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Pennsylvanian Gastropods of the Suborders Murchisoniina Cox et Knight, 1960 and Sinuspirina Mazaev subordo nov. from the Central Regions of the Russian Platform: Morphology, Taxonomy, and Phylogeny

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Abstract—The taxonomic composition and stratigraphic distribution of members of the suborders Murchisoniina and Sinuspirina subordo nov. in the deposits of the Moscovian, Kasimovian, and Gzhelian stages of the central regions of the Russian Platform is discussed. Based on detailed evaluation of the taxonomic value of the teleoconch and protoconch and also on evolutionary phylogenetic reconstructions, a fundamentally new scenario for the evolution of the murchisoniid gastropods and a new system for the suborder Murchisoniina Cox et Knight, 1960 are proposed. Several genera which were traditionally considered within the Murchisoniidae are assigned to the new family Sinuspiridae fam. nov. Five families are recognized in the suborder Murchisoniina: Ptychocaulidae fam. nov., Farewelliidae fam. nov., Plethospiridae Wenz, 1936, Murchisoniidae, and Orthonematidae Nützel et Bandel, 2000. The generic composition of the Orthonematidae and Murchisoniidae is revised. Diagnoses are given of the two suborders, five families, ten genera, and also descriptions of 33 species. Of these, one suborder, three families, and three species are new. Five of the described species are recorded for the first time.

Keywords: Carboniferous, gastropods, Russian Platform, morphology, phylogeny, taxonomy.

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"Character evolution within the clade Gastropoda is a mosaic of repeated patterns..."
W.F. Ponder and D.R. Lindberg, 1997

INTRODUCTION

Shells of murchisoniid gastropods and their imprints are widespread in the Paleozoic beds all over the world and are readily recognized due to very specific morphological characters. At the same time, shells of the suborder Sinuspirina Mazaev subordo nov. are relatively uncommon in the Paleozoic beds. Their external appearance is somewhat similar to that of Murchisoniina, and until now a few genera of sinuspirin gastropods have been assigned to the family Murchisoniidae. The earliest occurrences of murchisoniid gastropods are known from the Lower Ordovician. During the entire Paleozoic, the taxonomic diversity of the group has generally increased and reached its peak in the Late Carboniferous. The latest members of the suborder became extinct by the end of the Permian, or possibly, at the beginning of the Triassic. Sinuspirin gastropods apparently first appeared in the Early Ordovician. The latest occurrences of members of this group are known from the Upper Carboniferous. In general, the taxonomic diversity of sinuspirins was extremely low during the entire Paleozoic.

Although remains of murchisoniid gastropods are diverse in the Middle and Upper Carboniferous of the Russian Platform, until now their taxonomy and stratigraphic distribution have been poorly known. Perhaps, this can be explained in part by their preservation as casts and imprints. Occurrences of sinuspirin gastropods in this region are extremely rare.

The first mention of murchisoniid gastropods in the Middle and Upper Carboniferous of the Russian Platform and adjacent regions (Urals Foreland, Bakhmut Basin) can be found in the works of Trautschold (1874), Stuckenberg (1898, 1905), and Yakovlev (1899). Unfortunately, the earliest ("classical") works have certain deficiencies, which have already been mentioned by Licharew (1968, 1975) in his very detailed literature reviews. Most often we come across extremely brief descriptions combined with poor illustrations, in most cases aggravated by the lack of the type material. Therefore, the use of many of the taxa of Paleozoic gastropods established by the classics of Russian geology, despite their validity, is impossible for a variety of reasons. Unless material is found for such problematic taxa, their use will only become possible if neotypes are established, as was done by Yakovlev for the Permian of Kulogory (Mazaev, 2006). In cases when there are several morphologically similar species, such actions can be difficult and to a large extent formal. For example, because of the absence of types, *Murchisonia nikitini* Stuckenberg, 1905 (based on the illustration and description by Stuckenberg (1905)) could equally be considered as a senior synonym of *Cibecuia magnum* Mazaev, 2002 *Orthonema cochleoides* (Yin, 1932), or *O. silinae* (Licharew, 1975). The species *Murchisonia biarmica* Kutorga, 1842 requires a separate study. This taxon is mentioned in most "classical works" on the Carboniferous, Permo–Carboniferous, and Permian of the Russian Platform and adjacent regions, including Stuckenberg's (1905) study of the Upper Carboniferous series of the Samara Bend, but, in all cases, the identification of the taxon remained uncertain. Among the above works, Yakovlev's monograph stands out because of the precise photographic illustrations of the material studied, very detailed descriptions, and the absence of modern taxa among generic taxa (such as *Turbo, Turritella, Natica*, etc.). Of 11 murchisoniid species, including those assigned by Yakovlev to *Promatildia*, only two come from the Upper Carboniferous beds of the Bakhmut Basin, whereas the remaining nine come from the Permian Oka–Tsna Swell, northern wing of the Moscow Syneclise, and the Bakhmut Basin. Imprints of gastropod shells (not only of murchisoniids) collected in the "Permo–Carboniferous" outcrops northwest of the town of Murom (Denyatino, Muskovo) are of considerable interest. This assemblage contains species that have not yet been discovered anywhere else.

The modern stage in the study of Paleozoic gastropods by Russian paleontologists begins with Licharew's studies. Many species from the Carboniferous beds of the Russian Platform have been shown to be with the same as species described by Licharew from the Middle–Upper Carboniferous boundary beds and the Upper Carboniferous–Lower Permian of southern Fergana (Licharew, 1967, 1968) and also from the Middle and Upper Carboniferous beds of the eastern slope of the Ural Mountains (Licharew, 1975). In total, at least 65 species of murchisoniid gastropods were described in these papers. Later, Licharew's collection was partly revised, generic assignments of some species were revised, and some were synonymized (Mazaev, 2001, 2002, 2003).

Based on published data, it has been established that many species of murchisoniid gastropods discovered in the Carboniferous of the East European Platform are characterized by broad geographical ranges and found in the synchronous beds of western China and North America. The stratigraphic distribution of these species varies and may include intervals from one substage to several stages.

Originally, the main purpose of this paper was to establish the taxonomic composition and stratigraphic distribution of murchisoniid gastropods in the Middle and Upper Carboniferous beds of the Russian Platform. However, from the very beginning, it has become clear that the limited set of morphological characters of the shell of murchisoniid gastropods and the independent appearance of the same characters in different families present considerable difficulties for both the reconstruction of the systematics of the group and the taxonomic assignment of its members. There is no a well-defined system of ranking of morphological

characters in this group. The same characters have been given different taxonomic interpretations by different authors, resulting in erroneous generic and familial attribution of many Late Paleozoic species. In addition, discovery of morphologically similar protoconchs in modern cenogastropods and some representatives of *Goniasma* Tomlin, 1930. *Cerithioides* Haughton, 1859, and *Stegocoelia* Donald, 1889, casts doubt on their traditional placement in the Murchisoniidae Koken, 1896 (Nützel and Bandel, 2000; Bandel et al., 2002; Nützel and Pan, 2005).

Based on a detailed evaluation of the systematic value of characters of the teleoconch and protoconch and on evolutionary phylogenetic reconstructions, a fundamentally new scenario of the evolution of murchisoniid gastropods and a new system of the suborder Murchisoniina Cox et Knight, 1960 are proposed. At the same time, several genera, which were traditionally considered within Murchisoniidae, were included in the new family Sinuspiridae Mazaev fam. nov. A new suborder Sinuspirina Mazaev subordo nov. was proposed to accommodate Sinuspiridae fam. nov. in the order Pleurotomariida Cox et Knight, 1960. At the same time, five families are included in the suborder Murchisoniina: Ptychocaulidae Mazaev fam. nov., Farewelliidae Mazaev fam. nov., Plethospiridae Wenz, 1936, Murchisoniidae, and Orthonematidae Nützel et Bandel, 2000. The generic composition of the families Orthonematidae, Plethospiridae, and Murchisoniidae was revised. Two subfamilies, Murchisoniinae Koken, 1896 and Cheeneetnukiidae Blodgett et Cook, 2002, were recognized in the Murchisoniidae. The family Orthonematidae was described in detail because its content and taxonomy are highly debatable. In addition, it includes over 80% of species described in this paper. The new data on morphology and taxonomy of murchisoniid gastropods allow a new interpretation of the stages of this mollusk group in the Paleozoic.

The chapter on systematic paleontology contains the diagnoses of two suborders, five families, two subfamilies, ten genera, and 33 species. Of these, one suborder, three families, and three species are new. Five of the species described are recorded for the first time in this region. The species assignment of specimens that had previously been identified by me (Mazaev, 2003) as *Orthonema frequens* Licharew, 1968, and the taxonomic assignment of the genus *Callispira* Nelson, 1947, previously placed by me in the Orthonematidae (Mazaev, 2002) has been reconsidered.

At the same time, with the study of fossil material from the Middle and Upper Carboniferous of the Russian Platform, I examined and, in some cases, revised the collection of Carboniferous gastropods of the eastern slope of the Ural Mountains (Tchernyshev Central Geological Museum (TsNIGR Museum), collection no. 9758) described by Licharew (1975); the collection of Late Carboniferous and Early Permian gastropods of southern Fergana (TsNIGR Museum, collection no. 8336) described by Licharew in two other monographs (Licharew, 1967, 1968), and the collection of Late Carboniferous and Early Permian gastropods of the Russian Platform (TsNIGR Museum, collection no. 325) described by Yakovlev (1899). The comparison of fossil gastropods from the above collections with those from my collection, which formed a basis for this paper, was invaluable for gaining an understanding of features and importance of many morphological characters of the groups examined.

CHAPTER 1. MATERIAL AND METHODS

This study is based on extensive material, which I collected from 1989 to 2003. In addition, I used fossil material donated by V.N. Sinelnikova (Geological Institute, Russian Academy of Sciences). This material included Sinelnikova's private collections and some specimens collected in the late 19th century and the beginning of the 20th century by A.P. Ivanov. A few imprints of murchisoniid gastropods were received from P.B. Kabanov and A.G. Kuznetsov. Altogether, the material examined includes specimens from 38 sections of the Middle and Upper Carboniferous of the Moscow Basin, Oka–Tsna Swell, and Onega Area (table, Fig. 1). The collection includes over 5000 specimens and is housed in the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN), collection no. 4471. In addition, I examined collections of Licharew (TsNIGR Museum): collection no. 9758 for Licharew's (1975) monograph and collection no. 8336 for his 1967 and 1968 monographs.

In the sections studied, fossilized shells were only preserved in a few mollusk groups: completely in Platyceratidae and partly in Euomphalacea and Conocardiidae, in which only the external calcitic layer was preserved, whereas the internal aragonite layer was dissolved (Mazaev, 1994, 1996). Shells of other mollusk groups are only represented by imprints, which is due to the post-sedimentary dissolution of aragonite. There is only one locality known (no. 4471-8 = no. 4471-32), an outcrop near the railroad station "55th km" near the village of Gzhel', in which preservation of gastropod shells is similar to that of material from the Pennsylvanian of the American Midcontinent. Unfortunately, only a very small number of specimens come from this level, whereas shells of murchisoniid and sinuspirin gastropods have not been found at all.

Cavities left by aragonite shells are well preserved in sediments capable of resisting compaction during lithogenesis. Compacted rocks, such as marl or limestone, with a large siliciclastic content contain only strongly distorted molds at the very best. They represent something between the internal cast (mold) and the external mold, and often possess prominent reflections of fragments of ornamentation. Therefore, the fossil material was mainly collected from the carbonate portions of the section containing "horizons" of mass lenticular cavities developed in spaces occupied

Table 1. The list of localities and collectors: (MR) Moscow Region, (VR) Vladimir Region, (RR) Ryazan Region, (KR) Kaluga Region, and (VLGR) Vologda Region

Section no.	Locality, details	Locality number in section	Collector
1	MR, Shchelkovo quarry	4471-4	A.V. Mazaev
		4471-2	A.V. Mazaev
2	MR, outcrop on the Klyazma River, near the village of Amerevo	4471-37	A.V. Mazaev
3	MR, Rusavkino quarry	4471-3	A.V. Mazaev
		4471-84	A.V. Mazaev
4	MR, Gzhel' brick clay quarry	4471-6	A.V. Mazaev
5	MR, outcrop near the "55 km" Railway Station	4471-7	A.V. Mazaev
		4471-8	A.V. Mazaev
		4471-75	A.V. Mazaev
		4471-32	A.P. Ivanov
6	MR, road quarry east of the village of Gubino	4471-76	A.V. Mazaev
7	VR, Dyukino quarry	4471-99	A.V. Mazaev
8	VR, Georgievskoe quarry	4471-12	A.V. Mazaev
		4471-13	A.V. Mazaev
9	VR, Dobryatino quarry	4471-16	A.V. Mazaev
		4471-17	A.V. Mazaev
10	Moscow, construction pit "City"	4471-97	A.V. Mazaev
		4471-98	A.V. Mazaev
11	Moscow, Dorogomilovo, outcrop	4471-29	A.P. Ivanov
12	Moscow, Zamoskvorechie, bottom hole of the Serpukhovsko–Timiryazevskaya underground metro line	4471-20	A.V. Mazaev
13	Moscow, Fili, Moscow River dredge	4471-31	A.G. Kuznetsov
14	Moscow, southwest, bottom hole of the underground metro line	4471-39	A.V. Mazaev
15	MR, limestone pit near the village of Yamskoe	4471-23	V.N. Sinelnikova
16	MR, outcrop on the Rozhaika River near the village of Sudakovo	4471-33	V.N. Sinelnikova
17	MR, Domodedovo quarry	4471-24	A.V. Mazaev
		4471-50	A.V. Mazaev
18	MR, Myachkovo quarry	4471-25	V.N. Sinelnikova
		4471-34	A.P. Ivanov
19	MR, quarry near the village of Kamennaya Tyazhina	4471-30	P.B. Kabanov
20	MR, Podolsk quarry	4471-22	V.N. Sinelnikova

Table 1. (Contd.)

Section no.	Locality, details	Locality number in section	Collector
21	MR, Afanasievo quarry	4471-18	A.V. Mazaev
		4471-88	A.V. Mazaev
		4471-89	A.V. Mazaev
		4471-90	A.V. Mazaev
22	MR, outcrop near the village of Shifernaya	4471-19	A.V. Mazaev
23	MR, quarry near the Konev Bor Station	4471-14	A.V. Mazaev
		4471-21	A.V. Mazaev
		4471-54	A.V. Mazaev
		4471-103	A.V. Mazaev
24	MR, road cutting on the Federal Highway "Ural", near the village of Korobcheevo	4471-70	A.V. Mazaev
25	MR, Akatievo quarry	4471-92	A.V. Mazaev
		4471-93	A.V. Mazaev
26	MR, outcrop near the town of Kashira	4471-38	A.P. Ivanov
27	MR, right bank of the Oka River, road cutting on the Federal Highway "Don"	4471-101	A.V. Mazaev
28	MR, Grigorovo quarry near Tuchkovo	4471-28	V.N. Sinelnikova
29	MR, outcrop on the Moscow River, near the village of Lutsino (west of Zvenigorod)	4471-40	A.P. Ivanov
30	KR, outcrop "Roshcha", right bank of the Protva River, opposite the Pafnutiev Monastery	4471-94	A.V. Mazaev
31	RR, Kasimov quarry, near the village of Tashenka	4471-26	N.V. Zernetskaya
		4471-86	A.V. Mazaev
		4471-87	A.V. Mazaev
		4471-96	A.V. Mazaev
		4471-81	A.V. Mazaev
32	RR, Maleevo quarry	4471-74	A.V. Mazaev
		4471-82	A.V. Mazaev
33	RR, Akishinskii quarry, near the village of Lashma	4471-77	A.V. Mazaev
		4471-78	A.V. Mazaev
		4471-79	A.V. Mazaev
		4471-80	A.V. Mazaev
		4471-85	A.V. Mazaev
34	RR, quarry near the village of Yambirno	4471-73	A.V. Mazaev
		4471-83	A.V. Mazaev
35	VLGR, Aleksandrovskii quarry	4471-102	A.V. Mazaev
		4471-91	A.V. Mazaev

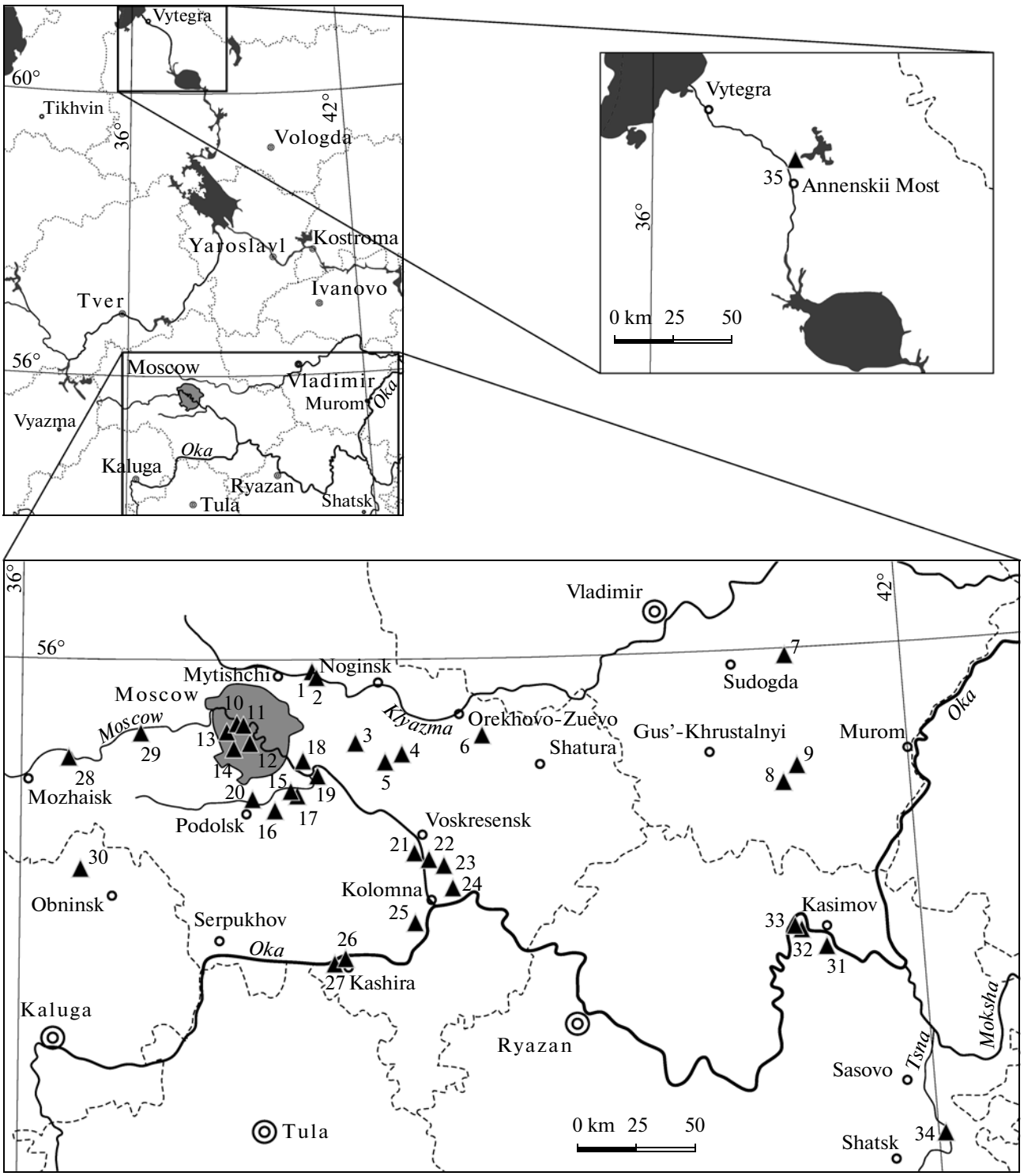


Fig. 1. Map showing localities of the material studied: (1) Shchelkovo quarry; (2) outcrop on Klyazma River, near village of Amerevo; (3) Rusavkino quarry; (4) Gzhel' Brick Clay quarry; (5) outcrop near the "55 km" Railway Station; (6) road quarry east of the village of Gubino; (7) Dyukino quarry; (8) Georgievskoe quarry; (9) Dobryatino quarry; (10) Moscow, construction pit "City"; (11) Dorogomilovo; (12) bottom hole of Serpukhovsko-Timiryazevskaya underground railway; (13) Moscow, Fili, Moscow River dredge; (14) Moscow, Southwest, bottom hole of the underground railway; (15) limestone pit near the village of Yamskoe; (16) outcrop on the Rozhaika River near the village of Sudakovo; (17) Domodedovo quarry; (18) Myachkovo quarry; (19) quarry near the village of Kamennaya Tyazhina; (20) Podolsk quarry; (21) Afanasievo quarry; (22) outcrop near the village of Shifernaya; (23) quarry near the Konev Bor Station; (24) road cutting on the "Ural" Federal Highway, near the village of Korobcheevo; (25) Akatievo quarry; (26) outcrop near the town of Kashira; (27) right bank of the Oka River, road cutting on the "Don" Federal Highway; (28) Grigorovo quarry near Tuchkovo; (29) outcrop on the Moscow River, near the village of Lutsino (west of Zvenigorod); (30) "Roshcha" outcrop, right bank of the Protva River, opposite the Pafnutiev Monster; (31) Kasimov quarry, near the village of Tashenka; (32) Maleevo quarry; (33) Akishinskii quarry, near the village of Lashma; (34) quarry near the village of Yambirno; (35) Aleksandrovskii quarry.

by mollusk shells, rocks which are in fact coquinas. These accumulations are found in transgressive and regressive portions of cyclothems (the most prominent cyclites separated by parallel subaerial unconformities). In the central parts of the cyclothems, shell imprints are found relatively rarely and randomly and are usually poorly preserved. The quality of imprints in regressive and transgressive portions of cycles is not always satisfactory for study, which can be explained by three reasons: (1) Burial of strongly rounded shells (lacking some ornamentation characters before the burial. (2) Burial of shells in coarse-grained rocks lacking fine cementing mass. (3) Postsedimentary growth of small calcite crystals on the surface of imprints inside the cavities. The best imprints come from "sealed" grainstone and packstone under conditions where crystals of calcite do not occur on their surface. Such imprints reflect the finest detail of ornamentation and, in some cases, allow making casts of shell with a complete aperture and the apical whorl. In the synchronous beds in other regions, where shells are substituted by calcites, the aperture margin and the umbonal region are usually broken off or it is extremely difficult to clear them of the rock matrix. Therefore, preservation as imprints, strangely, can be advantageous.

The above preservation features affected the methods of sampling from natural outcrops and quarries studied. Despite the seeming abundance of mollusk imprints, each section contained one, or rarely, up to five fossil occurrences suitable for study. In addition, the sections studied are widely affected by secondary dolomitization leading to texture and structural changes in the rocks and is often accompanied by complete loss of macrofossils. Therefore, some stratigraphic intervals are poorly characterized by fossils and the collection studied does not allow equally complete taxonomic characterization of different stratigraphic levels.

The fossil material described in this study was collected in 64 occurrences across 35 sections (Figs. 2–7) and constitutes approximately 10% of the total fossil collection at my disposal. Each occurrence has been given a unique number, which follows the collection number after a slash (e.g., 4471/32, where 4471 is collection no. and 32 is occurrence number). In the figures of sections the occurrences are shown by arrows. The occurrences with their geographic position and collectors' data are listed in the table.

This paper uses the local scheme of stratification of the Middle and Upper Carboniferous, accepted by the Interdepartmental Regional Stratigraphic Meeting on the Middle and Upper Paleozoic of the Russian Platform (*Reshenie* ..., 1988), while the stratigraphic subdivision of particular sections is based on various papers (Ivanova and Khvorova, 1955; Makhlina et al., 1979, 1984, 2001; Shik, 1979; Alekseev et al., 1984; Davydov and Dorofeeva, 1991; Kabanov, 2003; Baranova and Kabanov, 2003).

Methods. All the samples with imprints collected in the sections were first cleared of excess rock matrix using a power stone cutting saw. After having been numbered, they were sorted using a binocular microscope, and casts were taken from the best ones using stomatological latex. The best results were obtained using "Bayer" impression materials, which do not require special preparation of the sample and allow taking impressions with negative angles and complex morphological elements. The impression material reflects all the fine detail of the imprint with a resolution at least 10 lines per 1 mm. The casts were photographed using a digital camera Nikon CoolPix 990 and SEM ComScan (PIN).

CHAPTER 2. MORPHOLOGY

The shell of murchisoniid gastropods is described using the following major morphological characters and parameters: dimensions, shell shape, ornamentation, selenizone, growth lines, apertural morphology, juvenile whorl morphology, and protoconch morphology. Similar characters are also observed in sinuspirin gastropods, although they do not have a selenizone, whereas the juvenile whorl and protoconch morphology is unknown.

Dimensions. The size of the gastropod shell in the families Murchisoniidae and Orthonematidae varies widely. In the majority of known species, shell height ranges from 0.5 to 2 cm. Some species of *Goniasma* and *Cibecuia* Winters, 1956 very rarely reach the maximum size of 12 cm. Three size classes can be recognized: small shells—from 0.5 to 2 cm, medium-sized shells—from 2 to 5 cm, and large shells—over 5 cm. In some cases, the shell size of gastropods is not considered as a separate character, but the shell size in combination with other characters can be used to recognize taxa of subspecific rank. Wide variations of the shell size were observed in the following species: *Goniasma lasallensis* (Worthen, 1890) (Licharew, 1967, p. 73); *Orthonema salteri* (Meek et Worthen, 1860) (Batten, 1995, p. 29; Kues and Batten, 2001, p. 52); and *Orthonema frequens* (Licharew, 1968, p. 43). Licharew proposed varieties corresponding to subspecies for the first and the last species. Considering a wide geographic and stratigraphic distribution of these species, far more subspecies than previously recognized can be established for them. Shells of the families Sinuspiridae fam. nov. and Ptychocaulidae fam. nov. are distinguished by the large size; for example, the type species of *Ptycocaulus* could apparently reach 120 mm in height.

For all the species described in this monograph, I measured the shell height and the maximum diameter. For some species, it was necessary to calculate the width-to-height ratio of the last whorls or the ratio of the height of the upper whorl face to that of the lower whorl face (Fig. 8).

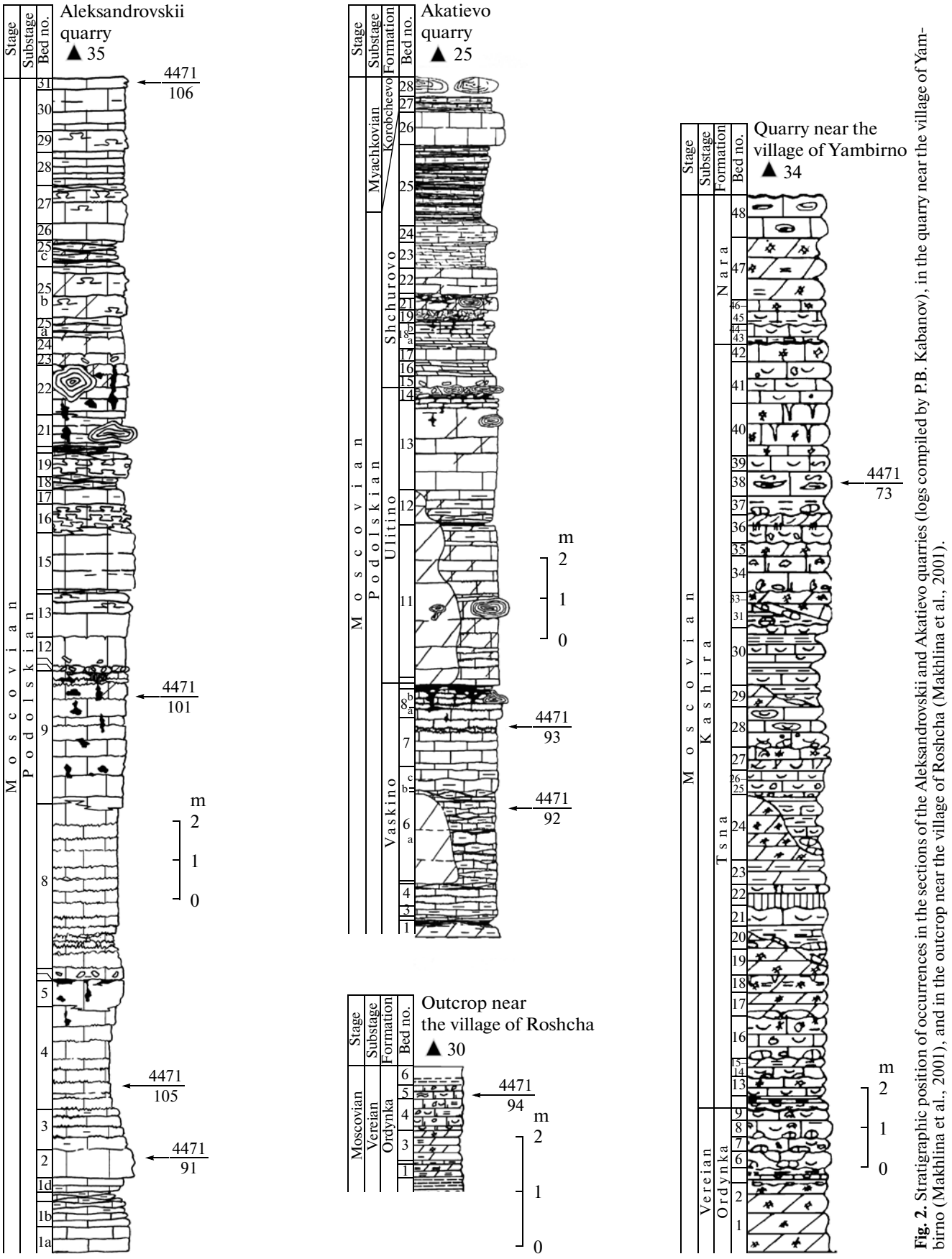


Fig. 2. Stratigraphic position of occurrences in the sections of the Aleksandrovskii and Akatievo quarries (logs compiled by P.B. Kabanov), in the quarry near the village of Yambirno (Makhlina et al., 2001), and in the outcrop near the village of Roshcha (Makhlina et al., 2001).

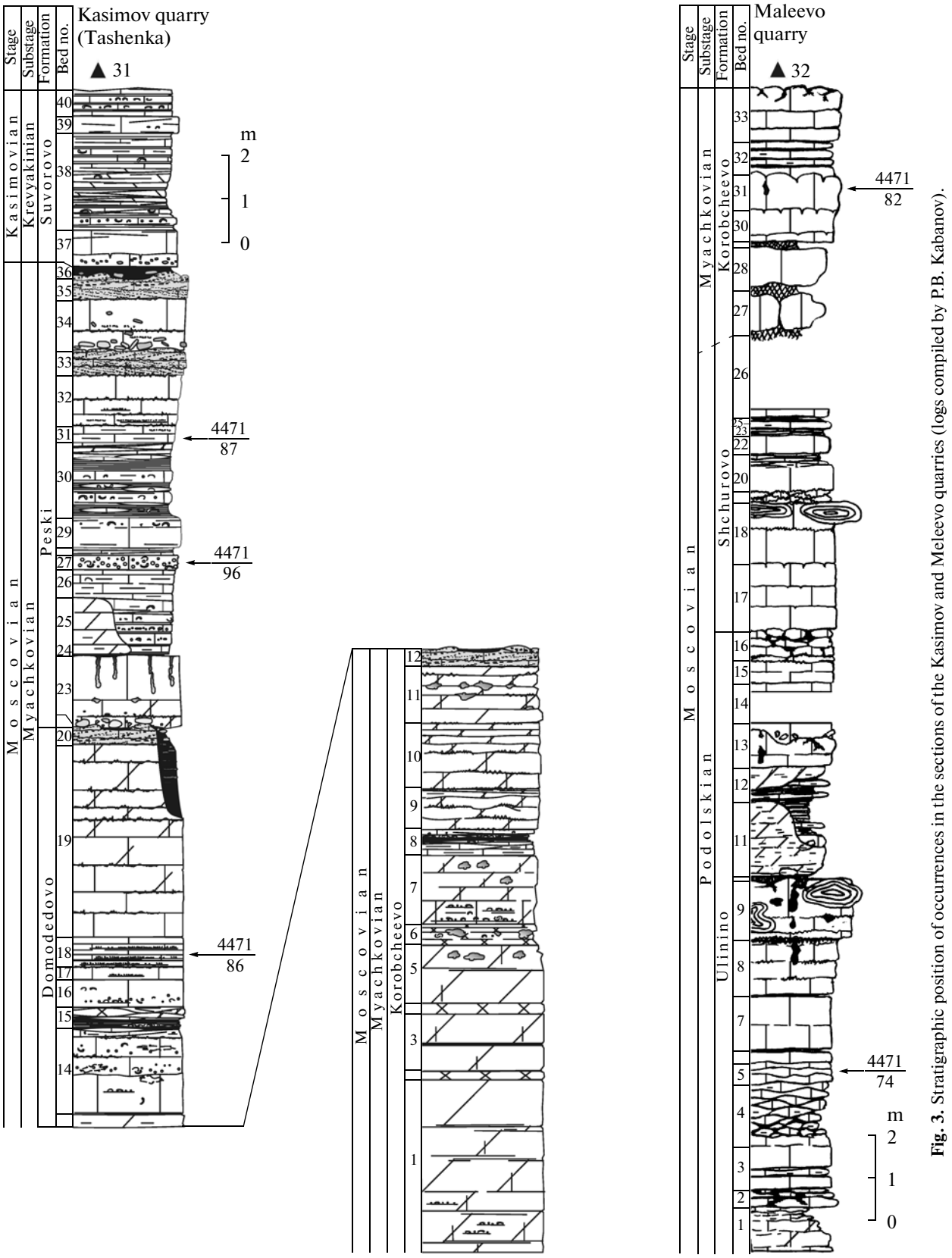


Fig. 3. Stratigraphic position of occurrences in the sections of the Kasimov and Meleevo quarries (logs compiled by P.B. Kabanov).

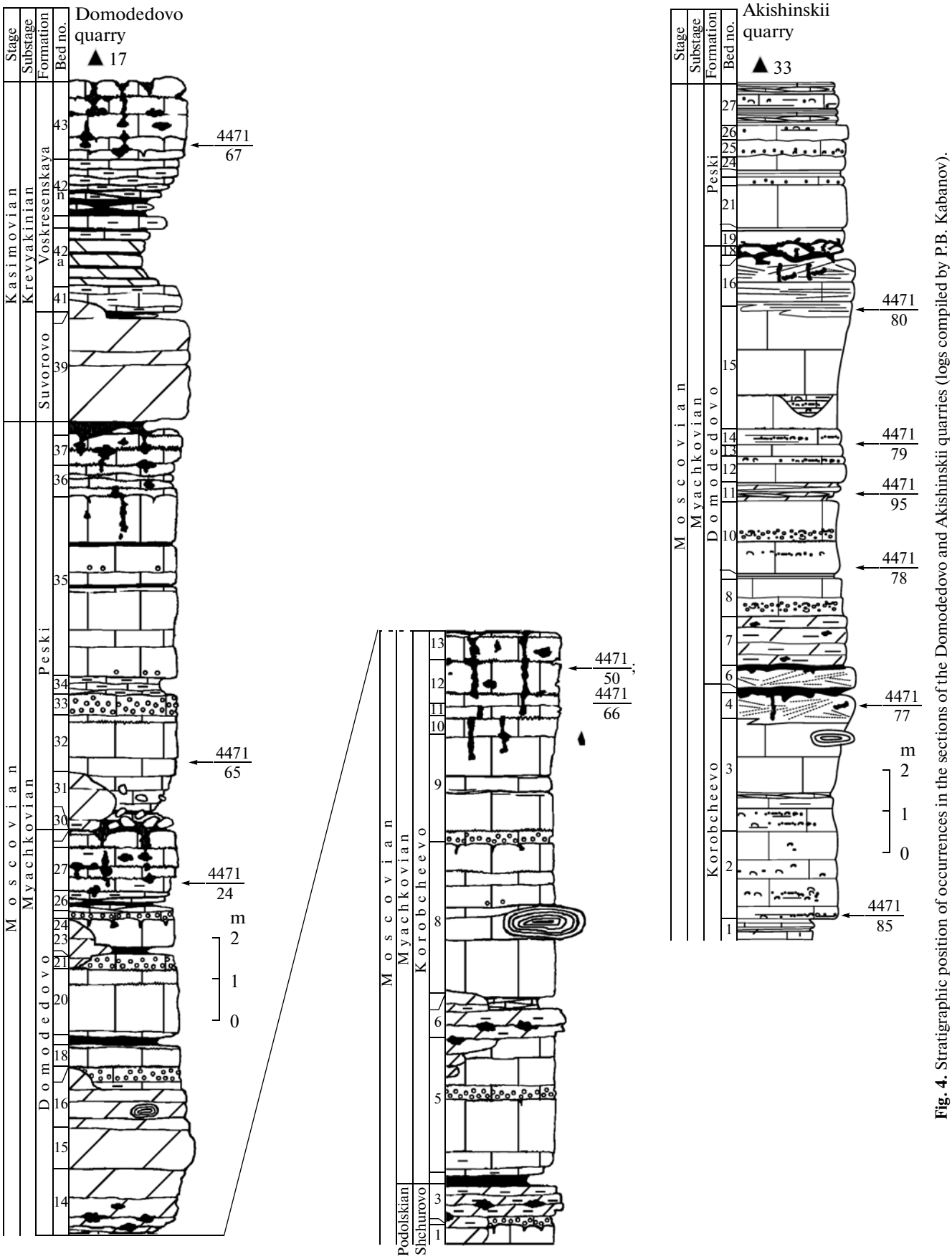


Fig. 4. Stratigraphic position of occurrences in the sections of the Domodedovo and Akishinskii quarries (logs compiled by P.B. Kabanov).

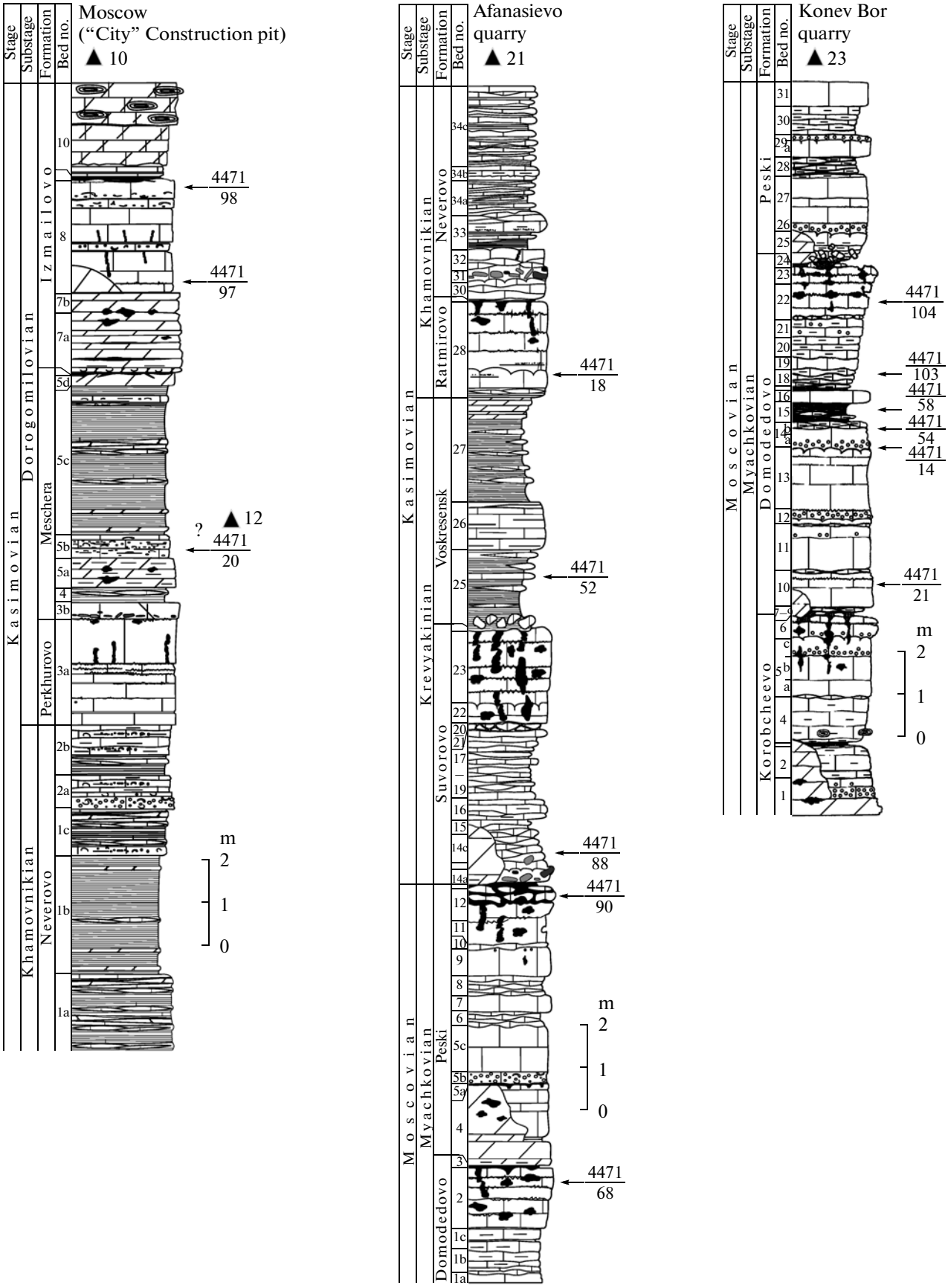


Fig. 5. Stratigraphic position of occurrences in the sections of the of the Moscow City construction pit, Afanasievo quarry, and quarry near the Konev Bor Station (logs compiled by P.B. Kabanov).

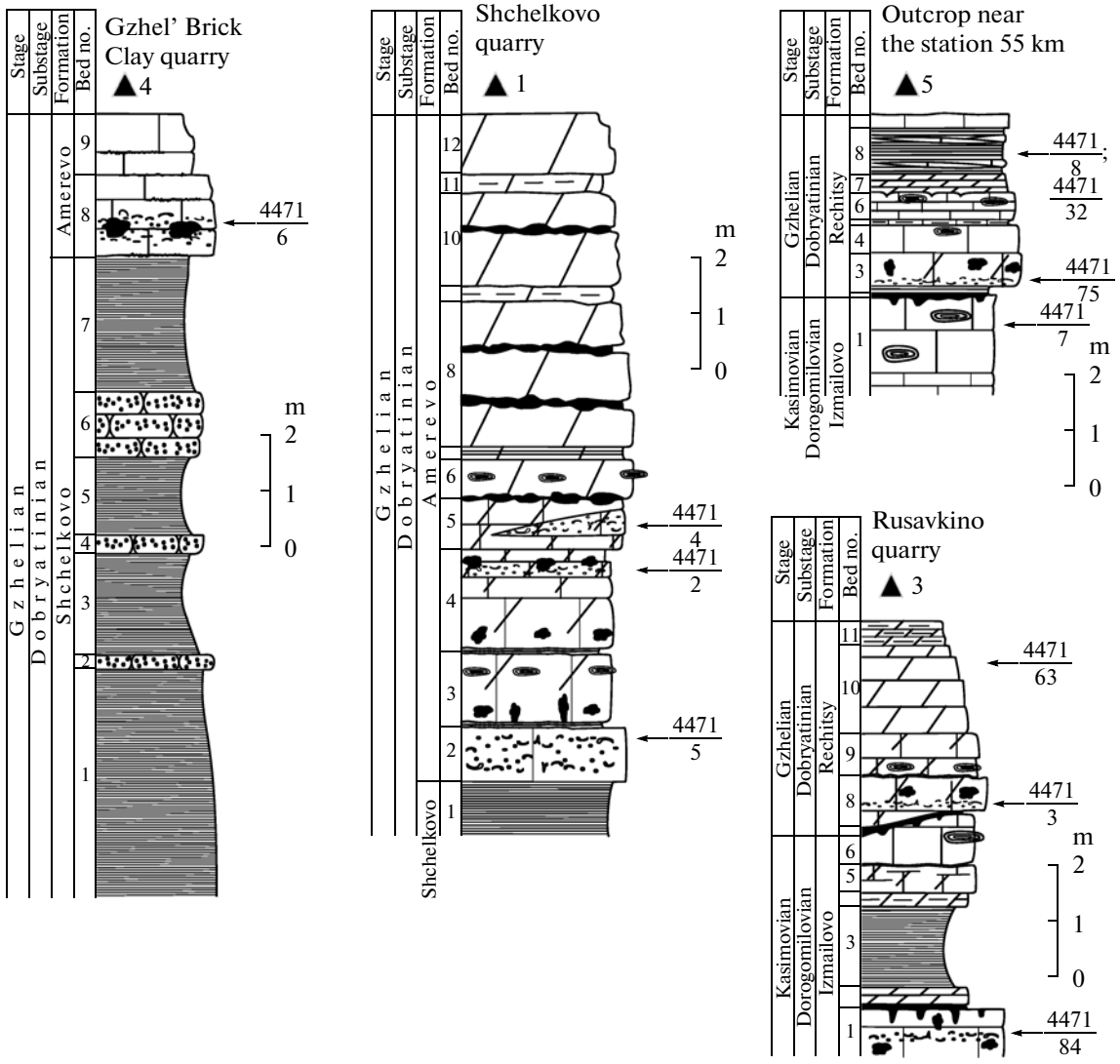


Fig. 6. Stratigraphic position of occurrences in the sections of the Gzhel' brick clay quarry, Shchelkovo quarry, quarry near the village of Rusavkino, and in the outcrop near "55 km" Railroad Station (Mazaev, 1994, modified).

The shell shape of murchisoniid gastropods varies from turbinate, with not more than eight whorls (Plethospiridae), to turreted, with up to 20 whorls (Murchisoniidae, Orthonematidae, and Farewelliidae fam. nov.) (Fig. 9). The number of whorls is characteristic of the Ptychocaulidae fam. nov.

The shell shape largely depends on the whorl profiles. In most murchisoniid and orthonematid species, the whorl profile usually changes in ontogeny and, in this case, the juvenile whorls are different from the adult ones (Fig. 10, *jw*, *aw*). The adult whorls have at least two surfaces: whorl face and whorl base (Fig. 10, *wf*, *wb*). When the whorl face is subdivided by a carina or a distinct shoulder, the lower whorl face and upper whorl face are recognized (Fig. 10, *lwf*, *uwf*). The largest variations are observed in the profile of the whorl face, whereas that of the whorl base varies from flattened to convex and, in addition, the whorl base may be extended downwards, or can be subhorizontal. The following major types of the whorl profile are recognized: (1) angular, with a sharp or massive rounded carina, approximately in the middle of the whorl face (Fig. 11a); (2) rounded, when an evenly curved whorl face relatively smoothly continues as the whorl base (Figs. 11b, 11c); (3) subcylindrical (drum-shaped), when the whorl face is subparallel to the shell axis, smoothly continues as the whorl base or forms a sharp basal carina at the point of transition; it can be separated from the suture by a subsutural ramp with a variously developed shoulder (Figs. 11d, 11e); (4) trapezoidal (conical), with an almost straight, weakly concave or weakly convex whorl face, which is distinctly oblique in relation to the shell axis; often there is a shoulder with a narrow subsutural ramp and, in addition, the whorl face may be separated from the whorl base by a sharp carinate ridge (Figs. 11f, 11g).

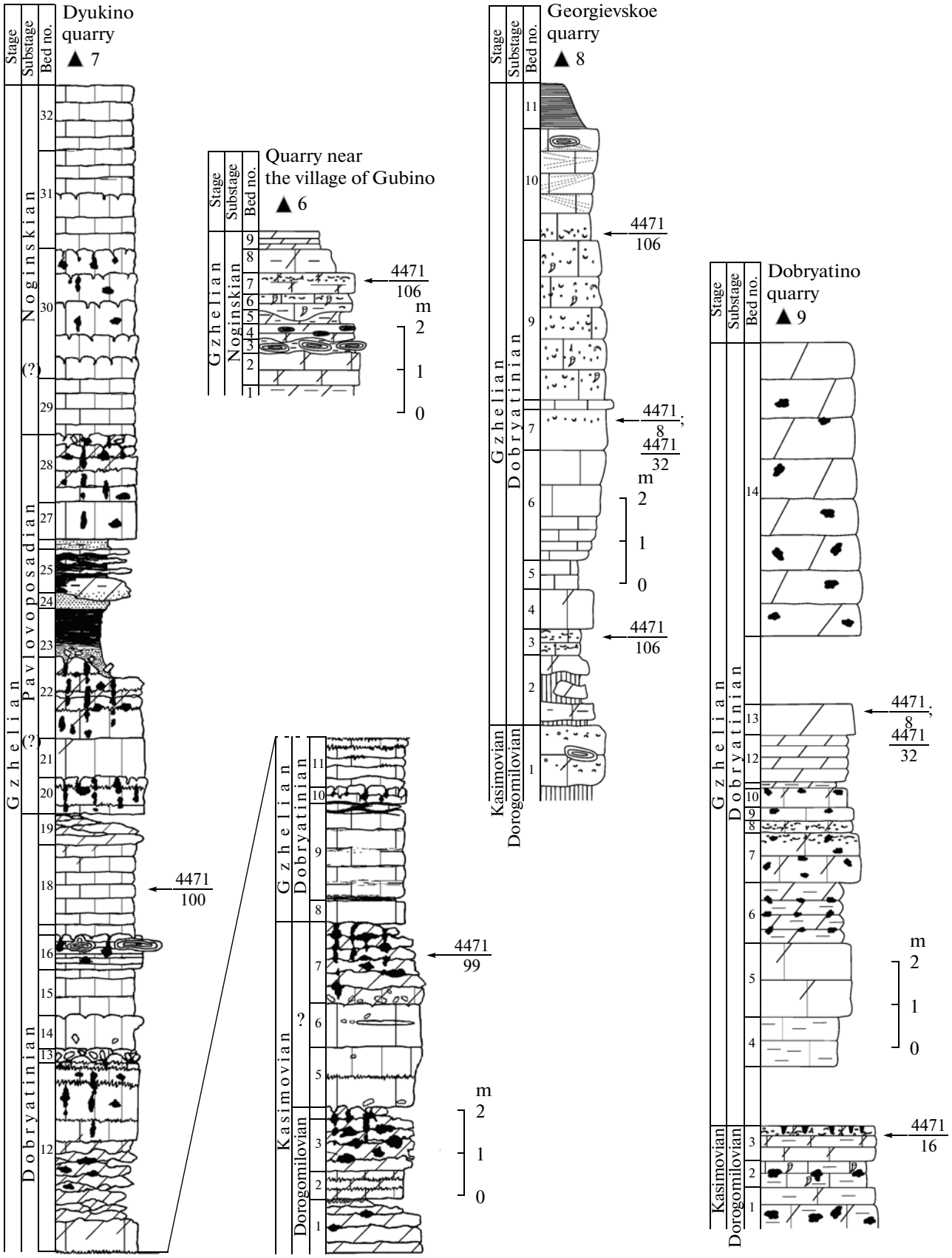


Fig. 7. Stratigraphic position of occurrences in the sections of the Dyukino quarry (logs compiled by P.B. Kabanov), quarry near the village of Gubino (Mazaev, 1997, modified), Georgievskoe and Dobryatino quarries (logs compiled by the author).

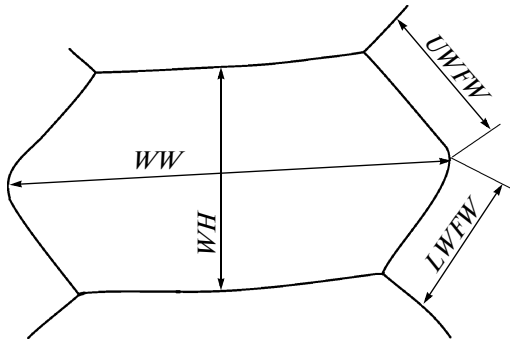


Fig. 8. Measurements of the whorl width (*WW*), whorl height (*WH*), upper whorl face width (*UWFW*), and lower whorl face width (*LWFW*).

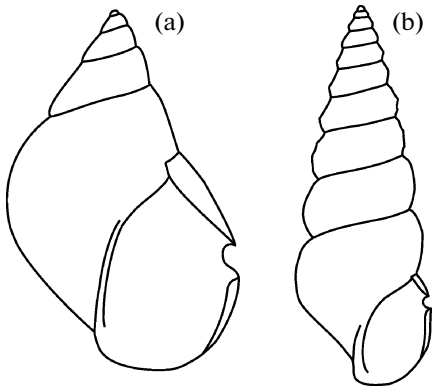


Fig. 9. Main morphotypes of murchisoniid gastropods: (a) high-spired ovate, *Pithodea ampulissima* Konink, 1881; (b) turreted, turriform, *Stegocoelia klyazmaensis* Mazaev, 2001.

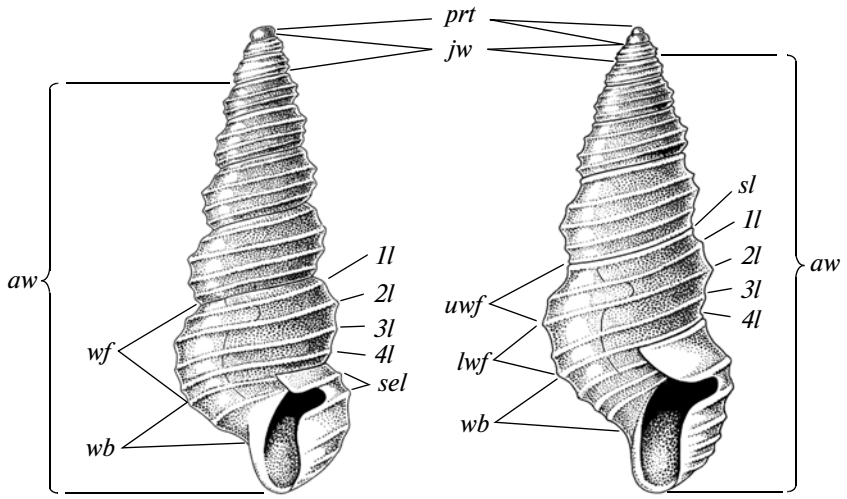


Fig. 10. Main ornamentation features of *Stegocoelia acutiformis* and *S. okaensis*. Designations: (*prt*) protoconch; (*jw*) juvenile whorls; (*aw*) adult whorls; (*wf*) whorl face; (*wb*) whorl base; (*uwf*) upper whorl face; (*lwf*) lower whorl face; (*sel*) selenizone; (*sl*) sutural lira; (*1l, 2l, 3l, 4l*) main spiral lirae on whorl face, their number on juvenile and adult whorls changing (Mazaev, 2001, modified).

The whorl profile is an important taxonomic character of generic rank. This is most prominent in the succession of the genera *Stegocoelia, Taosia* Girty, 1939, *Vebericochlis* Licharew, 1967, and *Orthonema* Meek et Worthen, 1862 which have a similar type of ornamentation and, apart from the morphology of the apical whorls, are different in the whorl shape only. The identification at the species level is based on less pronounced changes in the whorl shape.

The **shell ornamentation** of murchisoniid gastropods sensu lato is generally not very diverse. The shell surface in many plethospiroids, murchisoniids, ptychocauliids, and orthonematids is smooth or almost smooth, possessing only a band of selenizone, whereas shells of other members of these families have spiral ornamentation. In each of the above families, ornamentation shows a trend towards increased complexity. Shells of the family Farewelliidae fam. nov., currently represented solely by *Farewellia heidelbergerae* Frida et Blodgett, 2004, have a well-developed collabral ornamentation in the form of relatively thick lirae, which outline apparently repeat the apertural margin. Slightly below the seam, the collabral lirae are separated by a well-developed selenizone and, in the place of intersection, they sharply change their direction. The upper ones are prosocline and lower ones are opisthocline or, in Licharew's (1975, p. 13) terminology, the upper and lower lirae are inclined posteriorly and anteriorly, respectively.

To a lesser extent, collabral ornamentation is developed in early members of Sinuspiridae fam. nov. The type species *Sinuspira tenera* Perner, 1907 is ornamented with distinct, thin, cordlike lirae, which form a deep sinus on the whorl face, apparently following

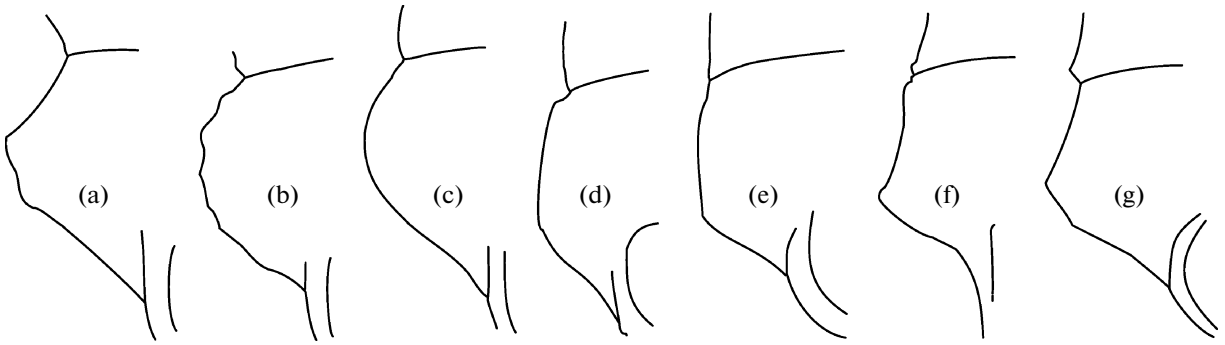


Fig. 11. Main types of whorl profiles: (a) angular, *Goniasma lasallensis*; (b, c) rounded: (b) *Stegocoela* sp. and (c) *Altadema altadema*; (d, e) subcylindrical: (d) *Vebericochlis maclayi* and (e) *Orthonema frequens*; (f, g) trapezoidal: (f) *Cibecuia sinelnikovae* and (g) *Taosia crenulata*.

the apertural margin (Knight, 1941, pl. 45, figs. 7a, 7b). In the majority of sinuspirid genera, the shells are almost smooth, lacking a selenizone, and are ornamented mostly by growth lines. Only the latest genera possess spiral ornamentation, whereas *Micrentoma* Donald, 1898 shows both spiral and collabral ornamentation (Knight, 1941, pl. 44, figs. 5a, 5b).

The collabral ornamentation in Plethospiridae can be represented by thin cordlike lirae. The spiral ornamentation is frequently represented by thin grooves separating wide, flattened spiral lirae.

The shells of Murchisoniidae and Orthonematidae show a more developed ornamentation, which is primarily observed in the distinctness of spiral lirae and in their greater number. Several ornamentation-based morphogroups can be recognized within Carboniferous members of the family Murchisoniidae: (1) whorl base and whorl face are smooth: *Bellazona* Gordon et Yochelson, 1987, *Cheeneetnukia* Blodgett et Cook, 2002, and *Ulungaratoconcha* Blodgett et Cook, 2002; (2) whorl face is smooth, while the whorl base is ornamented by two spiral lirae: *Cerithioides*; (3) whorl face is ornamented by two spiral lirae developed to a varying extent: *Murchisonia* d'Archiac et deVerneuil, 1841; (4) whorl face and whorl base are ornamented with a few spiral lirae: *Goniasma, Donaldospira* Batten, 1966; (5) whorl face and whorl base are ornamented with numerous thin spiral lirae separated by thin spiral grooves: *Aclisina* Konink, 1881.

Morphogroups homologues to the above described may be recognized within the family Orthonematidae: (1) whorl face and whorl base are smooth: *Ferganispira* Licharew, 1967, *Loxosonia* Batten, 1985, and *Arribazona* Kues, 1990; (2) whorl face is smooth, the whorl base possesses spiral lirae: *Cibecuia*; (3) whorl face is ornamented with four major spiral lirae, whereas the whorl base is variously ornamented: *Stegocoelia*, *Taosia, Vebericochlis, Orthonema, Concinnispira* Zernetskaja, 1983, *Hermosanema* Kues et Batten, 2001, and *Altadema* Kues, 2002; (4) whorl face and whorl base possess numerous narrow spiral lirae separated by thin spiral grooves: Laschmaspira Mazaev, 2003.

The above ornamentation types are mainly repeated in the two families. Their combination with the whorl profile types provides a clear generic diagnosis. The variations (lirae size, their arrangements on the shell surface, the appearance of intercalating lirae, or transformation of lirae into spiral lines of nodes) are good species identifiers within each type.

In this paper, particular attention is paid to the following succession of genera: *Stegocoelia, Taosia, Vebericochlis, Orthonema, Concinnispira, Hermosanema*, and *Altadema*. Spiral ornamentation in *Concinnispira* and *Hermosanema* secondarily disappears in the last whorls. In *Altadem*a, ornamentation can be expressed extremely weakly, up to the complete disappearance. Many species of the genus *Orthonema* also secondarily drop one or even all spiral lirae. However, the type of ornamentation apparently evolved from a single common archetype, with the whorl face possessing four major regularly spaced lirae and selenizone between the upper pair of lirae, which is characteristic of *Stegocoelia, Taosia*, and *Vebericochlis*.

For unification of the taxonomic descriptions of the above taxa, the spiral lira separating the selenizone from the top, was proposed to refer to as the first lira (Mazaev, 2001) (Figs. 10, *1l*; 12, *1l*). Some species of *Stegocoelia, Orthonema, Vebericochlis*, and possibly other genera can possess an additional subsutural lira (Figs. 10, *sl*; 12, *sl*). The subsutural lira is most commonly located immediately below the suture and is slightly different in size from other main spiral lirae. Its presence is an important species-rank character (*Orthonema silinae* (Fig. 12f) and *O. cochleoides* Yin, 1932 (Fig. 12e). In several species of *Stegocoelia, Vebericochlis*, and *Altadema*, like in *Goniasma*, the whorl face and/or the whorl base may possess additional spiral lirae (of smaller size), located between the main lirae (*S. gzheliensis* Mazaev, 2001, *S. laschmaensis* Mazaev, 2001, *V. arguta* (Licharew, 1975)) (Fig. 12, *al*). Occasionally, some species of *Stegocoelia, Vebericochlis, Orthonema*, and *Altadema* have an additional lira positioned on the selenizone (*Stegocoelia knighti* (Licharew, 1975), *S. gzheliensis, Vebericochlis maclayi*

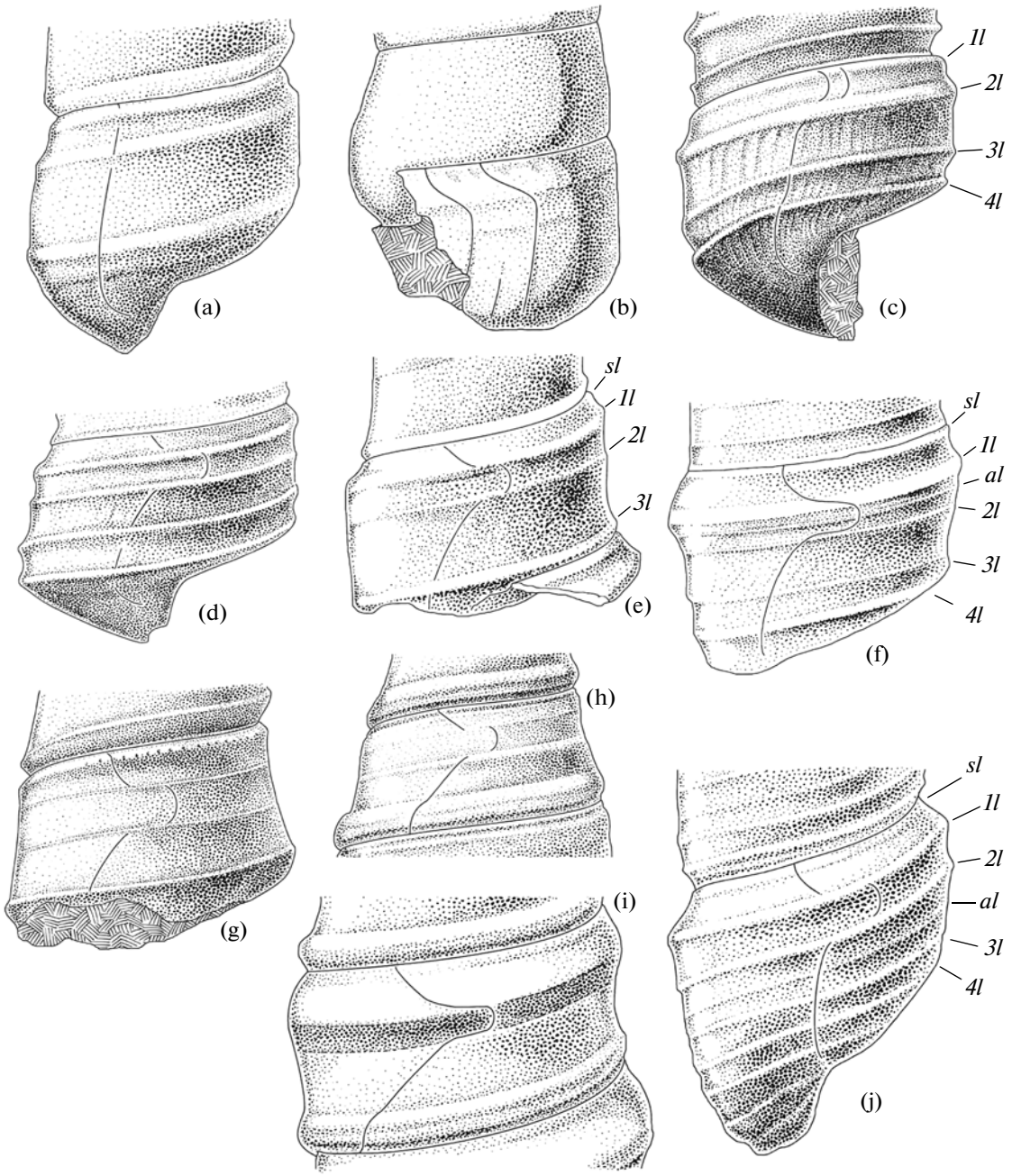


Fig. 12. Adult whorl morphology in Orthonematidae: (a) *Orthonema salteri* (Meek et Worthen, 1860), PIN, no. 4471/6/34; (b) *Orthonema inoratum* Knight, 1934 (Knight, 1934, pl. 57, fig. 1d); (c) *Orthonema marvinwelleri* Knight, 1934, PIN, no. 4471/50/30; (d) *Orthonema simplex* sp. nov., PIN, no. 4471/2/13; (e) *Orthonema cochleoides* (Yin, 1932), PIN, no. 4471/2/24; (f) *Orthonema silinae* (Licharew, 1975), TsNIGR Museum, no. 109, collection no. 9758; (g) *Cibecuia sinelnikovae* Mazaev, 2002, PIN, no. 4471/22/9; (h, i) *Cibecuia magnum* Mazaev, 2002, PIN, no. 4471/78/50; adult whorls and last whorls; (j) *Vebericochlis arguta* (Licharew, 1975), TsNIGR Museum, no. 193, collection no. 9758. Designations: (*sl*) sutural lira; (*al*) auxiliary lira; (*1l*, *2l*, *3l* and *4l*) the first, second, third, and fourth main lira (after Mazaev, 2002, modified).

Licharew, 1967, *Orthonema silinae, Altadema convexa* Kues, 2002, *A. lira* Mazaev, 2003) (Fig. 12f).

The even spacing and prominence of the main spiral lirae on the whorl face is an important morphological character. However, some genera do not follow this scheme. For instance, one or all primary lirae of some *Orthonema* species may be weakly developed or even completely disappear in some individuals (*O. silinae* (Fig. 12f), *O. cochleoides* (Fig. 12e), *O. frequens* (Fig. 12a)). The main spiral lira of many species of *Orthonema* and also *Vebericochlis arguta* (Licharew, 1975) are separated into the upper and lower pairs, whereas, in other species of these genera, the lirae are arranged evenly, which is typical of *Stegocoelia* and *Taosia*.

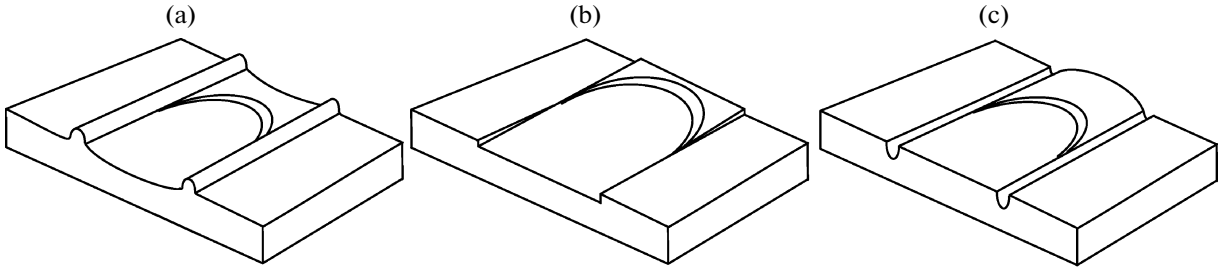


Fig. 13. Main types of selenizone of murchisoniid gastropods (explanations in text).

The development of spiral lirae on the whorl base is only known in some species of *Stegocoelia, Vebericochlis*, and *Altadema* (Figs. 10a, 10b). The number of spiral lirae on the whorl base may increase as the shell grows and reach six in some species. The last whorl of some species may also possess auxiliary spiral striae (*Stegocoelia knighti, S. okaensis* Mazaev, 2001, and *Altadema lira*). The presence of auxiliary striae is very variable and is attributed to species variability.

A spiral row of nodes is extremely rarely present. Most commonly a row of nodes substitutes one of spiral lirae. This character independently appears in species of different genera: *Taosia crenulata* Girty, 1939 and *Vebericochlis maclayi*. Rows of nodes are occasionally observed in some species of particular genera, which in general are characterized by extremely weak or absent spiral ornamentation: *Cibecuia cedarensis* Winters, 1956, *Altadema nodolira* Mazaev, 2003, and *Arribazona tschernyschewi* (Yakowlew, 1899). Middle Devonian species of *Cheeneetnukia* and *Ulungaratoconcha*, which also lack pronounced spiral ornamentation, show the presence of massive nodes.

The selenizone is a band formed in place of the mantle slit during the shell growth. This element of ornamentation is characteristic of most Zygobranchia. In the suborder Murchisoniina, the selenizone is usually organized more simply than in other Zygobranchia and the recognized selenizone types are repeated in different groups of Vetigastropoda. The morphology and position of the selenizone (in combination with other characters) is one of the most important features of generic rank. At the same time, the family Sinuspiridae fam. nov. lacks a selenizone, which is apparently related to the morphology of the slit in members of this family. Three types of selenizone are recognized in the Plethospiridae, Murchisoniidae Ptychocaulidae, and Orthonematidae: (1) concave, smooth selenizone, with thin lunulae, which is bounded on either side by a spiral lira (Fig. 13a); (2) flat selenizone above or below the shell surface, with very weak lunulae (Fig. 13b); (3) weakly convex or flat selenizone bounded on either side by a thin groove, and lying almost on the same plane with the shell surface; lunulae are inconspicuous (Fig. 13c). The first type is considered as the initial for the second and third. The second and third types are very similar and can be observed at different growth stages of the same shell. The three types are prominently correlated with the development of spiral ornamentation. It is clear that the appearance of the second and third types is primarily related to the absence of spiral ornamentation. The extremely thin selenizone of *Lodanaria* Dahmer, 1925 and the festoon-shaped selenizone of *Helicospira* Girty, 1915 are derived from the first type. The channel selenizone of *Farewellia* and *Loxosonia* is apparently derived from the second type. The selenizone marking the carina of *Donaldospira* represents yet another type. The surface of the selenizone is sharply curved and its lower region is on the lower lateral surface of the whorl, whereas the upper region is located on the upper whorl face (Batten, 1966, pl. 7, fig. 23). A similar selenizone structure is observed in another group of vetigastropods, the genus *Biarmeaspira* Mazaev, 2006 (Mazaev, 2006, pl. 4, figs. 1–22).

Growth lines are developed to varying extents. In smooth shells lacking ornamentation, they are only observed in the selenizone as lunulae or absent altogether. Most commonly, the growth lines are observed as threadlike grooves and, less commonly, as sharp collabral lirae. Because almost all shells of Murchisoniina had a pleural slit, the growth lines form a sinus on the whorl face.

Shells of the family Sinuspiridae fam. nov. have a relatively wide and shallow sinure. Its morphology is especially clearly visible on the shells of the type series of *Sinuspira tenera* (Knight, 1941, p. 322, pl. 45, figs. 7a, 7b) (Fig. 14a). Because the slit in shells of this family is not parallel-sided, they lack a selenizone. As a result, the depth of the sinus is usually apparent. The U-shaped and V-shaped sinuses are clearly different (Figs. 14a, 14b). In later genera, the sinus is shallower and wider (Fig. 14c).

In Murchisoniina, the morphological pattern of growth lines is approximately the same. From the upper suture, the growth lines are opisthocline to form lunulae on the selenizone, and are prosocline beneath the selenizone. The position of the selenizone is the primary difference. Less significant differences include the character of the curvature of lines (convex forward or straight) and the angle of inclination of the growth lines to the shell axis, which are important for identification of species or subspecies. The depth of

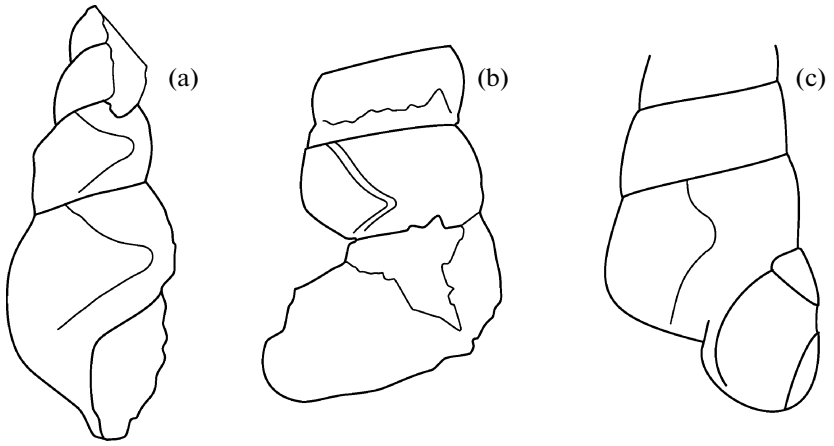


Fig. 14. Growth lines: (a) *Sinuspira tenera* Perner, 1907 (Knight, 1941, pl. 45, fig. 7b; drawing on photograph); (b) *Michelia cylindrical* Roemer, 1854 (Knight, 1941, pl. 42, fig. 1; drawing on photograph); (c) *Micrentoma nana* (Koninck, 1881) (Donald 1898, pl. 5, figs. 12, 13; drawing on photograph).

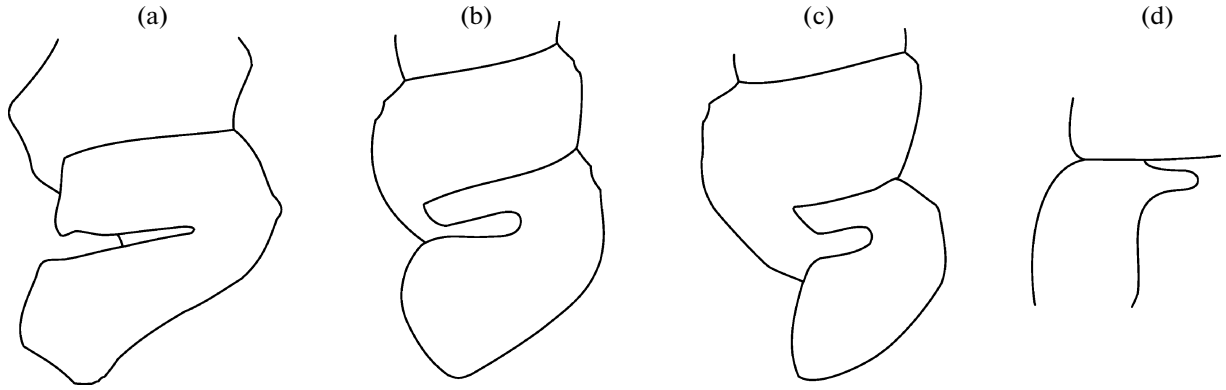


Fig. 15. Palatal apertural margin morphology: (a) *Goniasma lasallensis* (Worthen, 1890), PIN, no. 4471/99/51; (b) *Altadema lira* Mazaev, 2003, PIN, no. 4471/77/1; (c) *Vebericichlis arguta* (Licharew, 1975), PIN, no. 4471/73/17; (d) *Arribazona devispira* Mazaev, 2003, PIN no. 4471/50/48.

the sinus is a very important character. However, because the opposite margins of the sinus in their extremum are usually parallel, the growth lines along the margins of the selenizone are superimposed on the lunulae; therefore, the depth of the sinus can only be inferred from the growth lines when more prominent lines showing growth arrests are observed. Hence, the depth of the sinus remains unknown for most species of Murchisoniina. The depth of the sinus in some species of Orthonematidae was apparently two to four times its width (Figs. 12d–12j, 15b–15d).

In the genus *Orthonema*, the growth line morphology was not as simple as in the other orthonematid genera. Originally, when Meek and Worthen (1862) established this genus, they emphasized that the type species *O. salteri* (Meek et Worthen, 1861) has straight, almost vertical growth lines; this is reflected in the generic name. With time, species with a small labral sinus and, later, those with a well-developed labral sinus were also assigned to the genus *Orthonema*. Known growth line types form a succession from completely straight to those with a sharp and deep labral sinus corresponding to a pleural slit. For instance, *O. frequens*, like the type species, has almost straight growth lines (Fig. 12a). *O. inornatum* Knight, 1934 (Knight, 1934, pl. 57, fig. 1d) has a sharp but shallow labral sinus (Fig. 12b). *O. marvinwelleri* Knight, 1934 has a narrow and apparently deep labral sinus shifted almost to the upper suture (Fig. 12c). A prominent sinus is observed in *O. simplex* Mazaev, 2002, *O. cochleoides* (Fig. 12e), *O. nacazawai* Batten (Batten, 1985, text-fig. 26), and *O. subtaeniatum* (Geinitz, 1866) (Anderson et al., 1985, text-fig. 3.10). The same type of growth lines is observed in numerous specimens of *O. silinae* (Licharew, 1975), although on the last whorl of the two largest specimens from the type series, growth lines clearly reflect the depth of the sinus (Fig. 12f). It is evident that these specimens had a true, deep pleural slit. It is noteworthy that here I am talking about the last (adult) whorls of the shell, whereas at the

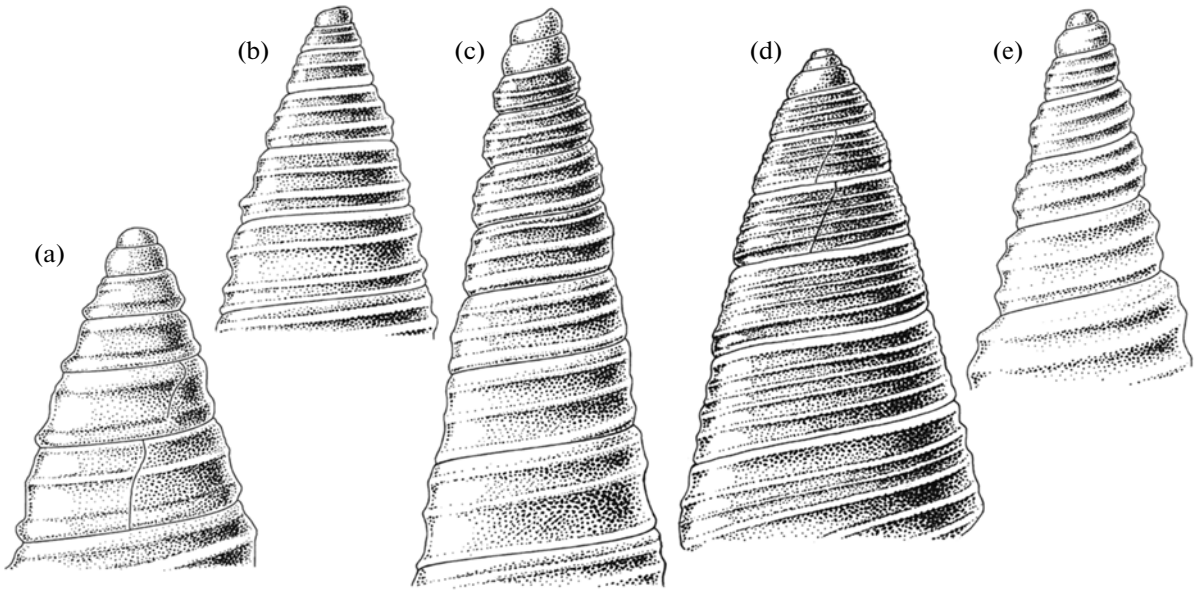


Fig. 16. Juvenile whorl morphology: (a) *Orthonema salteri* (Meek et Worthen, 1860), PIN, no. 4471/79/184; (b) *Orthonema marvinwelleri* Knight, 1934, PIN no. 4471/85/74; (c) *Orthonema cochleoides* (Yin, 1932), PIN, no. 4471/79/173; (d) *Orthonema silinae* (Licharew, 1975), TsNIGR Museum, no. 264, collection no. 9758; (e) *Vebericochlis arguta* (Licharew, 1975), PIN, no. 4471/73/26 (Mazaev, 2002, modified).

juvenile stages of this species, growth lines are almost straight (Fig. 16d).

Juvenile whorls of many genera are clearly distinct from the adult whorls of the teleoconch. The best example is the juvenile whorls of the genera *Stegocoelia, Concinnispira,* and *Hermosanema*. They are distinguished by the number of spiral lirae (not more than three) and the angular profile; the lower two lirae are always positioned close to one another, whereas the middle lira forms a distinct carina (Fig. 7). Juvenile whorls of *Goniasma* are similar in morphology (Bandel et al., 2002, pl. 8, figs. 70, 75, 76, 79; pl. 9, figs. 80, 81). In species of the genus *Orthonema*, juvenile whorls have varying ornamentation and the whorl profile. The number of lirae varies from three to six, whereas the whorl face shape varies from weakly concave to round. Some lirae in species with more than three spiral lirae become primaries in the ontogeny, whereas other lirae become secondaries (Figs. 16a–16d). Juvenile whorls of *Vebericochlis* and possibly some species of *Cibecuia* have a similar morphology (Fig. 16e). Juvenile whorls of *Altadema* are rounded with one or two weak spiral lirae, restricting the selenizone. Juvenile whorls of *Arribazona* and *Cerithioides* are rounded and lacking spiral ornamentation. The morphology of the juvenile whorls in other genera is still unexamined.

The aperture morphology is one of the most important conchological characters. A characteristic feature of the aperture in Murchisoniina is the presence of pleural slit. Some taxa show a weakly developed "incipient" abapical apertural canal. The parieto-palatal canal in this group is absent; it is not developed even in taxa that have partially or completely lost the pleural slit in the course of evolution. At the same time, occurrences of shells of murchisoniid gastropods with completely preserved apertural margin are extremely rare. Several specimens described in this study, one way or another demonstrate the shape and the depth of the slit and are exceptional (Pl. 1, figs. 10–16; Pl. 3, fig. 13; Pl. 6, fig. 3; Pl. 7, figs. 3, 5). In most cases, the interpretations of the possible apertural morphology are based on the observation of the growth line course (Pl. 6, fig. 6; Pl. 7, figs. 6, 11, 14). This is commonly the only possible method.

The fossil material showing de facto the presence of the pallial slit and its morphology in *Stegocoelia, Cibecuia, Vebericochlis, Altadema, Arribazona*, and *Orthonema* appeared only recently (Mazaev, 2001, 2002, 2003) and, in the present paper, I for the first time describe the apertural morphology of *Goniasma lasallensis* (Fig. 15a).

In genera of Orthonematidae, the depth of the pallial slit is usually approximately twice its width. The margins of the pallial slit are parallel and expand or narrow towards the aperture. The slit is always located above the middle of the whorl face. As mentioned above, species of *Orthonema* show an extreme variety of the palatal margin of the aperture. Within one genus, it is possible to observe a complete succession from an aperture with a well-developed pallial slit to the aperture with a virtually even palatal margin without a slit. Interestingly, the sinus, irrespective of its depth, is always bounded by the upper pair of spiral lirae, exactly as in *Stegocoelia, Taosia*, and *Vebericochlis*. If the sinus is absent, the upper pair of lirae are still developed to this or that extent (Figs. 12a, 12b).

Among genera of Murchisoniidae, the slit morphology is only known for *Goniasma*, and its depth is from 5 to 10 times greater than its width. The morphology of the slit in Plethospiridae, although shown for many genera in *Treatise* (Knight et al, 1960), is probably only known for certain for the type species of *Plethospira* (Knight, 1941, pl. 24, fig. 2b).

In Sinuspiridae, the slit margins are never parallel, and the depth and shape of the slit is relatively comparable with the course of the growth lines (Figs. 14a–14c). For the genus *Micrentoma*, the course of growth lines was relatively clearly shown by Donald (1898, p. 69, pl. 5, figs. 12, 13) (Fig. 14c). Similar growth lines were shown for the type material of *Callispira* (Nelson, 1947, pl. 65, figs. 6a, 6b). The sinus of these genera resembles somewhat that typical for loxonematid gastropods. However, it is relatively prominent in its extremum, its width being almost the same as its depth. In this group, a selenizone is not formed in the places of overgrown relatively wide U- or V-shaped slit even when the spiral lirae are well developed, which is a very important morphological character for this group. The pallial cavity of these mollusks was apparently shallow. The morphology of the slit and its development without formation of a selenizone is a characteristic feature of Sinuspiridae.

Columella and umbilicus. The columella is formed by the columellar lip either as a tube, or as a solid rod. Within the aperture, the columella may be long, or short, straight or gently curved. In most cases, the columella of sinuspirin, murchisoniid, and orthonematid gastropods is solid, and the umbilicus is absent. Less commonly the columella is formed as a very thin tube and, in this case, the shell may possess a narrow, slitlike umbilicus. Sometimes, despite a small width of the umbilicus, its depth may be comparable to the shell height. In ptychokaulids, the columella is formed in completely different way, i.e., as a wide tube. In this case, the umbilicus is relatively wide and phaneromphalous. Its width is usually comparable with the last whorl height.

CHAPTER 3. COMPARATIVE AND ADAPTIVE MORPHOLOGY OF THE SUBORDERS MURCHISONIINA AND SINUSPIRINA AND THEIR PHYLOGENY

In this chapter, based on the functional morphological analysis of conchological characters, I attempted to reveal possible scenarios of the evolution of the suborders Murchisoniina and Sinuspirina. Taking into account the diversity and a vast geochronological span of both suborders, detailed analysis of the entire Early Paleozoic material, or the revision of the family Plethospiridae are beyond the scope of this study. On the other hand, it seemed impossible to leave out some Silurian and Devonian taxa. The study focused on the morphology and phylogeny of the families Murchisoniidae and Orthonematidae and on the morphology and origin of the family Sinuspiridae.

From the time of the establishment of the family Murchisoniidae by E. Koken until recently, the combination of the two major characters: the pleural slit and highly conical shells, relatively sufficiently characterized and bounded the murchisoniid gastropods from all other gastropod groups. The presence of a pronounced labral sinus or of a pronounced labral sinus in combination with the selenizone is the only argument in support of the opinion that the murchisoniid gastropods may have been zygobranchiate gastropods. Cox and Knight (Knight et al., 1960, p. I290) noted that, despite the presence of a slit, there are certain other characters that are shared by murchisoniid gastropods and Cerithiacea, including the absence of a nacreous layer and turreted shell. However, the nacreous layer is absent in Scissurelidae and Fissurellidae, and its absence does not contradict the placement of this group in Vetigastropoda, whereas instances of the maximum shift of the spire to the right are observed in several groups of Paleozoic gastropods which certainly belong to zygobranchiate gastropods. Another character which is, according to Cox and Knight, shared by murchisoniid gastropods and Cerithiacea, is the tendency to develop an incipient abapical apertural (inhalant) canal. This character is rather problematic when its significance for morphology and taxonomy is considered. Firstly, occurrences of the fossil material with a well-developed basal and palatal apertural margin are rare. Secondly, shells with a broken apertural margin, which are the majority in collections, can mistakenly be interpreted as siphonostomic, because the columellar part of shells is stronger and usually remains intact when the palatal margin is broken off (Pl. 2, figs. 2, 3. pl. 3, figs. 9, 16). The degree of the development of the abapical apertural canal varies in different genera. In the collection studied it is not expressed in specimens of *Altadema, Arribazona*, and *Stegocoelia*, although is relatively well developed in adult specimens of *Goniasma lasallensis* (Pl. 1, figs. 10, 15). Cox and Knight (Knight et al., 1960, p. I290) defined this morphological character as a tendency to the appearance of the abapical apertural (inhalant) canal, essentially giving it a functional morphological explanation, which is easy to agree with. However, in my opinion, its morphology has nothing in common with that of the abapical apertural canal of recent Cerithiacea, as on the occasions when it is developed, it appears as a weakly developed relatively wide groove or slightly flattened area between the columella and the basal margin of the aperture. The tendency to the development of such morphology can be observed in some Recent Trochacea, in the Jurassic Eucyclinae (Hickman and McLean, 1990, text-figs. 38, 39), and also in some Paleozoic Vetigastropoda, e.g., in *Biarmeaspira verideclinata* Mazaev (Mazaev, 2006, pl. 4, figs. 14, 15b). At the same time, the largest specimens of *Goniasma lasallensis*, the abapical apertural

canal is hypertrophically developed in the group under consideration. The shells of *Goniasma lasallensis* show a unique combination of contradictory characters: (1) the morphology of the teleoconch of *Goniasma lasallensis* in the overwhelming number of characters is strikingly similar to that of the teleoconch of *Murchisonia*; (2) the position and morphology of the slit can indicate the clear division of the pallial cavity into two approximately equal parts. The length of the slit is at least one-fifth of the length of the last whorl's circumference and, hence, the depth of the pallial cavity can be comparable with the depth of the pallial cavity of extant *Pleutomaria* (Voltzow et al., 2004); (3) adult shells of this species show the maximum development of the abapical apertural canal; (4) protoconchs show a well-developed sinusigera (Nützel and Bandel, 2000, text-figs. 2, 3; Bandel et al., 2002, text-figs. 70, 71).

Protoconchs with a well-developed sinusigera and composed of more than one whorl were discovered on many specimens of other species collected on different continents from the Carboniferous and Permian deposits (Yoo, 1988, 1994; Pan and Erwin, 2002; Nützel et al., 2002). With a varying degree of certainty, they were assigned to the following genera: *Goniasma, Cerithioides, Stegocoelia, Orthonema, Platyzona*, and also *Microlampra* and *Erwinispira* (the morphology of teleoconchs in the two latter genera is unknown). The peculiar morphology of protoconchs suggests (1) the longer pelagic larval development than in the extant Vetigastropoda, (2) the larval stage was probably planktonotrophic. Based on the evident similarity of the morphology of these protoconchs with those of some caenogastropods (both fossil and extant) and on the fact that no planktonotrophic stage is known for extant Vetigastropoda, all the above genera are assigned in the majority of recent studies to Caenogastropoda (Nützel and Bandel, 2000; Nützel et al., 2002; Bandel et al., 2002; Nützel and Pan, 2005). While the presence of the selenizone and the slit in these genera may indicate the plesiomorphic subdivision of the pallial cavity into two parts, Nützel and Bandel (2000, p. 558) write that the "the teleoconch morphology is often homeoplastic in this group," although accepting based on the protoconch structure that these gastropods belong to Caenogastropoda. Although these authors did not cite any explanation or examples of the homeoplasticity of teleoconch characters in caenogastropods, perhaps, in this case, they implied the development of slits in turrids.

Ya.I. Starobogatov (personal communication) said in one of his reviews that "any hypothesis on the taxonomy of extinct organisms is virtually unfalsifiable. The most plausible (i.e., most likely) hypothesis has to be chosen from a number of competing hypotheses, although this choice will be evaluated as 'very likely,' 'less likely,' etc." It is absolutely clear that, in this case, the term "taxonomy" of Late Paleozoic murchisoniid gastropods is primarily based on the morphology of their pallial cavity. In other words, the hypothesis of *Goniasma, Cerithioides*, and *Stegocoelia* being caenogastropods suggests that the right pallial organs are reduced. If the slit had functional significance, the pallial organs of these mollusks were plesiomorphic, as in Zygobranchia.

I suggest that this controversy should be considered at a different angle. The protoconch morphology can also be homeoplastic, especially considering that, in extant gastropods, different modes of larval ontogeny can be present even within one population of one species or in closely related species (Bouchet, 1989). At the same time, as mentioned above, the planktotrophic development is unknown in extant Vetigastropoda (Sasaki, 1998). However, the question is to which extent these present day data can be safely applied to the past. The independent appearance of planktotrophy in Neritopsina and Caenogastropoda, based on different hypotheses of their phylogeny, was considered in several papers (Haszprunar et al., 1995; Ponder and Lindberg, 1997). Which factors could prevent the independent appearance of planktotrophy in ancient Vetigastropoda? Many of these taxa have a short pelagic stage (Hickman, 1992 and others), whereas a transition from the lecithotrophic to planktotrophic development can be relatively simply achieved (Dodd, 1955). In other words, planktotrophic larva could still appear in Vetigastropoda, at least as a kind of an "evolutionary experiment." Modern data suggest that the appearance of planktotrophy at the Devonian–Carboniferous boundary could have been widespread. On the other hand, the mass appearance of larvae with a prolonged pelagic stage of development can be considered as an adaptation to the changing environment, following the biotic events at the Frasnian–Famennian boundary. Ponder and Lindberg (1997) list at least two possible factors that could have initiated planktotrophy in the Early Carboniferous: appearance and increase in number of benthic predators, and the appearance of phytoplankton.

The discovery of Paleozoic Vetigastropoda with a different protoconch morphology (lacking a sinusigera), with no analogues among the extant Vetigastropoda may be directly related to this problem. These taxa include *Apachella* spp. from the Early Permian of Arizona (Winters, 1956, pl. 3, fig. 4a; pl. 4, figs. 1b, 3c, 4b); *Campbellospira* Yoo, 1994 from the Tournaisian of Australia (Yoo, 1994, pl. 5, fig. 12), *Mourlonia* sp. from the Devonian of Poland (Dzik, 1994, text-figs. 35F, 35G), *Mourlonia* sp. and *Composonema* sp. from the Visean of the United States (Nützel and Mapes, 2001, text-figs. 5F–5I, 5N, 5O; 6A–6C), *Platyzona pulchella* Pan et Erwin, 2002 and *P. nitella* Pan et Erwin, 2002 from the Late Permian of China (Pan and Erwin 2002, text-figs. 8.1–8.4, 9.2). Apparently, similar protoconch morphology occurs in *Biarmeaspira verideclinata* and *Euconospira? pinegensis* Mazaev, 2006 (Mazaev, 2006, pl. 4, figs. 18, 19, pl. 5, fig. 4b), in all species of *Baylea* and *Biarmeaspira* from the Sakmarian and Kazanian

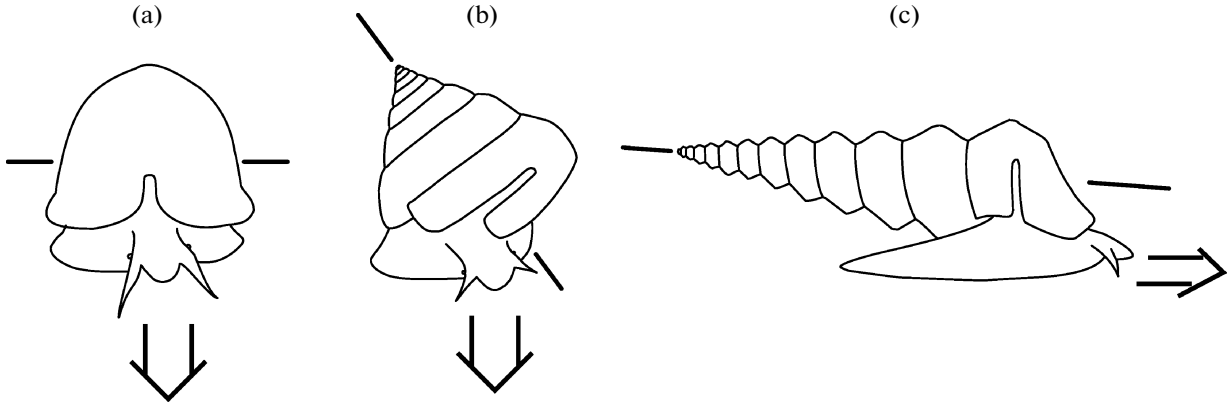


Fig. 17. Position of the shell axis in relation to the pedal-visceral mass: (a) Bellerophontida, (b) Pleurotomariida, (c) Murchisoniina (after Knight, 1952; Hickman, 1985; and Linsley, 1978; modified).

of the Russian Platform, and in all species of *Baylea* from the Pennsylvanian of the Russian Platform. Protoconchs of the above taxa are composed of approximately two smooth low spiral whorls with a sharp transition to the teleoconch. In opinion of Nützel and Mapes (2001, pp. 156, 158), such morphology is more typical of caenogastropods and even can suggest planktotrophy. These authors commented that the discovery of this morphology in Vetigastropoda is at surprising.

Thus, Late Paleozoic gastropods with a normal slit and selenizone have at least three kinds of protoconchs: (1) the protoconch composed of approximately one whorl with an abrupt transition to the teleoconch characteristic of all Vetigastropoda, beginning from the Mesozoic; (2) the protoconch composed of more than one whorl with a distinct sinusigera observed in extant and fossil Caenogastropoda; (3) the protoconch composed of approximately two smooth low conical whorls with an abrupt transition to the teleoconch lacking sinusigera, which is more typical of Caenogastropoda, with no analogues in extant Vetigastropoda. Based on this, it is either necessary to accept the plasticity of this character in ancient Vetigastropoda or, following the paradigm accepted by Bandel, Nützel, and others, to assign taxa with the protoconchs of the (2) and (3) kinds within the Caenogastropoda. In this case, the answer to the question of whether the present can adequately represent the past does not seem unequivocal. The gap between the extant and Late Paleozoic Vetigastropoda is over 250 m.y. The diversity and taxonomic composition of extant Vetigastropoda are very much different from those from the Paleozoic. This suggests differences in the biology of extant and Paleozoic Vetigastropoda. On the other hand, larval development in extant gastropods can be very diverse even in closely related species, suggesting the adaptive significance of protoconch morphology rather than its taxonomic value, which was suggested by Thorson (1950). In other words, if it is assumed that the extant Vetigastropoda lacked planktotrophic larvae, the similarity of the protoconch structure of all the above taxa with that of the extant caenogastropods does not suggest a phylogenetic relationship, but only similar larval ontogeny. The hypothesis of realization of the maximum number of possible ontogenetic patterns in ancient Vetigastropoda seems more likely than the retention of a plesiomorphic character (slit) that has lost its functional significance. Moreover, it should be taken into account that the slit weakens the shell, which is relatively thin and almost lacking ornamentation (compared to the majority of extant mollusks). For instance, the majority of deepwater *Perotrochus maureri* show 7–12 healed shell injuries, which apparently resulted from unsuccessful crustacean attacks (Harasevich and Askew, 1993, p. 134). Numerous examples of parallel evolution in murchisoniid gastropods are important arguments supporting the hypothesis that *Goniasma, Cerithioides, Stegocoelia*, and *Orthonema* had the pallial cavity similar to that of Zygobranchia. The evolution of the families Murchisoniidae and Orthonematidae show independent appearance of similar morphological structures of teleoconch, i.e., the whorl profile and ornamentation. The similarity of the selenizone and slit morphology in Plethospiridae, Murchisoniidae, and Orthonematidae is obvious.

The appearance and adaptive changes in teleoconch morphology of murchisoniid gastropods appear to be logical. Apparently, attempts to form a shell with various positions of the axis in relation to the foot occurred early in the evolution of Zygobranchia (Fig. 17). Changes in the shell shape were directly related to the regulatory torsion processes defining the position of the visceral sac. The effect of these processes on the position of the pallial cavity in various gastropod clades has been repeatedly discussed (Naef, 1911; Knight, 1952; Linsley, 1978; Hickman, 1985; Golikov and Starobogatov, 1989). Because the pallial cavity in Zygobranchia is divided into two parts, during torsion, one of these parts should decrease along with the decrease in the function of one of the

ctenidia. The order Pleurotomariida has the most diverse shells. Among its members, Murchisoniina show the maximum shift of the spire to the right. The sagittal plane of the pallial cavity in species with a trochoid shell is inclined at approximately 45° and turned anticlockwise from the sagittal surface of the foot base. The shell axis is at an angle of at least 45° to the place of the foot base (Fig. 17b), while the pallial cavity is turned to 45° clockwise, and the right portion of the pallial cavity is larger than the left (Golikov and Starobogatov, 1989). Hence, the function of the left ctenidium decreases with a subsequent downward displacement of the slit. If the shell is elongated and turriform, the shell axis is almost parallel to the direction of the mollusk's movement (Fig. 17c), whereas the pallial cavity is turned to 90° clockwise. In this position, the left portion of the pallial cavity hangs over the head, while the right portion is strongly reduced and, hence, the function of the right ctenidium decreases. These changes in theory should affect the position of the slit that serves as a passage for the exhalant water, i.e., when the right portion of the pallial cavity decreases, the slit should be shifted towards the suture. In reality, we observe the following: the turriform shells of Murchisoniina show the slit either in the middle, or in the upper part of the whorl face, which, however, does not indicate the plasticity of this character. In contrast, in murchisoniid gastropods, the position of the slit usually differs in different epochs and is fixed in various phylogenetically distinct groups at different time planes. It should be taken into account that the supposed position of the shells in murchisoniid gastropods in relation to the foot base is here accepted as the most energy efficient. Despite the fact that, during movement, extant mollusks can easily and widely rotate their shell in relation to the foot, changes in the shell shape without a change in the general arrangement of the pallial organs can lead to a need for constant calibration of the shell axis. In addition, the observed retention of the subcentral position of the slit on the whorl face of murchisoniid gastropods during relatively long periods suggests that changes in the general arrangement of the pallial organs are not easy and, hence, the symmetrical subdivision of the pallial cavity is important as a plesiomorphic character of these gastropods.

Four major evolutionary trends are recognized within the Murchisoniina, which correspond to four families Plethospiridae, Murchisoniidae, Orthonematidae, and Ptychocaulidae Mazaev fam. nov. Members of these families show the presence of a narrow and, in most cases, relatively deep slit, which forms a selenizone as the shell grows. Even in the species where shells lack a spiral ornamentation, the selenizone is always distinct. However, it never becomes as complex as in some bellerophontid or pleurotomariid gastropods, in which its surface is ornamented with massive elements, such as lunulae or nodes (except for Triassic *Vistilia* Koken, 1896 and *Trypanocochlea* Tomlin, 1931, if these are reallymurchisoniid gastropods). The first Plethospiridae (*Plethospira, Seelya*) appeared in the Early Ordovician, while the earliest Murchisoniidae (*Hormotoma, Ectomaria*) first appeared later, in the Middle Ordovician. If this is true, it would be logical to suggest that Murchisoniidae evolved from Plethospiridae, whereas the latter evolved from ancient Pleuromariida, from which they inherited a "simplified" selenizone, typical of all murchisoniid gastropods. The suggested lineage agrees with the interpretation of a stable morphological trend, from the low conical shell to the high-spired ovate shell and,then, to the turreted shell. Thus, the two major evolutionary trends within Murchisoniina were primarily related to the development of two types of high-spired shells (ovate high-spired and turreted) and, then, to the realization of possible changes in the general arrangement of the pallial organs.

The trend comprising species with ovate high-spired shells includes at least eight genera assigned to the family Plethospiridae Wenz, 1938. The genus *Plethospira* Ulrich, 1897, confirmed from the Lower Ordovician beds, has an ovate high-spired shell with rapidly expanding whorls. The incipient abapical canal is well discernible. The slit is located almost in the middle of the outer lip, and the selenizone is distinct. The development of the incipient abapical canal and presence of other above characters show that the axis of the shell was more likely inclined toward the substrate during the movements of the mollusk, and was almost in parallel with the anteroposterior axis of the body. In other words, the pallial cavity was rotated clockwise. In this position, as described above, the left portion of the pallial cavity hangs over the head, whereas the right portion is strongly reduced. Because of the unequal water flows in the right and left portions of the pallial cavity, the functional significance of the right ctenidium should have been reduced, which in turn led to the slit shifted towards the suture. However, no expressed trend in the slit changing position from subcentral to sutural can be observed, which is apparently connected with the shell shape intermediate between almost trochoid shells of pleurotomariids and turriform shells of most murchisoniid gastropods.

Other two major trends in Murchisoniina (Murchisoniidae and Orthonematidae) are characterized by high-spired or turriform shells and a narrow slit similar to that of Plethospiridae, which forms a selenizone. During the motion of the mollusk, the axis of the turriform shell of *Murchisonia* should have been parallel to the anteroposterior axis of the body (Linsley, 1978, p. 204, text-fig. 14). As in Plethospiridae, the pallial cavity of Murchisoniidae was rotated clockwise. However, because the shell axis was parallel to the anteroposterior axis of the body, the right portion of the pallial organs should have been reduced even greater. As the functional pressure to the left ctenidium, the abapical canal is developed to a varying degree in most Murchisoniidae. It is evident that the

mollusks, in which the slit was formed at the midwhorl face had to support the shell in this way to provide water flows in the approximately equal portions of the pallial cavity. The shift of the slit towards the suture and a considerable decrease of the left portion of the pallial organs should have led to the reduction of the energy expenditure to support the shell. From this point of view, the appearance of taxa with a displaced slit is logical and expected. However, the evolution of Murchisoniidae shows that, in these gastropods, which inherited the symmetrical arrangement of the pallial organs, such changed were neither easy nor fast. During the entire time of the existence of this evolutionary trend from the Early Ordovician to at least the Late Permian, the selenizone retains its position at or below the middle of the whorl face.

The first and essential changes, which could lead to almost complete disappearance of the right portion of the pallial organs are at present based on the discovery in the Lower Devonian of Alaska of *Farewellia heidelbergerae* Frida et Blodgett, 2004. Teleoconchs of this species have a specific combination of characters: selenizone shifted to the maximum towards the suture and well-developed collabral ornamentation. The position and type of the selenizone in this species shows an apparent morphological similarity to *Loxosonia zygopleura* Batten, 1985 from the Lower Permian of Malaysia. However, the geochronological ranges of members of these genera are separated by a large gap; hence, the appearance of similar characters in both genera was most likely independent. The appearance of *Farewellia* marked the dead end side branch in the evolution of the second major trend in murchisoniid gastropods, while representatives of this evolutionary branch constitute the family Farewelliidae Mazaev fam. nov.

The contradiction between the symmetrical arrangement of the pallial organs and the turriform shell was also resolved in a different way, through the increased control of the shell spatial position. This strategy was performed through the following morphological changes: (1) the formation of a wide columella (which increased the lever function of the columellar muscle), (2) increased number of whorls due to a decrease in height in relation to width (increased value of the function of the application of the lever), (3) the development of the columellar fold (essential increase in efficiency of the columellar muscle). The above morphological characters can to the full extent be observed in *Ptychocaulus verneuili* (Koken, 1889) from the Lower Devonian of Bohemia and, to a lesser extent, in *Vetotuba brazier* (Etheridge, 1890) from the Silurian beds in the vicinity of Melbourne, in *Melissosoa compacta* (Hall, 1860) from the Lower Devonian of New York, in *Medfracaulus turriformis* (Chernyshev, 1893), and also in *Coelocaulus karlae* Rohr, Blodgett et Frida, 2003 from the Upper Silurian of Alaska. The assignment of the latter species to the genus *Coelocaulus* (Rohr et al., 2003; Rohr and Blodgett, 2008) seems erroneous because the type species of this genus has a narrow phaneromphalous umbilicus and relatively high whorls and, therefore, it should be classified within *Medfracaulus*, or assigned to a new genus). Thus, the above five species constitute the fourth evolutionary trend in murchisoniid gastropods. Based on the degree of morphological disparity and fixation of new characters that are not found in the related groups (the development of the phaneromphalous umbilicus, shells composed of numerous low whorls (up to 30 in the holotype of *Ptychocaulus verneuili* (Knight, 1941, p. 285)), representatives of this evolutionary branch are assigned to the family Ptychocaulidae Mazaev fam. nov. It is possible that the new family should also include the genus *Gaskonadia* Weller et St. Clair, 1928, which, however, differs in the expanded aperture of the last whorl.

With regard to Murchisoniidae, it should be noted that this trend shows two tendencies: (a) gradually increasing complexity of shell ornamentation and (2) appearance of the new variation of the whorl profile. The relatively recently discovered *Cheeneetnukia* and *Ulungaratoconcha* with subcylindrical whorl profile look very unusually among the other representative of this trend, but certainly belong to it (Blodgett and Cook, 2002). Like other Murchisoniidae, they have a selenizone not exceeding the middle of the whorl face. In the view of the theory of homologous series, their appearance is logical because in its whorl profile these two genera are very similar to the orthometid genus *Cibecuia*. Similar examples of parallelisms in the whorl profile can be observed while comparing other genera in the families Murchisoniidae and Orthonematidae.

Ectomaria, the earliest known member of Murchisoniidae, has a relatively wide selenizone, which is bounded by two spiral lirae, the depth of the slit on the shells of these genera remains unknown. Other members have a narrower selenizone. The morphology of the slit is known for certainty only for *Goniasma* (Fig. 15a). Similar slit morphology (very narrow and deep) is observed in *Murchisonia, Lodanaria*, and *Helicospira*. These four genera form a phylogenetic lineage which differentiated in the Early Devonian and existed until the Triassic. The length of their pallial cavity was approximately one-fourth of the last whorl. Interestingly, the terminal genus *Helicospira* has a scalloped selenizone, which was most likely formed as a series of openings preceding the slit. Similar structures in a more hypertrophic expression are observed in extant Fissurellidae and Haliotidae and in some Paleozoic and Mesozoic members of Vetigastropoda. The transformation of the slit in various structures (slit + opening, series of openings, one opening) is determined by specific arrangement of water flows in the pallial cavity similar to that in extant pleurotomariids, in which the exhalant canal is formed by the pallial fold (Voltzow et al., 2004).

Apparently, *Goniasma* in the Early Carboniferous gave rise to species of the third of the major evolution-

ary trends in murchisoniid gastropods, family Orthonematidae. *Goniasma* and *Stegocoelia* are similar in ornamentation, whorl profile, selenizone morphology, morphology of the juvenile whorls and the protoconch. However, *Stegocoelia*, like other orthonematid genera, is characterized by an important character, selenizone shifted toward the suture. Thus, in the history of the suborder Murchisoniina the appearance of this character occurs at least twice and independent from each other. The appearance in the Early Carboniferous of taxa with this important apomorphy later resulted in explosive radiation. In the Lower Pennsylvanian, there are at least nine genera of Orthonematidae, and only three of Murchisoniidae. The position of the selenizone (which reflects the position of the slit) should not be considered as a fixed morphological character, but as a trend in the evolution of this character, judging from the adaptations of the pallial organs to the torsion. The evolutionary trend of orthonematids shows the entire succession of changes in the position of the slit from almost subcentral (but always above the midwhorl face), as in *Stegocoelia*, to a more strongly shifted towards the suture, as in the majority of orthonematid species, and eventually to the position approximating the suture, like, e.g., in *Arribazona devispira* Mazaev, 2003, *Orthonema marvinwelleri*, *Vebericochlis arguta* (Licharew, 1975), etc. (Figs. 12c; 15b–15d). In the last case, it is evident that the position of the slit does not leave space sufficient for the right ctenidium, and it was more likely reduced in species at the terminal ends of this evolutionary trend. This explains the appearance of species, in which the slit did not at all develop in ontogeny, while the morphology of the palatal apertural margin, reflected by the growth lines, retains characters of the apical whorls (the delayed development of the slit at the beginning of the teleoconch morphogeny), primarily in the type species *O. salteri*. Various types of growth lines, reflecting the shape of the apertural margin in several *Orthonema* species, are considered in detail in the Chapter "Morphology."

Representatives of Orthonematidae show a greater morphological diversity than Murchisoniidae. In general, many homologous characters (kind of ornamentation, selenizone, and whorl profile) independently evolve in both evolutionary trends.

The differentiation (radiation) within orthonematids primarily followed various models of spiral ornamentation and, secondarily, the appearance of various types of whorl profiles within each model, i.e., realization of all possible combinations.

Evidently, the earliest model in this succession of models is that including *Stegocoelia, Taosia, Vebericochlis*, and *Orthonema*. These genera are characterized by the presence on the whorl surface of four major, well-developed spiral ridges and are clearly distinct in the whorl profile. The succession of genera: *Concinnispira, Hermosanema*, and *Altadema* are characterized by the trend toward the reduction of spiral elements of ornamentation on the last whorls. Despite the morphological similarity, the last three genera do not form a phylogenetic succession, since they existed in different time and different geographical provinces and most likely evolved from different species of *Stegocoelia*.

The genus *Orthonema* is quite distinct in this respect. As shown in the Chapter "Morphology", almost all species of this genus irrespective of the degree of the development retain to a varying extent the set of the other characters. The genus *Orthonema*, along with the genus *Metaorthonema*, form a separate phylogenetic branch.

The next group comprises the genera *Cibecuia, Arribazona*, and *Ferganispira* and is characterized by the smooth whorl faces with a selenizone, the only spiral element of ornamentation. Like in the previous group of genera, they are clearly distinguished by the whorl profile. In *Cibecuia* and *Arribazona*, the basal parts of the adult whorls may show extremely weak spiral ornamentation. The genus *Arribazona* most likely evolved from *Stegocoelia* and, perhaps, is ancestral to *Ferganispira* and *Laschmaspira*. The origin of *Cibecuia* is less evident. In some *Cibecuia*, juvenile whorls show spiral lirae. The morphology of this genus is similar to that of *Orthonema* and *Taosia* and possibly this genus has a common ancestor *Stegocoelia*, with these genera. The genus *Loxosonia*, from the Lower Permian of Malaysia with a grooved selenizone is morphologically similar to *Arribazona* and *Ferganispira* in a number of characters (smooth whorls rounded in cross section).

The genus *Laschmaspira* together with the species described by Licharew (1967, pp. 57, 58) from the Early Permian of Fergana as *Stegocoelia* ? *diversicostata* Licharew, 1967 and *S.* ? *kirgisica* Licharew, 1967, which should certainly be assigned to a new genus, form a separate group within Orthonematidae. All these are clearly distinct morphologically, i.e., their spiral ornamentation is composed of narrow or wide grooves and, depending on their arrangement, the shell possesses either densely spaced spiral lirae with narrow grooves in between, or lirae alternating with relatively wide bands separated by variously wide grooves. A homologous type of ornamentation is observed in Plethospiridae (*Plethospira*) and in Murchisoniidae (*Aclisina*).

Thus, the family Orthonematidae evolved by forming groups with different types of ornamentation and, within those, through differentiation of the whorl profile. This interpretation allows the following hierarchy of the morphologically significant characters in the family Orthonematidae.

The identification at the generic level is based on the following characters: the morphology of slit and selenizone and the combination of major types of ornamentation and whorl profile. The identification to species is based on the following characters: various whorl profile and ornamentation within the recognized major types, the whorl width-to-height ratio, appearance and number of auxiliary spiral lirae or

nodes, slight fluctuations of the growth line shape, general shell outline, whorl expansion rate, shape and size of the columella, the formation of the pseudoumbilicus by the extension of the columellar lip.

Another evolutionary trend, which included, according to the paradigm proposed in this paper, members of the family Sinuspiridae, evolved in parallel and independently from the evolutionary trends within the suborder Murchisoniina. The morphology of shells in this family is somewhat similar to that of shells of Murchisoniidae, although they have one character in common, a wide U- or V-shaped slit, which does not form a selenizone. A similar type of slit is observed in other large Paleozoic gastropod groups: in the bellerophontid family Sinuitidae Dall, 1913 and pleurotomariid family Sinuopeidae Wenz, 1938. Golikov and Starobogatov (1989, p. 34) considered such a slit to be very primitive, marking the early evolution of the order Pleurotomariida. Apparently, Sinuspiridae inherited this slit morphology from the family Sinuopeidae and evolved independently from the family Murchisoniidae. Early Sinuspiridae (*Sinuspira* Perner, 1907, *Catozone* Perner, 1907, *Mishelia* Roemer, 1852) have a rounded whorl profile, with shell surface covered by distinct, prominent growth lines, sometimes becoming threadlike sinusoid lirae. Later members of Sinuspiridae show well-developed elements of spiral ornamentation (*Callispira*), which are sometimes combined with collabral elements (*Micrentoma* Donald, 1898). The sinus in early members of this family is subcentral and, in *Catozone*, it is considerably shifted towards the suture. Apparently, like in murchisoniids, Sinuspiridae showed a tendency to develop asymmetry of the pallial organs as a result of torsion.

CHAPTER 4. SYSTEM OF THE SUBORDERS MURCHISONIINA AND SINUSPIRINA

The taxonomy of Murchisoniidae proposed by Wenz (1938, p. 159) can be considered as the first attempt to develop the systematics of this group. He proposed to consider the family Murchisoniidae as including four subfamilies: Murchisoniinae Wenz, 1938, Hormotominae Wenz, 1938, Pithodeinae Wenz, 1938, and Omospirinae Wenz, 1938 (the latter two provisionally), and the family was included in the superfamily Pleurotomariacea.

In *Osnovy paleontologii* (Pchelintsev and Korobkov, 1960) the taxa proposed by Wenz as families and subfamilies were elevated to superfamilies and families, respectively, and the generic content of some of these was expanded.

A more justified emendation of the murchisoniid gastropod taxonomy was proposed in *Treatise* (Knight et al., 1960). A new suborder, Murchisoniina Cox et Knight, 1960, was introduced to tentatively accommodate them in the order Archaeogastropoda. The suborder included two families: Murchisoniidae and Plethospiridae Wenz, 1938, within one superfamily Murchisoniacea Koken, 1896. The family Murchisoniidae included almost all genera previously listed by Wenz within the Hormotominae, which was listed as a synonym of Murchisoniidae. Another group, Omospirinae with slightly emended content, was taken out of Murchisoniacea and placed in Pleurotomariacea. The subfamily Plethospirinae Wenz, 1938 was excluded from Pleurotomariidae and placed in Murchisoniacea as a family, with two subfamilies Plethospirinae (sensu stricto) and Pithodeinae.

In general, except for the system proposed by Wagner (2002), which I cannot comment on as not understandably substantiated, this taxonomy of murchisoniid gastropods is currently uniformly accepted, with small changes in the recent decades, as addition of new generic taxa, and the family Cheeneetnukiidae Blodgett et Cook, 2002. At the same time, detailed analysis of the family Murchisoniidae implies that its taxonomy cannot be logically explained from the point of view of character hierarchy. In fact, a considerable number of generic taxa were established declaratively. However, the absence of indications in the original diagnoses which characters in particular and why were chosen to distinguish a genus or subgenus, did not influence the correctness of their recognition, but rather influenced the absence of any hierarchy of characters within the family Murchisoniidae. In practice, the presence of the selenizone or of a prominent sinus in a turreted shell was considered a sufficient criterion to place it in this family.

The placement of the family Orthonematidae is another key question in the systematics of murchisoniid gastropod. This family is here considered as a sister group of the family Murchisoniidae. This point of view, on the one hand, is based on the facts and their correspondence to the subsequent conclusions, which are discussed in the previous chapter, but, on the other hand, can be disproved from the point of view developed by Nützel and Bandel.

A detailed consideration of plethospirids and early Early Paleozoic murchisoniids is beyond the scope of this study. It is evident that detailed morphological analysis of Early Paleozoic mollusks will in the future introduce essential corrections in the proposed interpretation. The question of the possible assignment of the Triassic genera *Vistilia* Koken, 1896 and *Trypanocochlea* Tomlin, 1931 to murchisoniid gastropods is also beyond the scope of this work.

With regard to the rank and placement of murchisoniid gastropods, I completely agree with the systematics proposed by Golikov and Starobogatov (1989), in which murchisoniid gastropods are treated as the suborder Murchisoniina Cox et Knight, 1960 and included in the order Pleurotomariida Cox et Knight, 1960, which, along with the other two orders, Bellerophontida Ulrich et Scofield, 1897 and Trochonematida Golikov et Starobogatov, 1989, constitute the subclass Scutibranchia. Apart from Murchisoni-

ina, the suborders *Sinuopeina* Golikov et Starobogatov, 1989, *Fissurellina* Golikov et Starobogatov, 1989, *Pleurotomariina* Cox et Knight, 1960, and *Haliotiina* Golikov et Starobogatov, 1989 were included in the order Pleurotomariida.

Thus, in the present paper, murchisoniid gastropods are accepted as the suborder Murchisoniina, with the murchisoniid and pleurotomariid gastropods being sister groups, while pleurotomariid gastropods are regarded as an ancestral group. Murchisoniid gastropods are accepted as a family deviating from its ancestral group being characterized by the maximum protrusion of the spire to the right. These groups differentiated at a different (lower) level of differences than the pleurotomariid gastropods and bellerophontid or trochonematid gastropods.

In contrast to Murchisoniidae, which evolved from Pleurotomariina with a normally formed selenizone, Sinuspiratidae fam. nov. probably evolved from Sinuopeina and retained a primitive U-shaped slit, which did not form a selenizone. Like murchisoniid gastropods, members of Sinuspiratidae fam. nov. show the maximum shift of the spire to the right. The Sinuspiratidae fam. nov. are distinct from members of the suborder Sinuopeina and, therefore, a new suborder, Sinuspirina Mazaev subordo nov., is proposed to accommodate them in the order Pleurotomariida.

Seven genera that have been traditionally assigned to the family Murchisoniidae are now included in Sinuspiratidae. The genus *Callispira*, with its set of characters similar to that of *Micrentoma* is also assigned to Sinuspiratidae. The systematic position of *Callispira* has been for a long time unresolved. Nelson (1947) placed it in the Loxonematacea. In *Treatise*, the genus *Callispira*, like *Orthonema*, was placed in Turritellidae (Knight et al., 1960). Later, based on the fact that the U-shaped sinus is somewhat displaced towards the suture, *Callispira* was erroneously assigned to the family Orthonematidae (Mazaev, 2003).

The suborder Murchisoniina, according to the taxonomy accepted in the present paper, includes five families. This taxonomy is based on the change in several major characters, primarily the evolution of the main aromorphosis (change in the morphology of the pallial cavity), which is reflected in the position of the selenizone. In this case, the shell shape is one of the major characters.

Representatives of the family Plethospiridae with their high-spired ovate shells occupy an intermediate position between the low-spired shells of ancient Pleurotomariida and turreted shells of Murchisoniidae. The taxonomic composition of Plethospiridae is not discussed in this paper and requires a thorough revision. Provisionally, I am not inclined to accept its subdivision into Plethospirinae and Pithodeinae proposed by Cox and Knight (Knight et al., 1960), probably based on the development of the subapical canal. The family includes shells with diverse ornamentation, including the collabral ornamentation in the shape of lirae following the growth lines, while the selenizone which is similar to that of Murchisoniidae and located approximately at midwhorl, but, in *Leptorima* Perner, 1907 from the Upper Silurian of Bohemia, it is strongly shifted to the suture. The genus *Wortheniopsis* Borm, 1825, based on the morphology of its aperture and ornamentation, should be transferred to Pleurotomariida. The same is true of *Plathyzona* Knight, 1945, which has an extremely wide and variously ornamented selenizone. The generic content of Plethospiridae is low, including at least eight genera.

The family Murchisoniidae contains turreted shells with a prominent selenizone, which is located below or near the midwhorl. From at least 18 genera included in the family, only *Donaldospira, Goniasma*, and *Cerithioides* are known from the Pennsylvanian. *Donaldospira* was originally proposed as a subgenus of the genus *Murchisonia* (Batten, 1966). Later, Batten (1985) considered *Donaldospira* and *Goniasma* as subgenera of *Stegocoelia*. Because the selenizone in *Donaldospira* and *Goniasma* is below or at the midwhorl, both taxa belong to the family Murchisoniidae, and the level of their morphological disparity corresponds to the generic level. Nützel and Bandel (2000) established the family Goniasmatidae Nützel et Bandel (originally Goniasmidae), with the type genus *Goniasma*, in the order Cerithiomorpha. Two more genera, *Stegocoelia* and *Cerithioides*, were included in the family based on the combination of the cerithiomorphic protoconch and a slit on the palatal margin of the aperture. The phylogenetic reconstructions advocated in the present paper are mostly based on the observed changes in the apertural morphology and other characters of the teleoconch. Therefore, the genus *Stegocoelia* is here assigned to Orthonematidae, while *Cerithioides*, to Murchisoniidae. Goniasmatidae and Hormotominae are here considered as junior synonyms of Murchisoniidae. Other taxa included in Murchisoniidae require serious revision with subsequent recognition of phylogenetically-based hierarchic system of characters. I completely agree with the opinion of Blodgett et al. (1999) that all taxa listed by Knight et al. (1960) as subgenera within *Murchisonia*, and *M.* (*Ostioma*) Tassel, 1980 should be considered as separate genera. *Cheeneetnukia* Blodgett et Cook, 2002 and *Ulungaratoconcha* Blodgett et Cook, 2002, which were originally (Blodgett et Cook, 2002) included in the family Cheeneetnukiidae Blodgett et Cook, 2002, are here also included in Murchisoniidae. However, the level of disparity (whorl profile) between these two genera and other Murchisoniidae genera does not allow their assignment to different families. If such an approach was accepted, genera with a rounded whorl profile, like *Cerithioides*, should have been assigned to a separate family, whereas the rank of the family Murchisoniidae would have been raised to superfamily. Therefore, following the proposed phylogenetic reconstruction for murchisoniid gastropods

and resulting weight of characters, it is proposed to lower the rank of the family Cheeneetnukiidae to subfamily, place it in the family Murchisoniidae, and establish the subfamily Murchisoniinae to accommodate other taxa included in Murchisoniidae.

The Ptychocaulidae include genera with the selenizone position similar to that in Murchisoniidae, but with idioadaptations (perforated umbilicus, with subsequent appearance of the columellar fold, and with low and wide whorls). It is evident that the above characters allow clear recognition of this group and their taxonomic weight corresponds to that of a family. Thus, the family includes six genera, while the genus *Gaskonadia* Weller et St. Clair, 1928 is included tentatively.

As shown in the previous chapter, the evolution of the main aromorphosis in Murchisoniina (trend to asymmetry of the pallial cavity) led to separation from Murchisoniidae first of Farewelliidae and later of Orthonematidae. The former family presently includes only one species, while the family Orthonematidae includes 13 genera. Morphology of selenizones, ornamentation, and whorl profiles are repeated in Orthonematidae and Murchisoniidae, indicating lowering of their taxonomic value, i.e., they correspond to ever decreasing branches in a huge phylogenetic tree. The differentiation (radiation) within Orthonematidae was primarily directed towards diversification of spiral ornamentation and, secondarily, towards the appearance of different whorl profiles within each of the resulting groups, thereby towards all possible combinations of these characters. The systematic position of the family Orthonematidae and its type genus *Orthonema* was for a long time a subject of many discussions. Wenz (1938) assigned *Orthonema* to the subfamily Acanthonematinae, which he assigned to Loxonematidae. Following Knight's approach, the genus *Orthonema* was included in the family Turritellidae Woodward, 1851 (Knight, 1934; Knight et al., 1960; Anderson et al., 1985; Batten, 1985; Erwin, 1988; Ponder and Waren, 1988). On the other hand, many authors assigned *Orthonema* to acanthonematid gastropods, the taxonomic position of which was constantly under discussion. For instance, Tracey et al. (1993) provisionally included Acanthonematidae in Murchisonioidea. Nützel (1997) stated that Acanthonematidae was a cerithiomorphic sister group or the order Ptenoglossa and possibly closely related to Cerithioidea, Murchisonioidea, and Pleurotomarioidea. Later, Nützel and Bandel (2000) accepted that the family Acanthonematidae was not a good choice for accommodating *Orthonema*. Based on the protoconch morphology, they assigned *Orthonema* to the order Cerithiomorpha Golikov et Starobogatov, 1975. Four genera, *Knightella* Longstaff, 1933, *Paleostylus* Mansuy, 1914, *Spiromphalus* Hayasaka, 1939, and *Metorthonema* Erwin, 1988, were stated to be closely related to *Orthonema* and a new family, Orthonematidae (Orthonemidae prior to 2005), was proposed to accommodate these genera (Bouchet and Rocroi, 2005). Of the above genera, the protoconch morphology was studied only for *Orthonema*. The same paper showed protoconchs morphologically similar to protoconchs of *Orthonema*, but because teleoconchs of these species have a slit on the palatal edge of the aperture, a new family, Goniasmatidae Nützel et Bandel, 2000 (Goniasmidae in publications prior to 2005) (Bouchet and Rocroi, 2005), was proposed to accommodate these taxa. Thus, *Goniasma, Stegocoelia*, and *Cerithioides* were excluded from murchisoniid gastropods and assigned to caenogastropods.

Although the genus *Orthonema* was traditionally considered to be separate from murchisoniids (except for the study of Tracey et al. (1993), where it was traditionally assigned to Murchisoniidae), it has many characters in common with the genus *Stegocoelia*. Because the original diagnosis of *Orthonema* allowed the assignment to this genus only of species with straight growth lines, whereas more species with a labral sinus continued to be described, many species were erroneously assigned to *Stegocoelia, Orthonema*, or *Murchisonia*. A detailed analysis of variability of morphological characters in various *Orthonema* species shows that the genera *Orthonema, Vebericochlis, Taosia*, and *Stegocoelia* are closely related (Mazaev, 2002). The family includes *Orthonema, Metorthonema, Stegocoelia, Taosia, Vebericochlis, Altadema, Concinnispira, Hermosanema, Cibecuia, Arribazona, Ferganispira, Loxosonia*, and *Lashmaspira*. The genera *Knightella, Paleostylus*, and *Spiromphalus*, which were originally listed by Nützel and Bandel in this family, are excluded from the family and assigned to loxonematid gastropods.

In the overwhelming majority of papers, some of the listed taxa are considered as subgenera of the genus *Stegocoelia*. *Stegocoelia* was established by Donald (1889) as a "section" of *Murchisonia*. Later, Donald established the "section" *Hypergonia* as an auxiliary taxon, which "agrees with *Stegocoelia* in the position of the sinus, but differs in the absence of the inner lip reflected on the columella and the absence of umbilicus" (Donald, 1892, p. 564). Longstaff (1926, p. 529) (née Donald), after detailed studies, concluded that *Stegocoelia* can be a synonym of *Hypergonia* and raised the latter taxon to a genus. In *Treatise*, the priority of *Stegocoelia* was restored and three subgenera were included in *Stegocoelia: Stegocoelia, Hypergonia*, and *Taosia* Girty, 1939 (Knight et al., 1960). The last taxon was established by Girty as a genus. Batten (1995) included two more taxa in *Stegocoelia*: *Donaldospira* and *Goniasma* Tomlin, 1930, regarding them as subgenera (Batten, 1995). Kues and Batten (2001) maintained this taxonomy and rank. However, considering the position of the selenizone, *Donaldospira* and *Goniasma* should be taken out of *Stegocoelia* and regarded as separate genera in the family Murchisoniidae.

Vebericochlis was proposed by Licharew (1967) within *Stegocoelia* and described as a monotypic

taxon. The well-developed spiral and collabral rows of nodes in the type species *S.* (*Vebericochlis*) *maclayi* Licharew, 1967 the author of the genus considered to be an important diagnostic character. The subsequent revision of the Fergana material showed that, in some shells of the type series, the nodes are closely approximated to form normally developed spiral lirae. Such shells Licharew described as *Stegocoelia* (*Hypergonia*) *ambigua* Licharew, 1967, which was later treated (Mazaev, 2001) as a junior synonym of the type species of *Vebericochlis*; this resulted in the revision of the original diagnosis of *Vebericochlis*. It is evident that the accumulation of new material required revision of all other above taxa to establish an understandable hierarchy of characters.

Batten (1966, p. 76) noted that "the principal difference between the three subgenera of *Stegocoelia* is based on the relative height of the spire, the position of the periphery on the whorl, and the whorl profile... In *S.* (*Stegocoelia*), the shell is low spired, and the periphery is high on the whorl which is usually rounded. In *S.* (*Hypergonia*) Donald, the shell tends to be high spired, with the periphery located about the midwhorl. Finally, *S.* (*Taosia*), which is also high spired, has periphery low on the whorl and, in addition, may develop nodes or other forms of collabral ornament." Indeed, *Taosia* is clearly distinguished by the low periphery and the angular whorl profile, which is responsible for the position of the periphery. With regard to the other two taxa, *Stegocoelia* sensu stricto and *Hypergonia*, the diagnostic characters are not exactly the best to diagnose the taxa, since as the time passed, a number of species have become known that exhibit a reverse combination of characters: low spire–angular whorls profile (*S. knighti*) and high spire–rounded whorl profile (*S. acuta*). Moreover, many species show varying whorl profiles, both at different ontogenetic stages (*S. alta, S. klyazmaensis*) and in the series of intraspecific variation (*S. acutiformis*). Thus, *Hypergonia* is a junior synonym of *Stegocoelia*. It is clear that *Stegocoelia, Taosia*, and *Vebericochlis* are sufficiently distinct in their whorl profile. In addition, there is no reason to consider the latter two taxa as subgenera, as their differences are at a similar level; hence, they should be considered as genera. At the same time, their separation based solely on the whorl profile is insufficient because of the existence of adjacent taxa similar in the number of primary lirae on the whorl face: *Orthonema, Concinnispira, Hermosanema*, and *Altadema*. Therefore, to diagnose them a combination of several characters should be taken into account: the whorl profile type, characters of spiral ornamentation on juvenile whorls and basal surface of the last. The combination of these characters in unique for each of the above taxa.

The genera *Cibecuia, Arribazona, Ferganispira*, and *Loxosonia* have an almost smooth whorl face, but are relatively clearly distinguished by their whorl profile, except the last one, with a narrow, grooved selenizone.

The genus *Laschmaspira* Mazaev, 2003 has a principally different morphology of spiral ornamentation, formed by grooves separated by numerous spiral costae. The genus *Microlampra* established by Pan and Erwin (2002) within Microdomatidae was later transferred to the family Orthonematidae (Nützel, Pan, and Erwin, 2002). Unfortunately, it was based on juvenile shells, with one or 1.5 whorls after the protoconch. Morphologically these are almost identical to juvenile shells of the genus *Stegocoelia* and, therefore, until the teleoconchs of the type species are studied, it would be impossible to confirm whether or not *Microlampra* is a synonym *of Stegocoelia*.

The following system of the suborders Sinuspirina and Murchisoniina is proposed in the present paper:

Order Pleurotomariida Cox et Knight, 1960

Suborder Sinuspirina Mazaev, 2012, subordo nov.

Family Sinuspiridae Mazaev, 2012, fam. nov.

Sinuspira Perner, 1907;
Catozone, Perner, 1907;
Coelocaulus Oehlert and Oehlert, 1888;
(?) *Donaldiella* Cossmann, 1903;
Michelia Roemer, 1852;
Micrentoma Donald, 1898;
Callispira Nelson, 1947.

Suborder Murchisoniina Cox et Knight, 1960

Family Murchisoniidae Koken, 1896

Subfamily Murchisoniinae Koken, 1896

Murchisonia d'Archiac et deVerneuil, 1841;
Solenospira Ulrich et Scofield, 1897;
(?) *Ectomaria* Koken, 1896;
(?) *Turritoma* Ulrich, 1897;
Hormotoma Salter, 1859;
Hormotomina Grabau et Shimer, 1909;
Biangularia Spitz, 1907;
Morania Horny, 1953;
Ostioma Tassel, 1980;
Lodanaria Dahmer, 1925;
Aclisina deKonink, 1881;
Cerithioides Haughton, 1859;
Goniasma Tomlin, 1930;
Donaldospira Batten, 1966;
Helicospira Girty, 1915;
Bellazona Gordon et Yochelson, 1987.

Subfamily Cheeneetnukiinae Blodgett et Cook, 2002

Cheeneetnukia Blodgett et Cook, 2002;
Ulungaratoconcha Blodgett et Cook, 2002.

Family Plethospiridae Wenz, 1938

Plethospira Ulrich et Scofield, 1897;
Seelya Ulrich et Scofield, 1897;
Gyrodoma Etheridge, Jr., 1898;
Diplozone Perner, 1907;
Pithodea Koninck, 1881;

Caliendrum Brown, 1838;
Kirkospira Rohr et Blodgett, 2003;
(?) *Leptorima* Perner, 1907;

Family Ptychocaulidae Mazaev, fam. nov.

Ptychocaulus Perner, 1907;
Medfracaulus Rohr, Blodgett et Frida, 2003;
Vetotuba Etheridge, 1890;
Melissosoa Clarke, 1909;
Barroisocaulus Gubanov, Blodgett et Litochkin, 1995;
(?) *Gaskonadia* Weller et St. Clair, 1928.

Family Farewelliidae Mazaev fam. nov.

Farewellia Frida et Blodgett, 2004.

Family Orthonematidae Nützel et Bandel, 2000

Orthonema Meek et Worthen, 1862;
Metorthonema Erwin, 1988;
Stegocoelia Donald, 1889;
Taosia Girty, 1939;
Vebericochlis Licharew, 1967;
Altadema Kues, 2002;
Concinnispira Zernetskaja, 1983;
Hermosanema Kues et Batten, 2001;
Cibecuia Winters, 1956;
Arribazona Kues, 1990;
Ferganispira Licharew, 1967;
Loxosonia Batten, 1985;
Lashmaspira Mazaev, 2003.

CHAPTER 5. SYSTEMATIC PALEONTOLOGY

Order Pleurotomariida Cox et Knight, 1960

Suborder Sinuspirina Mazaev, subordo nov.

Diagnosis. High-spired turreted shells, outer lip with U-shaped slit, selenizone not developed.

Composition. Sinuspiridae, from the Ordovician to Carboniferous inclusive.

Comparison. The suborder is distinguished from Murchisoniina by the absence of selenizone.

Family Sinuspiridae Mazaev, fam. nov.

Type genus. *Sinuspira* Perner, 1907.

Diagnosis. High, turreted shells, outer lip with U-shaped slit, selenizone not developed. Umbilicus absent or narrow, slitlike. Shells smooth or with spiral ornamentation, occasionally with coarse growth lines. Growth lines forming relatively narrow and deep sinus on whorl face and archlike curved forward on basal surface.

Generic composition. Seven genera, Ordovician to Carboniferous inclusive, worldwide: *Sinuspira* Perner, 1907; *Catozone*, Perner, 1907; *Coelocaulus* Oehlert and Oehlert, 1888, (?) *Donaldiella* Cossmann, 1903; *Michelia* Roemer, 1852; *Micrentoma* Donald, 1898; and *Callispira* Nelson, 1947.

Remarks. As mentioned above, several Devonian species previously assigned to *Coelocaulus* (Rohr et al., 2003; Rohr and Blodgett, 2008; Gubanov et al., 1995) should be assigned to other generic taxa within the family Ptychocaulidae. The type species of *Coelocaulus* according to its illustration and descriptions (Knight, 1941) does not have a wide umbilicus and distinct selenizone.

Genus *Callispira* Nelson, 1947

Callispira: Nelson, 1947, p. 463; Knight et al., 1960, p. I317; Kues and Batten, 2001, p. 59; Mazaev, 2003. p. 98.

Type species. *Callispira quinquecostata* Nelson, 1947.

Diagnosis. Shells medium-sized or relatively large, turriform; whorl face profile generally rounded or weakly convex, below suture nearly straight or slightly concave; whorl face ornamented with relatively wide, rounded in cross section spiral lirae (five or less), separated by evenly concave spaces, at least as wide as lirae; upper lira shifted from suture, sometimes thinner than others, smooth or absent; whorl base evenly convex, smooth or ornamented with indistinct weak growth lines, growth lines on whorl face very thin, nearly parallel to shell axis; developing shallow, relatively narrow U-shaped labral sinus, located near two upper spiral lirae, but not bounded by those.

Species composition. Two species from the Pennsylvanian of North America and three species from the Pennsylvanian of the central Russian Platform.

Comparison. This genus is very similar to *Micrentoma* Donald and distinguished from it by the absence of collabral ornamentation.

Remarks. Four species from the Pennsylvanian of North America were described and included in *Callispira* (Nelson, 1947; Hoare, 1961; Hoare et al., 1997; Kues and Batten, 2001). However, only two of those can reliably be assigned to this genus: *C. quinquecostata* Nelson, 1947 and *C. grossa* Hoare, Anderson et Sturgeon, 1997. The systematic assignment of *C. novemcostata* Nelson, 1947, and *Callispira?* sp. *A* Kues et Batten, 2001 is unresolved, since the former species has many spiral lirae on whorl face (over five), while the latter has a distinct selenizone with a smooth flattened band below it. Evidently, new genus-group taxa are needed to accommodate these species. In addition, Licharew (Licharew 1968, p. 46), "somewhat tentatively" assigned four species from the Lower Permian of southern Fergana to the genus *Callispira*. Three of these species were later assigned to *Laschmaspira* (Mazaev, 2003), whereas the systematic assignment of the fourth species *Callispira* ? *nana* Licharew, 1968 remains unclear and requires reexamination.

Callispira okaensis Mazaev, 2003

Plate 1, fig. 1

Callispira okaensis: Mazaev, 2003, p. 98, fig. 3M.

Holotype. PIN, no. 4471/96-1, shell imprint, Ryazan Region, Kasimovskii quarry (near the village of Tashenka); Moscovian Stage, Myachkovian Sub-

stage, Peski Formation, white coral–foraminiferal grainstone series.

Description. The shell is from medium-sized to large, high, turreted, without an umbilicus, composed of at least ten rounded whorls. The suture is distinct, thin, impressed. The whorl face profile is pendant. The whorl face is convex, just below the suture flattened or slightly concave, in the lower part gradually meets the moderately convex whorl base. The whorl face is ornamented with five distinct spiral lirae, the upper lira is slightly smaller than the rest, hardly discernible rounded ridge on the last whorls appear just below the suture. The lirae are separated by equal spaces, while the upper and lower lirae are shifted from the sutures to the same distances. The whorl base is smooth. The apertural margin is not preserved. The columella is massive, nearly straight, inclined to the shell axis. Growth lines are hardly discernible. The protoconch and apical whorls are unknown.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/96-1 holotype	>23.0	9.5
4471/96-2 paratype	>12.0	5.5

Comparison. This species is clearly distinguished from *C. quinquecostata* Nelson, 1947 and *C. bellula* Mazaev, 2003 by the more strongly convex whorl profile and the absence of the prominently concave zone under the suture. It differs from *C. grossa* Hoare, Anderson et Sturgeon, 1997 in the slender shell. The whorl width-to-height ratio in *C. okaensis* ranges from 1.8 to 1.6, whereas in *C. grossa*, it ranges from 2 to 2.4.

Occurrence. Central Russian Platform, Pennsylvanian, Moscovian Stage (Kashirian, Myachkovian, and Krevyakian substages).

Material. Altogether six imprints: one from locality no. 4471/20, one from locality no. 4471/21, two from locality no. 4471/39, and two from locality no. 4471/96.

Callispira bellula Mazaev, 2003

Plate 1, fig. 2

Callispira bellula: Mazaev, 2003. p. 99, fig. 3N.

Holotype. PIN, no. 4471/2-19, shell imprint, Moscow Region, Shchelkovo quarry; Gzhelian Stage, Dobryatinian, Amerevo Formation, top of thick (2 m) member of yellow dolomitized limestone, approximately 3.5 m above the top of the variegated clay series.

Description. The shell is medium-sized, turriform, without an umbilicus, composed of at least ten weakly convex whorls. The suture is impressed, very thin and shallow. The whorl face profile is pendant, the whorl face is moderately convex in the lower regions and moderately concave in the upper region. The whorl face is ornamented with five distinct spiral lirae. Two upper lirae are slightly smaller than the others and the space between them is equal to that between the upper lira and the suture. The space between the second and third lirae is considerably wider than the space between the upper pair of lirae and equal to the space between the other lirae. The third lira separates the upper concave face from the lower convex whorl face and forms a weak shoulder. The fifth lira clearly separates the whorl face from the whorl base and forms a week carina. The whorl base is weakly convex, smooth. Growth lines indiscernible. The protoconch, apical whorls, and aperture are not preserved.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/2-19, holotype	>26	10

Comparison. This species is similar to *C. quinquecostata*, but is distinguished from it by the relatively closely located upper lira and the suture. It clearly differs from *C. grossa* and *C. okaensis* in the whorl profile.

Material. Holotype.

Callispira tricostata Mazaev, sp. nov.

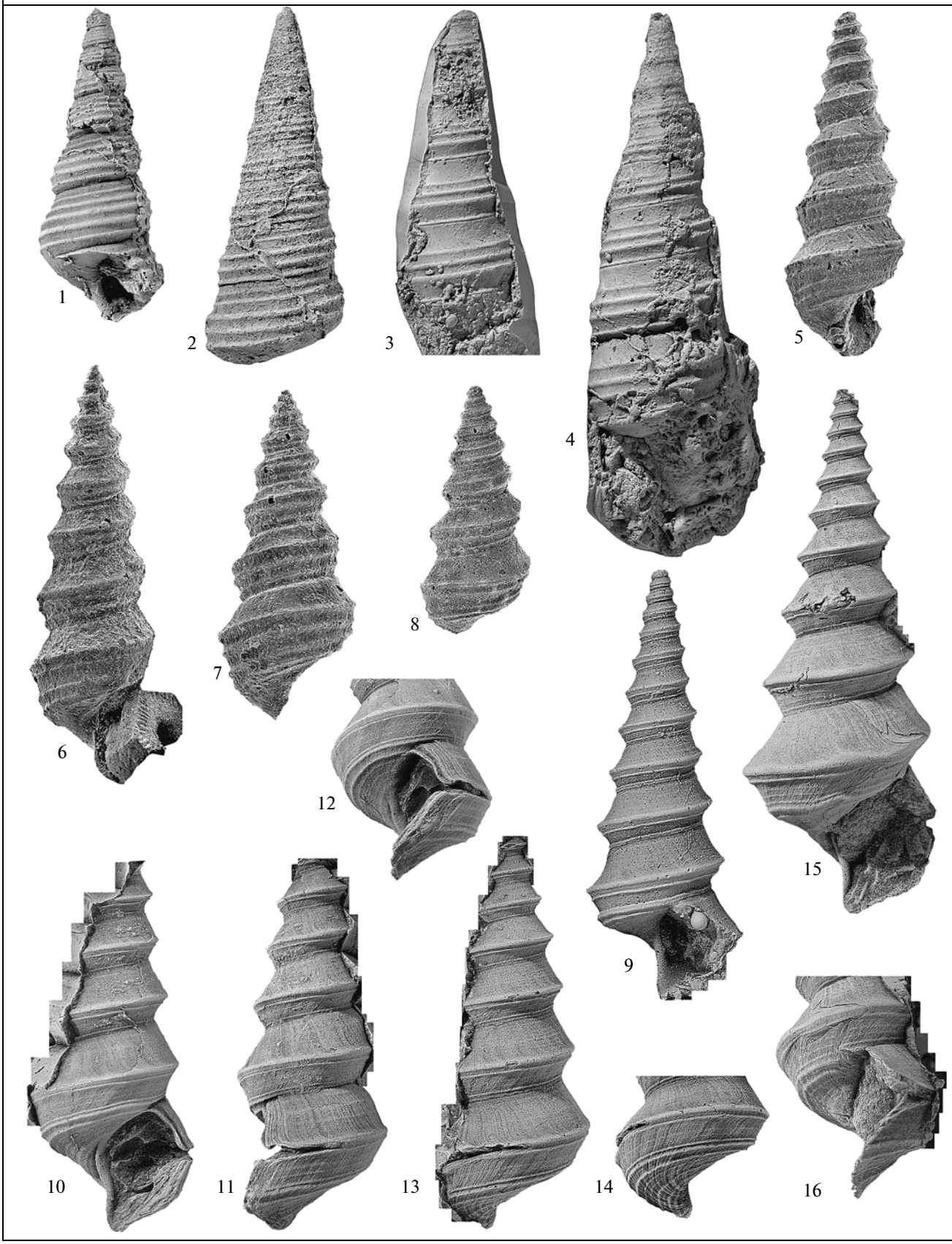
Plate 1, figs. 3 and 4

Etymology. From the Latin *tri* (three) and *costum* (rib).

Holotype. PIN, no. 4471/91-39, paratype PIN, no. 4471/91-38, Vologda Region, Vytegorsk Region, Aleksandrovskii quarry; Moscovian Stage, Podolskian Substage, thick member (up to 1 m) coral–foraminiferal grainstone at the base of the lower tier.

Description. The shell is large, turriform, composed of over ten weakly convex whorls. The suture is impressed, very thin, and shallow. The whorl face profile is pendant: moderately convex in the lower part and moderately concave in the upper part. The whorl face is ornamented with four distinct equally wide spiral lirae. The second spiral lira separates the upper concave and lower convex surfaces of the whorl face and forms a weak shoulder. The fourth lira clearly separates the whorl face from the whorl base and forms a weak carina. Three upper lirae are located approximately at midwhorl and are grouped, separated by even spaces. The fourth (lower) lira is shifted directly to the lower suture, while the lower space between lirae is always slightly wider than the spaces between three upper lirae. The space between the suture and the upper lira is 1.5–2 times wider than the spaces between the three upper lirae and forms a wide, slightly concave, smooth spiral band. The whorl base is weakly convex and smooth. Growth lines are indiscernible. The protoconch, apical whorls and aperture are not preserved.

Plate 1



Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/91-39 (holotype)	>61	>20

Comparison. This species is largely similar to *C. bellula* and distinguished by the number of spiral lirae and the wide band just below the suture.

Material. Holotype and paratype.

Suborder Murchisoniina Cox et Knight, 1960

Family Murchisoniidae Koken, 1896

Type genus. *Murchisonia* d'Archiac et deVerneuil, 1841.

Diagnosis. Turreted, mostly high-spired shells formed of many whorls, ornamented with spiral ornamentation and selenizone or selenizone alone. Selenizone located at midwhorl height or below it. Selenizone not wide, may be narrow and grooved, bounded by either spiral lirae or thin grooves, or located slightly above or below the rest of shell. Selenizone profile straight, convex, or concave; surface of selenizone smooth or ornamented with thin lunulae, may be ornamented with one or several thin auxiliary spiral lirae. Growth lines thin, prosocline above selenizone, forming lunulae on selenizone, beneath selenizone nearly straight or slightly bent forward, opisthocline.

Composition. Two subfamilies, worldwide; Cheeneetnukiinae from the Devonian and Murchisoniinae from the Ordovician to Permian inclusive.

Comparison. Shells of Murchisoniidae share many characters with shells of Orthonematidae (types of ornamentation, whorl profile, and selenizone), differing in the position of the selenizone, which is at or under the midwhorl. This family is distinguished from Farewelliidae fam. nov. by the position of the selenizone and development of primarily spiral ornamentation.

Subfamily Murchisoniinae Koken, 1896

Type genus. *Murchisonia* d'Archiac et deVerneuil, 1841.

Diagnosis. Shells turreted, turriform, whorl face profile trapezoid, convex or angular. Selenizone relatively wide or narrow, bounded by spiral lirae or grooves, or its profile different from rest of whorl profile. Ornamentation absent or mainly spiral.

Generic composition. At least 16 genera, from the Ordovician to Permian inclusive, worldwide: *Murchisonia* d'Archiac et deVerneuil, 1841; *Solenospira* Ulrich et Scofield, 1897; (?) *Ectomaria* Koken, 1896; (?) *Turritoma* Ulrich, 1897; *Hormotoma* Salter, 1859; *Hormotomina* Grabau et Shimer, 1909; *Biangularia* Spitz, 1907; *Morania* Horny, 1953; (?) *Ostioma* Tassel, 1980; *Lodanaria* Dahmer, 1925; *Aclisina* de Koninck, 1881; *Cerithioides* Haughton, 1859; *Goniasma* Tomlin, 1930; *Donaldospira* Batten, 1966; *Helicospira* Girty, 1915; and *Bellazona* Gordon et Yochelson, 1987.

Comparison. Shells of Murchisoniinae are different from Cheeneetnukiinae in the rounded or angular whorl face profile.

Genus *Goniasma* Tomlin, 1930

Goniospira: Girty, 1915, p. 356.

Goniasma: Tomlin, 1930, p. 23; Knight, 1941, p. 133; Knight et al., 1960, p. I293.

Stegocoelia (*Goniasma*) Batten, 1995, p. 22.

Type species. *Murchisonia lasallensis* Worthen, 1890.

Diagnosis. Shell turreted, formed by many slowly expanding whorls, umbilicus absent. Face of adult whorls subdivided by sharp carina into upper and lower faces. Upper whorl face nearly straight, slightly convex or concave; sutural lira absent or developed extremely weakly. Lower whorl face ornamented with four variously developed main spiral lirae. Carina marking first primary lira. Selenizone located immediately below carina, bounded by first and second primary lirae. Whorl separated from whorl face by rela-

Explanation of Plate 1

All photographs are taken from latex casts.

Fig. 1. *Callispira okaensis* Mazaev, 2003, ×2.5: holotype PIN, no. 4471/96-1; Ryazan Region, Kasimov quarry (near the village of Tashenka); Moscovian Stage, Myachkovian Substage, Peski Formation, white coral–foraminiferal grainstone member.

Fig. 2. *Callispira bellula* Mazaev, 2003, ×2.5: holotype PIN, no. 4471/2-19; Moscow Region, Shchelkovo quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation.

Figs. 3 and 4. *Callispira tricostata* Mazaev, sp. nov., ×1.5: (3) specimen PIN, no. 4471/91-38; (4) holotype PIN, no. 4471/91-39, Vologda Region, Aleksandrovskii quarry; Moscovian Stage, Podolskian Substage, white coral–foraminiferal grainstone member at the base of the quarry.

Figs. 5–7. *Goniasma gzheliensis* Mazaev, sp. nov.: (5) holotype PIN, no. 4471/6-17, ×6; (6) specimen PIN, no. 4471/6-1, ×6; (7) specimen PIN, no. 4471/6-58, ×10. Moscow Region, Gzhel' brick clay quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation.

Figs. 8–16. *Goniasma lasallensis* (Worthen, 1890): (8) specimen PIN, no. 4471/99-78, ×10; (9) specimen PIN, no. 4471/99-61, ×4 (10–12) specimen PIN, no. 4471/99-51, ×2; (10) cast of imprints of an intact aperture; (11) cast of imprints of intact palatal margin with a slit; (12) oblique palatal margin apertural and basal view; (13, 14) specimen PIN, no. 4471/99-46, ×2: (13) cast with imprints of shells with an intact slit, (14) the same imprint, basal view; (15, 16) specimen PIN, no. 4471/99-15, ×2: (15) apertural view, (16) palatal margin apertural view; Vladimir Region, Dyukino quarry; Kasimovian Stage, Dorogomilovian Substage (?).

tively sharp shoulder, smooth or with one variously developed basal lira, shifted towards fourth primary lira. Upper and lower lateral surfaces, and whorl base on last whorls can be ornamented with auxiliary thin spiral lirae. Growth lines on upper whorl face prosocline, beneath selenizone opisthocline; selenizone smooth or with very thin lunulae.

Species composition. About ten species; Mississippian of Central Asia; Pennsylvanian of North America; Pennsylvanian of the Russian Platform, Ural Mountains, Central Asia, and northwestern China; Permian of the Russian Platform, Central Asia, North America, and southwestern China.

Comparison. *Goniasma* is distinguished from *Donaldospira* by the selenizone, i.e., by its flat or concave surface, bounded by a pair of spiral lirae. It differs from *Murchisonia* mainly by ornamentation composed of variously developed spiral lirae, and in the presence of a sharp shoulder between the whorl face and whorl base.

Remarks. The ornamentation in the type species of *Goniasma* can be considered as the initial type: the upper whorl face is smooth, while the lower whorl face possesses four main spiral lirae; whorl base is ornamented with one primary basal lira. The first primary lira on the whorl face marks a sharp carina and bounds the selenizone on the top. Modifications of this scheme result from recombination of variations, such as a decrease in width of several main spiral lirae or their complete absence or, in contrast, by an increase of spiral ornamentation with subsequent appearance of auxiliary, thinner spiral lirae on the upper and lower whorl face and on whorl base.

The number of main spiral lirae and the position of the selenizone between the first and second lirae and its morphology coincide in *Goniasma* and *Stegocoelia*, which supports the hypothesis of the origin of *Stegocoelia* from *Goniasma*.

Goniasma gzheliensis Mazaev, sp. nov.

Plate 1, figs. 5–7

Etymology. From the village of Gzhel'.

Holotype. PIN, no. 4471/6-17, shell imprint; paratypes: PIN, nos. 4471/6-1, 4471/6-58, 4471/6-62, 4471/6-64, 4471/6-85, shell imprints, Moscow Region, Gzhel' brick clay quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation, base of the yellow dolomitized limestone member overlying a variegated clay member.

Description. The shell is small, turreted, turriform, composed of at least ten carinate whorls. The suture is very thin, hardly discernible. The protoconch is orthostrophic, composed of one or two rounded whorls. Juvenile whorls are composed of at least four whorls, carinate in profile, ornamented with four spiral lirae separated by equal spaces; the sutural lira is well developed, the carina marks the second main lira. The first main lira is at the middle of the upper whorl face between the sutural lira and carina. In adult whorls, the carina marks the first main lira, whereas the sutural lira gradually weakens to become obsolete on the last whorls. The upper whorl face between the suture and carina in the first adult whorl is nearly the same as the spaces between the first and second and second and third main lirae; then, it gradually widens and, in the last whorls, the ratio of the upper whorl face width to the lower whorl face width varies from 0.83 to 0.93. The whorl face above and below the carina is nearly straight or slightly concave in the profile. The lower whorl face is ornamented with four main spiral lirae; the first lira (as mentioned above) marks the carina, while the suture is developed immediately on or under the fourth lira. The spaces between the lirae are almost equal, and only in the last whorls they are paired. The spaces within both pairs of lirae are equal, and at least two-thirds of the size of the spaces between the pairs. Whorl base is ornamented with one basal spiral lira. In the first adult whorls, this lira is thinner than the others, positioned considerably closer to the fourth main lirae, whereas, in the last whorls, the thickness of the lira increases and matches that of the main spiral lirae; the space between it and the fourth main spiral lirae is equal to that between any pair. The selenizone in adult whorls is located immediately under the carina and bounded by the first and second main spiral lirae, and its surface is smooth and concave. Sometimes, its surface possesses a very thin auxiliary spiral lira. The aperture is pentagonal in cross section, the columella is moderately long, arcuate at the base. The outer lip margin and slit are not preserved. Growth lines are indiscernible.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/6-17, holotype	10.4	3.4
4471/6-1, paratype	12.8	>4.0
4471/6-58, paratype	6.0	2.6
4471/6-62, paratype	13.4	4.0

Comparison. Shells of this species are very similar to juvenile shells of *G. lasallensis*, although they are clearly different in the width of the upper whorl face, which is always less than the lower whorl face. This species is distinguished from *G. ferganica* Licharew, 1967 by the nearly straight upper whorl face profile and clear subdivision of the shell surface into whorl face and whorl base, which is marked by the position of the fourth main spiral lira.

Material. Sixteen specimens from the type locality.

Goniasma lasallensis (Worthen, 1890)

Plate 1, figs. 8–16

Murchisonia lasallensis: Worthen, 1890, p. 141, pl. 25, figs. 7 and 7a.

Worthenia? *lasallensis:* Girty, 1903, p. 457.

Murchisonia fischeri: Stuckenberg, 1905, p. 90, pl. XII, figs. 8 and 9.

Goniospira lasallensis: Girty, 1915, p. 356, pl. 30, figs. 7 and 8a.

Solenospira cf. *fischeri*: Yin, 1932, p. 19, pl. 20, fig. 19.

Murchisonia angulata: Stuckenberg, 1898, p. 197, pl. 1, fig. 7 (non *Murchisonia angulate* Phillips, 1836).

Goniasma lasallensis: Girty, 1939, p. 30, text-figs. 15–19; Knight, 1941, p. 133, pl. 42, figs. 6a–6e; Knight, 1944, p. 459, pl. 185, fig. 21; Sturgeon, 1964, p. 217, pl. 34, fig. 20, pl. 36, fig. 1; Kues: 1985, p. 14, text-fig. 2M; 1991, p. 228, text-fig. 3.14; 1996, p. 182, text-fig. 7.19.

Goniasma lasallensis vulgaris: Licharew, 1968, p. 73, pl. 16, figs. 1–10.

Goniasma cf. *lasallense:* Licharew, 1975, p. 63. pl. 9, figs. 6–8.

Stegocoelia (*Goniasma*) *lasallensis*: Batten, 1995, p. 22, text-fig. 31.

Murchisonia subangulata: Yakovlev, 1899, p. 31 (non *Murchisonia subangulata* Verneuil, 1845).

Murchisonia multilineata: Yakovlev, 1899, p. 37 (non *Murchisonia multilineata* Netschaev, 1894).

Solenospira sp. indet. aff. *conjungens:* Yin, 1932, p. 20, pl. 2, fig. 20.

Holotype. (According to Knight, 1941, p. 133), Illinois State Museum, no. 2603; Illinois, La Salle; Pennsylvanian, La Salle Limestone.

Description. The shell is large, turreted, turriform, formed by at least ten carinate whorls; the suture is very fine, hardly discernible. The protoconch is orthostrophic, composed of one or two smooth rounded whorls, terminated by a distinct sinusigera. The first one or two juvenile whorls are almost rounded, ornamented with four spiral lirae separated by almost equal spaces, while the sutural and the following lirae are positioned slightly closer. The remaining two or three juvenile whorls are sharply carinate in cross section, ornamented with a sutural lira and four main spiral lirae with equally wide spaces. The sutural lira becomes thinner with each subsequent whorl and disappears in adult whorls. The second main lira marks the carina, the upper and lower whorl faces are nearly straight or slightly convex in profile, and approximately equal in width. The first and third main lirae are located approximately in the middle of the upper and lower whorl faces, respectively; and the fourth main lira is overlapped by the subsequent whorl. In the first adult whorls, the sutural lira is directly under the suture, very weak or obsolete. The second lira is shifted to the whorl periphery and marks the carina, while the space between the sutural and second lirae becomes at least twice as wide and forms the upper whorl face. The upper whorl face is moderately concave in profile and becomes nearly straight or slightly convex in the last whorls; it is smooth or covered by many thin auxiliary spiral lirae (up to seven), with equal spaces between them. The lower whorl face is straight or slightly concave in profile, ornamented with four main spiral lirae, grouped in pairs. The upper whorl face width to lower whorl face width ratio varies from 1.16 to 1.6. The first lira marks the carina, while the fourth lira marks a sharp, carinate transition from the whorl face to whorl base. Each subsequent whorl forms a suture immediately below the fourth lira. The space between the lirae of the lower pair is nearly the same as the space of the upper pair or half its size; occasionally, two lower lirae are coalesce to make one or separated by a very narrow groove. The width of the main lirae is the same or the second and third lirae are noticeably thinner than the first and fourth. The space between the pairs is nearly straight in profile, smooth or ornamented with two thin auxiliary spiral lirae; it forms the larger part of the lower whorl face. In the last whorls, its width is three time greater than the space between lirae in the upper pair. The whorl base in the first adult whorls is ornamented with one main spiral lira, which is as wide as the fourth main lira, while the space between them is smaller than the space between lirae in any pair of lirae. In the last whorls, the space between the basal lira and the fourth main lira equals the space in the upper pair and, in addition, there appear five auxiliary spiral lirae separated by approximately equal spaces, some of these are as wide as the first or fourth main spiral lirae. The selenizone in adult whorls is located immediately below the carina and is bounded by the first and second main spiral lira, and its surface is smooth and concave. The aperture is pentagonal in cross section, the columella is attenuated in its lower part; in the last whorls, it is spirally bent, formed by the reflection of the inner lip. The shell possesses a weakly developed abapical canal and a narrow and deep slit, bounded by the first and second main lirae. In some specimens, its depth it is one-fourth of the last whorl circumference. The growth lines are very thin, sometimes distinct and prominent; on the upper whorl face, they are weakly bent and prosocline downwards at an angle of 25°–35°. On the selenizone, they form hardly noticeable lunulae, beneath the selenizone being weakly bent and opisthocline at 30°–35°.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/99-15	>48.0	18.2
4471/99-73	35.0	12.5
4471/99-14	>40.0	14.0
4471/4-2	>51.0	19.0

Variability. The species variability is manifested in slight changes in the size of the apical angle and the upper whorl face width to the lower whorl face width ratio. The material studied, as that described by Licharew (1967, p. 74), show auxiliary spiral lirae. This character was noted by Licharew as the main difference of these shells from similar ones described from North America. However, the auxiliary spiral lirae are only observed in the last whorls, and this ornamentation is very fine (its presence may depend on the state of preservation of the material). The shells of this species recorded from the Pennsylvanian of North America are small, i.e., they belong to younger individuals than those collected in Central Asia and the Russian Platform. Hence, the appearance of auxiliary spiral lirae in this case cannot be considered as a distinguishing character even at the subspecies level.

Comparison. This species is distinguished from *G. gzheliensis* by the upper whorl face width,

which is always greater than that of the lower whorl face; it differs from *G. ferganica* Licharew, 1967 in the clear subdivision of the shell surface into the whorl face and whorl base and in the position of the fourth main spiral lira.

R e m a r k s. Yakovlev (1899) identified *Murchisonia subangulata* Vern. (Pl. 4, fig. 25) and *M. multilineata* Netsch. (Pl. 4, fig. 30) from his fossil material. These shells certainly belong to the species described here as *G. lasallensis*. Species of Verneuil and Netschaev also belong to the genus *Goniasma*, but their precise identification is impossible without additional collecting from the type localities. The species described is extremely widespread in the sections studied and, unlike most other gastropod species, does not show affinity to any specific facies.

O c c u r r e n c e. Pennsylvanian of North America and the Russian Platform; Middle Carboniferous of the eastern slope of the Ural Mountains; Pennsylvanian and Lower Permian (Asselian) of Central Asia.

M a t e r i a l. The collection studied includes more than 290 imprints: 12 from locality no. 4471/2, one from locality no. 4471/3, two from locality no. 4471/4, 12 from locality no. 4471/6, one from locality no. 4471/7, eight from locality no. 4471/12, one from locality no. 4471/14, one from locality no. 4471/16, eight from locality no. 4471/17, 12 from locality no. 4471/18, one from locality no. 4471/19, 15 from locality no. 4471/20, six from locality no. 4471/21, two from locality no. 4471/22, one from locality no. 4471/23, two from locality no. 4471/24, 24 from locality no. 4471/25, one from locality no. 4471/26, one from locality no. 4471/27, three from locality no. 4471/29, one from locality no. 4471/30, two from locality no. 4471/31, two from locality no. 4471/32, eight from locality no. 4471/34, nine from locality no. 4471/35, one from locality no. 4471/50, one from locality no. 4471/54, six from locality no. 4471/74, one from locality no. 4471/76, four from locality no. 4471/77, one from locality no. 4471/78, eight from locality no. 4471/79, two from locality no. 4471/80, one from locality no. 4471/81, seven from locality no. 4471/82, seven from locality no. 4471/84, one from locality no. 4471/85, two from locality no. 4471/86, three from locality no. 4471/87, two from locality no. 4471/88, one from locality no. 4471/89, one from locality no. 4471/90, three from locality no. 4471/94, three from locality no. 4471/97, one from locality no. 4471/98, over 80 from locality no. 4471/99, three from locality no. 4471/101, and 16 from locality no. 4471/102.

***Goniasma pygmaea* Mazaev, sp. nov.**

Plate 2, fig. 1

E t y m o l o g y. From the Latin *pygmaeum* (small).

H o l o t y p e. PIN, no. 4471/86-84, shell imprint, Ryazan Region, Kasimov quarry (near the village of Tashenka); Moscovian Stage, Myachkovian Substage, Domodedovo Formation, basal part of the white mudstone member.

D e s c r i p t i o n. The shell is very small, turreted, composed of many slowly expanding sharply carinate whorls. The suture is very thin, hardly discernible. The protoconch and juvenile whorls are not preserved. Adult whorls are subdivided by a prominent carina into two approximately equal upper and lower whorl faces. The upper whorl face is moderately concave and smooth, bounded in the periphery by the first main spiral lira, while the sutural lira is absent. The lower whorl face is slightly convex, ornamented with the second main spiral lira, occurring slightly above the middle of the lower whorl face. The rest of the lirae are indiscernible. The basal part of the shell is not preserved. The first and second spiral lirae are very massive, with their width approximately equal to the space

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

All photographs are taken from latex casts.

Fig. 1. *Goniasma pygmaea* Mazaev, sp. nov., ×17: holotype PIN, no. 4471/86-84; Ryazan Region, Kasimov quarry (near the village of Tashenka); Moscovian Stage, Domodedovo Formation.

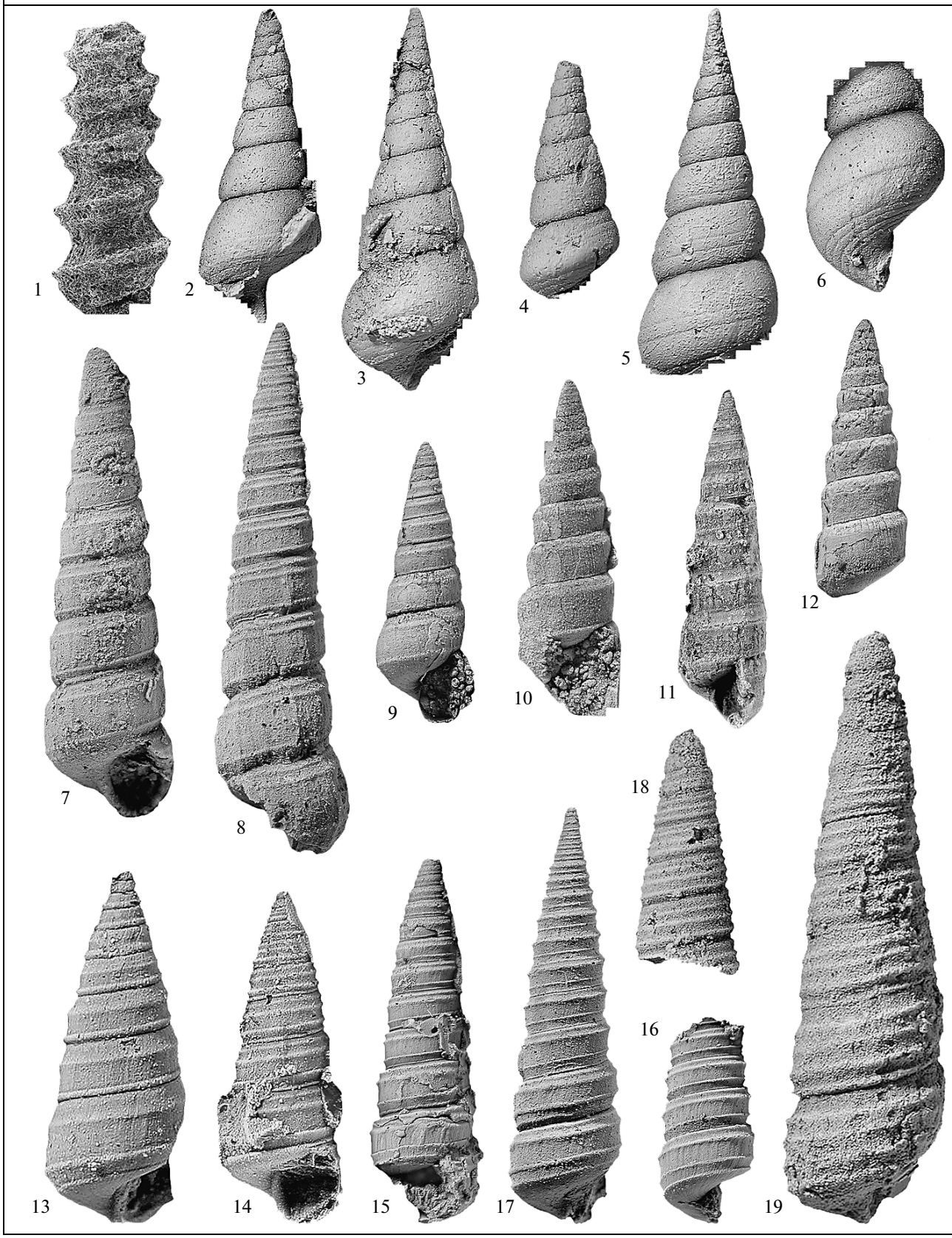
Figs. 2–6. *Cerithioides permicum* Licharew, 1967, ×6: (2, 3) specimen PIN, no. 4471/79-115, casts of various side of the imprint, Ryazan Region, Akishinskii quarry (near the village of Lashma); Moscovian Stage, Domodedovo Formation; (4) specimen PIN, no. 4471/87-101; (5, 6) specimen PIN, no. 4471/87-31, casts of various side of the imprint; Ryazan Region, Kasimov quarry (near the village of Tashenka); Moscovian Stage, Peski Formation.

Figs. 7–13. *Orthonema salteri* (Meek et Worthen, 1960): (7) specimen PIN, no. 4471/6-57, ×7; Moscow Region, Gzhel' quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation; (8) specimen PIN, no. 4471/85-9, ×7; Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, Korobcheevo Formation; (9, 10) specimen PIN, no. 4471/102-69, specimen PIN, no. 4471/102-68 ×7, Vologda Region, Aleksandrovskii quarry, middle part of the section, oblique-bedded grainstone with *Meekella eximia*; (11) specimen PIN, no. 4471/80-7, ×7, Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, Domodedovo Formation; (12) specimen PIN, no. 4471/92-28, ×7, Moscow Region, Akatievo quarry; Moscovian Stage, Podolskian Substage; (13) specimen PIN, no. 4471/79-184, ×15, Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, Domodedovo Formation.

Figs. 14–17. *Orthonema marvinwelleri* Knight, 1934: (14) specimen PIN, no. 4471/50-32, ×15; (15) specimen PIN, no. 4471/50-136, ×7; (16) specimen PIN, no. 4471/50-30, ×7; Moscow Region, Domodedovo quarry; Moscovian Stage, Myachkovian Substage, Korobcheevo Formation; (17) specimen PIN, no. 4471/85/74, ×7, Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, Korobcheevo Formation.

Figs. 18 and 19. *Orthonema borovskensis* Mazaev, 2002; ×7: (18) specimen PIN, no. 4471/94-42; (19) holotype PIN, no. 4471/94-41; Kaluga Region, outcrop Roshcha, near the town of Borovsk; Moscovian Stage, Vereian Substage, Ordynka Formation.

Plate 2



between them, while the width of the space is approximately one-third of the width of the lower whorl face. The morphology of the aperture and growth lines is unknown.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/86-84 holotype	>3.5	1.34

Comparison. This species is somewhat similar to *G. fesuiensis* Pan et Erwin, 2002, differing in the relatively massive first and second main lirae.

Remarks. Despite only one (poorly preserved) specimen at my disposal, I find it possible to describe it as a new species. This species definitely belongs to *Goniasma*, firstly, because of the morphology of the selenizone, which is bounded by two closely spaced lirae with a characteristic concave space between them and, secondly, based on its position immediately below the prominent carina, which subdivides the whorl surface into two nearly equal zones. This species is distinguished from other species of this genus by the extremely small, almost indistinguishable whorl expansion rate. On average, the diameter of each subsequent whorl increases only by 6.5 %.

Material. Holotype.

Genus *Cerithioides* Haughton, 1859

Cerithioides Haughton, 1859, p. 282.

Glyphodeta Donald, 1895, p. 212.

Type species. *Cerithioides telescopium* Haughton, 1859.

Diagnosis. Shell from small to large, turreted, composed of many slowly expanding whorls. Umbilicus absent. Whorl face in early whorls nearly straight, weakly convex, relatively abruptly transiting into whorl base, but without forming carina. In last whorls, whorl face rounded, smoothly passing into whorl base forming evenly curved arch. Whorl face smooth, selenizone narrow, straight or slightly convex in cross section, smooth, bounded by two thin grooves or slightly elevated over adjacent surface, in adult whorls, positioned immediately below midwhorl face. Whorl base ornamented with wide, spiral lirae rounded in cross section separated by thin grooves. Growth lines thin, prosocline above selenizone, opisthocline beneath selenizone. Selenizone smooth or with very fine lunulae.

Species composition. At least six species: Middle Devonian of Central Europe and North America, Mississippian of Europe, Pennsylvanian of North America, Pennsylvanian of Eastern Europe, Lower Permian of Central Asia.

Comparison. This genus is similar to *Bellazona* Gordon et Yochelson; however, in the latter, the selenizone is in the lower part of the whorl face, whorl base being smooth.

Remarks. The genus *Cerithioides* should include some species previously assigned to *Glyphodeta* Donald, 1895, whereas the genus *Glyphodeta* should be considered as a junior synonym of *Cerithioides*. The genus *Glyphodeta* was established by Donald (1895, p. 212) as a "section" (subgenus) of *Murchisonia*, with the type species *Murchisonia zonata* Donald, 1887. Knight (1941, p. 132) noted that many characters described and figured by Donald are absent in the type material. On the other hand, the assignment to this genus of *M.* (*Glyphodeta*) *fimbricarinata* Young et Armstrong, 1874 and *M.* (*G.*) *taeniata* Phillips, 1836, making its identification virtually impossible. Longstaff (1926, p. 529) did not use this taxon, saying that "the names *Stegocoelia* (...) and *Glyphodeta* (...) suggested for other sections by me are inadvisable, as the former was on a mistaken characteristic, and the latter on a very imperfectly preserved specimen as type." However, the authors of *Treatise* (Knight et al., 1960) resurrected this genus and figured *G. terebriformis* (Hall). Although this was not specified, it is evident that the authors of *Treatise* distinguished between *Cerithioides* and *Glyphodeta* solely based on the whorl cross section, since the position and the type of the selenizone and ornamentation are identical. On the other hand, in several species of *Cerithioides*, including the type species (Knight, 1941, p. 75, pl. 47, figs. 3a–3d), the whorl cross section changes as the shell grows, and the terminal whorls become evenly rounded. Thus, there are no characters that can be used as distinct criteria for separating these taxa, hence, the genus *Glyphodeta* should not be used.

Cerithioides permicum Licharew, 1967

Plate 2, figs. 2–6

Cerithioides permicum: Licharew, 1967, p. 53, pl. 13, fig. 15.

Holotype. TsNIGR Museum, collection no. 8336, no. 136, Uzbekistan, Karachatyr Range, outcrop no. 32/69; Lower Permian, Asselian.

Description. The shell is turreted, composed of many slowly expanding whorls; the umbilicus is absent. The suture is thin, impressed, and shallow. The protoconch is not preserved. The whorl face in the early whorls is nearly straight, weakly convex, relatively abruptly passing smoothly into the whorl base, but without forming a carina. In the last whorls, the whorl face is rounded, gradually fusing with the whorl base, forming a evenly curved arch. The width-to-height ratio of the whorl is about 0.5. The whorl face is smooth. The selenizone is narrow, straight or slightly convex in cross section, smooth, bounded by two thin grooves or is slightly elevated over the adjacent shell surface, positioned below the midwhorl face. The band between the lower suture and selenizone is equal to, or 1.5 times greater than its width. The whorl base is ornamented with slightly flattened spiral lirae rounded in cross section. Their width equals or slightly less than the selenizone width, while the lirae are sep-

arated by thin grooves. In the last whorl, the number of spiral lirae is up to six. The growth lines are thin, prosocline over the selenizone at 45°; beneath the selenizone, they are opisthocline at 13°. On the selenizone, growth lines are indiscernible. Apertural margins are not preserved.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/79-115	12.0	4.3
4471/87-31	>10.8	4.1
4471/87-101	>7.4	3.1

Comparison. This species is similar to *C. telescopium* Haughton, 1859 and distinguished from it by the width whorl to height ratio of approximately 0.5, whereas in *C. thelescopium*, this ratio is nearly 1.7.

Occurrence. Pennsylvanian, Myachkovian Substage, central Russian Platform; Lower Permian, Asselian; Central Asia, Karachatyr Range.

Material. Three imprints: one specimen from locality no. 4471/79 and two from locality no. 4471/87.

Subfamily Cheeneetnukiinae Blodgett et Cook, 2002

Type genus. *Cheeneetnukia* Blodgett et Cook, 2002.

Diagnosis. Shells turreted, whorl profile cylindrical, with subsutural ramp and pronounced shoulder. Whorl face straight or concave, separated from base by distinct shoulder. Selenizone relatively wide, positioned approximately in midwhorl face. Ornamentation weak, except spiral nodes on shoulder.

Generic composition. *Cheeneetnukia* Blodgett et Cook, 2002; Eifelian of Alaska and Givetian of Australia, *Ulungaratoconcha* Blodgett et Cook, 2002, Eifelian of Alaska.

Comparison. Shells of Cheeneetnukiinae differ from those of Murchisoniinae in the pronounced subsutural ramp and shoulder.

Family Ptychocaulidae Mazaev fam. nov.

Type genus. *Ptychocaulus* Perner, 1907.

Diagnosis. Turreted, turriform shells, composed of many whorls; whorl profile subcylindrical, and slightly convex. Whorl width twice its height. Selenizone positioned at or below midwhorl face. Umbilicus wide, perforated, its width comparable to last whorl height. Ornamentation either represented solely by selenizone, or by combination of selenizone with collabral or spiral lirae. Growth lines thin, prosocline above selenizone and opisthocline beneath selenizone.

Generic composition. *Ptychocaulus* Perner, 1907; *Medfracaulus* Rohr, Blodgett et Frida, 2003; *Vetotuba* Etheridge, 1890; *Melissosoa* Clarke, 1909; *Barroisocaulus* Gubanov, Blodgett et Litochkin, 1995; and (?) *Gaskonadia* Weller et St. Clair, 1928. Ordovician (?), Silurian, Devonian, worldwide.

Comparison. This family is distinguished from all other families in the suborder by a relatively wide perforated umbilicus.

Family Farewelliidae Mazaev fam. nov.

Type genus. *Farewellia* Frida et Blodgett, 2004.

Diagnosis. Turreted, turriform shells. Whorl profile convex. Selenizone located above midwhorl face. Ornamentation mostly collabral, following growth line direction, which prosocline above selenizone and opisthocline below it.

Generic composition. Type genus from the Emsian of Alaska.

Comparison. This family is distinguished from Ptychocaulidae by the absence of a perforated umbilicus. It is distinguished from Murchisoniidae by the position of the selenizone above the midwhorl face. It does not differ formally from Orthonematidae; however, a geochronological gap between the two families suggests their independent origin.

Family Orthonematidae Nützel et Bandel, 2000

Type genus. *Orthonema* Meek et Worthen, 1862.

Diagnosis. High-spired shells, possessing spiral ornamentation and selenizone or only selenizone; selenizone located above midwhorl face; growth lines thin, prosocline above selenizone, forming lunulae on selenizone; beneath selenizone, nearly straight or slightly bent forward, opisthocline; in some species, growth lines retaining neanic characters, remaining straight or forming shallow labral sinus.

Generic composition. *Orthonema* Meek et Worthen, 1862, *Metorthonema* Erwin, 1988, *Stegocoelia* Donald, 1889, *Taosia* Girty, 1939, *Vebericochlis* Licharew, 1967, *Altadema* Kues, 2002, *Concinnispira* Zernetskaja, 1983, *Hermosanema* Kues et Batten, 2001, *Cibecuia* Winters, 1956, *Arribazona* Kues, 1990, *Ferganispira* Licharew, 1967, *Loxosonia* Batten, 1985, and *Lashmaspira* Mazaev, 2003. Mississippian–Middle Permian; worldwide.

Comparison. Genera of this family are similar to those of the family Murchisoniidae in the shell shape, ornamentation, and whorl profile, but distinctly differing in the position of the selenizone, which in Orthonematidae is located strictly above midwhorl face.

Genus *Orthonema* Meek et Worthen, 1862

Orthonema: Meek and Worthen, 1862, p. 146; Knight, 1934, p. 435; 1941, p. 220; Knight et al., 1960, p. I317; Anderson et al., 1985, p. 1012; Batten, 1985, p. 18; Erwin, 1988, p. 567; Mazaev, 2002, p. 97.

Geolcomia: Licharew, 1975, p. 115.

Type species. *Eunema*? *salteri* Meek et Worthen, 1861.

Diagnosis. Shell turreted, lacking umbilicus. Protoconch conical, composed of one or two smooth whorls. Juvenile whorls rounded or nearly straight, ornamented with three or four spiral lirae with equal spaces between them. Adult whorls subcylindrical, with variously developed subsutural ramp, forming shoulder, and basal carina or angulation. Shell whorl face parallel to shell axis, straight, weakly convex or concave, usually ornamented with four main spiral lirae with equal spaces between them or paired. Auxiliary spiral lira occasionally located between first and second lirae. Whorl base rounded, smooth or ornamented with one relatively wide lira, rounded in cross section. Growth lines thin, forming variously developed labral sinus; shells lacking sinus—orthocline; with developed sinus, prosocline on subsutural ramp; between first and second spiral lira forming lunulae, below second lira opisthocline. In species with well-developed sinus, selenizone present; in species lacking sinus, lunulae between first and second lirae absent.

Species composition. Over 15 species. Mississippian–Lower Permian, worldwide.

Comparison. The genus *Orthonema* is distinguished from *Stegocoelia*, *Taosia*, and *Vebericochlis* by its subcylindrical whorl profile, characterized by variously developed sutural ramp and basal carina or angulation. In contrast to *Vebericochlis*, the whorl base of *Orthonema* shells is never attenuated basally and is clearly separated from whorl face by a basal carina or angulation. *Orthonema* differs from *Cibecuia* in the presence of the whorl face and variously developed spiral lirae.

***Orthonema salteri* (Meek et Worthen, 1860)**

Plate 2, figs. 7–13

Eunema salteri: Meek and Worthen, 1860, p. 461.

Orthonema salteri: Meek and Worthen, 1866, p. 381, pl. 31, figs. 14a–14c; Knight, 1934, p. 438, pl. 56, figs. 1a–1d; 1936, p. 533; 1941, pp. 220–221, pl. 50, fig. 3; 1944, p. 475, pl. 195, fig. 1; Knight et al., 1960, p. I317, text-fig. 210.5; Anderson et al., 1985, p. 1012, text-figs. 2.8, 3.1, and 3.2; Batten, 1995, p. 29, text-figs. 40a and 40b; Kues and Batten, 2001, p. 52, text-figs. 10.1–10.5.

Orthonema liratum: Sayre, 1930 (1931), p. 151, pl. 17, figs. 2 and 3.

Orthonema sayrei: Knight, 1934, p. 439, pl. 56, fig. 3.

Orthonema bilineatum: Mark, 1912, p. 316, pl. 16, fig. 14; Knight, 1934, p. 440, pl. 56, fig. 2.

Orthonema schucherti: Knight, 1934, p. 441, pl. 56, figs. 6a and 6b.

Orthonema werneri: Knight, 1934, p. 441, pl. 56, figs. 7a–7c; Anderson et al., 1985, p. 1013, text-figs. 3.3 and 3.4.

Orthonema frequens: Mazaev, 2002, p. 97, text-figs. 1A, 2A, 4A–4F (non *Orthonema frequens* Licharew, 1967).

Holotype. (According to Knight, 1941, p. 220) specimen no. X-246? (11031); Paleontology Collection, Illinois University, Urbana, Illinois; Macoupin County, Hodges Creek; Pennsylvanian, Carbondale Formation, St. David Limestone.

Description. The shell is small, up to 18.5 mm high, turreted, composed of 15 subcylindrical whorls, without an umbilicus. The suture is clear and shallow. The pleural angle is from 8° to 27°. The protoconch is conical, composed of one or two smooth whorls. The whorl face of juvenile whorls is slightly concave, inclined to the shell axis at 20°, ornamented with three spiral lirae separated by equal spaces. The upper and lower lirae are immediately near the sutures, while the median lira is weakly developed. Adult whorls are ornamented with four paired spiral lirae. The fourth main lira is usually overlapped by the subsequent whorl; the suture is between the third and fourth lirae. Both pairs of lirae have equal spaces between the lirae, a fourth or a sixth as wide as the space between the pairs; the last occupies most of the whorl face, which is slightly concave, straight or slightly convex. The subsutural ramp is very narrow, its width is slightly less than the space between the first and second lirae. The shoulder is marked by the first or second spiral lira, its position may several times change in ontogeny. The basal carina is marked by the third lira. The whorl base of shells is rounded, smooth or ornamented with the fourth main spiral lira. At different ontogenetic stages, lirae can be weakly developed or absent. Growth lines are thin, lacking a labral sinus, orthocline or opisthocline at an angle of 5°. The aperture is suboval, the outer lip is thin, while the inner lip is thickened, and the columella is slightly bent.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/6-37	>7.2	2.3
4471/85-9	>13.6	3.4
4471/79-184	4.2	1.6

Comparison. *O. salteri* is distinguished from *O. frequens* Licharew, 1968 in the upper pair of spiral lirae being closer to the suture (in specimens with normally developed spiral lirae). In addition, *O. salteri* is noticeably smaller than *O. frequens*. *O. salteri* differs from *O. marvinwelleri* in the nearly orthocline growth lines, slightly inclined backwards.

Remarks. Batten (1995, p. 29) and Kues and Batten (2001, p. 52) noted a considerable range of variability for this species, including in shell size, number of whorls, size of the pleural angle, whorl profiles, position of the suture, degree of development of spiral elements of ornamentation, which can be completely absent. Based on their own observations, the above authors considerably increased the synonymy list for this species. Interestingly, such variations of characters were recorded by Licharew for *O. frequens*. Originally (Mazaev, 2002, 2004), I identified specimens described in this paper as *O. frequens*; however, characters mentioned under *Comparison* are in my opinion sufficient to distinguish between *O. salteri* and *O. frequens* and, based on these, I identify these specimens as *O. salteri*.

Occurrence. Central Russian Platform, Pennsylvanian (Myachkovian, Krevyakian, and Dobryatinian substages); Pennsylvanian of North America.

Material. Twenty-five imprints: ten from locality no. 4471/3, five from locality no. 4471/6, two from locality no. 4471/18, two from locality no. 4471/20, one from locality no. 4471/75, one from locality no. 4471/79, one from locality no. 4471/80, one from locality no. 4471/82, one from locality no. 4471/84, and one from locality no. 4471/85.

Orthonema marvinwelleri Knight, 1934

Plate 2, figs. 14–17

Orthonema marvinwelleri: Knight, 1934, p. 444, pl. 57, figs. 3a–3c; Knight, 1944, p. 477, pl. 195, figs. 3 and 4; Mazaev, 2002, p. 101, text-figs. 1C, 2B, 4O–4S.

Holotype. Yale Peabody Museum, no. 13944; paratype no. 13945, United States, Illinois, St. Louis, locality no. 6; Pennsylvanian, base of Pawnee Limestone Formation.

Description. The shell is small, to 10 mm high, turreted, composed of 17 cylindrical whorls; the suture is thin and shallow, lacking an umbilicus. The protoconch is composed of two smooth rounded whorls. Three juvenile whorls are subconical in profile, ornamented with three spiral lirae separated by equal, concave spaces. The first lira is located immediately below the suture; the second lira is of the same size or slightly wider, located at midwhorl face; the third lira is massive, located immediately above the basal suture. The whorl face in adult whorls is ornamented with four similar spiral lirae, which are paired. The subsutural ramp is inclined towards the shell axis at up to 27° and is formed by the upper pair. The first lira is near the suture or slightly shifted from it. The second lira forms the shoulder. The shell surface between the pairs is flat or slightly concave, it is approximately twice as wide as the spaces between the lirae within the upper or lower pairs. The suture is very thin and shallow, lies immediately under the fourth lira. The whorl base is weakly convex and smooth. The growth lines are relatively coarse, form lunulae between the first and second lirae; below the second lira, they are weakly convex forward and inclined at approximately 10°. The apertural outline in cross section is close to a parallelogram. The outer lip is thin, the inner lip is thickened. The columella is relatively long, nearly straight or slightly bent.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/50-32	5.2	1.8
4471/50-136	9.4	3.0
4471/85-74	10.7	3.0

Comparison. This species is very similar to *O. salteri* and *O. frequens* and differs in the position of the fourth lirae, which separates the whorl face from the whorl base and forms the lower carina, whereas, in *O. salteri* and *O. frequens*, this lira is shifted to the whorl base; in addition, growth lines in *O. marvinwelleri* show a distinct labral sinus. It differs from *O. nakazawai* Batten, 1985 in the absence of the subsutural lira and the first lira being positioned extremely close to the suture.

Occurrence. North American Microcontinent; Pennsylvanian, Desmoinesian; central Russian Platform, Pennsylvanian, Myachkovian Substage.

Material. Forty-eight imprints: four from locality no. 4471/22, four from locality no. 4471/23, 11 from locality no. 4471/24, one from locality no. 4471/28, two from locality no. 4471/40, 15 from locality no. 4471/50, one from locality no. 4471/54, two from locality no. 4471/70, one from locality no. 4471/74, and seven from locality no. 4471/85.

Orthonema borovskensis Mazaev, 2002

Plate 2, figs. 18 and 19

Orthonema borovskensis: Mazaev, 2002, p. 99, text-figs. 4K and 4L.

Holotype. PIN, no. 4471/94-41; shell imprint; paratype no. 4471/94-42; shell imprint, Kaluga Region, vicinity of the town of Borovsk, right bank of the Protva River, opposite the Pafnutiev Monastery, near the village of Roshcha, a road cutting outcrop; Moscovian Stage, Vereian Substage, Ordynskaya Formation, yellow dolomitized limestone.

Description. The shell is small, up to 15.5 mm high, turreted, composed of at least 11 subcylindrical whorls, without an umbilicus. The suture is thin, distinct, and very shallow. The protoconch and juvenile whorls are not preserved. Adult whorls are ornamented with four spiral lirae with equally wide spaces between them. The subsutural ramp is flat or slightly concave, as wide as the spaces between the lirae, inclined towards the shell axis at approximately 27°, forms a shoulder, which is indistinct in the early whorls and distinct on the last whorls. The shoulder is marked by the first spiral lira. The fourth spiral lira marks the lower carina. The whorls are overlapped by subsequent whorls immediately below the fourth lira. The whorl face between the shoulder and the lower carina is weakly convex. The whorl base is also weakly convex, with an indistinct spiral lira, lying below the suture. The growth lines are not preserved.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/94-41 PIN holotype	15.5	4.3

Comparison. This species is similar to *O. simplex* Mazaev, 2002 in having the evenly spread spiral lirae, although being clearly distinguished from the latter by the more strongly rounded whorls and the presence of indistinct spiral lirae on the whorl base.

Material. Holotype and paratype.

***Orthonema paulum* Mazaev, 2002**

Plate 3, figs. 1 and 2

Orthonema paulum: Mazaev, 2002, p. 99, text-figs. 4M and 4N.

Holotype. PIN, no. 4471/74-11; shell imprint, paratype no. 4471/74-8, shell imprint, Ryazan Region, Maleevo quarry; Moscovian Stage, Podolskian Substage, white packstone underlying the cross-bedded grainstone at the base of the quarry.

Description. The shell is very small (up to 4 mm in height), turreted, composed of at least ten subcylindrical whorls. The suture is very thin and shallow. The protoconch is poorly preserved, apparently composed of two rounded whorls. Juvenile whorls (not more than five) are conical in outline, ornamented with three spiral lirae; the first and third spiral lirae are thin, lying near the upper and lower sutures, respectively. The second lira is very massive, forming a carina between the first and third lirae. The whorl face in adult whorls is nearly straight, parallel to the shell axis, ornamented with three spiral lirae similar in size. The two upper lirae form the upper pair, while the third lies immediately above the suture. The space between the second and third lirae is twice or three times as large as the space between the lirae of the upper pair. The width of the subsutural ramp is half the width of the space between the lirae of the upper pair. The upper shoulder is marked by the first lira. The growth lines, whorl base, and aperture are not preserved.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/74-11 holotype	4.0	1.3
4471/74-8 paratype	3.0	1.0

Comparison. This species is very similar to *Orthonema* ? *retrosum* Licharew, 1975, but is distinguished by the massive median lira in juvenile whorls.

Material. Holotype and paratype.

***Orthonema silinae* (Licharew, 1975)**

Plate 3, figs. 3 and 4

Goniasma silinae: Licharew, 1975, p. 65, pl. 9, figs. 10–12.
Geolcomia rara: Licharew, 1975, p. 115, pl. XIX, fig. 1–3.
Geolcomia ? sp. indet. *a*: Licharew, 1975, p. 116, pl. 19, fig. 4.
Orthonema silinae: Mazaev, 2002, p. 102, text-figs. 1F, 2D, 5A–5E.

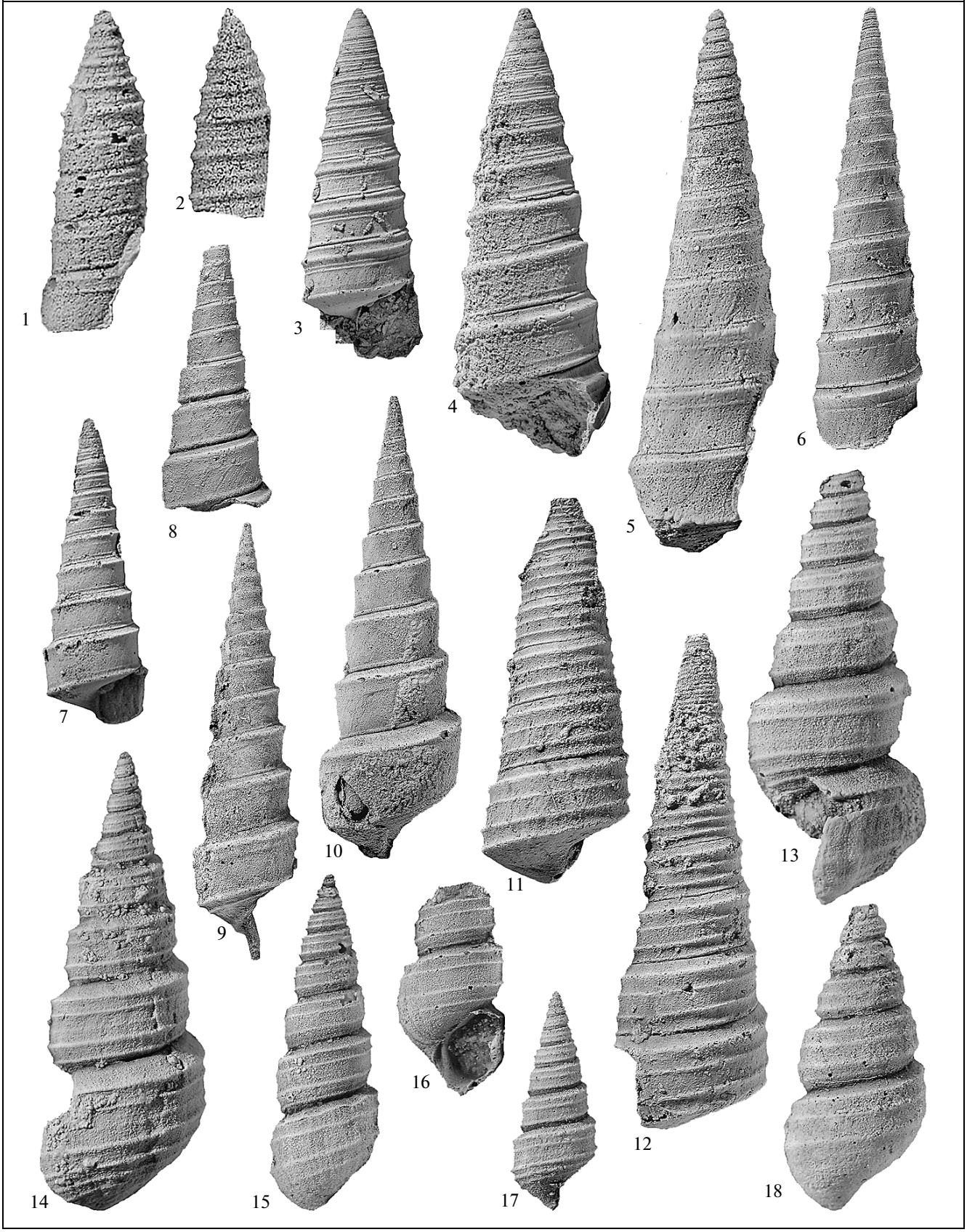
Holotype. TsNIGR Museum, collection no. 9758, no. 109, eastern slope of the Ural Mountains, Karabolka River, outcrop near the village of Ust'-Karabolka; Moscovian Stage, Myachkovian Substage.

Description. The shells are medium-sized (up 36 mm high), turreted, composed of 15 subcylindrical whorls, without an umbilicus. The protoconch is composed of two or three smooth rounded whorls. Six or seven juvenile whorls are subconical, ornamented with six spiral lirae of equal size, the upper lira lying immediately below suture. In adult whorls, the upper lira is developed as a weak sutural lira lying immediately below the suture. The second and fourth lirae form the upper pair of lirae, which delineate the selenizone, whereas the third lira lies between them as a weak auxiliary lira; the fifth and sixth spiral lirae form the lower pair of lirae. The upper and lower pairs of lirae have equal spaces between the lirae. The width of the subsutural ramp is approximately equal to that of the selenizone or slightly wider in the last whorl. Its surface is flattened or slightly concave, inclined toward the shell axis at an angle up to 30°. The shoulder is marked by the first main lira (upper lira of the upper pair); the lower carina is marked by the fourth main lira (lower lira of the lower pair). These lirae in adult whorls are relatively massive; in the last whorl, the fourth main lira becomes indistinct and disappears. The whorl face between the shoulder and lower carina is straight or slightly concave. In the early whorls, the space between the pairs is approximately the same as the space in either pair of lirae, while, in the last whorls, it gradually increases to become twice as wide. The suture is very thin and shallow, lying below the fourth main lira. The shell base is weakly convex and smooth.

Explanation of Plate 3

All photographs are taken from latex casts.
Figs. 1 and 2. *Orthonema paulum* Mazaev, 2002, ×15: (1) holotype PIN, no. 7741/74-11; (2) specimen PIN, no. 7741/74-8, Ryazan Region, Maleevo quarry; Moscovian Stage, Podolskian Substage.
Figs. 3 and 4. *Orthonema silinae* (Licharew, 1975), ×4: (3) specimen PIN, no. 7741/91-34, (4) specimen PIN, no. 7741/91-35, Vologda Region, Aleksandrovskii quarry; Moscovian Stage, Podolskian Substage, white coral–foraminiferal grainstone member at the base of the quarry.
Figs. 5–10. *Orthonema cochleoides* (Yin, 1932): (5) specimen PIN, no. 4471/79-173, ×10; (6) specimen PIN, no. 4471/79-59, ×4; Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, Domodedovo Formation; (7) specimen PIN, no. 7741/91-33, ×4, Vologda Region, Aleksandrovskii quarry, Moscovian Stage, Podolskian Substage, white coral–foraminiferal grainstone member at the base of the quarry; (8) specimen 4471/2-24, ×2, Moscow Region, Shchelkovo quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation; (9) specimen PIN, no. 4471/21-10, ×2, Moscow Region, Konev Bor quarry; Moscovian Stage, Myachkovian Substage, Korobcheevo Formation; (10) specimen PIN, no. 4471/78-51, ×2, Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, Domodedovo Formation.
Figs. 11 and 12. *Orthonema simplex* Mazaev, 2002, ×3.5: (11) specimen PIN, no. 4471/2-13, (12) holotype PIN, no. 4471/2-17, Moscow Region, Shchelkovo quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation.
Figs. 13–18. *Vebericochlis arguta* (Licharew, 1975), ×6: (13) specimen PIN, no. 4471/73-17, slit morphology and depth are clearly visible; (14) specimen 4471/73-26; (15) specimen PIN, no. 4471/73-52; (16) the same specimen, apertural view; (17) specimen PIN, no. 4471/73/16; (18) specimen PIN, no. 4471/73/5, Ryazan Region, Yambirno quarry; Tsna Formation.

Plate 3



The apertural outline in cross section is close to parallelogram. The shell has a weakly developed abapical canal and a well-developed slit below the shoulder. The slit depth is approximately twice its width. The columella is nearly straight or slightly bent. The growth lines are distinct, thin, bent forward above the selenizone, prosocline, inclined to the shell axis approximately at an angle of 45°; below the selenizone, slightly bent forward, opisthocline, inclines to the shell axis approximately at an angle of 30°, and form thin lunulae on the selenizone.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/91-35	20.5	7.0
4471/91-34	16.0	5.6

Comparison. *O. silinae* is very similar to *O. cochleoides*, being distinguished by the smooth whorl base, lacking spiral ornamentation. It is distinguished from *O. simplex* by the paired arrangement of lirae in adult whorls.

Remarks. During the growth, the shell of *O. silinae* undergoes considerable morphological changes. Seven or eight juvenile whorls of *O. silinae* have a larger apical angle than adult whorls and lack a subsutural ramp and a shoulder. Moreover, the whorl face of the first five whorls is ornamented with six spiral lirae (Pl. 2, figs. 7, 8). It is noteworthy that the type material shows clearly the change in the growth lines: in juvenile whorls, they are nearly straight, opisthocline (specimens nos. 261 and 264). A weak labral sinus appears later to be transformed in the later whorls into a narrow deep slit (specimens nos. 415 and 109, TsNIGR Museum collection, no. 9758).

Occurrence. Eastern slope of the Ural Mountains, Karabolka River, outcrop near the village of Ust'-Karabolka; Moscovian Stage, Myachkovian Substage; Vologda Region, Aleksandrovskii quarry; Moscovian Stage, Podolskian Substage.

Material. Two imprints from locality no. 4471/91.

***Orthonema cochleoides* (Yin, 1932)**

Plate 3, figs. 5–10

Solenospira cochleoides: Yin, 1932, p. 20, pl. 2, figs. 21–23.

Orthonema cochleoides (Yin, 1932): Mazaev, 2002, p. 102, text-figs. 1E, 2C, 5F–5J.

Orthonema teliscopiforme: Kues and Batten 2001, p. 52, text-figs. 10.6–10.8 (non *Orthonema teliscopiforme* Erwin, 1988).

Holotype. No. 4808; paratypes nos. 4807 and 4709, North China, Kansu (now Gansu) Province, Mokou; Pennsylvanian, Mokou Formation, Penchi Series.

Description. The shells are medium-sized (up to 45 mm high), turreted, composed of 20 subcylindrical whorls, without an umbilicus. The protoconch is composed of approximately two smooth, rounded whorls. Three or four juvenile whorls are rounded in profile, ornamented with three distinct thin spiral lirae with concave equal spaces between them. Adult whorls are ornamented with four spiral lirae, which are paired. The first and third main spiral lirae are thin in early whorls, becoming indistinct, wide and low in the last whorls. The second and fourth lirae either remain thin and distinct in the last whorls, or disappear. The spaces between lirae in each pair are equally wide slightly concave. The space between the pairs is at least twice as large as the space between lirae in each pair; its surface is nearly straight, parallel to the shell axis and forms most of the whorl face. Adult whorls possess a narrow subsutural ramp, which is slightly convex, flat or slightly concave, inclined toward the shell axis at an angle of 30°, its width being approximately equal to the width of the upper or lower pairs of lirae. The shoulder is marked by the first lira, the basal angulation or carina are marked by the third lira. The whorl base is nearly straight, slightly attenuated below, smooth or ornamented with the fourth spiral lira, which lies below the basal angulation; the auxiliary lira (rounded in profile) can be positioned near the columella. The suture is very thin and shallow, lies immediately below the third lira. The columella is straight or spirally bent, relatively long. The aperture is parallelogram-shaped in cross section, with a weak abapical canal. The outer lip is relatively wide, apparently, with a slit of unknown depth lying just under the shoulder. The growth lines are very thin or indistinct, nearly straight and prosocline on the subsutural ramp; in the space between the pairs of lirae, they form lunulae; on the remaining whorl face, they are nearly straight, opisthocline, and inclined towards the shell axis at an angle of up to 30°.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/78-51	43.0	13.0
4471/21-10	40.5	10.0
4471/2-26	19.5	6.5
4471/79-59	>21.0	5.0
4471/79-173	10.0	ca. 3.0

Comparison. This species is very similar to *O. silinae*, but is clearly distinguished by the position of the fourth spiral lirae in the basal region of adult whorls and by the considerably smaller angle of juvenile whorls and fewer spiral lirae (not more than four) on the whorl face.

Remarks. Kues and Batten (2001, p. 52, text-figs. 10.6–10.8) described several specimens from the Flechado Formation in New Mexico, which they identified as *Orthonema teliscopiforme* Erwin, 1988. However, their material is indistinguishable from the material described in this paper, and both sets of specimens are likely to belong to the same species. In the original description of this species, Yin noted the sim-

ilarity between *O. cochleoides* and *Murchisonia nikitini* Stuckenberg (Stuckenberg, 1905, p. 90, pl. 12, fig. 10). Unfortunately, Stuckenberg's types have been lost, whereas the quality of the illustrations and description in his monograph does not allow positive identification. The illustrations could equally be of *Cibecuia magnum*.

Occurrence. Central Russian Platform; Pennsylvanian, Kashirian, Myachkovian, and Dobryatinian substages; northern China, Kansu (now Gansu) Province; Pennsylvanian, Penchi Series.

Material. Twenty-six imprints: ten from locality no. 4471/2, two from locality no. 4471/8, one from locality no. 4471/16, one from locality no. 4471/21, one from locality no. 4471/24, one from locality no. 4471/39, one from locality no. 4471/47, two from locality no. 4471/54, one from locality no. 4471/74, two from locality no. 4471/78, two from locality no. 4471/79, and two from locality no. 4471/102.

Orthonema simplex Mazaev, 2002

Plate 3, figs. 11 and 12

Orthonema simplex: Mazaev, 2002, p. 103, text-figs. 1D, 5K, and 5L.

Holotype. PIN, no. 4471/2-17, shell imprint; paratype PIN, no. 4471/2-13; shell imprint; Moscow Region, Shchelkovo quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation, top of the thick member (2 m) of yellow dolomitized limestone, approximately 3.5 m above the top of variegated clay series.

Description. The shell is small turreted (up to 18.5 mm high), composed of at least 15 subcylindrical whorls, without an umbilicus. The protoconch is not preserved. Juvenile whorls are poorly preserved. Adult whorls have a distinct shoulder, ornamented with four spiral lirae, with equal concave spaces between them. The subsutural ramp is flat or slightly concave, with a width equal to the spaces between the lirae, inclined towards the shell axis at approximately 30°. The whorl face below the upper shoulder is nearly straight in profile, inclined towards the shell axis not more than at 5°. The upper shoulder is marked by the first spiral lira, the lower carina is marked by the fourth spiral lira. The suture is very thin and shallow, positioned immediately below the fourth lira; sometimes, the subsequent whorl partly overlaps this lira. The whorl base is weakly convex and smooth. The columella is short. The aperture is trapezoidal in cross section, with a weak abapical canal; the outer lip apparently had a slit just below the upper shoulder. The growth lines are thin, prosocline on the subsutural ramp; between the first and second lirae, they form thin lunulae. Below the second lira, the growth lines are straight, opisthocline, inclined to the shell axis at approximately 30°.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/2-17 holotype	18.5	5.6
4471/2-16 paratype	>14.5	5.0

Comparison. This species is similar to *O. borovskensis* in having regularly spaced spiral lirae, although being distinguished from the latter by the straight whorl face and the smooth basal surface.

Material. Holotype and paratype.

Genus *Vebericochlis* Licharew, 1967

Stegocoelia (Vebericochlis): Licharew, 1967, p. 69.
Vebericochlis: Mazaev, 2001, p. 140.

Type species. *Stegocoelia* (*Vebericochlis*) *maclayi* Licharew, 1967.

Diagnosis. Shell turreted, lacking umbilicus. Protoconch conical, composed of one or two smooth whorls. Juvenile whorls rounded or nearly straight, ornamented with three or four evenly spaced spiral lirae. Whorl face of adult whorls with narrow subsutural ramp forming shoulder. Shell surface below shoulder weakly convex or straight, ornamented with four main spiral lirae; upper lira forming shoulder. Auxiliary spiral lira occasionally lying on selenizone. Some spiral lirae can be expressed as spiral row of nodes. Selenizone band concave, smooth, bounded by first and second main lirae. Whorl face passing smoothly into whorl base near fourth lirae. Whorl base rounded, smooth or ornamented with spiral lirae. Growth lines thin, prosocline on subsutural ramp, forming lunulae on selenizone, opisthocline beneath selenizone and slightly bent forward.

Species composition. Two species from the Pennsylvanian of Eastern Europe and the Middle Ural Mountains, and from the Lower Permian of Central Asia.

Comparison and remarks. *Vebericochlis* was established as a subgenus of *Stegocoelia* (Licharew, 1967). Mazaev (2001) elevated the rank of *Stegocoelia, Taosia*, and *Vebericochlis* to genus, and *Orthonema* was shown later to be a closely related genus (Mazaev, 2002). All four genera have the same number of the main spiral lirae on the whorl face, but are readily distinguished by the whorl profile. Species of the genus *Vebericochlis*, like some species of *Orthonema*, have a narrow subsutural ramp, but lack a basal angulation, clearly separating the whorl face from the whorl base, whereas the whorl base is attenuated downwards.

Vebericochlis arguta (Licharew, 1975)

Plate 3, figs. 13–18

Stegocoelia (*Hypergonia*?) *arguta*: Licharew, 1975, p. 72, pl. 11, fig. 7.
Stegocoelia (*Hypergonia*?) *scalaris*: Licharew, 1975, p. 72, pl. 10, fig. 16.
Vebericochlis arguta: Mazaev, 2002, p. 95, text-figs. 1J, 2E, 3A–3I.

Holotype. TsNIGR Museum, collection no. 9758, no. 139, eastern slope of the Ural Mountains, Karabolka River, outcrop near the village of Ust'-Karabolka; Moscovian Stage, Myachkovian Substage.

Description. The shell is turreted, medium-sized, composed of approximately 11 subcylindrical whorls with a narrow subsutural ramp. The whorl face is nearly straight or slightly convex. The suture is impressed and shallow. The protoconch is composed of two smooth, rounded whorls. Juvenile whorls are ornamented with three or sometimes four spiral lirae separated by equally wide spaces. The first juvenile whorls are nearly rounded, while the last whorls have a nearly straight whorl face, inclined towards the shell axis at an angle up to 10°. Adult whorls have a sharply angular shoulder, which is marked by the first main spiral lira. The subsutural ramp is flat, inclined toward the shell axis at 50°, as wide as the selenizone or slightly larger on the last whorl. The sutural lira is absent or very weakly developed on the last whorl. The whorl face below the shoulder is nearly parallel to the shell axis and ornamented with four main spiral lirae, which are grouped in the upper and lower pairs, the spaces within these pairs are of the same size, half the width of the space between the pairs. The auxiliary lira can appear between the pairs in the last whorl. The selenizone is located immediately below the shoulder, concave, bounded by the first and second main lira. The whorl face gradually fuses with the whorl base near the fourth main lirae. The whorl base is smooth or ornamented with three spiral lirae with equally wide spaces between them. The aperture is suboval with a weak, incipient abapical canal and a prominent slit immediately below the shoulder. The depth of the slit is at least twice as large as its width. The slit margins are parallel. The outer and inner lips are thin, the columella is relatively long and nearly straight. The growth lines are very thin, prosocline on the subsutural ramp, weakly opisthocline below the selenizone, gently arcuate forward. The selenizone is smooth or with very fine lunulae.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/73-26	14.0	5.0
4471/73-17	>13.0	2.5
4471/73-52	10.0	3.5
4471/73-56	15.0	5.5
4471/73-54	6.0	2.5
4471/73-50	4.5	2.5
4471/73-16	7.0	2.5

Comparison. This species is distinguished from *V. maclayi* by the paired arrangement of the main spiral lirae on the last whorls.

Remarks. The majority of specimens studied show high variability, including the pleural angle ranging from 12° to 27°, and the whorl face profile varying from weakly convex to weakly concave.

Occurrence. Central Russian Platform; Pennsylvanian, Kashirian and Myachkovian substages; eastern slope of the Ural Mountains; Pennsylvanian, Myachkovian Substage.

Material. Seventy imprints: two from locality no. 4471/26, one from locality no. 4471/38, 38 from locality no. 4471/73, one from locality no. 4471/74, six from locality no. 4471/82, one from locality no. 4471/92, four from locality no. 4471/101, eight from locality no. 4471/102, and nine from locality no. 4471/103.

Genus *Stegocoelia* Donald, 1889

Murchisonia (Stegocoelia): Donald, 1889, p. 623.
Murchisonia (Hypergonia): Donald, 1892, p. 564.
Hypergonia: Longstaff, 1926, p. 529.
Stegocoelia (Stegocoelia): Knight et al., 1960, p. I293; Thein and Nitecki, 1974, p. 161.
Stegocoelia (Hypergonia): Knight et al., 1960, p. I293; Batten, 1966, p. 77; Thein and Nitecki, 1974, p. 167; Licharew, 1975, p. 66.
Stegocoelia: Knight et al., 1960, p. I293; Batten, 1966, p. 76; Licharew, 1967, p. 55; Thein and Nitecki, 1974, p. 161; Licharew, 1975, p. 66; Kues and Batten, 2001, p. 45; Mazaev, 2001, p. 140.

Type species. *Murchisonia* (*Stegocoelia*) *compacta* Donald, 1889.

Diagnosis. Shell turreted, composed of at least ten rounded or carinate whorls. Protoconch formed by one or three smooth whorls. Juvenile whorls from one to four, angular in profile, ornamented with three spiral lirae. Upper lira weak lying immediately below suture, two other more prominent lirae forming pair shifted away from upper lira and forming carina approximately at midwhorl; spaces between lirae concave, upper being twice as wide as that between lower pair of lirae. Selenizone or labral sinus lying in upper space between lirae. Whorl face in adult whorls rounded or carinate, ornamented with four main spiral lirae. Upper lira in adult whorls shifted away from suture forming first main lira. Spaces between lirae in adult whorls usually equal in size and slightly concave, sometimes in last whorls space between second and third lira becoming larger than others, main lirae grouped in pairs. Selenizone smooth, concave, lying between first and second lira. Second lira always forming periphery of whorl; in species with angular whorl profile, this lira forming carina and subdividing whorl face into lower and upper zones. Last whorls of some species occasionally possessing auxiliary sutural lira and/or weaker and thinner auxiliary spiral lirae in spaces between main lirae. Whorl face gradually fusing into rounded whorl base, smooth or ornamented with spiral lirae, sometimes with auxiliary, weaker spiral lirae in between. Aperture suboval in profile, with weak abapical canal and well-developed slit above midwhorl face. Its depth twice as large as width. Growth lines thin and distinct, above selenizone slightly bent forward, prosocline; on selenizone forming lunulae;

beneath selenizone gradually bent forward, opisthocline.

Species composition. Several dozen species. Mississippian (possibly Upper Devonian)–uppermost Middle Permian. Worldwide.

Comparison and remarks. The genus *Stegocoelia* is very similar to *Taosia*, *Vebericochlis*, and *Orthonema*. They are similar in ornamentation on the whorl faces, composed of four main spiral lirae, while the selenizone is always between the upper pair. This basic type can be made more complex by the appearance of the subsutural spiral lirae and thin auxiliary spiral lirae. The development of spiral lirae is more typical of *Stegocoelia*. These four taxa are different chiefly in the whorl profile. In *Vebericochlis* and *Orthonema*, the whorl face is subcylindrical, with a relatively well-developed subsutural ramp; whereas in *Taosia*, the whorl face profile is carinate, with a periphery noticeably below the midwhorl face. In the *Stegocoelia* species, the whorl face profile is rounded or carinate, with the periphery about midwhorl. Species with a carinate whorl profile have been traditionally assigned to *Hypergonia*. However, in some species, the carinate whorl profile can become rounded in ontogeny and vice versa. To distinguish between those, Batten (1966) proposed to use a combination of two characters: relatively large apical angle combined with a rounded whorl profile, relatively small apical angle combined with an angular whorl profile. It is evident that characters of *S. knighti* and *S. acuta* contradict the two suggested schemes, hence, *Hypergonia* was proposed to be regarded as a junior synonym of *Stegocoelia* (Mazaev, 2001). *Stegocoelia*, *Vebericochis*, and *Taosia* have the same rank of differences and, therefore, the latter two were suggested to be regarded as separate genera. *Donaldospira* and *Goniasma*, which Batten (1995, p. 20) included in *Stegocoelia* as subgenera, were excluded from *Stegocoelia* and transferred to Murchisoniidae based on the position of the selenizone.

Stegocoelia laschmaensis Mazaev, 2001

Plate 4, figs. 1–4

Stegocoelia laschmaensis: Mazaev, 2001, p. 149, text-figs. 3I–3L.

Holotype. PIN, no. 4471/77-60; shell imprint; paratypes: PIN, nos. 4471/77-17, 4471/77-30. 4471/77-53. 4471/77-91; shell imprints, Ryazan Region, Akishinskii quarry (near the village of Lashma); Moscovian Stage, Myachkovian Substage, top of the Korobcheevo Formation, gray cross-bedded grainstone with *Meekella*.

Description. The shell is small, turreted, composed of ten rounded whorls, without an umbilicus; the suture is shallow and impressed. The protoconch is composed of two smooth rounded whorls. One or two juvenile whorls weakly angular in profile, ornamented with three spiral lirae, The second lira forms a weak carina. Whorl face of adult whorls is ornamented with four spiral lirae with equal spaces between them. The sutural lira is absent. The fourth lira is near the lower suture. Two spiral lirae are in the upper whorl base. The selenizone is bounded by the first and second lirae. The whorl profile is rounded. The aperture is rounded, the outer lip is thin, the inner lip is thickened and gently curved. The growth lines are very thin, prosocline above the selenizone, form hardly noticeable lunulae above the selenizone, while beneath selenizone they form an even arch, concave forward and slightly opisthocline. The pallial slit is not preserved.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/77-60, holotype	5.5	2.5
4471/77-17, paratype	6.0	3.0
4471/77-30, paratype	5.5	2.5
4471/77-53, paratype	6.0	3.0
4471/77-91, paratype	7.0	3.0

Comparison. This species is similar to *S. acutiformis* and distinguished by the presence of two spiral lirae on the shell base.

Material. Nineteen imprints from the type locality.

Stegocoelia klyazmaensis Mazaev, 2001

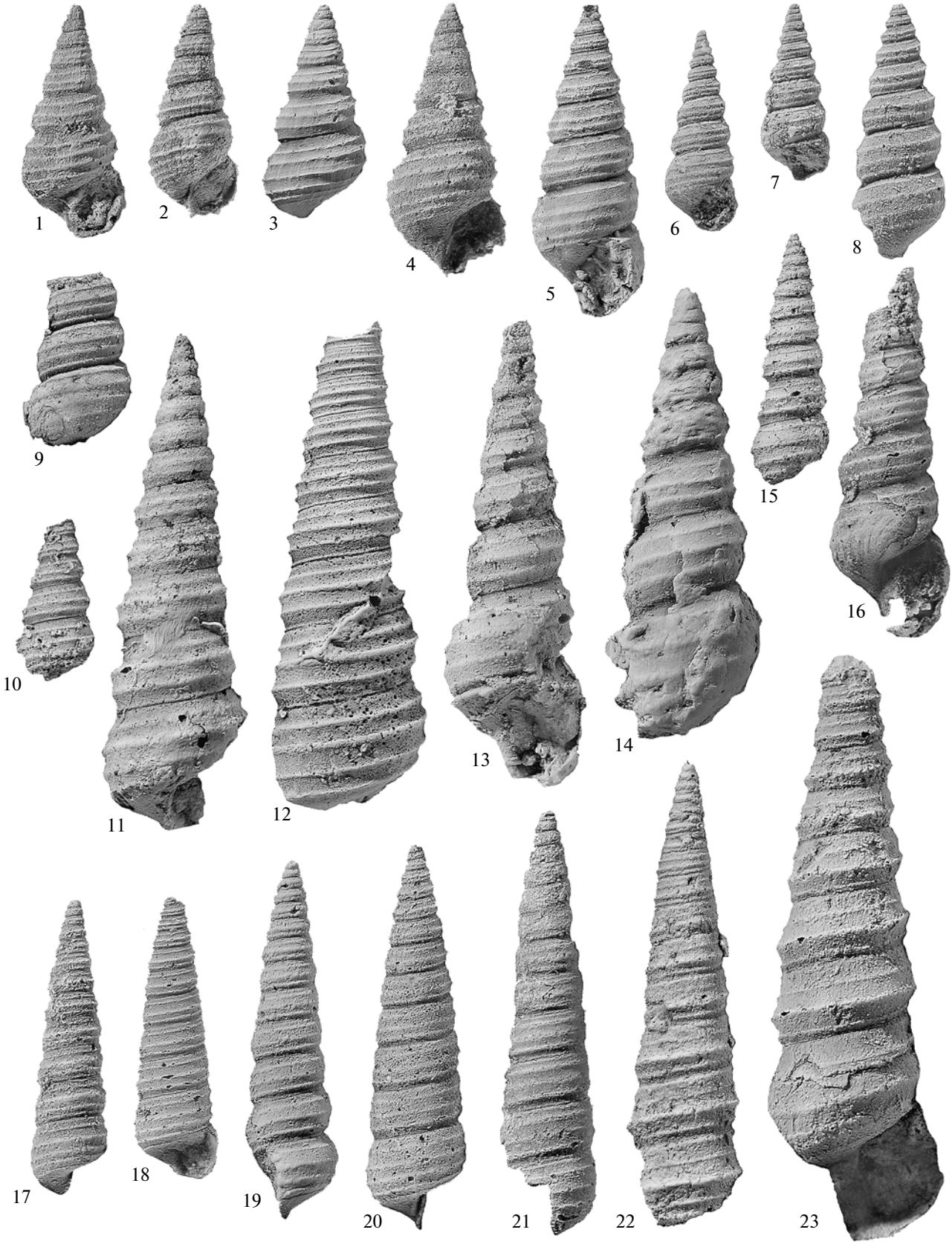
Plate 4, figs. 5–9

Stegocoelia klyazmaensis: Mazaev, 2001, p. 141, text-fig. 2F.

Holotype. PIN, no. 4471/4-5, shell imprint; paratype PIN, no. 4471/4-29, shell imprint, Moscow Region, Shchelkovo quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation, top of a thick member (2 m) of yellow dolomitized limestone, approximately 3.5 m above the top of the variegated clay member.

Description. The shell is small, turreted, composed of at least ten whorls, without an umbilicus; the suture is impressed and relatively deep. The protoconch is not preserved. Two juvenile whorls are slightly angular in profile, ornamented with three spiral lirae. The upper lira is weak and located just under the upper suture; two other lirae are very closely spaced and form an angular whorl profile. The whorl face of adult whorls is ornamented with four main spiral lirae. The sutural lira is absent, the selenizone is between the first and second lirae, and it is noticeably wider than other spaces between the lirae. On the first three adult whorls, the second lira forms a distinct carina; the profile of these whorls is angular. The profile of the next four whorls is rounded. The whorl base is smooth, with one spiral lira similar in size to the main spiral lirae, and is spaced from these by a distance equal to spaces between the main lirae. The aperture is suboval in cross section. The columella is relatively long, weakly bent. The outer lip is thin, while the inner lip is thick. The growth lines and pallial slit are not preserved.

Plate 4



Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/4-5 holotype	8.0	3.0
4471/84-3	4.5	2.0

Comparison. This species is very similar to *S. gzheliensis, S. acuta*, and *S. acutiformis*, being distinguished by the wide selenizone, which is at least 1.1–1.2 times wider than the other spaces between the lirae. The band between the first main lira and suture is approximately half of the width of spaces between the second, third, and fourth main lirae.

Occurrence. Central Russian Platform; Gzhelian Stage, Dobryatinian Substage.

Material. Eighteen imprints: four from locality no. 4471/3, two from locality no. 4471/4, eight from locality no. 4471/6, one from locality no. 4471/16, and three from locality no. 4471/84.

***Stegocoelia berestovensis* Zernetskaja, 1983**

Plate 4, figs. 10–12

Solenospira amana: Yin, 1932, pp. 18, 19, pl. 2, figs. 14–17 (non *Solenospira amana* Konink, 1883).

Stegocoelia (Stegocoelia) berestovensis: Zernetskaya, 1983, pp. 111, 112; pl. 63, figs. 5–7.

Stegocoelia berestovensis: Mazaev, 2001, p. 146, text-figs. 2S–2U.

Holotype. Institute of Geological Sciences, Academy of Science of Ukraine, no. 1936/8, Ukraine, Donetsk Region, left bank of the Berestovaya River, near the village of Fenino; Bashkirian, limestone E.

Description. The shell is medium-sized, turreted, composed of 11–12 weakly angular whorls, lacking an umbilicus. The suture is distinct and shallow. The protoconch is not preserved. Two or three juvenile whorl are poorly preserved, angular in profile, ornamented with three spiral lirae, The second lira forms a prominent carina. The second and third lirae are closely spaced. The whorl face of adult whorls is ornamented with four spiral lirae. The sutural lira is absent or very weak. The first lira is approximately at the middle of the upper whorl face. The second lira forms a weak carina. The third lira is on the lower whorl face, while the fourth is above the suture or overlapped by the subsequent whorl. All spaces between lirae are nearly equal. The definitive whorl is nearly rounded in profile. The selenizone is bounded by the first and second lira. The whorl base is smooth and weakly convex. The growth lines and slit are not preserved.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/21-11	>23.0	6.5
4471/21-9	21.5	6.0

Comparison. The definitive whorls of this species are similar to those of *S. acutiformis*, but differ in the shallower suture and greater width-to-height whorl ratio (from 2.0 to 2.2).

Remarks. This species is very similar to North American *S. wortheni* Knight, 1942, the assignment of which to *Taosia* has been suggested (Kues and Batten, 2001, p. 50). In addition, this material is evidently similar to the shells identified as *Orthonema chorda* Aderson et al., 1985 (Aderson et al., 1985, p. 1019, text-figs. 2.2, 4.4–4.6). Perhaps, all or some of these taxa are synonyms. However, based on the literature only, this synonymy cannot be confirmed.

Occurrence. Central Russian Platform; Moscovian Stage, Myachkovian Substage, Korobcheevo Formation; Donets Basin; Bashkirian, limestone E; northern China, Mokou Formation, Penchi Series.

Explanation of Plate 4

All photographs are taken from latex casts.

Figs. 1–4. *Stegocoelia laschmaensis* Mazaev, 2001, ×7: (1) specimen PIN, no. 4471/77-17; (2) specimen PIN, no. 4471/77-30; (3) holotype PIN, no. 4471/77-60; (4)specimen PIN, no. 4471/77-91; Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, top of the Korobcheevo Formation.

Figs. 5–9. *Stegocoelia klyazmaensis* Mazaev, 2001, ×7: (5) holotype PIN, no. 4471/4-5, Moscow Region, Shchelkovo quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation; (6) specimen PIN, no. 4471/6-174; (7) specimen PIN, no. 4471/6-172; Moscow Region, Gzhel' brick clay quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation; (8) specimen PIN, no. 4471/99-210; (9) specimen PIN, no. 4471/99-168; Vladimir Region, Dyukino quarry, Kasimovian Stage, Dorogomilovian Substage(?).

Figs. 10–12. *Stegocoelia berestovensis* Zernetskaja, 1983, ×4: (10) specimen PIN, no. 4471/70-40, Moscow Region, outcrop near the village of Korobcheevo; Moscovian Stage, Myachkovian Substage, Korobcheevo Formation; (11) specimen PIN, no. 4471/21-9; (12) specimen PIN, no. 4471/21-11; Moscow Region, Konev Bor quarry; Moscovian Stage, Myachkovian Substage, Korobcheevo Formation.

Figs. 13–16. *Stegocoelia acuta* Mazaev, 2001, ×8: (13) specimen PIN, no. 4471/18-147; (14) specimen PIN, no. 4471/18-177; (15) specimen PIN, no. 4471/18-183; (16) holotype PIN, no. 4471/18-182; Moscow Region, Afanasievo quarry; Kasimovian Stage, Khamovnikian Substage, Ratmirovo Formation.

Figs. 17–21. *Stegocoelia alta* Licharew, 1975, ×7: (17) specimen PIN, no. 4471/74-237, Ryazan Region, Maleevo quarry; Moscovian Stage, Myachkovian Substage, Korobcheevo Formation; (18) specimen PIN, no. 4471/79-89; (19) specimen PIN, no. 4471/79-254; (20) specimen PIN, no. 4471/79-3; (21) specimen 4471/79-46; Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, Domodedovo Formation.

Figs. 22 and 23. *Stegocoelia turabievoensis* Mazaev, 2001, ×7: (22) specimen PIN, no. 4471/2-16, (23) holotype PIN, no. 4471/2-15; Moscow Region, Shchelkovo quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation.

Material. Three imprints: two from locality no. 4471/21 and one from locality no. 4471/70.

***Stegocoelia acuta* Mazaev, 2001**

Plate 4, figs. 13–16

Stegocoelia acuta: Mazaev, 2001, p. 144, text-figs. 2I–2L.

Holotype. PIN, no. 4471/18-182, shell imprint, paratypes: no. 4471/18-147, 4471/18-177, 4471/18-183, shell imprints; Moscow Region, Afanasievo quarry; Kasimovian Stage, Khamovniki Substage, Ratmirovo Formation, base of the white mudstone member (2.5 m).

Description. The shell is small, turreted, composed of at least 14 rounded whorls, lacking an umbilicus. The suture is impressed and relatively deep. The protoconch is poorly preserved. Six juvenile whorls are very slender, angular in profile, ornamented with three spiral lirae. The second lira forms a carina. The whorl face of adult whorls is rounded, ornamented with four main spiral lirae separated by even, slightly concave spaces. The sutural lira is not developed. The second lira is approximately at the midwhorl face. The fourth lira is located immediately above the lower suture. The selenizone is smooth, bounded by the first and second lirae. The whorl base is smooth, with one spiral lira similar in size to the main spiral lirae, and is spaced by a distance equal to the space between the main lirae. The aperture is suboval in cross section. The columella is moderately long and straight. The upper lip is thin, while the inner lip is thick. The growth lines are very thin, prosocline above the selenizone, form weak lunulae on the selenizone and a gentle arch on the lower whorl face, which is convex and slightly inclined forward from the selenizone. The pallial slit is not preserved.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/18-182, holotype	>9.0	2.8
4471/18-147, paratype	12.0	4.0
4471/18-177, paratype	11.5	3.7
4471/18-183, paratype	6.5	2.3

Comparison. This species is very similar to *S. acutiformis* being distinguished by the more slender, elongated spire and by the width-to-height whorl ratio, which ranges from 1.4 to 1.7. It differs from *S. gzheliensis* in the rounded whorl profile and equal spaces between lirae on the definitive whorls.

Occurrence. Central Russian Platform; Moscovian Stage, Myachkovian Substage, Kasimovian Stage, Krevyakian Substage, Gzhelian Stage, Dobryatinian Substage.

Material. Twenty-nine imprints: two from locality no. 4471/12, 24 from locality no. 4471/18, two from locality no. 4471/36, and one from locality no. 4471/87.

***Stegocoelia alta* Licharew, 1975**

Plate 4, figs. 17–21

Stegocoelia (*Hypergonia*?) *alta*: Licharew, 1975, pp. 69–70, pl. 10, figs. 7–9; Mazaev, 2001, p. 141, text-fig. 2A–2E.

Stegocoelia (*Hypergonia*?) *altiformis*: Licharew, 1975, p. 70, pl. 10, figs. 10–12.

Stegocoelia (*Hypergonia*?) *acris*: Licharew, 1975, pp. 70, 71, pl. 10, figs. 13 and 14.

Stegocoelia (*Hypergonia*?) sp. aff. *acris*: Licharew, 1975, p. 71, pl. X, fig. 15.

Stegocoelia (*Hypergonia*?) *procera*: Licharew, 1975, p. 72, pl. XI, figs. 4 and 5.

Stegocoelia (*Hypergonia*?) *korobkovi*: Licharew, 1975, p. 72, pl. 11, figs. 1 and 3; non fig. 2.

Stegocoelia (*Hypergonia*?) sp. indet. *c*: Licharew, 1975, pp. 73, 74, pl. 11, fig. 8.

Holotype. TsNIGR Museum, collection no. 9758, no. 124, paratypes: nos. 125, 351, 352, 353; eastern slope of the Ural Mountains, Karabolka River, outcrop near the village of Ust'-Karabolka; Moscovian Stage, Myachkovian Substage.

Description. The shell is small, turreted, composed of 13 slowly expanding whorls, lacking an umbilicus. The suture is thin and shallow. The protoconch is formed by two smooth whorls, the next four–six juvenile whorls are prominently angular, ornamented with three spiral lirae, the median lira forms a carina, while the two lower lirae are closely spaced. The whorl face profile of adult whorls is nearly straight or slightly convex. The whorl face is ornamented with a weak sutural lira and four main spiral lirae with equal spaces between them. The space between the sutural lira and first main lira can be narrower than the others. The selenizone is bounded by the first and second main spiral lirae, can be slightly wider than the remaining spaces between the lirae. The whorl base is smooth, with one spiral lira of the same size as the main spiral lirae, and is positioned at a distance from them similar to the space between the main lirae. The aperture is semirounded in cross section. The columella is short. The growth lines are very thin, prosocline above the selenizone, form lunulae on the selenizone, and below the selenizone are weakly bent forward, opisthocline. The slit is not preserved.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/79-89	6.0	1.5
4471/74-7	6.5	1.5
4471/74-237	6.5	1.5
4471/74-76	>9.0	2.5
4471/20-18	9.0	2.5
4471/31-3	6.0	2.0

Comparison. This species is distinguished from *S. acuta* by the more slowly increasing number of whorls and the greater width-to-height ratio of the whorl. It is distinguished from *S. gzheliensis* by the disappearance of the carinate whorl profile in the last whorls.

Remarks. Shells of this species show considerable ontogenetic variability. The whorl profile changes in ontogeny from carinate to rounded, then, changes almost to subcylindrical, but lacking a shoulder and lower carina. Several species established by Licharew are listed here as junior synonyms of this species. Most of the original specimens represent apical, or definitive shell fragments.

Occurrence. Central Russian Platform; Moscovian Stage, Myachkovian Substage, Kasimovian Stage, Krevyakian and Khamovniki substages; eastern slope of the Ural Mountains; Moscovian Stage, Myachkovian Substage.

Material. Thirty-eight imprints: locality no. 4471/18 – 5 specimens, locality no. 4471/20 – 3 specimens, locality no. 4471/26 – 1 specimen, locality no. 4471/31 – 1 specimen, locality no. 4471/74 – 10 specimens, locality no. 4471/79 – 13 specimens, locality no. 4471/87 – 7 specimens.

Stegocoelia turabievoensis Mazaev, 2001

Plate 4, figs. 22 and 23

Stegocoelia turabievoensis: Mazaev, 2001, p. 142, text-figs. 2G and 2H.

Holotype. PIN, no. 4471/2-15, shell imprint; paratypes: PIN, nos. 4471/2-14, 4471/2-16, 4471/2-20, 4471/2-27, 4471/2-85, shell imprints; Moscow Region, Shchelkovo quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation, top of the thick (2 m) yellow dolomitized limestone, approximately 3.5 m above the top of the variegated clayey member.

Description. The shell is turreted, medium-sized, composed of 16 weakly angular whorls, lacking an umbilicus. The suture is distinct, shallow. The protoconch is composed of one and a half to two rounded, smooth whorls. Six juvenile whorls are poorly preserved, angular in profile, ornamented with three spiral lirae. The second lira forms a carina, two lower lirae are closely spaced. The whorl face of adult whorls is ornamented with four main spiral lirae and variously developed sutural lira. The first main lira is slightly thinner than the rest of main lirae and located in the center of the upper part of the angular whorl face. The second lira is relatively massive, forms a distinct carina. The selenizone is bounded by the first and second main lirae. All lirae are separated by equal, weakly concave or nearly straight in profile spaces. The fourth main lira is overlapped by a subsequent whorl, separates the whorl face from the base. On definitive whorls, it lies in the peripheral zone of the whorl base. The aperture is trapezoidal. The outer lip is thin, whereas the inner lip is thick. The columella is long and straight. The growth lines are very thin, prosocline above the selenizone; on the selenizone, they form weak lunulae and, below the selenizone, gradually arch forwards, opisthocline. The slit is not preserved.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/2-15 holotype	>15.0	4.0
4471/2-16 paratype	12.0	3.0

Comparison. In its whorl profile, number and position of spiral lirae, this species is similar to *S. percostata* (Girty, 1939), although being relatively readily distinguished from that by the smaller apical angle and completely different width-to-height whorl ratio.

Material. Seven imprints from the type locality.

Stegocoelia knighti (Licharew, 1975)

Plate 5, figs. 1–3

Cyclozyga knighti: Licharew, 1975, pp. 113–114, pl. 18, figs. 13–15.

Stegocoelia (*Stegocoelia*?) *compactiformis*: Licharew, 1975, p. 67, pl. 10, figs. 3 and 4.

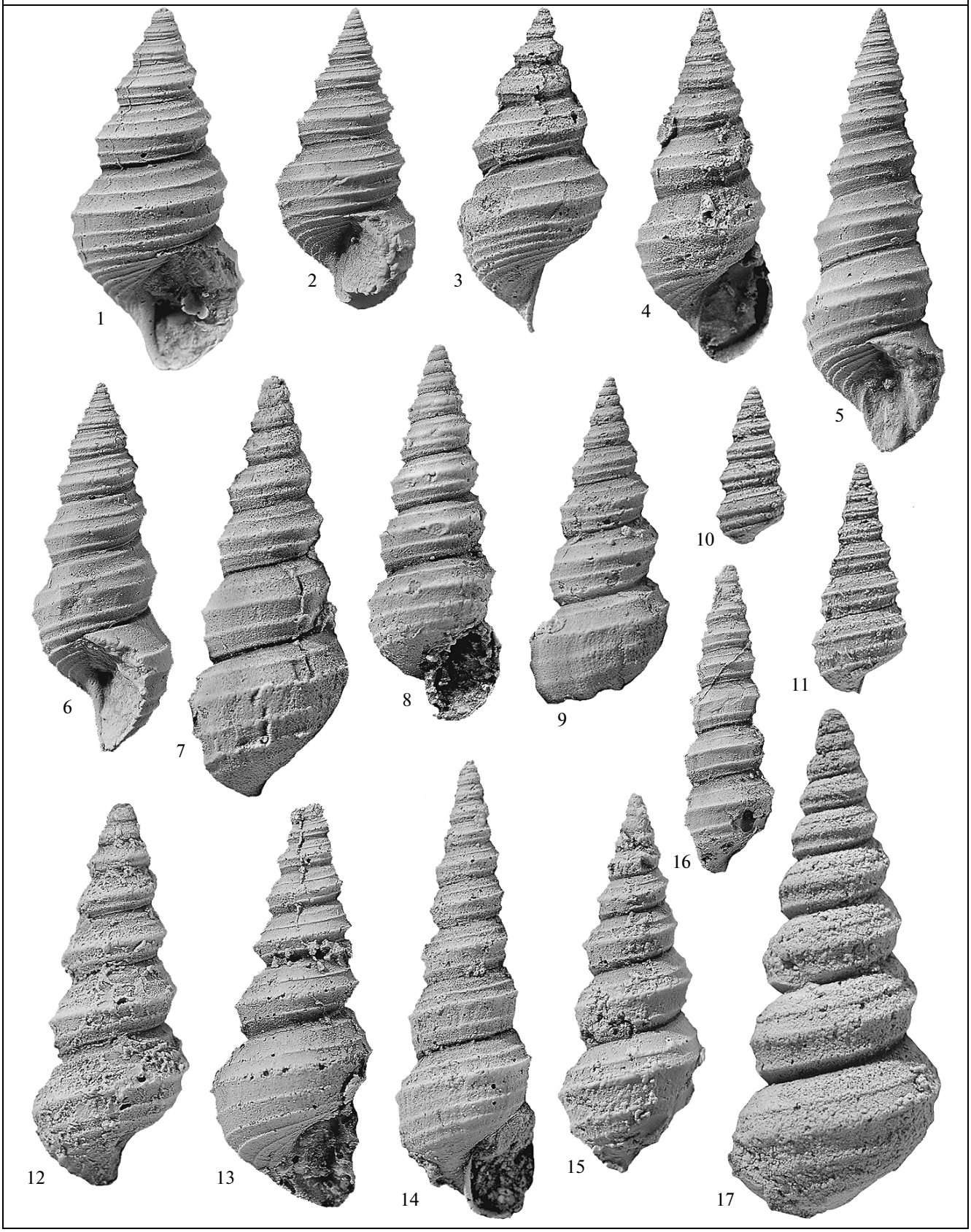
Stegocoelia (*Stegocoelia*?) *rara*: Licharew, 1975, pp. 67, 68, pl. 10, figs. 5 and 6.

Stegocoelia knighti: Mazaev, 2001, p. 147, text-figs. 3A–3C.

Holotype. TsNIGR Museum, collection no. 9758, no. 257; paratypes nos. 258, 259, 368; eastern slope of the Ural Mountains, Karabolka River, outcrop near the village of Ust'-Karabolka; Moscovian Stage, Myachkovian Substage.

Description. The shell is small, turreted, composed of eight prominently angular whorls, lacking an umbilicus. The suture is impressed and shallow. The protoconch consists of approximately two smooth rounded whorls. Three juvenile whorls are angular in profile, ornamented with three spiral lirae. The upper lira is weak and is located immediately near the suture. The second and third lirae are prominent, closely spaced in a pair, which forms an angular whorl profile. A weak auxiliary sutural lira appears on the last juvenile whorl. The whorl face of adult whorls is ornamented with the sutural lira and four main spiral lirae. The lirae are equal in size and are separated by equal spaces. The sutural lira is prominently shifted away from the suture. The second main lira forms a prominent carina. The fourth main lira is located slightly above suture and slightly nearer to the third lira. The selenizone is bounded by the first and second lirae; on the definitive whorls, a very thin auxiliary lira may appear on the selenizone slightly above the second lira. The whorl base is nearly straight in profile, ornamented with at least five spiral lirae of the same size as the main lirae on the whorl face. Weak auxiliary spiral lirae may appear between them on the definitive whorls. The aperture is suboval. The outer lip is thin; the inner lip is thickened. The columella is moderately long, weakly bent; the abapical canal is weakly developed. The growth lines are very thin, prosocline above the selenizone, on the selenizone, form weak lunulae, below the selenizone, form a broad convex opisthocline arch. The slit is not preserved.

Plate 5



Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/79-222	8.0	4.0
4471/79-142	8.5	4.0
4471/22-7	5.0	3.0
4471/6-26	7.0	3.5
4471/76-9	5.0	3.0

Comparison. This species is very similar to *S. okaensis* and is distinguished only in the larger apical angle of about 50°.

Occurrence. Central Russian Platform, Moscovian Stage, Myachkovian Substage, Kasimovian Stage, Krevyakian Substage, Gzhelian Stage, Dobryatinian Substage; eastern slope of the Ural Mountains; Moscovian Stage, Myachkovian Substage.

Material. Thirty-one imprints: five from locality no. 4471/3, one from locality no. 4471/4, one from locality no. 4471/6, one from locality no. 4471/18, three from locality no. 4471/20, two from locality no. 4471/22, one from locality no. 4471/26, one from locality no. 4471/30, two from locality no. 4471/50, one from locality no. 4471/74, one from locality no. 4471/76, ten from locality no. 4471/79, one from locality no. 4471/84, and one from locality no. 4471/85.

***Stegocoelia okaensis* Mazaev, 2001**

Plate 5, figs. 4–6

Stegocoelia okaensis: Mazaev, 2001, p. 147, text-figs. 3D–3F.

Holotype. PIN, no. 4471/79-262; shell imprint; paratypes PIN, nos. 4471/79-19, 4471/79-52, 4471/79-76, 4471/79-91, shell imprints; Ryazan Region, Akishinskii quarry (near the village of Lashma); Moscovian Stage, Myachkovian Substage, Domodedovo Formation, base of a member (5 m) of white thickly bedded mudstone.

Description. The shell is small, turreted, composed of 11 prominently angular whorls, lacking an umbilicus. The suture is impressed and shallow. The protoconch is composed of two smooth whorls. Two or three juvenile whorls are angular in profile, ornamented with three spiral lirae; the upper lira is weak, located immediately below the upper suture, two other lirae are closely spaced in a pair, which forms an angular whorl profile. A weak auxiliary sutural lira appears on the last juvenile whorl. The whorl face of adult whorls is ornamented with four main spiral lirae and a sutural lira with equal spaces between them. The sutural lira is located immediately below the suture. The second main lira usually forms a carina. The fourth lira is near the lower suture or overlapped by the subsequent whorl. The selenizone is bounded by the first and second lirae; on the definitive whorl, the distance between the sutural and first lira is nearly two times wider than the band of the selenizone. The whorl base on the last whorl has up to five spiral lirae. The aperture is suboval. The outer lip is thin; the inner lip is thick. The columella is moderately long. The growth lines are very thin, prosocline above the selenizone, on selenizone form weak lunulae, beneath selenizone form a broadly curved forwards, slightly opisthocline arch. The pallial slit is not preserved.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/79-262 holotype	11.5	3.5
4471/79-19 paratype	9.0	3.5
4471/79-52 paratype	7.5	3.0
4471/79-76 paratype	8.0	2.5
4471/79-91 paratype	9.0	3.0
4471/2-12	11.5	4.5

Comparison. This species is very similar to *S. knighti* and distinguished from it only by the smaller

Explanation of Plate 5

All photographs are taken from latex casts.

Figs. 1–3. *Stegocoelia knighti* (Licharew, 1975), ×7: (1) specimen PIN, no. 4471/79-290; (2) specimen PIN, no. 4471/79-222; (3) specimen PIN, no. 4471/79-142; Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, Domodedovo Formation;

Figs. 4–6. *Stegocoelia okaensis* Mazaev, 2001, ×7: (4) specimen PIN, no. 4471/79-91; (5) holotype PIN, no. 4471/79-262; (6) specimen, no. 4471/79-19; Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, Domodedovo Formation;

Figs. 7–11. *Stegocoelia acutiformis* Mazaev, 2001, ×7: (7) specimen PIN, no. 4471/90-3; (8) holotype PIN, no. 4471/90-1; (9) specimen PIN, no. 4471/90-2; Moscow Region, Afanasievo quarry, Moscovian Stage, Peski Formation; (10) specimen PIN, no. 4471/6-173; (11) specimen PIN, no. 4471/6-161; Moscow Region, Gzhel' brick clay quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation.

Figs. 12 and 13. *Stegocoelia korobcheevoensis* Mazaev, 2001, ×7: (12) specimen PIN, no. 4471/50-140; (13) holotype PIN, no. 4471/50-150; Moscow Region, Domodedovo quarry; Moscovian Stage, Korobcheevo Formation.

Figs. 14–17. *Stegocoelia gzheliensis* Mazaev, 2001, ×7: (14) specimen PIN, no. 4471/37-1; Moscow Region, outcrop on the bank of the Klyazma River near the village of Amerevo; Gzhelian Stage, Amerevo Formation (collection by A.P. Ivanov); (15) specimen PIN, no. 4471/3-36; (16) specimen PIN, no. 4471/3-5 (holotype); Moscow Region, Rusavkino quarry; Gzhelian Stage, Rechitsy Formation; (17) specimen PIN, no. 4471/97-18; Moscow, construction pit beneath the City center, Kasimovian Stage, Dorogomilovian Substage, Izmailovo Formation.

apical angle of about 40°. It differs from *S. korobcheevoensis* in the larger number of spiral lirae on the whorl base and in the wider space between the sutural and the first main lira on the definitive whorls.

Occurrence. Central Russian Platform; Moscovian Stage, Myachkovian Substage, Gzhelian Stage, Dobryatinian Substage.

Material. Sixty-nine imprints: one from locality no. 4471/2, one from locality no. 4471/13, three from locality no. 4471/22, two from locality no. 4471/25, six from locality no. 4471/26, one from locality no. 4471/28, one from locality no. 4471/33, seven from locality no. 4471/70, 14 from locality no. 4471/74, 28 from locality no. 4471/79, one from locality no. 4471/80, and five from locality no. 4471/85.

***Stegocoelia acutiformis* Mazaev, 2001**

Plate 5, figs. 7–11

Stegocoelia acutiformis: Mazaev, 2001, p. 145, text-figs. 2M–2O.

Holotype. PIN, no. 4471/90-1; shell imprint; paratypes: PIN, nos. 4471/90-2; 4471/90-3. 4471/90-4, 4471/90-5, shell imprints; Moscow Region, Afanasievo quarry; Moscovian Stage, Myachkovian Substage, Peski Formation, coarse cross-bedded gray grainstone with *Meekella*, underlying the Turaevo dolomite.

Description. The shell is small, turreted, composed of 12 angular whorls, lacking an umbilicus. The suture is impressed, relatively deep. The protoconch is composed of approximately two smooth rounded whorls. One juvenile whorl is slightly angular in profile, ornamented with three spiral lirae. The band between the first and second lirae is twice as wide as that between the second and third lirae. The whorl face of the adult whorls is ornamented with four main spiral lirae. The sutural lira is not developed. The first lira is approximately in the middle of the upper whorl face or slightly shifted towards the suture. The second lira subdivides the whorl face into the upper and lower zones and usually forms a carina. The third lira is approximately in the middle of the lower whorl face, whereas the fourth is near the lower suture. The selenizone is bounded by the first and second lira. The whorl base is rounded, possesses one spiral lira below the fourth lira. All spaces between lirae are approximately equal in width, while the band between the first lira and the suture is narrower. The aperture is suboval. The outer lip is thin. The inner lip is thick. The abapical canal is weakly developed; the depth of the slit is twice as large as its width. The columella is moderately long, straight. The growth lines are very thin, prosocline above the selenizone, on the selenizone form weak lunulae, and beneath selenizone forming a broad slightly opisthocline arch.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/90-1, holotype	10.0	3.5
4471/90-2, paratype	9.0	3.5
4471/90-3, paratype	10.5	4.0

Comparison. *S. acutiformis* is distinguished from *S. gzheliensis* by approximately equal spaces between lirae, while the distance between the suture and the first main lira is equal to, or less than, the width of the selenizone. This species is distinguished from *S. acuta* in the less elongated shell with more rapidly expanding whorls. The width-to-height ratio of the whorl ranges from 1.7 to 1.9

Remarks. The intraspecific variability is observed in the change in the proportions of juvenile whorls and in the profile of the definitive whorls, which varies from carinate to rounded.

Occurrence. Central Russian Platform; Moscovian Stage, Podolskian and Myachkovian substages, Kasimovian Stage, Krevyakian Substage, Gzhelian Stage, Dobryatinian Substage.

Material. Sixty-seven imprints: two from locality no. 4471/6, 27 from locality no. 4471/18, three from locality no. 4471/19, seven from locality no. 4471/74, one from locality no. 4471/83, two from locality no. 4471/87, 18 from locality no. 4471/90, and seven from locality no. 4471/93.

***Stegocoelia korobcheevoensis* Mazaev, 2001**

Plate 5, figs. 12 and 13

Stegocoelia korobcheevoensis: Mazaev, 2001, p. 148, text-figs. 3G and 3H.

Holotype. PIN, no. 4471/50-150, shell imprint; paratypes PIN, nos. 4471/50-140, 4471/50-145, shell imprints; Moscow Region, Domodedovo quarry; Moscovian Stage, Myachkovian Substage, Korobcheevo Formation, top of the thick member (2 m) of the coral–foraminiferal grainstone.

Description. The shell is small, turreted, composed of eight angular whorls, lacking an umbilicus. The suture is impressed and moderately deep. The protoconch is not preserved. Juvenile whorls are angular, ornamented with three spiral lirae. The second lira forms a carina. The whorl face of adult whorls is ornamented with four main spiral lirae and an auxiliary sutural lira. The sutural lira is shifted away from the suture. The first main spiral lira is in the middle of the upper region of the prominently angular whorl face. The second main lira forms a carina, while the third main lira is in the middle of the lower zone of the whorl face. The fourth spiral lira is overlapped by the subsequent whorl or is located immediately above the lower suture. The selenizone is bounded by the first and second lirae. The whorl base on the last whorl possesses three spiral lirae. All lirae are separated by equal

spaces. The aperture is suboval. The outer lip is thin, while the inner lip is thick. The growth lines are very thin, prosocline above the selenizone. On the selenizone, they form lunulae, and beneath the selenizone, form a broad arch, bent forward and slightly opisthocline. The pallial slit is not preserved.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/50-150, holotype	9.0	4.0
4471/50–140, paratype	9.5	4.0
4471/50-145, paratype	>10.0	>4.5

Comparison. This species is very similar to *S. okaensis*, but distinguished by the sutural lira shifted downward and by fewer spiral lirae on the whorl base. It differs from *S. acutiformis* and *S. gzheliensis* in the presence on the whorl base of three spiral lirae and the well-developed sutural lira.

Occurrence. Central Russian Platform; Moscovian Stage, Myachkovian Substage, Kasimovian Stage, Krevyakian Substage.

Material. Fourteen imprints: one from locality no. 4471/18, one from locality no. 4471/28, six from locality no. 4471/50, five from locality no. 4471/70, and one from locality no. 4471/87.

***Stegocoelia gzheliensis* Mazaev, 2001**

Plate 5, figs. 14–17

Stegocoelia gzheliensis: Mazaev, 2001, p. 146, text-figs. 2P–2R.

Holotype. PIN, no. 4471/3-5, shell imprint; paratypes: PIN, nos. 4471/3-3. 4471/3-36; shell imprints; Moscow Region, Rusavkino quarry; Gzhelian Stage, Dobryatinian Substage, Rechitsy Formation, yellow dolomitized limestone, 0.5 m above the variegated clay.

Description. The shell is small, turreted, consisting of up to 13 prominently angular whorls, lacking an umbilicus. The suture is impressed and deep. The protoconch is not preserved. Juvenile whorls are poorly preserved, apparently composed of two angular whorls with three spiral lirae. The second lira forms a prominent carina. The second and third lirae are closely spaced. The whorl face of adult whorls is ornamented with four spiral lirae. The sutural lira is absent or weakly developed on the last whorl. The first main spiral lira is approximately in the middle of the upper part of the prominently angular whorl face. The second lira forms a carina or shoulder. The third lira is developed on the lower whorl face and the fourth is near the lower suture. The selenizone is bounded by the first and second lirae. The whorl base possesses one or two weak spiral lirae. On the last whorl, the distance between the second and third lirae can be nearly twice as large as the width of the selenizone. This space may possess a thin, threadlike auxiliary lira. The aperture is suboval; the outer lip is thin; the inner lip is thick. The columella is moderately long and straight. The growth lines are very thin, prosocline above the selenizone. They form weak lunulae on the selenizone, broadly arcuate below the selenizone, bent forward and opisthocline. The slit is not preserved.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/3-5, holotype	8.0	2.5
4471/3-36, paratype	9.5	4.0
4471/37-1	12.0	4.0

Comparison. This species is very similar to *S. acutiformis*, but distinguished by the considerably more slender, elongated juvenile whorls and the wide space between the second and third main lirae on the definitive whorls. In addition, the width of the space between the suture and the first spiral lira is the same or slightly greater than that of the selenizone. It is distinguished from *S. acuta* by the carinate whorl profile.

Remarks. Intraspecific variability is observed in the changes in the whorl profile from angular with a prominent carina to nearly subcylindrical with a shoulder on the definitive whorls.

Occurrence. Central Russian Platform; Gzhelian Stage, Dobryatinian Substage.

Material. Eleven imprints: three from locality no. 4471/3, three from locality no. 4471/4, three from locality no. 4471/6, one from locality no. 4471/37, and one from locality no. 4471/75.

Genus *Arribazona* Kues, 1990

Arribazona: Kues, 1990, p. 252; Kues and Batten, 2001, p. 51; Mazaev, 2003, p. 96.

Type species. *Arribazona hesperia* Kues, 1990.

Diagnosis. Shell small or medium-sized, turreted; suture impressed, shallow; juvenile whorls smooth, weakly convex; whorl face profile of adult whorls weakly convex or nearly flat, weakly rounded near sutures; whorl face passing smoothly into whorl base on definitive whorls, but separated by weak rounded angulation on intermediate whorls. Whorl base weakly convex; selenizone positioned above midwhorl, slightly elevated or lying at level of adjacent shell surface, occasionally bounded by thin grooves. Weakly developed sutural ramp and very thin or indistinct spiral lirae beneath selenizone or spiral rows of weakly developed nodes present in some species on definitive whorls. Growth lines very thin, weakly prosocline above selenizone, on selenizone form lunulae, beneath selenizone gradually bent forward and opisthocline.

Species composition. Species of this genus come from the Middle Pennsylvanian of Texas and New Mexico and the Pennsylvanian to Lower Permian of Eastern Europe and Central Asia.

Comparison. This genus is very similar to *Altadema* and *Laschmaspira*, distinguished by the flattened whorl profile, without variously developed spiral lirae near the selenizone. In addition, a weak angulation between the whorl face and whorl base is formed in the intermediate whorls. This angulation is never developed as a distinct carina, and disappears on the definitive whorls. This genus is clearly distinguished from *Ferganispira* by the absence of a subsutural ramp, which forms a distinct shoulder above the selenizone.

Remarks. Kues (1990, p. 252) showed that some shells of the type species show weakly developed (very thin or hardly discernible) spiral lirae below the selenizone. A few, apparently teratological specimens of another species, *A. tschernyschewi* (Yakovlev, 1899) possess indistinct, relatively wide spiral rounded ridges or a spiral row of nodes on the transition from the whorl face above the suture, below the selenizone on the whorl face and partly on the whorl base (Mazaev, 2006, p. 50). It should be said that spiral ornamentation in *Arribazona* is never developed as strongly as in *Laschmaspira* or *Stegocoelia*.

Arribazona devispira Mazaev, 2003

Plate 6, figs. 1–8

Arribazona devispira: Mazaev, 2003, p. 97, text-figs. 3D–3K.

Holotype. PIN, no. 4471/79/166, shell imprint; paratypes PIN, nos. 4471/79-5, 4471/79-45, 4471/79-123, 4471/79-140, 4471/79-154, 4471/79-157, 4471/79-186, 4471/79-217, 4471/79-253, shell imprints; Ryazan Region, Akishinskii quarry (near the village of Lashma); Moscovian Stage, Myachkovian Substage, Domodedovo Formation, base of the tick member (5 m) of while thickly bedded mudstone.

Description. The shell is small, up to 14 mm high, turreted, composed of ten smooth rounded whorls. The protoconch is not preserved. Juvenile whorls are smooth, weakly convex. The whorl face profile of adult whorls in its central zone varies from flat to slightly convex, weakly rounded near the upper suture, to the same extent or more strongly rounded near the lower suture up to the development of a distinct angulation. The last whorl usually becomes more strongly convex, evenly rounds into the whorl base, deviates from the previous growing mode, and is shifted down away from the suture. The whorl base is smooth and weakly convex. The suture is sunken, shallow, deeper on the last whorl. The selenizone is above the midwhorl face. The distance between the selenizone and the upper suture is approximately equal in size to the selenizone. The selenizone is flat or slightly convex, bounded by thin grooves, lies in the same plane as the whorl surface or weakly elevated above it. The aperture is suboval. The outer, basal, and columellar lips are thin, the reflection of the columellar lip forms a columella and a very small umbilicus. The columella is moderately long and nearly straight. The outer lip has a pallial slit. The slit is three times as deep as wide. The growth lines are very thin, bent above the selenizone and are weakly prosocline. On the selenizone, they form lunulae, while beneath the selenizone, they are bent forward and weakly opisthocline.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/79-166, holotype	11.5	4.0
4471/79-5, paratype	7.5	2.5
4471/79-123, paratype	11.0	3.5
4471/79-140, paratype	7.5	3.0
4471/79-154, paratype	11.5	3.5
4471/79-157, paratype	9.0	3.5
4471/79-253, paratype	9.0	3.0

Comparison. This species is distinguished from *A. hesperia* Kues, 1990 by the smooth surface of the whorl below the selenizone (lacking thin spiral lirae). It differs from *Arribazona tschernyschewi* (Yakovlev, 1899) and *Arribazona permiana* (Yakovlev, 1899) in the more strongly flattened whorl face and in the width-to-height ratio of the median whorls varying from 1.8 to 2.0.

Remarks. The last whorls deviate from the growth direction of the preceding whorls, and their whorl width-to-height ratio is 1.35. This deviation is also observed in the change in the whorl profile.

Explanation of Plate 6

All photographs are taken from latex casts.

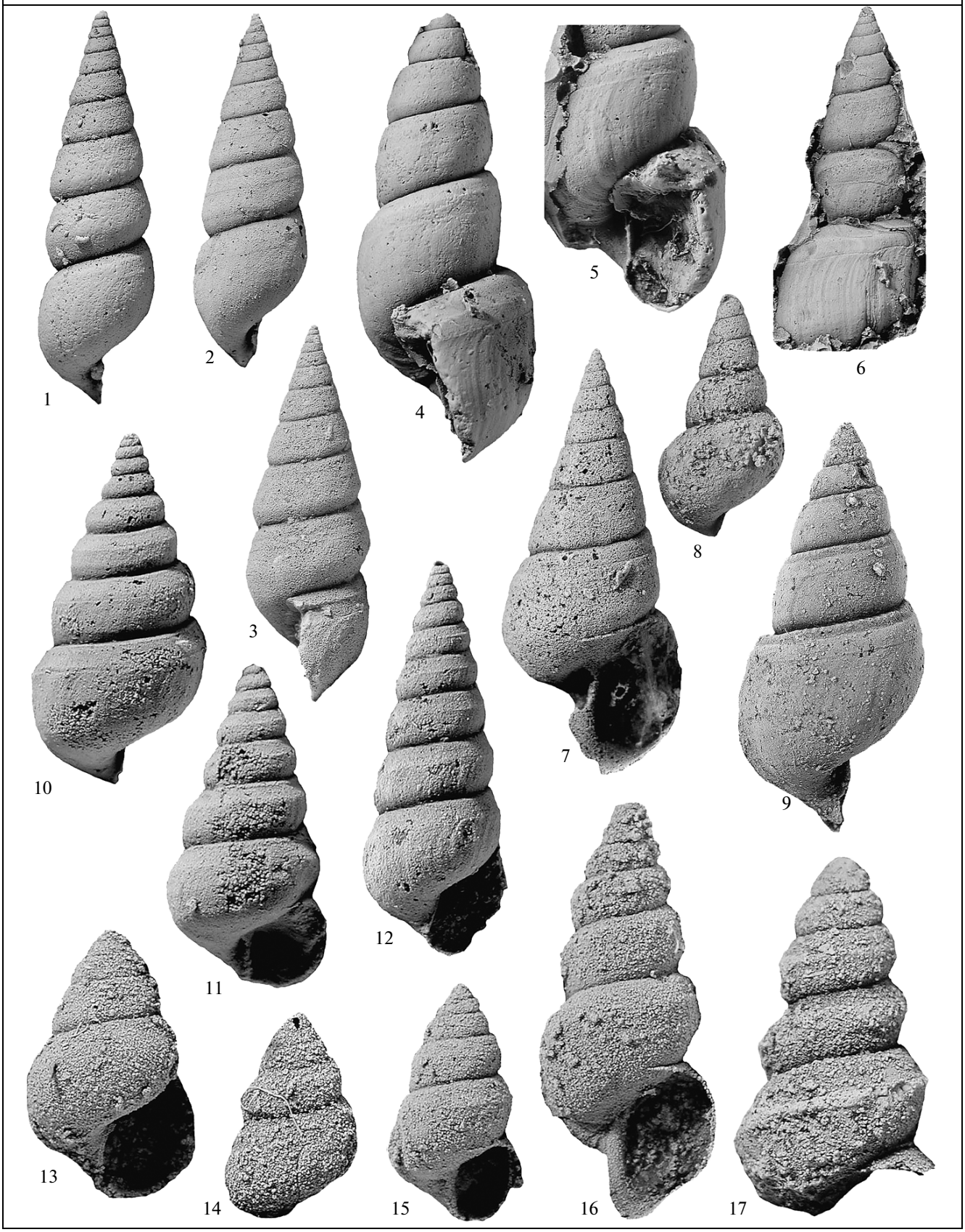
Figs. 1–8. *Arribazona devispira* Mazaev, 2003, ×6: (1) specimen PIN, no. 4471/79-154; (2) specimen PIN, no. 4471/79-123; (3) holotype PIN, no. 4471/79-166; Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, Domodedovo Formation; (4, 5, 6) specimen PIN, no. 4471/50-48: (4) palatal margin view, (5) apertural view, (6) cast of the spire with imprints from the same specimen, on the last whorl, growth lines clearly show slit morphology and depth; Moscow Region, Domodedovo quarry; Moscovian Stage, Myachkovian Substage, Korobcheevo Formation; (7) specimen PIN, no. 4471/78-56; (8) specimen PIN, no. 44/78-31; Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, Domodedovo Formation.

Fig. 9. *Arribazona nodolira* Mazaev, 2003, holotype PIN, no. 4471/6-61, ×5; Moscow Region, Gzhel' quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation.

Figs. 10–12. *Altadema altadema* Mazaev, 2003, ×12: (10) specimen 7741/16-17; (11) holotype PIN, no. 4471/16-8; (12) specimen PIN, no. 4471/16-13; Vladimir Region, Dobryatino quarry; Kasimovian Stage, Dorogomilovian Substage.

Figs. 13–17. *Altadema cryptocarina* Mazaev, 2003, ×11: (13) specimen PIN, no. 4471/76-14; (14) specimen PIN, no. 4471/76-28; (15) holotype PIN, no. 4471/76-18; (16) specimen PIN, no. 4471/76-1; (17) specimen PIN, no. 4471/76-11; Moscow Region, quarry near the village of Gubino; Gzhelian Stage, Noginskian (?) Substage.

Plate 6



Occurrence. Central Russian Platform; Moscovian Stage, Myachkovian Substage, Kasimovian Stage, Krevyakian Substage, Gzhelian Stage, Dobryatinian Substage.

Material. Sixty-six imprints: one from locality no. 4471/16, one from locality no. 4471/18, one from locality no. 4471/26, two from locality no. 4471/50, one from locality no. 4471/70, 52 from locality no. 4471/79, seven from locality no. 4471/78, and one from locality no. 4471/86.

Arribazona nodolira Mazaev, 2003

Plate 6, fig. 9

Arribazona nodolira: Mazaev, 2003, p. 97, text-fig. 3L.

Holotype. PIN, no. 4471/6-61, shell imprint; paratype PIN, no. 4471/6-113, shell imprint; Moscow Region, Gzhel' brick clay quarry; Gzhelian Stage, Dobryatinian Substage, Amerevo Formation, base of the member of yellow dolomitized limestone, overlying the variegated clay member.

Description. The shell is medium-sized, up to 15 mm high, turreted, composed of seven rapidly expanding smooth whorls. The protoconch is not preserved. Juvenile whorls are smooth and slightly convex. Adult whorls are slightly convex, the lower region of the whorl face is nearly straight, the subsequent whorls are weakly convex, rounding smoothly into the slightly convex whorl base. The suture is impressed and shallow. A weak sutural lira with many small nodes appears on the last whorls. The space between the suture and selenizone is as wide as the selenizone. The selenizone is flat or slightly convex, bounded by thin grooves, lies in the same plane as the whorl surface or weakly elevated over it. The apertural margin morphology is unknown. The growth lines are very thin, bent forward above the selenizone and are weakly prosocline; on selenizone, they form lunulae; beneath selenizone, they are bent forward and weakly opisthocline.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/6-61, holotype	15.0	7.0
4471/17-23	7.2	3.5
4471/17-12	9.0	4.3

Comparison. This species is clearly distinguished from congeners by the presence of an ornamented subsutural lira on the last whorls.

Occurrence. Central Russian Platform; Gzhelian Stage, Dobryatinian Substage.

Material. Eight imprints: two from locality no. 4471/6, five from locality no. 4471/17, and one from locality no. 4471/99.

Genus *Altadema* Kues, 2002

Altadema: Kues, 2002, p. 53; Mazaev, 2003, p. 91.

Type species. *Altadema convexa* Kues, 2002.

Diagnosis. Shell small or medium-sized, turreted; juvenile whorls smooth, rounded, with weak angulation near suture; profile of definitive whorls rounded, sometimes weakly angular near selenizone; suture impressed; selenizone positioned above midwhorl weakly concave, bounded on either side by spiral lira or thin groove or straight in cross section, which clearly separates selenizone surface from adjacent shell surface; spiral ornamentation absent or represented by one to four distinct or weak evenly spaced spiral lirae; two upper lirae (if present) bound selenizone. Growth lines very thin, prosocline above selenizone, forming lunulae on selenizone, gradually bent forward and opisthocline beneath selenizone.

Species composition. One species from the Middle Pennsylvanian of Texas and three species from the Pennsylvanian of the central Russian Platform.

Comparison. This genus is distinguished from *Arribazona* in the evenly rounded whorl profile (excluding occasions when a weak carina is present near the selenizone), whereas the whorl face of the intermediate whorls of *Arribazona* are nearly flat or slightly convex in profile, and rather prominently rounds into the whorl base, forming a rounded angulation. This genus differs from *Concinnispira* and *Hermosanema* in the smooth and nearly rounded juvenile whorls.

Remarks. *Altadema* is very similar to *Concinnispira, Hermosanema*, and *Arribazona*. These genera share many characters, but in different combinations. The number of spiral lirae on the whorl face of some species may reach four and in this *Altadema* is similar to *Stegocoelia, Taosia* Girty, 1939, *Vebericochlis, Concinnispira, Hermosanema*, and *Orthonema*. The similarity of *Altadema* to *Concinnispira* and *Hermosanema* is observed in the disappearance of spiral ornamentation on the definitive whorls.

Altadema altadema Mazaev, 2003

Plate 6, figs. 10–12

Altadema altadema: Mazaev, 2003, p. 92, text-figs. 2F–2H.

Holotype. PIN, no. 4471/16-13, shell imprint; paratypes PIN, nos. 4471/16-8, 4471/16-17, shell imprints; Vladimir Region, Dobryatino quarry; Gzhelian Stage, Dorogomilovian Substage.

Description. The shell is very small (up to 5.5 mm high), turreted, composed of ten nearly rounded whorls. The suture is impressed. The protoconch is not preserved. The spiral angle varies from 25° to 40°. The whorl surface is smooth. The selenizone is flattened, weakly impressed or lies at the same level as the whorl surface, may be bounded by weak spiral groove on either side, and is located almost immediately below the upper suture. The whorl profile

is convex, with a periphery near midwhorl, slightly angular beneath the selenizone. Some specimens have a thin, indistinct spiral lira, which appears beginning from the third whorl and disappears in the last two whorls. The shell lacks an umbilicus or has a pseudoumbilicus, which is formed as a reflection of the inner lip. The outer lip margin and the slit are not preserved; the depth of the slit is unknown. The aperture is rounded, angular in the parieto-palatal region. The outer and inner lips are thin, the columella is nearly straight. The growth lines are thin, distinct; on the selenizone, they form lunulae, beneath the selenizone, they curve forward and are slightly opisthocline.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/16-13, holotype	6.0	2.2
4471/16-8, paratype	5.0	2.4
4471/16-11, paratype	5.4	2.0
4471/16-17, paratype	5.3	2.7
4471/16-22, paratype	4.5	2.3

Comparison. This species is readily distinguished from congeners by the position of the selenizone, which is set very close to the suture.

Remarks. Available shells exhibit a wide range of intraspecific variation, which is manifested in various values of the apical angle (from 25° to 40°).

Occurrence. Central Russian Platform; Kasimovian Stage, Krevyakian Substage; Gzhelian Stage, Dorogomilovian Substage.

Material. Eleven imprints: ten from locality no. 4471/16 and one from locality no. 4471/20.

Altadema cryptocarina Mazaev, 2003

Plate 6, figs. 13–17

Altadema cryptocarina: Mazaev, 2003, p. 91, text-figs. 2A–2E.

Holotype. PIN, no. 4471/76-18, shell imprint; paratypes PIN, no. 4471/76-1, 4471/76-11. 4471/76-14, 4471/76-18, 4471/76-28, shell imprints; Moscow Region, Shatura District, road cutting near the village of Gubino; Gzhelian Stage, Noginsk (?) Substage.

Description. The shell is very small, turreted (approximately 7 mm high), composed of six or seven nearly rounded or weakly angular whorls. The suture is impressed. The protoconch is not preserved. The whorl expansion rate is variable. The apical angle varies from 35° to 50°. The whorl face is smooth or ornamented at adult stages with one weak spiral lira, occurring beneath the selenizone. In some large specimens, this lira forms a carina on the last whorl. The selenizone is indistinct, lying in the same plane as the whorl surface. It is distinguished by the flattened profile, shifted from the upper suture for a distance approximately equal to its width. The aperture is rounded, angular in the parieto-palatal region. The outer and inner lips are thin; the columella is slightly bent or straight; at adult stages, the reflection of the inner lip forms a very small pseudoumbilicus. The growth lines are not preserved. One specimen exhibits one deeply impressed growth line, which is slightly prosocline between the upper suture and selenizone, forming a sinus inside the selenizone; the depth of the sinus is slightly greater than its width. Beneath the selenizone, the growth line is weakly bent and slightly opisthocline.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/76-18, holotype	6.0	2.4
4471/76-1, paratype	6.2	2.7
4471/76-11, paratype	>6.0	3.2
4471/76-14, paratype	4.7	2.5

Comparison. This species is similar to *A. altadema*, but distinguished by the slowed whorl expansion rate. It differs from *A. convexa* Kues, 2002 in the whorl profile, which becomes angular near the selenizone at the definitive stage.

Material. Ten imprints from the type locality.

Altadema lira Mazaev, 2003

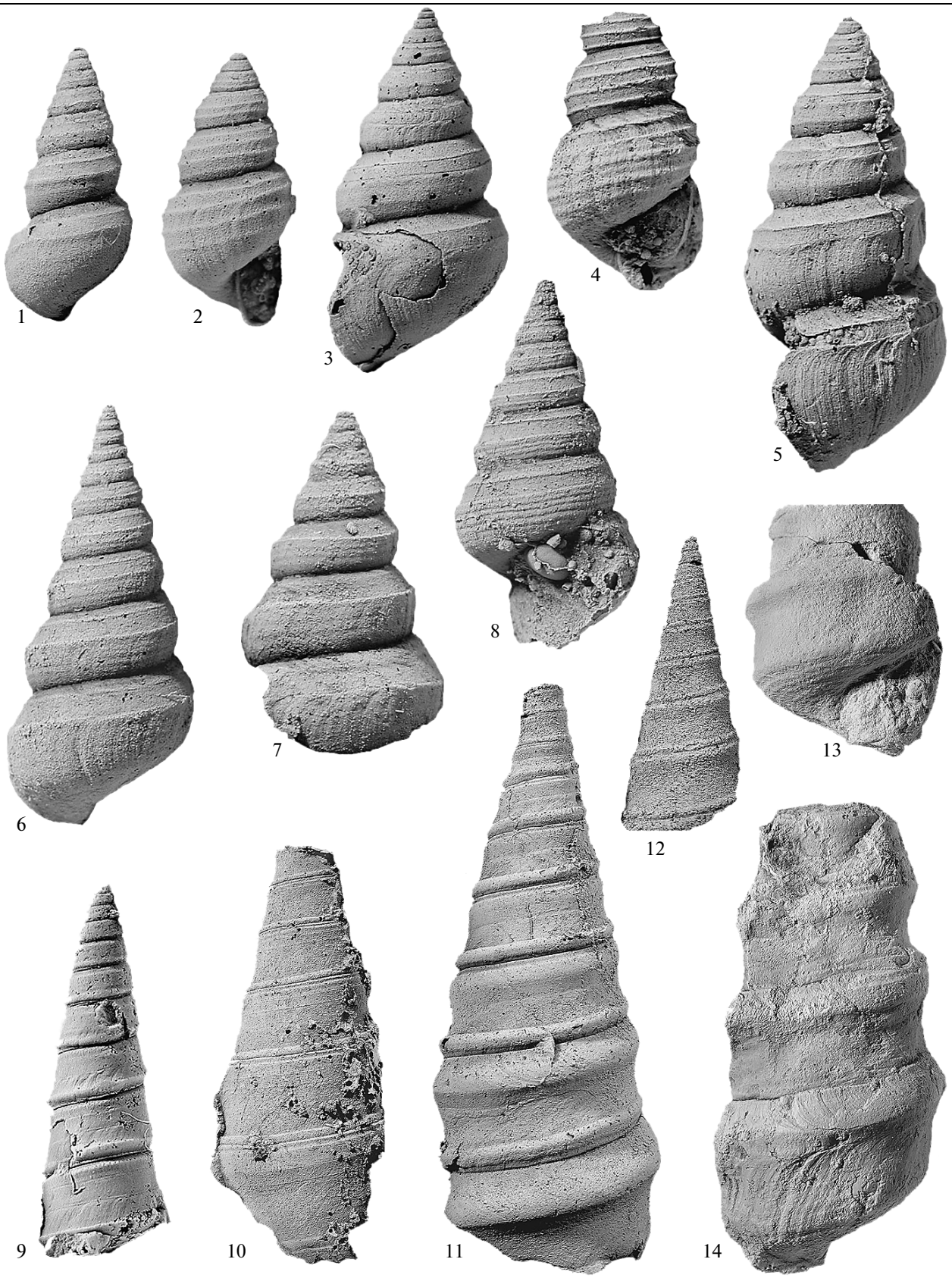
Plate 7, figs. 1–5

Altadema lira: Mazaev, 2003, p. 92, text-figs. 2I–2M.

Holotype. PIN, no. 4471/77-1, shell imprint; paratypes PIN, no. 4471/77-19, 4471/77-32, 4471/77-66, 4471/77-68, 4471/77-110, 4471/77-142, 4471/77-147, 4471/77-152, shell imprints; Ryazan Region, Akishinskii quarry (near the village of Lashma); Moscovian Stage, Myachkovian Substage, top of the Korobcheevo Formation, gray cross-bedded grainstone with *Meekella*.

Description. The shell is small, turreted (up to 10 mm high), composed of nine rapidly expanding, rounded whorls. The suture is impressed. The protoconch is poorly preserved, composed of two smooth rounded whorls. Juvenile whorls are nearly rounded, slightly angular below the slightly concave selenizone. The profile of adult whorls is rounded. The whorl surface is only ornamented with the selenizone or four indistinct or distinct spiral lirae. The lirae are separated by equally wide spaces. The upper and lower lirae are shifted away from sutures at the same distances. The upper pair of lirae bounds the selenizone. Weak auxiliary lirae occasionally appear below the second, third, and fourth lirae. The selenizone of some specimens is at the same level as the whorl surface and bounded by a weak spiral groove on either side or defined only by a concave or convex profile. The aperture is rounded, angular in the parieto-palatal zone. The outer and inner lips are thin, the columella is short and weakly bent. The growth lines are thin, distinct, slightly bent forward above the selenizone and prosocline. They form lunulae on the selenizone, and bent

Plate 7



forward and opisthocline beneath the selenizone. Sometimes, the selenizone is smooth, lacking growth lines. One specimen shows an almost completely preserved slit; the depth of the slit is four times its width; the slit edges narrow towards the apertural edge.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/77-1, holotype	10.0	4.5
4471/77-32, paratype	8.0	4.0
4471/77-19, paratype	7.0	3.5
4471/77-152, paratype	7.5	3.5
4471/77-110, paratype	6.0	3.5
4471/74-66 paratype	6.0	2.5
4471/74-142 paratype	7.0	3.0

Comparison. *A. lira* is distinguished from congeners by the well-developed spiral ornamentation.

Remarks. The material studied shows extremely wide intraspecific variability, which is observed in the development of various number of spiral lirae (from 0 to 4) and in the development various types of the selenizone. The majority of specimens have two indistinct or prominent spiral lirae, which bound selenizone. Several specimens lack a spiral ornamentation. Other specimens studied are ornamented with three or four indistinct or distinct spiral lirae. Well-developed spiral ornamentation can disappear on the definitive whorls (specimen PIN, no. 4471/77/9), which is typical for species of *Concinnispira* and *Hermosanema*.

Some specimens have a weak auxiliary spiral lira near the second lirae on the selenizone (specimen PIN, no. 4471/77/142). The appearance of this morphological element is observed in many species of other genera: *Altadema convexa* (Kues, 2002, text-figs. 2.3, 2.4), *Vebericochlis maclayi* (Licharew, 1967), *Orthonema silinae* (Licharew, 1975), (Mazaev, 2002, text-figs. 3J, 5D, 5E), *Stegocoelia gzheliensis* Mazaev, 2001 and *S. knighti* (Licharew, 1975) (Mazaev, 2001, text-figs. 2P, 3A, 3C).

Several specimens show gradual changes in the morphology of selenizone throughout growth (Plate 7, fig. 3). The selenizone is flat, positioned at the same level as the adjacent shell surface or slightly beneath it; it can also be bounded by thin grooves, as is typical of species of other genera: *Cibecuia, Arribazona, Fergani-spira*, and *Cerithioides*. The selenizone can also be concave, bounded by spiral lirae, as is typical of species of some other genera: *Stegocoelia, Taosia, Vebericochlis, Orthonema*, and *Goniasma*.

Material. Forty-nine imprints from the type locality.

Genus *Laschmaspira* Mazaev, 2003

Laschmaspira: Mazaev, 2003, p. 94.

Type species. *Laschmaspira rara* Mazaev, 2003.

Diagnosis. Shell small or medium-sized, turreted; juvenile whorls slightly angular; profile of adult whorls convex, sometimes with weak angulation beneath selenizone. Base of last whorl moderately convex, rounding smoothly into whorl face. Selenizone positioned above midwhorl face, nearly flat, bounded by two thin grooves, when lying in one plane with whorl surface or slightly lower; whorl face beneath selenizone ornamented with many (at least six) closely spaced, indistinct or distinct spiral lirae. Growth lines thin, distinct, above selenizone bent forward and slightly prosocline, on selenizone forming lunulae, beneath selenizone bent forward and slightly opisthocline.

Species composition. One species from the Myachkovian Substage of the Ryazan Region, three species from the Asselian of southern Fergana, and one species from the Bashkirian of the Chelyabinsk Region (Shartymka River).

Comparison. This genus is clearly distinguished from other genera of the family by the presence on the whorl face beneath the selenizone of at least six spiral lirae, separated by grooved spaces, which are narrower than the lirae.

Explanation of Plate 7

All photographs, except Fig. 14, are taken from latex casts.

Figs. 1–5. *Altadema lira* Mazaev, 2003, ×8: (1) specimen PIN, no. 4471/77-66; (2) specimen PIN, no. 4471/77-110; (3) specimen PIN, no. 4471/77-32; (4) specimen PIN, no. 4471/77-147; (5) holotype PIN, no. 4471/77-1, slit morphology and depth are clearly visible; Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, Korobcheevo Formation.

Figs. 6–8. *Laschmaspira rara* Mazaev, 2003, ×8: (6) specimen PIN, no. 4471/77-160; (7) specimen PIN, no. 4471/77-117; (8) holotype PIN, no. 4471/77-22; Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, Korobcheevo Formation.

Fig. 9. *Cibecuia sinelnikovae* Mazaev, 2002, holotype, PIN, no. 4471/22-9 (), ×10; Moscow Region, Podolsk quarry; Moscovian Stage, Myachkovian Substage, Korobcheevo Formation.

Figs. 10–14. *Cibecuia magnum* Mazaev, 2002: (10) specimen PIN, no. 4471/21-8, × 2.5, Moscow Region, Konev Bor quarry; Moscovian Stage, Myachkovian Substage, Korobcheevo Formation; (11) holotype PIN, no. 4471/78-50, ×2 (), Ryazan Region, Akishinskii quarry; Moscovian Stage, Myachkovian Substage, Domodedovo Formation; (12) specimen PIN, no. 4471/39-10, ×4, southwestern Moscow, underground metro pit; Moscovian Stage, Kashirian Substage; (13) specimen PIN, no. 4471/65-2, ×1.5, Moscow Region, Domodedovo quarry; Moscovian Stage, Myachkovian Substage, Peski Formation; (14) specimen TsNIGR Museum, no. 212, ×1.5, Central Asia, Kizil-Kaya Mountain, Lower Pennsylvanian, on last whorl growth lines clearly demonstrate slit morphology and depth.

Remarks. The selenizone in cross section is nearly flat or slightly concave, bounded by weak lirae or grooves, positioned slightly beneath or slightly above adjacent shell surface. No specimens with preserved aperture is present. Prominent growth lines on one specimen of *Laschmaspira rara* suggest that the slit, as in *Stegocoelia*, had nearly parallel margins, whereas the depth is four times its width.

It was previously shown (Mazaev, 2003, p. 94) that *Laschmaspira* should include the following species described by Licharew under *Callispira*: *Laschmaspira* sp. indet. (Licharew, 1968), *L. conulus* (Licharew, 1968), and *L. volgini* (Licharew, 1968). In the same paper, I erroneously assigned to *Laschmaspira Glyphodeta karatshatyrensis* Licharew, 1967. In fact, some material described by Licharew under this species name should be assigned to *Laschmaspira* under a different species name, whereas remaining specimens, including the holotype, should be assigned to a new taxon of at least generic rank within the Orthonematidae.

***Laschmaspira rara* Mazaev, 2003**

Plate 7, figs. 6–8

Laschmaspira rara: Mazaev, 2003, p. 96, text-figs. 3A–3C.

Holotype. PIN, no. 4471/77-22, shell imprint; paratypes PIN, no. 4471/77-117, 4471/77-153, 4471/77-155, 4471/77-156, 4471/77-160. 4471/77-170, shell imprints; Ryazan Region, Akishinskii quarry (near the village of Lashma); Moscovian Stage, Myachkovian Substage, top of the Korobcheevo Formation, gray cross-bedded grainstone with *Meekella*.

Description. The shell is small, turreted, lacking an umbilicus, composed of 11 whorls; the suture is impressed and shallow. Juvenile whorls are ornamented with two spiral lirae, which are positioned beneath the selenizone, whereas the upper lira forms a weak angulation. The profile of adult whorls is moderately convex; indistinct or clear angulation appears immediately beneath the selenizone. The base of the last whorl is moderately convex, round smoothly into the whorl face. The selenizone is positioned above the midwhorl, whereas the distance between the suture and the selenizone is less than the width of the selenizone. The selenizone is flat, positioned mostly at the same level as the shell surface or distinctly impressed, can be bounded by a thin groove or very indistinct lira on either side. The whorl surface beneath the selenizone and the whorl base are ornamented with at least six distinct or indistinct, closely spaced lirae. The spaces between the lirae are approximately half the width of the lirae. The growth lines are distinct, thin, above the selenizone bent forward and are slightly prosocline; on the selenizone, they form lunulae, beneath the selenizone, they curve forward and are slightly opisthocline. The slit is four times as deep as wide.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/77-22, holotype	8.0	4.0
4471/77-153, paratype	12.5	>5.5
4471/77-156, paratype	6.5	3.3
4471/77-160, paratype	9.3	4.2
4471/77-170, paratype	7.0	3.8

Comparison. This species is very similar to *L. volgini* (Licharew, 1968), from which it is distinguished by the rounded whorl profile.

Remarks. The intraspecific variability of the material studied is observed in the extent of the development of the spiral lirae beneath the selenizone, which sometimes forms a weak shoulder. The spiral lirae in many specimens are very weak, which, however, can be attributed to the postmortem erosion of shells and their burial in rounded state. Some shells show strongly impressed coarse growth lines (Pl. 7, fig. 6).

Material. Twelve imprints from the type locality.

Genus *Cibecuia* Winters, 1956

Cibecuia: Winters, 1956, p. 44; Knight et al., 1960, p. I293; Winters, 1963, p. 38; Batten, 1985, p. 9; Mazaev, 2002, p. 103.

Type species. *Cibecuia cedarensis* Winters, 1956.

Diagnosis. Shell turreted, composed of many subcylindrical or subconical whorls, lacking umbilicus. Protoconch composed of one or two smooth whorls. Whorl face of adult whorls straight and concave in profile, nearly parallel or weakly inclined to shell axis. Suture thin, distinct. Basal carina or basal angulation well developed, clearly separating whorl face from whorl base. Whorl face smooth, ornamented with spiral lira or spiral row of nodes below suture, which forming very weak shoulder with very narrow subsutural ramp. Selenizone flat, smooth, bounded by thin grooves, may also be slightly elevated or impressed in relation to rest of shell surface, positioned above midwhorl, but beneath shoulder. Whorl base moderately rounded, smooth or ornamented with relatively wide and low spiral lirae. Growth lines distinct, thin, sometimes prominent and coarse, above selenizone convex forward and prosocline, on selenizone forming lunulae, beneath selenizone convex forward and opisthocline.

Species composition. Several species from the Permian of Arizona, West Texas, and Malaysia. Two species from the Pennsylvanian of Eastern Europe.

Comparison. This genus is morphologically similar to *Orthonema* in whorl profile, but in its species, the selenizone is never bounded from above by

spiral lira or shoulder. The spiral lirae are always absent.

***Cibecuia sinelnikovae* Mazaev, 2002**

Plate 7, fig. 9

Cibecuia sinelnikovae: Mazaev, 2002, p. 104, text-figs. 1G and 5M.

Holotype. PIN, no. 4471/22-9, shell imprint; Moscow Region, Podolsk quarry; Moscovian Stage, Myachkovian Substage, Domodedovo Formation, white coral–foraminiferal grainstone.

Description. The shell is small turreted, composed of ten subconical whorls. The protoconch consists of one smooth rounded whorl. Juvenile whorls are subconical, with a slightly convex surface; the suture is deeply impressed. The surface of adult whorls is slightly concave in profile. The suture is thin, distinct. The shoulder is very small, sharp, marked by a spiral row of small nodes, separated from the suture by a very narrow subsutural ramp, its width is one-third of the width of the selenizone. The lower carina is rounded and relatively massive, lies above the suture. The selenizone is flat, lies in the same plane as the shell surface, bounded by two thin grooves. The selenizone is shifted away from the suture at a distance slightly smaller than its width. The whorl base is poorly preserved, apparently weakly convex, and smooth. Growth lines are distinct, thin, sometimes coarse, prosocline, positioned at an angle about 30° to the shell axis; thin lunulae are formed on the selenizone; beneath the selenizone, growth lines are slightly convex, opisthocline, and inclined to the shell axis at almost 30°.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/22-9, holotype	6.6	2.4

Comparison. Despite this species is represented in the collection by a single specimen, it has unique characters, e.g., a narrow subsutural ramp, morphology of which readily distinguishes it from other few congeners.

Material. Holotype.

***Cibecuia magnum* Mazaev, 2002**

Plate 7, figs. 10–14

Ferganispira sp. indet: Licharew, 1967, p. 52, pl. 17, fig. 19; Orthonema sp. 2: Kues and Batten, 2001, p. 57, text-fig. 10.30.

Cibecuia magnum: Mazaev, 2002, p. 104, text-figs. 1H, 1I, and 5N–5R.

Holotype. PIN, no. 4471/78-50, shell imprint; paratype PIN, no. 4471/78-74, shell imprint; Ryazan Region, Akishinskii quarry (near the village of Lashma); Moscovian Stage, Myachkovian Substage, Domodedovo Formation, white coral–foraminiferal grainstone.

Description. The shell is large turreted (to 50 mm in height), composed of at least ten subconical or subcylindrical whorls. A massive rounded shoulder is formed at adult stage. The protoconch is not preserved. Juvenile whorls are poorly preserved, formed by three slightly convex whorls, ornamented with three spiral lirae. The whorl face of adult whorls is concave in profile. The suture is thin, impressed. The shoulder is very small and sharp, separated from the suture by a subsutural ramp, representing a very narrow concave band, inclined to the shell axis at 30°. The width of the subsutural ramp is half the width of the selenizone. The lower carina is rounded and relatively massive, lies immediately above the suture. The selenizone is flattened, lies in the same plane as the shell surface, above, or beneath it, bounded by two thin grooves. The selenizone is shifted from the shoulder to a distance equal to its width. In the last whorls, the narrow subsutural ramp and shoulder bounding it disappear, and another massive rounded shoulder is formed immediately above the selenizone. The selenizone on the last whorls is shifted from the suture to a distance approximately twice the width of the selenizone. The whorl base is weakly convex, ornamented with six evenly spaced indistinct spiral lirae. The aperture is parallelogram-like in cross section and shows an incipient siphonal canal and a slit, which on the last whorls occurs immediately below the upper shoulder. The slit is twice as deep as wide. The columella is short and slightly bent. Growth lines are very distinct, thin above selenizone prosocline, inclined to the shell axis at almost 35°; on the selenizone, they form thin lunulae; beneath the selenizone, they are slightly convex, opisthocline at almost 48°.

Dimensions in mm:

Specimen PIN, no.	Shell height	Max. diameter
4471/78-50, holotype	>52.0	ca. 21.0
4471/39-10	>14.0	ca. 6.0

Comparison. *Cibecuia magnum* is distinguished from all other members of the genus by the absence of spiral elements, which are reduced to a row of nodes.

Remarks. Shells of this species are unusually large for the genus. They show high variability of morphology throughout growth, especially at the last growth stages.

Occurrence. Central Russian Platform; Moscovian Stage, Vereian, Kashirian, and Myachkovian substages; Central Asia, North America (New Mexico); Flechado Formation, Early Desmoinesian.

Material. Eighteen imprints: two from locality no. 4471/21, 13 from locality no. 4471/39, two from

locality no. 4471/78, one from locality no. 4471/94, and one cast from locality no. 4471/65.

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