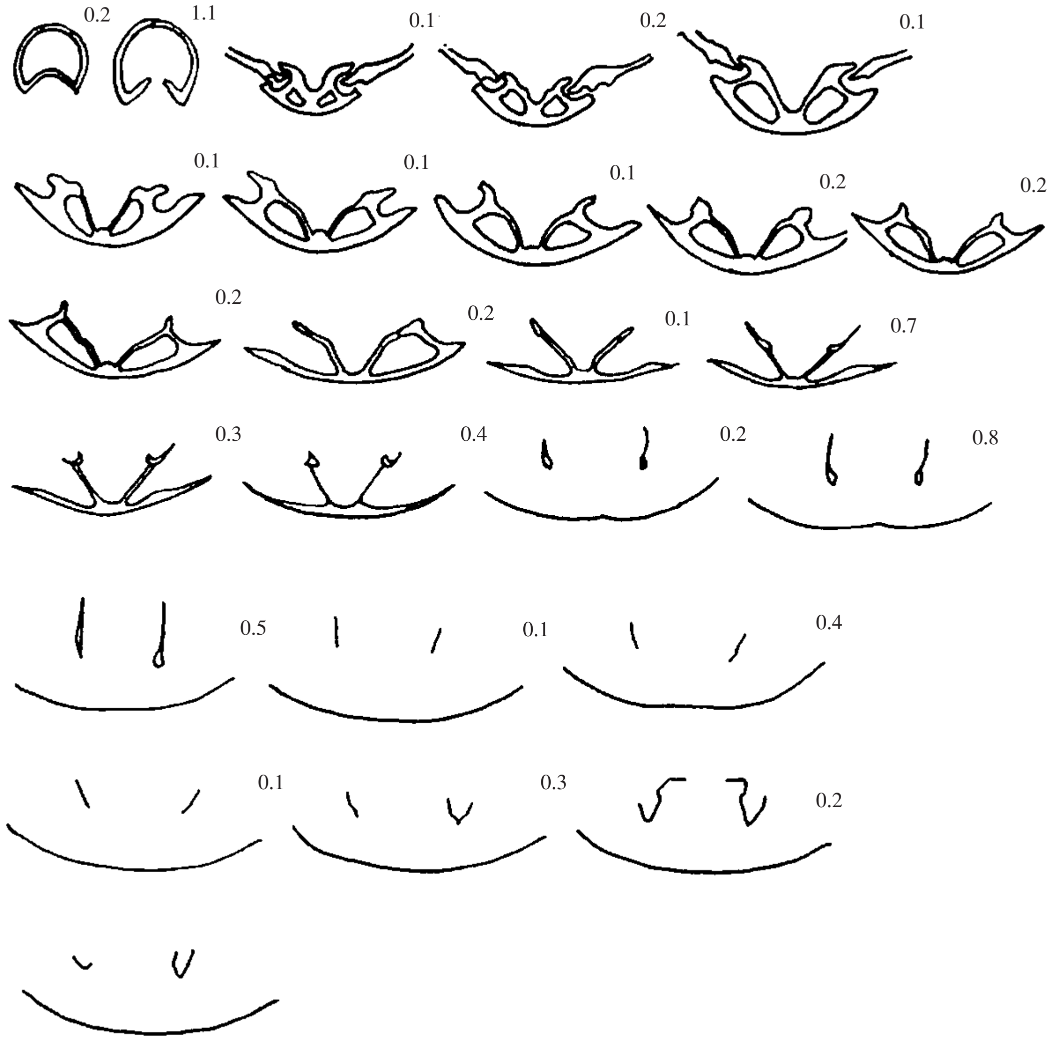


Fig. 48. *Hemiptychina kutorgi* sp. nov.; specimen PIN, no. 2073/1041, serial sections through the shell, figures indicate distances between the sections.

strongly curved. The false area is slightly concave. The umbonal keels are absent. The apical angle is 75°–80°. The dorsal valve is flattened in the middle and strongly convex in the anterior half. A deep sulcus is developed near the anterior margin. It is angular in cross section and bordered by short and sharp folds.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
Holotype 2073/1036	17.8	13.3	10.8	0.75	0.61
2073/1037	16.6	12.3	10.6	0.74	0.63
2073/1038	16.5	12.0	10.5	0.73	0.63
2073/1039	13.8	9.8	8.0	0.71	0.58
2073/1040	13.2	10.0	8.6	0.75	0.63

S h e l l i n t e r i o r. The pedicle collar is gently arched. The outer hinge plates are narrow and slightly raised in the relief of the cardinalia. The inner hinge plates are supported by a low septum in the apical region. Anteriorly they are convex and rest on the bottom of the valve on each side of the euseptoid. The crural bases continue the inner hinge plates. The border between these two structures is well-pronounced. The dorsal tips of the crural bases are concave anteriorly. The crural processes are poorly developed. The loop branches are wide and subparallel. The transverse band of the loop is not preserved.

C o m p a r i s o n. The new species differs from *H. sublaevis* Waagen, 1882 in the strongly convex shell, W-shaped anterior commissure, and in the presence of a sulcus and two short folds near the anterior margin of the dorsal valve. It differs from *H. himalayensis* Waagen, 1882 in the strongly convex valves, almost straight lateral commissures, biplicate anterior margin, and in the location of the maximum thickness of the shell.

R e m a r k s. In his original description of the genus *Hemiptychina*, Waagen (1882) noted that the type of plication “is not absolutely indispensable” for the genus. He meant that in the presence of numerous fine

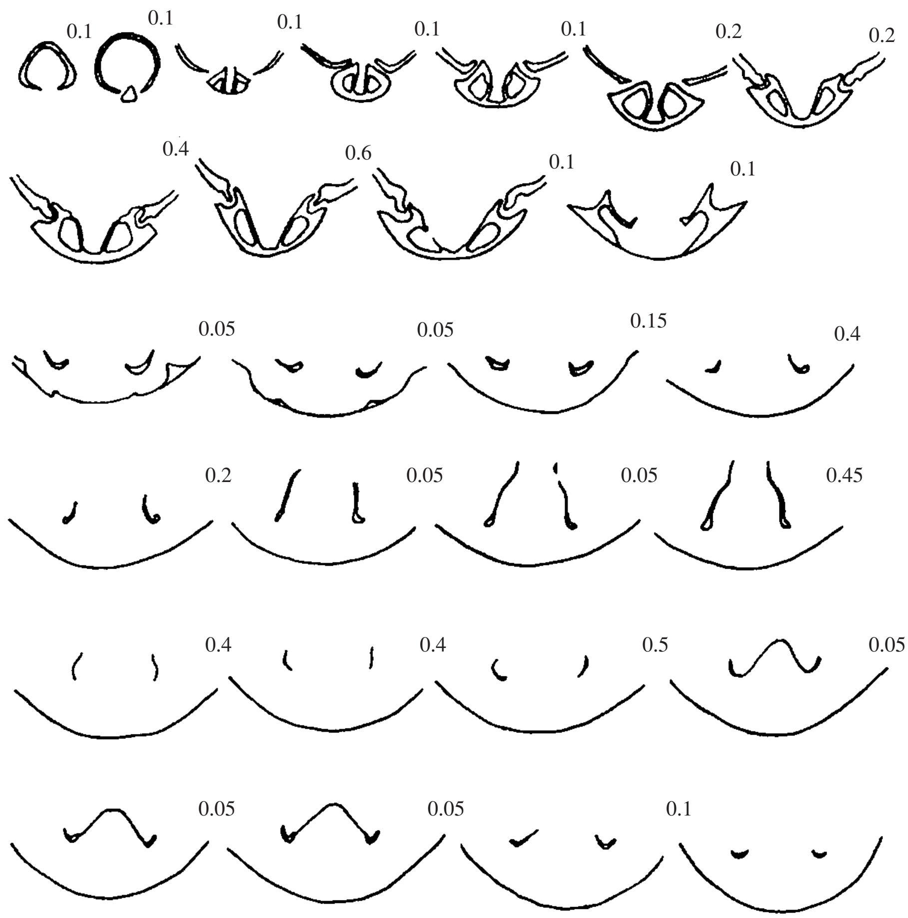


Fig. 49. *Hemiptychina himalayensis* (Davidson, 1862); specimen PIN, no. 2073/1045, serial sections through the shell; figures indicate distances between the sections in mm.

folds not only juvenile but occasionally also adult shells might be smooth, although these are probably exceptional. In our material, most of the shells are smooth. Only two short folds are developed near the anterior margin. The new species is referred to *Hemiptychina* based on the bend of the shell, flattened surfaces on the both valves, wide and strongly curved umbo, and shell interior.

O c c u r r e n c e. Upper Permian, Guadalupian Stage, Gnishik horizon; Transcaucasia.

M a t e r i a l. Four complete shells and nine shells with broken margins from the Vedi River, one complete shell and three shells with broken margins from the Avush River, five complete shells from the Ogbin River, and one shell with broken margins from the village of Geranos.

Hemiptychina himalayensis (Davidson, 1862)

Plate 1, fig. 13

Terebratula himalayensis: Davidson, 1862, p. 27, pl. 2, fig. 1.

Hemiptychina himalayensis: Waagen, 1882, pp. 368–371, pl. 26, figs. 6–10.

L e c t o t y p e. Specimen figured by Davidson (1862), pl. 2, fig. 1.

D e s c r i p t i o n (Fig. 49). The shell is elongated oval and equiconvex. The umbo is narrow and elongated. The anterior margin bears small, short folds. A few more folds are located on the lateral sides of the shell. The anterior and lateral commissures are multiplicate. The hinge line is long. The sulcus and fold are absent. The anterior margin is rounded. The maximum width is in the anterior third of the shell. The maximum thickness is in the middle. The ventral valve is moderately convex in the umbonal region and slightly flattened in the anterior half. The number of small folds is 12. The umbo is straight and high. The foramen is small. The false area is narrow. The umbonal keels are rounded. The apical angle is 67°–75°. The dorsal valve is uniformly convex and slightly flattened in the anterior half. The number of small folds is 12 or 13.

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

Specimen, no.	L	W	T	W/L	T/L
2073/1041	18.0	13.5	10.2	0.75	0.57
2073/1042	17.0	12.0	10.0	0.70	0.59
2073/1043	16.5	11.7	10.5	0.70	0.67
2073/1044	15.7	11.5	9.0	0.73	0.57

Shell interior. The pedicle collar is unknown. The outer hinge plates are narrow and slightly raised. The inner hinge plates are subparallel in the apical region and rest on the bottom of the dorsal valve separately. The crural bases are directed ventrally. The crural processes are long. The loop is short. The transverse band of the loop is shaped like a regular arc.

Comparison. This species differs from *H. sparsiplicata* Waagen, 1882 in the elongated shell, narrow umbo, sharper folds, and more convex ventral valve. It differs from *H. inflata* Waagen, 1882 in the less convex valves, larger number of folds, and narrow and less curved umbo.

Material. Four complete shells and 16 shells with broken margins from the outskirts of the village of Ogbin (Transcaucasia).

***Hemiptychina morrisi* Grabau, 1931**

Plate 1, fig. 14

Hemiptychina morrisi: Grabau, 1931, pp. 92–95, pl. 3, figs. 1–5.

Holotype. American Museum of Natural History, New York, no. 315. Cat. G.S.C. 1392; northern China (Inner Mongolia), Zhesi Hongor; Upper Permian, Murgabian.

Description. The shell is middle-sized and almost round, with a strongly convex ventral valve. The anterior margin and the anterior half of the lateral margins bear numerous small folds. The hinge line is long and strongly curved. The sulcus and fold are absent. The maximum width is slightly shifted from the middle to the anterior margin. The maximum thickness is within one-third of the valve length from the anterior margin. The ventral valve is strongly convex along the entire length and curved at a right angle in the anterior third of the shell. The lateral sides of the valve are rounded. The anterior margin is wide, flattened, and perpendicular to the surface of the valve, with large number (up to ten) of small folds. Each lateral side bears four or five folds. The umbo is high, curved, and massive, with coarse umbonal keels. The false area fuses with the lateral sides of the umbo. The apical angle is 75°–80°. The foramen is large; the shape of the foramen has not been observed. The dorsal valve is slightly convex in the posterior half and strongly convex near the anterior margin. The anterior margin and narrow lateral margins are perpendicular to the flattened surface of the valves.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
5133/1	17.4	13.5	13.5	0.77	0.77
5133/2	16.5	13.7	12.5	0.83	0.76
5133/3	14.0	12.0	10.4	0.81	0.75

Comparison. This species differs from *H. himalayensis* Davidson, 1862 in the rounded shell, massive and curved umbo, less convex dorsal valve, and larger apical angle. It differs from *H. inflata* Waagen, 1882 in the rounded shell, short and more numerous folds, and narrower umbo. From *H. sublaevis* Waagen, 1882 it differs in the rounded shell, more convex valves, presence of small folds on the shell margins, and in the bend of both valves at a right angle near the anterior margin.

Material. Three complete shells, five shells with damaged umbos, and eight shells with broken margins from Zhesi Hongor.

***Hemiptychina sparsiplicata* Waagen, 1882**

Plate 1, fig. 15

Hemiptychina sparsiplicata: Waagen, 1882, pp. 366 and 367, pl. 27, figs. 4, 5, and 6.

Morrisina sparsiplicata: Grabau, 1931, pp. 98–100, pl. 8, fig. 2.

Lectotype. Specimen figured by Waagen (1882), pl. 27, fig. 4 from northern China (Inner Mongolia), Zhesi Hongor; Upper Permian, Murgabian.

Description (Fig. 50). The shell is small and rounded pentagonal or oval. Five or six folds are present near the anterior margin. The lateral sides of the shell rarely bear one or two folds. The ventral valve is uniformly and strongly convex. The dorsal valve is slightly convex or flattened. The sulcus and fold are absent. The anterior margin is rectimarginate and denticulate. The lateral commissures are slightly arched. The hinge line is short and strongly curved. The maximum width is in the middle or slightly shifted to the anterior margin. The ventral valve is uniformly and strongly convex. The umbo is low and high. The foramen has not been observed. The false area is wide. The umbonal keels are short and sharpened. The apical angle is 80°–82°. The dorsal valve is flattened in the middle and convex near the margins.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
5133/17	18.0	14.0	8.0	0.77	0.44
5133/18	17.0	14.2	9.8	0.83	0.87
5133/19	14.8	13.0	10.0	0.87	0.67

Shell interior. The pedicle collar is deep and steeply curved. The teeth are narrow and enter the sockets obliquely. There is an outer denticle. The outer hinge plates are narrow. The inner hinge plate is curved and consists of two parts resting on the valve bottom at a large distance from each other. The crural bases are concave, wide, and located between the inner hinge plates and socket ridges. The crural processes are very short. The loop branches are narrow and subparallel. The transverse band of the loop is widely arched. The flanks are short. The loop length is about one-half of the dorsal valve length.

Comparison. This genus differs from *H. himalayensis* (Davidson, 1862) in the lower umbo, rectimarginate anterior margin, flattened dorsal valve, wide false area, large apical angle, presence of the pedicle

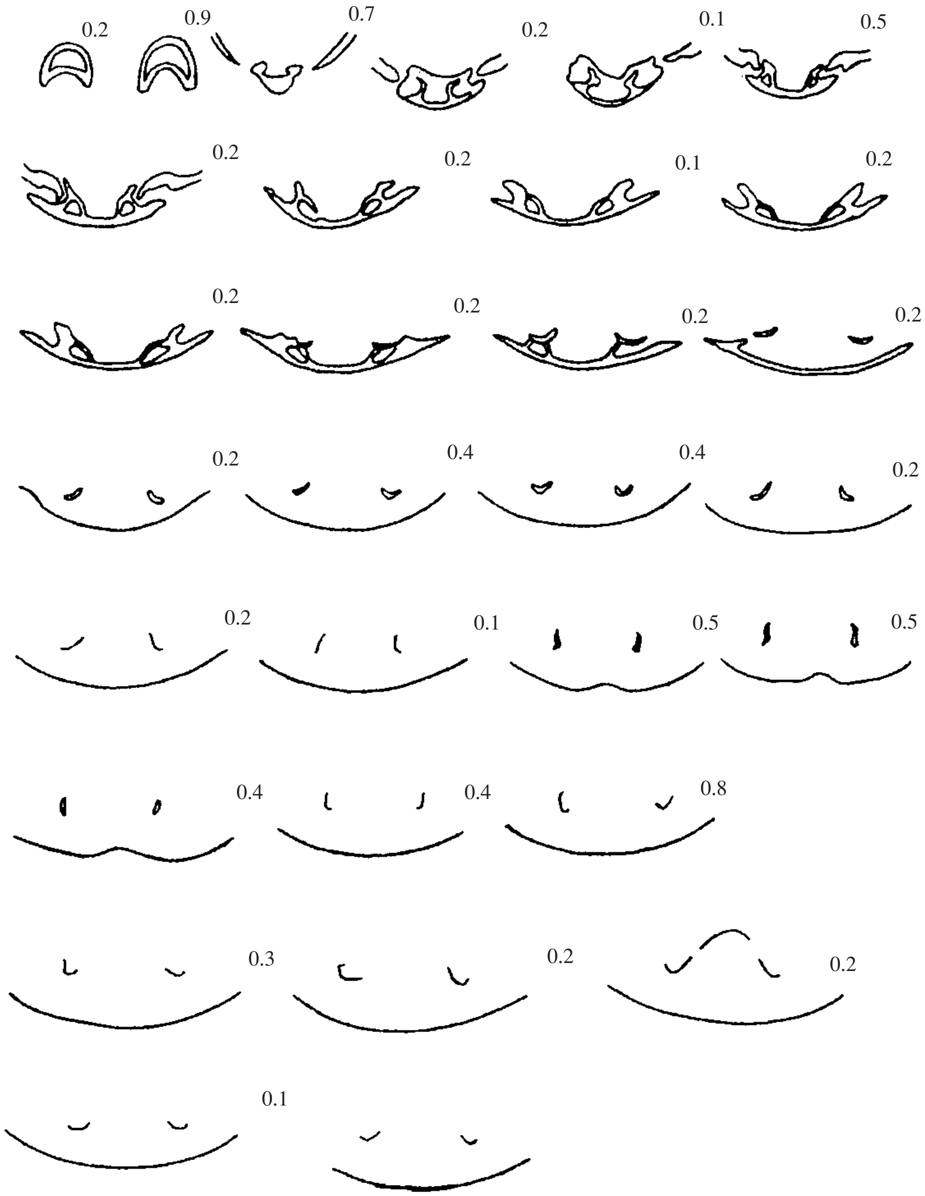


Fig. 50. *Hemiptychina sparsiplicata* Waagen, 1882; specimen PIN, no. 5133/20, serial sections through the shell; figures indicate distances between the sections in mm.

collar, short crural processes, and longer loop. It differs from *H. morrisi* Grabau, 1931 in the shell outline, smaller number of folds on the anterior margin, uniformly convex ventral valve, and narrower anterior margin.

R e m a r k s. Grabau (1931) selected this species as a type species of a new genus *Morrisina*, which he established from the genus *Hemiptychina*. He included in this genus the species *H. crebliplicata* and *H. inflata*, which he considered to be a special evolutionary branch, although all of them were found in the middle part of the *Productus* limestones. Stehli (1962) studied the interior of the aforementioned species and concluded that they belong to the genus *Hemiptychina.* However, he did not describe or figure the interior of *H. sparsiplicata*. We studied specimens of *H. sparsiplicata* from the type locality Zhesi Hongor in northern China. The interior of *H. sparsiplicata* is figured here for the first time.

M a t e r i a l. Two complete shells and one shell with broken umbo from Zhesi Hongor.

Genus *Mongolina* Grabau, 1931

Mongolina: Grabau, 1931, pp. 102 and 103.

Rostranteris: Stehli, 1965, H759.

T y p e s p e c i e s. *Mongolina subdieneri* Grabau, 1931.

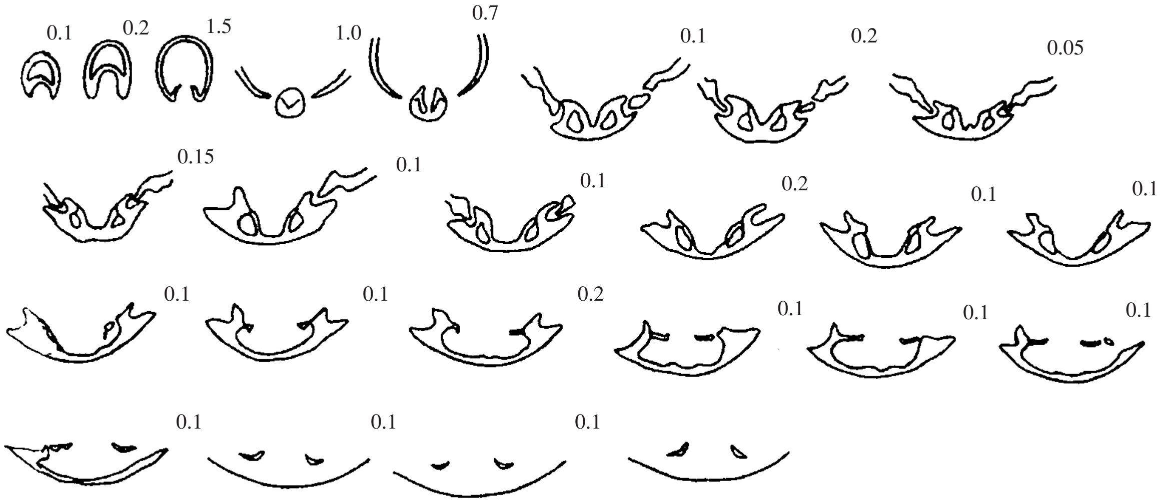


Fig. 51. *Mongolina subdieneri* Grabau, 1931; specimen PIN, no. 5133/23, serial sections through the shell; figures indicate distances between the sections in mm.

D i a g n o s i s. Shell small or middle-sized, equiconvex, elongated, and terebratulid-like. Anterior margin biplicate and rounded. Fold weakly pronounced on the dorsal valve. Shallow sulcus developed on the ventral valve. Lateral margins of the shell sharpened. Anterior commissure biplicate. Umbo curved. Foramen large. Pedicle collar present. Outer hinge plates narrow. Inner hinge plates rest on the valve bottom separately. Crural bases ventrally directed and slightly raised. Loop short and narrow.

S p e c i e s c o m p o s i t i o n. Type species.

C o m p a r i s o n. This genus differs from *Hemiptychina* Waagen, 1882 in the uniformly convex shell, biplicate anterior margin, and the absence of numerous small folds on the shell margins.

R e m a r k s. Grabau (1931) established a monotypic genus *Mongolina* with a type species *M. subdieneri* Grabau, 1931 based on the shell exterior of the single specimen. He supposed that the shell interior of the genus was identical with *Hemiptychina a*nd *Morrisina*. Stehli (1962) pointed to the absence of data on the internal structures and referred *Mongolina* to the genus *Rostranteris* emphasizing considerable resemblance in their external appearance. He also supposed that *Mongolina* might be a synonym of *Gefonia* or separate genus. Smirnova and Grunt (2001) for the first time studied the internal structures of the type species *M. subdieneri* from the Murgabian deposits of the valley of Zhesi Hongor (Baotege) (type locality) in northern China (Inner Mongolia). The absence of the dental plates, inner hinge plates resting on the valve bottom, and terebratuloid loop are evidence that this species belongs to the family Gillediidae Campbell, 1965. The biplicate shell with uniformly convex valves and sharpened margins allow *Mongolina* to be considered a separate genus.

Mongolina subdieneri **Grabau, 1931**

Plate 2, fig. 1

Mongolina subdieneri: Grabau, 1931, pp. 103–105, pl. 8, figs. 5a–5f.

H o l o t y p e. American Museum of Natural History, New York, no. 70, Cat. G.S.C. 1300; Zhesi Hongor, northern China (Inner Mongolia); Upper Permian, Murgabian.

D e s c r i p t i o n (Fig. 51). The shell is small or middle-sized, equiconvex, and rounded pentagonal, with two weakly developed folds near the anterior margin. The anterior commissure is paraplicate, with rounded bends. The lateral commissures are arched. The hinge line is long and slightly curved. The maximum width and thickness are in the middle. The ventral valve is uniformly curved, with slightly flattened lateral surfaces. Only two sharpened folds separated by a shallow sulcus are present near the anterior margin. The umbo is strongly curved. The foramen is large and round. The false area fuses with the lateral sides of the umbo. The apical angle is 78°–80°. The dorsal valve is uniformly convex and slightly flattened laterally. The sulcus is gentle and bordered by the poorly pronounced and short folds, which are only visible near the anterior margin.

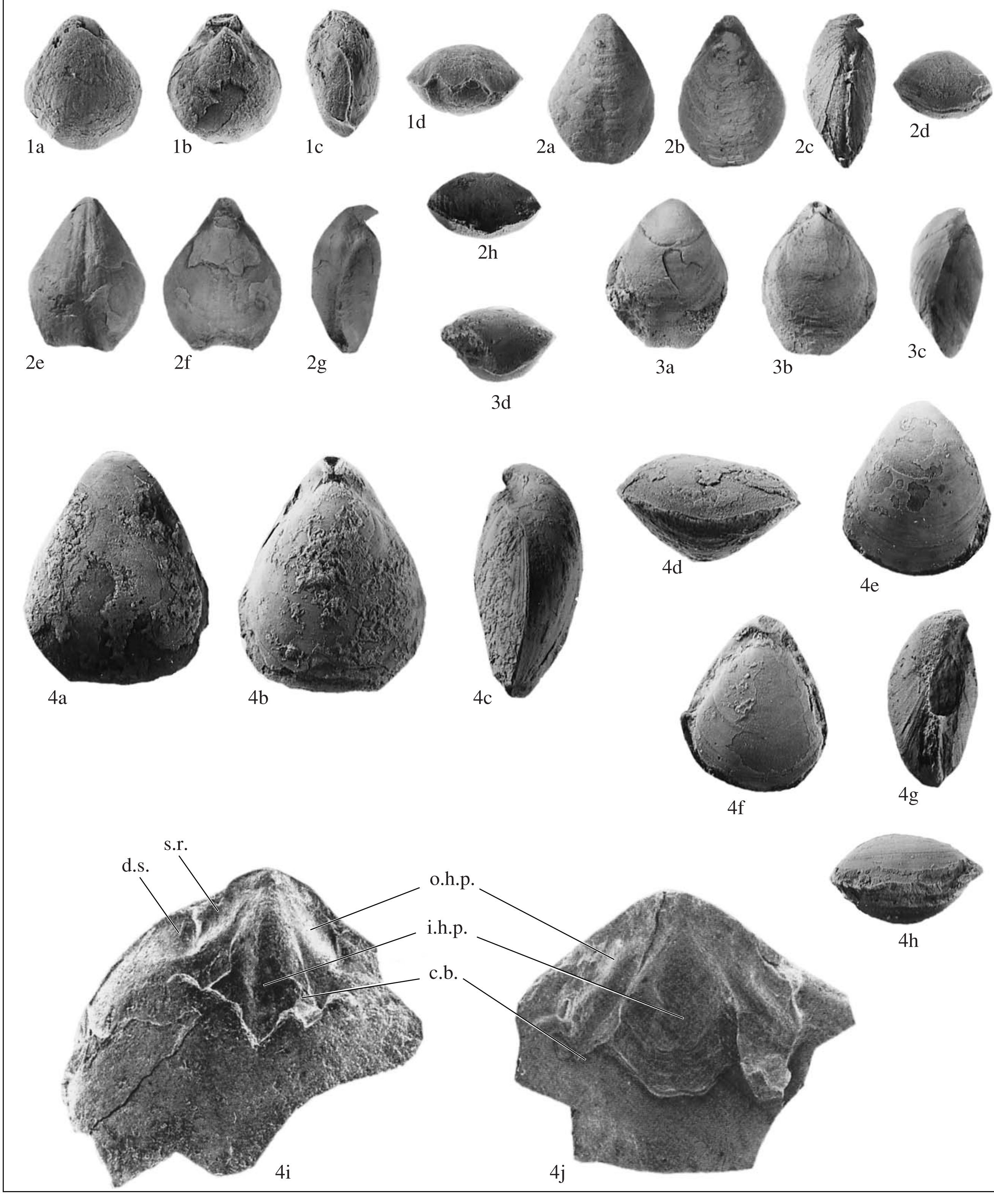
D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
5133/20	21.0	15.3	11.8	0.73	0.56
5133/21	16.4	13.0	11.0	0.79	0.67
133/22	15.6	13.6	8.7	0.87	0.56

S h e l l i n t e r i o r. The pedicle collar is deep and sharply curved. The teeth are narrow and steeply enter the sockets. The socket ridges are high. The outer hinge plates are wide. The inner hinge plates are steeply inclined to the bottom of the dorsal valve and rest on the bottom separately. The crural bases are not raised.

Material. Eight shells: two complete shells and six shells with broken umbos from the valley of Zhesi Hongor (Baotege and Bulege-2 localities).

Plate 2



Genus *Pyandzhelasma* Smirnova et Grunt, 2002

Pyandzhelasma: Smirnova and Grunt, 2002, pp. 44–45.

T y p e s p e c i e s. *Hemiptychina juresanensiforme* Licharew, 2002.

D i a g n o s i s. Shell large, moderately biconvex, pyriform or oval, with narrow sulcus on the ventral valve. Anterior commissure monoplicate or straight. Umbo strongly curved. Foramen large. Pedicle collar present. Outer hinge plates wide and steeply inclined to the plane of symmetry. Inner hinge plates rest on the valve bottom and form deep septalium. Crural bases are poorly pronounced in the relief of septalium. Crural processes wide. Loop branches narrow. Transverse band of the loop widely trapezoidal.

S p e c i e s c o m p o s i t i o n. Type species, *P. piriforme* Smirnova et Grunt, 2002, and *P. juresanense* (Tschernyschew, 1902).

C o m p a r i s o n. This genus differs from *Lowenstamia* Stehli, 1961 in the larger shell, less massive umbo, less convex valves, deep septalium, and small crural bases poorly pronounced in the relief of septalium. It differs from *Maorielasma* Waterhouse, 1964 in the less convex valves, strongly curved umbo, the presence of a sulcus on the ventral valve, and in the wide outer hinge plates.

Pyandzhelasma juresanensiforme (Licharew, 2002)

Plate 2, fig. 2

Dielasma juresanense: Tschernyschew, 1914, p. 7, pl. 2, figs. 9 and 10.

Hemiptychina juresanensiforme: Licharew, 2002, p. 42, text-figs. 1a–1d.

Pyandzhelasma juresanensiforme: Smirnova and Grunt, 2002, pp. 45–47, text-figs. 4i–4p.

H o l o t y p e. TsNIGR Museum, no. 23/340, complete shell; kishlak Safetdaron, Tangi-Gor Gorge, southwestern Darvaz; Lower Permian, Safetdaron Formation.

D e s c r i p t i o n (Fig. 52). The shell is large, rounded pentagonal, and equiconvex or with a slightly more convex ventral valve. The anterior margin is obtuse and often sinuate. The umbo is high and narrow. The sulcus extends along the entire length of the ventral valve. The lateral commissures are slightly arched. The anterior commissure is wide and sinuate, rarely straight. The hinge line is long and curved at an angle about 90°. The maximum width is slightly shifted anteriorly from the valve midlength, more rarely in the middle. The maximum thickness is in the middle or slightly shifted posteriorly. The ventral valve is moderately and uniformly convex lengthwise and transversely. The sulcus is shaped like a narrow groove, bordered by two rounded folds, and runs from the umbo to the anterior margin, where it assumes the form of a narrow, dorsally directed linguiform extension. The umbo is high, strongly curved, and compressed laterally. The umbonal keels are rounded and border the high false area. The apical angle is 60°–65°. The foramen is large, labiate, and submesothyrid. The dorsal valve is slightly curved transversely and longitudinally and lacks plication. Only the largest specimens have a weakly developed elevation near the anterior margin.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
4104/564	31.3	24.3	15.2	0.77	0.48
4104/565	28.4	21.6	13.5	0.79	0.47
4104/567	27.6	20.0	13.0	0.72	0.47
4104/566	26.7	18.7	12.5	0.70	0.47

S h e l l i n t e r i o r. The pedicle collar is deep. The outer hinge plates are steeply inclined to the plane of symmetry, fuse with the inner socket ridges near the hinge line, and are raised over the ridges in relief in the anterior half of the cardinalia. The inner hinge plates rest on the bottom of the dorsal valve on the each side of the euseptoid to form septalium with an angle of 35°–40°. The crural bases are weakly raised in relief along the full length of septalium, ventrally directed in its anterior part, and form a concave surface with the hinge plate. The loop branches are narrow, angular in section, and have a concave surface. The crural processes are long. The transverse band of the loop is widely trapezoidal. The loop length is about one-third of the dorsal valve length.

C o m p a r i s o n. This species differs from *P. juresanense* (Tschernyschew, 1902) in the less convex valves, low umbo, and in the absence of the sharp folds on the dorsal valve.

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

Fig. 1. *Mongolina subdieneri* Grabau, 1931; specimen PIN, no. 5133/25, ×1.5: (1a) ventral valve; (1b) dorsal valve; (1c) lateral view; (1d) anterior margin; Murgabian Stage, Upper Permian; northern China (Inner Mongolia).

Fig. 2. *Pyandzhelasma juresanensiformis* (Licharew, 2002); specimen PIN, no. 4104/565, ×1: (2a) ventral valve; (2b) dorsal valve; (2c) lateral view; (2d) anterior margin; specimen PIN, no. 4104/566, ×1: (2e) ventral valve; (2f) dorsal valve; (2g) lateral view; (2h) anterior margin; Gundara Formation, Upper Permian; southwestern Darvaz.

Fig. 3. *Pyandzhelasma piriforme* Smirnova et Grunt, 2002; holotype PIN, no. 4104/587: (3a) ventral valve; (3b) dorsal valve; (3c) lateral view; (3d) anterior margin; Gundara Formation, Upper Permian; southwestern Darvaz.

Fig. 4. *Compositelasma evolutum* Smirnova, 2006; holotype PIN, no. 4898/2391, ×2: (4a) ventral valve; (4b) dorsal valve; (4c) lateral view; (4d) anterior margin; specimen PIN, no. 4898/2396, ×2: (4e) ventral valve; (4f) dorsal valve; (4g) lateral view; (4h) anterior margin; specimen PIN, no. 4898/2404, ×15: (4i) dorsal valve, detail of the cardinalium structure; specimen PIN, no. 4898/2405, ×15: (4j) dorsal valve, detail of the cardinalium structure; designations: (i.h.p.) inner hinge plate, (o.h.p.) outer hinge plate, (d.s.) dental sockets, (c.b.) crural bases, (s.r.) socket ridges; Lower Kazanian Substage, Upper Permian; Russian Platform.

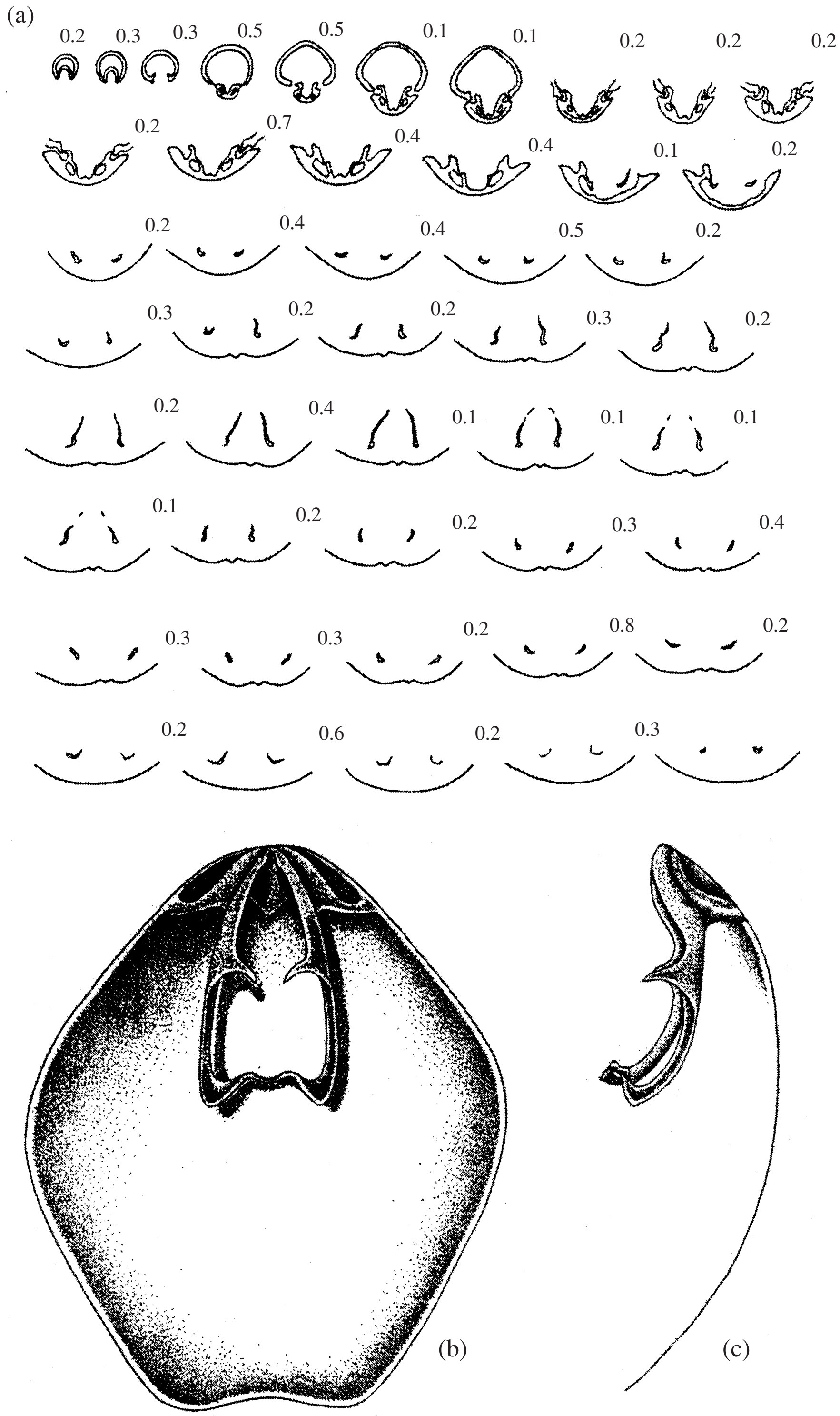


Fig. 52. *Pyandzhelasma juresanensiformis* (Licharew, 2002); specimen PIN, no. 4104/568: (a) serial cross sections; figures indicate distances between the sections in mm; reconstruction of the internal structures: (b) dorsal valve and (c) lateral view.

O c c u r r e n c e. Lower Permian, Bolorian Stage (rarely); Upper Permian, Kubergandian Stage (usually); southwestern Darvaz.

M a t e r i a l. Three complete shells from the outskirts of the kishlak of Safedaron, Tangi-Gor Gorge (collected by Tschernyschew); five complete shells and

18 shell fragments from the Gundara River basin (collected by Grunt).

Pyandzhelasma piriforme Smirnova et Grunt, 2002

Plate 2, fig. 3

Pyandzhelasma piriforme: Smirnova and Grunt, 2002, pp. 47 and 48, text-figs. 4q–4t.

H o l o t y p e. PIN, no. 4104/587, complete shell; Tajikistan, southwestern Darvaz, Gundara River, at height 3660.0 m; Upper Permian, Gundara Formation.

D e s c r i p t i o n (Fig. 53). The shell is middle-sized or large, oval or pyriform, and equiconvex. The umbo is wide. The sulcus is narrow and extends from the middle of the ventral valve up to the anterior margin. The lateral commissures are steeply arched. The anterior margin is short and sinuate. The anterior commissure is arched dorsally. The hinge line is long and curved almost at a right angle. The maximum width is in the middle of the shell or slightly shifted to the anterior margin. The maximum thickness is in the middle. The ventral valve is strongly and uniformly curved. The shallow sulcus is bordered by weakly developed elevations. The umbo is wide, low, and strongly curved. The umbonal keels are smooth and border the low false area. The apical angle is 62°–73°. The foramen is middle-sized, rounded and submesothyrid. The dorsal valve is curved rooflike, with flattened lateral slopes.

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

Specimen, no.	L	W	T	W/L	T/L
4104/589	36.8	28.9	18.0	0.78	0.49
4104/588	29.0	21.0	16.0	0.73	0.55
4104/587	27.4	21.4	14.0	0.78	0.51

S h e l l i n t e r i o r. The pedicle collar is gently arched. The inner hinge plates rest on the valve bottom to form a deep, narrow, V-shaped septalium near the top of the umbo. The septalium rapidly broadens anteriorly. The outer hinge plates are wide and poorly pronounced. The crural bases develop after the disappearance of septalium and form a right angle with the outer hinge plates. The crural processes are long, curved, and parallel to the plane of symmetry. The loop branches are slightly ventrally concave and angular in section. The transverse band of the loop is widely trapezoidal. The loop length is slightly more than one-third of the dorsal valve length.

C o m p a r i s o n. This species differs from *P. juresanense* (Tschernyschew, 1902) in the larger and pyriform shell and arched anterior commissure. It differs from *P. juresanensiforme* (Licharew, 2002) in the oval or pyriform shell, steeply curved lateral commissures, and dorsally arched anterior commissure.

O c c u r r e n c e. Gundara Formation, Upper Permian; southwestern Darvaz, Tajikistan.

M a t e r i a l. Three complete specimens from the type locality.

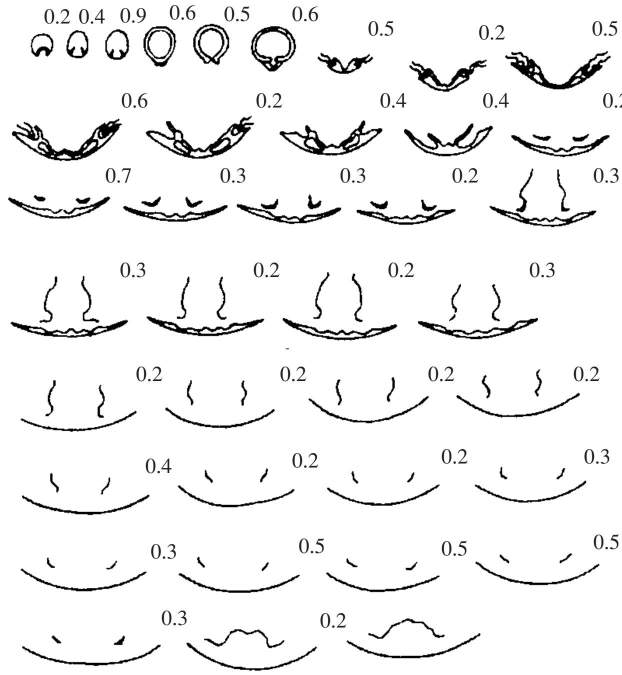


Fig. 53. *Pyandzhelasma piriforme* Smirnova et Grunt, 2002, specimen PIN, no. 4104/590, serial cross sections; figures indicate distances between the sections in mm.

S u p e r f a m i l y Compositelasmatoidea Smirnova, 2006

Compositelasmatoidea: Smirnova, 2006a, p. 64.

D i a g n o s i s. Dental plates and outer hinge plates well-developed. Inner hinge plate supported by septum, rests on the bottom of the dorsal valve, or free. Crural plates present or absent. Crural bases connected with outer hinge plate or crural plates. Brachidium development complicated. Secondary elements involved. Both dielasmoid and angustothyridid types of development exist.

C o m p a r i s o n. This superfamily differs from other superfamilies in the type of brachidium development.

C o m p o s i t i o n. Families Compositelasmatidae Smirnova, 2006 and Beecheriidae Smirnova, 2004.

Family Compositelasmatidae Smirnova, 2006

Compositelasmatidae: Smirnova, 2006a, p. 64.

T y p e g e n u s. *Copmositelasma* Smirnova, 2006.

D i a g n o s i s. Shell smooth or with shallow ventral sulcus. Dental plates well-pronounced from middle developmental stages onward. Outer hinge plates present throughout ontogeny. Inner hinge plates supported by septum or free. Crural bases connected with outer hinge plates. Loop narrow, of dielasmoid type.

C o m p a r i s o n. This family differs from the family Beecheriidae Smirnova, 2004 in the absence of crural plates, crural bases connected with outer hinge plates, which are present throughout ontogeny, and in the possible presence of free inner hinge plates.

C o m p o s i t i o n. Type genus, *Gruntelasma* Smirnova, 2004, *Grigorjevaelasma* Smirnova, 2004, and *Campbellelasma* Smirnova, 2004.

Genus *Compositelasma* Smirnova, 2006

Compositelasma: Smirnova, 2006a, p. 65.

T y p e s p e c i e s. *Compositelasma evolutum* Smirnova, 2006.

D i a g n o s i s. Shell small and variously shaped, mainly rounded triangular. Sulcus poorly developed and running along full length of ventral valve. Dorsal valve curved rooflike. Anterior commissure angularly arched. Pedicle collar well-developed. Dental plates long and subparallel. Outer hinge plates horizontal or slightly inclined. Inner hinge plate variously shaped and supported by septum to form septalium, rests on the bottom of the dorsal valve, or free. Ridge may be developed in the middle of the inner hinge plate. Crural bases with ventral tips. Loop branches narrow. Transverse band of the loop arched.

S p e c i e s c o m p o s i t i o n. Type species.

C o m p a r i s o n. This genus differs from *Gruntelasma* Smirnova in the angularly arched anterior commissure, long dental plates, and in the presence of septalium.

Compositelasma evolutum Smirnova, 2006

Plate 2, fig. 4

Compositelasma evolutum: Smirnova, 2006a, pp. 65–69, pl. 8, figs. 1–4.

H o l o t y p e. PIN, no. 4898/2391; eastern Russian Platform, Sok River, village of Chuvashskii Bajtugan; Upper Permian, Lower Kazanian.

D e s c r i p t i o n (Fig. 32). The shell is small, rounded pentagonal or pyriform, and equiconvex or the ventral valve may be slightly more convex than the dorsal. The umbo is elongated. The anterior commissure is arched and slightly angular in the middle. The lateral commissures are widely arched. The hinge line is long and curved at a right angle. The maximum width is near the anterior margin. The maximum convexity is in the middle. The ventral valve is narrow in the umbonal region and broadens considerably to the anterior margin. The sulcus is shallow, with gentle slopes, and starts almost in the umbo. The lateral surfaces are flattened in the anterior half of the valve. The umbo is high and curved. The foramen is umbonal and labiate. The false area is high, concave, and bordered by sharpened umbonal keels. The apical angle is 65°–70°. The dorsal valve is curved rooflike, with a median elevation extending along the full length of the valve. The lateral sides of the valve are flattened.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
Holotype					
4898/2391	20.5	15.5	9.6	0.75	0.47
4898/2392	17.3	14.5	8.5	0.84	0.49
4898/2393	16.7	14.4	7.8	0.86	0.48
4898/2394	15.9	13.4	7.8	0.84	0.49
4898/2395	14.3	11.8	7.2	0.82	0.51

S h e l l i n t e r i o r. The pedicle collar is angular. The dental plates are long and border narrow umbonal cavities. The teeth enter the sockets obliquely. The additional denticles are well-developed. The inner hinge plate in the adult shell is supported by a septum in the umbonal region. Anteriorly it first becomes free and then rests on the valve bottom. A high, narrow crest is visible in the middle concave part of the inner hinge plate and extends for a considerable distance from the umbo. The outer hinge plates are wide, horizontal, and inclined to the inner socket ridges. The crural bases are narrow, with pronounced ventral tips in adult developmental stages. The crural processes are short. The loop branches are narrow. The transverse band of the loop is strongly arched. The length of the loop is two-fifths of the length of the dorsal valve.

O c c u r r e n c e. Upper Permian, Lower Kazanian; eastern Russian Platform.

M a t e r i a l. Forty well-preserved specimens from the type locality.

Genus *Gruntelasma* Smirnova, 2004

Gruntelasma: Smirnova et al., 2004, p. 38.

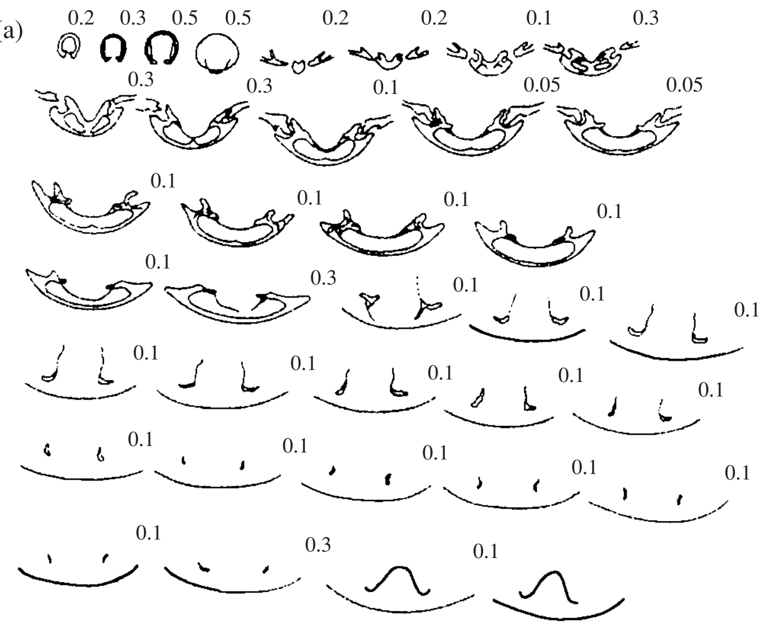
T y p e s p e c i e s. *Gruntelasma bajtuganensis* Smirnova, 2004.

D i a g n o s i s. Shell small, almost equiconvex, rounded triangular, and longitudinally elongated. Anterior commissure straight or slightly arched dorsally. Shallow sulcus present or absent on ventral valve. Pedicle collar present. Dental plates short. Outer hinge plates and crural bases horizontal. Inner hinge plate cup-shaped in cross section and not supported by septum. Crural processes long. Loop length about one-third of dorsal valve length. Transverse band of loop strongly curved.

S p e c i e s c o m p o s i t i o n. Type species and *G. disciformis* sp. nov. from the Lower Kazanian Substage (Upper Permian) of the eastern Russian Platform.

C o m p a r i s o n. This genus differs from *Campbellelasma* Smirnova, 2004 and *Compositelasma* Smirnova, 2004 in the absence of septalium at all developmental stages and in the cup-shaped inner hinge plate.

(a)



(b)

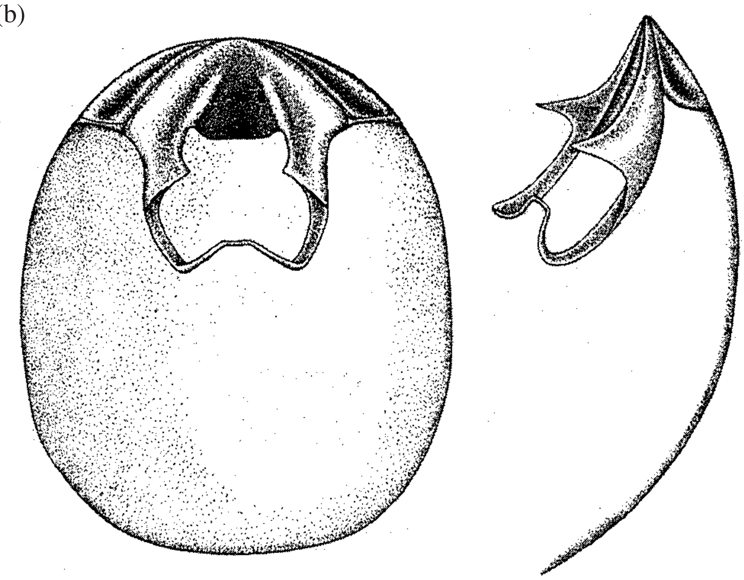


Fig. 54. *Gruntelasma bajtuganensis* Smirnova, 2004; specimen PIN, no. 4898/7: (a) serial cross sections; figures indicate distances between the sections in mm; (b) reconstruction of the internal structures.

Gruntelasma bajtuganensis **Smirnova, 2004**

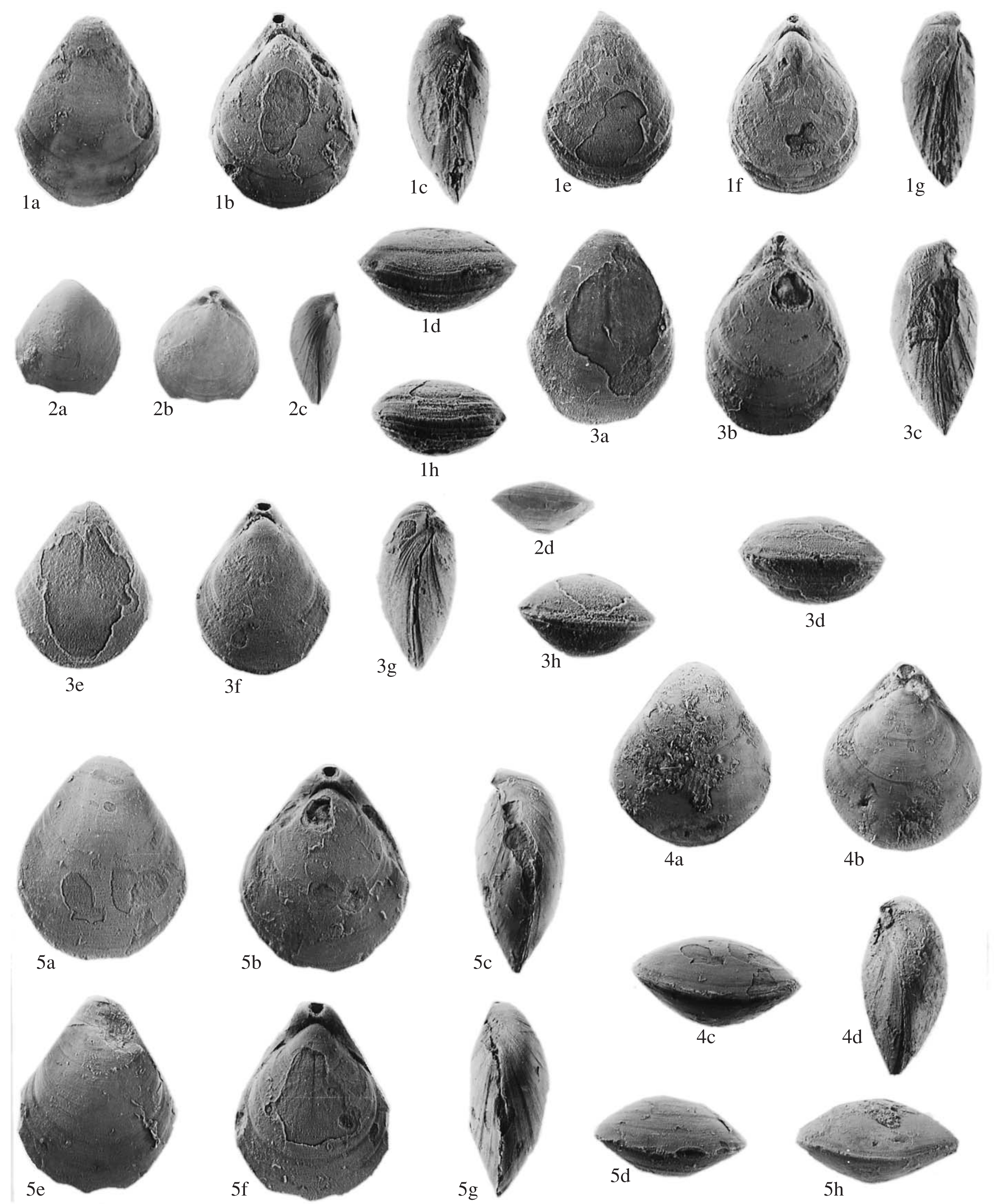
Plate 3, fig. 1

Gruntelasma bajtuganensis: Smirnova et al., 2004, pp. 38 and 39, text-figs. 2, 3, and 4a–4h.

Holotype. PIN, no. 4898/1, complete shell; eastern Russian Platform, Bajtugan River; Upper Permian, Lower Kazanian.

Description (Fig. 54). The shell is rounded triangular, equiconvex, and slightly to strongly elongated. The umbonal region is strongly elongated. The anterior margin is straight to slightly curved dorsally. The lateral sides flattened or slightly convex. The lateral commissures are curved only slightly, as a broad arch. The anterior commissure is shaped like a regular arch and may be curved in the middle. The maximum width is in the anterior third of the shell. The maximum thickness is in the middle. The ventral valve is uniformly convex along the full surface. The sulcus is narrow, shallow, and restricted to the anterior half of the valve. The umbo is high, narrow, and curved to strongly curved. The false area is well-pronounced and bordered by sharpened umbonal keels. The apical angle is 60°–62°. The foramen is labiate, apical, and ovally elongate. The dorsal valve is slightly convex near the umbo and flattened in the anterior half. A weakly developed elevation extends along the full length of the dorsal valve.

Plate 3


1a
1b
1c
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2a
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3f
3g
3h
4a
4b
5a
5b
5c
4c
4d
5e
5f
5g
5d
5h

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
Holotype 4898/1	15.4	11.5	6.5	0.75	0.42
4898/2	15.8	11.8	7.3	0.75	0.46
4898/3	14.7	11.0	6.7	0.75	0.47
4898/4	14.7	11.3	6.8	0.76	0.46
4898/5	12.8	10.0	6.0	0.78	0.46

Shell interior. The pedicle collar is gently arched. The dental plates are slightly diverging. The teeth are narrow and enter the sockets at an angle of 45°. The denticle is located at the border with the valve and one or two denticles are located on the inner socket ridge side. The outer hinge plates are narrow and horizontal. The inner hinge plate is cup-shaped, supported by a low septum in the apical region, and becomes free at the subsequent stages to form a single, wide, and concave surface hanging freely over the bottom of the dorsal valve. The inner socket ridges are high and inclined to the plane of shell symmetry at an angle of 45°. The crural bases are horizontal and located in one plane with the outer hinge plates. The crural processes are long and subparallel. The loop branches are narrow. The transverse band of the loop is high-arched. The length of the loop is about one-third of the length of the dorsal valve.

Comparison. In the description of *G. disciformis.*

Occurrence. Upper Permian, Lower Kazanian Substage; eastern Russian Platform.

Material. One hundred and forty-seven well-preserved shells from the right bank of the Bajtugan River, northern outskirts of the village of Tatarskii Bajtugan; 100 well-preserved shells from the right bank of the Sok River, eastern outskirts of the village of Chuvashskii Bajtugan.

Gruntelasma disciformis Smirnova, sp. nov.

Plate 3, fig. 2

Etymology. From the Latin *disciformis* (disk-shaped).

Holotype. PIN, no. 4898/2539, complete shell; eastern Russian Platform, Sok River, Kamyshla quarry; Upper Permian, Lower Kazanian, Bajtugan Beds.

Description (Fig. 55). The shell is smooth and rounded, with flattened margins. The width is almost equal to the length. The anterior and lateral commissures are very slightly curved. The maximum width is in the anterior third of the shell. The maximum thickness is in the middle. The ventral valve is more convex than the dorsal one and slightly curved rooflike. The umbo is high, curved, and almost touches the dorsal valve. The pseudoarea is high, concave, and bordered by sharpened umbonal keels. The foramen is large, round, and mesothyrid. The apical angle is 84°–85°. The dorsal valve is flattened and slightly and uniformly curved along the full length.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
Holotype 4898/2539	19.0	17.1	9.1	0.90	0.47
4898/2540	17.7	17.7	8.5	1.0	0.48

Shell interior. The pedicle collar is deeply arched. The dental plates are short, massive, and subparallel. The umbonal cavities are slitlike. The teeth are narrow, tongue-shaped, and enter the sockets steeply or at a right angle. The inner and outer denticles are well-developed. The outer hinge plates are horizontal to slightly concave and wide anteriorly. The single inner hinge plate is sessile, touches the bottom of the dorsal valve, and curved at an angle from 70° in the apical region to 120° in the anterior region. The inner socket ridges are high and vertical. The crural bases deviate ventrally at a right angle from the outer hinge plates. The crural processes are widely spaced. The loop branches are narrow. The transverse band of the loop is unknown.

Comparison. The new species differs from *G. bajtuganensis* Smirnova, 2004 in the rounded shell, unequally convex valves, absence of the sulcus on the ventral valve, large apical angle, deeply arched pedicle

Explanation of Plate 3

All specimens come from the Lower Kazanian (Upper Permian) of the Russian Platform.

Fig. 1. *Gruntelasma bajtuganensis* Smirnova, 2004; holotype PIN, no. 4898/1, ×2: (1a) ventral valve; (1b) dorsal valve; (1c) lateral view; (1d) anterior margin; specimen PIN, no. 4898/7, ×2: (1e) ventral valve, (1f) dorsal valve; (1g) lateral view; (1h) anterior margin.

Fig. 2. *Gruntelasma disciformis* sp. nov.; holotype PIN, no. 4898/2539, ×1: (2a) ventral valve; (2b) dorsal valve; (2c) lateral view; (2d) anterior margin.

Fig. 3. *Grigorjevaelasma rossica* Smirnova, 2004; holotype PIN, no. 4898/45, ×2: (3a) ventral valve; (3b) dorsal valve; (3c) lateral view; (3d) anterior margin; specimen PIN, no. 4898/52, ×2: (3e) ventral valve; (3f) dorsal valve; (3g) lateral view; (3h) anterior margin.

Fig. 4. *Campbellelasma variiforme* Smirnova, 2004; holotype PIN, no. 4898/1710, ×2: (4a) ventral valve; (4b) dorsal valve; (4c) lateral view; (4d) anterior margin.

Fig. 5. *Campbellelasma vulgaris* Smirnova, 2004; holotype PIN, no. 4898/2251, ×2: (5a) ventral valve; (5b) dorsal valve; (5c) lateral view; (5d) anterior margin; specimen PIN, no. 4898/2254, ×2: (5e) ventral valve; (5f) dorsal valve; (5g) lateral view; (5h) anterior margin.

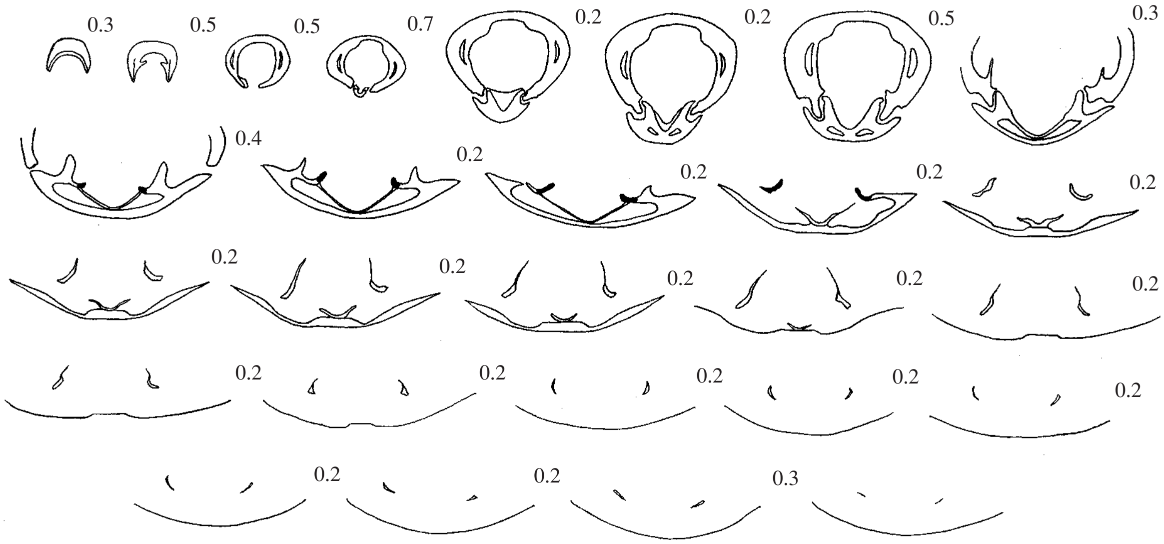


Fig. 55. *Gruntelasma disciformis* sp. nov., specimen PIN, no. 4898/2540, serial cross sections; figures indicate distances between the sections in mm.

collar, ventrally directed crural bases, sessile inner hinge plate, and in the massive dental plates.

R e m a r k s. The new species differs from the typical representatives of *Gruntelasma* in the sessile inner hinge plate and massive dental plates.

O c c u r r e n c e. Upper Permian, Lower Kazanian Substage; eastern Russian Platform.

M a t e r i a l. Two well-preserved specimens from the type locality.

Genus *Grigorjevaelasma* Smirnova, 2004

Grigorjevaelasma: Smirnova et al., 2004, p. 40.

T y p e s p e c i e s. *Grigorjevaelasma rossica* Smirnova, 2004.

D i a g n o s i s. Shell small, rounded rhombic or rounded pentagonal, and not plicate. Anterior commissure arched dorsally. Pedicle collar present. Dental plates long. Outer hinge plates slightly concave. Inner hinge plate V-shaped, supported or not supported by septum or euseptoid at early stages. Crural processes long. Crural bases inclined to the plane of symmetry. Length of the loop is about two-fifths of the length of the dorsal valve. Transverse band of the loop widely arched.

S p e c i e s c o m p o s i t i o n. Type species.

C o m p a r i s o n. This genus differs from *Gruntelasma* Smirnova, 2004 in the absence of the sulcus on the ventral valve, rounded rhombic or rounded pentagonal shell, long dental plates, shape of the inner hinge plate, and widely arched transverse band of the loop.

Grigorjevaelasma rossica Smirnova, 2004

Plate 3, fig. 3

Grigorjevaelasma rossica: Smirnova et al., 2004, pp. 41 and 42, text-figs. 4i–4p, 5, and 6.

H o l o t y p e. PIN, no. 4898/45, complete shell; eastern Russian Platform, Sok River, village of Chuvashskii Bajtugan; Upper Permian, Lower Kazanian.

D e s c r i p t i o n (Fig. 56). The shell is small and variously shaped, mainly rounded rhombic, more rarely rounded pentagonal. The valves are equiconvex or the ventral valve may be slightly more convex than the dorsal one. The lateral sides of the shell are moderately convex. The anterior margin is arched. The maximum width is slightly shifted from the middle to the anterior margin, more rarely within one-third of the valve length from the anterior margin. The maximum thickness is in the middle. The ventral valve is convex in the umbonal region and flattened in the anterior half. The umbo is small, massive, curved or strongly curved, and bordered by smooth umbonal keels. The apical angle is 65°–72°. The false area is high and concave. The foramen is labiate, middle-sized, and apical. The dorsal valve is convex in the middle and flattened near the margins. A weakly developed elevation may or may not be present near the anterior margin.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.		L	W	T	W/L	T/L
Holotype	4898/45	14.7	12.0	7.2	0.81	0.49
	4898/46	16.7	12.8	7.3	0.76	0.43
	4898/47	16.5	13.2	8.4	0.80	0.51
	4898/48	15.5	13.0	7.8	0.84	0.54

S h e l l i n t e r i o r. The pedicle collar is deeply arched. The teeth enter the sockets almost vertically and bear one or two denticles. The dental plates are diverging and separate narrow umbonal cavities from a wide delthyrial cavity. The inner hinge plate is narrowly V-shaped and connected with a low septum or eusep-

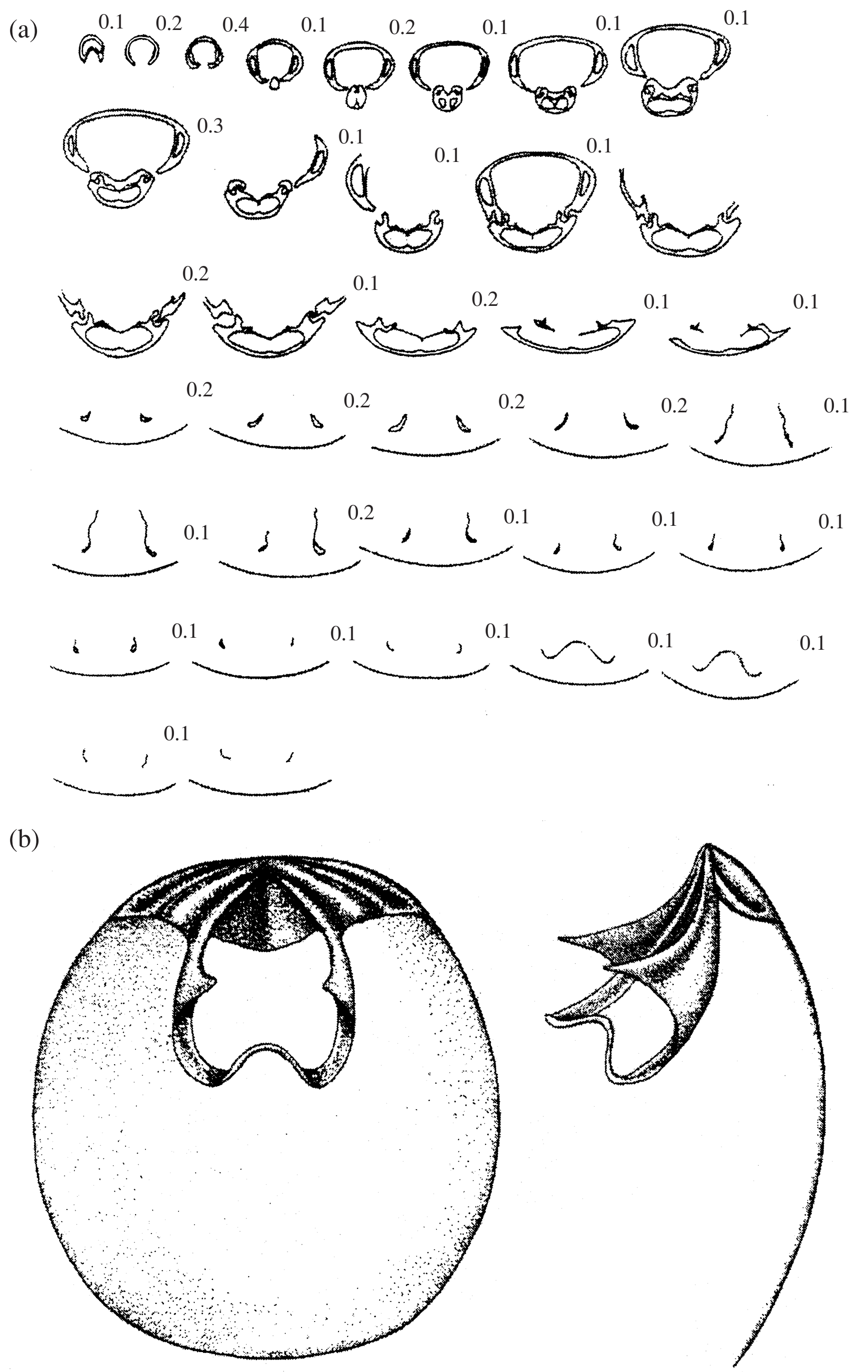


Fig. 56. *Grigorjevaelasma rossica* sp. nov.; specimen PIN, no. 4898/51: (a) serial cross sections; figures indicate distances between the sections in mm; (b) reconstruction of the internal structures.

toid in the umbonal region. Anteriorly it becomes free from the septal structures and remains V-shaped along the full length. A small vertical structure may or may not be developed at the junction of two parts of the hinge plate. The inner socket ridges are high and perpendicular to wide, horizontal outer hinge plates. The crural bases are almost perpendicular to the outer hinge plates. The crural processes are long and subparallel. The loop branches are narrow and short. The transverse band of the loop is low and widely arched. The length of the loop is about two-fifths of the length of the dorsal valve.

O c c u r r e n c e. Upper Permian, Lower Kazanian Substage; eastern Russian Platform.

M a t e r i a l. Three hundred and twelve well-preserved specimens from the right bank of the Sok River, eastern outskirts of the village of Chuvashskii

Bajtugan; 86 well-preserved specimens from the right bank of the Bajtugan River, northern outskirts of the village of Tatarskii Bajtugan.

Genus *Campbellelasma* Smirnova, 2004

Campbellelasma: Smirnova, 2004b, pp. 24 and 25.

Type species. *Campbellelasma variiforme* Smirnova, 2004.

Diagnosis. Shell small or middle-sized, equiconvex, and variously shaped. Weakly developed sulcus present or absent on the ventral valve. Anterior and lateral commissures slightly arched, more rarely straight. Pedicle collar present. Dental plates short. Outer hinge plates concave. Inner hinge plates supported by septum of varying height along the full length to form septalium. Crural processes wide. Loop branches narrow. Transverse band unknown.

Species composition. Type species; *C. vulgaris* Smirnova, 2004 from the Lower Kazanian Substage (Upper Permian) of the eastern Russian Platform, Sok River basin.

Comparison. This genus differs from *Compositelasma* Smirnova, 2004 in the concave outer hinge plates lacking ridge and in the presence of a septum and septalium along the full length of the cardinalia. It differs from *Grigorjevaelasma* Smirnova, 2004 in the presence of sulcus on the ventral valve, short dental plates, and in the presence of septum and septalium in the cardinalium.

Campbellelasma variiforme Smirnova, 2004

Plate 3, fig. 4

Campbellelasma variiforme: Smirnova, 2004b, pp. 25 and 26, pl. 4, figs. 1a–1h.

Holotype. PIN, no. 4898/1710, complete shell; eastern Russian Platform, Sok River, village of Chuvashskii Bajtugan; Upper Permian, Lower Kazanian.

Description (Fig. 57). The shell is small or middle-sized, wide, rounded quadrangular to rounded pentagonal in outline. The maximum width is slightly shifted from the middle to the anterior margin. The maximum thickness is in the middle. The anterior commissure is straight or slightly dorsally curved to form a wide arc. The lateral commissures are almost straight. The ventral valve is strongly convex in the umbonal region and flattened in the anterior half. A poorly pronounced sulcus may or may not be developed on the anterior margin, being accompanied by a slight bend of the anterior commissure. The lateral sides of the ventral valve are rounded in the posterior half and flattened anteriorly. The umbo is low, curved, and slightly overhanging the dorsal valve. The false area is narrow and bordered by well-pronounced sharpened umbonal keels. The apical angle is 70°–72°. The foramen is labiate, umbonal, middle-sized, and almost touches the dorsal valve. The dorsal valve is uniformly curved in all directions, being flattened near the margins.

Dimensions in mm and ratios:

	Specimen, no.	L	W	T	W/L	T/L
Holotype	4898/1710	18.8	16.2	8.8	0.89	0.47
	4898/1711	19.6	17.5	8.1	0.89	0.41
	4898/1712	16.7	14.8	7.1	0.89	0.43
	4898/1713	16.2	14.3	7.5	0.89	0.47
	4898/1714	15.8	14.9	7.8	0.94	0.49

Shell interior. The pedicle collar is gently arched. The dental plates are short and divide narrow umbonal cavities and a wide delthyrial cavity. The teeth are narrow, curved, bear thickening at the end, and enter the sockets at an angle of 50°–60°. A denticle is present on the inner side of the tooth. The outer hinge plates are wide and strongly concave. The inner hinge plates are supported by a high septum to form septalium. The parts of the hinge plates are joined at an angle of 120°. The crural bases are well-pronounced. The crural processes are wide and drawn together ventrally. The loop branches are narrow and subparallel. The transverse band of the loop is unknown.

Comparison. In the description of *C. vulgaris*.

Occurrence. Upper Permian, Lower Kazanian Substage; eastern Russian Platform.

Material. Three hundred and ninety-four well-preserved specimens from the village of Chuvashskii Bajtugan, 136 specimens from the northern outskirts of the village of Tatarskii Bajtugan.

Campbellelasma vulgaris Smirnova, 2004

Plate 3, fig. 5

Campbellelasma vulgaris: Smirnova, 2004b, pp. 26 and 27, pl. 4, figs. 2a–2h.

Holotype. PIN, no. 4898/2251, complete shell; eastern Russian Platform, Sok River, village of Chuvashskii Bajtugan; Upper Permian, Lower Kazanian.

Description (Fig. 58). The shell is smooth, small or middle-sized, pyriform, moderately convex, and equiconvex. The lateral commissures are straight or slightly arched. The anterior commissure is slightly curved dorsally to form a wide arc. The anterior margin is flattened. The maximum width is within one-third of the valve length from the anterior margin. The maximum thickness is within one-third of the valve length from the umbo. The ventral valve is convex in the umbonal region and flattened in the anterior half. The sulcus is absent. The umbo is high, curved, and slightly overhanging the dorsal valve. The deltidium is high and wide. The false area is high and concave. The umbonal keels are smooth. The apical angle is 65°–78°. The foramen is large, labiate, and round or almost oval. The dorsal valve is slightly convex in the middle and flattened near the margins.

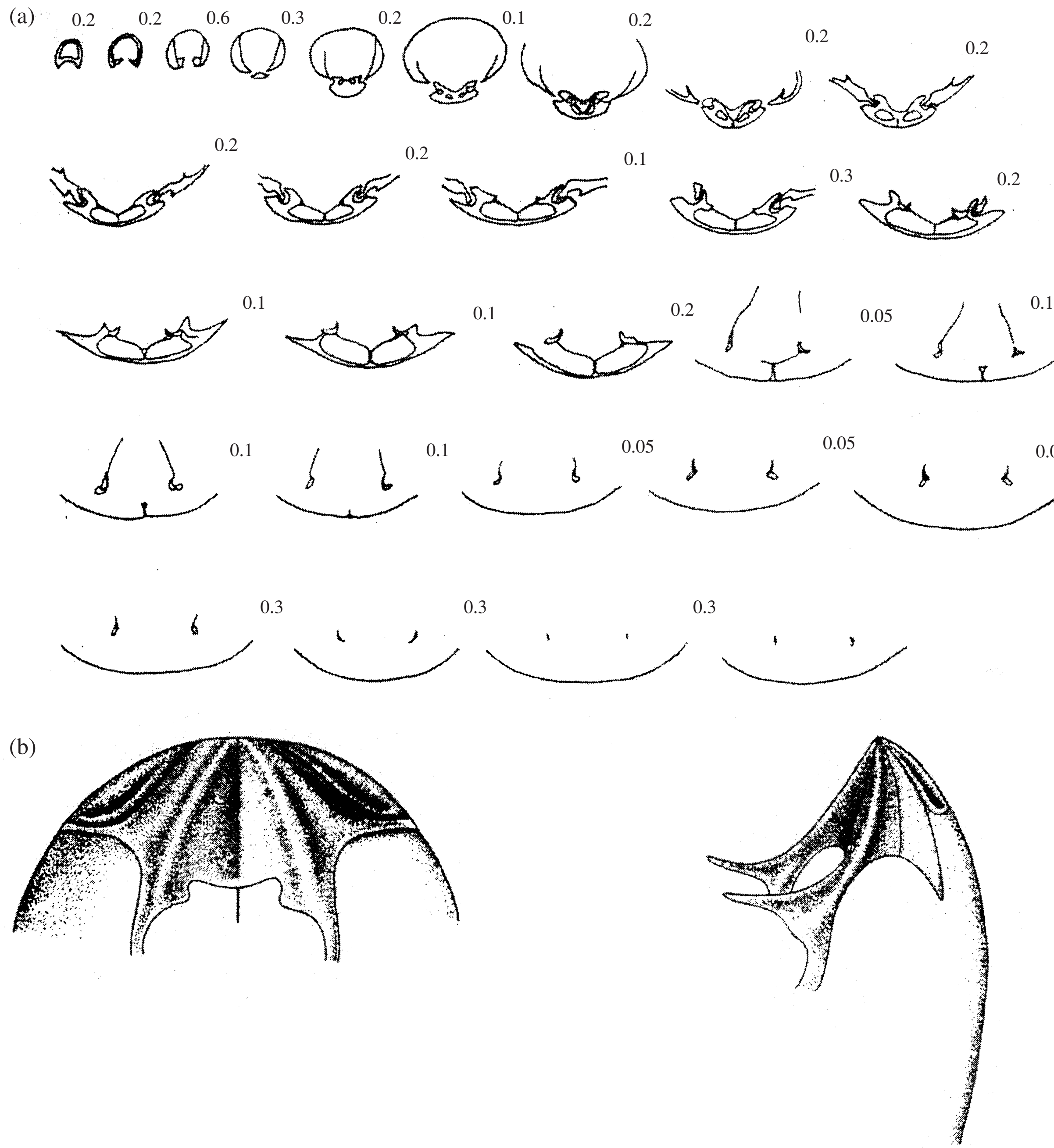


Fig. 57. *Campbellelasma variiforme* Smirnova, 2004; specimen PIN, no. 4898/1715: (a) serial cross sections; figures indicate distances between the sections in mm; (b) reconstruction of the internal structures.

Dimensions in mm and ratios:

Specimen, no.		L	W	T	W/L	T/L
Holotype	4898/2251	17.3	14.5	7.7	0.84	0.44
	4898/2252	17.5	13.8	7.5	0.78	0.43
	4898/2253	17.5	13.4	7.0	0.76	0.40
	4898/2254	16.5	13.0	7.0	0.78	0.43
	4898/2255	15.0	12.0	7.0	0.80	0.46

Shell interior. The pedicle collar is gently arched. The teeth are narrow, obliquely enter the sockets, and bear an additional denticle on the outer side. The dental plates are short and divide the umbo into narrow umbonal cavities and a wide dethyrial cavity. The outer hinge plates are wide, slightly concave, and parallel to the bottom of the valve. The inner hinge plates are supported by a low septum to form septalium. The parts of the inner hinge plate are connected at an angle of 90°–100°. The crural bases are slightly raised over the outer hinge plate. The crural processes are wide and subparallel. The loop branches are narrow. The transverse band of the loop is unknown.

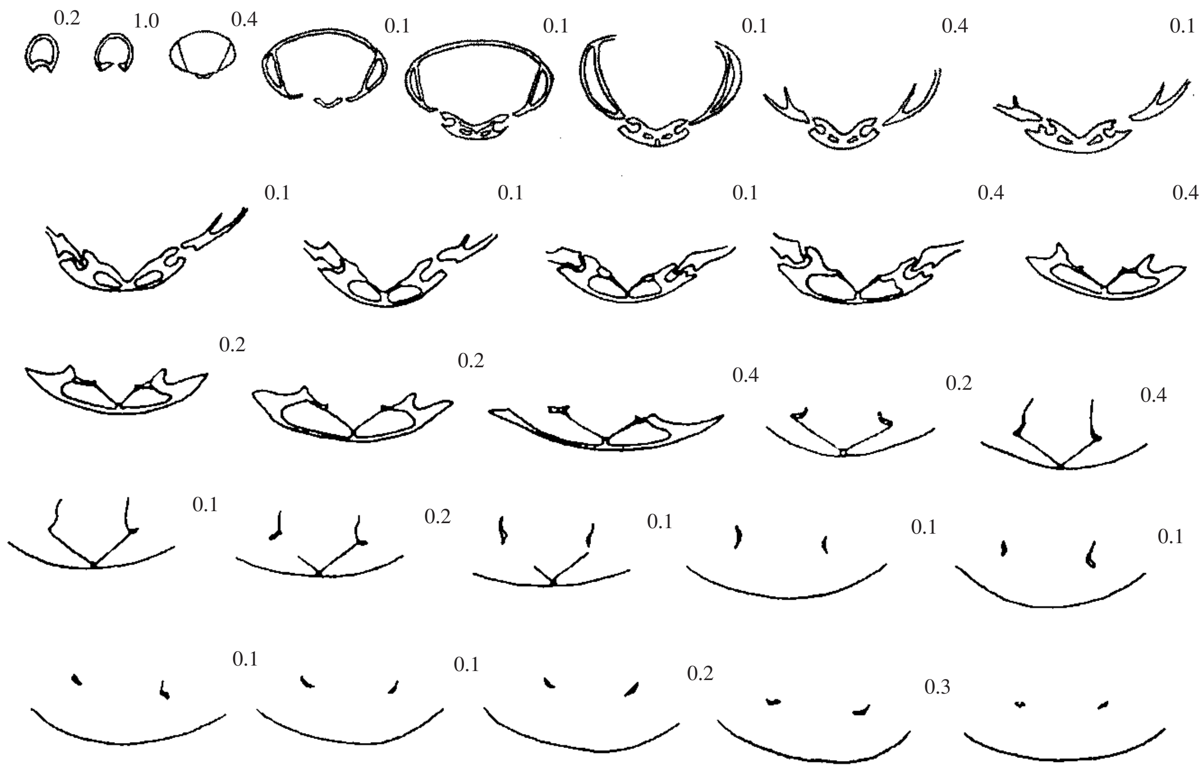


Fig. 58. *Campbellelasma vulgaris* Smirnova, 2004; specimen PIN, no. 4898/2256, serial cross sections; figures indicate distances between the sections in mm.

C o m p a r i s o n. This species differs from *C. variiforme* Smirnova, 2004 in the pyriform shell, absence of the sulcus on the ventral valve, higher umbo, smooth umbonal keels, large apical angle, low septum, slightly concave outer hinge plates, and in crural bases that are poorly pronounced in relief.

O c c u r r e n c e. Upper Permian, Lower Kazanian Substage; eastern Russian Platform.

M a t e r i a l. Twenty-three specimens: 18 well-preserved specimens from the Sok River basin, village of Chuvashskii Bajtugan, and 73 well-preserved specimens from the village of Tatarskii Bajtugan.

Family Beecheriidae Smirnova, 2004

Beecheriidae: Smirnova, 2004a, p. 50.

T y p e g e n u s. *Beecheria* Hall et Clarke, 1893.

D i a g n o s i s. Shell smooth. Dental plates well differentiated. Outer hinge plates present or absent at early developmental stages. Inner hinge plate supported by septum or euseptoid or rest on the bottom of the dorsal valve. Crural plates rest on the valve bottom. Crural bases connected with crural plates. Narrow loop of dielasmoid type.

C o m p o s i t i o n. Type genus, *Hoskingia* Campbell, 1965, *Sokelasma* Smirnova, 2004, *Calycelasma* gen. nov., and *Tapetulasma* gen. nov.

C o m p a r i s o n. In the description of the family Compositelasmatidae Smirnova.

Genus *Beecheria* Hall et Clark, 1893

Beecheria: Hall et Clark, 1893, p. 300; Stehli, 1956, p. 302; 1965, H761; Licharew et al., 1960, p. 292; Grigorjeva, 1967, p. 72; Cooper et Grant, 1976, pp. 2908 and 2909.

T y p e s p e c i e s. *B. davidsoni* Hall et Clarke, 1893; Upper Carboniferous; the USA.

D i a g n o s i s. Shell oval, from small to large, and smooth or monoplicate. Anterior commissure from straight to slightly arched. Ventral valve is more convex than the dorsal. Pedicle collar arched. Dental plates well-pronounced. Outer hinge plates absent. Crural plates at varying distances from inner socket ridges. Inner hinge plates connected with the valve bottom to form septalium and bordered by the crural plates laterally. Loop length about one-half of the dorsal valve length. Transverse band of the loop rounded triangular.

S p e c i e s c o m p o s i t i o n. Type species, *B. elliptica* Cooper et Grant, 1976, and *B. expansa* Cooper et Grant, 1976 from the Guadalupian Stage (Upper Permian) of western Texas; *B. samarica* sp. nov., *B. kargaliensis* sp. nov., *B. angusta* (Netschajew, 1894), and *B. netschajewi* Grigorjeva 1967 from the Lower Kazanian Substage (Upper Permian) of the eastern Russian Platform.

C o m p a r i s o n. This genus differs from *Sokelasma* Smirnova, 2004 in the variously sized and non-equiconvex shell and in the absence of outer hinge plates and septum. It differs from *Tapetulasma* gen. nov. in the shape of the inner hinge plates, which form the septalium, and in the high crural plates.

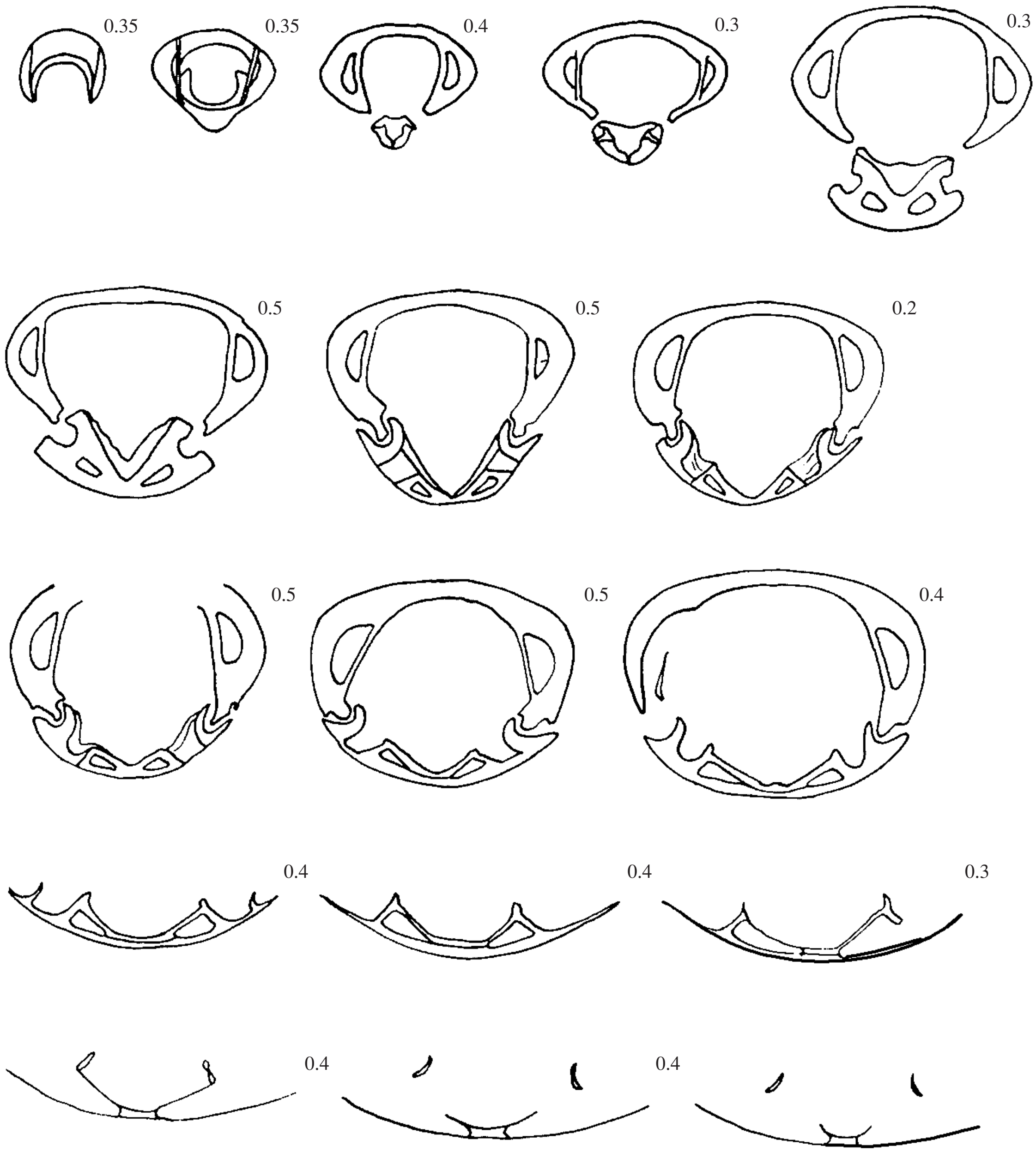


Fig. 59. *Beecheria samarica* sp. nov.; specimen PIN, no. 4898/2537, serial cross sections; figures indicate distances between the sections in mm.

R e m a r k s. Stehli (1956) noted that the genus *Beecheria* was abundant in the Middle and Upper Carboniferous, rare in the Lower and Middle Permian, and has not been found in the younger deposits. In our collection, we have three *Beecheria* species from the Kazanian of the Russian Platform. These species are probably the last representatives of the genus. Thus, *Beecheria* existed from the Lower Carboniferous to the Permian. Grigorjeva (1967) was the first to mention *Beecheria* from the Kazanian of the Russian Platform based on her study of the internal structures of her new species *B. netschajewi.* She suggested that not all Kazanian terebratulids belong to the genus *Dielasma*, as it was previously supposed, and that part of them might be referred to the genus *Beecheria*. Our studies confirm this suggestion.

Beecheria samarica Smirnova, sp. nov.

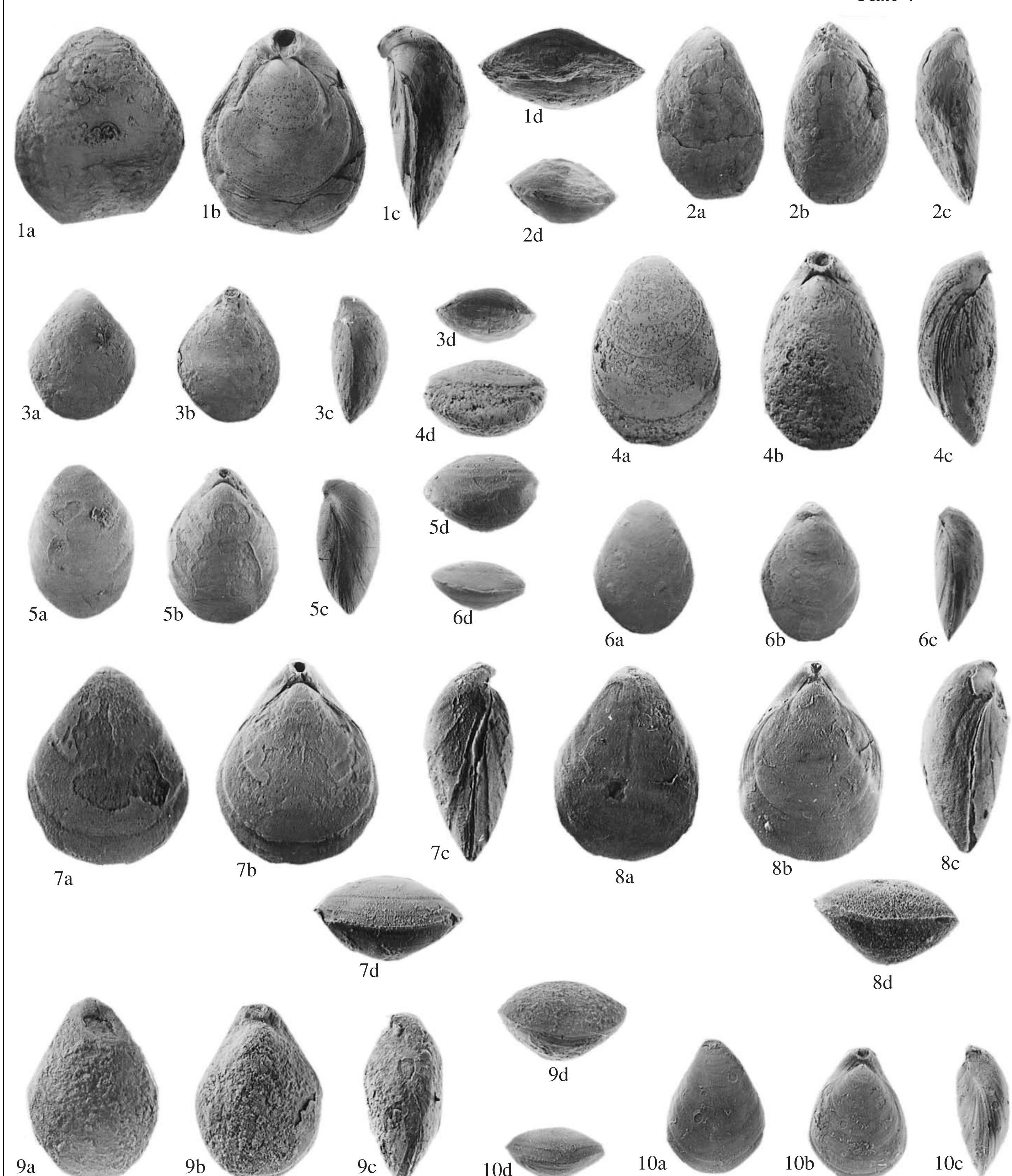
Plate 4, fig. 1

E t y m o l o g y. From the town of Samara.

H o l o t y p e. PIN, no. 4898/2535, complete shell; Samara Region, Sok River, village of Kamyshla, Kamyshla quarry; Upper Permian, Lower Kazanian, Bajtugan Beds.

D e s c r i p t i o n (Fig. 59). The shell is large and oval, with a slightly convex dorsal valve and more convex ventral valve. The lateral sides of the shell are flattened. The anterior margin is wide. The anterior commissure is gently and widely arched. The lateral commissures are almost straight. The hinge line is long and strongly curved. The maximum width is in the anterior third of the shell. The maximum thickness is in the posterior third of the shell. The ventral valve is strongly convex in the umbonal region and may have a poorly pronounced sulcus near the anterior margin. The umbo is massive, strongly curved, overhanging the dorsal

Plate 4



valve. The foramen is large, round, apical, and labiate, with a strongly projecting lip. The false area is high and concave. The umbonal keels are sharpened. The apical angle is 62°–64°. The entire surface of the pseudodeltidium is convex. A poorly pronounced elevation may be present.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
Holotype 4898/2535	33.9	28.2	13.8	0.83	0.41
4898/2536	25.7	20.5	9.5	0.79	0.37

Shell interior. The pedicle collar is arched. The dental plates are long, massive, and parallel in the apical region and slightly converging anteriorly. The teeth enter the sockets vertically. The inner and outer denticles are developed. The outer hinge plates are absent. The crural plates early separate from the inner socket ridges and are located at a considerable distance from them. The inner hinge plate is entire, concave, and connected with the valve bottom.

Comparison. The new species differs from *B. angusta* Netschajew, 1894 in the flattened margins, wider shell, wide anterior margin, almost straight lateral commissures, umbo overhanging the dorsal valve, well-pronounced pedicle collar, and in the presence of a solid inner hinge plate resting on the valve bottom. It differs from *B. kargaliensis* sp. nov. in the wider shell, larger foramen, well-pronounced umbonal keels, straight lateral commissures, flattened dorsal valve, long dental plates, teeth that enter the sockets vertically, and in the single inner hinge plate.

Occurrence. Upper Permian, Lower Kazanian Substage; Samara Region.

Material. Three specimens: two complete shells and one shell with broken margins from the type locality.

Beecheria kargaliensis Smirnova, sp. nov.

Plate 4, fig. 2

Dielasma sp. indeed: Netschajew, 1911, p. 117, pl. 15, fig. 13.

Etymology. From Kargali quarry.

Holotype. PIN, no. 4898/2516, complete shell; Tatarstan, 25 km southeast of the town of Chistopol', Kargali quarry; Upper Permian, Lower Kazanian.

Description (Figs. 60, 61). The shell is middle-sized, oval, and strongly elongated, with flattened lateral and anterior margins. The ventral valve is more convex than the dorsal one. The lateral commissures are widely arched. The anterior commissure is straight to slightly arched. The hinge line is strongly curved. The maximum width is in the anterior third of the shell. The maximum thickness is in the posterior third of the shell. The ventral valve is strongly convex in the umbonal region and flattened in the anterior half. The molds show the middle groove extending along the full length of the valve. A barely visible sulcus may be present at the end of the anterior margin. The umbo is massive and curved. The foramen is small. The false area is high, slightly concave, and bordered by smooth umbonal keels. The apical angle is 55°–60°. The pseudodeltidium is unknown. The dorsal valve is slightly convex, rooflike, with a low elevation extending along the full length of the valve and flattening near the anterior margin.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
Holotype 4898/2516	29.0	17.7	10.3	0.61	0.35
4898/2517	19.8	13.0	7.5	0.65	0.37
4898/2518	22.5	14.7	–	0.65	–
4898/2519	16.0	11.3	4.5	0.71	0.27
4898/2520	16.8	11.5	6.8	0.68	0.34

Explanation of Plate 4

All specimens come from the Lower Kazanian (Upper Permian) of the Russian Platform.

Fig. 1. *Beecheria samarica* sp. nov.; holotype PIN, no. 4898/2535, ×1: (1a) ventral valve; (1b) dorsal valve; (1c) lateral view; (1d) anterior margin.

Fig. 2. *Beecheria kargaliensis* sp. nov.; holotype PIN, no. 4898/2516, ×1: (2a) ventral valve; (2b) dorsal valve; (2c) lateral view; (2d) anterior margin.

Fig. 3. *Beecheria netschajewi* Grigorjeva, 1967; specimen PIN, no. 4898/2494, ×1: (3a) ventral valve; (3b) dorsal valve; (3c) lateral view; (3d) anterior margin.

Fig. 4. *Beecheria angusta* (Netschajew, 1894); specimen PIN, no. 4898/125, ×1.5: (4a) ventral valve; (4b) dorsal valve; (4c) lateral view; (4d) anterior margin.

Fig. 5. *Calycelasma kalaschnikovi* sp. nov.; holotype PIN, no. 4898/2406, ×1: (5a) ventral valve; (5b) dorsal valve; (5c) lateral view; (5d) anterior margin.

Fig. 6. *Tapetulasma boltaevae* sp. nov.; holotype PIN, no. 4898/2482, ×1: (6a) ventral valve; (6b) dorsal valve; (6c) lateral view; (6d) anterior margin.

Fig. 7. *Sokelasma guttiformis* Smirnova, 2004; holotype PIN, no. 4898/76, ×2: (7a) ventral valve; (7b) dorsal valve; (7c) lateral view; (7d) anterior margin.

Fig. 8. *Sokelasma esaulovae* Smirnova, 2004; holotype PIN, no. 4898/100, ×2: (8a) ventral valve; (8b) ventral valve, (8c) lateral view; (8d) anterior margin.

Fig. 9. *Sokelasma tatarstanica* sp. nov.; holotype PIN, no. 4898/2416: (9a) ventral valve; (9b) dorsal valve; (9c) lateral view; (9d) anterior margin.

Fig. 10. *Sokelasma chuvaschensis* sp. nov.; holotype PIN, no. 4898/2466: (10a) ventral valve; (10b) dorsal valve; (10c) lateral view; (10d) anterior margin.

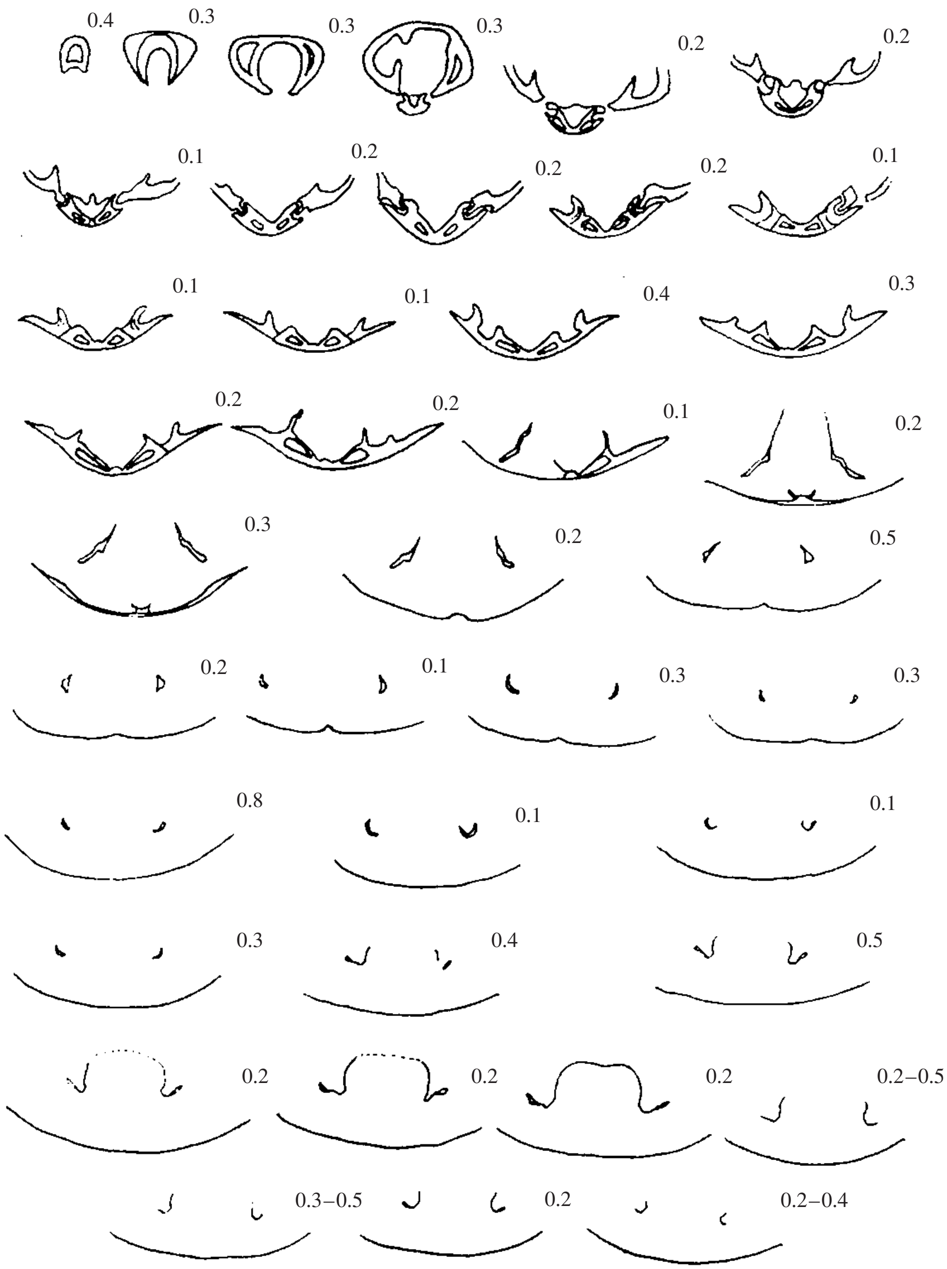


Fig. 60. *Beecheria kargaliensis* sp. nov.; specimen PIN, no. 4898/2521, serial cross sections; figures indicate distances between the sections in mm.

S h e l l i n t e r i o r. The pedicle collar is arched. The dental plates are massive, subparallel, and short. The teeth are narrow and enter the sockets obliquely. Outer and inner denticles are present. There is a ridgelike projection resembling the cardinal process. The outer hinge plates are absent. The socket ridges are fused with the inner hinge plate in the apical region. The parts of the inner hinge plate separately rest on the valve bottom on each side of the euseptoid and, together with the valve bottom, form wide cavities. The crural plates deviate from the socket ridges near the apex of the dorsal umbo, are directed perpendicular to the bottom of the dorsal valve, and support laterally the inner hinge plates. The crural processes are wide, slightly converging, and deviate from the crural plates. The loop branches are narrow, concave in cross section, and parallel. The transverse band of the loop is rounded rectangular and wide. The loop bears long flanks. The loop length is about one-half of the dorsal valve length.

C o m p a r i s o n. The new species differs from *B. angusta* (Netschajew, 1894) in the longer shell, less

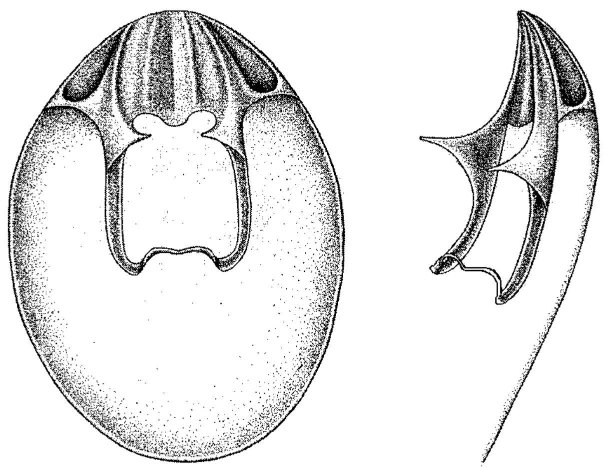


Fig. 61. *Beecheria kargaliensis* sp. nov.; specimen PIN, no. 4898/2521, reconstruction of the internal structures.

convex valves, small foramen, location of the maximum convexity of the valves, flattened lateral sides, short dental plates, teeth that enter the sockets vertically, and in the absence of outer hinge plates. It differs from *B. netschajewi* Grigorjeva, 1967 in the larger, narrow, and elongated oval shell, less convex valves, straight anterior commissure, and flattened margins.

O c c u r r e n c e. Upper Permian, Lower Kazanian Substage; Tatarstan.

M a t e r i a l. Thirteen well-preserved specimens and 15 specimens with compressed lateral sides from the Samara Region, village of Kamyshla; four complete shells, one specimen with broken umbo, and seven specimens with broken margins from the Kargali quarry, 25 km southeast of the town of Chistopol'.

Beecheria netschajewi Grigorjeva, 1967

Plate 4, fig. 3

Beecheria netschajewi: Grigorjeva, 1967, pp. 73 and 74, pl. 8, fig. 11.

H o l o t y p e. PIN, no. 1119/1204; eastern Russian Platform, Sok River, village of Kamyshla; Upper Permian, Lower Kazanian, Bajtugan Beds.

D e s c r i p t i o n (Fig. 62). The shell is small, oval or pyriform, and usually longitudinally elongated. Some shells are slightly rounded rectangular or rounded pentagonal. The lateral commissures are almost straight. The anterior commissure is slightly arched. The anterior margin is rounded. The plication is absent. The lateral sides of the shell are from slightly rounded to flattened. The maximum width and thickness are in the middle. The ventral valve is slightly more convex than the dorsal one and uniformly curved, more rarely rooflike in the umbonal region. The umbo is high and curved. The foramen is large, circular, and apical. The false area is bordered by rounded umbonal keels. The apical angle is 68°–75°. The pseudodeltidium is unknown. The dorsal valve is slightly convex, varying in shape from uniformly curved along the full length to slightly flattened near the margins.

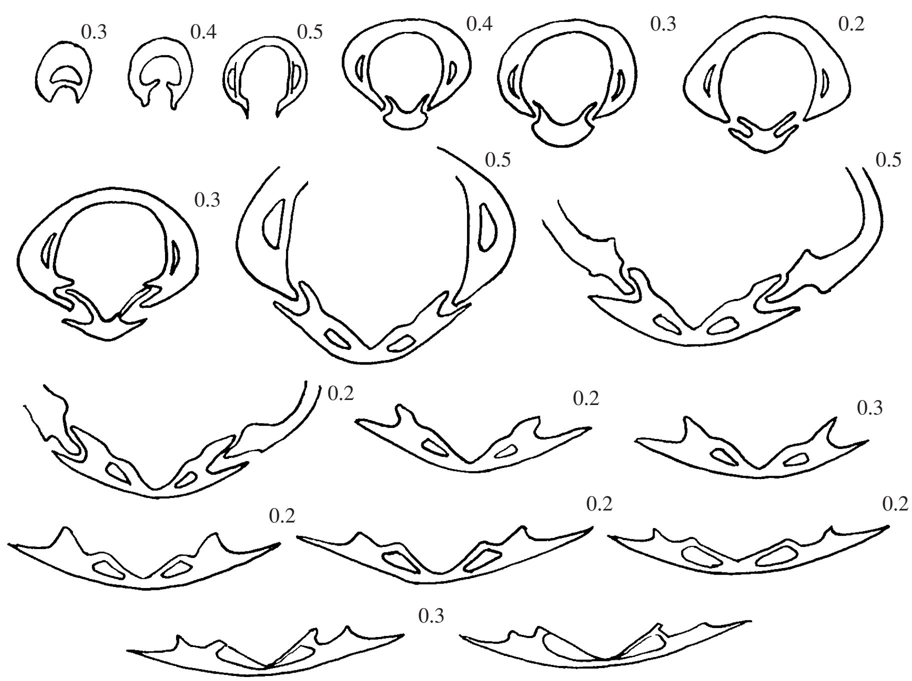


Fig. 62. *Beecheria netschajewi* Grigorjeva, 1967; specimen PIN, no. 4898/2491, serial cross sections; figures indicate distances between the sections in mm.

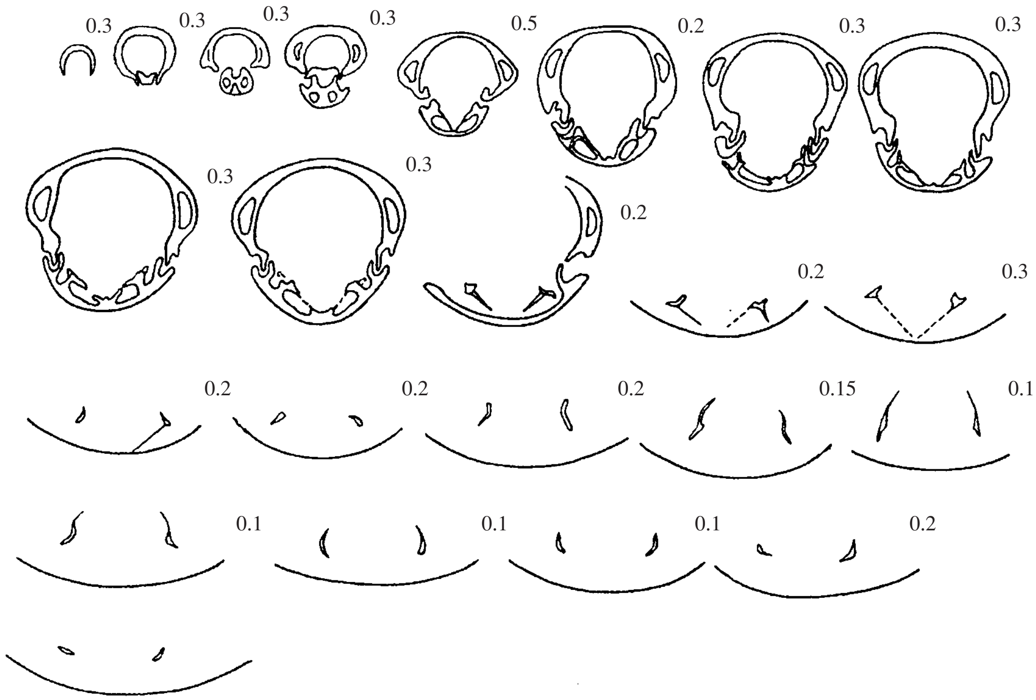


Fig. 63. *Beecheria angusta* Netschajew, 1894; specimen PIN, no. 4898/128, serial cross sections; figures indicate distances between the sections in mm.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
4898/2485	22.4	16.2	10.9	0.72	0.48
4898/2486	21.7	17.4	9.5	0.81	0.44
4898/2487	17.8	13.3	8.3	0.74	0.46
4898/2488	14.5	11.0	7.0	0.75	0.48
4898/2489	19.6	14.6	8.2	0.74	0.42
4898/2490	18.0	14.2	7.8	0.78	0.43

S h e l l i n t e r i o r. The pedicle collar is arched. The dental plates are wide, short, and parallel. The teeth are narrow and enter the dental sockets obliquely. Outer and inner denticles are present. The outer hinge plates are absent. The inner socket ridges are high and are connected with the inner hinge plates in the apical region. The inner hinge plates rest on the valve bottom. The crural plates are separated from the inner socket ridges. The cavities between the inner hinge plates and valve bottom are narrow. The septum and euseptoid are absent. The loop has not been preserved.

C o m p a r i s o n. This species differs from *B. kargaliensis* sp. nov. in the elongated and more convex shell, location of the maximum width and convexity, larger apical angle, large foramen, absence of the euseptoid, and in the narrow cavities between the inner hinge plates and valve bottom. It differs from *B. angusta* Netschajew, 1894 in the less elongated shell, location of the maximum width, almost straight lateral commissures, rounded anterior margin, larger apical angle, short dental plates, teeth, and in the narrow cavities between the inner hinge plates and valve bottom.

R e m a r k s. The species is redescribed in order to describe in detail the shell exterior and cardinalium.

O c c u r r e n c e. Samara Region; Upper Permian, Lower Kazanian Substage.

M a t e r i a l. Thirty-one well-preserved specimens and 40 specimens with partly broken margins from the Sok River basin, Kamyshla quarry.

Beecheria angusta (Netschajew, 1894)

Plate 4, fig. 4

Dielasma angusta: Netschajew, 1894, pp. 187 and 188, pl. 5, fig. 16; Netschajew, 1911, pp. 111 and 112, pl. 15, fig. 9.

Beecheria angusta: Smirnova, 2004a, pp. 50–54, pl. 6, figs. 3a–3h.

H o l o t y p e. Kazan State University, Museum of Geology and Mineralogy, no. 76/13; northeastern Russian Platform; site of ancient settlement on the right bank of the Vyatka River, in the mouth of the Pizhma River; Upper Permian, Kazanian.

D e s c r i p t i o n (Fig. 63). The shell is small, smooth, oval, longitudinally elongated, with moderately convex valves. The maximum width is within one-third of the valve length from the anterior margin. The maximum convexity is in the middle. The anterior commissure is gently arched. The lateral commissures are widely arched. The lateral margins are rounded. The ventral valve is considerably more convex than the dorsal one. The maximum convexity is in the posterior half of the shell. The maximum width is shifted to the anterior margin. The valve is flattened in the posterior half. The anterior margin is slightly stretched to form a linguiform extension. The umbo is high and narrow. The umbonal keels are smooth. The deltidium is low. The false area is concave and high. The apical angle is 56°–62°. The foramen is large, round, and umbonal. The dorsal valve is flattened, with the convexity as low as half to two-thirds of that of the ventral valve. A longitudinal elevation with gentle slopes may be present in the middle of the valve. The lateral sides of the valve are flattened.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
4898/121	22.0	13.8	9.3	0.63	0.42
4898/122	21.7	14.4	9.0	0.66	0.41
4898/123	19.7	12.8	8.5	0.65	0.43
4898/124	18.5	13.2	8.2	0.71	0.44

Shell interior. The pedicle collar is poorly pronounced. The dental plates are long, located close to the ventral valve, slightly diverging in the apical region of the umbo, and subparallel anteriorly. The denticle is well-pronounced. The outer hinge plates are steeply inclined to the commissural plane. They deviate from the inner socket ridges at early developmental stages and disappear anteriorly. The inner hinge plates are connected at an angle of 90°–100° and are supported by the euseptoid to form the septalium. They are supported by the crural plates that rest on the bottom of the dorsal valve and are perpendicular to the latter. The inner hinge plates are remote from the inner socket ridges. The crural processes are short. The loop branches are narrow.

Comparison. This species differs from *B. davidsoni* Hall et Clarke, 1893 in the smaller shell, location of the maximum width that is shifted to the anterior margin, less convex valves, less curved umbo, slightly curved commissures, long dental plates, well-pronounced outer plates, and in the septalium resting along the full length on the bottom of the dorsal valve.

Occurrence. Upper Permian, Kazanian Stage; northeastern Russian Platform.

Material. Three hundred and five complete shells from the Sok River basin near the village of Chuvashskii Bajtugan; 34 specimens from the northern outskirts of the village of Tatarskii Bajtugan; three specimens from the Chimbulatskii quarry, Kirov Region; four specimens from the Dema River, 2 km downstream from the village of Nikiforovo; one specimen from the right bank of the Nemda River, bluff near the village of Kamen'.

Genus *Calycelasma* Smirnova, gen. nov.

Etymology. From the Greek *calyx* (cup) and *elasma* (plate).

Type species. *Calycelasma kalaschnikovi* sp. nov.

Diagnosis. Shell small, oval, smooth, and equiconvex. Anterior commissure gently arched. Pedicle collar tube-shaped. Dental plates short. Outer hinge plates narrow, located in the apical region. Inner hinge plate cup-shaped and supported by septum. Crural plates drawn together with the inner socket ridges. Loop branches narrow. Loop length about one-half of the dorsal valve length. Transverse band of the loop strongly curved.

Species composition. Type species.

Comparison. The new genus differs from *Sokelasma* Smirnova, 2004 in the oval shell, tube-shaped pedicle collar, cup-shaped inner hinge plate, well-pronounced ventral and dorsal tips of the crural bases, and in the long flanks of the loop. It differs from *Beecheria* Hall et Clarke, 1893 in the crural plates drawn together with the inner socket ridges and in the cup-shaped inner hinge plate supported by the septum.

Calycelasma kalaschnikovi Smirnova, sp. nov.

Plate 4, fig. 5

Etymology. In honor of the geologist N.V. Kalashnikov.

Holotype. PIN, no. 4898/2406, complete shell; eastern Russian Platform, Sok River, village of Chuvashskii Bajtugan; Upper Permian, Lower Kazanian.

Description (Fig. 64). The shell is small, ovally elongate longitudinally, and equiconvex or the ventral valve may be slightly more convex than the dorsal one. The lateral margins are rounded. The lateral commissures are almost straight. The anterior commissure is slightly arched dorsally. The hinge line is long and strongly curved. The maximum width and thickness are in the middle of the shell. The ventral valve is moderately convex in the posterior half and slightly flattened in the anterior half. The plication is absent. The umbo is high and curved. The umbonal keels are sharpened. The false area is high and slightly concave. The apical angle is 68°–70°. The foramen is round and apical. The dorsal valve is strongly convex along the full length and slightly flattened near the margins.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
Holotype					
4898/2406	13.1	9.4	7.0	0.71	0.53
4898/2408	14.5	10.2	6.9	0.71	0.48
4898/2409	13.3	10.3	7.5	0.77	0.56
4898/2410	14.7	11.8	7.9	0.78	0.44
4898/2411	14.8	11.6	6.5	0.78	0.51
4898/2407	15.8	12.8	8.2	0.78	0.49

Shell interior. The pedicle collar is tube-shaped and circular in cross section. The teeth are massive and vertically enter the dental sockets. The outer

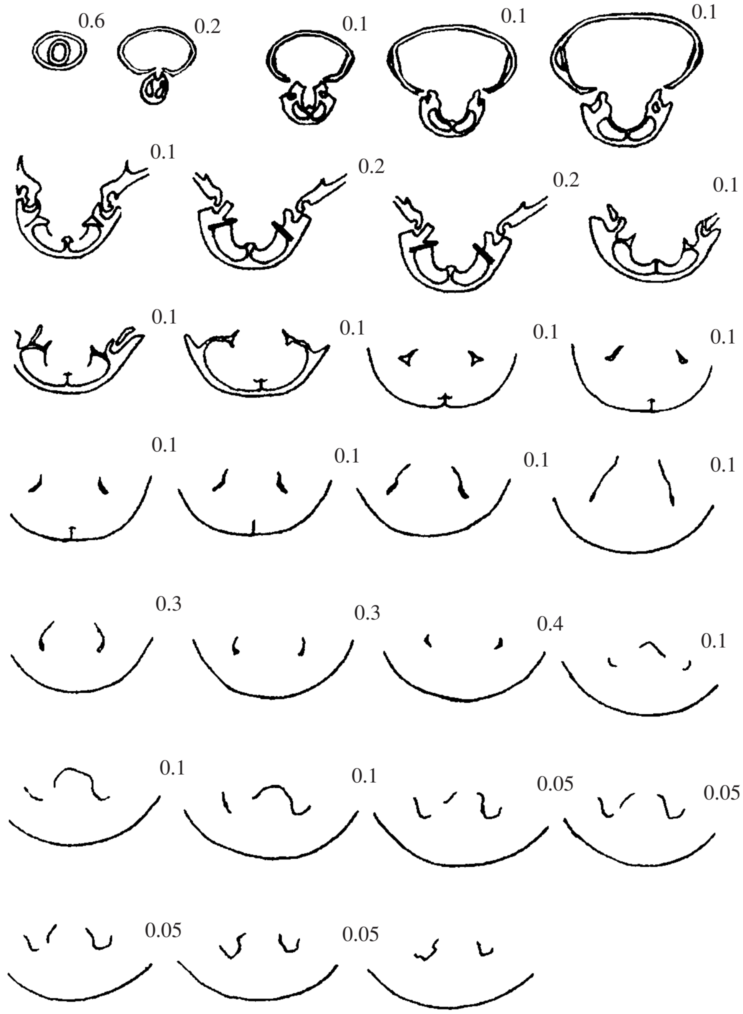


Fig. 64. *Calycelasma kalaschnikovi* sp. nov.; specimen PIN, no. 4898/2612, serial cross sections; figures indicate distances between the sections in mm.

and inner denticles are well-developed. The dental plates are slightly diverging and border narrow umbonal cavities. The outer hinge plate is short, poorly pronounced in the cardinalium relief, and developed only in the apical region. The inner hinge plate is cup-shaped and supported by a septum along the full length. The crural plates are distinctly separated from the inner socket ridges in relief, are located close to them, and rest on the valve bottom anteriorly. The crural bases have ventral and dorsal tips. The crural processes are wide and slightly curved. The loop branches are narrow. The transverse band of the loop is rounded triangular to trapezoidal. The loop length is about one-half of the dorsal valve length.

Occurrence. Upper Permian, Lower Kazanian Substage; east of the Russian Platform.

Material. Seventy-six well-preserved specimens from the type locality.

Genus *Tapetulasma* Smirnova, gen. nov.

Etymology. From the Latin *tapetum* (covering) and Greek *elasma* (plate).

Type species. *Tapetulasma boltaevae* sp. nov.

Diagnosis. Shell middle-sized and not plicate, with moderately convex valves and flattened margins. Anterior commissure slightly curved. Pedicle collar arched. Dental plates long and massive. Outer hinge plates absent. Inner hinge plate covering the bottom of the dorsal valve. Crural plates resting on the bottom of the dorsal valve, distinctly separated by considerable distances from the inner socket ridges. Loop narrow and long. Loop length about one-half of the dorsal valve length. Transverse band of the loop wide and rounded rectangular.

Species composition. Type species.

Comparison. The new genus differs from *Sokelasma* Smirnova, 2004 in the absence of the sep-

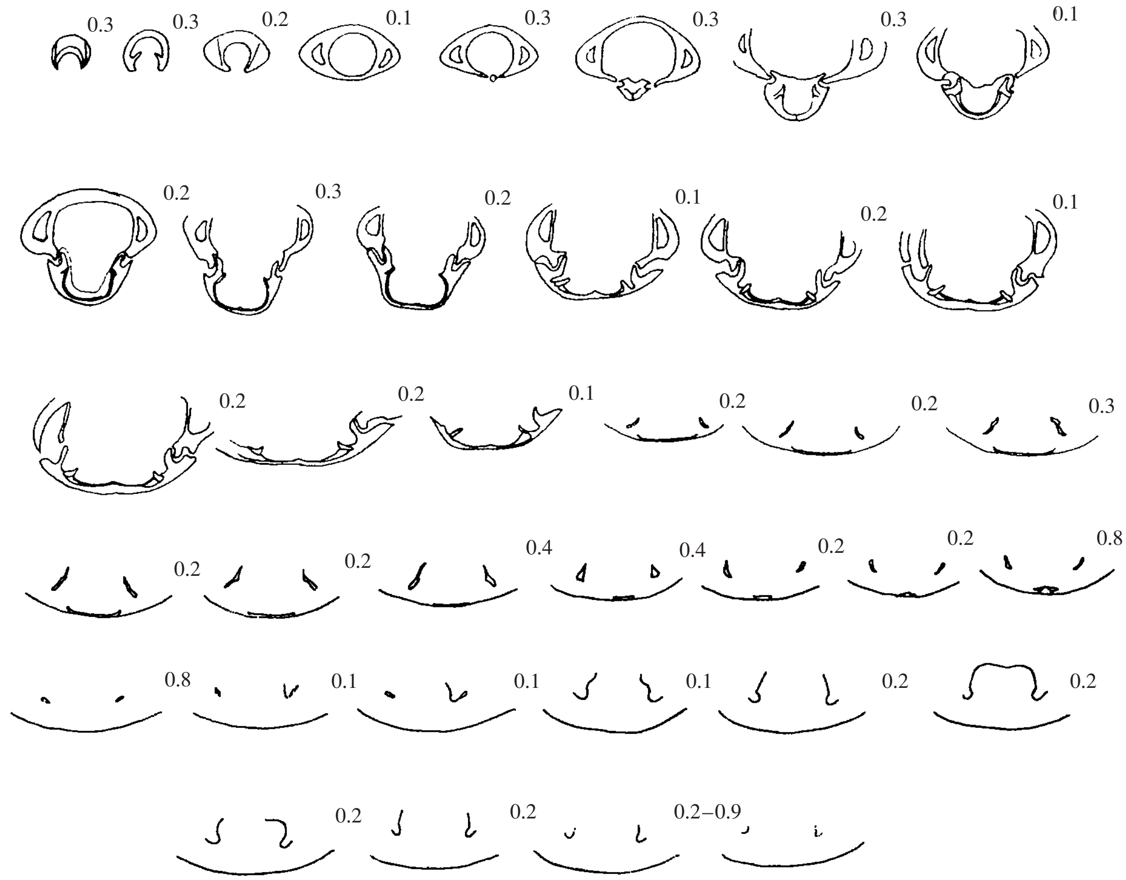


Fig. 65. *Tapetulasma boltaevae* sp. nov.; specimen PIN, no. 4898/2485, serial cross sections; figures indicate distances between the sections in mm.

tum, inner hinge plate covering the shell bottom, low crural plates remote from the socket ridges, and in the shape of the transverse band of the loop. It differs from *Calycelasma* gen. nov. in the larger shell, arched pedicle collar, long dental plates, absence of the dorsal septum and outer hinge plates, shape of the inner hinge plates, rounded rectangular shape of the transverse plate of the loop, and in the crural plates resting on the valve bottom.

Tapetulasma boltaevae **Smirnova, sp. nov.**

Plate 4, fig. 6

Etymology. In honor of the geologist V.P. Boltaeva.

Holotype. PIN, no. 4898/2482, complete shell; Samara Region, Sok River, village of Kamyshla, Kamyshla quarry; Upper Permian, Lower Kazanian, Bajtugan Beds.

Description (Figs. 65, 66). The shell is shaped like a regular oval, with flattened dorsal and slightly convex ventral valves. The lateral sides and anterior margins are flattened. The anterior and lateral commissures are slightly arched. The hinge line is strongly curved. The maximum width is in the anterior third of the shell. The maximum thickness is in the posterior third of the shell. The ventral valve is convex in the posterior and flattened in the anterior halves. The plication is absent. The umbo is slightly curved. The false area is high, concave, and bordered by sharpened umbonal keels. The apical angle is 70°–73°. The foramen is large, circular, and apical. The dorsal valve is slightly curved along the full length and bears a weakly pronounced elevation near the anterior margin.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
Holotype					
4898/2482	23.8	18.0	9.0	0.75	0.38
4898/2483	20.0	16.0	8.2	0.80	0.41
4898/2484	21.2	16.5	8.1	0.78	0.38

Shell interior. The pedicle collar is wide and arched. The dental plates are long and parallel. The teeth enter the dental sockets vertically. Outer and inner denticles are present. The inner socket ridges are high, perpendicular to the valve bottom, and well-pronounced in relief. The crural plates are contiguous with the inner socket ridges and inner hinge plate in the apical region. The crural plates are perpendicular to the bottom of the dorsal valve along their full length. The

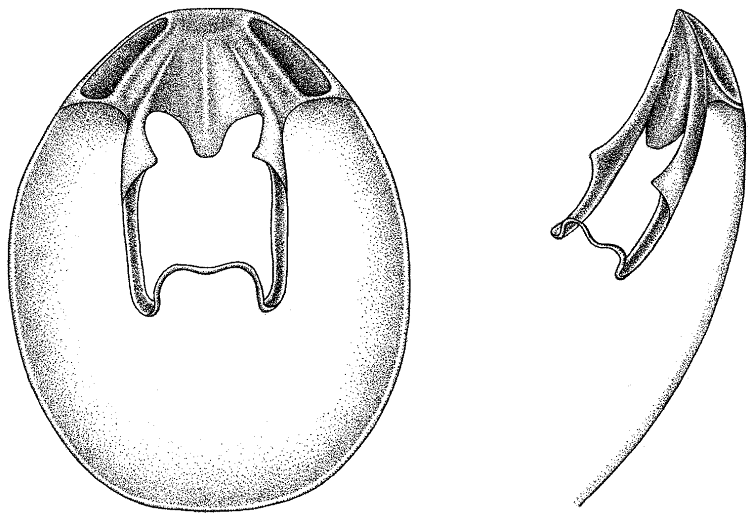


Fig. 66. *Tapetulasma boltaevae* sp. nov.; specimen PIN, no. 4898/2485, reconstruction of the internal structures.

inner hinge plate is a single structure lining the cavity of the dorsal valve. It is connected with the crural plates along its full length. The inner hinge plate gradually increases and disappears in the middle of the dorsal valve. The crural processes are narrow. The loop branches narrow, subparallel, and slightly concave. The transverse band of the loop is wide and rounded rectangular, with long flanks. The loop length is about one-half of the dorsal valve length.

Occurrence. Upper Permian, Lower Kazanian Substage; Samara Region.

Material. Three specimens from the type locality.

Genus *Sokelasma* Smirnova, 2004

Sokelasma: Smirnova, 2004a, pp. 50 and 51.

Type species. *S. guttiformis* Smirnova, 2004.

Diagnosis. Shell small, rounded, and equiconvex. Anterior commissure arched dorsally. Pedicle collar from gently arched to deep. Dental plates variously developed. Outer hinge plates narrow or absent. Inner hinge plates supported by septum to form septalium. Crural plates high, resting on the bottom of the dorsal valve at varying distances from the inner socket ridges. Loop narrow. Loop length about one-half of the dorsal valve length. Transverse band of the loop widely arched.

Species composition. Type species, *S. esaulovae* Smirnova, 2004, *S. tatarstanica* sp. nov., and *S. chuvaschensis* sp. nov. from the Lower Kazanian Substage (Upper Permian) of the eastern Russian Platform.

Comparison. This genus differs from *Hoskingia* Campbell, 1965 in the small and rounded shell, slightly curved valves, and in the inner hinge plate supported by the septum.

Sokelasma guttiformis Smirnova, 2004

Plate 4, fig. 7

Sokelasma guttiformis: Smirnova, 2004a, pp. 51–52.

Holotype. PIN, no. 4898/76; eastern Russian Platform, Sok River, village of Chuvashskii Bajtugan; Upper Permian, Lower Kazanian.

Description (Fig. 67). The shell is tear-shaped or rounded, equiconvex or the ventral valve may be slightly more convex than the dorsal one. The width and length are almost equal. The lateral sides of the shell are flattened. The maximum width is in the anterior third or in the middle of the shell. The maximum thickness is in the posterior third or in the middle of the shell. The anterior commissure is slightly dorsally arched. The lateral commissures are widely arched. The ventral valve is strongly convex in the umbonal region and flattened in the anterior half, where a weakly developed sulcus may be present. The anterior margin is curved dorsally as a linguiform extension. The umbo is high, curved, and bordered by well-pronounced umbonal keels. The false area is concave. The apical angle is 65°–70°. The foramen is circular, middle-sized, and apical. The dorsal valve is curved rooflike in the middle and flattened near the margins.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
Holotype 4898/76	17.2	14.0	7.9	0.81	0.46
4898/77	15.2	12.7	7.1	0.83	0.46
4898/78	14.4	12.2	6.9	0.84	0.48
4898/79	13.6	11.5	7.1	0.85	0.52
4898/80	12.8	11.0	6.0	0.86	0.47

Shell interior. The pedicle collar is gently arched. The teeth are narrow and enter the dental sock-

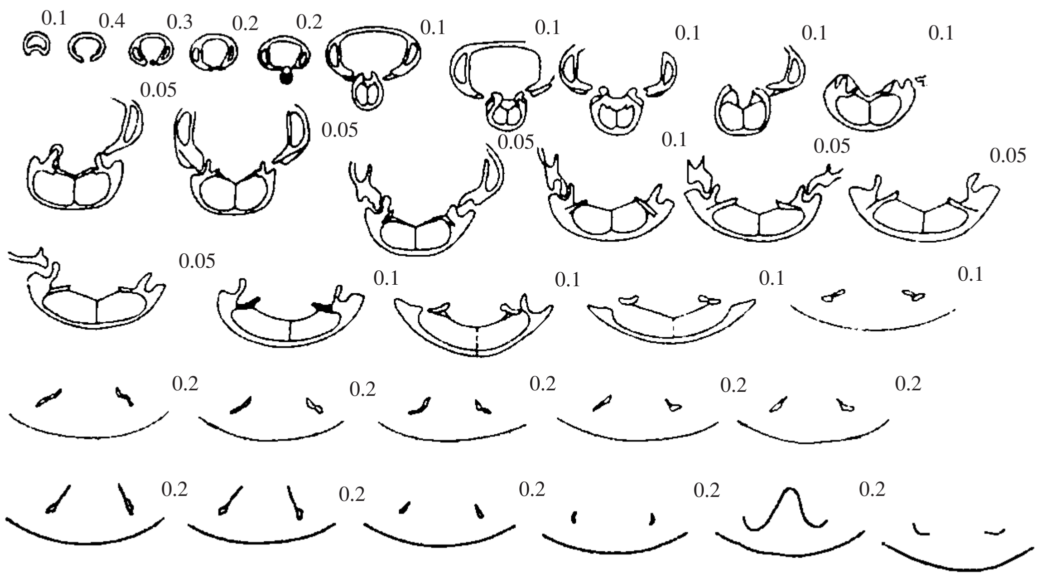


Fig. 67. *Sokelasma guttiformis* Smirnova, 2004; specimen PIN, no. 4898/81, serial cross sections; figures indicate distances between the sections in mm.

ets vertically. The denticle is large. The dental plates are subparallel and divide small umbonal cavities and a large delthyrial cavity. The outer hinge plates are strongly curved and very short. The inner hinge plates are supported by a high septum to form a septalium and are bordered by crural plates from outside. The inner socket ridges are high. The crural plates are high, perpendicular to the bottom of the dorsal valve, partly penetrate into the shell wall, and are drawn together with the inner socket ridges. The transverse band of the loop is highly arched.

C o m p a r i s o n. This species differs from *S. chuvaschensis* in the tear-shaped or rounded shell, slightly arched anterior commissure, flattened lateral sides of the shell, high umbo, rooflike curved dorsal valve, teeth that obliquely enter the dental sockets, presence of outer hinge plates, high dorsal septum, and in the highly arched transverse band of the loop.

O c c u r r e n c e. Upper Permian, Lower Kazanian Substage; eastern Russian Platform.

M a t e r i a l. Two hundred and eighty well-preserved specimens from the Sok River basin, near the village of Chuvashskii Bajtugan; 52 specimens from the northern outskirts of the village of Tatarskii Bajtugan.

Sokelasma esaulovae Smirnova, 2004

Plate 4, fig. 8

Sokelasma esaulovae: Smirnova, 2004a, pp. 52 and 53, pl. 6, figs. 2a–2h.

H o l o t y p e. PIN, no. 4898/100; eastern Russian Platform, Sok River, village of Chuvashskii Bajtugan; Upper Permian, Lower Kazanian.

D e s c r i p t i o n (Fig. 68). The shell is ovally elongate or pyriform, with flattened lateral and anterior margins. The valves are equiconvex or the ventral valve may be slightly more convex than the dorsal one. The length considerably exceeds the width. The maximum width is in the middle or is slightly shifted to the anterior margin. The maximum thickness is in the middle. The anterior commissure is dorsally curved to form a wide arc. The lateral commissures are slightly curved. The lateral sides may be parallel. The ventral valve is uniformly curved along its full length. The anterior margin is slightly dorsally stretched to form a wide linguiform extension. The umbo is high, curved, and bordered by sharpened umbonal keels. The false area is well-pronounced and concave. The apical angle is 70°–78°. The foramen is small and umbonal. The dorsal valve is curved rooflike in the posterior half and flattened in the anterior half. Some shells have a poorly pronounced elevation near the anterior margin. The lateral sides of the valve are flattened to slightly concave.

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

Specimen, no.		L	W	T	W/L	T/L
Holotype	4898/100	16.6	12.5	7.2	0.75	0.43
	4898/101	15.6	12.1	7.8	0.77	0.50
	4898/102	15.2	11.8	7.1	0.77	0.46
	4898/103	14.7	11.7	6.7	0.79	0.45
	4898/104	13.2	10.8	6.0	0.81	0.45

S h e l l i n t e r i o r. The pedicle collar is gently arched. The teeth are narrow, enter the dental sockets obliquely, and bear one or two denticles. The dental plates are short, slightly diverging, and divide a large delthyrial cavity and small umbonal cavities. The outer hinge plates are well-pronounced in the umbonal

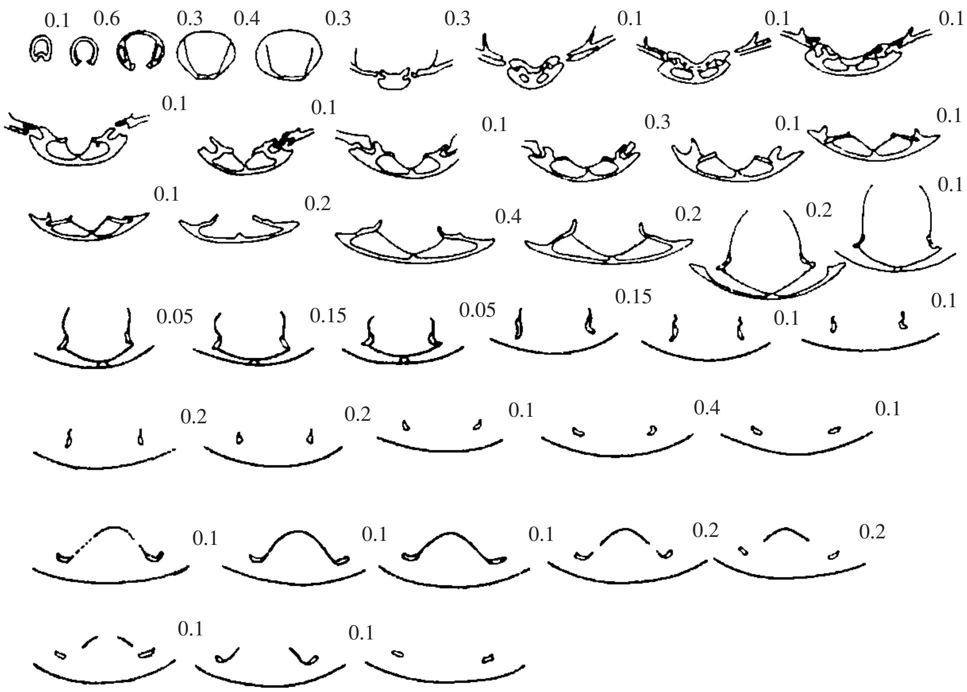


Fig. 68. *Sokelasma esaulovae* Smirnova, 2004; specimen PIN, no. 4898/105, serial cross sections; figures indicate distances between the sections in mm.

region. They are slightly concave plates at early developmental stages, horizontal plates at the subsequent stages, and reduce before the appearance of the crural plates. The inner hinge plates are cup-shaped and are supported by the euseptoid. The crural plates are drawn together with the inner socket ridges, rest on the bottom of the dorsal valve, and penetrate into the shell wall. After the outer hinge plates disappear, the inner hinge plates are supported by the crural plates. The crural processes are long. The loop branches are narrow. The length of the loop is about two-fifths of the length of the dorsal valve. The transverse band of the loop is widely arched.

C o m p a r i s o n. This species differs from *S. guttiformis* Smirnova, 2004 in the ovally elongate or pyriform shell, large apical angle, teeth that obliquely enter the dental sockets, short dental plates, presence of euseptoid, and in the well-pronounced outer hinge plates. It differs from *S. tatarstanica* sp. nov. in the large apical angle, large foramen, absence of the sulcus on the ventral valve, gently arched pedicle collar, and in the presence of the outer hinge plates.

O c c u r r e n c e. Upper Permian, Lower Kazanian Substage; eastern Russian Platform.

M a t e r i a l. Three hundred and ten well-preserved shells from the Sok River basin near the village of Chuvashskii Bajtugan; 78 specimens from the northern outskirts of the village of Tatarskii Bajtugan.

Sokelasma tatarstanica Smirnova, sp. nov.

Plate 4, fig. 9

E t y m o l o g y. From the republic of Tatarstan.

H o l o t y p e. PIN, no. 4898/2416; eastern Russian Platform, Sok River basin, village of Chuvashskii Bajtugan; Upper Permian, Lower Kazanian.

D e s c r i p t i o n (Fig. 69). The shell is oval to rounded triangular and equiconvex or, more rarely, the dorsal valve is slightly more convex than the ventral one. The lateral sides of the shell are flattened. The hinge line is long and strongly curved. The lateral commissures are widely arched. The anterior commissure is widely and steeply arched. The maximum width is in the middle or is slightly shifted to the anterior margin. The maximum thickness is in the middle. The ventral valve is flattened in the anterior half. A narrow and poorly pronounced sulcus may be developed along the full length of the valve. The anterior margin projects to form a wide linguiform extension. The umbo is high, curved, and narrow. The false area is high and concave. The apical angle is 60°–65°. The foramen is large, round, and labiate. A weakly developed fold extends along the full length of the dorsal valve. The lateral slopes of the dorsal valve are rounded.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
Holotype					
4898/2416	20.3	15.0	10.0	0.73	0.49
4898/2417	17.7	12.5	9.0	0.71	0.51
4898/2418	15.1	11.5	7.2	0.76	0.47
4898/2419	16.0	11.0	7.7	0.68	0.48
4898/2420	16.0	12.5	7.8	0.78	0.48
4898/2421	13.5	10.2	6.8	0.75	0.50

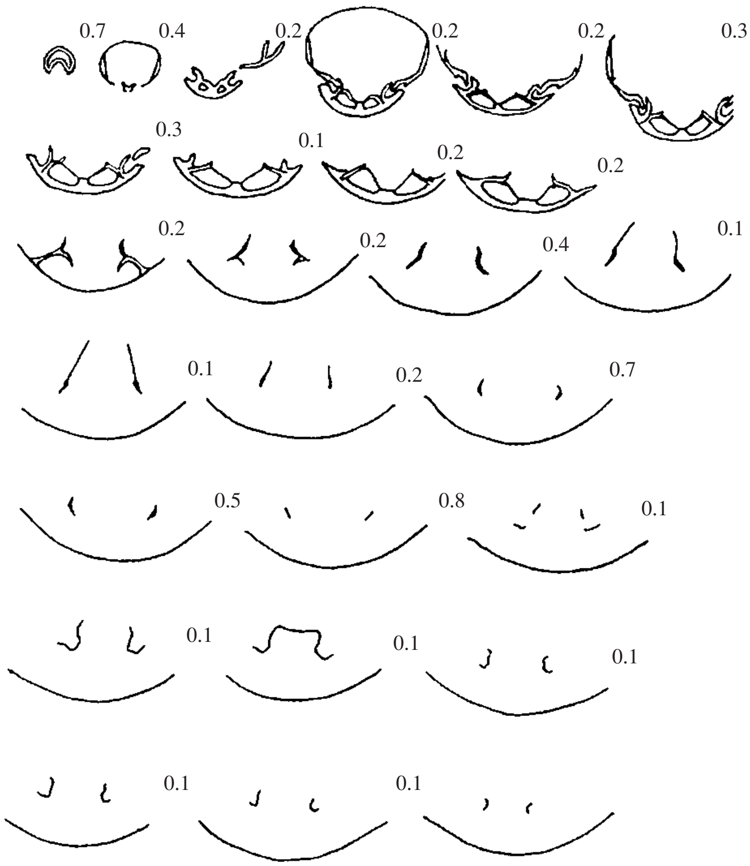


Fig. 69. *Sokelasma tatarstanica* sp. nov.; specimen PIN, no. 4898/2422, serial cross sections; figures indicate distances between the sections in mm.

S h e l l i n t e r i o r. The pedicle collar is deep. The teeth enter the dental sockets obliquely. The outer denticle is developed. The dental plates are short, slightly diverging, and located close to the valve wall. The outer hinge plates are absent. The inner hinge plates are supported by a massive, low septum and adjoin the crural plates. The crural plates are perpendicular to the plane of symmetry, drawn near the socket ridges, distinctly separated from the latter in relief, and penetrate into the valve wall. The crural bases are concave toward the lateral sides. The crural processes are wide and slightly curved. The loop branches are narrow. The transverse band of the loop is widely rectangular. The flanks are long. The loop length is about one-half of the dorsal valve length.

C o m p a r i s o n. The new species differs from *S. guttiformis* Smirnova, 2004 in the narrower, oval shell, strongly curved anterior margin, teeth obliquely entering the dental sockets, low septum, smaller angle between the crural plates, widely rectangular transverse band of the loop, and in the long flanks. It differs from *S. esaulovae* Smirnova, 2004, which is similar in external appearance, in the ventral valve flattened near the anterior margin, absence of the outer hinge plate, widely rectangular transverse band of the loop, and in the long flanks.

O c c u r r e n c e. Upper Permian, Lower Kazanian Substage; eastern Russian Platform.

M a t e r i a l. Fifty well-preserved specimens from the type locality.

Sokelasma chuvaschensis **Smirnova, sp. nov.**

Plate 4, fig. 10

E t y m o l o g y. From the republic of Chuvashia.

H o l o t y p e. PIN, no. 4898/2466, complete shell; eastern Russian Platform, Sok River, village of Chuvashskii Bajtugan; Upper Permian, Lower Kazanian.

D e s c r i p t i o n (Fig. 70). The shell is oval or rounded rhombic and equiconvex. The lateral sides of the shell are moderately convex. The hinge line is short and curved. The lateral commissures are almost straight. The anterior commissure varies in shape from narrowly arched and pointed in the middle to widely arched. The maximum width is in the middle or, more rarely, is slightly shifted to the anterior margin. The maximum thickness is in the middle. The ventral valve is uniformly curved along the entire surface. The anterior margin is stretched dorsally to form a linguiform

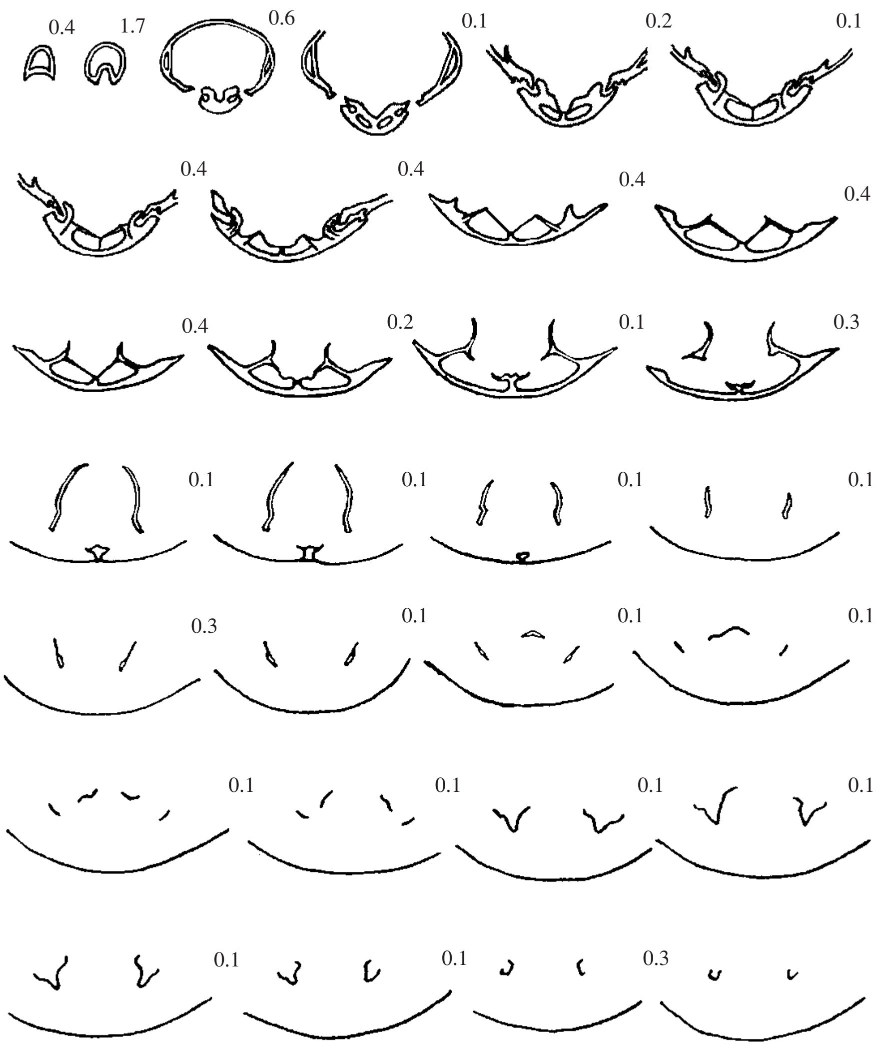


Fig. 70. *Sokelasma chuvaschensis* sp. nov.; specimen PIN, no. 4898/2472, serial cross sections; figures indicate distances between the sections in mm.

extension, usually narrow or, more rarely, wide. The umbo is curved and low. The false area is concave and bordered by rounded umbonal keels. The foramen is middle-sized, umbonal, and labiate. The apical angle is 60°–72°. The dorsal valve is moderately and uniformly convex. A weakly pronounced elevation is visible near the anterior margin in the region of the linguiform extension.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
Holotype 4898/2466	15.5	11.9	6.5	0.83	0.45
4898/2467	15.7	12.8	7.5	0.81	0.48
4898/2468	15.0	12.0	7.0	0.80	0.47
4898/2469	16.0	11.8	7.9	0.74	0.49
4898/2470	17.8	14.5	8.6	0.82	0.48
4898/2471	16.4	12.6	8.3	0.76	0.51

S h e l l i n t e r i o r. The pedicle collar is gently arched to deep. The teeth are narrow and enter the dental sockets obliquely. Two additional denticles are present. The dental plates are short, slightly diverging, and drawn near the valve wall. The outer hinge plates are absent. The inner hinge plates are perpendicular to each other and supported by a low, massive septum. The crural plates are located close to the inner socket ridges in the apical region and at a distance from them in the anterior region, where they are oriented perpendicular to the valve wall. The crural bases have long ventral tips that are concave toward the lateral sides of the valve. The crural processes are long and falcate. The loop branches are narrow. The transverse band of the loop is wide and rectangular in cross section. The flanks of the loop are long. The loop length is about half of the dorsal valve length.

C o m p a r i s o n. The new species differs from *S. tatarstanica* Smirnova, sp. nov. in the wider, rounded rhombic shell, moderately convex lateral sides of the shell, short hinge line, straight lateral commissures, narrow linguiform extension on the anterior margin, uniformly curved ventral valve, large apical angle, curved crural processes, and in the crural plates located at a distance from the inner socket ridges. It differs from *S. esaulovae* Smirnova, 2004 in the rounded rhombic shell with convex lateral sides, narrow bend of the anterior margin, straight lateral commissures, smaller apical angle, uniformly curved dorsal valve, absence of the outer hinge plates, and in the widely rectangular transverse band of the loop.

Occurrence. Upper Permian, Lower Kazanian Substage; eastern Russian Platform.

Material. Fifty-eight well-preserved specimens from the type locality.

Superfamily Terebratuloidea Gray, 1840

[Nom. transl. Schuchert et Le Vene, 1929 (ex Terebratulidae Gray, 1840)].

Terebratulacea: Dagys, 1974, p. 194.

Diagnosis. Dental plates and inner hinge plates absent. Outer hinge plates usually well-developed. Crural plates present or absent. Loop short and triangular. Secondary elements involved in brachidium development. Brachidium passes through centronelloid and mutationelliform stages.

Occurrence. Late Carboniferous (?), Late Permian–recent.

Composition. Terebratulidae Gray, 1840; Cancellothyrididae Thomson, 1927; Nucleatidae Schuchert et Le Vene, 1921; Gibbithyrididae Muir-Wood, 1965; and Heterelasminidae Licharew, 1956.

Family Heterelasminidae Licharew, 1956

Heterelasminidae: Licharew, 1956, p. 293; Licharew, 1956b, p. 68; Campbell, 1965, p. 104; Stehli, 1965, H760; Koczyrkewicz, 1976, p. 74; Cooper et Grant, 1976, p. 2907.

Diagnosis. Shell smooth or ribbed and variously sized. Dental plates absent. Outer hinge plates rudimentary or absent. Inner hinge plates and septal structures absent. Crural plates resting on bottom of the dorsal valve. Crural bases connected with the crural plates. Loop terebratuloid, developing without secondary elements.

Occurrence. Permian.

Composition. *Heterelasmina* Licharew, 1939; *Gundarolasmina* Smirnova et Grunt, 2003; *Permicola* Koczyrkewicz, 1976; and *Amurothyris* Koczyrkewicz, 1976.

Comparison. This family differs from Terebratulidae Gray, 1840 in the rudimentary or absent outer hinge plates, absence of the inner hinge plates, presence of crural plates, and in the crural bases connected with the crural plates. It differs from Cancellothyrididae Thomson, 1927 in the smooth shell, triangular loop, poorly pronounced outer hinge plates, presence of the crural plates, and in the crural bases connected with the crural plates.

Genus *Heterelasmina* Licharew, 1939

Heterelasmina: Licharew, 1939, p. 120; Licharew, 1956, p. 68; Licharew et al., 1960, p. 293; Grunt and Dmitriev, 1973, pp. 152 and 153; Koczyrkewicz, 1976, p. 74.

Jisuina: Stehli, 1962, p. 103; 1965, H760.

Type species. *Hemiptychina dieneri* Gemmellaro, 1899; Upper Permian, Murgabian, *Fusulina* limestones; Sicily.

Diagnosis. Shell small and smooth, with flattened dorsal valve and rooflike ventral valve, and variously shaped: rounded pentagonal, rounded rectangular, rounded triangular, or oval. Two or three deep folds present in the anterior half of the shell. Lateral commissures strongly curved. Anterior commissure with two or three sharp bends. Umbo massive. Foramen small. Pedicle collar present or absent. Outer hinge plates rudimental. Crural plates rest on the bottom of the dorsal valve in the umbonal region. Crural processes long. Loop terebratuloid. Loop length about one-third of the dorsal valve length.

Species composition. Type species; *H. genuflexa* (Gemmellaro, 1899) from the uppermost Kubergandian–lowermost Murgabian (Upper Permian) of Sicily; *H. latesinuata* (Licharew, 2002), *H. planoventrum* (Licharew, 2002), and *H. cuboides* Licharew in Smirnova, 2001 from the Safetdaron Formation (Bolorian Stage, Lower Permian) of the southwestern Darvaz; and *H. regularis* Smirnova et Grunt, 2003 and *H. costata* sp. nov. from the Gundara Formation (Upper Permian) of the southwestern Darvaz.

Comparison. This genus differs from *Permicola* Koczyrkewicz, 1976 in the larger shell, presence of plication along the full length of the ventral valve, and in the strongly curved lateral commissures. It differs from *Amurothyris* Koczyrkewicz, 1976 in the absence of ribs, presence of plication on both valves, and in the type of commissures.

Remarks. Stehli (1962, 1965) believed the genus *Heterelasmina* to be a junior synonym of *Jisuina* Grabau, 1931. The type species of the latter is *J. elegantula* Grabau, 1931 from the Upper Permian of northern China, represented by a single damaged specimen. Without any explanation, Grabau (1931) assigned *Hemiptychina genuflexa* Gemmellaro, 1899, *H. nikitini* Gemmellaro, 1899, *H. waageni* Stuckenberg, 1905, and *H. bokharica* Tschernyschew, 1914 to *Jisuina*. Stehli (1962) studied the internal structures of *H. genuflexa* in cross section and considered its interior to be typical of *Jisuina*. In fact, this species is not the type species for the genus *Jisuina* and its interior cannot characterize this genus. The interior of *Jisuina* is still unknown and its taxonomic position is controversial. We accept the position of Grunt (Grunt and Dmitriev, 1973) and Koczyrkewicz (1976) on the validity of the genus *Heterelasmina*. This genus has a distinct systematic position and is a type genus for the family Heterelasminidae Licharew, 1956, which is recognized by all Paleozoic terebratulid researchers.

Plate 5


1a
1b
1c
1d
1e
1f
1g
1h
2a
2b
2c
2d
3a
3b
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3d
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15c
15d
16a
16b
16c
16d
17a
17b
17c
17d
18a
18b
18c
18d

When establishing the genus *Heterelasmina,* Licharew (1939) listed *Heterelasmina dieneri* (Gemmellaro, 1899) first. According to the rules of the Zoological Nomenclature, this species is the type species. Licharew (1956) later incorrectly designated *Heterelasmina schucherti* Licharew, 1956 from the Upper Permian of the Northern Caucasus as the type species.

Heterelasmina cuboides **Licharew in Smirnova, 2001**

Plate 5, fig. 1

Hemiptychina dieneri: Tschernyschew, 1914, pp. 10 and 11, pl. 3, figs. 9–11.

Heterelasmina dieneri: Licharew, 1939, p. 120, pl. 29, fig. 11.

Holotype. TsNIGR Museum, no. 999/4424; Tajikistan, southwestern Darvaz, Tangi-Gor Gorge; Lower Permian, Bolorian, Safetdaron Formation.

Description (Fig. 13). The shell is small and equiconvex, with rounded quadrangular or rounded pentagonal and strongly convex valves. The length and width are almost equal. The lateral sides of the shell are rounded, subparallel, and wide. The hinge line is long and slightly curved. The lateral commissures are strongly arched. The anterior margin is triplicate. The anterior commissure has three pointed bends. The maximum width is slightly shifted to the anterior margin. The maximum thickness is in the middle or is slightly shifted to the anterior margin. The ventral valve is curved in the middle at a right angle. In cross section the ventral valve closely resembles a rectangle with rounded corners. The sulcus is narrow, extends from the umbo up to the anterior margin, and broadens only slightly. Two high folds extend from the umbo up to anterior margin bordering the sulcus. Shallow hollows running from the middle of the valve are present outside the folds. The umbo is wide, strongly inflated, overhanging the dorsal valve. The umbonal keels are short and smooth. The apical angle is 78°–82°. The foramen is very small and submesothyrid. The dorsal valve is curved rooflike along the full length. The middle elevation is high and has a smooth or sharpened surface. The lateral sides are inclined to each other at an angle of 70°–80°. Three folds are well-pronounced.

Explanation of Plate 5

Fig. 1. *Heterelasmina cuboides* Licharew in Smirnova, 2001; holotype TsNIGR Museum, no. 999/4424, ×1: (1a) ventral valve; (1b) dorsal valve; (1c) lateral view; (1d) anterior margin; Bolorian Stage, Safetdaron Formation, Lower Permian; southwestern Darvaz; specimen PIN, no. 4104/322, ×1: (1e) ventral valve; (1f) dorsal valve; (1g) lateral view; (1h) anterior margin; Gundara Formation, Upper Permian; southwestern Darvaz.

Fig. 2. *Heterelasmina regularis* Smirnova et Grunt, 2003; holotype PIN, no. 4104/1054, ×1: (2a) ventral valve; (2b) dorsal valve; (2c) lateral view; (2d) anterior margin; Gundara Formation, Upper Permian; southwestern Darvaz.

Fig. 3. *Heterelasmina planoventris* (Licharew, 2002); specimen PIN, no. 4104/750, ×1: (3a) ventral valve; (3b) dorsal valve; (3c) lateral view; (3d) anterior margin; Bolorian Stage, Safetdaron Formation, Lower Permian; southwestern Darvaz.

Fig. 4. *Heterelasmina latesinuata* (Licharew, 2002); specimen PIN, no. 4104/77, ×1: (4a) ventral valve; (4b) dorsal valve; (4c) lateral view; (4d) anterior margin; Kubergandian Stage, Upper Permian; southwestern Darvaz.

Fig. 5. *Heterelasmina costata* sp. nov.; holotype PIN, no. 4104/1079, ×1: (5a) ventral valve; (5b) dorsal valve; (5c) lateral view; (5d) anterior margin; Gundara Formation, Upper Permian; southwestern Darvaz.

Fig. 6. *Gundarolasmina gundarensis* Smirnova et Grunt, 2003; holotype PIN, no. 4104/619, ×1: (6a) ventral valve; (6b) dorsal valve; (6c) lateral view; (6d) anterior margin; Gundara Formation, Upper Permian, southwestern Darvaz.

Fig. 7. *Gundarolasmina ordinata* Smirnova et Grunt, 2003; holotype PIN, no. 4104/623, ×1: (7a) ventral valve; (7b) dorsal valve; (7c) lateral view; (7d) anterior margin; Gundara Formation, Upper Permian; southwestern Darvaz.

Fig. 8. *Gundarolasmina schucherti* (Licharew, 1956); specimen PIN, no. 4918/60, ×1.5: (8a) ventral valve; (8b) dorsal valve; (8c) lateral view; (8d) anterior margin; Urushten Horizon, Upper Permian; Northern Caucasia.

Fig. 9. *Gundarolasmina itaitubense* (Derby, 1874); specimen PIN, no. 5133/28, ×1: (9a) ventral valve; (9b) dorsal valve; (9c) lateral view; (9d) anterior margin; Murgabian Stage, Upper Permian; northern China.

Fig. 10. *Gundarolasmina acutangulum* (Waagen, 1882); specimen PIN, no. 5133/31, ×1.5: (10a) ventral valve; (10b) dorsal valve; (10c) lateral view; (10d) anterior margin; Murgabian Stage, Upper Permian; northern China.

Fig. 11. *Fredericksolasma lata* (Licharew, 1939); holotype TsNIGR Museum, no. 33/340, ×1.5: (11a) ventral valve; (11b) dorsal valve; (11c) lateral view; (11d) anterior margin; Gundara Formation, Upper Permian; southwestern Darvaz.

Fig. 12. Fredericksolasma lata (Licharew, 1939); specimen PIN, no. 4104/16, ×1: (12a) ventral valve; (12b) dorsal valve; (12c) lateral view; (12d) anterior margin; Gundara Formation, Upper Permian; southwestern Darvaz.

Fig. 13. *Fredericksolasma rhomboidale* Smirnova et Grunt, 2003; holotype PIN, no. 4104/361, ×1: (13a) ventral valve; (13b) dorsal valve; (13c) lateral view; (13d) anterior margin; Gundara Formation, Upper Permian; southwestern Darvaz.

Fig. 14. *Fredericksolasma darvasica* Smirnova et Grunt, 2003; specimen PIN, no. 4104/235, ×1: (14a) ventral valve; (14b) dorsal valve; (14c) lateral view; (14d) anterior margin; Bolorian Stage, Safetdaron Formation, Lower Permian; southwestern Darvaz.

Fig. 15. *Levenolasma concava* Smirnova et Grunt, 2003; holotype PIN, no. 4104/283, ×1: (15a) ventral valve; (15b) dorsal valve; (15c) lateral view; (15d) anterior margin; Gundara Formation, Upper Permian; southwestern Darvaz.

Fig. 16. *Levenolasma leveni* Smirnova et Grunt, 2003; holotype PIN, no. 4104/1083, ×1: (16a) ventral valve; (16b) dorsal valve; (16c) lateral view; (16d) anterior margin; Gundara Formation, Upper Permian; southwestern Darvaz.

Fig. 17. *Levenolasma sinuosa* sp. nov.; holotype PIN, no. 4104/1076, ×1: (17a) ventral valve; (17b) dorsal valve; (17c) lateral view; (17d) anterior margin; Gundara Formation, Upper Permian; southwestern Darvaz.

Fig. 18. *Levenolasma mongolica* (Grabau, 1931); specimen PIN, no. 5133/31, ×1.5: (18a) ventral valve; (18b) dorsal valve; (18c) lateral view; (18d) anterior margin; Midian Stage, Upper Permian; northern China.

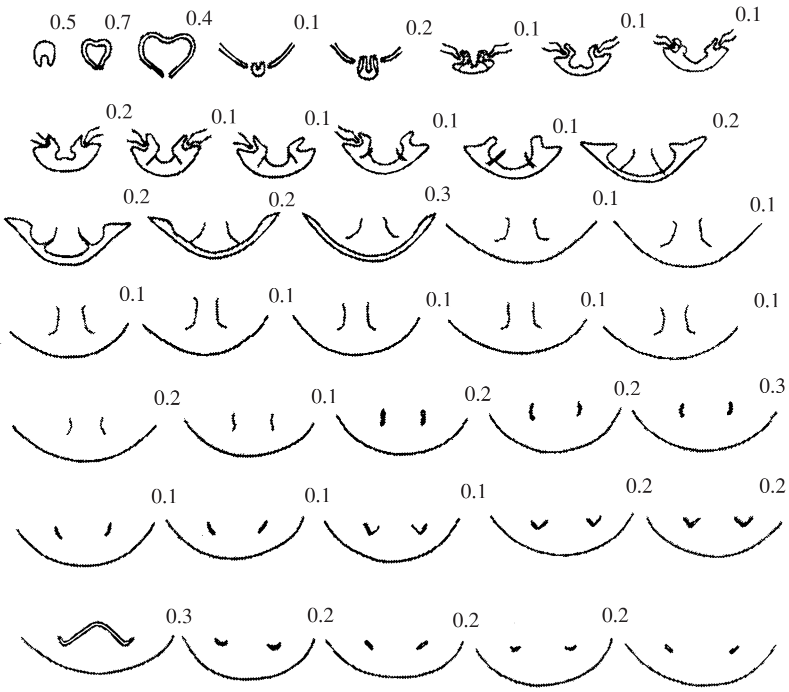

Fig. 71. *Heterelasmina regularis* Smirnova et Grunt, 2003; specimen PIN, no. 4104/1055, serial cross sections; figures indicate distances between the sections in mm.

The middle fold continues the elevation, and the two lateral folds are located in the anterior third of the valve. Two narrow sinuses that are deep near the anterior margin are located between the folds.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
Holotype 999/4424	12.1	10.6	9.2	0.88	0.76
4104/3	14.8	12.1	11.0	0.82	0.74
4104/4	14.7	13.1	10.7	0.89	0.73
4104/5	14.8	12.3	11.0	0.83	0.74
4104/6	14.8	12.8	10.9	0.86	0.74

S h e l l i n t e r i o r. The pedicle collar is poorly pronounced. The teeth are hammer-shaped and have a projection at the boundary with the inner socket ridges. The outer hinge plate is only present in large shells, in which it is represented by small parts that are poorly pronounced in the relief. The inner socket ridges are high and almost perpendicular to the plane of symmetry. The crural plates are high, widely spaced, and rest on the bottom of the dorsal valve. The crural processes are wide, strongly curved, and laterally convex. The loop branches are wide and subparallel. The transverse band of the loop is rounded triangular and strongly curved. The loop length is about one-third of the dorsal valve length.

C o m p a r i s o n. This species differs from *H. dieneri* (Gemmellaro, 1899) in the more convex valves, almost globe-shaped shell, strongly curved ventral valve, rounded lateral sides of the shell, and in the better pronounced plication of the anterior margin. It differs from *H. genuflexa* (Gemmellaro, 1899) in the smaller, rounded quadrangular, and equiconvex shell, width almost equal to length, smaller apical angle, and in the small foramen.

O c c u r r e n c e. Lower Permian, Bolorian Stage, Safetdaron Formation (several records); Upper Permian, Gundara Formation (numerous records); Tajikistan, southwestern Darvaz.

M a t e r i a l. Two hundred and twenty complete shells from the left bank of the Zidadara River near its headstream; 17 complete shells and 16 specimens with broken umbos from the right bank of the Gundara River, at height 3661 m; 26 complete shells and 23 fragments from the headstream of the Zidadara River.

Heterelasmina regularis Smirnova et Grunt, 2003

Plate 5, fig. 2

Heterelasmina regularis: Smirnova and Grunt, 2003, pp. 28 and 29, text-figs. 4a–4h, and 5.

H o l o t y p e. PIN, no. 4104/1054, complete shell; Upper Permian, Gundara Formation; Tajikistan, southwestern Darvaz, Zidadara River.

D e s c r i p t i o n (Fig. 71). The shell is middle-sized, moderately biconvex, and oval. The length considerably exceeds the width. The maximum length and width are in the middle of the shell. The lateral sides of the shell are flattened. The hinge line is long and slightly curved. The lateral commissures are arched. The anterior commissure is sinuate and gently biplicate. The anterior margin is biplicate. The ventral valve is slightly more convex than the dorsal valve and is uniformly curved both transversely and longitudinally. The sulcus is narrow, shallow, and extends from the umbo to the anterior margin. It is bordered by two narrow and rounded folds developed in the anterior half of the valve. The umbo is strongly curved and narrow. The umbonal keels are short and well-pronounced. The false area is short and high. The apical angle is 70°–78°. The foramen is small and submesothyrid. The dorsal valve is rooflike, with flattened lateral surfaces and two high, sharpened folds in the middle and one low fold between them. All folds start from the middle of the valve.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.		L	W	T	W/L	T/L
Holotype	4104/1054	15.6	11.7	8.0	0.75	0.51
	4104/1050	18.7	13.4	10.7	0.72	0.57
	4104/1051	18.6	13.7	10.0	0.73	0.54
	4104/1052	18.1	13.0	8.8	0.72	0.43
	4104/1053	16.7	12.2	10.0	0.73	0.59

S h e l l i n t e r i o r. The pedicle collar is unknown. The teeth are narrow and enter the dental sockets obliquely. The outer hinge plates are poorly developed. The crural plates rest on the bottom of the dorsal valve and are closely spaced. The crural processes are long, wide, and laterally convex. The loop branches are narrow and subparallel. The transverse band of the loop is angularly arched. The flanks of the loop are long. The loop length is one-third of the dorsal valve length.

C o m p a r i s o n. This species differs from *H. cuboides* Licharew in Smirnova, 2001 in the larger and oval shell, less convex valves, less curved umbo, low folds on both valves, shape of the teeth, closely spaced crural plates, and in the narrower crural processes. It differs from *H. latesinuata* (Licharew, 2002) in the narrower, oval shell, high folds on the dorsal valve, shape of the anterior margin, smaller apical angle, poorly pronounced outer hinge plates, and in the shape of the transverse band of the loop.

M a t e r i a l. Ten complete specimens and 13 specimens with broken margins from the type locality.

Heterelasmina planoventris **(Licharew, 2002)**

Plate 5, fig. 3

Hemiptychina planoventrum: Licharew, 2002, p. 42, text-figs. 1e–1h.

Heterelasmina planoventris: Smirnova and Grunt, 2003a, pp. 29 and 30, text-figs. 4i–4l.

H o l o t y p e. TsNIGR Museum, no. 1003/4424, complete shell; southwestern Darvaz, kishlak of Safedaron, Adamak cliff; Lower Permian, Bolorian, Safetdaron Formation.

D e s c r i p t i o n. The shell is middle-sized, compressed laterally, elongated longitudinally, and from ovally triangular to ovally rectangular in outline. The maximum width is in the middle. The maximum thickness is in the middle or is slightly shifted to the anterior margin. The hinge line is from slightly curved to straight. The lateral commissures are steeply arched. The anterior commissure is wide and sharply W-shaped. The ventral valve is less convex than the dorsal one, curved almost at a right angle, and is flattened in the umbonal region. The sulcus is deep, narrow, and bordered by two high, rounded, and subparallel folds. The folds extend along the full length of the valve and are bordered by shallow grooves. The lateral sides of the valve are narrow and ridge-shaped. The umbo is strongly curved, massive, and high, with a flattened surface. The apical angle is 78°–80°. The foramen is very small, round, and submesothyrid. The dorsal valve is strongly inflated, rooflike posteriorly, and rounded quadrangular anteriorly. A wide, high elevation that is angular in cross section is present in the middle of the valve. Three high and sharpened folds are present in the anterior region of the valve. They are separated by two deep grooves that are sharply angular in cross section. The lateral sides of the valve are wide, flattened, and inclined to the plane of symmetry at a sharp angle.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.		L	W	T	W/L	T/L
Holotype	1003/4424	13.0	10.5	9.0	0.80	0.69
	4104/750	13.6	9.6	10.5	0.71	0.77
	4104/751	13.7	11.3	10.5	0.82	0.76
	4104/752	14.3	11.5	10.4	0.80	0.72
	4104/753	14.5	10.8	10.3	0.74	0.71

C o m p a r i s o n. This species differs from *H. cuboides* Licharew in Smirnova, 2001 in the laterally compressed, more longitudinally elongated, and rounded rectangular shell, flattened surface of the umbo, and non-equicovex valves. It differs from *H. genuflexa* (Gemmellaro, 1899) in the less elongated shell, more convex ventral valve, flattened umbo, and in the smaller apical angle.

M a t e r i a l. Eighteen complete shells and 20 shells with broken margins from the interfluve between the Charymdara and Zidadara rivers, at height 3837.4 m.

Heterelasmina latesinuata **(Licharew, 2002)**

Plate 5, fig. 4

Hemiptychina orientalis: Tschernyschew, 1914, p. 9, pl. 3, figs. 6 and 7.

Hemiptychina latesinuata: Licharew, 2002, p. 41.

Heterelasmina latesinuata: Smirnova and Grunt, 2003a, pp. 30 and 31, text-figs. 4m–4p, and 6.

H o l o t y p e. TsNIGR Museum, no. 42/340, complete shell; southwestern Darvaz, kishlak of Safedaron,

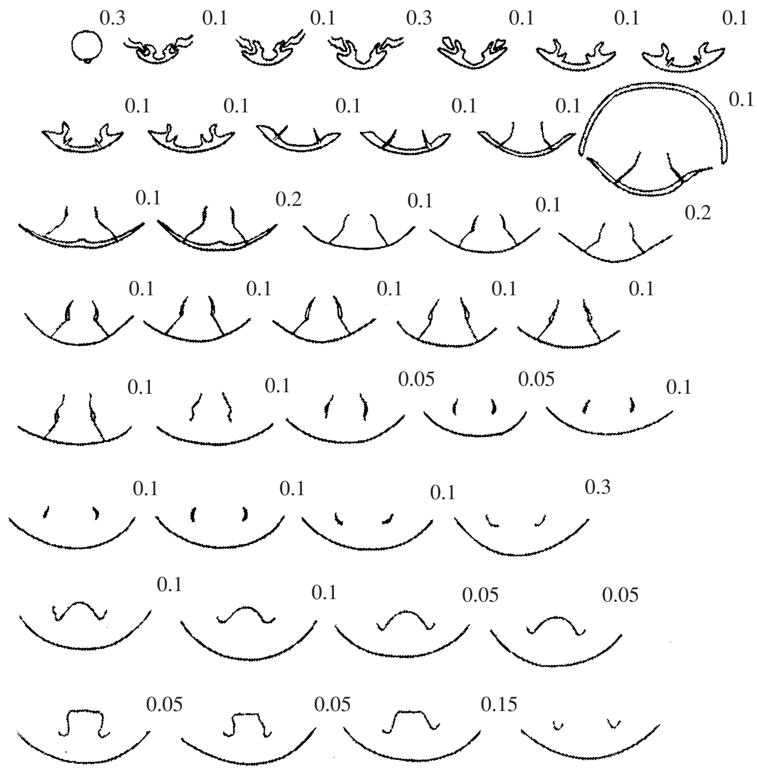

Fig. 72. *Heterelasmina latesinuata* (Licharew, 2002); specimen PIN, no. 4104/1011, serial cross sections; figures indicate distances between the sections in mm.

Tangi-Gor Gorge; Lower Permian, Bolorian, Safetdaron Formation.

D e s c r i p t i o n (Fig. 72). The shell is middle-sized, rounded regular pentagon shaped, almost isometric, and moderately biconvex. The maximum width and thickness are in the middle. The hinge line is slightly curved. The lateral commissures are steeply curved. The anterior commissure is regularly W-shaped. The ventral valve is convex in the middle and flattened near the margins. The sulcus is wide, extends from the umbo to the anterior margin, and slightly broadens anteriorly. The sulcus is bordered by two rounded folds with shallow grooves alongside. The umbo is curved, low, and wide. The umbonal keels are short and smooth. The apical angle is 83°–88°. The foramen is small and submesothyrid. The dorsal valve is rooflike, with flattened lateral sides. Three sharpened folds, separated by grooves, are well-pronounced in the anterior third of the shell. Shallow hollows are located alongside the grooves and transform into slightly concave surfaces.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.		L	W	T	W/L	T/L
Holotype	42/340	17.0	15.5	9.5	0.91	0.56
	4104/900	15.9	14.6	8.8	0.92	0.55
	4104/902	15.0	13.4	9.5	0.89	0.63
	4104/903	15.0	12.3	8.7	0.82	0.58
	4104/904	14.8	12.6	9.0	0.85	0.61

S h e l l i n t e r i o r. The pedicle collar is unknown. The teeth are narrow and rounded. The outer hinge plates are short and narrow. The crural plates are inclined to each other at almost a right angle and connected with the valve bottom for a considerable distance. The crural processes are long, convex toward the lateral sides of the valve, and separated in relief from the crural bases. The loop branches are narrow, short, and laterally convex. The transverse band of the loop is low, widely arched, and trapezoidal anteriorly.

C o m p a r i s o n. This species differs from *H. planoventris* (Licharew, 2002) in the rounded pentagonal shell, less convex valves, less curved umbo, flattened lateral sides, absence of the pedicle collar, better pronounced outer hinge plates, less curved crural processes, laterally convex loop branches, and in the shape of the transverse band of the loop.

M a t e r i a l. Twenty-eight complete specimens and 18 damaged specimens from the left bank of the Zidadara River.

Heterelasmina costata Smirnova, sp. nov.

Plate 5, fig. 5

E t y m o l o g y. From the Latin *costa* (rib).

H o l o t y p e. PIN, no. 4104/1079, complete shell; Tajikistan, southwestern Darvaz, left bank of the Zidadara River; Upper Permian, Gundara Formation.

D e s c r i p t i o n. The shell is ovally elongate, moderately to strongly convex. The anterior margin is straight. Four folds are located on the dorsal valve and three folds are located on the ventral valve. The ventral valve is more convex than the dorsal one. The sulcus extends along the full length of the ventral valve. The lateral sides of the shell are rounded. The hinge line is short and slightly curved. The lateral commissures are almost straight. The anterior commissure is trapezoidal and notched anteriorly. The maximum width is in the anterior third of the shell. The maximum thickness is in the middle. The ventral valve is strongly and uniformly convex. The sulcus is deep, narrow, and slightly broadens anteriorly. Three folds are present: one narrow fold in the middle of the sulcus and two higher, rounded folds on each side of the sulcus. All folds extend in the anterior two-thirds of the shell. The umbo is narrow, high, and curved. The umbonal keels are short and rounded. The apical angle is 75°. The foramen is large, round, and submesothyrid. The dorsal valve is moderately and uniformly convex. The elevation is weakly developed and bordered by two low folds. Two low, well-pronounced folds are developed in the middle of the elevation. All folds extend from the midlength of the valve up to the anterior margin. The lateral surfaces of the valve are moderately convex.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.		L	W	T	W/L	T/L
Holotype	4104/1079	15.3	10.5	8.5	0.68	0.55

C o m p a r i s o n. The new species differs from *H. cuboides* Licharew in Smirnova, 2001, *H. planoventris* Licharew, 2002, and *H. latesinuata* Licharew, 2002 in the shell outline, moderately convex dorsal valve, straight lateral commissures, and in the presence of four folds on the dorsal valve and four folds on the ventral valve. It differs from *H. regularis* Smirnova et Grunt, 2003 in the number of folds on the valves, the type of the anterior and lateral commissures, the location of the maximum width, and in the more convex ventral valve.

M a t e r i a l. One complete shell from the type locality.

Genus *Gundarolasmina* Smirnova et Grunt, 2003

Gundarolasmina: Smirnova and Grunt, 2003a, pp. 24 and 25.

T y p e s p e c i e s. *Gundarolasmina gundarensis* Smirnova et Grunt, 2003.

D i a g n o s i s. Shell middle-sized, ovally elongate, ovally pentagonal, elongated pyriform, smooth or with one axial fold and widely uniplicate anterior commissure. Umbo narrow. Pedicle collar present or absent. Outer hinge plates separated, narrow, and short. Crural plates rest on the bottom of the dorsal valve for a considerable distance. Vinculum between crural processes present or absent, making the loop ring-shaped when present. Loop branches not differentiated, forming a single structure with crural plates and crural bases. Loop length about one-third of the dorsal valve length. Loop flanks usually long.

S p e c i e s c o m p o s i t i o n. Type species, *G. ordinata* Smirnova et Grunt, 2003 from the Gundara Formation (Upper Permian) of the southwestern Darvaz, *G. acutangulum* (Waagen, 1882) from the Murgabian and Midian stages of Pakistan, *G. itaitubense* (Derby, 1874) from the Murgabian Stage (Upper Permian) of northern China, and *G. schucherti* (Licharew, 1956) from the Urushten Horizon (Upper Permian) of Northern Caucasia.

C o m p a r i s o n. This genus differs from *Heterelasmina* Licharew, 1939 in the larger shell, character of the valves curvature, narrow umbo, not differentiated loop branches, and in the widely spaced crural bases resting on the bottom of the dorsal valve. It differs from *Permicola* Koczyrkewicz, 1976 and *Amurothyris* Koczyrkewicz, 1976 in the smooth shell, presence of the outer hinge plates, crural plates resting on the bottom of the valve for a long distance, and in the presence of a vinculum between the crural processes.

Gundarolasmina gundarensis Smirnova et Grunt, 2003

Plate 5, fig. 6

Gundarolasmina gundarensis: Smirnova and Grunt, 2003a, p. 25, text-figs. 1a–1d, and 2.

H o l o t y p e. PIN, no. 4104/619, complete shell; southwestern Darvaz, right bank of the Gundara River; Upper Permian, Gundara Formation.

D e s c r i p t i o n (Fig. 73). The shell is middle-sized to large, elongated pyriform, and moderately biconvex. The maximum width is in the anterior third of the shell. The maximum thickness is in the posterior third of the shell. The hinge line is curved almost at a right angle. The lateral commissures are arched in the anterior half of the shell. The anterior commissure is widely uniplicate and dorsally curved. The anterior margin is wide and uniplicate. The ventral valve is more convex than the dorsal one, not plicate, and moderately and uniformly convex, with maximum convexity in the umbonal region. The umbo is narrow. The umbonal keels are smooth. The apical angle is 66°–73°. The foramen is unknown. The dorsal valve is strongly convex in the umbonal region, with flattened lateral and anterior sides. A poorly pronounced elevation is located in the anterior region of the valve.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.		L	W	T	W/L	T/L
Holotype	4104/619	23.3	15.6	10.0	0.67	0.43
	4104/620	21.0	12.3	9.5	0.59	0.45
	4104/621	19.3	13.3	9.5	0.67	0.49

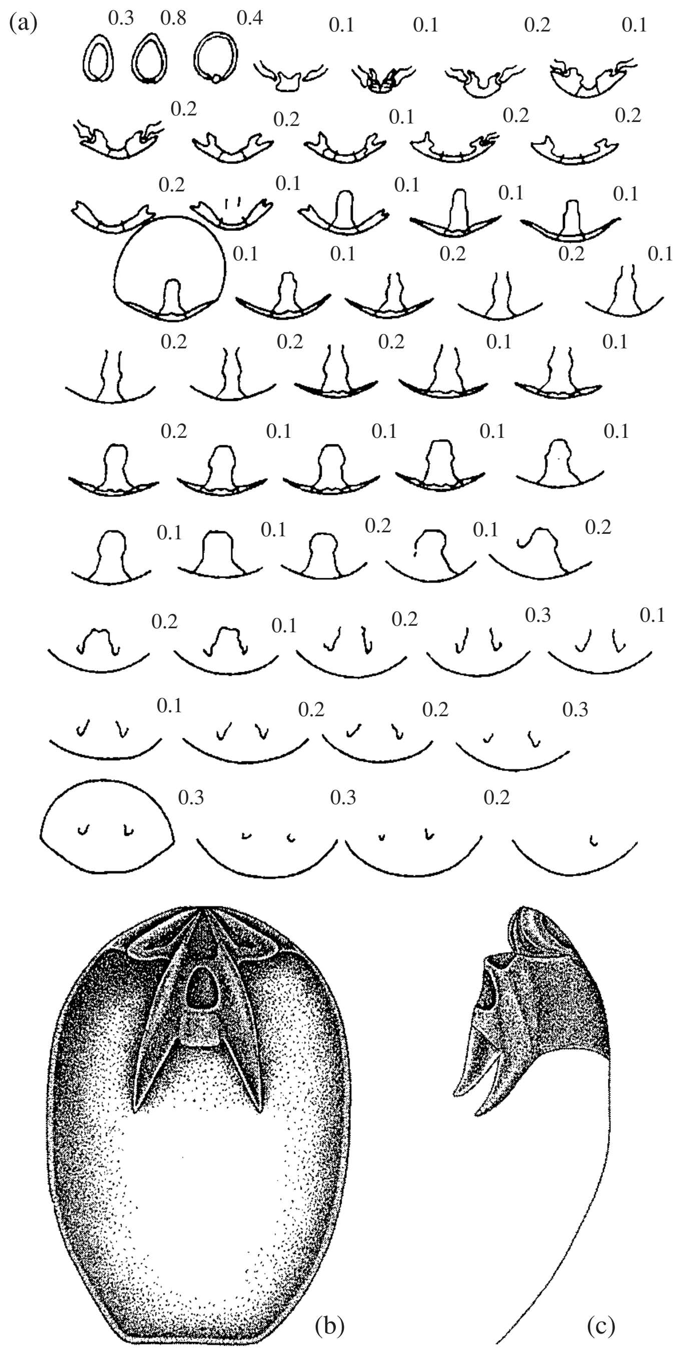

Fig. 73. *Gundarolasmina gundarensis* Smirnova et Grunt, 2003; specimen PIN, no. 4104/622: (a) serial cross sections; figures indicate distances between the sections in mm; reconstruction of the internal structures: (b) ventral valve and (c) lateral view.

Shell interior. The pedicle collar is absent. The teeth are narrow, tongue-shaped, and bear a small additional denticle. The outer hinge plates are narrow, short, inclined to the plane of symmetry, and slightly separated in relief from the inner socket ridges. The crural plates are well-pronounced, low, inclined to the plane of symmetry at an angle of 30°, and penetrate into the valve wall. The crural processes are long, curved, and connected by a thin vinculum that makes the loop ring-shaped. Anteriorly the crural plates remain connected with the crural processes for a considerable distance even after the rounded trapezoidal transverse band of the loop appears. The loop branches are not differentiated. The loop flanks are long and angularly curved in cross section. The flanks length is about one-third of the loop length. The loop length is one-third of the dorsal valve length. The transverse band of the loop is wide and rounded trapezoidal in section.

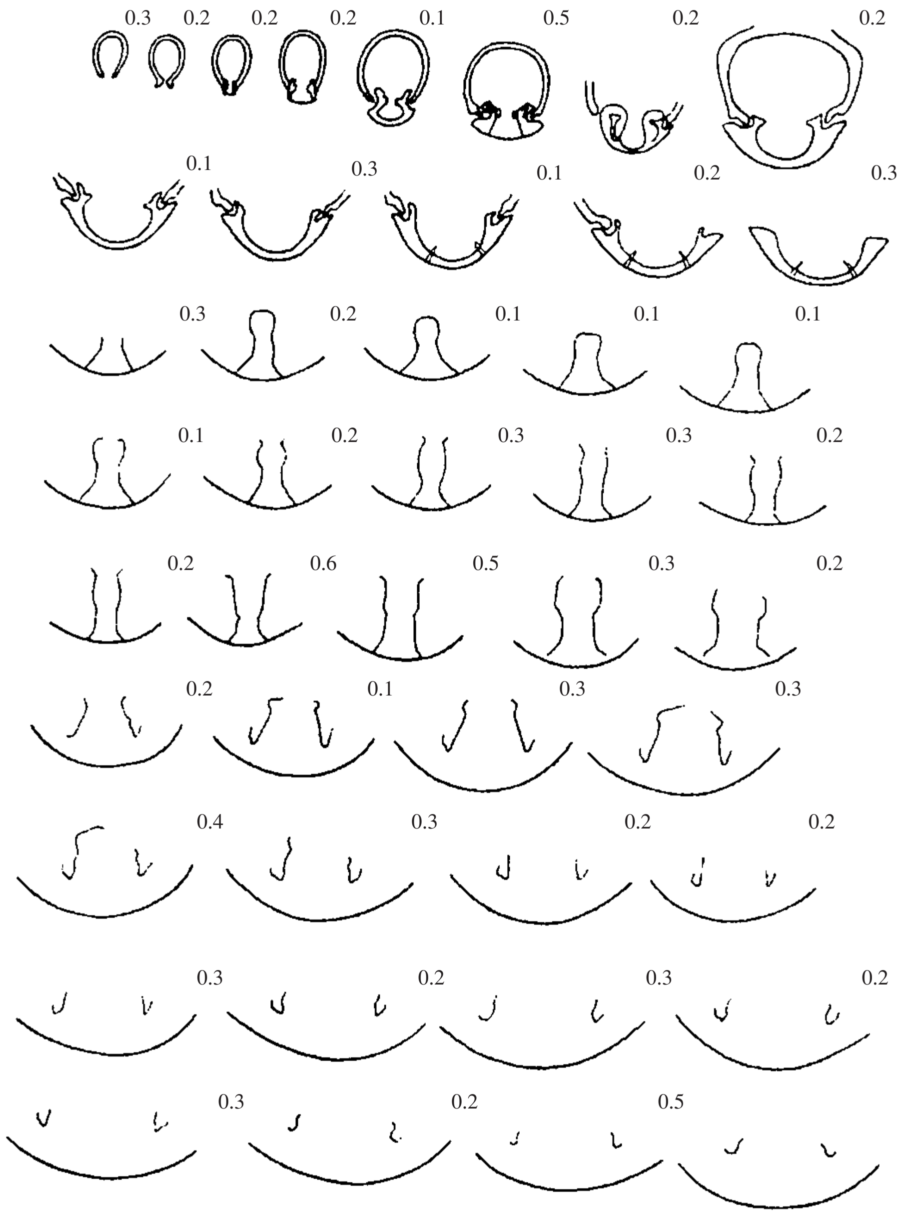

Fig. 74. *Gundarolasmina ordinata* Smirnova et Grunt, 2003; specimen PIN, no. 4104/626, serial cross sections; figures indicate distances between the sections in mm.

C o m p a r i s o n. This species differs from *G. acutangulum* (Waagen, 1882) in the uniplicate anterior margin, location of the maximum width and thickness, non-equiconvex valves, uniformly convex ventral valve, smaller apical angle, presence of the elevation on the dorsal valve, and in the presence of outer hinge plates.

M a t e r i a l. Four well-preserved specimens from the type locality.

Gundarolasmina ordinata Smirnova et Grunt, 2003

Plate 5, fig. 7

Gundarolasmina ordinata: Smirnova and Grunt, 2003a, pp. 25–28, text-figs. 1e–1h, and 3.

H o l o t y p e. PIN, no. 4104/623, complete shell; southwestern Darvaz, headstream of the Gundara River; Upper Permian, Gundara Formation.

D e s c r i p t i o n (Fig. 74). The shell is middle-sized, oval or ovally pentagonal, moderately biconvex, and equiconvex. The maximum width is in the middle. The maximum thickness is slightly shifted to the umbo. The hinge line is strongly curved. The anterior margin is rounded. The lateral commissures are gently arched. The anterior commissure is widely rounded, slightly dorsally curved, and straightened in the middle. The lateral sides are flattened. The ventral valve is smooth, strongly convex in the umbonal region, and moderately convex in the anterior half. The umbo is low, moder-

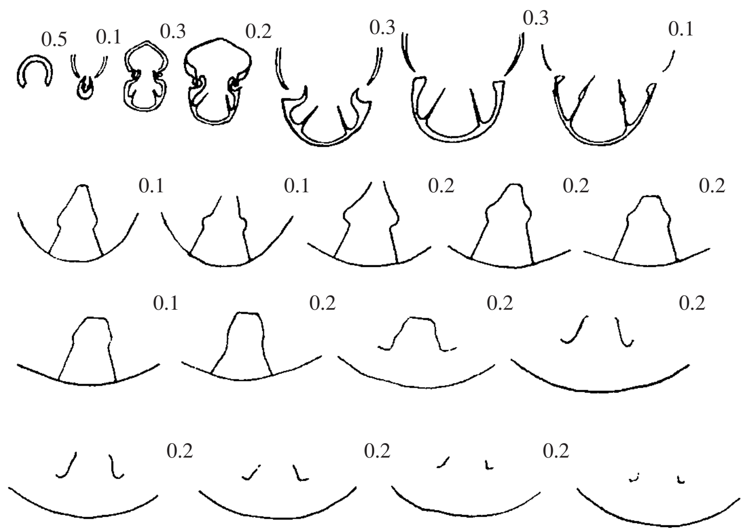

Fig. 75. *Gundarolasmina schucherti* (Licharew, 1956); specimen PIN, no. 4918/62, serial cross sections; figures indicate distances between the sections in mm.

ately curved, and bordered by smooth umbonal keels. The apical angle is 70°–75°. The foramen is small, oval, and submesothyrid. The dorsal valve has flattened lateral sides and bears low elevation extending along the full length of the valve.

D i m e n s i o n s i n m m a n d r a t i o s:

	Specimen, no.	L	W	T	W/L	T/L
Holotype	4104/623	22.2	16.3	11.0	0.73	0.49
	4104/622	24.3	15.5	11.0	0.64	0.45
	4104/624	18.3	13.3	9.2	0.72	0.51

S h e l l i n t e r i o r. The pedicle collar is absent. The teeth are narrow, enter the sockets obliquely, and bear a small denticle. The outer hinge plates are narrow, widely spaced, observed for a short distance, distinctly separated from the steeply inclined inner socket ridges, and have a horizontal surface. High crural plates are inclined to the plane of symmetry at an angle of 30°. The crural processes are long and are connected to form a ring-shaped loop. The crural plates are fused with the crural processes along the full length. The loop is supported by this structure until the transverse band appears. The transverse band is widely trapezoidal. The flanks of the loop are long. The flanks length is one-third of the loop length. The loop length is one-third of the dorsal valve length.

C o m p a r i s o n. This species differs from *G. gundarensis* Smirnova et Grunt, 2003 in the wider shell, maximum width located in the middle, equiconvex valves, and in the higher crural plates. It differs from *G. schucherti* (Licharew, 1956) in the equiconvex valves, absence of the sulcus on the ventral valve, smaller apical angle, lower crural plates, and in the presence of outer hinge plates.

O c c u r r e n c e. Upper Permian, Gundara Formation; southwestern Darvaz.

M a t e r i a l. Two complete shells from the Gundara River basin, at height 3661.0 m, and 4 complete shells from the headstream of the Gundara River.

Gundarolasmina schucherti (Licharew, 1956)

Plate 5, fig. 8

Heterelasmina schucherti: Licharew, 1956, pp. 68–70, pl. 14, figs. 8–11, text-fig. 15.

H o l o t y p e. TsNIGR Museum, no. 2002/2139, complete shell; Northern Caucasia, 4 km from the mouth of the Urushten River, Armovka ravine; Upper Permian, Urushten Horizon.

D e s c r i p t i o n (Fig. 75). The shell is ovally elongate, an with obtuse anterior margin. The sulcus is deep, wide, and extends along the full length of the ventral valve. The anterior commissure is arched or slightly straightened. The lateral commissures are steeply arched. The anterior margin is flattened. The hinge line is long and strongly curved. The maximum width and thickness of the shell are in the middle. The ventral valve is concave along the full length. The sulcus remains equally wide and deep along the full length of the ventral valve and flattens in the anterior region of the valve. The lateral margins of the valve are parallel and sharpened. The umbo is very small and low. The foramen is spotlike. The false area is shaped like a narrow band. The apical angle is 100°–110°. The dorsal valve is curved rooflike along the full length and steeply arched in cross section. The lateral surfaces of the valve are wide and subparallel.

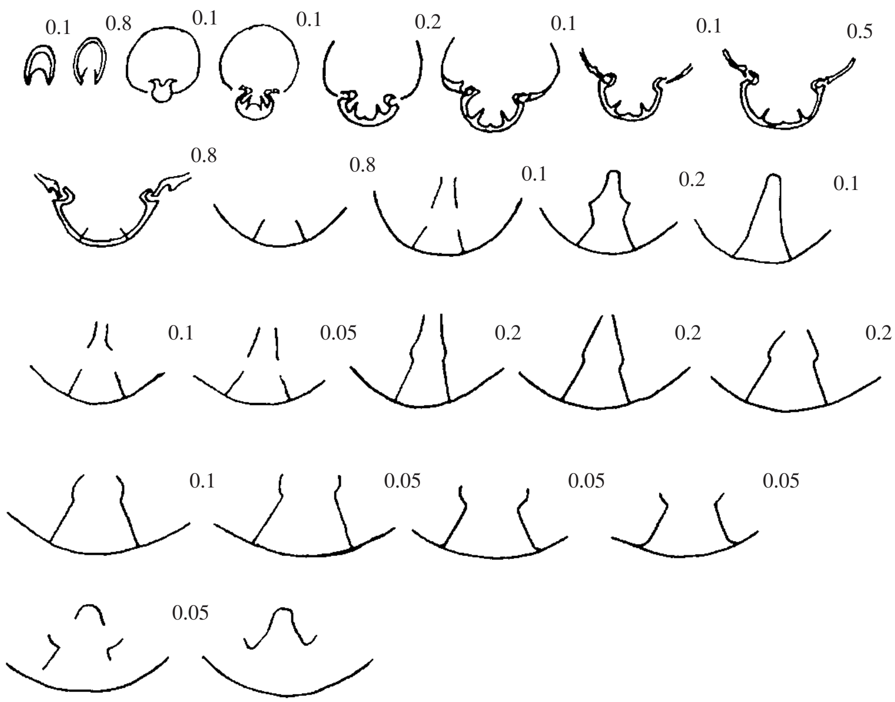

Fig. 76. *Gundarolasmina itaitubense* (Derby, 1874); specimen PIN, no. 5133/30, serial cross sections; figures indicate distances between the sections in mm.

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

Specimen, no.	L	W	T	W/L	T/L
4918/57	18.8	13.7	10.0	0.73	0.53
4918/60	17.0	12.0	9.0	0.70	0.53
4918/61	13.0	8.8	6.0	0.61	0.46

S h e l l i n t e r i o r. The pedicle collar is absent. The outer and inner hinge plates are undeveloped. The inner socket ridges are high. The crural plates are high, long, and remote from the inner socket ridges. The crural processes deviate from the crural plates and connect to form a thin vinculum. The joined crural plates and crural processes are traced for a considerable distance. A second vinculum, a transverse band of the loop, appears anteriorly and is trapezoidal in cross section. The loop flanks are long. The loop length is one-third of the dorsal valve length.

C o m p a r i s o n. This species differs from *G. gundarensis* Smirnova et Grunt, 2003 and *G. ordinata* Smirnova et Grunt, 2003 in the deep and wide sulcus extending along the full length of the ventral valve, more convex dorsal valve, parallel lateral margins of the shell, larger apical angle, absence of the outer hinge plates, and in the long crural plates.

R e m a r k s. Licharew established *Heterelasmina schucherti* in 1956 as the type species of *Heterelasmina.* However, while establishing the genus *Heterelasmina* in 1939, Licharew listed the species *Heterelasmina dieneri* (Gemmellaro, 1899) first, making that species the type species of *Heterelasmina.* We studied the internal structure of *H. schucherti* and found it to differ considerably from that of *H. dieneri* in the long and complicated loop. This species cannot be referred to *Heterelasmina* and has characteristic features of the genus *Gundarolasmina.*

M a t e r i a l. Two complete shells and two shells with broken margins from Mt. Yatyrgvarta, near the frontier post of Chernaya Rechka.

Gundarolasmina itaitubense (Derby, 1874)

Plate 5, fig. 9

Dielasma itaitubense: Derby, 1874, p. 1, pl. 2, figs. 1, 3, 8, and 16; pl. 3, fig. 24; Waagen, 1882, pp. 348 and 349, pl. 26, fig. 5; Netschajew, 1911, p. 113, pl. 15, fig. 8.

L e c t o t y p e. Specimen figured by Derby (1874, pl. 2, fig. 1) from the limestones near Itaituba, Tapajós River basin, tributary of the Amazon River, northern Brazil (depository of specimen unknown).

D e s c r i p t i o n (Fig. 76). The shell is ovally elongate and equiconvex. The anterior margin is stretched and uniplicate. The sulcus on the ventral valve and the elevation on the dorsal valve are poorly developed. The anterior commissure is narrowly arched. The lateral commissures are gently arched. The lateral sides are flattened. The hinge line is short and slightly curved. The maximum width and thickness are in the middle of the shell. The ventral valve is moderately convex in the umbonal region and flattened in the anterior half. The sulcus is shallow and is located near the anterior mar-

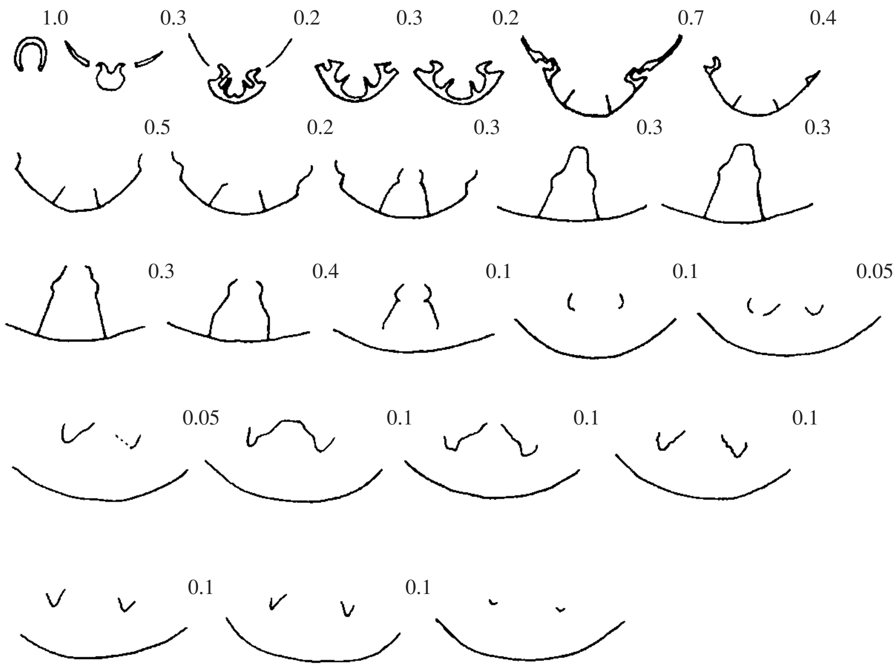

Fig. 77. *Gundarolasmina acutangulum* (Waagen, 1882); specimen PIN, no. 5133/37, serial cross sections; figures indicate distances between the sections in mm.

gin. The umbo is strongly curved and overhangs the dorsal valve. The umbonal keels are absent. The foramen is small. The apical angle is 75°. The dorsal valve is convex along the full length. The elevation is high. The valve is arched in cross section. The anterior margin forms a linguiform extension.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
5133/28	20.5	15.2	9.2	0.74	0.45
5133/29	18.5	14.0	8.0	0.76	0.43
5133/30	18.2	11.3	9.5	0.62	0.52

Shell interior. The pedicle collar is deeply arched and steeply curved. The inner socket ridges are high. The outer and inner hinge plates are absent. The crural plates are high and extend from the apical region to the end of the loop. The crural processes connect to form a thin vinculum. The crural plates and crural bases form a single structure. The loop branches are not differentiated. The transverse band of the loop is narrowly arched and located in the anterior part of the loop. The loop flanks are short. The loop length is about one-third of the dorsal valve length.

Comparison. This species differs from *G. gundarensis* Smirnova et Grunt, 2003 in the narrower shell, narrow and elongated anterior margin, presence of the pedicle collar, short loop flanks, absence of the outer hinge plates, and in the narrowly arched transverse band of the loop. It differs from *G. ordinata* Smirnova et Grunt, 2003 in the ovally elongate shell, narrow and uniplicate anterior margin, presence of the pedicle collar, absence of the outer hinge plates, and in the short loop flanks.

Occurrence. Upper Permian(?) of Brazil; Upper Permian, Murgabian Stage of southwestern China.

Material. Two complete shells and one shell with a broken umbo from southwestern China, foothills of the Zonliang Ridge, Sichuan Province.

Gundarolasmina acutangulum (Waagen, 1882)

Plate 5, fig. 10

Dielasma acutangulum: Waagen, 1882, pp. 355 and 356, pl. 26, figs. 1 and 2; pl. 25, fig. 7.

Lectotype. Specimen figured by Waagen (1882, pl. 26, fig. 1) from northern China (Inner Mongolia), Zhesi Hongor; Upper Permian, Murgabian.

Description (Fig. 77). The shell is oval, strongly elongated, and equiconvex, or the ventral valve may be slightly more convex than the dorsal one. The anterior margin is biplicate. The maximum width and thickness are in the middle. The anterior commissure is roundly biplicate. The lateral commissures are straight to arched. The ventral valve bears rooflike elevation extending from the umbo to the anterior margin. More rarely the valve surface is uniformly convex. The elevation is bordered by two shallow hollows. The lateral sides of the valve are flattened. The umbo is short, slightly curved, and pointed. The umbonal keels are smooth. The foramen is round and small. The apical angle is 78°–85°. The dorsal valve is strongly convex in the umbonal region and flattened in the anterior half. The sulcus is well-pronounced, shallow, located in the anterior third of the shell, and bordered by two low, sharpened folds. Wide and weakly pronounced hollows are located on the lateral sides in the anterior half of the valve.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
5133/32	24.7	16.2	11.0	0.65	0.45
5133/33	22.5	15.5	10.8	0.68	0.48
5133/34	22.0	13.6	11.3	0.62	0.51
5133/35	18.7	13.0	9.8	0.69	0.52
5133/36	17.3	12.0	8.2	0.68	0.47

Shell interior. The pedicle collar is absent. The inner and outer hinge plates are absent. The crural plates are low, appear in the apical region, and run up to the midlength of the dorsal valve, where they become higher. The inner socket ridges are strongly curved. The crural processes deviate from the crural plates. The ventral tips of crural processes fuse to form a thin transverse vinculum. The descending branches of the loop are not differentiated. The transverse band of the loop is arched and forms after the crural plates disappear. The loop flanks are long. The loop length is about one-half of the dorsal valve length.

Comparison. This species differs from *G. schucherti* (Licharew, 1956) in the biplicate anterior margin, equiconvex shell, smaller apical angle, flattened lateral sides of the shell, low crural plates, and in the arched transverse band of the loop.

Occurrence. Three complete shells and three specimens with broken margins from the foothills of the Zonliang Ridge, Sichuan Province, southwestern China.

Superfamily Loboidothyridoidea Makridin, 1964

[Nom. transl. Dagys, 1968 (ex Loboidothyrinae Makridin, 1964)].
Loboidothyridacea: Dagys, 1974, p. 198.

Diagnosis. Dental plates and crural plates absent. Outer hinge plates well-developed. Inner hinge plates present or absent. Adult loop relatively long, often with projecting flanks. Brachidium development based on secondary elements and characterized by centronelloid, quasicampagiform, campagiform, and dictiothyridiform stages.

Occurrence. Upper Permian–Cretaceous.

Composition. Loboidothyrididae Makridin, 1964; Dictiothyrididae Makridin, 1964; Boreiothyrididae Dagys, 1968; and Pseudodielasmatidae Cooper et Grant, 1976.

Family Pseudodielasmatidae Cooper et Grant, 1976

Pseudodielasmatidae: Cooper et Grant, 1976, p. 2910.

Diagnosis. Shell small and almost equiconvex, with plicate anterior margin. Outer hinge plate separated. Inner hinge plate absent. Crural bases located on the outer hinge plate. Loop short, triangular, and terebratuloid.

Composition. *Pseudodielasma* Brill, 1940; *Pleurolasma* Cooper et Grant, 1976; *Levenolasma* Smirnova et Grunt, 2003; and *Frederiksolasma* Smirnova, 2001.

Comparison. This family differs from the family Loboidothyrididae Makridin, 1964 in the short loop lacking long flanks and in the absence of cardinal process and inner hinge plates. It differs from Boreiothyrididae Dagys, 1968 in the small shell, plicate anterior margin, and in the absence of the inner hinge plate.

Remarks. Cooper and Grant (1976) established the family Pseudodielasmatidae in the superfamily Dielasmatoidea. Dagys (1974) noted a possible relationship between the Permian *Pseudodielasma* with Mesozoic terebratulids based on the disappearance of dental plates and inner hinge plates and the acquisition of the terebratuloid loop. Campbell (1965) attributed the absence of data on the ontogeny of the internal structures of Pseudodielasmatidae to the poor preservation of the material. We have abundant well-preserved shells of different ages from the collection of the Upper Permian terebratulids collected by Grunt in the northern Pamirs (southwestern Darvaz) and studied the ontogeny in the genus *Fredericksolasma* Smirnova, 2001 (Smirnova, 2001). We discovered a type of brachidium development that involves secondary elements, and which corresponds to that of the Mesozoic Loboidothyroidea. Dagys called this type loboidothyridid. This type of development considerably differs from the dielasmoid type (superfamily Dielasmatoidea), which is simple and lacks secondary elements. The family Pseudodielasmatidae may be regarded as the oldest group in the superfamily Loboidothyridoidea based on the similarity in the structure of cardinalium and adult brachidium and the identical ontogenetic changes. This group possibly gave rise to the large Mesozoic terebratulid taxa.

Genus *Fredericksolasma* Smirnova, 2001

Fredericksolasma: Smirnova, 2001, p. 38.

Type species. *Hemiptychina pseudoelongata* var. *lata* Licharew, 1939.

Diagnosis. Shell small or middle-sized and rounded or ovally elongate, with moderately convex valves. Shallow sulcus present or absent on the ventral valve. Anterior commissure uniplicate. Outer hinge plate separated and narrow. Inner hinge plate absent. Socket ridges high. Crural bases and hinge plate joined at almost a right angle. Loop triangular and short. Loop length less than one-third of the dorsal valve length. Transverse band of the loop widely trapezoidal or rounded triangular.

Species composition. Type species, *F. rhomboidale* Smirnova et Grunt, 2003 from the Chapsai Formation (Djulfian Stage, Upper Permian) of southwestern Darvaz, *F. darvasica* (Tschernyschew, 1914) from the Safetdaron Formation (Bolorian Stage, Lower Permian) of the southwestern Darvaz, *F. nummulus* (Waagen, 1882) and *F. sublaevis* (Waagen, 1882) from the Murgabian and Midian stages (Upper Permian) of Pakistan.

C o m p a r i s o n. This genus differs from *Pseudodielasma* Brill, 1940 and *Pleurolasma* Cooper et Grant, 1976 in the smooth and equiconvex shell, uniplicate anterior commissure, and in the presence of the outer hinge plate.

Fredericksolasma lata (Licharew, 1939)

Plate 5, figs. 11 and 12

Hemiptychina pseudoelongata var. *lata*: Licharew, 1939, p. 119, pl. 29, fig. 7.

Fredericksolasma lata: Smirnova, 2001, text-figs. 7–10.

H o l o t y p e. TsNIGR Museum, Tschernyschew's collection, no. 33/340; southwestern Darvaz, Gundara River; Upper Permian, Gundara Formation.

D e s c r i p t i o n (Fig. 20). The shell is small, rounded or rounded rectangular, more rarely ovally elongate, almost equiconvex, and lacks well-pronounced plication. The hinge line is long and strongly curved. The lateral commissures are slightly arched. The anterior commissure is dorsally arched and tongue-shaped. The maximum width is slightly shifted from the middle to the anterior margin. The maximum thickness is in the middle. The ventral valve is slightly convex both longitudinally and transversely and flattened in the anterior half. The anterior margin is stretched to form a linguiform extension. The umbo is wide, massive, and strongly curved. The umbonal keels are smooth and short. The false area is high and concave. The apical angle is 82°–92°. The foramen is small, circular, and submesothyrid. The dorsal valve is strongly convex in the middle, with flattened lateral sides. The middle elevation is weakly pronounced in the anterior third of the valve.

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

Specimen, no.	L	W	T	W/L	T/L
4104/9	16.5	14.5	9.6	0.88	0.58
4104/10	16.5	14.8	9.6	0.89	0.58
4104/11	15.6	13.4	8.9	0.86	0.57
4104/12	15.9	13.1	8.3	0.82	0.52
4104/13	15.1	13.8	7.9	0.85	0.52

S h e l l i n t e r i o r. A pedicle collar may be present. The teeth bear an additional denticle on the outer side and a ridgelike elevation on the inner side. The outer hinge plate is shaped like two narrow, almost horizontal surfaces that are distinctly separated from the inner socket ridges. The crural bases are located on the inner surface of the hinge plate and are almost perpendicular to the latter. The loop is short and narrow. The flanks are well-pronounced and slightly diverging. The loop branches are narrow. The transverse band of the loop is widely trapezoidal and curved in the middle.

C o m p a r i s o n. This species differs from *F. nummulus* (Waagen, 1882) in the equiconvex and smaller shell, larger apical angle, and curved lateral commissures. It differs from *F. sublaevis* (Waagen, 1882) in the wider and equiconvex shell and in the wide umbo.

O c c u r r e n c e. Upper Permian, Gundara Formation; southwestern Darvaz, Trans-Alay Range.

M a t e r i a l. Sixty-five well-preserved specimens and 56 specimens with broken margins from the Zidadara River basin, southwestern Darvaz; 122 well-preserved specimens and 63 damaged shells from the Kashkasu River basin, Trans-Alay Range.

Fredericksolasma rhomboidale Smirnova et Grunt, 2003

Plate 5, fig. 13

Hemiptychina (Beecheria) *pseudoelongata*: Tschernyschew, 1914, pp. 8 and 9, pl. 2, figs. 14–17.

Fredericksolasma rhomboidale: Smirnova and Grunt, 2003b, p. 35, text-figs. 1i-1n, and 3.

H o l o t y p e. PIN, no. 4104/361, complete shell; southwestern Darvaz, Gundara River; Upper Permian, Djulfian, Chapsai Formation.

D e s c r i p t i o n (Fig. 78). The shell is middle-sized, ovally rhombic, longitudinally elongated, moderately biconvex, and equiconvex. The maximum width is in the anterior half of the shell. The maximum thickness is in the middle or is slightly shifted posteriorly. The hinge line is curved at a right angle. The anterior margin is flattened. The lateral commissures are straight to slightly curved near the anterior margin. The anterior commissure forms a narrow, well-pronounced, and dorsally directed linguiform extension. The ventral valve is uniformly curved along the full length and not plicate. The umbo is high, narrow, and moderately curved. The umbonal keels are smooth. The false area is slightly concave. The apical angle is 70°–80°. The foramen is small, rounded, and submesothyrid. The elevation on the dorsal valve is well-pronounced in the middle and may be bordered by small depressions. The lateral sides of the valve are convex.

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

Specimen, no.		L	W	T	W/L	T/L
Holotype	4104/341	16.5	13.0	7.9	0.79	0.48
	4104/502	17.5	13.9	7.9	0.74	0.45
	4104/372	16.4	11.4	8.3	0.69	0.50
	4104/405	16.0	11.0	7.5	0.68	0.47
	4104/406	14.6	10.0	6.4	0.67	0.43

S h e l l i n t e r i o r. The pedicle collar is absent. The teeth are narrow, pointed, and bear additional denticle. The socket ridges are low. The outer hinge plates are shaped like narrow surfaces inclined to the plane of symmetry. The crural bases are ventrally directed and

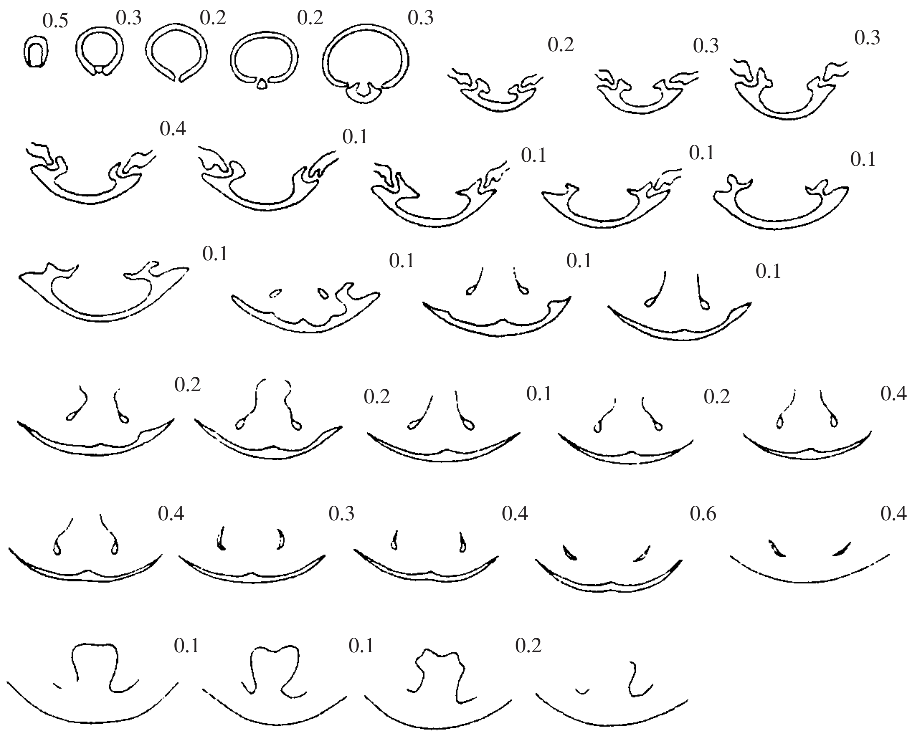

Fig. 78. *Fredericksolasma rhomboidale* Smirnova et Grunt, 2003; specimen PIN, no. 4104/365, serial cross sections; figures indicate distances between the sections in mm.

join the outer hinge plates at an angle of 110°. The crural processes are well-pronounced and laterally curved. The loop branches are short. The transverse band of the loop is roundly trapezoidal and curved in the middle. The loop is laterally compressed at the junction of the descending branches and the transverse band. The loop length is about one-third of the dorsal valve length.

Comparison. This species differs from *F. lata* (Licharew, 1939) in the narrower and elongated shell with a typical ovally rhombic outline, better pronounced elevation on the dorsal valve, smaller apical angle, less curved umbo, absence of the pedicle collar, lower socket ridges, and in the well-pronounced crural processes.

Material. Seventy complete specimens and 150 damaged specimens from the type locality.

Fredericksolasma darvasica (Tschernyschew, 1914)

Plate 5, fig. 14

Dielasma darvasicum: Tschernyschew, 1914, p. 6, pl. 2, figs. 5–7.

Fredericksolasma darvasica: Smirnova and Grunt, 2003b, pp. 36 and 37, text-figs. 1o–1r, and 4.

Lectotype. TsNIGR Museum, no. 23/340, complete shell; southwestern Darvaz, kishlak of Safedaron, Tangi-Gor Gorge; Lower Permian, Bolorian, Safedaron Formation.

Description (Fig. 79). The shell is middle-sized, almost equiconvex, longitudinally elongated, pyriform or rounded pentagonal, and moderately convex. The maximum width is in the middle. The maximum thickness is shifted to the umbo. The lateral surfaces are flattened. The hinge line is long and strongly curved. The lateral commissures are steeply arched. The anterior commissure is dorsally curved, straightened, or arched. The anterior margin is widely arched in cross section. The ventral valve is moderately and uniformly curved. The sulcus is sharply pronounced, widely arched in cross section, extends from the middle of the valve, and broadens towards the anterior margin, where its bottom becomes flattened. The anterior margin may be stretched to form a linguiform extension. The umbo is low, wide, strongly curved, and overhang the dorsal valve. The umbonal keels are rounded. The apical angle is 78°–80°. The false area is low and slightly concave. The dorsal valve is usually strongly convex posteriorly, more rarely along the full length. In the latter case it is rooflike with steep lateral sides in cross section. A low, rounded elevation is located in the anterior third of the shell.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
4104/329	20.4	14.9	9.7	0.73	0.47
4104/327	19.1	12.8	8.6	0.67	0.45
4104/328	15.5	10.5	5.4	0.68	0.35
4104/330	11.8	9.2	3.5	0.78	0.30

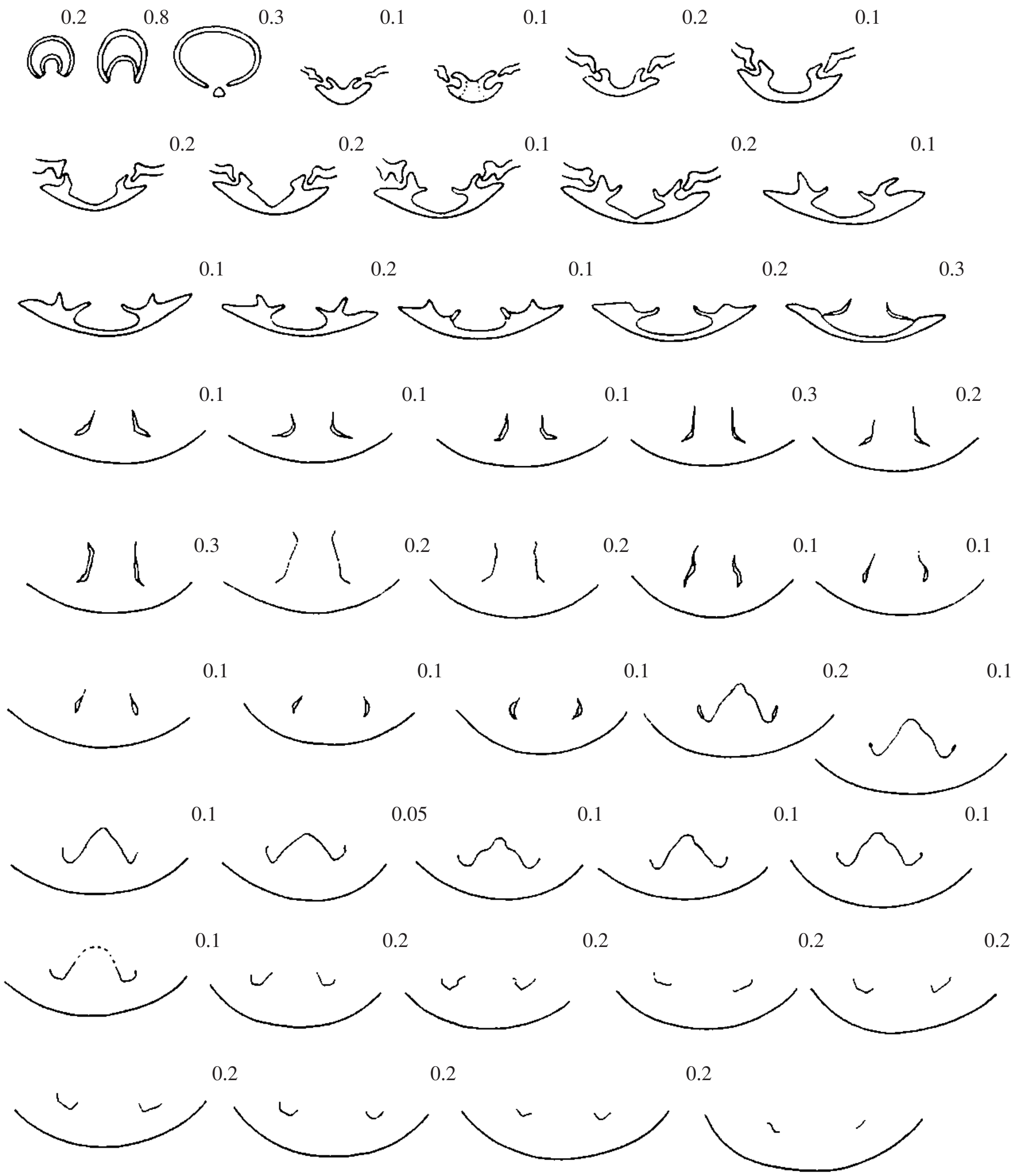

Fig. 79. *Fredericksolasma darvasica* (Tschernyschew, 1914); specimen PIN, no. 4104/127, serial cross sections; figures indicate distances between the sections in mm.

Shell interior. The pedicle collar is deeply arched. The teeth are narrow, wedge-shaped, and bear an additional lateral denticle. The outer hinge plates are concave and indistinctly separated from the low socket ridges. The crural bases are shaped like well-pronounced plates inclined to the plane of symmetry at an angle about 45°. The crural processes are wide and subparallel, with slightly diverging ventral tips. The loop branches are short. The transverse band of the loop is rounded triangular. The loop flanks are long. The loop length is less than one-third of the dorsal valve length.

Comparison. This species differs from *F. lata* (Licharew, 1939) in the elongated shell, presence of the sulcus on the ventral valve, steeply curved lateral commissures, smaller apical angle, low false area, well-pronounced pedicle collar, direction of the crural bases, presence of a well-developed outer hinge plate, wide crural processes, and in the rounded triangular transverse band of the loop. It differs from *F. rhomboidale* Smirnova, Grunt, 2003 in the shape of the shell, widely arched anterior margin, steeply curved lateral commissures, presence of the sulcus on the ventral valve, presence of the pedicle collar, and in the rounded triangular transverse band of the loop.

Remarks. This species has not been restudied since it was established by Tschernyschew (1914).

Tschernyschew did not describe it and only compared it with other species of the genus *Dielasma.* Some morphological features of the species can be revealed from the comparison: "… differing in the relative length of the young and larger specimens" and "… presence of the sharply pronounced longitudinal depression on the dorsal valve." We described in detail the shell exterior and interior in this species. The species is referred to the genus *Fredericksolasma* based on the analysis of series of cross sections.

Material. Eight complete shells and three shells with broken margins from the type locality.

Genus *Levenolasma* Smirnova et Grunt, 2003

Levenolasma: Smirnova and Grunt, 2003b, p. 33.

Type species. *L. concava* Smirnova et Grunt, 2003.

Diagnosis. Shell middle-sized or large and ovally elongate or rounded pentagonal, with flattened ventral and rooflike dorsal valves. Anterior commissure uniplicate with few small folds. Sulcus extending along the full length of the ventral valve. Outer hinge plates separated and parallel to the bottom of the dorsal valve. Crural bases shaped like small projections. Inner hinge plate absent. Crural processes fused to form high transverse band. Loop short. Loop branches not differentiated.

Species composition. Type species; *L. leveni* Smirnova et Grunt, 2003 and *L. sinuosa* sp. nov. from the Gundara Formation (Upper Permian) of the southwestern Darvaz, *L. nikitini* (Gemmellaro, 1899) from the uppermost Kubergandian–lowermost Murgabian of Sicily, and *L. mongolica* sp. nov. from the Midian Stage (Upper Permian) of northern China (Inner Mongolia).

Comparison. This genus differs from *Pleurolasma* Cooper, 1976 in the larger shell, flattened ventral valve, fused crural processes, and short loop. It differs from *Pseudodielasma* Brill, 1940 in the larger shell, absence of the inner hinge plate, and in the transverse band of the loop formed by the fusion of the crural processes.

Levenolasma concava Smirnova et Grunt, 2003

Plate 5, fig. 15

Levenolasma concava: Smirnova and Grunt, 2003b, pp. 33 and 34, text-figs. 1a–1d, and 2.

Holotype. PIN, no. 4104/283, complete shell; southwestern Darvaz, Zidadara River; Upper Permian, Gundara Formation.

Description (Fig. 80). The shell is middle-sized, ovally pentagonal, longitudinally elongated, and moderately biconvex. The maximum width is in the posterior third of the shell. The maximum thickness is in the middle. The hinge line is slightly curved. The lateral commissures are semicircular. The anterior commissure is narrowly arched with a small, weakly pronounced, dorsally directed bend in the middle. The anterior margin is narrow and rounded. The ventral valve is strongly curved. The sulcus is wide, gently sloping, starts from the umbo, and deepens towards the anterior margin. The lateral sides are flattened. The umbo is low and wide. The umbonal keels are poorly pronounced. The apical angle is 95°–102°. The foramen is small and submesothyrid. The dorsal valve is rooflike, with steep slopes. The lateral surfaces are flattened and inclined to each other at an angle of 70°–75°. Three gentle, short folds are poorly developed near the anterior margin.

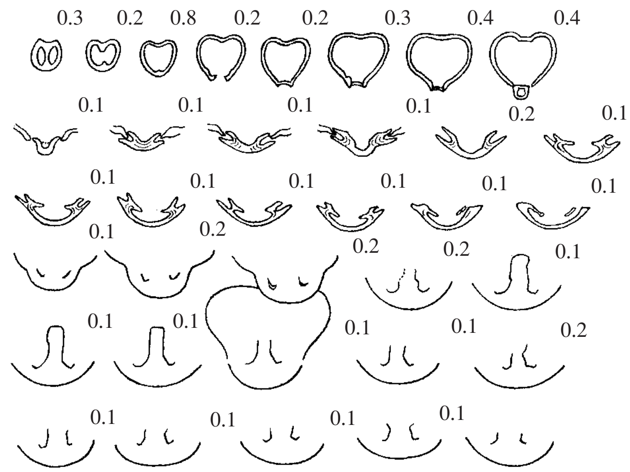

Fig. 80. *Levenolasma concava* Smirnova et Grunt, 2003; specimen PIN, no. 4104/1077, serial cross sections; figures indicate distances between the sections in mm.

Dimensions in mm and ratios:

Specimen, no.	L	W	T	W/L	T/L
Holotype 4104/283	19.3	13.7	9.6	0.71	0.49
4104/284	19.0	13.5	12.2	0.71	0.64

Shell interior. The pedicle collar is unknown. The teeth are narrow, pointed, and bear small additional denticles. The outer hinge plates have wide, flat surfaces that are inclined to the plane of symmetry at a sharp angle. The inner socket ridges are low and wide. The crural bases are small, ventrally directed projections on the inner margins of the hinge plate. The transverse band of the loop is formed by the fused crural processes and is rectangular in section. The loop branches are short. The loop flanks are long, wide, and subparallel.

Comparison. This species differs from *L. nikitini* (Gemmellaro, 1899) in the wider umbo, less convex dorsal valve, deeper sulcus of the ventral valve, and narrow and rounded anterior margin. It differs from *L. leveni* Smirnova et Grunt, 2003 in the smaller and rounded pentagonal shell, slightly curved hinge line, shape of the anterior commissure, wide sulcus on the ventral valve, and in the wide umbo.

Material. Holotype and one more specimen from the Gundara River basin.

***Levenolasma leveni* Smirnova et Grunt, 2003**

Plate 5, fig. 16

Levenolasma leveni: Smirnova and Grunt, 2003b, pp. 34 and 35, text-figs. 1e–1h.

H o l o t y p e. PIN, no. 4104/1083, complete shell; southwestern Darvaz, Zidadara River; Upper Permian, Gundara Formation.

D e s c r i p t i o n. The shell is large, narrowly oval, laterally compressed, strongly longitudinally elongated, and moderately biconvex. The anterior margin is narrow, elongated, and rounded. The maximum width is in the anterior third of the shell. The maximum thickness is in the middle. The hinge line is curved at a right angle. The lateral commissures are steeply arched. The anterior commissure is narrowly arched dorsally. The ventral valve is considerably less convex than the dorsal one. The sulcus is narrow, shallow, starts from the umbo, and slightly broadens anteriorly. The lateral margins of the ventral valve are steeply curved in the posterior half and flattened in the anterior half. The umbo is massive and strongly curved. The umbonal keels are rounded. The apical angle is 66°–70°. The foramen is unknown. The dorsal valve is rooflike, with steep slopes. The lateral sides are flattened and inclined to the axis at an angle of 75°.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.		L	W	T	W/L	T/L
Holotype	4104/1083	33.0	19.0	15.2	0.51	0.46
	4104/1084	39.3	20.0	18.5	0.57	0.47

C o m p a r i s o n. This species differs from all other *Levenolasma* species in the larger and narrowly oval shells, strongly curved hinge line, dorsally curved anterior commissure, and in the narrow and massive umbo.

M a t e r i a l. Two complete shells from the type locality.

***Levenolasma sinuosa* Smirnova, sp. nov.**

Plate 5, fig. 17

E t y m o l o g y. From the Latin *sinuosa* (sinuous).

H o l o t y p e. PIN, no. 4104/1076, complete shell; Tajikistan, southwestern Darvaz, right bank of the Gundara River; Upper Permian, Gundara Formation.

D e s c r i p t i o n. The shell is pyriform. The anterior margin is wide, arched, and bears two or three small folds. The dorsal valve is strongly convex. The hinge line is short and strongly curved. The lateral commissures are steeply arched. The anterior commissure is widely arched and finely plicate in the middle. The anterior margin is wide and flattened. The maximum width is in the anterior third of the shell. The maximum thickness is in the middle. The ventral valve is slightly convex in the umbonal region and flattened in the anterior half. The sulcus is shaped like a narrow groove, starts from the umbo, and broadens towards the anterior margin. Two poorly pronounced folds border the sulcus and are located in the anterior third of the shell. The lateral sides of the ventral valve are flattened anteriorly. The umbo is narrow, low, and curved. The umbonal keels are rounded. The foramen is large, ovally elongate, and submesothyrid. The apical angle is 65°–70°. The dorsal valve is curved rooflike: strongly in the posterior half and gently in the anterior half. The lateral sides of the valve are flattened. Three low and rounded folds are located on the anterior margin.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.		L	W	T	W/L	T/L
Holotype	4104/1076	20.0	15.0	10.6	0.75	0.53

C o m p a r i s o n. The new species differs from *L. concava* Smirnova et Grunt, 2003 in the wider shell, less concave ventral valve, wide and flattened anterior margin, location of the maximum width, shallower sulcus on the ventral valve, strongly curved hinge line, and in the narrow umbo. It differs from *L. nikitini* (Gemmellaro, 1899) in the wider anterior margin, poorly pronounced plication on the anterior half of the shell, and in the more convex dorsal valve.

M a t e r i a l. One complete shell and one shell with a broken ventral valve from the type locality.

***Levenolasma mongolica* (Grabau, 1931)**

Plate 5, fig. 18

Dielasma millepunctatum Hall var. *mongolicum*: Grabau, 1931, pp. 57–60, pl. 4, figs. 5a–5d.

H o l o t y p e. American Museum of Natural History, New York, no. 25, Cat. G.S.C. 1267; northern China (Inner Mongolia), Zhesi Hongor; Upper Permian, Midian.

D e s c r i p t i o n. The shell is oval and middle-sized. The sulcus on the ventral valve is wide. Both valves are slightly convex. The anterior margin is elongated and rounded. The anterior commissure is widely arched. The lateral commissures are steeply arched. The lateral sides of the shell are slightly convex. The hinge line is long and strongly curved. The maximum width and thickness are in the middle. The ventral valve is slightly convex near the umbo. The sulcus starts within one-third of the valve length from the umbo and rapidly broadens towards the anterior margin. The sulcus deepens within one-third of the valve length from the anterior margin and extends upon the full width of the ventral valve. The umbo is low. The false area is narrow and bordered by well-pronounced umbonal keels. The foramen is unknown. The apical angle is 77°. The dorsal valve is curved rooflike. The lateral sides are wide and flattened.

D i m e n s i o n s i n m m a n d r a t i o s:

Specimen, no.	L	W	T	W/L	T/L
5133/31	17.6	13.8	8.0	0.78	0.45

C o m p a r i s o n. This species differs from *L. concava* Smirnova et Grunt, 2003 in the oval shell, widely arched anterior commissure, absence of fine plication on the anterior margin, and in the strongly curved hinge line. It differs from *L. leveni* Smirnova et Grunt, 2003 in the smaller and oval shell and in the wide sulcus on the ventral valve.

M a t e r i a l. One shell with a broken apex of the umbo from Zhesi Hongor.

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