

**Jurassic Gastropods  
of European Russia  
(Orders Cerithiiformes,  
Bucciniformes,  
and Epitoniiformes)**

**A. V. Guzhov**

**Paleontological Institute, Russian Academy of Sciences,  
Profsoyuznaya ul. 123, Moscow, 117997 Russia**

e-mail: [gva@tavrida.ru](mailto:gva@tavrida.ru)

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# Contents

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INTRODUCTION	S457
CHAPTER 1. THE HISTORY OF THE STUDY OF JURASSIC GASTROPODS FROM THE RUSSIAN PLATFORM	S457
CHAPTER 2. SHELL MORPHOLOGY	S461
CHAPTER 3. SOME PROBLEMS OF THE TAXONOMY, NOMENCLATURE, AND EVOLUTION OF JURASSIC GASTROPODS	S464
Families Procerithiidae and Cryptaulacidae	S464
Families Purpurinidae and Purpuroideidae	S476
Family Cerithiopsidae	S480
Family Eumetulidae	S482
Family Polygyrinidae	S482
Family Maturifusidae	S483
Family Epitoniidae	S484
CHAPTER 4. SYSTEMATIC PALEONTOLOGY	S485
Family Cryptaulacidae	S485
Family Procerithiidae	S508
Family Purpurinidae	S511
Family Cerithiopsidae	S515
Family Eumetulidae	S520
Family Polygyrinidae	S520
Family Maturifusidae	S521
Family Epitoniidae	S531
CHAPTER 5. STRATIGRAPHIC AND FACIAL DISTRIBUTION OF JURASSIC GASTROPODS FROM EUROPEAN RUSSIA	S537
The Role of Gastropods in Faunal Assemblages of European Russia	S537
Ecological Features of Gastropods from European Russia	S548
List of Localities of Jurassic Gastropods Studied	S552
REFERENCES	S554

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**Abstract**—The study is devoted to Jurassic gastropods of the Central and Central Chernozem regions of Russia. Thanks to the exact locality data on the collected material, the stratigraphic ranges of many species were refined. Several beds are recognized by the change in the dominant gastropod species in the Middle and Upper Jurassic clay sediments. Detailed characteristics of facial distribution of gastropod taxa are given. New material displays a high diversity of gastropod species. The study covers 42 species of 16 genera from 8 families (among them, 1 family, 1 subfamily, 5 genera, 1 subgenus, and 18 species are new).

*Key words:* gastropods, systematics, ecology, Jurassic, biostratigraphy, European Russia.

## INTRODUCTION

The gastropod taxa studied (subclass Pectinibranchia, orders Bucciniformes and Cerithiiformes, and subclass Sinistrobranchia, order Epitoniiformes) compose one of the most diverse groups of Mesozoic gastropods in the Northern Hemisphere. The system mainly worked out by Cossmann over a century ago is currently in use for the classification of these mollusks. However, in the last thirty years, there were numerous studies concerning the embryonic and postembryonic morphology of various gastropods from different taxonomic groups. This work has provided new characters never previously used in gastropod classification. These new characters can be used to improve and correct the existing gastropod systematics. There is a necessity to produce a gastropod classification that would completely incorporate the new data on the embryonic and postembryonic shell development and phylogeny of gastropods.

The study of Jurassic gastropods from central European Russia has not kept pace with similar investigations abroad. Despite the outstanding achievements of P.A. Gerasimov in the study of Jurassic gastropods from European Russia, which were published in several monographs (1955, 1969, 1992), his extensive material has not been used to improve the gastropod classification. The perfect preservation of Oxfordian and, to some extent, Callovian and Volgian gastropods and their wide distribution in the Jurassic sediments of European Russia provide a good basis for solving different problems in systematics, biogeography, ecology, and diversity dynamics. Some of these problems have never previously been addressed. The present study endeavors to fill in some of these gaps.

## MATERIAL

Most of the material used in the present study was collected by the author during 1994–2000 in the Moscow, Yaroslavl, Kursk, Ryazan, Kostroma, and Bryansk regions. In addition, the specimens collected in Moscow, Kursk, Ryazan, Voronezh, Nizhni Novgorod, and Ulyanovsk regions were kindly granted me by D.N. Kiselev, D.B. Gulyaev, M.A. Rogov, V.A. Eliseev,

V.R. Lyapin, and K.M. Shapovalov. I also studied the paleontological collections of E. Eichwald (1840, 1865–68), V.N. Riabinin (1912), E. Hoffmann (1863), and H. Trautschold, housed in the laboratory of St. Petersburg State University, and the collections of P.A. Gerasimov (1955, 1969, 1992), housed at the State Geological Museum of the Russian Academy of Sciences and the Paleontological Institute of the Russian Academy of Sciences (PIN). The study of Cretaceous gastropods was based on the collections of V.A. Korotkov from Central Asia, housed at the Institute of Geology and Exploration of Combustible Fuels (IGIRGI).

Quantitative (calculation of the number of shells of each species) and qualitative (species composition) analyses of the gastropod assemblages were performed during collecting. On the basis of the gastropod assemblages, corresponding beds were established. The fossils were collected using common methods and water flushing of rock samples in sieves with 1 and 0.5 mm mesh. Shells were picked from the sieved residue. During laboratory studies, latex casts were produced in some cases, since the majority of specimens from coarse-grained rocks were represented by imprints. Light microscopy and scanning electron microscopy were used in the study.

## CHAPTER 1. THE HISTORY OF THE STUDY OF JURASSIC GASTROPODS FROM THE RUSSIAN PLATFORM

In this chapter, I briefly review the publications that contributed to the study of species diversity of Jurassic gastropods from the Russian Platform. Citing the publications, I retain the original determination of the species; wherever possible, my own redeterminations, corrections, and comments are given in brackets. Some species are treated according to the generally recognized system proposed by Gerasimov (1992). Although I do not accept all of these species, a comprehensive taxonomic study is required to resolve this matter. It should be mentioned that only the publications containing the gastropod illustrations or, at least, descriptions of new species, are considered. Publications giving only lists of gastropod species are omitted in this

review, since even recent papers often contain incorrect identifications (even at the family level).

The study of Jurassic gastropods from Russia has a 150-year history. It comes as no surprise that the first examples described from Russia were from the direct vicinity of Moscow, an area rich in excellent sections of Oxfordian and Volgian deposits. The first data on gastropods from the Volgian Stage are given by Fischer von Waldheim (1837, 1843), Eichwald (1840), and Auerbach and Frears (1846). Fischer von Waldheim (1837) undertook the geological study of Moscow and its vicinity. He depicted an internal mold of the gastropod *Nassa* dated as Lias in accordance with contemporaneous ideas concerning the age of the Jurassic strata in the Moscow Region. This species is here considered as an internal mold of the Volgian species *Khetella incerta* (d'Orbigny). The second paper by Fischer von Waldheim (1843) contains brief diagnoses of the following gastropods from Khoroshovo (at present, Moscow): *Turbo undulatus* Phillips, *T. sulcostomus* Phillips, *T. cyclostoma* Zieten, *T. heliciformis* Zieten, *Auricula obsoleta* Phillips [= *Sulcoactaeon* sp. or *Parvulactaeon* sp.], *Cirrus rotundatus* Sowerby, and a new species, *Melania inaequata* Fischer. All species came from the Volgian strata. The first three are probably *Eucyclus jasikofianus* (d'Orbigny) and *E. secundaris* (Rouillier). Eichwald described the Volgian gastropod *Orbicula maeotis* Eichwald [= *Berlieria maeotis* (Eichwald)] and treated it as a brachiopod. Auerbach and Frears depicted *Natica* sp. [=? *Oonia? incerta* Gerasimov] from the Upper Volgian of Moscow.

After the study of the Jurassic fossils collected by expedition of S. Murchison, A. d'Orbigny described several new gastropods, including the first species from the Oxfordian (Murchison *et al.*, 1845). Very accurate lithographs accompanied the descriptions. The Oxfordian species came from the limestone of the Izyum Formation (Kamenka River, Kharkov Region, Ukraine), i.e., *Nerinea eichwaldiana* d'Orbigny and *Cerithium russiense* d'Orbigny [= *Procerithium russiense* (d'Orbigny)], and from the Middle Oxfordian clays near the town of Makar'ev (Unzha River, Kostroma Region), i.e., *Actaeon frearsiana* d'Orbigny [= *Tornatellaea frearsiana* (d'Orbigny)], *A. peroskiana* d'Orbigny, and *Pleurotomaria buchiana* d'Orbigny [= *Bathrotomaria muensteri* (Roemer)]. Volgian gastropods were collected chiefly in Khoroshovo, i.e., *Turbo jasikofianus* d'Orbigny and *T. meyendorffii* d'Orbigny. Both taxa represent the same species, i.e., *Eucyclus jasikofianus* (d'Orbigny); *T. meyendorffii* was described based on poorly preserved specimens (internal mold and fragments of the nacreous layer of the shell). *Pleurotomaria bloedeana* d'Orbigny [unidentifiable pleurotomariid] and *Buccinum incertum* d'Orbigny [= *Khetella incerta* (d'Orbigny)] come from the Volgian of the Orenburg Region. In addition, the report on the expedition to the Pechora River Basin with descriptions of several Callovian and Oxfordian gastropods was published at that time (Eichwald, 1846).

However, the majority of the species established before the 20th century were described by Rouillier (Rouillier, 1846; Rouillier and Vosinsky, 1847, 1849). All of the species were collected along the banks of the Moskva River in the area of recent Moscow (Khoroshovo, Mnevniky), near the village of Gal'evy in the vicinity of the town of Krasnogorsk, and in a quarry of Upper Volgian sandstone near the village of Kotel'niki. This important collection was not deposited in any museum or institution, but was part of the private collection of Fahrenkohl, a Moscow pharmacist; consequently its whereabouts was unknown for a long time. Only fifty years later, part of the collection was found among material donated to the Peter the Great Geological Museum [now the Central Institute of Geological Exploration for Base and Precious Metals (TsNIGRI)] from the Rybinsk estate of the Mikhalkovs family. Due to the diligence of Sokolov (1912), the surviving material from the Gal'evy locality was preserved and restudied.

During the thirty years following the publications of Rouillier, numerous short papers devoted to Volgian and Oxfordian deposits of the Moscow Region were published. They mainly depicted other fossil groups, and descriptions of gastropods were rarely present. Trautschold (1858, 1859, 1860, 1866, 1877, 1878) was the most significant contributor of that period. The results of studies of the Jurassic fauna from the vicinity of Moscow are presented in his brief publications. The first paper was devoted to fossils from the Upper Volgian sandstone near the village of Kotel'niki and contained descriptions of two new species, i.e., *Turbo auerbachii* Trautschold [= *Neritopsis auerbachi* (Trautschold)] and *Trochus torosus* Trautschold [= *Pleurotomaria trautscholdi* (Gerasimov)]. In the second paper, which is devoted to the fauna of the Upper Oxfordian clays from the Dorogomilovo Turnpike (Moscow), the species *Cerithium septemplex* Roemer is depicted; this is most likely a poor illustration of *Cosmocerithium contiae* Guzhov. Three new gastropod species are described in the paper on the Oxfordian clay near the village of Gal'evy (Trautschold, 1860). One species, *Cerithium januale* Trautschold, is a juvenile shell, which is probably a synonym of *Proacirsa struvii* (Lahusen, 1883).

In 1866, Trautschold published a most interesting work in the context of the present study. He depicted several perfectly preserved shells of scarce gastropod species from the Volgian strata of modern Moscow, i.e., *Scurria bicanaliculata* Trautschold, *Emarginula exigua* Trautschold, *Turbo neritoides* Trautschold [= *Vanicoropsis neritoides* (Trautschold)], *Nerita jurensis* Münster [= *Vanicoro psammobia* Gerasimov], and *Trochus cottaldanus* d'Orbigny. In addition, it is the sole publication dealing with the Middle Oxfordian gastropods from the Vladimir Region (village of Mishino in the vicinity of the town of Murom). These species are *Cerithium quinarium* Trautschold [= *Exelissa* (Exelissa) *quinaria* (Trautschold)], *Fusus sabatieri* Trautschold [*Pietteia russiensis* Gerasimov is its junior synonym],

*Fusus corniculatus* Trautschold [= *Khetella corniculata* (Trautschold)], and *Turbo formosus* Trautschold [= *Eucyclus formosus* (Trautschold)]. In 1877, two species of Oxfordian gastropods were described, i.e., *Pleurotomaria buvignieri* d'Orbigny [= *Bathrotomaria buvignieri* (d'Orbigny) sensu Gerasimov, 1992] and *Natica semistriata* Trautschold. The latter species is not provided with an illustration, while the description suggests only that it is an opisthobranchiate gastropod.

Eichwald continued his studies concurrently with Trautschold. He mentioned two gastropods from the Upper Volgian sandstone of the *nodiger* Zone, i.e., *Natica congrua* Eichwald [= *Oonia? congrua* (Eichwald)] and *N. cretacea* Goldfuss, and gave brief diagnoses for them. Later, he published a summary, which included the data on the distribution and species composition of the Jurassic fauna (Eichwald, 1865, 1868). In these studies, the Volgian strata were assigned to the Lower Cretaceous. Each gastropod species is provided with a more detailed diagnosis and list of localities. Several new species were described, including gastropods from Popilani and Nigranden (Lithuania). Unfortunately, only a few species were illustrated, and the illustrations are far from perfect.

Nikitin (1877), in a paper on the geological structure of the Vorob'evy Gory, described the gastropod *Pileolus? sp.* [= *Crepidula? nikitini* Gerasimov, 1992]. Milashevitch (1879) described a limpet-like gastropod *Patella inornata* Milashevitch from the Lower Callovian of the Nizhni Novgorod Region. Earlier, works with descriptions of Oxfordian gastropods from the vicinity of Izyum (Ukraine) (Gurov, 1869) and from the southern Ural Mountains (Orenburg Region) (Hoffmann, 1863) had been published. Both publications contain poor drawings, so that it is difficult to recognize any gastropod species. The paper by Trautschold (1878) also devoted to the Oxfordian of the Izyum area followed the Gurov's publication. It includes illustrations of two gastropod species, i.e., *Phasianella buvignieri* d'Orbigny and *Nerinea quadrilobata* Trautschold.

Gastropods from the Oxfordian of the Ryazan Region were treated in the *Proceedings of the Geological Committee* (Lahusen, 1883). Numerous Upper Callovian-Oxfordian gastropods were described and illustrated, including several new forms, i.e., *Chemnitzia struvii* Lahusen [= *Proacirsa struvii* (Lahusen)], *Turbo* (Eunema) *spinosus* Lahusen [= *Metriomphalus spinosus* (Lahusen)], and *Fusus clathratus* Lahusen [= *Brachytrema clathrata* (Lahusen)]. In 1882, Gurov published a second book. It lacks illustrations but includes the description of a new species, *Turritella murchisoni* Gurov [= ? a species of the genus *Fibula*], earlier referred to by the same author as *Turritella* n. sp. (Gurov, 1869).

The study of Ilovaisky (1903) was of outstanding importance to the study of the Oxfordian fauna. It differs from the preceding publications in its detailed analysis of the stratigraphic distribution of fossils in the

Oxfordian of the Moscow and Ryazan regions and, thus, provides valuable data on gastropod stratigraphy. This study retains its significance even today. The species composition of Oxfordian gastropods was also studied in more detail. Among the new species he described, the following are noteworthy: *Turritella divisa* Ilovaisky [= *Clathrobaculus fahrenheitii* (Rouillier)] and *T. bicostata* Ilovaisky [= *Clathrobaculus krantzi* (Rouillier)].

Several subsequent works were devoted to the Jurassic of the Baltic Region, i.e., the Callovian and Oxfordian faunas of Popilani and Nigranden. One work (Boden, 1911) treated the Middle Oxfordian and included the following gastropod species: *Fusus? eichwaldi* Boden [= *Pietteia russiensis* Gerasimov], *Alaria ritteri* Thurmann [= *Bicorempterus pseudopellati* (Gerasimov)], *Alaria gagnebini* (Thurmann) [= *Dicroloma cochleata* (Quenstedt)], *Turritella complanata* Brösamlen [= *Clathrobaculus fahrenheitii* (Rouillier)], *Amauropsis calypso* (d'Orbigny) [= *Oonia calypso* (d'Orbigny) sensu Gerasimov, 1992], *Purpurina concava* Brösamlen, *P. bicarinata* Boden, *Pleurotomaria muensteri* Roemer [= *Bathrotomaria muensteri* (Roemer)], *P. buchana* d'Orbigny [= *Bathrotomaria muensteri* (Roemer)], and *P. buvignieri* d'Orbigny. Surprisingly, none of the species dominating in the Middle Oxfordian of Central Russia (see below) had been described at that time.

Krenkel (1915) studied the Callovian fauna, and described a small number of gastropod species, mainly poorly preserved, and some without illustrations, i.e., *Pleurotomaria punctata* Goldfuss [= *Bathrotomaria muensteri* (Roemer)], *P. granulata* (Sowerby) [= *Bathrotomaria buvignieri* (d'Orbigny) sensu Gerasimov, 1992], *Turbo meyendorfi* d'Orbigny [internal mold of *Eucyclus* sp. indet.], *Trochus* n. sp., *Alaria myurus* Eudes-Deslongchamps, *Purpurina orbignyana* Hebert et Deslongchamps, and *Patella* sp. A very important contribution to the study of Callovian gastropods was made by Riabinin (1912). He described numerous species and gave detailed diagnoses, but almost without any illustrations. Therefore, many species are difficult to distinguish. Riabinin (1912) studied a great variety of species of the genus *Pleurotomaria* [= *Bathrotomaria*] and combined several species of the family Pleurotomariidae into one, characterized by high intraspecific diversity. He illustrated only three species, i.e., *Pleurotomaria buchana* d'Orbigny [= *Bathrotomaria muensteri* (Roemer) + *B. buvignieri* (d'Orbigny) + *Obornella* sp.], *Pseudomelania variabilis* (Morris et Lycett) [= ?*Infacertium sensu stricto*], and *Turbo meyendorffii* d'Orbigny.

A few years later, the most important monographic work on the Jurassic gastropods from the northern Ukraine was published (Nalivkin and Akimov, 1917). The work showed a great species diversity of this group, and included the first description of a Bajocian gastropod (*Cylindobullina* cf. *disjuncta* Terquem et Jourdy, 1869). Most of the gastropod fauna was dated

as Oxfordian. Because of southern position of the region and the different type of sediments (mainly clayish and oolitic limestone with bioherms), Ukrainian gastropod assemblages substantially differ from those of the Moscow Region, although some common species do occur.

After that publication, the study of Jurassic gastropods from the Russian Platform was set aside for almost forty years. Only in the 1950s, the famous paleontologists P.A. Gerasimov and I.M. Yamnichenko resumed active investigations in this field and almost simultaneously published the results of their candidate's dissertations (Gerasimov, 1955; Yamnichenko, 1958). Based on the long-term collecting activity during the geological mapping of the Moscow Region and adjacent areas, Gerasimov published a summary of the Jurassic fauna. Among other fossil groups, he described many gastropods and established a number of new species: *Scurria impressa* Gerasimov, *Emarginula foveolata* Gerasimov, *Pleurotomaria mosquensis* Gerasimov [= *Bathrotomaria mosquensis* (Gerasimov)], *Cochleochilus carinatus* Gerasimov [= *Proconulus carinatus* (Gerasimov) sensu Gerasimov, 1992], *Cochleochilus subvinealis* Gerasimov [= *Calliomphalus subvinealis* (Gerasimov) sensu Gerasimov, 1992], *Amberleya pulchra* Gerasimov [= *Eucyclus pulchrus* (Gerasimov)], *Brachytrema kostromensis* Gerasimov [= *Maturifusus kostromensis* (Gerasimov)], *Cryptaulax pseudoechinata* Gerasimov [= *Cryptaulax* (*Cryptaulax*) *pseudoechinatus* (Gerasimov)], *Procerithium? volgensis* Gerasimov [= *Procerithium* (*Plicacerithium*) *volgensis* Gerasimov, 1992], *Natica tenuistriata* Gerasimov [in subsequent papers, he erroneously assigned it to *Euspira gerasimovi* Beisel], *Actaeonina laevis* Gerasimov [= *Cryptonatica? laevis* (Gerasimov)], *Vanicoro psambobia* Gerasimov [= *Trachynerita? psambobia* (Gerasimov)], and *Pseudomelania? mutabilis* Gerasimov [= *Cryptaulax* (*Neocryptaulax*) *mutabilis* (Gerasimov)]. Many species were first recorded in the Jurassic deposits of Russia. However, in subsequent papers Gerasimov correctly noted that a number of original determinations were incorrect. Gerasimov was the first to estimate the frequency of occurrence of gastropod species within different stratigraphic intervals.

Interesting and finely preserved material of Toarcian, Aalenian, and Bajocian zygopleuriid gastropods [I am in doubt whether all of the species described in this work belong to zygopleuriids] collected from boreholes in the Donets Basin and the Dnieper–Donets Depression was described by Yamnichenko (1958). Unfortunately, Yamnichenko almost completely ignored the foreign literature on this subject, so that the extent of endemism of the fauna in relation to adjacent regions was not discussed. Somewhat later, Lapkin (1959) published a short paper with the description of a new nerineid species *Nerinella gurovi* Lapkin from the Izyum Formation of the Oxfordian. However, the priority of *Nerinella gurovi* Lapkin over the form *Nerinea visurgis* var. *minima* Gurov, 1869 is doubtful. In an ear-

lier paper, Gurchik (1951) described *Berlieria maetotis* (Eichwald) from the Volgian strata of the Saratov Region.

Several papers of different authors were published in the 1960s–1970s. Ivanova (1965) described material from the Oxfordian of the Khanskaya Gora locality in the Orenburg Region. She referred to the poor preservation and scarcity of the material and described the following species: *Pleurotomaria muensteri* Roemer [= *Bathrotomaria muensteri* (Roemer) + *B. buvignieri* (d'Orbigny)], *P. buvignieri* d'Orbigny [= *Bathrotomaria* sp. indet.], *P. buchana* d'Orbigny [= *B. muensteri* (Roemer)], *Turbo meyendorfi* d'Orbigny [= *Eucyclus* sp. indet. + *Maturifusus* ex gr. *M. keyserlingianus* (Rouillier)], and *Alaria ganebini* (Thurmann) [= *Bicorempterus pseudopellati* (Gerasimov)].

Preobrazhenskaya (1966) studied the stratigraphy and petrography of Jurassic and Lower Cretaceous deposits of the Voronezh Syncline. Several plates with figured faunal and floral fossils are present in the book, including gastropods from boreholes in the Belgorod Region. However, all of the gastropods are incorrectly identified: *Nerinea* sp. [= *Pseudomelania* sp., Volgian Stage], *Procerithium russiense* (d'Orbigny) [= *Cryptaulax* (*Cryptaulax*) *protortilis* (Cox), Middle Callovian], *Phaneroptyxis* (?) sp. [= unidentifiable gastropod, Middle Callovian], *Pleurotomaria muensteri* Roemer and *P. buchi* d'Orbigny [= unidentifiable pleurotomariids, Lower Oxfordian], *Amberleya* sp. [= unidentifiable gastropod, Lower Oxfordian], and *Dicroloma hamus* (Deslongchamps) [= *D. cochleata* (Quenstedt), Upper Oxfordian].

The most important publication of that time is a book by Gerasimov (1969) on the stratigraphy and fauna of the Middle and Upper Volgian of the Russian Platform. The previously studied material was treated in the gastropod section of the book and only one new species, *Metriomphalus rouillieri* Gerasimov [= *Eucyclus jasikofianus* (d'Orbigny)] was described. Subsequently, Gavrilishin (1972) studied core material from boreholes in the Brest Region, Belarus. He described one gastropod species, *Pleurotomaria thouetensis* (Hebert et Deslongchamps), but it is poorly preserved; therefore, I can only assume its relation to the genus *Amphitrochus*.

The last publication of that period (Romanovitsch, 1978) presents a rather interesting study of gastropods from the Komi Republic (Sysola, Pizhma, Tsil'ma, and Ad'zva rivers). Unfortunately, the preservation of the shell material is far from perfect. The species *Amberleya adzvensis* Romanovitsch, *A. pushiana* (d'Orbigny), *A. meyendorfi* (d'Orbigny), and *Eucyclus jasikofianus* (d'Orbigny) were described based on internal molds with fragments of the nacreous layer. The external layer of the shell is rarely preserved; therefore its morphology is difficult to understand from figures. However, in spite of the poor preservation of the material, it is possible to recognize that the specimens are incorrectly

determined. For instance, the name *Eucyclus jasikofianus* is used for a Callovian form, while the actual *E. jasikofianus* is only found in Volgian strata. The form named as *Pleurotomaria muensteri* Roemer is of particular interest, because it is well-preserved and possibly represents a new species.

The 1980s and 1990s are prominent in the largest compilations on Jurassic gastropods. The results of the study of Ukrainian gastropods were published by Yamnichenko and Astakhova (1984), Yamnichenko (1987), and Dykan' and Makarenko (1990). The first publication is a handbook to the Mesozoic mollusks of Ukraine. It is largely composed of figures of shells from earlier works (Nalivkin and Akimov, 1917; Yamnichenko, 1958). Nevertheless, several species new to the Jurassic of Ukraine are also present. Later, a comprehensive work on gastropods from the Lower and Middle Jurassic of the Donets Basin and Dnieper-Donets Depression was published (Yamnichenko, 1987). In addition, it contains a few species from the Oxfordian and Kimmeridgian. It is rather strange that the work does not consider the Upper Jurassic gastropods of this region that were repeatedly discussed in earlier studies (Gurov, 1869; Nalivkin and Akimov, 1917; etc.). The book mainly considers finely preserved material from boreholes. It should be noted that a significant shortfall of this publication is its complete disregard of earlier works on Jurassic gastropods. This results in a striking apparent endemism of the Ukrainian gastropod assemblage, of over 150 (!) gastropod species, not one occurred in neighboring regions (i.e., all species were considered to be endemic!). Moreover, many of the newly described species are synonyms.

The book by Dykan and Makarenko (1990) covers mainly the pelecypods, while gastropods are few and poorly preserved. The gastropods were collected in Oxfordian carbonate rocks of the Donets Basin, and their determinations leave much to be desired. Two new species were established in this study, i.e., *Procerithium tortilis* Makarenko [= a species of the superfamily Nerineoidea] and *Turritella isjumensis* Makarenko [= *Clathrobaculus fahrenheitii* (Rouillier, 1847)].

The data on the Jurassic gastropods from the Moscow Syncline and Voronezh Anticline were summarized in the book by Gerasimov (1992). He devoted the last years of his life to this outstanding study. The book covers over a hundred gastropod species, including many new forms. This had become possible due to his cooperation with amateur paleontologists, whose private collections significantly augmented the material. Gerasimov provided the description of each species with brief characteristics of the facial distribution. The book contains significantly enlarged data on the stratigraphical distribution and intraspecific variability of many species. A few years later, the atlases on the Volgian (Gerasimov *et al.*, 1995) and Callovian (Gerasimov *et al.*, 1996) faunas of European Russia were pub-

lished. Both guides mainly reproduce the illustrations from the previous monograph by Gerasimov (1992), but of a better quality. In addition, there are several photographs of shells that have never been figured earlier.

Finally, in the recent years, Guzhov (2002a, 2002b, 2003) touched some aspects of gastropod systematics and described several new gastropod species and genera from the Jurassic of European Russia.

## CHAPTER 2. SHELL MORPHOLOGY

When describing gastropod shells, I follow the commonly accepted terminology defined in Korobkov's manual (1950), *Paleontological Dictionary* (1965), and partly in *Treatise on Invertebrate Paleontology* (1960). However, the terminology varies from author to author, as is clearly shown in the *Paleontological Dictionary*. In addition, I had to introduce some new terms. Therefore, I should explain the terminology used in the present study.

All shells of the groups examined are dextrally coiled and conospiral, i.e., the shell is formed by a tube coiled along a descending conical spiral. All the whorls of the shell, except the last, form the spire. Each whorl embraces the preceding one up to the line of contact between whorls, designated as the suture. The suture varies in depth, depending on the angle between the surfaces of contacting whorls. If the whorl surface joins the suture gently sloping, at a small angle, the suture looks like a furrow (superficial suture). If the whorls are plumb near the suture, it lies in a wide slit and designated as a slitlike suture. In all other cases, the suture is more or less angular and deep.

The mollusk shell passes through several ontogenetic stages. The first whorls are formed at the embryonic and larval stages, the rest of the whorls grow after the metamorphosis of a larva into a young mollusk. The whorls formed prior to metamorphosis are positioned in the apical part of the shell and named the protoconch. The whorls lying below the protoconch form the teleoconch. The protoconch either pass into the teleoconch without any visible boundary or differs in shape and (or) ornamentation. In the first case, the boundary between the protoconch and teleoconch is placed conventionally or transitional whorls are designated. It is noteworthy that the axes of coiling of the protoconch and teleoconch either coincide or not. When the coiling direction of the protoconch differs from that of the teleoconch, the protoconch is called heterostrophic (the shell is also called heterostrophic, i.e., with the heterostrophic protoconch). In the case where whorls of the protoconch are clearly coiled in the same direction as those of the teleoconch, the protoconch is called homeostrophic.

The direction of coiling of the protoconch and teleoconch are always slightly misaligned in the groups of gastropods studied, and this feature is not mentioned in the description. Only the significant misalignment of

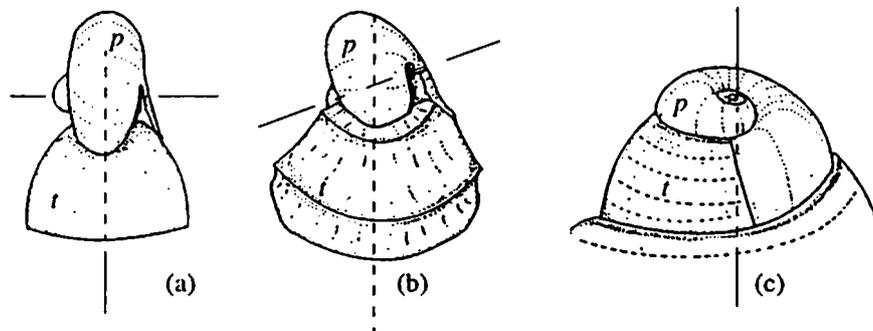


Fig. 1. Various heterostrophic protoconchs: (a) transaxial, (b) medial, and (c) coaxial (after Schröder, 1995, modified). Designations: (*p*) protoconch and (*r*) teleoconch.

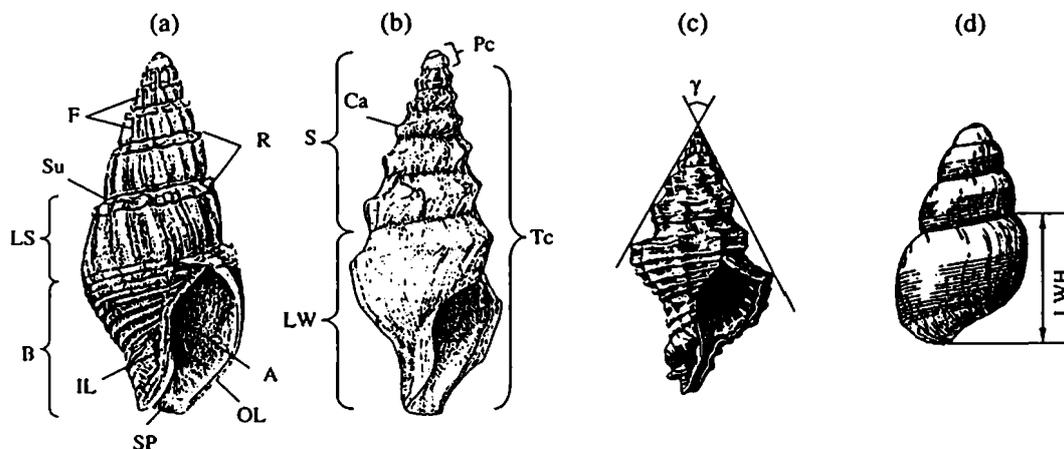


Fig. 2. Shell morphology: (a) bucciniform shell; (b) carinate shell, (c) teleoconch angle measurement, and (d) measurement of the last whorl height. Designations: (A) aperture, (B) base, (Ca) carina, (F) fold, (IL) inner lip, (LS) lateral side, (LW) last whorl, (LWH) last whorl height, (OL) outer lip, (Pc) protoconch, (R) rib, (S) spire, (SP) siphonal projection, (Su) suture, (Tc) teleoconch, and ( $\gamma$ ) teleoconch angle.

the axes is noteworthy. In the present study, I consider several genera with a heterostrophic protoconch. According to Schröder (1995), several types of the heterostrophic protoconchs are distinguished by the angle between the axes of the protoconch and teleoconch, i.e., the transaxial, medial, and coaxial types (Fig. 1). In the transaxial heterostrophic protoconch, the coiling axes are positioned at, or almost at, right angles, i.e., the protoconch is perpendicular to the top of the teleoconch. In the coaxial heterostrophic protoconch, the two axes almost coincide, but the directions of protoconch and teleoconch coiling are opposite. In this case, the protoconch lies on the top of the teleoconch or is partially submerged in its initial whorls. In all other cases, with a transitional angle between the protoconch and teleoconch axes, the protoconch is called medial.

The spire is a cone whose generatrix is composed of tangents drawn through the external points of each whorl. The generating lines may be straight, convex, or concave. The shape of the spire also depends on the

coiling angle, i.e., double angle between the axis of the shell and the generating line. The coiling angle always changes during ontogeny, although these changes are sometimes very slight. In the present study, I use the term *teleoconch angle* to designate the angle between two opposite generating lines composing its arms. This angle is estimated differently in the case of convex (carinate) and flattened whorls. In the first case, the sides of the angle are drawn through the most projecting elements of sculpturing of the first and last whorls. In the shell with noncarinate whorls, the sides of the angle are drawn through the midpoints of the first and last whorls.

Depending on the teleoconch angle, I divide the shells into three groups, i.e., high-turriculate (angle less than  $15^\circ$ ), turriculate (angle varies between  $15^\circ$  and  $30^\circ$ ), and low-turriculate (angle varies between  $30^\circ$  and  $60^\circ$ ). The shells with the teleoconch angle exceeding  $60^\circ$  are called lowly conical. Some shells have rapidly expanding and involute whorls, consequently, their spire is

low, and the last whorl is large. Thus, the form of such a shell approaches a sphere. In addition, ornamented shells with a relatively high spire and a large and rounded last whorl bearing a siphonal canal below occur among the specimens examined. Such a shell resembles that of the family Buccinidae and, hence, is called a bucciniform shell (Fig. 2a). The cerithiform shell is long, multispiral, siphonostomatous, and ornamented (see Pl. 1). The purpuriniform shell is a siphonostomatous shell composed of a large or small number of gradate whorls, which resemble the shell of *Purpurina sensu stricto* (Pl. 6, figs. 6–11). The term *extent of involution* (Fig. 3) characterizes the extent to which the last whorl envelops the earlier one and is expressed as a percentage. A part of the last whorl that is located below the continuation of the suture is designated as the base, which varies in height. A part of the whorl that is always visible is designated as the lateral side. The extent of involution is the ratio (in percent) of the base height to the total whorl height,  $h_1 : h$  100% (Fig. 3).

The aperture is either simple, with an even outline (holostomatous), or has a siphonal notch or projection (siphonostomatous). The projection varies widely in development. In the simplest case, it is a slightly expanded and curved basal apertural margin. A more advanced aperture has a short and concave groove-like canal. The extreme variant is a half-closed or even completely closed siphonal canal resembling a tube. Other siphonostomatous shells have a notch in the basal part of the aperture. This notch discharges the same function as the canal, i.e., allows the water inflow into the mantle cavity. The terms *circular aperture* and *oval aperture* describe the internal outline of the aperture, while the external outline is determined by the whorl shape.

The whorls are variable in shape, i.e., flat, angular, or convex. A convex whorl is either evenly convex or the greatest convexity is confined to a certain part of the whorl. The whorls often bear spiral angulations. A strongly prominent or even sharpened angulation is called a carina. An angulation often bears a spiral rib on its edge that is called a carinate rib. The number of angulations varies from one to several. Whorls that have one carina are called carinate, those with two carinae are called bicarinate. For the purpose of descriptive convenience, the lateral surface of carinate whorls is divided into supracarinate and subcarinate surfaces, according to the position relative to the carina.

The lateral surface of the last whorl in adult shells is sometimes similar to that of the spire whorls, but often displays more or less prominent age-related changes: changes in the suture inclination, weakness or absence of ornamentation, growth interruption marks, and changes in the pattern of the growth lines. Some taxa demonstrate open coiling of the last whorl, which is then called a vermiform whorl.

The main shell parameters (height and width of the shell and height of the last whorl) are measured along

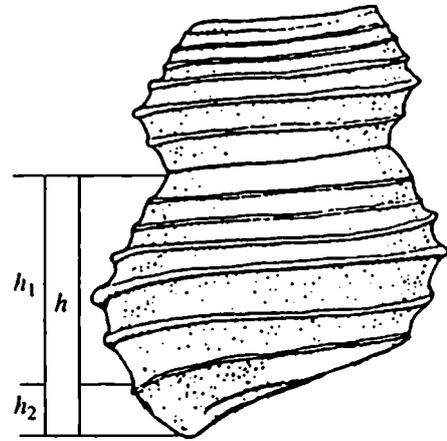


Fig. 3. Estimation of the extent of involution. Designations: ( $h$ ) last whorl height, ( $h_1$ ) height of the lateral side, and ( $h_2$ ) height of the shell base.

the projection on the axis of coiling. According to the shell size, they are regarded as small-sized (below 10 mm), medium-sized (from 10 to 40 mm), and large-sized shells (over 40 mm).

The gastropods of the groups under discussion always have ornamented whorls (except for some embryonic whorls with a smooth surface). The ornamentation is mainly represented by elongated elevations, which are called ribs and folds. It is commonly accepted that folds differ from ribs by the larger size and less prominently delineated borders. In the present study, ribs and folds are mainly distinguished by their direction; the spiral elements are regarded as ribs, while the folds are collabral, parallel to the growth lines (Fig. 2a). The growth lines are traces on the whorl surface that mark the positions of the aperture edge at different stages of the shell growth.

Spiral elements vary in width and height. The width usually exceeds the height, so that ribs are ribbonlike. If the width is equal to the height, the rib is square in cross section. The ornamentation of the teleoconch either appears initially or later in the course of its growth. The ribs that develop from the beginning of the teleoconch or even appear in the protoconch are called primary ribs. The ribs that are formed at the later stages of the teleoconch growth are called secondary. In the present study, the ribs are numbered in descending order from the top to the base.

The folds are usually larger and less distinct than the ribs, so they are defined herein in much the same way as commonly accepted elsewhere. However, the collabral elements are sometimes similar to the spiral elements in shape and prominence. The folds can run from one suture to another, changing insignificantly, or can become more prominent in places. Sometimes, the folds extend onto the shell base. The genus *Exelissa* has strongly developed folds that continue each other on neighboring whorls. It appears that the folds form sev-

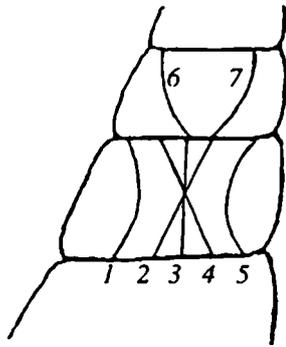


Fig. 4. Classification of growth lines based on their directions: (1) opisthocyrt, (2) opisthocline, (3) orthocline, (4) prosocline, (5) prosocyrt, (6) prosocline-prosocyrt, and (7) opisthocline-opisthocyrt.

eral vertical rows, and the shell of *Exelissa* looks like a polyhedral pyramid. For conciseness, such shells are called, for instance, octahedral (if eight vertical rows are present).

Depending on the general direction, the collabral ornamentation and growth lines are divided into the following types (Fig. 4): orthocline (positioned perpendicular to the sutures and straight in outline), prosocline (the lower part is closer to the aperture than the upper), and opisthocline (the upper part is closer to the aperture than the lower). The folds that are perpendicular to the sutures and posteriorly convex are called opisthocyrt folds; those anteriorly convex are called prosocyrt. If the prosocline elements are convex posteriorly, they are called prosocline-prosocyrt, while, if they are opisthocline and convex anteriorly, they are called opisthocline-opisthocyrt elements.

Grain-like tubercles are formed at the intersection of ribs and folds. These tubercles are variable in size and shape; occasionally, they are absent. Large, pointed tubercles are called spines.

The type of ornamentation composed of the equally prominent spiral and collabral elements is called reticulate. Shells with such ornamentation are called reticulate-ribbed.

### CHAPTER 3. SOME PROBLEMS OF THE TAXONOMY, NOMENCLATURE, AND EVOLUTION OF JURASSIC GASTROPODS

This chapter revises the taxonomy of several gastropod families with similar shell morphologies: Cerithiopsidae H. Adams et A. Adams, Cryptaulacidae Gründel, Epitoniidae Berry, Eumetulidae Golikov et Starobogatov, Maturifusidae Gründel, Procerithiidae Cossmann, Polygyrinidae Bandel, and Purpurinidae Zittel. In addition, a new family, Purpuroideidae fam. nov., is established. Below, these families are discussed either individually or in groups. In most cases we will first discuss the placement of taxa in families and then some sub-

duced taxa, including their composition, interrelationships, and patterns of evolutionary changes in shell morphology.

#### Families Procerithiidae and Cryptaulacidae

To date, the family Procerithiidae Cossmann, 1906 includes many taxa. Cossmann (1906) placed many turriculate, anomphalous, holostomatous (in fact, siphonostomatous) shells with reticulate or tuberculate ornamentation in the family Procerithiidae. The aperture is rounded from the anterior or bears an angular notch. However, the notch does not form a true canal. Cossmann split the family into three subfamilies, i.e., Procerithiinae, Paracerithiinae, and Metacerithiinae. Procerithiinae are characterized by an aperture that is rounded and slightly notched anteriorly, Paracerithiinae display a slightly angular aperture with a notch that does not project beyond the outline of the aperture. Metacerithiinae have a notch that resembles a canal in appearance and distinctly projects beyond the aperture outline.

The diagnoses of the family and its subfamilies are based on a single feature and do not take embryonic or postembryonic developments, or ontogenetic or age-related changes in shell morphology into account. Nevertheless, the family and its subfamilies have changed only slightly in composition since Cossmann's time. Cossmann placed the genera *Procerithium* Cossmann, 1902 with the subgenera *Procerithium* sensu stricto (sections *Procerithium* sensu stricto and *Cosmocerithium* Cossmann, 1906), *Rhabdocolpus* Cossmann, 1906, and *Xystrella* Cossmann, 1906); *Cerithinella* Gemmellaro, 1878 (sections *Cerithinella* sensu stricto and *Laevibaculus* Cossmann, 1906); *Nerineopsis* Cossmann, 1906; *Gymnocerithium* Cossmann, 1906; *Cryptaulax* Tate, 1869 with the subgenera *Cryptaulax* sensu stricto and *Cryptoptyxis* Cossmann, 1906; and *Exelissa* Piette, 1860 (sections *Exelissa* sensu stricto and *Teliiochilus* Cossmann, 1906) in the Procerithiinae; the genera *Paracerithium* Cossmann, 1902; *Rhynchocerithium* Cossmann, 1906; *Terebrella* Andreae, 1887; and *Cirsocerithium* Cossmann, 1906 in the subfamily Paracerithiinae; and the new genera *Bathraspira* Cossmann, 1906; *Metacerithium* Cossmann, 1906; and *Uchauxia* Cossmann, 1906 and, tentatively, *Cimolithium* Cossmann, 1906 and *Rostrocereithium* Cossmann, 1906 in the subfamily Metacerithiinae.

Subsequently, Wenz (1940) added several taxa to the family Procerithiidae. He placed the genera *Urgonella* Cossmann, 1916; *?Nudivagus* Wade, 1917; and *Cupaniella* Gemmellaro, 1911 in the subfamily Procerithiinae and the subgenera *Eocerithium* Bonarelli, 1927 and *Apicaria* Kutassy, 1937 in the genus *Procerithium* Cossmann, 1902. In addition, he questioned the assignment of *Cerithinella* Gemmellaro, 1878 to the subfamily. He added the genera *?Trachoeucus* Kittl, 1894; *?Pseudotrionium* Wenz, 1940; and *Diatrypesus* Tomlin, 1929 to the subfamily Paracerithiinae (instead of the preoccupied genus *Terebrella* Andreae, 1887)

and included the subgenera *Bigotella* Cossmann, 1913 and *Brachycerithium* Bonarelli, 1921 in the genus *Procerithium* Cossmann, 1902. He placed the genus *Protofusus* Bonarelli, 1921 in the subfamily Metacerithiinae and supported the position of the genus *Cimolithium* Cossmann, 1906 in this family. All of Cossmann's sections have been raised to the subgeneric level.

In 1974 Gründel (1974b) established a new subgenus of the genus *Procerithium* Cossmann, 1902, *Infacerithium* Gründel, 1974. Later, he suggested (Gründel, 1976a) that the family Procerithiidae was divided into two subfamilies, i.e., Procerithiinae and Cryptaulinae Gründel, 1976. The subfamily Procerithiinae contained the genera *Procerithium* Cossmann, 1902 (subgenera *Procerithium* sensu stricto, *Infacerithium* Gründel, 1974; *Cosmocerithium* Cossmann, 1906; and *Rhabdocolpus* Cossmann, 1906); *Bittolium* Cossmann, 1906; *Bittium* Leach, 1847 (subgenera *Bittium* sensu stricto, *Cerithidium* Monterosato, 1884 and *Rasbittium* Gründel, 1976); *Lirobittium* Bartsch, 1911 (subgenera *Lirobittium* sensu stricto; *Cacozeliana* Strand, 1928; and, probably, *Stylidium* Dall, 1907); and *Semibittium* Cossmann, 1896. The subfamily Cryptaulinae included the fossil genus *Cryptaulax* Tate, 1869 (subgenera *Cryptaulax* sensu stricto; *Pseudocerithium* Cossmann, 1884; and *Xystrella* Cossmann, 1906) and the two extant genera *Argyropeza* Melvill et Standen, 1901 and *Varicopeza* Gründel, 1976.

However, these subfamilies were not used by Gründel or by any other malacologists. In his latest publication, Gründel (1999b) implied another hierarchy of taxa in the family Procerithiidae; i.e., *Procerithium* Cossmann, 1902 (without subgenera); *Rhabdocolpus* Cossmann, 1906 (subgenera *Rhabdocolpus* sensu stricto and *Infacerithium* Gründel, 1974); *Rhynchocerithium* Cossmann, 1906; *Cryptaulax* Tate, 1869 (without subgenera); and *Exelissa* Piette, 1860 (without subgenera).

I studied the following taxa of Jurassic proceritiids: *Procerithium* Cossmann, 1902; *Rhabdocolpus* Cossmann, 1906; *Infacerithium* Gründel, 1974; *Cryptaulax* (*Cryptaulax*) Tate, 1869; *C.* (*Neocryptaulax*) Gerasimov, 1992; *Exelissa* Piette, 1860; *Cryptoxyxis* Cossmann, 1906; and *Cosmocerithium* Cossmann, 1906. In addition, I examined the Cretaceous material of *Cosmocerithium* Cossmann, 1906 [sensu Cossmann]; *Bathraspira* Cossmann, 1906; *Metacerithium* Cossmann, 1906; and *Rostrocerithium* Cossmann, 1906. My study of the published data on the embryonic and postembryonic developments of these and other taxa, and the correlation of them with my own data, have allowed me to modify the family composition.

The members of the family Procerithiidae (in the old sense) for which the embryonic development is known can be split into two groups. The first group includes *Procerithium* Cossmann, 1902 and *Rhabdocolpus* Cossmann, 1906 [= *Procerithium* Cossmann, 1902, see below]. I have assigned them to the family Procerithiidae. In addition, I tentatively assigned to this family a

new genus, *Tyrnoviella* gen. nov., the embryonic development of which is unknown (Table 1). Walther (1951) has shown that *Rhabdocolpus* Cossmann, 1906 is characterized by a protoconch with several smooth whorls. My own observations support this. The protoconch of *Procerithium russiense* d'Orb. I examined is composed of about 3.5 smooth and rounded whorls and is separated from the teleoconch by an opisthocyrt commissure, followed by folds. The folds are present on the entire shell, and the spiral ornamentation appears after the teleoconch has completed 0.5–3.5 whorls. The uppermost rib appears first, is more prominent, and bears more pronounced tubercles than all the other ribs, making the profile of the whorls steplike. Contrary to the opinions of Cossmann (1906) and Gründel (1974), this is not due to the development of a "ramp" or "horizontal platform" on the upper part of the whorl. The portion of the whorl that lies above the uppermost rib is very steep between the folds (not less than 70°–80°) and not so steep on the folds (45°–50°). The family Cryptaulacidae shows the same type of gradation.

A similar protoconch and development of ornamentation were shown in *Procerithium* sensu stricto by Gründel (1997, pl. 5, figs. 1–5; 1999b, pl. 1, figs. 4–14). Carination is present only in the lower parts of the protoconch whorls. The composition of the genus *Procerithium* Cossmann, 1902 remains uncertain. This primarily concerns its relationships with *Katosira* Koken, 1892 and *Rhabdocolpus* Cossmann, 1906. Studies of these three genera suggest that they are successive members of a single evolutionary lineage, and that the distinctions between them are rather vague. The genus *Katosira* (Middle Triassic–Middle Jurassic) includes turriculate and high-turriculate shells with a teleoconch ornamented by prominent folds and numerous spiral threads that appear later in life. The aperture is rounded and has an angular notch. In contrast to *Katosira*, the Early Jurassic *Procerithium* Cossmann, 1902 has fine ribs and folds (the latter dominate the former); small tubercles develop at their intersections. The aperture is the same as that in *Katosira*. The genus *Rhabdocolpus* Cossmann, 1906 (Early–Late Jurassic) is distinguishable from *Procerithium* Cossmann, 1902 by its more pronounced spiral ornamentation and the presence of indistinct gradate shoulders of the whorls. Thus, there is an evolutionary tendency towards the strengthening of spiral ornamentation (and, consequently, spreading of the ribs) and the appearance of a slightly stepped profile. I believe that the members of the Cretaceous *Uchauxia* Cossmann, 1906 are descendants of the Jurassic *Rhabdocolpus* Cossmann, 1906.

Thus, the evolutionary line *Katosira*–*Uchauxia* is characterized by the gradual development of spiral ornamentation and the transfer (?) of its appearance to progressively earlier ontogenetic stages and, perhaps, by the development of the apertural notch into a groove (see below). Thus, it is difficult to draw boundaries between these taxa: the difference between *Procerithium* Cossmann, 1902 and *Rhabdocolpus* Cossmann,

1906 is restricted to the whorls being slightly stepped (which is the result of more prominent ribs), and there is virtually no difference between *Rhabdocolpus* Cossmann, 1906 and *Uchauxia* Cossmann, 1906. The data suggesting the development of the siphonal groove in *Uchauxia* are questionable, since I myself long mistook the distinctive basal chips of *Procerithium russiense* (d'Orbigny) (= *Rhabdocolpus* Cossmann, 1906 according to Cossmann and Wenz) for a siphonal groove. Since the distinguishing characters in this evolutionary line are difficult to evaluate, little differentiated, and evolved slowly, I consider the genera *Rhabdocolpus* Cossmann, 1906 and *Uchauxia* Cossmann, 1906 to be synonyms of the genus *Procerithium* Cossmann, 1902.

Although there is no distinct boundary between *Katosira* and *Procerithium* Cossmann, 1902, I retain them as separate genera; the fact that *Katosira* belongs to the same line of morphological evolution as the Procerithiidae suggests that it should be assigned to this family rather than to the Zygopleuridae sensu stricto (Table 1).

The second group, which I here assign to the family Cryptaulacidae Gründel, was first established by Gründel (1976a) as the subfamily Cryptaulinae within the family Procerithiidae and subsequently renamed Cryptaulacinae (Gründel, personal communication). I recognize the following genera within the family Cryptaulacidae: *Infacerithium* Gründel, 1974; *Cryptaulax* Tate, 1869; *Exelissa* Piette, 1860; *Cupaniella* Gemmellaro, 1911; *Teliophilus* Cossmann, 1906; *Protocerithium* Bistram, 1903; *Microcerithium* gen. nov.; *Shurovites* gen. nov.; and the genus *Cimoliocentrum* Cossmann, 1908, which has been transferred from the family Purpurinidae. Protoconchs are known in *Infacerithium* Gründel, 1974; *Cryptaulax* Tate, 1869; *Exelissa* Piette, 1860; and *Microcerithium* gen. nov.

These protoconchs consist of the initial 1–1.5 smooth whorls, which are followed by two gradually developing angulations. Later the angulations become carinate, each bearing a rib or a row of tubercles. The remaining surface of the whorls may also have several rows of tubercles. Folds appear at the beginning of the teleoconch, while the existing ribs temporarily become flatter or disappear, and new ribs often appear. The aperture has a notch, a bend of the basal margin, or a poorly developed groove. The teleoconch ontogeny varies from genus to genus. The genera of the family are split into two subfamilies, i.e., Cryptaulacinae and Exelissinae subfam. nov., according to the pattern of the last whorl. The distinction is that in the subfamily Exelissinae the last whorl strongly deflects downward, narrows, becomes rounder, and loses folds, while its spiral ornamentation flattens and may even completely disappear near the aperture. In addition, the anterior end of the last whorl tends to become vermiform in appearance; it grows anteriorly uncoiled and slightly bent upwards, and its ornament is restricted to coarse growth lines. In the subfamily Cryptaulacinae, the last whorl may

become rounder and only slightly deflects downward, its ornamentation becomes less prominent only at the extreme end.

*Shurovites* gen. nov., which is placed here in the Exelissinae, differs from the other genera in that the lower carina and, sometimes, a fine rib corresponding to the upper carina develop at the latest stages of protoconch development. The preceding protoconch whorls are rounded. In *Shurovites* gen. nov., prominent ribs and folds appear at the earliest stages of teleoconch development. The high position of the carina on the protoconch, the early development of spiral ornamentation on the teleoconch, and the changes in the last shell whorl that are typical of the Exelissinae (see the descriptions of the species) suggest that *Shurovites* gen. nov. belongs to the family Cryptaulacidae rather than to the Procerithiidae. On the basis of the latter character, this genus is assigned here to the subfamily Exelissinae. Its position within the subfamily will be discussed in detail below.

I here assign the following genera to the subfamily Cryptaulacinae: *Cryptaulax* Tate, 1869 (subgenera *Cryptaulax* sensu stricto; *Pseudocerithium* Cossmann, 1884; and *Neocryptaulax* Gerasimov, 1992); *Infacerithium* Gründel, 1974 (subgenera *Infacerithium* sensu stricto and *Kuntseviella* subgen. nov.); and *Microcerithium* gen. nov. (Table 1). The following genera are assigned to the subfamily Exelissinae: *Exelissa* Piette, 1860 (subgenera *Exelissa* sensu stricto and *Pyrazopsis* Hacobjan, 1972); *Cupaniella* Gemmellaro, 1911; *Teliophilus* Cossmann, 1906; *Cimoliocentrum* Cossmann, 1908; and *Shurovites* gen. nov. In addition, the genus *Protocerithium* Bistram, 1903 is reassigned to this subfamily. Below I discuss some problems of the taxonomy, nomenclature, and evolution of members of the family Cryptaulacidae.

The genus *Cryptaulax* Tate, 1869. The type species was designated by Tate (1869) as *Cerithium tortile* Hebert et Deslongchamps, 1860. Nevertheless, Cossmann (1906) ignored the valid type species of the genus and introduced another species as a type, i.e., *Cerithium scobina* Eudes-Deslongchamps, 1842. He proposed the species *Cerithium armatum* Goldfuss, 1844 as the type for *Xystrella* Cossmann, 1906, another taxon of the subfamily Procerithiinae (sensu Cossmann). The species *Cerithium scobina* Eudes-Deslongchamps has a very high-turriculate (almost subcylindrical) shell with numerous whorls thus, it is rather distant morphologically from Tate's type species of the genus *Cryptaulax* Tate, 1869. *C. tortile* Hebert et Deslongchamps, 1860 has a high-turriculate shell with a lesser number of whorls. *C. armatum* Goldfuss, 1844 has a very high shell, which is atypical of species related to *C. tortile* but resembles that of *C. scobina*. Cossmann's choice of morphologically similar species, i.e., *C. scobina* and *C. armatum*, as the types for *Cryptaulax* Tate, 1869 and *Xystrella* Cossmann, 1906, respectively, led to a mistaken concept of the genus



Wenz (1939) restricted his illustrations of the genus *Cryptaulax* Tate, 1869 to that of Cossmann's plesio-type. More recently, Gründel (1974a) restored the priority of Tate's type species of the genus *Cryptaulax* Tate, 1869, and quite recently (Gründel, 1999b) synonymized *Xystrella* Cossmann, 1906 and *Cryptaulax* sensu stricto on the basis of a reexamination of *C. armatum*. I support both decisions of Gründel but believe that forms that are similar to *C. scobina* Eudes-Deslongchamps, 1842 should be considered to be members of a separate subgenus within *Cryptaulax* Tate, 1869. For this purpose, I suggest the restoration of the subgenus *Pseudocerithium* Cossmann, 1884, which had previously been included in the synonymy of *Cryptaulax* Tate, 1869.

The composition of the type species of the genus *Cryptaulax* Tate, 1869 also poses several problems. Tate (1869) did not list the forms that he included in *C. tortile* Hebert et Deslongchamps, despite the fact that the original description of this species (Hebert and Deslongchamps, 1860, pl. 6, figs. 1a–1e) included illustrations of five shells of different species and perhaps even different genera. The specimen illustrated in pl. 6, fig. 1c is probably an *Exelissa* Piette, 1860, while the others belong to either *Cryptaulax* sensu stricto (pl. 6, figs. 1a, 1b, 1d) or to *Cryptaulax* (*Neocryptaulax*) (pl. 6, fig. 1e). Cossmann (1906, 1913) proposed that the species be confined to the specimens given in pl. 6, figs. 1a and 1b, but his opinion has not been accepted. Haas (1953) considered the specimen in pl. 6, fig. 1c to be the true *Cryptaulax tortilis*, while Gerasimov included in this species specimens in pl. 6, figs. 1a, 1c, and 1e. Finally, Gründel (1999b) ascribed specimens in pl. 6, figs. 1a–1c to this species. In my view, the most correct opinion is that of Cossmann. I studied specimens from my own collection that are very similar to those illustrated in pl. 6, figs. 1a, 1b, and 1d. I believe that pl. 6, fig. 1d represents a similar but separate species, which is described below as *Cryptaulax* (*Cryptaulax*) *pseudoechinatus* Gerasimov. The other figures (i.e., pl. 6, figs. 1c, 1e) illustrate the other two species.

There are problems with the validity of the type species name of the genus *Cryptaulax* Tate, 1869. Eudes-Deslongchamps used the same name, i.e., *Cerithium tortile*, for a new species of turritelliform gastropod (Eudes-Deslongchamps, 1842a, p. 200, pl. 11, fig. 15). Thus, the name of the type species of the genus *Cryptaulax* Tate, 1869 is preoccupied. To correct this nomenclatorial problem, Cox (1965a, p. 15) proposed a new replacement name *Procerithium* (*Xystrella*) *protortile* for *Cerithium tortile* Hebert et Deslongchamps, non *Cerithium tortile* Eudes-Deslongchamps, 1842. Being unaware of this nomenclatorial act, Gründel (1999b, p. 16) introduced another replacement name, i.e., *Cryptaulax bellayensis*.

The taxon *Pseudocerithium* Cossmann, 1884 was established by Cossmann (Cossmann in Fischer, 1880–

1887, p. 685). Its type species was designated in a more recent work (Cossmann, 1885, p. 124) as *Cerithium undulatum* Quenstedt, 1858. Subsequently, *Pseudocerithium* Cossmann, 1884 was synonymized with *Cryptaulax* Tate, 1869 by Zittel (1895), who was supported by Cossmann (1906) and Wenz (1939). In my view, however, *Cryptaulax* sensu stricto and *Pseudocerithium* Cossmann, 1884 are easily distinguishable, and the intermediate (deviating) forms, like *Cerithium armatum* Goldfuss, are rare. I consider *Cryptaulax* sensu stricto to be comprised of gastropods with high-turriculate or, rarely, very high-turriculate shells composed of no more than 15 teleoconch whorls. The subgenus *Pseudocerithium* Cossmann, 1884 includes gastropods with very high-turriculate to subcylindrical shells composed of more than 15 (usually about 20) teleoconch whorls. It also clearly differs from the subgenus *Neocryptaulax* Gerasimov, 1992 in the slender multispiral shells and ornamentation pattern (see the description in Systematic Paleontology).

The relationships between *Exelissa* Piette, 1860 and *Cryptoptyxis* Cossmann, 1906. Both taxa are characterized by the presence of coarse angulated folds that are coterminous on neighboring whorls and form axial rows (similar rows are typical for most shells with colabral ornamentation, but they are usually characterized by rather compact bulging of folds and, quite often, by greater numbers per whorl). The species *Cerithium strangulatum* d'Archiac, 1843 (the type species of *Exelissa* Piette, 1860) has seven rows of folds and a convex generating line, whereas *Cerithium wrighti* Etallon, 1859 (the type species of *Cryptoptyxis* Cossmann, 1906) has five rows of folds and a straight generating line.

There are many species with five-, six-, seven-, and eight-faced shells that occur in coeval deposits. For instance, *Cerithium desplanchei* Piette, 1857 (five or six rows of folds and a straight generating line) and *C. strangulatum* d'Archiac, 1843 (seven rows of folds and a convex generating line) occur in the Bathonian of France. In addition, generating lines of shells in members of *Exelissa* Piette, 1860 are either convex or as straight as that of *Cryptoptyxis* Cossmann, 1906 (for example, the species *E. prismatophora* Cossmann, 1913 from the Toarcian of France has seven rows of folds and a straight generating line).

However, there are some trends in the evolution of shell morphology. The majority of species that have characters in common with the type species of the genus *Exelissa* Piette, 1860 occur in the Early Jurassic, and only a few of them occur in the Middle Jurassic–Early Cretaceous. They are extremely rare in the Late Jurassic and sometimes pass through stages in ontogeny that are typical of both genera. For instance, the shell of *Exelissa distans* Cossmann, 1913 from the Upper Oxfordian of France is eight-faced at the early teleoconch stages but abruptly loses three faces to become five-faced with a straight generating line on the

later teleoconch whorls. The species with features typical for the type species of the genus *Cryptoptyxis* Cossmann, 1906 are extremely rare in the Early Jurassic, appear in moderate numbers in the Middle Jurassic, and become widely distributed in the Late Jurassic. All of them have a straight or, occasionally, slightly convex generating line.

Hence, we can see a gradual evolution from the eight-faced and seven-faced shells with a convex generating line towards the five-faced and six-faced shells with a straight generating line through a complete set of transitional forms (detailed data are given in Systematic Paleontology).

I examined over 15 thousand specimens of the species *Cerithium quinarium* Trautschold, 1866 from the Middle Oxfordian. The majority of shells are five-faced, but four-faced and six-faced specimens also, even if quite rarely, occur. Thus, the shells with six rows of folds are morphologically intermediate between *Exelissa* Piette, 1860 and *Cryptoptyxis* Cossmann, 1906, whereas the four-faced forms are similar to some species of *Pyrazopsis* Hacobjan, 1972 (see below). It is probable that such a pattern of intraspecific variability is not uncommon, and the absence of similar data on other species can be explained by the lack of adequate study of the group.

Taking into consideration the gradual evolution of the eight-faced and seven-faced forms towards the five-faced and six-faced forms, it seems neither sensible nor possible to reliably separate the genera under discussion, and hence I regard them as a single genus, i.e., *Exelissa* Piette, 1860. In addition, the genus *Kilvertia* Lycett, 1863 is an objective synonym of *Exelissa* Piette, 1860 since it is based on the same type species, i.e., *Cerithium strangulatum* d'Archiac, 1843 (Lycett, 1863, p. 15).

The genus *Teliochilus* Cossmann, 1906, was originally designated by Gemmellaro (1878) as *Tomochelilus*. Later, Cossmann (1906) noted that *Tomochelilus* Gemmellaro, 1878 is a junior homonym of *Tomochilus* Laferté, 1851 and proposed a new name, *Teliochilus* Cossmann, 1906. The type species of the genus, i.e., *Tomochelilus deslongchampsii* Gemmellaro, 1878, has a small oval shell with a convex generating line. The shell is ornamented by spiral ribs and closely spaced axial folds. The last whorl descends, looses folds, and stretches anteriorly. These changes in the last whorl morphology were convincingly demonstrated by Fucini (1913). The aperture is rounded and sloped backwards from the base upwards. There is no contraction of the whorl. All these features suggest that the genus belongs to the subfamily Exelissinae. The genus distribution is limited to the carbonate rocks of the Lower Lias of Italy (Sicily). Wenz (1939, p. 731, text-fig. 2117) provided a rather strange illustration attributed to the type species of the genus *Teliochilus* Cossmann, 1906. The origin of the specimen he figured is unknown, and no similar form has been illustrated by

the author of the species or by any other specialist. This illustration has nothing in common with the actual type species of the genus and serves only to confuse.

The genus *Cupaniella* Gemmellaro, 1911 was described on the basis of a single species by Gemmellaro (1911). Its type species *Cupianella biplicata* Gemmellaro, 1911 is characterized by a teleoconch with a convex generating line and shell ornamented by spiral ribs and collabral plications. The last whorl is descending. The ornamentation of the last whorl is missing. The structure of the last whorl suggests that the genus belongs to the subfamily Exelissinae.

The genus *Protocerithium* Bistram, 1903, established by Bistram (1903), was synonymized with *Protocerithium* Cossmann, 1902 by Cossmann (1906) and Wenz (1940). However, illustrations in the original publication by Bistram prove the validity of *Protocerithium*. Some illustrations show shells that are very similar to *Cryptaulax* sensu stricto (pl. 5, fig. 17) or *C. (Neocryptaulax)* (pl. 5, figs. 15, 16). But other figures (pl. 5, fig. 19; pl. 6, figs. 1, 2) display such details of the last whorl and aperture of the type species that they exclude the possibility that this species belongs to the above-mentioned subgenera. A short and deep groove that is identical to that of *E. (Exelissa) quinaria* (Trautschold) (Pl. 2, fig. 5a) and strong change in ornamentation that resulted in disappearance of folds long before the aperture suggest that this species belongs to the subfamily Exelissinae. The chosen direction of the projection gives no way of providing data on the presence of diagnostic features of the subfamily (contraction, descending, and straightening of the last whorl). Unfortunately, Bistram did not illustrate any complete shell with the features that were illustrated separately. Thus, we cannot say whether or not the drawings of the last whorls (pl. 5, fig. 19; pl. 6, figs. 1, 2) belong to the complete shells shown in pl. 5, figs. 15–17. Bistram designated the type species of his genus as *Protocerithium lugdunense* (Dumortier, 1864). The comparison of the original illustration by Dumortier (1864) and the drawing by Bistram has convinced me that they represent different species. Thus, the type species of the genus *Protocerithium* was misinterpreted and illustrated by teleoconchs of several species, which are shown without the late whorls and aperture, bearing characteristic features of this genus. A reexamination of the type material is necessary to solve these problems.

### *The Evolution of Cryptaulids (Table 1)*

It is difficult to recognize members of the subfamily Cryptaulacinae using old-established species, since they usually convergently resemble the species of Procerithiidae and lack such conspicuous distinctive characters as the structure of the last whorl in Exelissinae. Thus, I have to use the protoconch structure, the absence of those morphological changes in whorls that are characteristic of Exelissinae, and the general similarity in

shell morphology to the undoubted members of the Cryptaulacinae. It is not surprising, then, that only a minor portion of this extensively illustrated material has been reliably attributed to genera of the Cryptaulacinae.

The genus *Cryptaulax* Tate, 1869 includes multispiral shells, usually more than 10 mm high, with prominent spiral and collabral ornamentation. The aperture is rounded, with a notch and thin outer lip at the base or without a notch but with a thickened inner lip and explanate (flared) outer lip. The last feature is typical for species of the subgenus *Neocryptaulax* Gerasimov, 1992. The genus *Microcerithium* gen. nov. includes forms the ontogenetic development of which was arrested at early stages. It is not surprising, then, that they are very small (three to four times smaller than the species of *Cryptaulax* Tate, 1869) and usually have underdeveloped and poorly defined spiral and collabral ornamentation (especially in specimens from the Volgian Stage). The aperture has a narrowly explanate basal margin. These species of the genus occur in Upper Jurassic clays. Possibly, they originated from *Cryptaulax* sensu stricto through neoteny. The genus *Infacerithium* Gründel, 1974 apparently originated in the Middle Jurassic, most likely from *Cryptaulax* sensu stricto. Its evolution is characterized by a progressive reduction in collabral ornamentation (the spiral elements are also often weaker than those in the genus *Cryptaulax* Tate, 1869). The folds of the last whorls were first to disappear (subgenus *Infacerithium* sensu stricto); later, in the Volgian Stage, the folds disappear from the entire shell (subgenus *Kuntseviella* subgen. nov.). The basal margin of the aperture is explanate as in *Microcerithium* gen. nov. The species of the genus *Infacerithium* Gründel, 1974 are as small as the species of *Microcerithium* gen. nov., and possibly they also are neotenic descendants of *Cryptaulax* Tate, 1869.

Now we examine the evolution of morphology of the genus *Exelissa* Piette, 1860 from the subfamily *Exelissinae*. Its first undoubted members are known from the Upper Triassic of South America (Haas, 1953). Already the Upper Jurassic material illustrated by Gemmellaro (1878) shows two morphologically distinct groups. The shells of the first group are relatively thin-walled and slender (as in typical *Exelissa* sensu stricto), the shells of the second group are of lower height and more robust (these forms still belong to *Exelissa* sensu stricto). Hence, both groups must have originated earlier, in the Triassic and diverged from their common ancestor. The first group is common in argillaceous, arenaceous-argillaceous, and calcareous-argillaceous shallow-water facies. The second group occurs predominantly in calcareous sediments and in reef communities and biostromes of Late Jurassic time. The Late Jurassic descendants of the second group developed folds on the internal surface of whorls in the fashion of nereneids or trochactaeonids, which inhabited the same environments. In addition to only two distinguishing features of Early Jurassic species, i.e., the low spire and hard shell, the Kimmeridgian–Tithonian

forms have two prominent columellar folds (Gemmellaro, 1869; Pirona, 1878, etc.). The species *Centrogonia cureti* Cossmann, 1899 from the Urgonian coral facies is very similar to this group. It has two folds on the columellar side; one fold on the outer lip; and a low, conical, five-faced shell like that of the Jurassic species; thus, I believe that it originated from those Late Jurassic forms. *C. cureti* Cossmann, 1899 is the type species of the genus *Cimoliocentrum* Cossmann, 1908, which has been misplaced in the family Purpurinidae. Thus, those members of the Exelissinae that evolved folds as an adaptation for reef or bioherm habitats, should be assigned to the genus *Cimoliocentrum*. Unfortunately, we have no data on the shell evolution of this group between the Toarcian and Oxfordian, i.e., the time when the fold pattern evolved. Gemmellaro's illustration of the Early Jurassic species *Cerithium pentaplocum* Gemmellaro, 1878 (Lower Lias of Italy), which has two columellar folds and one fold on the outer lip that are arranged in a different manner than those of the Late Jurassic species, suggests that apertural folds appeared repeatedly in the Exelissinae: there were apparently at least two attempts at such adaptation; i.e., at the beginning of the Jurassic and in the Middle Jurassic.

The other species of *Exelissa* Piette, 1860 lack any apertural folds and all modifications are restricted to the shell form or ornamentation. As previously mentioned, evolution reduced the number of folds from eight or nine to five, and the species with a convex generating line of whorls gradually disappeared. But some forms with a greater number of folds, e.g., *E. (E.) dollfusi* (Choffat, 1901) with seven rows of folds from the Senonian of Portugal, occurred even in the Cretaceous. Probably, such species should be considered as recurring forms, originating from mollusks with a lesser number of folds. At the same time, in some Cretaceous representatives (subgenus *Pyrazopsis*), the ribs turn into rows of tubercles that run between folds, and the number of folds per whorl reduces to four (one species).

Thus, there are two trends in the morphogenesis of the genus *Exelissa* Piette, 1860. The first trend is represented by the lineage *E. (Exelissa)* (Jurassic) → *E. (Pyrazopsis)* (Late Cretaceous), the second trend is represented by the lineage *E. (Exelissa)* (Early Jurassic) → *Cimoliocentrum* (Late Jurassic–Early Cretaceous). Despite these trends, some species retained most of the ancestral features.

Several Lower Jurassic forms that do not fit in any of the established genera of the Exelissinae have been described in the literature. Dubar (1948) described the species *Exelissa galenae* Dubar and *E. cf. prealpina* Cossmann, 1905. Both of them have numerous folds and a well-defined altered last whorl. *Exelissa galenae* has 11 folds per whorl, while *E. cf. prealpina* has 14 folds. Thus, these two species are similar to the genus *Shurovites* gen. nov.; or, more specifically, to the species of the *S. shurovensis* sp. nov.

The composition of the genus *Shurovites* gen. nov. is uncertain, since the genus has been established based on its protoconch structure (see above). However, the genus is not uniform in teleoconch morphology; thus, *Shurovites* gen. nov. may be divided into two groups, i.e., *S. unzhensis* sp. nov. and *S. shurovensis* sp. nov. In *S. unzhensis* sp. nov., the last whorl is not deflected downwards and has a low, broadly conical base. This form is similar to the species of Cryptaulacinae. In the type species of the genus, i.e., *S. shurovensis* sp. nov., the last whorl is deflected downwards and has a cup-shaped base like that of the members of the Exelissinae. Probably, *Shurovites* gen. nov. originates from forms that resemble *Exelissa galenae* Dubar and represents a group with a rather conservative morphology approaching that of the ancestral *Exelissa* Piette, 1860. In addition, the genus probably has an archaic protoconch with only the lower carina (the protoconch evolution is discussed below). I believe that species like *Exelissa* cf. *prealpina* Cossmann, 1905 (sensu Dubar), *Exelissa galenae* Dubar, and *S. shurovensis* possess many features that are probably typical of the ancestor of the Exelissinae.

In addition to the above-mentioned taxa, there is a group of species of uncertain affinities, bearing a four- or five-faced, very long and narrow shells with a straight generating line. These are *Cryptoptyxis? diversicostata* Imlay, 1941 (Middle–Upper Oxfordian of the southern United States; five or six rows of folds); *Cerithium pentagonum* d'Archiac, 1843 (Bathonian of France; five rows of folds); *Cryptaulax albus* Dubar, 1948 (Upper Pliensbachian of Morocco; five rows of folds); *C. angulodentatus* Dubar, 1948 (Upper Pliensbachian of Morocco; four rows of folds); and *C. tetraetianus* Cossmann, 1913 (Bajocian of France; four or five rows of folds). All of them have a high, cup-shaped base of the last whorl and prominent spiral ornamentation. However, the alteration of the last whorl is unknown in these taxa. Their position is somewhat intermediate between the subgenera *Exelissa* sensu stricto and *Cryptaulax* (*Pseudocerithium*). The last taxon has very long, narrow shells and a few rows of folds coterminous on several whorls.

Now we discuss the protoconch evolution of the family Cryptaulacidae and views on the elaboration of the spiral ornamentation in *Cryptaulax* Tate, 1869. I studied protoconchs of Callovian–Volgian members of the family. Gründel (1974d, 1990a, 1999b) described protoconchs of Middle Jurassic species. McDonald and Trueman (1921) examined protoconchs of Early Lias forms. The Middle Jurassic (Callovian–Bathonian) and Upper Jurassic species are identical in protoconch structure, whereas the Early Lias forms have a somewhat different developmental pattern of carinae. The first smooth whorl is followed by a single whorl with the lower carina, which in turn, is followed by one to two and a half whorls with two carinae. In the Middle–Late Jurassic forms, the initial smooth whorl is im-

mediately followed by bicarinate whorls. Thus, the younger species develop the upper carina earlier in ontogeny. According to McDonald and Trueman (1921), the upper carina of the Early Jurassic species *Exelissa* cf. *numismalis* (Tate) is weaker than the lower one along its entire length.

If the strengthening of the upper carina is a progressive trend, we may suppose that the most primitive forms must have had a protoconch with a single (lower) carina. From this point of view, the protoconch of the genus *Shurovites* is primitive and retains conservative features. Thus, *Shurovites* retains the slightly ornamented protoconch of the ancestor, whereas the other cryptaulacids evolved more elaborate ornamentation.

The evolution of ornamentation in the Cryptaulacidae has been already studied by McDonald and Trueman (1921) and Walther (1951). The former specialists thoroughly discussed the causes of this evolution and recognized so-called primitive (katagenetic) and progressive types. The acceleration was one of the morphogenetic routes considered by McDonald and Trueman. They used the word acceleration to mean the abridgement of embryonic shell and earlier development of the reticulate ornamentation and numerous secondary ribs on the teleoconch. In addition, they considered a reduction in the size of protoconchs to be a progressive feature, i.e., they believed that smaller shells of a taxon are more advanced in an evolutionary sense than larger shells. Hence, the most primitive form is characterized by a large shell, long protoconch with two or two and a half bicarinate whorls, and teleoconch with two ribs. In contrast, the most progressive forms are characterized by a small shell, short protoconch with one or one and a half bicarinate whorls, early appearance of the secondary ribs on teleoconchs, and considerable weakening of collabral ornamentation. The progressive features were attributed to shells that they assigned to the genus *Exelissa* Piette, 1860. Thus, the convexity or pupoid shape of the shell were also considered progressive. According to McDonald and Trueman, the progressive forms repeatedly evolved from the primitive members; thus, they considered the genus *Exelissa* Piette, 1860 to be an artificial taxon. This conclusion was supported by the great morphological variability of forms included within the genus. However, I should note that none of the species ascribed by McDonald and Trueman to *Exelissa* Piette, 1860 actually belong to the genus. On the one hand, the descriptions and illustrations suggest that all of the species lack rows of folds, which are typical for *Exelissa* Piette, 1860. The numerous folds and ribs and the convex generating line of teleoconch support the affinity of these forms to *Cupaniella* Gemmellaro, 1911 and *Cryptaulax* (*Neocryptaulax*) Gerasimov, 1992. On the other hand, it is unlikely that the morphological diversity of gastropods is due to the steady and rapid speciation of progressive species from those primitive forms that considerably differ from them in morphology. My own study of the evolution of cryptaulacids during half

of the Jurassic shows only a very gradual advance in shell ornamentation and insignificant changes in whorl shape. Thus, the conclusions of McDonald and Trueman should be rejected.

On the basis of the conclusions of McDonald and Trueman, Walther (1951) interpreted the evolution of ornamentation in *Cryptaulax* sensu stricto [named as *Procerithium* Cossmann, 1902 in Walther, 1951] and *Cryptaulax* (*Pseudocerithium*) [named as *Cryptaulax* Tate, 1869 in Walther, 1951].

Walther assumed that *Cryptaulax* sensu stricto experienced a general increase in the number of spiral ribs during the evolution, whereas *C.* (*Pseudocerithium*) underwent a reduction in prominent spiral ribs from three to two ribs (according to Walther, the middle prominent ribs was replaced by a series of finer ribs). However, my personal observations suggest that species with two, three, or even four ribs on the teleoconch existed simultaneously. For instance, the species *Cryptaulax* (*Cryptaulax*) *pseudoechinatus* Gerasimov with two ribs and *C.* (*C.*) *protortilis* (Cox) with three or four ribs were common during the Callovian and the species *C.* (*C.*) *strangwaysi* (Rouillier) with three or four ribs was replaced by *C.* (*C.*) *unzhensis* sp. nov, which had predominantly two ribs. I believe that many other examples of such coexistence can be found.

In addition to the above-mentioned taxa belonging to the Cryptaulacidae and Procerithiidae, there are a few genera that were ascribed by Cossmann and Wenz to Procerithiidae and the systematic position of which is discussed below.

The genera *Protofusus* Bonarelli, 1921; *Trachoeus* Kittl, 1894; and *Eocerithium* Bonarelli, 1927 have been based on the material that was too poorly preserved to be reliably identified.

The genus *Cosmocerithium* Cossmann, 1906 was assigned (Guzhov, 2002b) to the family Cerithiopsidae and, thus, is discussed in the corresponding section. The genus *Rhynchocerithium* Cossmann, 1906 was placed in the family Maturifusidae (order Bucciniformes). Possibly, the genera *Apicaria* Kutassy, 1937 and *Brachycerithium* Bonarelli, 1921 are also members of the family Maturifusidae, but the lack of data on their protoconch structure gives no way of determining their systematic position.

The genus *Paracerithium* Cossmann, 1902. Dealing with the Hettangian fauna, Cossmann established the genus *Paracerithium* Cossmann, 1902 with the type species *P. acanthocolpum* Cossmann (Charton and Cossmann, 1902, p. 175, pl. 3, figs. 20, 21). In the original description, the genus *Paracerithium* Cossmann, 1902 is characterized by a shell with a carinate or angulated shoulder, with fine and dense spiral ornamentation and coarse collabral ribs. The aperture is siphonostomatous, with rounded-angular bend of the basal margin (Charton and Cossmann, 1902, p. 174, text-fig. 2). Thus, these features of *Paracerithium* Cossmann, 1902 show that it is close to *Purpurina*

(*Purpurina*) d'Orbigny emend. Deslongchamps (family Purpurinidae) or *Khetella* Beisel, 1977 (family Maturifusidae in this study). The species *Paracerithium moorei* Cossmann, described in the same work, is especially similar to the above-mentioned genera. However, the type species of the genus *Paracerithium* Cossmann, 1902 differs considerably from the species of *Purpurina* sensu stricto and *Khetella* Beisel, 1977. The original illustrations of *P. acanthocolpum* suggest a question as to the completeness of preservation of the basal part of the aperture. It is evident that the aperture is broken from below; thus suggesting the presence of a basal groove. If it is true, the genus *Paracerithium* Cossmann, 1902 is a synonym of *Khetella* Beisel, 1977. It is quite possible that *P. acanthocolpum* Cossmann was the earliest member of *Khetella*, representatives of which undoubtedly occur in the Middle Jurassic (Callovian)–Lower Cretaceous. Many of the species that Cossmann (1906, 1913) has placed in the genus *Paracerithium* are assigned here to *Exelissa* sensu stricto, *Cryptaulax* sensu stricto, and *Procerithium* Cossmann, 1902, and some other forms are of uncertain position. Thus, there is a need for revision of the species composition of *Paracerithium* Cossmann, 1902 and its phylogenetic affinities with other gastropod taxa.

The genus *Metacerithium* Cossmann, 1906. This taxon should be considered within the separate family Metacerithiidae Cossmann, 1906. The protoconch of *Metacerithium* Cossmann, 1906 is unknown. The shell is multispiral, composed of low whorls divided by a shallow suture. The ornamentation is represented by spiral rows of tubercles, often with fine ribs between them, and collabral folds. The base of the shell is almost flat with weak ornamentation. The aperture is compressed along the shell axis, with a short canal. No other genera morphologically similar to *Metacerithium* Cossmann, 1906 are known in the present content of the family Procerithiidae. The members of the genus *Proceritella* Fischer, 1961 are very similar to *Metacerithium* Cossmann, 1906, but all of them are distinguished by the selenizone running under the suture. The systematic position of the family Metacerithiidae is still uncertain, but it is unlikely that it does not belong to the order Cerithiiformes.

The genus *Bathraspira* Cossmann, 1906 apparently belongs to the family Mathildidae Dall, 1889. The genus of Mathildidae, i.e., *Erratohilda* Gründel, 1997 is very similar to *Bathraspira* Cossmann, 1906 in general shell shape and size. All of them have a strongly carinate shell with fine spiral ornamentation and, usually, with two prominent ribs in the upper part of the base. However, the shell of *Erratohilda* Gründel, 1997 is slightly siphonostomatous, and its aperture has only the basal bend, whereas the shells of *Bathraspira* Cossmann, 1906 has a siphonal angulation that sometimes looks like a wide semicircular canal. However, in the Oxfordian of European Russia, there is a mathildid species, *Cerithium asperum* Rouillier, 1846 (original data), which is very similar to the cretaceous *Bathraspira*. I sup-

pose that *Bathraspira* Cossmann, 1906 is a descendant of this species.

The genus *Nerineopsis* Cossmann, 1906 [= *Diatrypesus* Tomlin, 1929] is very similar to members of the families Turritellidae and Mathildidae and, probably, can be assigned to one of them. It is more likely that it belongs to the family Mathildidae, because Cossmann (1913) has assigned some species of the genus *Clathrobaculus* Cossmann, 1912 (undoubted Mathildidae) to this genus. On the other hand, the type species of the genus is similar to Cretaceous representatives of the family Turritellidae, i.e., to the genus *Caucasella* Hacobjan, 1972. Usually, its species have rows of densely spaced tubercles rather than solid ribs. However, Cossmann also placed some species with tuberculate ornamentation in the genus *Nerineopsis* Cossmann, 1906.

The genus *Rostrocerithium* Cossmann, 1906 is possibly a member of the family Coelostylinidae, but no ornamented forms are currently known in this family. The genus *Cerithinella* Gemmellaro, 1878 certainly belongs to the Nerineoidea because of the presence of a selenizone bordered by a row of tubercles under the suture. The genus *Urgonella* Cossmann, 1916 is similar to mollusks, which are typical for the brackish-water Wealden deposits of France (see Favre and Richard, 1927).

Two genera of Paleozoic mollusks have been placed in the Procerithiidae in *Treatise on Invertebrate Paleontology*, i.e., *Kinishbia* Winters, 1956 from the Upper Permian of the United States and *Spanionema* Whidborne, 1891 from the Middle Devonian of Great Britain. Both genera are significantly older than the other Procerithiidae. They are similar to members of the family only in having a turriculate shell, while the pattern of ornamentation differs greatly. I have no data on the protoconch structure of *Spanionema* Whidborne, 1891 and *Kinishbia* Winters, 1956. Thus, I propose to remove these genera from the composition of the family Procerithiidae.

Since the systematic compilation by Wenz, two other genera from the Jurassic of France have been assigned to the family Procerithiidae, i.e., *Campanilopsis* P.-H. Fischer, 1956 and *Martignyella* J.-C. Fischer, 1969. Both genera differ from the typical Procerithiidae in the larger size (over 5 cm), the pattern of ornamentation, and the aperture with a separate parietal channel. Their type species, i.e., *Martignyella semiexcavata* (Cossmann, 1885) and *Campanilopsis margaritifera* (d'Archiac, 1843), have a spiral thickening under the suture (smooth in the former species and tuberculate in the latter). The whorls appear slightly concave because of this thickening. The rest of the whorl surface bears numerous spiral threads or several spiral bands. The Cretaceous genus *Cimolilopsis* Calzada, 1997 shows a similar morphology. Calzada placed this genus in the subfamily Metacerithiinae. The type species of the genus

is *Cerithium gassendii* Coquand, 1865 from the Aptian of Spain. It has a large turriculate shell (55–65 mm in height), with a slightly gradate spire. This gradate profile is formed by a spiral thickening running in the upper part of the whorls. The shell has no other ornamentation. The whorls are narrow in cross section, the aperture is unknown. All these features, i.e., the large size of shells, the spiral thickening in the upper part of whorls that results in their concave profile, and the absence of the ornamentation, show that *Cimolilopsis* Calzada, 1997 is close to *Campanilopsis* P.-H. Fischer, 1956 and *Martignyella* J.-C. Fischer, 1969. The supposed phylogenetic affinity between *Cimolilopsis* Calzada, 1997 and *Metacerithium* Cossmann, 1906 is in serious doubt.

#### *The Morphological Differences between the Family Cryptaulacidae and Some Other Families of Cerithioidei*

As previously mentioned in the beginning of the chapter, Gründel has (1976a) assigned the recent genera *Argyropeza* Melvill et Standen, 1901 and *Varicopeza* Gründel, 1976 to his newly erected subfamily Cryptaulinae. Indeed, this subfamily shows a striking similarity in protoconch and teleoconch morphology to the Jurassic *Cryptaulax* sensu stricto and *Infacerithium* sensu stricto, which also have been illustrated in this work. In the same publication, Gründel regarded the subfamily Bittiinae Cossmann as a synonym of Procerithiinae. However, the above-mentioned morphological features of the species that I place here in the family Procerithiidae clearly show that Bittiinae and Procerithiinae are not synonyms and originate from different ancestors. On the other hand, the protoconch and early teleoconch morphology suggests that the Bittiinae can fit in the Cryptaulacidae quite well. However, the similarity of the Cenozoic Procerithiinae and Cryptaulacinae (sensu Gründel, 1976a) to the Jurassic Cryptaulacidae (in my sense) may be deceptive. Undoubtedly, the morphology and ontogenetic development of the protoconch and the change in ornamentation on the protoconch–teleoconch boundary are the main unifying features of the Cryptaulacidae in the present study. However, similar features are present in some younger members of the Cerithioidei. Hence, they are inadequate to characterize the family. This is also evident from the studies of larval morphology of other families of this suborder (see Kowalke, 1998). The protoconch morphology of the family Cassiopidae Kollmann is almost unknown, except in a few species. According to Kowalke (1998), the protoconch of *Cassiope kefersteini* (Münster, 1844) (Upper Cretaceous) passes through two stages, the first is characterized by smooth whorls; and the second, by bicarinate whorls. The protoconch of another member of the family, *Paraglauconia tricarinata* (Sowerby, 1836), is composed of several smooth whorls (Cleevely and Morris, 1988) and

clearly differs from the protoconchs of the Cryptaulacidae. In both species of the family Cassiopidae, the morphology of postlarval whorls differs greatly from that of the Cryptaulacidae. A similar protoconch structure (smooth whorls followed by bicarinate whorls) was shown (Kowalke, 1998) in some representatives of the family Potamididae H. Adams et A. Adams, i.e., *Granulolabium muensteri* (Keferstein, 1829) and *Echinobathra stillans* (Vidal, 1874) (Upper Cretaceous). These and many other potamidids considerably differ from the cryptaulacids in the shell morphology and in the aperture with a well-developed siphonal groove (the latter is absent among the Cryptaulacinae but present at the initial stage of the Exelissinae).

Gründel (1976b) provided data on the juvenile morphology of the family Diastomidae Cossmann, 1895. The surprising thing is that Gründel almost simultaneously described the family Procerithiidae with the subfamilies Procerithiinae and Cryptaulacinae (see Gründel, 1976a); claimed the synonymy of and between the family Procerithiidae to Diastomidae; reduced the subfamilies Procerithiinae and Bittiinae to Diastominae; and splits the subfamily Diastominae into two tribes, i.e., Procerithiini and Diastomini (Gründel, 1976b). His papers give an accurate account of the early shell development in the Diastomidae. The protoconch of the Diastominae first evolved a smooth whorl followed by whorls with two or three ribs and subsequently several more ribs. A distinct boundary between the protoconch and teleoconch is absent, the larval ornamentation gradually transforms into the postlarval and becomes more elaborate, and, finally, the collabral elements appear. The protoconch of his Fenellinae [= Scaliolidae Jousseau] consists of several smooth whorls, sometimes with a fine ribs in the middle. The boundary between the protoconch and teleoconch is distinct. The teleoconch ornamentation is not a continuation of the protoconch ornamentation: it develops independently. Thus, the family Diastomidae is clearly distinguishable from the Cryptaulacidae.

The families Melanopsidae H. Adams et A. Adams, Planaxidae Gray, Thiaridae Troschel, and Batillariidae Houbriek easily differ from the Cryptaulacidae in the pattern of protoconch, developmental pattern of the postlarval ornamentation, and general shell morphology (see Kowalke, 1998).

A deep-water family Abysochrysidae Tomlin includes a single genus *Abysochrysos* Tomlin, 1927. Its systematic position was uncertain for a long time, and it was tentatively considered within the superfamily Cerithiacea. Finally, Houbriek (1979) assumed that the Abysochrysidae and Loxonematidae are related; thus, the family was tentatively placed within the superfamily Loxonematacea. To confirm or refute this assumption, we should consider the morphology of juvenile shell of *Abysochrysos*. The species *A. melvilli* (Schepman, 1909) and *A. melanoides* Tomlin, 1927 have multispiral turriculate shells composed of 13–

16 whorls. The shell of *A. melvilli* is ornamented by folds with tubercles on their upper and lower sides. I assume that these tubercles are rudimentary remains of the intersections of folds and spiral ribs that were well-developed in the ancestors of the recent *Abysochrysos* Tomlin, 1927. The presence of fine ribs on the earlier whorls supports this assumption. In addition, a rib running through the upper row of tubercles is visible even on the later whorls of *A. melvilli* (Houbriek, 1979, text-fig. 7h). The spiral ornamentation is much more developed in *A. melanoides*, but this species lacks the tubercles. The upper rib that is equivalent to that in *A. melvilli* is most prominent. The ribs are accompanied by several finer ribs on the lower side of the whorls (Houbriek, 1979, text-figs. 1d, 1f, 1g, 1i). The ribs disappear on later whorls. Houbriek (1979) described a smooth protoconch composed of half whorl or one complete whorl for both species. Unfortunately, the magnification of shells in the figures is inadequate to attest to this fact. However, one can see that protoconchs of the shells are undoubtedly broken off. At the same time, Houbriek noted that the early whorls were eroded in all of the shells studied. Thus, the question arises as to whether Houbriek meant the early whorls of the teleoconch that are worn down to the point of being smooth, or the truly well-preserved end of the protoconch. On the basis of similarity in shells, Houbriek suggested that the genus *Abysochrysos* Tomlin, 1927 is related to members of the family Loxonematidae. However, the presence of spiral ornamentation among the species of *Abysochrysos* Tomlin, 1927 refutes this suggestion. As a rule, the last whorls of the shell are most variable in morphology. Thus, the ornamentation first appears on the last whorls. If a new feature is advantageous, it can evolve on progressively earlier whorls. Thus, I believe that the juvenile spiral ornamentation of *Abysochrysos* Tomlin, 1927 is rudimentary ornamentation inherited from an ancestor with prominent spiral ribs.

As for the possible emergence of spiral ornamentation in the family Loxonematidae, it will suffice to mention that the family Procerithiidae supposedly evolved from the Loxonematidae. In this case, the spiral ornamentation first appeared as very weak ribs on the last whorls of the shell. Later, it became more prominent and evolved on the progressively earlier teleoconch whorls. It is difficult to determine the direct ancestor of *Abysochrysos* Tomlin, 1927; however, if we reject the Loxonematidae, the only possible ancestor will be the subgenus *Cryptaulax* (*Pseudocerithium*) with a similar multispiral turriculate shell and flattened whorls. But *Cryptaulax* (*Pseudocerithium*) has well-developed spiral ornamentation. Possibly this form evolved into *Abysochrysos* Tomlin, 1927 through some still unknown intermediate taxa.

Finally, it is interesting to discuss the phylogenetic relationships and morphological differences between

the members of Cryptaulacidae and Cerithiinae. Houbriek (1992) made a taxonomic revision of the Indo-Pacific species of the genus *Cerithium* Bruguière, 1789 and provided a great body of illustrative material for comparison with the Cryptaulacidae. He synonymized numerous taxa of the subfamily Cerithiinae with the genus *Cerithium* Bruguière, 1789; thus, this genus contains species that differ considerably in morphology. Houbriek himself noted that shell morphology varies considerably from species to species, but he emphasized that each of them had a similar anatomy. I cannot agree with this statement, since the work contains many cases of polymorphic species that were established by Houbriek on the basis of the shell material alone, while the soft body has not been preserved. It is impossible to claim the similarity of anatomy in conchologically different species, if the soft bodies are unknown! Some species in Houbriek's paper are strikingly similar to members of the family Cryptaulacidae in the morphology of protoconch and early teleoconch, i.e., *Cerithium abditum* Houbriek, 1992; *C. flemischi* Martin, 1933; *C. gloriosum* Houbriek, 1992; etc. The protoconch morphology varies greatly from species to species of the genus; thus, Houbriek noted that it is of little systematic significance (Houbriek, 1980a, pp. 4–5). In many species of the genus *Cerithium* Bruguière, 1789, as well as in members of the Cryptaulacidae, the protoconch evolves through two distinct stages: first, the development of the initial smooth whorls and, second, the development of the bicarinate whorls. However, there are a number of differences between the genus *Cerithium* and the family Cryptaulacidae. Many species of *Cerithium* have a scalloped outer lip (the spiral ribs become stronger near the aperture and project beyond its margin and look like teeth). In Cryptaulacidae, by contrast, the spiral ornamentation flattens near the aperture and, thus, their outer lip is almost even. The lips are thickened in many *Cerithium* species (they are thin in the Cryptaulacidae), or the outer lip is explanate (which is atypical of Cryptaulacidae). The main distinctive morphological feature of the genus *Cerithium* is the presence of a well-developed siphonal canal, and only a few species have a deep notch instead of this canal. The canal runs out beyond the aperture and looks like a half-closed tube. Almost all of the species have a well-developed parietal canal, which is unknown in the Cryptaulacidae.

The members of the subfamily Bittiinae Cossmann show considerable similarity to the family Cryptaulacidae. The shells of Bittiinae are very similar to *Cryptaulax* (*Neocryptaulax*) Gerasimov, 1992. This subgenus is characterized by an aperture in which both lips are slightly explanate and no morphological features occur in place of the siphons (Gerasimov, 1992, pl. 22, fig. 7). In Bittiinae the aperture evolves a short angular canal, notch, or groove, i.e., its basal part has a more advanced structure than that of the majority of the

Cryptaulacidae. Although protoconchs of Bittiinae illustrated by Gründel (1976a) in many respects are similar to those of Cryptaulacidae, they are usually easily distinguishable.

The above-mentioned genus *Varicopeza* Gründel, 1976, which was originally placed by Gründel (1976a) in the subfamily Cryptaulacinae, was described in detail by Houbriek (1980b). The ontogeny and the pattern of larval and postlarval ornamentation of the genus are identical to those of the genera *Cryptaulax* sensu stricto and *Microcerithium* gen. nov.; however, the apertural structure of *Varicopeza* Gründel, 1976 is quite different from that of the Cryptaulacinae and even Exelissinae in that its aperture has a very large siphonal groove that is inclined with respect to the columella.

The genus *Argyropeza* Melvill et Standen, 1901 is still closer to the family Cryptaulacidae in morphology. Its species were described in detail and extensively illustrated by Houbriek (1980a). I cannot see any significant differences between *Argyropeza* and *Cryptaulax* sensu stricto, and the combination of its morphological features suggests that *Argyropeza* should be placed in the family Cryptaulacidae.

The great morphological similarity between the Triassic–Jurassic members of the family Cryptaulacidae and other representatives of the suborder Cerithioidei, especially with the above-mentioned Quaternary Cerithiidae, suggests that the taxonomy of Cerithioidea cannot be based merely on protoconch morphology. They also show a great similarity in teleoconch morphology. Thus, I refrain from including some Cenozoic families (subfamilies) of Cerithiacea in the Cryptaulacidae, as was suggested by Gründel (1976a, 1976b), and from including some Cenozoic and Recent taxa of Cerithiacea in the Cryptaulacidae on the basis of the similarity in larval and postlarval morphology of their shells. At the same time, I believe that the family Cryptaulacidae should be separated as a distinct taxon combining several species group that can be clearly distinguished from other gastropods of the same age. The family Cryptaulacidae, as compared with the Cerithiidae, differs only in the more primitive aperture with a poorly developed siphonal canal and in the absence of a parietal canal. However, some members of the Cerithiinae and Bittiinae with simpler apertures differ from Cryptaulacidae in different arrays of characters each of which, in fact, have the same level of taxonomic significance as the features distinguishing genera within these three groups. A taxonomy of the Cerithioidea based merely on protoconch morphology fails. A more sound and natural taxonomy of the Mesozoic and Cenozoic Cerithiacea may be possible only on the basis of the analysis of the stratigraphical sequences of the species and their phylogenetic relationships. A thorough phylogenetic analysis considering all available morphological features is the sole way to accomplish this task.

### Families Purpurinidae and Purpuroideidae

The family Purpurinidae was established by Zittel (1895) with the following diagnosis: "Thick-walled shells with gradate spire, nacreous layer is absent. The whorls are angulated and with a flat suture in the upper part. The angulation is often ornamented by tubercles, the last whorl large. The aperture is oval, with a canal." He put the following genera within the family: *Scalites* Koninck, 1881; *Trachydomia* Meek et Worthen, 1866; *Pseudoscalites* Kittl, 1894; *Tretospira* Koken, 1892; *Purpurina* d'Orbigny, 1850 emend. Deslongchamps, 1860; *Purpuroidea* Lycett, 1848; *Brachytrema* Morris et Lycett, 1850; and *Tomochelilus* Gemmellaro, 1878.

Cossmann (1906) altered the composition of the family Purpurinidae as follows: *Purpurina* d'Orbigny, 1850 emend. Deslongchamps, 1860 (with the subgenera *Purpurina* sensu stricto, *Eucycloidea* Hudleston, 1888, and *Pseudalaria* Hudleston, 1888); *Ochetochilus* Cossmann, 1899; *Purpuroidea* Lycett, 1848; and *Centrogonia* Cossmann, 1899. Later, Cossmann (1909) proposed a new replacement name (*Cimoliocentrum* Cossmann, 1909) instead of *Centrogonia* Cossmann, 1899, since the latter was a junior homonym of a generic name from the insect order Hymenoptera (Stål, 1869). In addition, he enlarged the family by the following taxa: *Angularia* Koken, 1892 (subgenus *Angularia* sensu stricto [with sections *Angularia* sensu stricto and *Pseudoscalites* Kittl, 1894], and *Moerckeia* J. Böhm, 1895); *Tretospira* Koken, 1892; and *Kittlia* Cossmann, 1909 [pro *Ptychostoma* Laube, 1868].

Wenz (1939) retained all of the Triassic and Jurassic taxa suggested by Cossmann and introduced some other forms in the family Purpurinidae. Thus, the composition of the Purpurinidae was the following: *Tretospira* Koken, 1892; *Angularia* Koken, 1892 (with subgenera *Angularia* sensu stricto, *Pseudoscalites* Kittl, 1894, and *Moerckeia* J. Böhm, 1895); *Aristerostrophia* Broili, 1907; *Gonioconcha* Bonarelli, 1921; *Purpurina* d'Orbigny, 1850 emend. Deslongchamps, 1860 (with the subgenera *Purpurina* sensu stricto, *Eucycloidea* Hudleston, 1888, and *Pseudalaria* Hudleston, 1888); *Ochetochilus* Cossmann, 1899; *Purpuroidea* Lycett, 1848; and *Parangularia* Kutassy, 1937. He reestablished the validity of the genus *Ptychostoma* Laube, 1868, which had been treated as preoccupied by Cossmann, and tentatively assigned four more genera to the family Purpurinidae; i.e., *Coronatica* Blanckenhorn, 1927; *Cimoliocentrum* Cossmann, 1909; *Proper-murchisonia* Gregorio, 1896; and *Pseudomurchisonia* Koken, 1896.

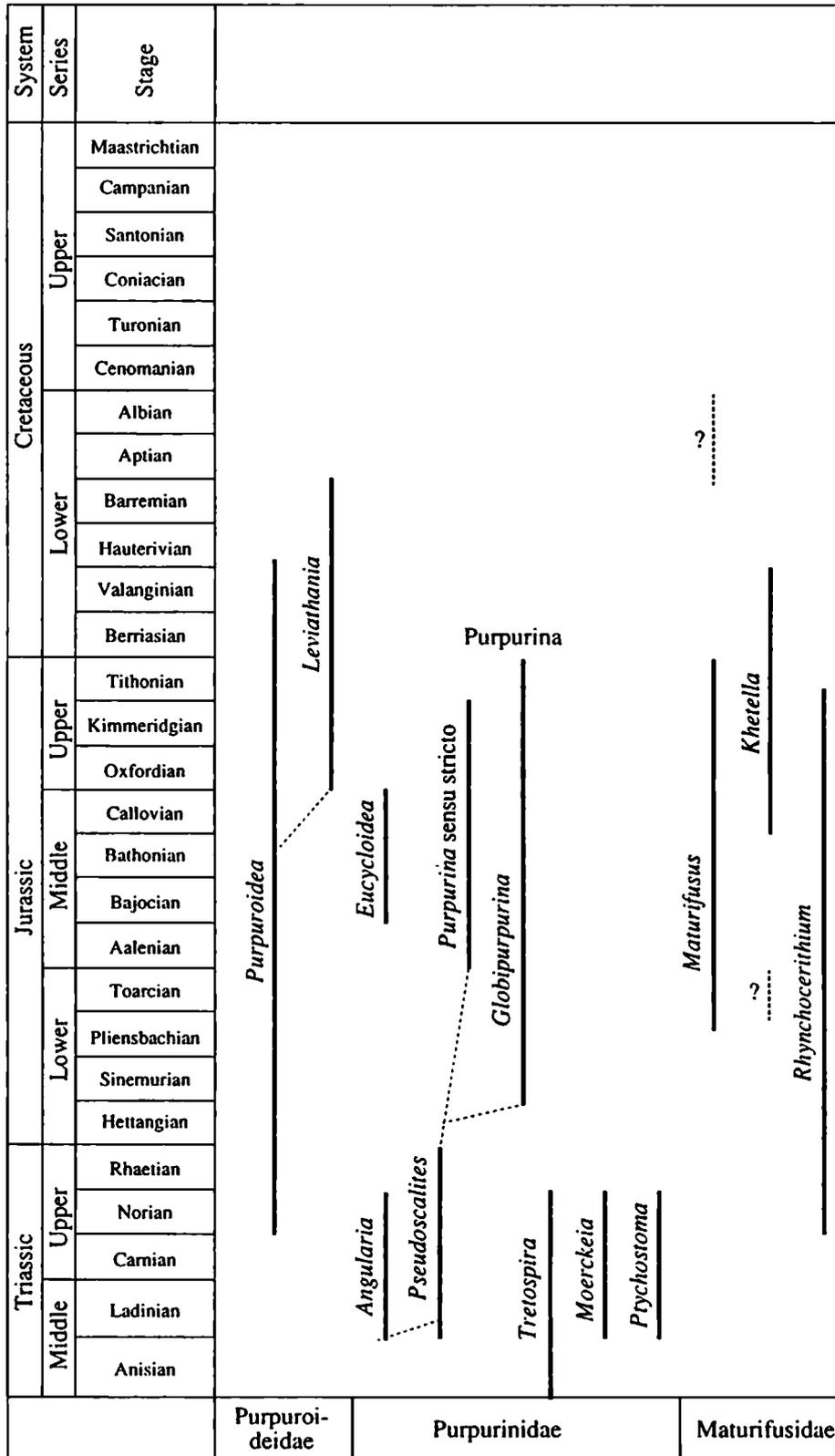
In later publications the composition of the family remained unchanged, except for the addition of the genus *Andangularia* Haas, 1953 (Haas, 1953).

Korotkov and Golovinova (1982) were the first to question the monophyly of the family Purpurinidae. They suggested that the genera *Leviathania* Pčelintsev, 1927 and *Purpuroidea* Lycett, 1848 belonged in a separate family. In addition, these authors pointed out the

"synthetic nature" of the Purpurinidae as a whole. There is actually a morphological inconsistency between different genera of the family, contradicting their assignment to a single family. The shell of the type genus of the family (*Purpurina* d'Orbigny) has a slightly siphonostomatous aperture, explanate lips, and a carina or angulation running along the upper sides of the whorls. The genus *Purpuroidea* Lycett, 1848 is distinguished by the distinctly siphonostomatous shell (the siphonal canal is short but deep) and by the size being significantly greater than in typical purpurinids. The genus *Leviathania* Pčelintsev, 1927 is very similar in morphology to the genus *Purpuroidea* Lycett, 1848, but its aperture is unknown. I suggest the establishment of a new family *Purpuroideidae* fam. nov. for these two genera (Table 2). The species *Tretospira carinata* (Terquem) from the Hettangian of France fits within the family Purpuroideidae fam. nov. quite well, especially in the genus *Leviathania* Pčelintsev, 1927. In the general appearance of the shell and last whorl morphology, it is very similar to *L. leviathan* (Pictet et Campiche, 1864). The species does not belong to the genus *Tretospira*, and the oldest species of *Leviathania* are known only from the Oxfordian. Thus, the generic position of *T. carinata* is unclear.

The genus *Purpuroidea* differs from *Leviathania* in having a row of large tubercles along the shoulder of the whorl. Sometimes, the tubercles cover the rest of the whorl surface, or coarse ribs can appear. The whorls are convex, lack prominent carinae, and attain their maximum width at the upper row of tubercles. Some species of *Leviathania* with large tubercles along the carina were referred by Golovinova and Korotkov (1986) to a new genus *Turboleviathania* Golovinova et Korotkov, 1986 (the type species *L. gerassimovi* Pčelintsev, 1931). Such species are marked by asterisks in the composition of the genus *Leviathania*. These authors mentioned the following characters that distinguish the genus *Turboleviathania* from the genus *Leviathania*: the greater shell size, tuberculate carina, wide last whorl, and different pattern of the shoulder platform (but without any detailed comparison). Actually, not all of the species that I have assigned to the genus *Leviathania* possess these distinguishing characters. It is worth noting, however, that the Cretaceous and Upper Jurassic species of *Leviathania* and *Turboleviathania* are preserved rather poorly, mainly as internal moulds (e.g., all *Turboleviathania* species). Hence, the presence or absence of tubercles is a rather unreliable character. Only the type species of the genus *Turboleviathania* and *L. beschterekensis* Golovinova, 1982 have prominent tubercles on the carinae, whereas the other species show indistinct or even dubious tubercles (at least, they are unidentifiable in photographs). The difference in size is also not a very safe criterion for a generic distinction. For instance, there is a species, *L. gigantea* (Makowsky, 1874), that has a huge shell, the last whorl of which lacks tubercles and is very sim-

**Table 2.** Stratigraphic distribution and phylogeny of the families Purpuroideidae, Purpurinidae, and Maturifusidae



ilar to that of *L. leviathan* (Pictet et Campiche). The shell size is comparable with the largest shells of *Turboleviathania*. Korotkov and Golovinova noted that some *Turboleviathania* are similar to *Purpuroidea* in shell shape and, consequently, to *Leviathania*. In addition, they mentioned the difference in the aperture structure in *Turboleviathania* and *Purpuroidea*. Since the aperture is unknown in *Turboleviathania* (and in *Leviathania*), I consider this comparison groundless.

Nevertheless, the attempt to split the later members of Purpuroideidae is valid, but it should be made more carefully and on the basis of more comprehensive material. For the time being, I suggest that the genera *Purpuroidea* and *Leviathania* be accepted with the composition given below.

Genus *Leviathania* Pčelintsev, 1927 with \**L. beschtereckensis* Golovinova, 1982 (Lower Valanginian of Crimea); \**L. borissjaki* Pčelintsev, 1931 (Valanginian of Crimea); \**L. gerassimovi* Pčelintsev, 1927 (Valanginian of Crimea); *L. gigantea* Makowsky, 1874 (Oxfordian of Germany); *L. leviathan* (Pictet et Campiche, 1864) (Valanginian of France and Portugal); *L. petrovensis* Pčelintsev, 1931 (Valanginian of Crimea); *L. pseudoleviathan* (Choffat, 1886) (Barremian of Portugal); *L. subnodosa* (Roemer, 1836) (Upper Kimmeridgian of Germany); and \**L. terrenaisensis* Pčelintsev, 1931 (Tithonian of Crimea).

Genus *Purpuroidea* Lycett, 1848 with *P. bicincta* (Piette, 1856) (Bathonian of France); *P. carpathica* Zittel, 1873 (Upper Tithonian of Europe, Tithonian of Turkmenistan); *P. deserti* H. Douville, 1925 (Callovian of the Sinai Peninsula, Egypt); *P. gigas* (Etallon, 1861) (Upper Kimmeridgian of France); *P. glabra* Morris et Lycett, 1850 (Bathonian–Lower Callovian of England and France); *P. gracilis* Loriol, 1886 (Lower Kimmeridgian of France); *P. insignis* Lycett, 1863 (Lower Callovian of England); *P. lapierrea* (Buvignier, 1843) (Oxfordian of France); *P. lorioli* Cossmann, 1913 (Kimmeridgian of France); *P. matheyi* Loriol, 1889 (Lower–Middle Oxfordian of France); *P. minax* (Piette, 1856) (Bathonian of France); *P. moreausea* (Buvignier, 1843) (Oxfordian of France); *P. multifilosa* (Cossmann, 1899) (Callovian of France); *P. neumayri* Pčelintsev, 1926 (Middle–Upper Oxfordian of Ciscaucasia); *P. nodulata* (Young et Bird, 1822) (after Hudleston, 1880a, Lower–Middle Oxfordian of England); *P. taurica* Pčelintsev, 1931 (Upper Oxfordian of Crimea); *P. turbinoidea* (Buvignier, 1843) (Oxfordian of France); *P. ufrensis* Korotkov, 1972 (Lower Valanginian of Kuba-Dag, Turkmenistan); and ?*P. longa* Pčelintsev, 1927 (Valanginian of Caucasus). In addition, several species from the Norian of Hungary (Kutassy, 1927) were assigned to *Purpuroidea*, i.e., *P. excelsior* Koken, 1897, *P. ferenczii* Kutassy, 1927 and *P. taramellii* (Stoppani, 1865). Like the Jurassic species of the genus, these Triassic forms have large shells with a row of tubercles along the shoulder. In addition, *P. ferenczii* is ornamented by ribs, whereas

*P. taramellii* is ornamented by ribs and supplementary rows of tubercles. Since their morphology fits well into the genus *Purpuroidea*, I include them in the composition of the genus.

Thus, the family Purpuroideidae fam. nov. is characterized by large or extremely large multispiral shells that lack an umbilicus, and possess a siphonostomatous aperture bearing a short half-closed siphonal canal.

The family *Purpurinidae* should include the following genera: *Angularia* Koken, 1892; *Eucycloidea* Hudleston, 1888; *Moerckeia* J. Böhm, 1895; *Pseudoscalites* Kittl, 1894; *Purpurina* d'Orbigny, 1850 emend. Deslongchamps, 1860 (with the subgenera *Purpurina* sensu stricto and *Globipurpurina* subgen. nov.); *Tretospira* Koken, 1892; and, probably, *Ptychostoma* Laube, 1868 (Table 2). It is desirable to remove all the other taxa from the family composition. The genus *Aristerotrophia* Broili, 1907 is similar to Zygopleuridae and has nothing in common with Purpurinidae. The genus *Cimoliocentrum* Cossmann, 1909 has been placed in the Cryptaulacidae (see above). It is known from the Late Jurassic–Early Cretaceous and represents a separate lineage of the genus *Exelissa* Piette, 1860 that is adapted for reef habitats. The genus *Coronatica* Blanckenhorn, 1927 is probably a member of the family Ampullariidae. *Pseudomurchisonia* Koken, 1896 should be placed in Murchisonioidea, since its type species bears a distinct selenizone along the periphery of the whorls. The systematic position of the genera *Propermurchisonia* Gregorio, 1896; *Pseudalaria* Hudleston, 1888; and *Ochetochilus* Cossmann, 1899 remains uncertain. The diagnosis of the genus *Gonioconcha* Bonarelli, 1921 is obscure because of the poorly preserved type material.

The upper angulation of the whorl, sometimes carinate, is typical for shells of the family Purpurinidae. The spiral ornamentation is present above and below the angulation and varies from fine threads to ribs. In addition, the collabral ornamentation represented by threads or folds is usually present. The spiral elements located above the angulation are usually weaker. The youngest members of the family come from the Tithonian.

There are some problems concerning the understanding of the genus *Purpurina* d'Orbigny, 1850 emend. Deslongchamps, 1860. The name was introduced by d'Orbigny (1850) for the Jurassic species. He provided a very brief and rather vague diagnosis for the genus: "Aperture large, with the single anterior furrow corresponding the semicircular notch of the genus *Purpura*. Internal margin is not flattened." he placed the following species in the genus: *Purpurina elegantula* d'Orbigny, 1850; *P. pulchella* d'Orbigny, 1850; *Fusus nassoides* Eudes-Deslongchamps, 1842 from the Bathonian–Bajocian (p. 270); *Fusus thorenti* d'Archiac, 1843; *Buccinum unilineatum* Sowerby, 1825 from the Bathonian (p. 302); *Purpurina brevis* d'Orbigny, 1850; *Buccinum pumilum* Sowerby, 1840 from the Callovian (p. 334); *Purpura lapierrea* Buvignier, 1843; and *Pur-*

*pura moreausia* Buvignier, 1843 from the Oxfordian (p. 357). In the atlas *Paléontologie française...* (d'Orbigny, 1850–1860), he illustrated many species under the name of *Purpurina*, while they were not mentioned in the text. At the same time, these species were assigned to the genus *Turbo* in the book *Prodrome de paléontologie* (d'Orbigny, 1850). These are the species described by d'Orbigny: *P. patroclus*, *P. philiasa*, *P. ornata*, *P. bathis*, *P. belia*, *P. bellona*, *P. bianor* and *P. bixa*. In the recent understanding, they are members of the families Purpurinidae (*Purpurina* and *Eucycloidea*) and Eucyclinidae (*Eucyclus*).

Thus, there is contradiction in the concept of the genus used by d'Orbigny. According to *Prodrome de paléontologie* all of the species are more or less siphonostomatous, while the *Paléontologie française...* suggests that almost all of them are holostomatous. Deslongchamps (1860) revised the position and content of the genus and reassigned numerous species of *Purpurina* to other genera, i.e., *Purpuroidea* Lycett, 1848; *Tubifer* Piette, 1856; *Eucyclus* Deslongchamps, 1860; *Littorina* Ferussac, 1821; and *Brachytrema* Morris et Lycett, 1850. He suggested a new diagnosis of the genus and designated a type species, *Turbo bellona* d'Orbigny, 1850. Although Deslongchamps' definition does not fit in the original diagnosis by d'Orbigny, I believe that his understanding of the genus remains valid for two reasons: the distinctness of Deslongchamps' diagnosis and the long practice of treating the genus in the sense of Deslongchamps.

In papers on the Triassic gastropods by Kittl (1892, 1894, 1895, 1899, 1912), there are several species assigned to the genera *Purpuroidea* and *Purpurina*, i.g., *Purpuroidea cerithiformis* Kittl, 1894; *P. subcerithiformis* Kittl, 1895; *P. crassenodosa* Klipstein in Kittl, 1894; *P. applanata* Kittl, 1894; *P. baconica* Kittl, 1912; and *Purpurina pleurotomaria* (Münster, 1841). All of them come from the St. Cassian Formation, Marmolata Limestone, and Triassic strata of the Bakony Mountains and do not belong to the genera *Purpuroidea* or *Purpurina*. They have small (2–4 cm high) low-turriculate shells with a slightly siphonostomatous aperture. The species *P. pleurotomaria* differs from *Purpurina* in the turriculate shell. Most of the species, except for *P. cerithiformis* and *P. subcerithiformis*, the position of which is unclear, can be assigned to Purpurinidae, but they do not fit any known genus. Only *Purpuroidea baconica*, which differs from all the other species in the larger tubercles, can be confidently assigned to *Pseudoscalites*. The species *Purpurina plicata* Kutassy, 1927 from the Norian of Hungary should also be placed in this genus.

Hudleston (1887) separated two groups in the genus *Purpurina*: *P. inflata* and *P. bellona*. Later, these groups were not used. However, I support Hudleston's opinion and consider his groups as two subgenera of *Purpurina*, i.e., "*Bellona group*" is the subgenus *Purpurina* sensu stricto, while "*Inflata group*" is the sub-

genus *Globipurpurina* subgen. nov. The first group, including the type species of the genus, is characterized by a higher spire and less involute whorls with a shoulder carination. Both the entire shell and last whorl are conical, the aperture is oval with a slightly concave flaring of the basal margin. The members of *Globipurpurina* subgen. nov. have spherical (rarely approaching to conical) shells. The last whorl has hemispherical or conical shape. The shoulder angulation is less pronounced than that of *Purpurina* sensu stricto and does not project beyond the shell contour. The basal flaring of the aperture is less developed, more narrow, and almost flat. More detailed descriptions of the subgenera are given in Systematic Paleontology.

Since I have no data for revising most genera of the family Purpurinidae, their diagnoses and composition here remain unchanged. I will discuss only three genera: *Andangularia* Haas, 1953; *Pseudoscalites* Kittl, 1894; and *Angularia* Koken, 1892. The last two genera are fairly similar morphologically. Both of them include conical shells with a gradate spire ornamented by growth lines (*Angularia*) or by tubercles along the carina, usually accompanied by faint folds and fine spiral ribs (*Pseudoscalites*). In addition, *Angularia* has an angulation, and *Pseudoscalites* has a sharp carina, which is frequently turned upwards. Thus, the presence of collabral and spiral ornamentation and sharp carina clearly distinguish the genus *Pseudoscalites* from *Angularia*.

The genus *Pseudoscalites* is, probably, a direct ancestor of *Purpurina* sensu stricto (see Table 2). This assumption is supported by the similarity in shell appearance, pattern of whorls, and the presence of spiral and collabral ornamentation. *Pseudoscalites* differs from *Purpurina* sensu stricto in the less prominent ornamentation, higher spire, and somewhat different pattern of aperture. The last feature is clearly visible on the shells of *Pseudoscalites armatus* (Stoppani, 1857) and *P. collariatus* Read (see Kittl, 1899; Broili, 1907). The aperture is pyriform, widens downwards, and has a rounded basal margin without flaring. The aperture of *Purpurina* sensu stricto is oval, evenly convex, with distinct flaring of the basal margin.

Consequently, we can conclude that the lineage *Pseudoscalites* → *Purpurina* sensu stricto shows a trend toward the increase in the collabral and spiral ornamentation and formation of the apertural structures in the anterior siphon.

The form described as *Pseudoscalites* n. sp. by Hass (1953) is, in fact, a member of the family Mathildidae. It has a wide carinate shell similar to that of the Jurassic species of *Erratohilda* Gröndel. The Upper Triassic form *Angularia* sp. (Nützel and Stenowbary-Daryan, 1999) with well-developed folds probably represents a new species of *Pseudoscalites*.

The genus *Andangularia* Haas, 1953 was erected to include the species *Pseudoscalites subarmatus* Jaworski and *Andangularia* aff. *subartmae* Haas from the

Upper Triassic of South America. The genus was originally placed within the family Purpurinidae (Haas, 1953). It is similar to *Pseudoscalites* in having a gradate spire and tuberculate carina. However, the species have a multispiral shell consisting of seven or eight whorls and different pattern of siphonostomatous aperture, i.e., they have a basal angulation of the aperture, as in the Procerithiidae-like or Loxonematidae-like fashion, which is absent from any other member of Purpurinidae. Thus, I suspect that it belongs to the superfamily Loxonematoidea.

Unfortunately, it is impossible to make a comparative analysis of the protoconchs of the Purpurinidae, since for the present time they are described only for two species of the family, i.e., *Purpurina* (*Globipurpurina*) *inflata* Tawney, 1873 (see Gründel, 1990a) and *P. (G.) plicata* (Quenstedt, 1858) (the present study). Any morphogenetic trends are also obscure (except for the lineage *Pseudoscalites* → *Purpurina* sensu stricto). The ancestors of the family or its descendants (if present) are unknown. Even the evidence for the monophyly of the family is not very convincing.

### Family Cerithiopsidae

Rouillier described the species *Cerithium renardi* from the Oxfordian in the vicinity of Moscow (Rouillier and Vosinsky, 1849). Much later, Gerasimov (1992) published the results of his study of an extensive gastropod collection that included description of three species of the genus *Procerithium* Cossmann, 1902, i.e., *P. (Rhabdocolpus) renardi* (Rouillier, 1849); *P. (R.) pumilum* Gerasimov, 1992; and *P. (R.) brateevense* Gerasimov, 1992. I studied the teleoconch of these species and came to the conclusion that they are very similar to *Cosmocerithium nysti* (d'Archiac, 1843) from the Bathonian of France. The genus *Cosmocerithium* Cossmann, 1906 was established by Cossmann (1906) as a subgenus of *Procerithium* Cossmann, 1902. *Cerithium nysti* d'Archiac was designated as the type species for the subgenus. However, the descriptions of Cossmann (1885, 1906, 1912) differ considerably from the material illustrated by d'Archiac (1843, p. 384, pl. 31, fig. 7) and Piette (1857, pl. 8, fig. 1). I studied the species *Cosmocerithium renardi* (Rouillier), *C. brateevense* (Gerasimov), *C. pumilum* (Gerasimov), and *C. contiae* Guzhov, 2002 and found out (Guzhov, 2002b) that they are close to *C. nysti* sensu d'Archiac. All of them clearly differ from *C. nysti* sensu Cossmann in having finely reticulate ornament, flattened whorls, and rhomboid aperture with a groove. At the same time, these features are typical for *C. nysti* sensu d'Archiac. Gründel (1997) presented Cossmann's opinion in his monographic work on the type species of gastropods from the Jurassic of France. Since d'Archiac and Cossmann had different views on *C. nysti*, the morphology of the genus *Cosmocerithium* strikingly differs from that of its type species. Thus, I have to modify the diagnosis of the genus *Cosmocerithium* Cossmann,

1906 and to reexamine its species composition (see Systematic Paleontology).

The species *C. nysti* sensu Cossmann has a multispiral turriculate shell consisting of slightly convex whorls divided by a shallow suture. The upper face of the whorl is ornamented by a few spiral ribs crossed by dominated folds. The lower half of the whorl bears two rows of nodes. The upper half of the whorl is convex, the lower one becomes concave. All these features can be seen on the illustrations by Cossmann (1885, pl. 5, figs. 20–22; 1906, pl. 8, figs. 15–16; 1912, pl. 3, figs. 61–62) and Gründel (1997, pl. 5, figs. 10, 12). *Procerithium picardi* Hirsch, 1980 from the Callovian of Israel (Hirsch, 1980, pl. 11, fig. 10 is another species similar to *C. nysti* sensu Cossmann. It has the shell composed of flat whorls ornamented by fine and dense ribs. The middle part of the whorl bears a furrow, short inflated folds appear below. *Procerithium* (*Cosmocerithium*) *dorvali* Cossmann, 1899 (p. 554, pl. 15, figs. 4, 5) has flat whorls with numerous threads crossed by short folds in the upper part of the whorl. A similar shell appearance occurs in *P. (C.) arabicum* Fischer, 2001.

The peculiarities of the shell ornamentation and the absence of data on the protoconch morphology do not allow me to assign these forms to any known taxa. However, the general shell appearance and the pattern of ornamentation of the species are similar to those of the genera *Cimolithium* Cossmann, 1906 [i.g., *C. belgicum* (d'Archiac, 1847)] and *Diatinostoma* [i.g., *D. nodosicinctum* (Schlosser, 1881), *D. achilles* (d'Orbigny, 1850), and *D. (Ditretus) mairei* Cossmann, 1912)] (see Cossmann, 1912b). The genus *Diatinostoma* is assigned to the family Eustomatidae Cossmann, 1906, whereas the genus *Cimolithium* Cossmann, 1906 is usually placed in Procerithiidae (but excluded from its composition in the present study). The study of the protoconchs of the genus *Cosmocerithium* suggests some similarity to the recent Triphoridae (especially in the case of *C. renardi*). The protoconchs of the genera *Euthymella* Thiele, 1929; *Nanophora* Laseron, 1958; *Viriola* Jousseume, 1884; etc. are composed of one or two rounded initial whorls with tubercles, followed by three or three and a half whorls with one or two ribs and dense fine folds (Nützel, 1998, pls. 8–12). In the Jurassic *Cosmocerithium renardi*, the first whorl is smooth and the next half-whorl or whorl has two ribs. The protoconch ends in two and a half or three and a half whorls bearing fine and densely spaced folds and two ribs, the latter usually accompanied by several threads. Thus, there are only some small differences in the whorl ornamentation, while the ontogeny and the protoconch shape are the same both in *C. renardi* and in triphorids (the spiral ornamentation of other species of *Cosmocerithium* Cossmann, 1906 differs considerably from that of the triphorids). The teleoconch morphology also has much in common. The shells of the Jurassic *Cosmocerithium* Cossmann, 1906 and recent triphorids are small and multispiral. The teleoconch ornamentation is reticulate, composed of thin dense folds

and ribs with nodes. Like the recent triphorids, the shell of *Cosmocerithium* bears a distinct siphonal canal; however, its structure is more primitive. No undamaged apertures of *Cosmocerithium* have been found; however, the broken aperture shows similarity to the aperture of recent triphorids, for instance "Triphoridae gelb-weiß-braun" (Nützel, 1998, p. 83, pl. 12, figs. A–D), or "Nov. Gen. D sp. rosa-weiß-braun" (Nützel, 1998, p. 81, pl. 11, figs. I–M). The most significant difference is in the coiling direction, i.e., *Cosmocerithium* has a dextral shell, while all triphorids are sinistral. However, Nützel (1998, pp. 121–123) suggested that triphorids could have evolved from the dextral forms. As an example, he mentioned the Eocene genus *Antiphora* Nützel, 1998, which only differs from typical triphorids in the coiling direction. He assigned this genus along with *Metaxia* Monterosato, 1884 and *Eorex* Nützel, 1998 to the subfamily Metaxiinae Marshall of the family Triphoridae. However, it is noteworthy that typical sinistrally coiled triphorids were already present in the Paleogene. The probability of the origin of sinistral forms from dextral mollusks was not excluded by Marshall, who was the first to include the subfamilies Metaxiinae Marshall and Adelacerithiinae Marshall with dextral representatives in the family Triphoridae (Marshall, 1977; 1983; 1984). Indeed, the origin of the triphorids from dextral ancestors is quite possible; thus, the genus *Cosmocerithium* could be a member of the ancestral group of the Triphoridae. On the other hand, a review of papers on Cerithiopsida suggests the similarity of *Cosmocerithium* Cossmann, 1906 to some of the Cenozoic genera of the family Cerithiopsidae. It is important that *Cosmocerithium*, like the cerithiopsids, has dextral shells and similar structure of the aperture and siphonal canal. In contrast to Triphoridae, the Cerithiopsidae lack the parietal canal, while the siphonal canal is opened anteriorly (I suppose the same condition for *Cosmocerithium* Cossmann, 1906). The cerithiopsin genus *Vatopsis* Gründel, 1980 has the most similar protoconch morphology, for instance, compare *V. bomonilifera* (Sandberger) and *Vatopsis* sp. from the Oligocene (Gründel, 1980, pp. 220–222), *Vatopsis* sp. 1 from the Miocene (Nützel, 1998, pl. 15, figs. I–J), *V. nodoliratum* (Wade) from the Campanian (Nützel, 1998, pl. 15, figs. S–V), etc. In addition, the genus *Tembrockia* Gründel, 1980 from the subfamily Seilinae has a similar protoconch shape (Gründel, 1980, pp. 234–235; Nützel, 1998, pl. 16, fig. F). However, *Tembrockia* significantly differs in the pattern of teleoconch ornamentation, which is composed of very thick ribs without folds. The genus *Vatopsis*, like *Cosmocerithium*, has reticulate ornamentation consisting of several ribs and numerous fine folds. The aperture can be rhomboidal. The similarity between these two genera is most readily seen when the genus *Cosmocerithium* Cossmann, 1906 is compared with *Vatopsis* sp. 1. The *Cosmocerithium* species differ from *Vatopsis* in the more complicated protoconch ornamentation composed of two or more ribs (threads) and prominent folds. *Cosmocerithium*

Cossmann, 1906 differs from other members of the Cerithiopsidae in the long and richly ornamented protoconch. Since there is no significant difference between the morphology of *Cosmocerithium* and Cerithiopsidae, and the Triphoridae has reverse coiling of the shell, I have suggested putting the genus *Cosmocerithium* into Cerithiopsidae (Guzhov, 2003).

As previously mentioned, Gerasimov (1992) assigned all three species of *Cosmocerithium*, i.e., *C. renardi* (Rouillier), *C. brateevense* (Gerasimov), and *C. pumilum* (Gerasimov) to the subgenus *Procerithium* (Rhabdocolpus) Cossmann, 1906. But according to Walther (1951) and my personal observations, the typical *Rhabdocolpus* has the protoconch composed of several smooth whorls, whereas the teleoconch contains numerous whorls ornamented only by folds at the early stages and by a combination of folds and ribs at later stages (see above). The shell of *Rhabdocolpus* is several times the size of *Cosmocerithium* and reaches 3 cm. Thus, the studied species of *Cosmocerithium* differs considerably from *Rhabdocolpus* Cossmann, 1906 [= *Procerithium* Cossmann, 1902, see above].

The Early Cretaceous monotypic genus *Prisciphora* Schröder, 1991 has an embryonic shell similar to that of *Cosmocerithium* Cossmann, 1906. The protoconch of its type species *P. beyschlagi* (Wollemann, 1903) from the Albian of Germany starts with two smooth whorls. The subsequent two and a half or three whorls are ornamented by densely spaced fine folds and two spiral ribs, a few additional ribs appear on the last whorl of the protoconch (according to Schröder, 1991; 1995). The teleoconch whorls and aperture pattern are similar to *Cosmocerithium*. Possibly, the genus *Prisciphora* originated from *Cosmocerithium*. Thus, I believed that the placement of *Prisciphora* in the families Triphoridae (see Schröder, 1991) or Eumetulidae (see Nützel, 1998) was in error and so I transferred it to the family Cerithiopsidae (Guzhov, 2003).

In addition, the newly discovered form *Novoselkella novoselkensis* Guzhov, 2003 was placed in the family Cerithiopsidae (Guzhov, 2003). The genus *Novoselkella* has a multispiral turriculate protoconch ornamented by strong folds and fine threads in the lower two-thirds of the whorl. Numerous microscopic granules appear on the last whorl of the protoconch. The teleoconch is composed of slightly convex whorls, ornamented by folds and ribs. The base of the shell is fairly high and convex and bears ribs. No undamaged aperture has been found, but the incomplete aperture bears a basal angulation. Its protoconch morphology is similar to that of the genera *Cosmocerithium*, with species *C. contiae* Guzhov, 2002 and *C. pumilum* (Gerasimov, 1992), and *Prisciphora*, which also have multispiral protoconchs with folds and spiral ribs on the later whorls. The genus *Novoselkella* Guzhov, 2003 differs from both genera in the shape of the shell base and teleoconch ornamentation. *Cosmocerithium* and *Prisciphora* have a more or less flattened base, and the last whorl has an angulation

in the basal-palatal area. The ornamentation of the lateral surface is coarse, composed of high ribs and thin but prominent folds. *Novoselkella* has a high, convex base; rounded periphery; and smooth ornamentation composed of rounded folds and rounded ribs.

### Family Eumetulidae

The family Eumetulidae is completed by the newly described genus *Longaevicerithium* Guzhov, 2003. The later was established to include the species *Procerithium* (*Plicacerithium*) *bitzae* Gerasimov, 1992. The genus differs from *Plicacerithium* Gerasimov, 1992 and *Procerithium* Cossmann, 1902, to which *P. bitzae* has been previously assigned, by the protoconch ornamentation. *Longaevicerithium* has a turriculate shell composed of convex whorls, which are ornamented by coarse folds and ribs. The protoconch is turriculate and multispiral, and its whorls are ornamented by folds and numerous microscopic granules. This type of the protoconch and teleoconch structure of *Longaevicerithium* is extremely similar to that of members of the subfamily Eumetulinae (see Gründel, 1980; Nützel, 1998). For instance, I compared it with the following eumetulin genera: *Eumetula* Thiele, 1912; *Ataxocerithium* Tate, 1893; *Cerithiopsilla* Thiele, 1912; and *Laiocochlis* Dunker et Metzger, 1874. *Longaevicerithium* is most similar to the first two genera but differs from *Eumethula* in the protoconch with widely spaced strong folds, rows of nodes, and absence of one or two ribs, which are usually present in *Eumethula*. In addition, it lacks large nodes on the teleoconch, which are typical for *Eumethula*. From *Ataxocerithium* the genus can be distinguished by the protoconch with widely spaced strong folds and rows of nodes; from *Cerithiopsilla*, by the high protoconch with widely spaced strong folds and rows of nodes and by the teleoconch with prominent folds and thinner ribs. From the genus *Laiocochlis*, it differs in the high protoconch with widely spaced strong folds and rows of nodes, along with the absence of the spiral ribs and threads, and in the prominent folds and thinner ribs on the teleoconch.

### Family Polygyrinidae

I assign the genus *Teutonica* Schröder, 1991 to this particular family. Earlier, the genus was placed in different families, i.e., Triphoridae (Schröder, 1991), Zygopleuridae (Nützel, 1998), Polygyrinidae (Gründel, 1999d), or Protorculidae (Guzhov, 2003). The comparison between *Teutonica* and members of these four families convinced me to put the genus within the family Polygyrinidae. However, I have some doubt in this decision; thus, it should be regarded as tentative. Let me explain the facts favoring this ambiguous position.

The significant similarity of the protoconch and early teleoconch appearance between the single genus of the family, i.e., *Polygyrina* Koken, 1892, and *Teutonica* Schröder, 1991 do exist. Two specimens of

*Polygyrina* type species, *P. lomelli* (Munster, 1841), are illustrated by Bandel (1991) and Nützel (1998). These figures, as well as drawings of the apical part of the shell made by Kittl (1894), provide data on the early ontogeny of the species.

Let us compare the morphology of *Polygyrina* and *Teutonica*. Both genera have highly spired multispiral shells with convex whorls. Width of the whorl exceeds its height. The protoconchs are very similar in shape. The earliest teleoconch whorls of *P. lomelli* are angular. But a rudimentary carination is also present near the protoconch–teleoconch boundary in the species *T. gramanni* Schröder, 1991 and *T. calloviana* Gründel, 2001. The difference in the ornamentation of the protoconch and teleoconch is noteworthy. The protoconch of *Polygyrina* bears collabral ornamentation composed of faint opisthocyrt threads in the lower part of the whorl. In the upper part of the whorl they are broken into randomly arranged tubercles. The species of *Teutonica* from Bajocian–Bathonian strata (Gründel, 1999d) show more pronounced collabral ornamentation, but it also is composed of rows of joint tubercles. These rows, like the threads of *Polygyrina*, disappear in the upper third of the whorl. The prosocline orientation of the collabral elements in *Teutonica* is an important difference from *Polygyrina*. And finally, in *T. calloviana* Gründel, 2001 (Callovian–Oxfordian), the thin but distinct folds, already lacking the tuberculate appearance, reach the suture without any visible weakening.

Thus, the evolution of the protoconch of the genus *Teutonica* reveals the development of the collabral ornamentation. In addition, the suture of the protoconch in all species of *Teutonica* is bounded by a row of tubercles from below, while in *Polygyrina* the sutural area lacks any tubercles. The difference of teleoconch morphology is the following: *Polygyrina* lacks the collabral ornamentation, whereas it is well-developed in *Teutonica*. Much of the mentioned differences are not strong enough to place *Teutonica* and *Polygyrina* in different families. The orientation of the larval collabral ornamentation is the most noticeable difference between them. But it is not constant even within *Teutonica* itself, i.e., all of the Bajocian and Bathonian species have prosocline folds, while in *T. calloviana* it varies from slightly prosocline to opisthocline-opisthocyrt. Thus, the significance of this particular feature is rather low.

As I have noted in my earlier paper (Guzhov, 2003), the genus *Teutonica* differs greatly from the members of the family Protorculidae in the structure of protoconch. However, in that publication I ascribed it to Protorculidae due to the similar tuberculate ornamentation of *Teutonica* and *Protorcula*. The position of *Teutonica* in the family Zygopleuridae is unlikely, because of the great difference in the protoconch pattern. The zygopleurid protoconch is smooth with a row of tubercles under the suture. The protoconch of the younger zygopleurids, for instance, *Laevipleura* Gründel et Nützel, 1998 (Lower Jurassic) (see Gründel and Nützel,

1998; Gründel, 1999c) and of their procerithiid descendants (*Katosira* Koken, 1892, *Procerithium* Cossmann, 1902) (see Gründel, 1999a; 1999b; present study) remains smooth. The similarity of postlarval ornamentation of zygopleurids and *Teutonica* is insignificant in this particular case.

### Family Maturifusidae

The family Maturifusidae Gründel, 2001 was erected quite recently. Gründel (2001) placed a single genus, *Maturifusus* Szabó, 1983, in the family. I here add two further genera, i.e., *Rhynchocerithium* Cossmann, 1906 and *Khetella* Beisel, 1977 (see Table 2). The family differs from all other Mesozoic gastropods by the pattern of protoconch and teleoconch. The maturifusid protoconch is composed of four to six and a half whorls. The first whorl is smooth and varies from planispiral to distinctly turbospiral. It is followed by the whorls with two angulation. The upper angulation is strong, almost right-angled, the lower one is faint. In *Khetella* all of the protoconch whorls may be rounded. The protoconch is conical or top-shaped (if some of the first whorls are planispiral). The protoconch-teleoconch boundary is sharp, marked by a commissure and appearance of ornamentation. The teleoconch is usually composed of a few whorls, but sometimes their number reaches 6.5. The whorls are convex and rounded or bear a shoulder angulation (carina) and, hence, are gradate. The ornamentation is composed of thick folds and strong ribs, thin ribs occur more rarely. The aperture bears a well-developed groove or pointed angulation. The family Maturifusidae is distinguishable from all of the gastropod families studied by a combination of a high protoconch, stocky shell with a low number of whorls, and the aperture with a well-developed siphonal groove. Similar protoconchs are present among the Cryptaulacidae, but they are smaller and shorter, with two coarse carinae.

The family was conventionally placed in the Buccinoidei, based on the similarity of teleoconch and the structure of apertures. The protoconch morphology of the Maturifusidae, except for *Khetella*, and recent Buccinoidei is different (the families Nassariidae and Buccinidae were compared).

The genus *Rhynchocerithium* Cossmann, 1906 was established by Cossmann (1906). He provided the generic diagnosis and composition (Cossmann, 1906; 1913), which were unchanged up to nowadays. Recently, the protoconch of several species of *Rhynchocerithium* have been described.

The genus *Maturifusus* Szabó, 1983. Prior to the establishment of the family Maturifusidae, the genus *Maturifusus* was a member of Purpurinidae (Szabó, 1983), but Schröder (1995) already doubted this position and suggested that the genus be reassigned to the family Buccinidae Rafinesque, 1815. And finally, Gründel (1998) claimed the problematic position of the genus *Maturifusus* somewhere within Bandel's order "Meta-Mesogastropoda."

The genus *Khetella* Beisel, 1977 was erected by Beisel (1977a). Later, it was characterized more precisely based on Early Cretaceous material (Beisel, 1983). In both of Beisel's publications, the genus is placed in the family Colombellinidae, but even a fleeting glance reveals a striking difference between *Khetella* and colombellinids in the structure of the aperture, the general shape of the shell, and the whorl morphology.

I had the opportunity to examine diverse and finely preserved material of the genera *Khetella* and *Maturifusus*, and compared the data obtained with foreign studies. In addition, I analyzed the published data on the morphology of the embryonic shell of other species of the genera *Maturifusus* (see Gründel, 1998; 1999c) and *Rhynchocerithium* Cossmann, 1906 (see Nützel, 1998; Gründel and Nützel, 1998; Gründel, 1999b; 1999c). A marked similarity between the genera *Maturifusus* and *Rhynchocerithium* is noted. Their protoconch is, in some cases, so similar that it cannot be distinguished. Generally, there are few differences in the protoconch morphology of these genera. Some species of *Rhynchocerithium* have a third rib above the upper carinae at the latest stages of protoconch ontogeny. In *Maturifusus* several rows of tubercles are present at the beginning of the protoconch, while the ribs and carinae appear much later (these data are based only on the single species, *M. conspicuus*). This "tuberculate" stage of the protoconch development is still unknown for *Rhynchocerithium*.

The ontogeny of the teleoconch ornamentation differs within the genera. In some species, i.e., *R. kochi* (Münster, 1844), *R. fusiforme* (Hebert et Deslongchamps, 1860) and *R. douglasi* Nützel et Senowbary-Daryan, 1999, the upper rib of the protoconch spreads onto the teleoconch and produces a gradate appearance of the whorls. The low number of supplementary ribs is typical for the genus *Rhynchocerithium*, while *Maturifusus* has many supplementary ribs. The differentiation of the ribs is well pronounced in *Rhynchocerithium*, while in *Maturifusus* the ribs are almost identical. The folds of *Rhynchocerithium* are thinner but sharper, in contrast to the wide and usually rounded folds of *Maturifusus*. Thus, there are some minor differences in the protoconch morphology and in the structure and ontogeny of teleoconch ornamentation that resulted in the cumulative distinction of these genera.

Nützel (1999) placed the species *R. douglasi* Nützel et Senowbary-Daryan, 1999 in the genus *Rhynchocerithium* Cossmann, 1906. The species differs significantly from the *R. fusiforme* group. *R. douglasi* has a gradate spire, two primary ribs, and sparse secondary ribs. The low number of ribs and gradate spire makes this species similar to members of the family Purpurinidae.

The genus *Khetella* Beisel, 1977 is distinguishable from other genera by its protoconch and teleoconch morphology. Its protoconch includes a few whorls. Two initial whorls are almost planispiral. Later, the whorls gain two angulation or remain rounded. The conical

teleoconch is composed of rounded or shouldered whorls. The rounded whorls are similar to those of the genus *Maturifusus* but clearly differ from them in the faint ribs and usually weak shoulder angulation. The study of *Khetella* shells revealed that the species are distinguishable not only in the teleoconch morphology but also have protoconchs of two distinct types. The first group of species has protoconchs with smooth and rounded whorls; in the second group, the last two protoconch whorls are bicarinate.

The attempt at using the teleoconch and protoconch morphology in reconstruction of phylogenetic links within the genus has shown that changes in the protoconch structure are not correlated with the changes in the teleoconch structure. In other words, the species that have very similar teleoconchs can have distinct protoconchs. I describe below four species of the genus *Khetella* from the Callovian–Oxfordian, i.e., *K. formosa* (Eichwald, 1868) and *K. formosiformis* sp. nov. with similar carinate shells but different in details of ornamentation and *K. makaryevensis* sp. nov. and *K. gradata* sp. nov. with bucciniform shells. However, they can be grouped in another manner on the basis of protoconch morphology, since *K. formosa* and *K. gradata* sp. nov. have protoconchs with bicarinate whorls, whereas *K. formosiformis* sp. nov. and *K. makaryevensis* sp. nov. have protoconchs with rounded whorls. This discrepancy prevents the evaluation of the systematic significance of the features, and as a result, does not allow the phylogenetic relationships of the species to be traced.

Schröder (1995) described the species *Procerithium kulickii* from the Valanginian of Poland, which has a multispiral conical protoconch similar to that of the Maturifusidae (compare the protoconch of *Maturifusus conspicuus* illustrated in the present publication, Pl. 7, fig. 11). I cannot surely assign *Procerithium kulickii* to the genus *Maturifusus*, since this species is represented by a juvenile specimen. The adult shell would probably have some specific features not typical for *Maturifusus*. Nevertheless, this find reveals maturifusid diversity even in the Neocomian.

### Family Epitoniidae

Three species of the genus *Plicacerithium* Gerasimov, 1992 from the Jurassic of European Russia were assigned by me (Guzhov, 2002a) to the epitoniids. These are as follows: *P. apicatum* (Eichwald, 1868); *P. altum* Guzhov, 2002; and *P. korobceevense* (Gerasimov, 1992). The last form significantly differs from the former two species in the presence of basal-palatal angulation that divides the base and lateral surface of the last whorl. The base of the shell is low and flattened in *P. korobceevense*. Two other species have rounded last whorl, its lateral surface gently transits into the rounded base of the shell. In epitoniids, such a difference in whorl morphology would suggest the different generic position of *P. korobceevense* and two other

species. *P. korobceevense* is rather similar to the Cretaceous species of the genera *Claviscala* Boury, 1910 and *Confusiscala* Boury, 1910.

However, the presence of *Claviscala* in the Cretaceous is doubtful. It is the result of Cossmann's misrepresentation of the generic diagnosis (Cossmann, 1912). He suggested the species *Scalaria clementina* d'Orbigny as the plesiotype for the genus. Under the term "plesiotype" he meant a supplementary taxon for the type species of a genus (see Cossmann, 1896, p. 3). The type species of the genus, *Claviscala*, i.e., *Scala richardi* Dautzenberg et Boury, was ignored and considered secondary. Cossmann explained his decision by stating the poor preservation of the single known specimen (i.e., the holotype) of *Scala richardi*. Boury reacted violently to this arbitrary decision (Boury, 1917). It is noteworthy that Boury mentioned the identical character of ornamentation in *S. richardi* and *S. clementina*. In addition, he supposed the existence of *Claviscala* since the Cretaceous. Unfortunately, neither Boury in his establishment of the genus *Claviscala* (Boury, 1910), nor Cossmann, nor Wenz in their compilations made a reference to the original description of the type species for the genus *Claviscala*. I also failed to find such a reference in modern publications. Thus, I have only the illustration by Wenz (1940, p. 794).

*S. richardi* differs from the Cretaceous species in the more numerous and thinner folds. It has low folds, in contrast to the coarse, crescent-like folds of *S. clementina*, which provide a very convex appearance to the whorls. It is not possible to find out the character of folds and ribs crossing in *S. richardi*. Judging from the difference in age between *S. clementina* and *S. richardi*, absence of any data on protoconch and the early teleoconch morphology of the type species of *Claviscala* and the Cretaceous forms, like *S. clementina*, the separation of these epitoniids into different genera is most likely.

The morphology of *P. korobceevense* is somewhat intermediate between the genus *Confusiscala* and *S. clementina* group. A stocky shell with a larger teleoconch angle, more inflated whorls, and a deep suture characterizes the genus *Confusiscala*. Probably, the shells of this genus are composed of a lesser number of whorls. In contrast, *S. clementina* has more slender and multispiral shell, than that of *P. korobceevense*. The type of ornamentation is almost identical in both species, only the basal-palatal angulation is less developed in the Jurassic form. This causes vagueness in the determination of the descendants of the Jurassic species. I here erect a new genus *Dubariscala* gen. nov. for *P. korobceevense*. Its phylogenetic relations with the genus *Confusiscala* and the *S. clementina* group remain unclear.

The species of the genus *Proscala* Cossmann, 1912 are most similar to *P. apicatum* and *P. altum* among the other Cretaceous forms. *Scalaria albensis* d'Orbigny, 1842, the type species of *Proscala*, has a rounded last whorl, similar to that of the genus *Plicacerithium*. The Jurassic forms differ from *Proscala* in the more stocky

shell with lower whorls and coarser folds. This strong plication increases the visible convexity of the whorls, whereas in *Proscala*, the whorls look fairly flat. Despite the great morphological similarity of *Plicacerithium* and *Proscala*, I am not sure that they belong to the same phylogenetic lineage. The Jurassic *Plicacerithium* is easily distinguished from any other Cretaceous epitoniids.

My earlier assumption (Guzhov, 2002a) that the angularity of broken whorls could be interpreted as evidence for a siphonostomatous aperture in Jurassic and Cretaceous epitoniids, in contrast to recent forms, should be considered doubtful. Undamaged apertures are unknown in both Jurassic and Cretaceous forms, while the broken aperture of the recent epitoniids can show a similar basal angulation.

#### CHAPTER 4. SYSTEMATIC PALEONTOLOGY

This chapter contains diagnoses of new and earlier established taxa of supraspecific rank. Most of the genera (and subgenera) are provided with a list of assigned species. In the species list, the original combination of the generic and species names is given in square brackets after the modern systematic treatment of the species, for example, *Shurovites binodosus* (Gründel, 1990) [= *Exelissa binodosa*]. When the modern and original combinations are identical, the comments in square brackets are omitted. In a few cases, in the species composition I indicate synonyms for species that are not described in the present study. The references include all publications that contain original descriptions of the species mentioned in the present work. The arrangement of families generally follows Golikov and Starobogatov (1987; 1988), except for Procerithiidae, which are included in the Cerithiiformes.

The following abbreviations are used for depositories in the present study: (GGM) Vernadsky State Geological Museum of the Russian Academy of Sciences, Moscow; (GM IGN) Geological Museum of the Institute of Geological Sciences, Kiev; (GMM) Geological and Mineralogical Museum of the Krupskaya Moscow Pedagogical University, Moscow; (PIN) Paleontological Institute of the Russian Academy of Sciences, Moscow; and (SPbGU) St. Petersburg State University.

### CLASS GASTROPODA

#### SUBCLASS PECTINIBRANCHIA BLAINVILLE, 1814

Superorder Calyptreiformii Férussac, 1822

Order Cerithiiformes Golikov et Starobogatov, 1975

Suborder Cerithioidei Golikov et Starobogatov, 1975

Superfamily Cerithioidea Férussac, 1819

#### Family Cryptaulacidae Gründel, 1976

**Diagnosis.** Shell small to medium-sized, multi-spiral, low- to high-turriculate, siphonostomatous, anomphalous. Protoconch composed of 3.0–4.0 whorls;

first whorls smooth and rounded, subsequent whorls bicarinate (except for those of genus *Shurovites* with *single carina*). First protoconch whorl almost planispiral. Boundary between protoconch and teleoconch marked by opisthocyrt commissure and appearance of folds. Teleoconch whorls convex or flattened. Starting from beginning of teleoconch, ornamentation represented by ribs and folds, usually with tubercles at their intersections. Sometimes folds reduced. Last whorl low. Shell base high, widely conical or cup-shaped. Aperture circular or oval, more or less angular from below in broken specimens. Growth lines opisthocyrt from suture to midheight of base, then bent to prosocyrt, and becoming opisthocyrt again in columellar area.

**Composition.** Subfamilies Cryptaulacinae Gründel, 1976 and Exelissinae subfam. nov.

**Comparison.** This family differs from the Procerithiidae in the protoconch composed of smooth and bicarinate whorls and in the appearance of the spiral ornamentation from the beginning of the teleoconch. It can be distinguished from the most similar family Cerithiidae by the less developed siphonal canal, the general shape of adult shell, and the protoconch morphology.

**Occurrence.** Middle Triassic, Ladinian–Upper Cretaceous of Eurasia, America, and Africa.

#### Subfamily Cryptaulacinae Gründel, 1976

**Diagnosis.** Shell from turriculate to high-turriculate. Generating line convex or straight. Smooth initial whorls of protoconch followed by bicarinate whorls. Teleoconch ornamentation composed of three or four primary and several secondary ribs. Folds present on entire teleoconch, sometimes, smoothed out on last whorls, or completely reduced. Last whorl rather similar to spire whorls, its folds and, occasionally, ribs often smoothed. Aperture circular, with basal notch or narrow explanate lip.

**Generic composition.** Four genera: *Cryptaulax* Tate, 1869, *Infacerithium* Gründel, 1974, *Argyropeza* Melvill et Standen, 1901, and *Microcerithium* gen. nov.

**Comparison.** The subfamily differs from the Exelissinae in the pattern of the last whorl, i.e., it is not deflected downward and lacks narrowing or straightening accompanied by smoothing of the collabral ornamentation.

**Occurrence.** Middle Triassic, Ladinian–Lower Cretaceous of Eurasia, Africa, America, and Australia.

#### Genus *Cryptaulax* Tate, 1869

*Cryptaulax*: Tate, 1869, p. 418; Cossmann, 1906, p. 37 (pars); 1913, p. 99 (pars); Wenz, 1940, p. 730 (pars); Gründel, 1974b, p. 840; 1999b, p. 14.

**Type species.** *Procerithium (Xystrella) protertile* Cox, 1965; Callovian of France.

**Diagnosis.** Shell medium-sized or, rarely, small, turriculate or high-turriculate, with convex or straight generating line. Protoconch composed of 1.0–1.5 smooth, rounded whorls, followed by 2.5–3.0 bicarinate whorls. Teleoconch composed of more than ten whorls. Whorls flattened or convex, nongradate or slightly gradate. Extent of involution 30–40%. Suture ranging from angular to superficial. Ornamentation composed of three or, rarely, four primary and several secondary ribs (lowermost primary rib usually partly covered by subsequent whorl and not always visible in apical view). Folds extending from suture to suture, forming tubercles at intersections with ribs. Shell base high, widely conical, and convex, with several ribs. Aperture circular or oval, with either explanate lips and round basal part, or with simple, downwardly elongated lips with basal notch.

**Composition.** Three subgenera: *Cryptaulax* Tate, 1869, *Neocryptaulax* Gerasimov, 1992, and *Pseudocerithium* Cossmann, 1884.

**Comparison.** This genus differs from *Infacerithium* in its always well-developed folds and from *Microcerithium* in its larger shell and usually more pronounced ornamentation.

**Occurrence.** Triassic, Ladinian–Carnian, Lower Jurassic–Lower Cretaceous, Valanginian of Europe; Upper Triassic, Norian–Rhaetian of the Near East; Jurassic, Upper Bajocian of the Middle Asia; Jurassic, Pliensbachian–Callovian of Africa; Upper Jurassic, Upper Oxfordian, ?Tithonian of North America; Upper Triassic, Rhaetian of South America (Peru).

#### Subgenus *Cryptaulax* Tate, 1869

*Cryptaulax*: Tate, 1869, p. 418.

**Type species.** *Procerithium (Xystrella) protortile* Cox, 1965; Callovian of France.

**Diagnosis.** Shell usually turriculate, with straight generating line. Teleoconch composed of up to 15 whorls. Whorls flattened or convex. Suture varying from shallow to deep. Ornamentation composed of three, rarely, four primary and several (0–3) secondary ribs. Aperture downwardly elongated, with basal angulation and wide notch. Outer lip simple, with sharp edge. Occasionally, apertural edge wavy because of spiral ornamentation. Age-related changes manifested in weakening and disappearance of folds and in weakening of spiral ribs. Whorls becoming rounded and covered by coarse growth lines near aperture. Whorls of this kind have maximum width in lower part, in contrast to preceding whorls reaching maximum width at midheight.

**Species composition.** Twenty-two species: type species; *C. (C.) acodiastrus* (Gründel, 1999) [= *Rhabdocolpus (R.) acodiastrus*] from the Callovian of Germany; *C. (C.) armatus* (Goldfuss, 1844) [= *Cerithium armatum*] from the Toarcian–Aalenian of Germany and France; *C. (C.) buccai* (Fucini, 1913) [= *Promathildia buccai*] from the Lower Lias of Italy; *C. (C.) canescens* (Dubar, 1948) [= *Procerithium canescens*] from the Upper Pliensbachian of Morocco; *C. (C.)*

*damonis* (Lycett, 1860) [= *Cerithium damonis*] from the Upper Callovian–Lower Oxfordian of England; *C. (C.) diplophysus* (Cossmann, 1912) (Cossmann, 1912, only text-figs. 62, 63) [= *Procerithium (Xystrella) diplophysum*] from the Bajocian of France; *C. (C.) echinophorus* (Cossmann, 1913) [= *Procerithium echinophorus*] from the Middle–Upper Oxfordian of France; *C. (C.) heptagonus* Conti, 1982 from the Lower Bajocian, *humphriesianum* Zone of Italy; *C. (C.) hunti* (Cox, 1935) [= *Procerithium hunti*] from the Pliensbachian of Somalia; *C. (C.) mandawaensis* (Cox, 1965) [= *Procerithium (Rhabdocolpus) mandawaensis*] from the ?Bajocian of Tanganyika Lake; *C. (C.) papillosus* (Eudes-Deslongchamps, 1842) [= *Cerithium papillosum*] from the Bajocian of France; *C. (C.) pleignensis* (Loriol, 1899) [= *Cerithium pleignensis*] from the Lower Oxfordian of France; *C. (C.) pseudoechinatus* Gerasimov, 1955 from the Callovian–Lower Oxfordian of Europe; *C. (C.) quenstedti* (Walther, 1951) [= *Procerithium (Xystrella) quenstedti*] from the Bathonian–Callovian of Poland and Germany; *C. (C.) scaliai* Fucini, 1913 [= *Promathildia scaliai*] from the Lower Lias of Italy; *C. (C.) strangwaysi* (Rouillier, 1849) [= *Cerithium strangwaysi*] from the Middle Oxfordian of European Russia; *C. (C.) tilarniocensis* Haas, 1953 from the Rhaetian of Peru; *C. (C.) trinoduliformis* (Smith, 1893) [= *Cerithium trinoduliforme*] from the Upper Kimmeridgian–Lower Tithonian of Germany; *C. (C.) unzhensis* sp. nov. from the Upper Oxfordian, *alteroides* Zone of European Russia; ?*C. (C.) brachymorphus* (Cossmann, 1913) [= *Procerithium (Rhabdocolpus) brachymorphe*] from the Lower Bathonian of France, Callovian of Tunisia (Cox, 1965); and ?*C. (C.) clathratus* (Gemmellaro, 1878) [= *Tomocheilus clathratus*] from the Lower Lias of Italy. In addition, several undetermined species of *Cryptaulax (C.)* were found in the Hettangian–Sinemurian of the Atlas Mountains, Morocco (Bourrouilh, 1966).

**Comparison.** This subgenus differs from the subgenus *Pseudocerithium* in its wider and lower shells and fewer teleoconch whorls (no more than 15). In *Pseudocerithium*, the secondary ribs are always faint (up to two in number), whereas in *Cryptaulax* sensu stricto, they are usually well-developed. It differs from the subgenus *Neocryptaulax* in the straight generating line, the structure of the aperture (simple outer lip, thin inner lip, and downward extension accompanied by the formation of the notch), and often in the ornamentation ontogeny (see *Neocryptaulax*).

#### *Cryptaulax (Cryptaulax) pseudoechinatus* Gerasimov, 1955

Plate 1, figs. 1–5

*Cerithium tortile*: Hebert and Deslongchamps, 1860, pl. 4, fig. 1d.  
*Procerithium (Xystrella) struckmanni*: Cossmann, 1906, pl. 5, fig. 25.

*Cryptaulax pseudoechinata*: Gerasimov, 1955, p. 191, pl. 40, figs. 6 and 7.

*Cryptaulax (Xystrella) echinatum*: Gründel, 1974b, p. 842, pl. 2, figs. 5–8.

*Procerithium aculeatus*: Yamnichenko, 1987, p. 85, pl. 9, figs. 3 and 4.

*Procerithium spinulentum*: Yamnichenko, 1987, p. 84, pl. 9, figs. 1 and 2.

*Cryptaulax (Xystrella) pseudoechinatum*: Gerasimov, 1992, p. 82 (pars), pl. 20, figs. 17 and 18; pl. 21, figs. 3–9.

*Cryptaulax* ex gr. *bellayensis* nom. nov. sp. 2: Gründel, 1999b, p. 17, pl. 3, fig. 19.

*Cryptaulax donosum*: Gründel, 1999b, p. 20, pl. 4, figs. 13 and 14.

?*Cryptaulax* sp. 1: Gründel, 1999b, p. 21, pl. 5, figs. 5–7.

**Holotype.** The specimen illustrated by Gerasimov (1955, pl. 40, fig. 7). Depository is unknown. Russia, Kaluga Region, Lyudinovskii District, borehole; Middle Callovian.

**Description.** The shell is up to 15.0–15.5 mm high. The protoconch is composed of 3.0–3.5 whorls. The first whorl is smooth, the rest of the whorls are bicarinate. Rows of tubercles run along the carinae. Several additional rows are present above the suture of the last whorl. The teleoconch is composed of 10.0–10.5 whorls; the teleoconch angle is 18°–34°. The maximum width of the whorl is at the upper rib. The extent of involution is about 38%. The suture is deep. The ornamentation is composed of three coarse primary ribs; the upper two are particularly prominent. Sometimes, after several teleoconch whorls, a faint secondary rib appears between the upper primary ribs. Two upper primary ribs often approach each other at the middle of the lateral surface of the whorl. Strong folds cross the ribs, their number per whorl is usually 9–11 or, rarely, 12–13 (in whorls 3.5–4.5 mm in diameter). The folds are orthocone in the early whorls and later become opisthocline–opisthocyrt or opisthocyrt. The ribs bear coarse spinelike tubercles at the crossing with the folds; tubercles are larger at the upper rib. The last whorl is 31–36% as high as the shell. The base of the shell bears four to six (rarely three) ribs. The folds disappear in the upper part of the shell base. The aperture is oval.

**Ontogenetic changes.** Two upper primary ribs often diverge with shell growth. In the first two whorls, the distance between them is 1.2–1.5 times narrower than the distance between the upper rib and the suture. But towards the aperture, these distances become equal, or the distance between the upper rib and the suture can be slightly less than the distance between the ribs. The folds become more densely spaced on the last two whorls. The last 0.2 of the whorl lack folds, while the ribs become faint, and the whorl becomes rounded. A series of coarse growth lines appears near the aperture.

**Comparison.** The species differs from the similar *C. (C.) damonis* (Lycett) from the Upper Callovian–Lower Oxfordian of England in the smaller size (15 mm instead of 20 mm), the more convex whorls, and the close position of the two upper primary ribs. The second primary rib is placed much higher relative to the suture, while in *C. (C.) damonis*, it is placed close to the suture. *C. (C.) pseudoechinatus* differs from

*C. (C.) echinophorus* (Cossmann) from the Middle–Upper Oxfordian in having three (instead of four) primary ribs.

**Remarks.** At the end of the Early Oxfordian, *C. (C.) pseudoechinatus* was replaced by *C. (C.) strangwaysi*. This was associated with a change in the type of spiral ornamentation. The Callovian *C. (C.) pseudoechinatus* has two strong ribs and, sometimes, a secondary rib that appears later, whereas Oxfordian members of this species have a less prominent ornamentation and the two upper primary ribs more distantly placed. Further evolution resulted in an even greater weakening of ribs and appearance of a secondary rib that was formed early in ontogeny. In the typical *C. (C.) strangwaysi*, the two upper primary ribs are widely spaced, while the secondary rib is strong and appears very early, sometimes, from the beginning of the teleoconch (as does the fourth primary rib). In addition, one or two extra secondary ribs are often present. However, the shells are morphologically very similar to the Early Oxfordian *C. (C.) pseudoechinatus* are found even in the *tenuiserratum* Zone. Thus, the evolution of *C. (C.) pseudoechinatus* shows the weakening of ornamentation, the sliding apart of the two upper primary ribs, and the appearance and enhancement of several secondary ribs.

**Occurrence.** Middle Callovian–Lower Oxfordian of European Russia; Middle–Upper Callovian of Baltic Region; Middle Callovian of Ukraine, Callovian–Oxfordian of France; Lower–Upper Callovian, *athleta* Zone of Germany; Callovian of Poland.

**Material.** Lower Callovian, *enodatum* Zone; Mikhailovskii Mine (299 specimens); Middle Callovian, *jason* Zone; village of Fokino (four specimens); Lower Oxfordian; village of Nikitino (four specimens).

*Cryptaulax (Cryptaulax) protortilis* (Cox, 1965)

Plate 1, figs. 6–13

*Cerithium tortile*: Hebert and Deslongchamps, 1860, pl. 4, figs. 1a and 1b.

?*Cryptaulax (Xystrella) quenstedtii*: Walther, 1951, p. 81 (pars), pl. 4, fig. 8.

*Procerithium (Xystrella) protortile*: Cox, 1965a, p. 15.

*Procerithium* sp.: Sasonova et Sasonov, 1967, pl. 45, fig. 3; pl. 51, fig. 1.

*Cryptaulax (Xystrella) quenstedtii*: Gründel, 1974b, p. 842, pl. 2, figs. 11–15.

*Cryptaulax (Xystrella) donosum*: Gründel, 1974b, p. 841, pl. 2, fig. 4.

*Cryptaulax (Cryptaulax) shiptonense*: Gründel, 1974b, p. 844, pl. 1, figs. 12 and 13.

*Procerithium explanatum*: Yamnichenko, 1987, p. 85, pl. 9, figs. 5 and 6.

*Procerithium accretum*: Yamnichenko, 1987, p. 86, pl. 9, figs. 7 and 8.

*Cryptaulax (Xystrella) pseudoechinatum*: Gerasimov, 1992, p. 82 (pars), pl. 21, figs. 1, 2, 11, 13, and 14; Gerasimov et al., 1996, pl. 23, fig. 8.

*Cryptaulax* ex gr. *bellayensis* nom. nov. sp. 1: Gründel, 1999b, p. 16, pl. 4, figs. 1–7.



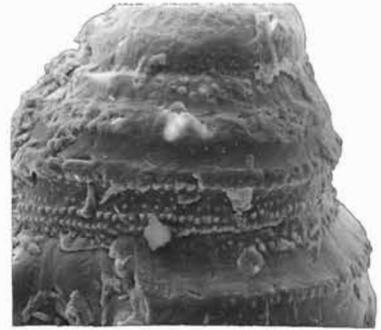
1a



1b



2a



2b



3



4



5



6



7



8



9



10



11a



11b



12



13a



13b



14



15a



15b



16a



16b



17



18



19

*Cryptaulax donosum*: Gründel, 1999b, p. 20, pl. 4, figs. 8–12, 15–19.

*Cryptaulax* sp. 1: Gründel, 1999b, p. 21, pl. 5, figs. 8, 9.

*Cryptaulax* sp. aff. *donosum*: Gründel, 1999b, p. 21, pl. 5, figs. 10–12.

**Lectotype.** The specimen figured by Hebert and Deslongchamps (1860, pl. 4, fig. 1a), France, Maine-et-Loire Department, Montreuil-Bellay Mountain; Callovian.

**Description.** The shell is up to 17 mm high. Only incomplete protoconchs, composed of 2.0–3.0 bicarinate whorls are known. The carinae are ornamented with ribs. The teleoconch is composed of 9.5–10.5 whorls, the teleoconch angle is 21.0°–33.5°. The maximum width of the whorl is at the upper rib. The extent of involution is about 35%. The suture is deep. The whorls are flat or slightly convex and slightly gradate. The ornamentation is composed of three primary and one or two secondary ribs. The secondary ribs run below the upper primary rib and vary from rather faint (in the early forms) to strong (in the late forms). The folds are strong, their number is 9–13 per whorl (whorl diameter is 4 mm), or rarely more (see below). The folds are orthocline in early whorls and later become slightly opisthocyrte and opisthocline, and near the aperture, they are distinctly opisthocyrte. The large, blunt tubercles are formed at the crossing of the folds and ribs. The largest tubercles run along the upper rib. The last whorl is 25% of the shell height. The shell base bears four or five (rarely six) ribs and the folds end in its upper part. The aperture is oval.

**Ontogenetic changes.** The folds become more opisthocyrte with shell growth. Gerontic changes consist of smoothing of the folds and tubercles (at first, the lower tubercles and later the upper ones) and weakening of the ribs. In a mature shell, morphological changes are observed in the last 0.15 of the whorl, where the folds disappear, the whorl becomes rounded, the ribs weaken, and the upper part of the lateral side becomes pressed in, which results in the appearance of the parietal canal. The whorl becomes incurved from

below, so that its maximum width is shifted in the lower part. Coarse growth lines appear near the apertural margin.

**Comparison.** The species differs from the similar *C. (C.) strangwaysi* in the slightly gradate profile of the whorls and more pronounced secondary ornamentation. It is distinguished from *C. (C.) pseudoechinatus* by its early appearance and the well-developed one or two secondary ribs on the lateral surface of the whorl.

**Remarks.** The study has revealed that the shell ornamentation strengthens during evolution. Accordingly, two subsequent intraspecific morphs are recognized. The first occurs from the *koenigi* Zone to the *jason* Zone. Shells with faint secondary ribs, usually, only one secondary rib (Pl. 1, figs. 6–9) prevailed at that time. The forms considered herein as *C. (C.) protortilis* β were found in the moraine deposits of Gzhel' and the Kamushki quarry. The fauna from these strata is dated to the Middle Callovian. This is most likely a higher interval, i.e., the upper part of the *jason* Zone to the *coronatum* Zone. The shells have two strong secondary ribs, which are equal in prominence to the primary ribs (Pl. 1, fig. 11). The deposits of the same age near the town of Shchelkovo and the Kazach'ya River contain the forms with deviating features, i.e., their whorls are flat and nongradate, the folds are densely placed, and one (Kazach'ya River locality) or two secondary ribs (Shchelkovo locality) are strong (Pl. 1, fig. 10).

Gründel (1999) described three varieties of the species *C. bellayensis*, i.e., *C. ex gr. bellayensis* 1, *C. ex gr. bellayensis* 2, and *C. ex gr. bellayensis* 3. Actually, they are treated as separate species, which are identical to *C. tortile* Hebert et Deslongchamps [= *C. (C.) protortilis*] in teleoconch morphology. However, they differ in the length of the protoconch. In the first, second, and third species the protoconchs are composed of 3.5–4.0, 4.0–4.5 whorls, and 4.5–5.5 whorls, respectively. In my opinion, this separation is well-grounded, since my own observation, based on extensive material on *C. (C.) strangwaysi* (Rouillier) and *Exelissa (E.) quinaria* (Traudschold), has revealed that the intraspecific vari-

#### Explanation of Plate 1

**Figs. 1–5.** *Cryptaulax (Cryptaulax) pseudoechinatus* Gerasimov: (1) PIN, no. 4863/161, ×3: (1a) apertural and (1b) abapertural views; village of Fokino; Middle Callovian, *jason* Zone; (2) GMM, no. 12/59: (2a) protoconch, ×71, (2b) fragment of protoconch ornamentation, ×205; (3) GMM, no. 12/61, abapertural view, ×3; (4) GMM, no. 12/60, abapertural view, ×3; Mikhailovskii Mine; Lower Callovian, *enodatum* Zone; (5) PIN, no. 4863/162, abapertural view, ×3; village of Fokino; Middle Callovian, *jason* Zone.

**Figs. 6–13.** *Cryptaulax (Cryptaulax) protortilis* Cox: (6) GMM, no. 12/51, abapertural view, ×3; (7) GMM, no. 12/50, abapertural view, ×3; (8) GMM, no. 12/49, abapertural view, ×3; (9) GMM, no. 12/48, abapertural view, ×3; Mikhailovskii Mine; Lower Callovian, *enodatum* Zone; (10) PIN, no. 4863/158, apertural view, ×3; town of Shchelkovo; Middle Callovian; (11) PIN, no. 4863/148, ×3: (11a) apertural view and (11b) left of the aperture; Moscow, Kamushki quarry; Middle Callovian; (12) GMM, no. 12/53, protoconch, ×55; (13) GMM, no. 12/52: (13a) left of the aperture, ×10, and (13b) protoconch, ×50; Mikhailovskii Mine; Lower Callovian, *enodatum* Zone.

**Figs. 14–18.** *Cryptaulax (Cryptaulax) strangwaysi* (Rouillier): (14) GMM, no. 12/81, abapertural view, ×3; (15) GMM, no. 12/79: (15a) apertural view, ×3, and (15b) protoconch, ×85; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone; (16) GMM, no. 12/111, ×3: (16a) apertural view and (16b) left of the aperture; town of Makar'ev; Middle Oxfordian, *densiplicatum* Zone; (17) GMM, no. 12/80, abapertural view, ×3; (18) GMM, no. 12/83, apertural view, ×3; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone.

**Fig. 19.** *Cryptaulax (Cryptaulax) unzhensis* sp. nov.: holotype GMM, no. 12/17, apertural view, ×4; town of Makar'ev, section northern Makar'ev; Upper Oxfordian, *alternoides* Zone, *ilovaiskii* Subzone.



1



2



3a



3b



4



5



6a



6b



7



8



9



10



12



13



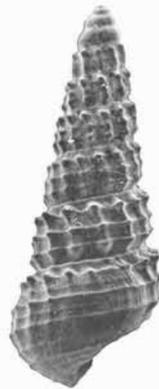
11



14



15



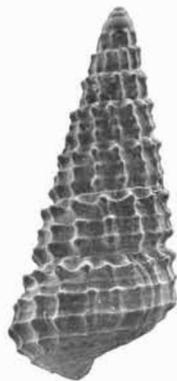
16a



16b



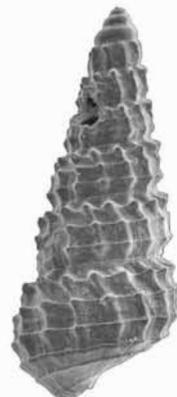
17a



17b



17c



18



19

ability of the protoconch length is at most half of a whorl. Judging from the preserved protoconchs, the species described here corresponds to *C. ex gr. bellayensis* 1. Gründel's publications provides no data on phylogenetic relationships of the three forms with other members of the subgenus *Cryptaulax*.

**Occurrence.** Lower Callovian, *koenigi* Zone, to the Middle Callovian of European Russia; Middle Callovian of Ukraine and Baltic Region; Callovian of France; Bathonian–Callovian of Germany; Upper Bathonian–Middle Callovian of Poland.

**Material.** Lower Callovian, *koenigi* Zone, *gowe-rianius* Subzone; village of Uzhovka (one specimen); Lower Callovian, *koenigi* Zone, *curtilobus* Subzone; village of Alpat'ev (one specimen), village of Ileshevo (one specimen), village of Burdovo (five specimens); Lower Callovian, *enodatum* Zone; Mikhailovskii Mine (227 specimens); Middle Callovian, *jason* Zone, *medea* Subzone; town of Makar'ev (one specimen), village of Vasil'kovo (one specimen); Middle Callovian, *jason* Zone; village of Fokino (603 specimens); Middle Callovian; village of Tyrnovo (two specimens), town of Shchelkovo (13 specimens), Moscow, Kamushki quarry (60 specimens).

*Cryptaulax (Cryptaulax) strangwaysi* (Rouillier, 1849)

Plate 1, figs. 14–18; Plate 2, figs. 1 and 2

*Cerithium strangwaysi*: Rouillier, 1849, p. 380, pl. L, fig. 97.

*Cerithium muricatoechinatum*: Andreae, 1887, p. 26, pl. A, figs. 13–19; Loriol, 1901, p. 39, pl. 3, fig. 11; Ilovaisky, 1903, p. 263, pl. 10, figs. 17 and 18.

?*Cerithium muricatoechinatum*: Andreae, 1887, pl. B, fig. 15; pl. C, fig. 11.

*Cerithium armatum*: Ilovaisky, 1903, p. 263, pl. 10, fig. 11.

*Cerithium echinatum*: Ilovaisky, 1903, p. 263, pl. 10, figs. 12–16.

?*Procerithium (Xystrella) struckmanni*: Cossmann, 1906, pl. 5, figs. 29 and 30.

*Cryptaulax echinata*: Gerasimov, 1955, p. 190, pl. 40, figs. 4 and 5.

*Cryptaulax (Xystrella) tortileoides*: Gerasimov, 1992, p. 80, pl. 20, figs. 1–13, 15, and 16.

*Cryptaulax (Xystrella) multituberculatum*: Gerasimov, 1992, p. 81, pl. 20, fig. 14 [mutatio].

*Cryptaulax (Xystrella) biseriatum*: Gerasimov, 1992, p. 82, pl. 18, fig. 40 [mutatio].

**Holotype.** The shell figured by C.F. Rouillier (1849, pl. 50, fig. 97); the specimen is lost. Russia, Moscow Region, Krasnogorskii District, right bank of the Moskva River, near the village of Gal'ev; upper Middle Oxfordian.

**Neotype.** GMM, no. 12/82; Moscow Region, Kolomenskii District, town of Shchurovo (Zarech'e), quarries; Middle Oxfordian, *tenuiserratum* Zone.

**Description.** The shell attains 15–16 mm in height. The protoconch is composed of 3.5–4.0 whorls. The first 1.5 whorls are smooth, and subsequent whorls are bicarinate. The rib running above the suture appears starting from the third whorl. The carinae have ribs. The teleoconch is composed of 12.0–12.5 whorls, its angle is 19°–30°. The whorls are flattened. The maximum width of the whorl is at the second primary rib. The extent of involution is 35%. The suture is deep. The ornamentation is composed of three or four strong primary ribs and up to two faint secondary ribs. The folds are orthocone or opisthocline, their number is 9–12 per whorl (whorl diameter is 5.5 mm). Large, blunt tubercles originate at the places of the folds and ribs crossing. In the first 3.0–3.5 teleoconch whorls, the tubercles of the upper primary rib are larger than those of the second primary rib; in the later whorls, the situation is opposite. The last whorl is 27% as high as the shell. The base of the shell bears from four to six ribs (or only two ribs in aberrant forms). The ends of the folds are present in the upper part of the shell base. The aperture is oval.

**Comparison.** *C. (C.) strangwaysi* is a direct descendant of *C. (C.) pseudoechinatus*, and this fact results in the absence of distinct morphological boundary between these species. However, *C. (C.) strangwaysi* never had a coarse ornamentation like its ancestor had

Explanation of Plate 2

**Figs. 1 and 2.** *Cryptaulax (Cryptaulax) strangwaysi* (Rouillier): (1) neotype GMM, no. 12/82, abapertural view, ×3; (2) GMM, no. 12/78, protoconch, ×102; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone.

**Figs. 3–5.** *Cryptaulax (Neocryptaulax) superstriatus* sp. nov.: (3) holotype GMM, no. 12/18, ×3; (3a) apertural and (3b) abapertural views; (4) GMM, no. 12/76, protoconch, ×61; (5) GMM, no. 12/77, abapertural view, ×3. Mikhailovskii Mine; Lower Callovian, *enodatum* Zone.

**Figs. 6–10.** *Cryptaulax (Neocryptaulax) mutabilis* (Gerasimov): (6) GMM, no. 12/45, ×3; (6a) apertural and (6b) abapertural views; village of Tyrnovo; Middle Callovian; (7) GMM, no. 12/46, abapertural view, ×3; village of Mikhailenino; Middle Callovian, *jason* Zone, *medea* Subzone; (8) GMM, no. 12/42, abapertural view, ×3; town of Makar'ev; Middle Callovian, *jason* Zone, *medea* Subzone; (9) GMM, no. 12/47 (cast), abapertural view, ×3; village of Alpat'ev; Lower Callovian, *koenigi* Zone, *curtilobus* Subzone; (10) GMM, no. 12/43, abapertural view, ×3; village of Tyrnovo; Middle Callovian.

**Figs. 11–15.** *Cryptaulax (Neocryptaulax) salebrosus* (Yamnichenko): (11) GMM, no. 12/44, abapertural view, ×3; village of Mikhailenino; Middle Callovian, *jason* Zone, *medea* Subzone; (12) GMM, no. 12/116, lateral to the aperture, ×3; (13) GMM, no. 12/117, abapertural view, ×3; Mikhailovskii Mine; Lower Callovian, *enodatum* Zone; (14) GMM, no. 12/128 (cast), abapertural view, ×3; village of Alpat'ev; Lower Callovian, *koenigi* Zone, *curtilobus* Subzone; (15) GMM, no. 12/129, abapertural view, ×3; village of Tyrnovo; Middle Callovian.

**Figs. 16–19.** *Microcerithium ostashovense* sp. nov.: (16) GMM, no. 12/108: (16a) abapertural view, ×15, and (16b) protoconch, ×80; (17) holotype GMM, no. 12/19: (17a) apertural view, ×13, (17b) abapertural view, ×13, and (17c) protoconch, ×67; (18) GMM, no. 12/107, abapertural view, ×16; (19) GMM, no. 12/123, abapertural view, ×19. Egor'evskii Phosphorite Mine, quarry no. 7-2bis; Upper Oxfordian, *serratum* Zone, *serratum* Subzone.

(even in the Lower Oxfordian), but obtained one or two early appearing secondary ribs. The comparison with other species is given in the description of those forms.

**Remarks.** Rouillier has illustrated *C. (C.) strangwaysi* with three strong ribs. I found many shells with a rather strong third rib (for example, see Pl. 1, figs. 17, 18) from the other Middle Oxfordian localities. Probably, these specimens correspond the form illustrated by Rouillier. Sokolov (1912) mentioned the poor preservation of fossils from the Middle Oxfordian layers near the village of Gal'evo, but he probably had insufficient material from this particular level. However, it must be taken into account that the outcrop was well exposed in Rouillier's time, so that he had better opportunity to collect a more representative sample from the Middle Oxfordian than did subsequent researchers.

*C. (C.) strangwaysi* is the ancestor of *C. (C.) unzhensis*. The evolution of *C. (C.) strangwaysi* led to weakening of ornamentation, to the point of being indistinct; however, the trend toward an increase in the density of the secondary ornamentation was retained. Because of that, *C. (C.) unzhensis* always has two or three ribs on the spire whorls and four or five ribs on the last whorl. The weakening of ornamentation makes the whorls rounded. It is noteworthy that this evolution leads to a decrease in the size of *C. (C.) unzhensis* (7 mm in contrast to 15–16 mm in *C. (C.) strangwaysi*).

**Occurrence.** Middle Oxfordian, *densiplicatum* Subzone of the *densiplicatum* Zone to the *tenuiserratum* Zone of European Russia; Middle–Upper Oxfordian of France.

**Material.** Middle Oxfordian; village of Nikitino (30 specimens), Afanas'evskii quarry (six specimens), village of Tynovo (13 specimens), village of Vasil'kovo (41 specimens), village of Mikhalenino (134 specimens); Middle Oxfordian, *densiplicatum* Subzone, *densiplicatum* Zone; village of Vasil'kovo (72 specimens), town of Makar'ev (119 specimens); Middle Oxfordian, *tenuiserratum* Zone; town of Shchurovo (Zarech'e) (983 specimens), rock debris of cement plant (28 specimens) and quarry near the cement plant (two specimens).

*Cryptaulax (Cryptaulax) unzhensis* Guzhov, sp. nov.

Plate 1, fig. 19

**Etymology.** From the Unzha River.

**Holotype.** GMM, no. 12/17; Kostroma Region, Makar'evskii District, town of Makar'ev, left bank of Unzha River, North Makar'ev locality; Upper Oxfordian, *alternoides* Zone, *ilovaiskii* Subzone.

**Description.** The shell reaches 7 mm in height. The protoconch is composed of 3.5 whorls. The first whorl is smooth, while subsequent whorls are bicarinate and have a spiral ridge below the suture and a rib above the suture. In the last half of the whorl, the carinae lose ribs and become rounded. The teleoconch is composed of 8.0–8.5 whorls, its angle is 20°–24°. The whorls are slightly convex at the beginning and later

become more inflated and rounded. The maximum width of the whorls corresponds their middle. The extent of involution is 35–40%. The suture becomes deeper with the shell growth. The ornamentation is composed of three primary and two or three secondary ribs of indistinct outlines. Two additional ribs are present on the last whorl. The folds are orthocone or opisthocline in the earlier whorls and become opisthocyrt in the last two and a half whorls. The folds are raised, but not very distinct, and become obscure in the last whorls. The last whorl has 13 or 14 folds. Large spherical tubercles appear on the crossing of ribs and folds. The last whorl is 30% as high as the shell. The base of the shell has four or five distinct ribs and weakened folds. The aperture is oval.

**Ontogenetic changes.** Ontogenetic changes are noticeable from the middle of the eighth teleoconch whorl, where the tubercles (except for the uppermost row) and folds rapidly weaken. The folds turn into indistinct elevations. In addition, the folds become more opisthocyrt, while the whorls become more rounded.

**Comparison.** The species differs from *C. (C.) strangwaysi* in its small shell, indistinct and weakened ornamentation, and convex whorls.

**Occurrence.** Upper Oxfordian, *alternoides* Zone, *ilovaiskii* Subzone of European Russia.

**Material.** Upper Oxfordian, *alternoides* Zone, *ilovaiskii* Subzone; town of Makar'ev (ten specimens).

#### Subgenus *Pseudocerithium* Cossmann, 1884

*Pseudocerithium*: Cossmann, 1884 (in Fischer, 1880–1887), p. 685; Cossmann, 1885, p. 124.

*Cryptaulax (Cryptaulax)*: Cossmann, 1906, p. 37 (pars).

**Type species.** *Cerithium undulatum* Quenstedt, 1858; Upper Bathonian–Lower Callovian substages; Germany.

**Diagnosis.** Shell high-turriculate, slender, with straight generating line. Protoconch unknown. Teleoconch composed of more than 15 flattened whorls. Suture deep. Ornamentation composed of two strong primary and several faint secondary ribs. Folds ranging from numerous to infrequent, forming rows. Aperture circular.

**Species composition.** Twelve species: type species; *C. (P.) bittneri* (Kittl, 1894) [= *Promathildia bittneri*] from the Ladinian–Carnian of Italy; *C. (P.) contortus* (Eudes-Deslongchamps, 1842) [= *Cerithium contortum*] from the Bajocian of France; *C. (P.) denses-triatum* Cossmann, 1885 [= *Pseudocerithium denses-triatum*] from the Bathonian of France; *C. (P.) heptacolpus* (Cossmann, 1913) [= *Cryptaulax heptacolpus*] from the Toarcian of France; *C. (P.) hystrix* (Eudes-Deslongchamps, 1842) [= *Cerithium hystrix*] from the Bajocian of France; *C. (P.) inaequelineatus* (Nützel et Senowbary-Daryan, 1999) [= *Xystrella inaequelineata*] from the Norian–Rhaetian of Iran; *C. (P.) obeliscus* (Scalia, 1903) [= *Chemnitzia obeliscus*] from the

Lower Lias of Italy (Fucini, 1913); *C. (P.) piettei* (Cossman, 1913) [= *Cryptaulax piettei*] from the Oxfordian of France; *C. (P.) rhabdocolpoides* (Haas, 1953) [= *Cryptaulax rhabdocolpoides*] from the Rhaetian of Peru; *C. (P.) scobina* (Eudes-Deslongchamps, 1842) [= *Cerithium scobinum*] from the Lower Pliensbachian of France; and *C. (P.) spiratus* (Moore, 1867) [= *Cerithium spiratum*] from the Hettangian of England.

Pčelintsev (1927c, 1937) mentioned the species *Cryptaulax armata* (Goldfuss) var. *ornata* Pčelintsev [= *C. (P.) ex gr. scobina*] from the ?Aalenian of the northern Caucasus.

**Comparison.** The subgenus differs from other members of the genus in its very slender and more multispiral shell.

#### Subgenus *Neocryptaulax* Gerasimov, 1992

*Cryptaulax (Neocryptaulax)*: Gerasimov, 1992, p. 84.

**Type species.** *Pseudomelania ? mutabilis* Gerasimov, 1955; Middle Callovian of Russia, Kaluga Region.

**Diagnosis.** Shell turriculate, usually with convex or, rarely, straight generating line. Teleoconch whorls convex, becoming flattened with shell growth. Extent of involution 20–37%. Suture ranging from deep to shallow. Spiral ornamentation composed of three to six usually identical ribs. Last two whorls strongly incurved in upper part. Aperture oval, with thickened inner lip and explanate outer lip. Edge of outer lip even and thin. Lips roundly join each other without canals or notches.

**Remarks.** The teleoconch ontogeny can be split into two stages. The first stage (folded whorls) is characterized by infrequent, strong varicose folds, which make the whorls appear inflated. The ribs are much weaker than the folds. The number of folds gradually increases to two or, rarely, four folds per whorl. The second stage (reticulate-ribbed whorls) is characterized by rapid weakening of the folds, their number rapidly increases. The folds can weaken so considerably that they become similar to ribs or even more faint. The number of folds reaches four to eight per whorl. The whorls become flattened. The transition between the stages is gradual or abrupt. The duration of each stage varies greatly within a species and between different species. The subgenus includes some species, for instance, *C. (N.) superstriatus*, which lacks the second ontogenetic stage. The apertural pattern is the most important morphological feature of the subgenus (see below); however, it has not been described in the type species.

**Composition.** Fifteen species: type species; *C. (N.) costaminuerus* (Gründel, 2000) [= *Exelissa costaminuera*] from the Upper Bajocian–Lower Bathonian of France; *C. (N.) decemcostatus* (Smith, 1893) [= *Cerithium decemcostatum*] from the Lower–Middle Oxfordian of Germany; *C. (N.) hausmanni* (Dunker, 1843)

[= *Potamides hausmanni*] from the Berriasian–Valanginian of Germany; *C. (N.) limaeformis* (Roemer, 1836) [= *Cerithium limaeforme*] from the Oxfordian of Germany (Goldfuss, 1844); *C. (N.) rugosus* (Dunker, 1843) [= *Potamides rugosus*] from the Portlandian of Germany; *C. (N.) salebrosus* Yamnichenko, 1987 [= *Procerithium salebrosium*] from the Lower Callovian of Ukraine; *C. (N.) superstriatus* sp. nov.; *C. (N.) tsibe* (d'Orbigny, 1850) [= *Cerithium tsibe*] from the Lias of France (Thevenin, 1908a); *C. (N.) vicinalis* (Thurmann, 1951) [= *Cerithium vicinale*] from the Lower Oxfordian of France (Loriol, 1899); *C. (N.) westfalicus* (Huckreide, 1967) [= *Procerithium (Rhabdocolpus) westfalicum*] from the Upper Kimmeridgian of Germany; *?C. (N.) carbonarius* (Goldfuss in Roemer, 1836) [= *Cerithium carbonarium*] from the Portlandian of Germany; *?C. (N.) guirandi* (Loriol, 1887) [= *Cerithium guirandi*] from the Lower Kimmeridgian of France; *?C. (N.) lorieri* (Hebert et Deslongchamps, 1860) [= *Cerithium lorieri*] from the Callovian of France; *?C. (N.) occidentalis* (Stanton, 1895) [= *Hypsipleura (?) occidentalis*] from the Tithonian of California, United States.

Imprints of several shells, which, possibly, can be assigned to the subgenus, are known from the Oxfordian–Kimmeridgian of China (Yu Wen and Zhu Xianggen, 1983).

**Comparison.** For comparisons, see descriptions of other subgenera.

#### *Cryptaulax (Neocryptaulax) superstriatus* Guzhov, sp. nov.

Plate 2, figs. 3–5

*Cryptaulax (Neocryptaulax) mutabilis*: Gerasimov et al., 1996, pl. 23, fig. 7.

**Etymology.** From the Latin *super* (upper) and *striatus* (striated).

**Holotype.** GMM, no. 12/18; Russia, Kursk Region, Zheleznogorskii District, Mikhailovskii Mine; Lower Callovian, *enodatum* Zone.

**Description.** The shell is up to 15 mm high, with straight generating line. The protoconch is composed of 3.5 whorls. The first whorl is smooth and rounded, the rest of the whorls are bicarinate. The carinae bear ribs. The teleoconch is composed of 9.5 whorls, its angle is 18.5°–33.0°. The whorls are convex; as the shell grows, they become less inflated and obtain more gentle folds. The suture is deep. The early and middle whorls of some specimens are expanded asymmetrically downwards. Usually, the whorls are evenly convex; their maximum width is at the midheight. The extent of involution is 37%. The ornamentation is composed of three strong primary ribs and one or, rarely, two secondary ribs. Two lower primary ribs are the strongest and often project considerably from the whorl surface. The folds are prominent, their number is 11–14 per whorl (in a whorl 5 mm in diameter). They transform from orthocline to opisthocyrt with the shell growth. Large, blunt tubercles ornament the ribs. In

early whorls, the tubercles are almost equal in size; in the middle whorls, the tubercles of the second rib become stronger; and in the last whorls, the tubercles of the third rib become stronger. The last whorl is 28% of the shell height. The base of the shell bears six to eight ribs and the fold ends in its upper part. The aperture is oval.

**Ontogenetic changes.** The folds gradually weaken and become more densely spaced on the last whorls, while the tubercles disappear in ascending order. A slight depression of the lateral whorl surface develops near the aperture. Adult shells probably vary in size and the number of whorls.

**Comparison.** The new species is distinguished from other species of the genus by its prominent and sparse spiral ornamentation and convex whorls. In addition, it is distinguished from *C. (N.) salebrosus* by the absence of the stage of reticulate-ribbed whorls.

**Occurrence.** Lower and Middle Callovian of European Russia.

**Material.** Lower Callovian, *enodatum* Zone, Mikhailovskii Mine (39 specimens); Middle Callovian, *jason* Zone, village of Fokino (one specimen).

*Cryptaulax (Neocryptaulax) mutabilis* (Gerasimov, 1955)

Plate 2, figs. 6–10

*Pseudomelania* ? *mutabilis*: Gerasimov, 1955, p. 186, pl. 40, figs. 15–17.

*Cryptaulax (Neocryptaulax) mutabilis*: Gerasimov, 1992, p. 84 (pars), pl. 22, figs. 9, 10, 13, 15, 17, 18, 20, 22.

*Procerithium octocostatum*: Yamnichenko, 1987, p. 82, pl. 8, figs. 11 and 12.

*Rhabdocolpus (Rhabdocolpus) multinodosum*: Gründel, 1999b, p. 7, pl. 1, figs. 15–20.

**Holotype.** The specimen illustrated by Gerasimov (1955, pl. 40, fig. 15); the depository is unknown. Russia, Kaluga Region, Lyudinovskii District, borehole; Middle Callovian.

**Description.** The shell is up to 10–13 mm high, with convex generating line. The teleoconch is composed of more than eight whorls. The teleoconch angle is 17°–26°. The early and middle whorls are convex, while the last whorls vary from slightly convex to flat. The maximum width of the whorl lies in its middle. The extent of involution is 32%. The suture is deep on early whorls, and becomes shallow later. The ornamentation is composed of six or seven equally developed ribs. The number of folds is 28–35 per whorl (whorl diameter is 3.2–3.5 mm). Small and rounded tubercles ornament the ribs. The last whorl is 26–28% as high as the shell. The base of the shell bears six to nine ribs. The aperture is circular. The parietal and siphonal grooves are present inside the last whorl, the grooves are smoothed out near the aperture.

The ontogeny of teleoconch ornamentation passes two stages. The first stage is observed in the early whorls or the early and middle whorls. At this stage, two to four folds are added in each subsequent whorl. The second stage is characterized by a decrease in coil-

ing angle, flattening of the whorls, and changes in the appearance of the folds. The folds become weaker and very densely spaced. Six to eight additional folds appear in each subsequent whorl. The folds are opisthocyrt, as prominent as, or weaker, than the ribs.

**Ontogenetic changes.** The last 1.5–2.0 whorls are characterized by the following changes: (1) the uppermost rib with large tubercles becomes more prominent; (2) the subsutural area of the whorl becomes more gently sloping, and this results in slightly gradate appearance of the whorls; and (3) the upper part of the whorl surface forms a depression below the upper rib.

**Comparison.** The comparison is given in the description of other species and below in the remarks.

**Remarks.** I recognize two morphological groups within this species, i.e., *C. (N.) mutabilis* α (Pl. 2, figs. 6, 8, 10) and *C. (N.) mutabilis* β (Pl. 2, figs. 7, 9). The two groups are connected by a series of transitional forms. Their definitions are concerned with the extreme intraspecific variability of *C. (N.) mutabilis*. The morph *C. (N.) mutabilis* α is characterized by a well-pronounced second stage (three-quarters of the shell) and a rather short first stage. The number of folds varies from 28 to 35 at the second stage. The second stage is shorter in morph *C. (N.) mutabilis* β. The folds are coarser and more widely spaced, they number 20–22; the whorls are more convex. In addition, the spire of *C. (N.) mutabilis* β lacks a convex profile. This morph displays a wide variety of intergrades to *C. (N.) salebrosus* (see below).

The species boundaries are difficult to distinguish due to a great variability of the shell morphology and variability in the ornamentation ontogeny. A wide range of transitional forms between the finely ornamented *C. (N.) mutabilis* α to coarsely ornamented *C. (N.) salebrosus* does exist. The morph *C. (N.) mutabilis* α occurs in various facies from medium-grained sands (Kostroma Region) to clayey silts (Kursk Region). Material in Gerasimov's collection and in my personal material comes mainly from sandy rocks. *C. (N.) mutabilis* β and *C. (N.) salebrosus* occur in the same range of facies both together with and without *C. (N.) mutabilis* α. Judging from the material available, the coarsely ornamented *C. (N.) salebrosus* prefers muddy sediments. For the time being, it is difficult to determine whether *C. (N.) mutabilis* and *C. (N.) salebrosus* represent a single, extremely variable species, or they are separate, ecologically isolated species with coincident morphology. This uncertainty caused Gerasimov to place all of them in a single species, *C. mutabilis*. *C. (N.) salebrosus* includes forms approaching *C. (N.) mutabilis*, but differing in the late and slight development of the stage of reticulate-ribbed whorls. This group exhibits polymorphism in the duration of the two stages of ornamentation ontogeny and in the extent to which the folded whorls are transformed into the reticulate-ribbed whorls.

**Occurrence.** Lower Callovian, *koenigi* Zone, to the Middle Callovian of European Russia; Lower Callovian of Ukraine; Bathonian of Poland.

**Material.** Lower Callovian, *koenigi* Zone, *gowe-rianius* Subzone; village of Uzhovka (one specimen); Lower Callovian, *koenigi* Zone; village of Burdovo (one specimen); Lower Callovian, *koenigi* Zone, *curtilobus* Subzone; village of Burdovo (17 specimens), village of Ileshevo (22 specimens), village of Alpat'ev (five specimens); Lower Callovian, *calloviense* Zone; town of Manturovo (two specimens); Lower Callovian, *?calloviense* Zone; town of Manturovo (one specimen); Lower Callovian, *enodatum* Zone; village of Burdovo (five specimens), Mikhailovskii Mine (five specimens); Middle Callovian, *jason* Zone, *medea* Subzone; village of Mikhalenino (48 specimens), town of Makar'ev (44 specimens); Middle Callovian, village of Tyrnovo (21 specimens).

*Cryptaulax (Neocryptaulax) salebrosus* (Yamnichenko, 1987)

Plate 2, figs. 11–15

*Procerithium salebrosus*: Yamnichenko, 1987, p. 83, pl. 8, figs. 13 and 14.

*Cryptaulax (Neocryptaulax) mutabilis*: Gerasimov, 1992, p. 84 (pars), pl. 22, figs. 3, 4, 7, 8, 21; Gerasimov *et al.*, 1996, pl. 23, figs. 5 and 6.

**Holotype.** GM IGN, no. 2152/82; Ukraine, Chernigov Region, borehole near the town of Shchors; Lower Callovian.

**Description.** The shell is about 12–13 mm high, with straight generating line. The protoconch is unknown. The teleoconch is composed of more than seven whorls, its angle is 19°–24°. The early whorls are convex; later whorls are often flattened. The maximum whorl width is at the midheight of the whorls. The extent of involution is 32%. The suture is relatively deep. The ornamentation is composed of five or six equally prominent ribs. The folds are strong, numbering 11–16 per whorl (whorl diameter is 3.5–4.0 mm). Large rounded tubercles ornament the places of folds and ribs crossing. The last whorl is about 27–29% of the shell height. The base of the shell bears six to nine ribs and the fold ends in its upper part. The aperture is oval.

The teleoconch ornamentation passes through the first stage or through the first and second stages. The first stage is observed in the entire teleoconch, except for the last 0–2 whorls. One or two slightly opisthocyrt folds are added in each subsequent whorl. At the second stage, the folds become densely spaced and slightly weakened, but still remain rather strong. Two, three, or four folds are added in each subsequent whorl of this part of the shell. The folds become more opisthocyrt (in some shells, the folds are opisthocyrt since the early whorls).

**Comparison.** The genus differs from *C. (N.) superstriatus* in the dense spiral ornamentation and from *C. (N.) mutabilis* in the coarser and more widely spaced folds and less developed reticulate-ribbed whorls only near the aperture (not in all specimens).

**Occurrence.** Lower–Middle Callovian of European Russia; Lower Callovian of Ukraine.

**Material.** Lower Callovian, *elatmae* Zone; village of Prosek (one specimen); Lower Callovian, *koenigi* Zone, *curtilobus* Subzone; village of Alpat'ev (three specimens), Unzha River, near the mouth of Pezhenga River (two specimens); Lower Callovian, *enodatum* Zone; Mikhailovskii Mine (ten specimens); Middle Callovian; village of Tyrnovo (two specimens).

#### Genus *Microcerithium* Guzhov, gen. nov.

**Etymology.** From the Greek *mikros* (small) and the generic name *Cerithium*.

**Type species.** *M. ostashovense* sp. nov.; Upper Oxfordian, *serratum* Zone, *serratum* Subzone; Russia, Moscow Region, Voskresenskii District, Egor'evskii Phosphorite Mine, quarry no. 7-2bis near the village of Ostashovo.

**Diagnosis.** Shell small, turriculate, with straight generating line. Protoconch composed of 1.0–1.5 rounded and smooth whorls, followed by 2.0–3.0 whorls with two carinae or rounded angulations. Teleoconch composed of 5.5–7.5 whorls. Whorls flattened or convex and nongradate. Ornamentation composed of two or three primary ribs and several (0–3) secondary ribs and folds. Folds extending from suture to suture, rather faint, indistinct, and forming small rounded tubercles at intersections of ribs and folds. Shell base high, convex, widely conical, with several ribs. Aperture circular, slightly deflected in the lower part.

**Species composition.** Two species: type species and *M. bicinctum* (Gerasimov, 1992).

**Comparison.** The genus differs from all other members of the subfamily in the smaller shell size. In addition, it is distinguished from *Infacerithium* by the constantly present folds; from *Cryptaulax* it differs by the underdeveloped teleoconch ornamentation and negative anaboly (see remarks).

**Remarks.** Negative anaboly is expressed in the loss of the latest stage of the teleoconch whorls with well-differentiated ornamentation. Possibly, the mollusks reached maturity earlier. The teleoconch length decreases, the development of the ornamentation becomes slower, and the shell size decreases threefold. Thus, neoteny takes place.

#### *Microcerithium ostashovense* Guzhov, sp. nov.

Plate 2, figs. 16–19

**Etymology.** From the village of Ostashovo.

**Holotype.** GMM, no. 12/19; Russia, Moscow Region, Voskresenskii District, Egor'evskii Phosphorite Mine, quarry no. 7-2bis; Upper Oxfordian, *serratum* Zone, *serratum* Subzone.

**Description.** The shell attains 4.8 mm in height. The protoconch is composed of 3.5–4.0 whorls. The first two whorls are smooth, followed by whorls with two rounded angulations without ribs. Two rows of



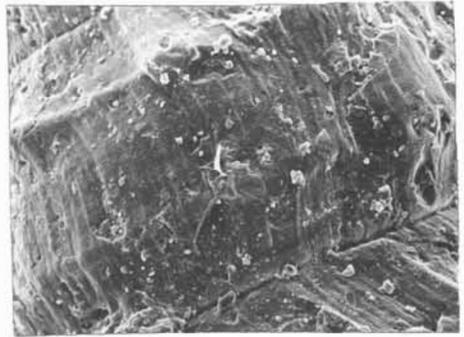
1



2a



2b



2c



3a



3b



4



5



6a



6b



7a



7b



7c



8



9



10



11



12a



12b



12c

tubercles appear above the suture since the 3.5 whorl. The teleoconch is composed of 7.0–7.5 whorls. The teleoconch angle is 22°–28°. The whorls become more convex with shell growth. The maximum width of the whorls is at their midheight. The extent of involution is 35%. The suture is angular and relatively deep. The ornamentation is composed of two primary ribs and one secondary rib (the last whorl has three faint secondary ribs). Strong and rather distinct folds cross the ribs; the number of folds is 13–16 per whorl (whorl diameter is 1.6 mm). The folds are opisthocyrt, more deflected in the lower part of the whorls. Rounded tubercles are formed at the intersections of the ribs and folds. The upper rib bears slightly larger tubercles. The last whorl is 24–28% as high as the shell. The base of the shell bears five ribs. The upper rib is strong and distinct; juvenile material suggests that it is a primary rib. The rest of the ribs are faint and indistinct. The aperture is widely lenticular.

**Ontogenetic changes.** Age-related variability is manifested in profound changes of ornamentation and whorl shape. From the 4.5–4.6 teleoconch whorl, a clear weakening of the folds and ribs occurs. The whorls become more inflated and rounded, and the folds become more opisthocyrt. Two additional ribs often develop; coarse growth lines sometimes appear.

**Comparison.** The comparison is given in the description of *M. bicinctum*.

**Occurrence.** Oxfordian, *praecordatum*–*serratum* zones, of Moscow Region.

**Material.** Upper Oxfordian, *serratum* Zone, *serratum* Subzone; Egor'evskii Phosphorite Mine, quarry no. 7-2bis (344 specimens).

*Microcerithium bicinctum* (Gerasimov, 1992)

Plate 3, figs. 1–3

*Procerithium* (*Rhabdocolpus*) *bicinctum*: Gerasimov, 1992, p. 73, pl. 18, figs. 5, 7–9, and 31; Gerasimov *et al.*, 1995, pl. 19, fig. 16.

**Holotype.** GGM, no. VI-222/33; Russia, Moscow, Kuntsevo District, Suvorovskii Park; Volgian Stage, *virgatus* Zone, *virgatus* Subzone (non *nikitini* sensu Gerasimov, 1992).

**Description.** The shell attains 4.5 mm in height. Probably, the protoconch is composed of about 3.5–

4.5 whorls. The first whorl is smooth, followed by bicarinate whorls. The carinae are well-developed, and bear ribs. A faint rib appears above the suture from the third whorl onwards. The protoconch–teleoconch boundary is usually marked by gradual development of collabral elevations. Therefore, there is no way to determine the exact protoconch length. The teleoconch is composed of 6.0–7.0 whorls. The teleoconch angle is 20.0°–23.5°. The whorls are flattened. The maximum width of the whorl is at the second primary rib. The extent of involution is 21–25%. The suture is rather deep. The ornamentation is composed of three, usually rather strong primary ribs and a single secondary rib (the latter is often absent). From the third teleoconch whorl, the ribs weaken and become faint. The upper primary rib is stronger than the second. The folds run across the ribs, the number of folds is 12–18 per whorl (in a whorl 1.2 mm in diameter). The folds are arched, faint, and indistinct. Slight bulges appear at the points of intersection of the folds with the upper rib. The folds are opisthocyrt and particularly prominent on the second whorl since their appearance (on earlier or later whorls, the folds weaken). The last whorl is 32–38% of the shell height. The base of adults bears four thin ribs. The aperture is trapezoid in immature shells and becomes oval in adult shells.

**Ontogenetic changes.** As the shell grows, the ornamentation is smoothed, i.e., the second primary rib is the first to disappear; then, the upper rib and the upper angulation are smoothed out. The folds almost disappear, become narrow, very faint, and densely spaced. The whorl gets rounded outlines.

**Comparison.** The species differs from *M. ostashovense* in the protoconch with well-developed carinae, the absence of any noticeable changes in ornamentation at the protoconch–teleoconch transition, and only slightly developed ornamentation.

**Remarks.** The early whorls of this species differ from those of *Infacerithium* (*Kuntseviella*) *kunceviense* in the straight-conical shell shape and, usually, in the more pronounced folds. The protoconch of *M. bicinctum* is wider and transits into the teleoconch, which is expanding in a similar rapid way. The protoconch and early teleoconch whorls of *I. (K.) kunceviense* expand

Explanation of Plate 3

**Figs. 1–3.** *Microcerithium bicinctum* (Gerasimov): (1) GMM, no. 12/36, abapertural view, ×15; (2) GMM, no. 12/34: (2a) abapertural view, ×20, (2b) protoconch, ×75, and (2c) microsculpture of the teleoconch, ×100; (3) GMM, no. 12/35, ×13: (3a) apertural and (3b) abapertural views. Moscow, Kuntsevo, Suvorovskii Park; Middle Volgian, *virgatus* Zone, *virgatus* Subzone.

**Fig. 4.** *Microcerithium* sp.; PIN, no. 4863/164, ×8; village of Undory; Upper Kimmeridgian, *eudoxus* Zone.

**Figs. 5–11.** *Infacerithium* (*Kuntseviella*) *kunceviense* (Gerasimov); Moscow, Kuntsevo, Suvorovskii Park; middle Volgian: (5) GMM, no. 12/64, abapertural view, ×15; (6) GMM, no. 12/63, ×10: (6a) apertural and (6b) abapertural views; (7) GMM, no. 12/62: (7a) apertural view, ×12, (7b) abapertural view, ×12, and (7c) protoconch, ×69; (8) GMM, no. 12/68, abapertural view, ×13; *virgatus* Zone, *virgatus* Subzone; (9) GMM, no. 12/67, lateral to the aperture, ×13; *nikitini* Zone; (10) GMM, no. 12/65, abapertural view, ×11; *virgatus* Zone, *virgatus* Subzone; (11) GMM, no. 12/66, abapertural view, ×10; *nikitini* Zone.

**Fig. 12.** *Infacerithium* (*Infacerithium*) *kirilli* sp. nov.: holotype GMM, no. 12/20: (12a) apertural view, ×19, (12b) abapertural view, ×12, and (12c) protoconch, ×75. Egor'evskii Phosphorite Mine, quarry no. 7-2bis; Upper Oxfordian, *serratum* Zone, *serratum* Subzone.

more slowly than subsequent whorls. Thus, the upper part of the shell is narrower, and the generating line is somewhat concave.

**Occurrence.** Volgian Stage, Middle Substage, *virgatus* Zone, *virgatus* Subzone of European Russia.

**Material.** Volgian Stage, Middle Substage, *virgatus* Zone, *virgatus* Subzone; Moscow, Kuntsevo (157 specimens).

*Microcerithium* sp.

Plate 3, fig. 4

Several shells of the genus *Microcerithium* from the Gerasimov's collection come from the Upper Kimmeridgian clays (*eudoxus* Zone) of the Ulyanovsk Region. Unfortunately, only the protoconchs and sometimes the earliest teleoconch whorls are preserved. Therefore, it was not possible to determine these specimens beyond the generic level. The protoconchs bear two angulations lacking ribs, as in *M. ostashovense*, while the first teleoconch whorl is ornamented with numerous well-developed folds. Several strong ribs are also visible on the scarce fragments of the later whorls.

**Material.** Upper Kimmeridgian, *eudoxus* Zone; village of Undory (two juvenile specimens and several small fragments).

**Genus *Infacerithium* Gründel, 1974**

*Procerithium* (*Infacerithium*): Gründel, 1974b, p. 832.

*Rhabdocolpus* (*Infacerithium*): Gründel, 1999b, p. 11.

**Type species.** *Procerithium* (*Infacerithium*) *klebyense* Gründel, 1974; Upper Bathonian–Lower Callovian of Poland [= *Procerithium* (*Infacerithium*) *satum* Gründel, 1974].

**Diagnosis.** Shell small, turriculate, with straight generating line. Protoconch composed of 1.0–1.5 smooth rounded whorls and 2.0–2.5 bicarinate whorls. Teleoconch whorls flat or slightly convex and slightly gradate or nongradate. Extent of involution 20–35%. Ornamentation composed of three primary ribs and several (from one to three) secondary ribs. Ribs constant in ontogeny, or smoothed out, except for upper rib. Folds ranging from very strong and distinct to faint and vestigial. In ontogeny, folds weaken on last several whorls, or on entire shell. Tubercles of upper rib (if present) significantly larger than those of other ribs. Shell base high, widely conical and convex, with several ribs. Aperture circular or oval.

**Composition.** Subgenera *Infacerithium* Gründel, 1974 and *Kuntseviella* subgen. nov.

**Comparison.** The genus differs from other representatives of the subfamily in the disappearance of collabral ornamentation on last several whorls or on the entire shell.

**Remarks.** The shell of *Infacerithium* is probably siphonostomatous, like that of *Cryptaulax* sensu stricto, which I consider to be the ancestor of *Infacerithium*. However, the demonstrative material has not yet been illustrated.

**Occurrence.** Bathonian–Volgian stages of Europe.

**Subgenus *Infacerithium* Gründel, 1974**

*Procerithium* (*Infacerithium*): Gründel, 1974b, p. 832.

*Rhabdocolpus* (*Infacerithium*): Gründel, 1999b, p. 11.

**Type species.** *Procerithium* (*Infacerithium*) *klebyense* Gründel, 1974; Upper Bathonian–Lower Callovian of Poland [= *Procerithium* (*Infacerithium*) *satum* Gründel, 1974].

**Diagnosis.** Protoconch composed of 1.0–1.5 smooth, rounded whorls followed by 2.5 bicarinate whorls. Ribs on carinae weaken at end of protoconch, and carinae become rounded. Teleoconch whorls usually slightly gradate, flat or slightly convex. Extent of involution about 35%. Ribs constant in ontogeny or smoothed out, except upper rib. Folds vary from faint and indistinct to strong and prominent. Folds cross ribs, forming tubercles, often only on upper rib. Largest tubercles always on upper rib. Folds usually weaken in ontogeny, completely absent from last whorls or transform into indistinct low elevations. Aperture circular or oval.

**Species composition.** Nine species: type species; *I. (I.) calloviense* (Gründel, 1999) [= *Rhabdocolpus* (*Infacerithium*) *calloviense*] from the Callovian of Germany; *I. (I.) kirilli* sp. nov., *I. (I.) medium* (Yamnichenko, 1987) [= *Procerithium medium*] from the Upper Bajocian of Ukraine, *I. (I.) regressum* (Yamnichenko, 1987) [= *Procerithium regressum*] from the Bajocian of Ukraine; *I. (I.) substriatum* (Gründel, 1974) [= *Procerithium* (*Infacerithium*) *substriatum*] from the Bathonian of Poland; *I. (I.) variabilis* (Morris et Lycett, 1850) [= *Chemnitzia variabilis*] from the Bathonian of England; *?I. (I.) gristowiense* (Gründel, 1999) [= *Procerithium* (?*Rhabdocolpus*) *gristowiense*] from the Callovian of Germany), and *?I. (I.) mysticum* (Yamnichenko, 1987) [= *Procerithium mysticum*] from the Upper Aalenian–Lower Bajocian of Ukraine.

**Comparison.** The comparison is given in the description of the subgenus *Infacerithium* (*Kuntseviella*).

***Infacerithium* (*Infacerithium*) *kirilli* Guzhov, sp. nov.**

Plate 3, fig. 12; Plate 4, figs. 1 and 2

**Etymology.** In honor of Kirill M. Shapovalov, amateur paleontologist, who found this species.

**Holotype.** GMM, no. 12/20; Russia, Moscow Region, Voskresenskii District, Egor'evskii Phosphorite Mine, quarry no. 7-2bis; Upper Oxfordian, *serratatum* Zone, *serratatum* Subzone.

**Description.** The shell attains 2.7 mm in height. The protoconch is composed of four whorls. The first 1.2 whorls are smooth, the remainder are bicarinate. In the last 1.5 whorls, a rib runs above the suture. It disappears under the suture just before the protoconch end. All ribs are tuberculate. In addition, a row of small tubercles runs below the suture. The teleoconch is dis-

tinguished by the appearance of the folds and disappearance of the ribs. The teleoconch is composed of 4.5 whorls, its angle is 13.5°. The whorls are convex, asymmetrically expanding downwards. The maximum width of the whorls is in the lower part. The suture is shallow. The ribs disappear on the first 0.5–1.0 teleoconch whorls. Subsequently, three to five wide, ribbon-like faint ribs appear. The ribs are separated by shallow furrows. The folds are strong on the early whorls, and weaken considerably on the last whorl. Tubercles are absent. The last whorl is not expanded, giving the shell a slightly pupoid appearance. Six ribs and nine folds ornament the last whorl. At the end of the shell, the collabral ornamentation is reduced below the suture and represented by a subsutural row of tubercles. The base of the shell bears two faint, wide ribbon-like ribs on the outer part. The aperture is circular.

**Comparison.** The species differs from all other members of the subgenus by a combination of well-developed folds and the very faint spiral ornamentation, and by the pupoid shape of the shell.

**Occurrence.** Upper Oxfordian, *serratum* Zone, *serratum* Subzone of European Russia.

**Material.** Upper Oxfordian, *serratum* Zone, *serratum* Subzone; Egor'evskii Phosphorite Mine, quarry no. 7-2bis (two specimens).

**Subgenus *Kuntseviella* Guzhov, subgen. nov.**

**Etymology.** From Kuntsevo (district of Moscow), where the type species has been found.

**Type species.** *Procerithium (Cosmocerithium) kunceviense* Gerasimov, 1992; Volgian Stage, ?*nikitini* Zone; Russia, Moscow.

**Diagnosis.** Protoconch composed of 1.0–1.5 rounded smooth whorls followed by 2.0–2.5 bicarinate whorls. Morphological boundary between protoconch and teleoconch indeterminable, since neither commissure nor decrease in cross section recognized. Teleoconch whorls flattened, nongradate. Extent of involution 20–25%. Secondary ribs present above upper primary rib. Collabral ornamentation absent or reduced to indistinct elevations, visible only on lateral surface. Tubercles absent. Aperture rounded trapezoid.

**Species composition.** Type species.

**Comparison.** This subgenus differs from the subgenus *Infacerithium* by the absence or weak development of collabral ornamentation, the absence of any morphological changes at the protoconch and teleoconch transition, and the presence of the secondary ribs above the upper primary rib (this feature has not been recorded in other members of the *Cryptaulacidae*).

***Infacerithium (Kuntseviella) kunceviense* (Gerasimov, 1992)**

Plate 3, figs. 5–11

*Procerithium (Cosmocerithium) kunceviense*: Gerasimov, 1992, p. 75, pl. 18, figs. 25–27, 29, 31, 32, and 41; Gerasimov *et al.*, 1995, pl. 19, figs. 14 and 15.

**Holotype.** GGM, no. VI 222/32; Moscow, Kuntsevo, Suvorovskii Park; Volgian Stage, ?*nikitini* Zone.

**Description.** The shell attains 5.7 mm in height. The protoconch includes about 3.5 whorls. The first 1.0–1.5 whorls are smooth, the rest protoconch whorls are bicarinate. The carinae bear ribs. The teleoconch is composed of about 11.0–11.5 whorls, its angle is 23°–29°. The maximum whorl width is at the second primary rib. The extent of involution is 22–25%. The suture is deep in early whorls and later usually becomes shallow. The early teleoconch whorls are bicarinate; later, the angulations are retained or disappear; in the latter case, the whorls become rounded. The whorls conically expand downwards. The ornamentation is composed of three primary ribs and two to four (rarely only one) secondary ribs (in a whorl 1.7–2.0 mm in diameter). One or, rarely, two ribs run above the upper primary rib. The ribs become equal in prominence on the last whorls. The second primary rib is the strongest. From the 5.5–6.5 whorls counted from the aperture, the secondary ribs appear below the upper primary rib; and from the 7.0–9.5 whorls, the secondary ribs appear above this rib. The ribs are crossed by the folds, which are reduced to wide indistinct procline elevations between two upper primary ribs. The folds are wedge-shaped, i.e., they are wide near the second primary rib and wedge out at the uppermost primary rib. The elevations give the ribs a finely undulating appearance and often disappear in several last whorls. In addition, a spiral microornamentation composed of tiny threads is visible in many specimens. The last whorl is 27–33% of the shell height. The base of the shell bears from three to five ribs.

**Occurrence.** Volgian Stage, *virgatus* Subzone of the *virgatus* Zone, to the *mosquensis* Subzone of the *nodiger* Zone; European Russia.

**Material.** Volgian Stage, Middle Substage, *virgatus* Zone, *virgatus* Subzone; Moscow, Kuntsevo (129 specimens); Volgian Stage, Middle Substage, *nikitini* Zone; Moscow, Kuntsevo (68 specimens).

**Subfamily *Exelissinae* Guzhov, subfam. nov.**

**Type genus.** *Exelissa* Piette, 1860.

**Diagnosis.** Shell ranging from low conical to high-turriculate, with straight or convex generating line. First protoconch whorls smooth, later whorls with one or two carinae. Teleoconch ornamentation composed of three primary and several secondary ribs and folds. Last whorl considerably modified. It deflected downwards, narrowed, and lacking collabral ornamentation. Shell base with numerous ribs. Aperture circular, with short, deep, narrow groove in basal area.

**Generic composition.** Six genera: *Cimolio-centrum* Cossmann, 1908; *Cupaniella* Gemmellaro, 1911; *Exelissa* Piette, 1860; *Protocerithium* Bistram,



1



2



3



4a



4b



5a



5b



5c



6



7



8



9



10



11



12



13a



13b



14



15



16



17a



17b



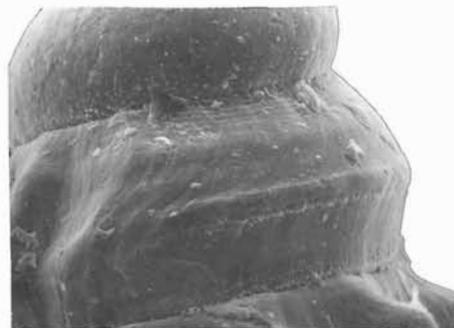
18



19a



19b



19c

1903; *Shurovites* gen. nov.; and *Teliochilus* Cossmann, 1906.

**Comparison.** The new subfamily is distinguished from the *Cryptaulacinae* by the modified last whorl and the presence of the groove.

**Occurrence.** Jurassic and Cretaceous of Europe, North America, and Africa.

### Genus *Exelissa* Piette, 1860

*Exelissa*: Piette, 1860, p. 14; Zittel, 1881–1885, p. 208; Cossmann, 1913, p. 112 (pars).

*Kilvertia*: Lycett, 1863, p. 15.

*Exelissa* (*Exelissa*): Cossmann, 1906, p. 40; Wenz, 1940, p. 731.

*Cryptaulax* (*Cryptoptyxis*): Cossmann, 1906, p. 39; Wenz, 1940, p. 730.

**Type species.** *Cerithium strangulatum* d'Archiac, 1843; Bathonian (?Middle); France, Aisne Department, Eparcy.

**Diagnosis.** Shell small or medium-sized, turriculate or, rarely, high-turriculate, with convex or straight generating line. Protoconch composed of one rounded and smooth whorl followed by three bicarinate whorls (subgenus *Exelissa*). Whorls flattened, nongradate. Suture shallow. Ornamentation composed of three primary ribs and several (0–3) secondary ribs. Spiral ornamentation sometimes composed of rows of tubercles. Ribs crossed by folds, which constitute from four to nine axial rows. Folds prominent and coarse, carinate, forming tubercles originating at intersections with ribs. Last whorl narrowed and rounded, with tendency toward vermiform shape. Shell base high, cup-shaped, with numerous ribs and ends of folds. Aperture circular or oval.

**Composition.** Two subgenera, *Exelissa* sensu stricto and *Pyrazopsis* Hacobjan, 1972.

**Comparison.** The genus differs from *Cupaniella* in the robust folds, arranged into four to nine axial rows; from *Cimoliocentrum* it is distinguished by the absence of internal folds.

**Occurrence.** Jurassic–Cretaceous of Europe; Upper Cenomanian of Asia (Armenia); Pliensbachian of North Africa (Morocco); Aalenian–Oxfordian of

North America (USA); ?Campanian–Maastrichtian of South America (Peru).

### Subgenus *Exelissa* Piette, 1860

*Exelissa*: Piette, 1860, p. 14; Zittel, 1881–1885, p. 208; Cossmann, 1913, p. 112 (pars).

*Exelissa* (*Exelissa*): Cossmann, 1906, p. 40; Wenz, 1940, p. 731.

*Cryptaulax* (*Cryptoptyxis*): Cossmann, 1906, p. 39; Wenz, 1940, p. 730.

**Type species.** *Cerithium strangulatum* d'Archiac, 1843; Bathonian (?Middle); France, Department Aisne, Eparcy.

**Diagnosis.** Shell turriculate, rarely high-turriculate, with convex or straight generating line. Ornamentation composed of three primary ribs and several (1–3) secondary ribs. Ribs crossed by fold, arranged into four to nine axial rows. Last whorl always modified (see generic diagnosis).

**Species composition.** Thirty species: type species (seven rows of folds, convex generating line); *E. (E.) angistoma* (Hebert et Deslongchamps, 1860) [= *Cerithium angistomum*] from the Callovian of France (five rows of folds, straight generating line); *E. (E.) barremica* Sayn, 1932 [= *Cryptoptyxis barremicum*] from the Barremian of Spain (six rows of folds, straight generating line); *E. (E.) bathonica* (Lycett, 1863) [= *Cerithium bathonica*] from the Bathonian of England (seven rows of folds, convex generating line); *E. (E.) bourgeati* (Loriol, 1887) [= *Cerithium bourgeati*] from the Lower Kimmeridgian of France (five rows of folds, straight generating line); *E. (E.) desplanchei* (Piette, 1857) [= *Cerithium desplanchei*] from the Bathonian of France (five or six rows of folds, straight generating line); *E. (E.) destefanii* (Simonelli, 1882) [= *Cerithium destefanii*] from the Lower Lias of Italy (five rows of folds, ? generating line); *E. (E.) distans* Cossmann, 1913 from the Upper Oxfordian of France (eight rows of folds, abruptly changed for five rows of folds in the last whorls, straight generating line); *E. (E.) distephanoi* (Parona, 1883) [= *Cerithium distephanoi*] from the Lower Lias of Italy (six rows of

### Explanation of Plate 4

**Figs. 1 and 2.** *Infacerithium (Infacerithium) kirilli* sp. nov.: (1) holotype GMM, no. 12/20, fragment of protoconch ornamentation,  $\times 135$ ; (2) GMM, no. 12/103, abapertural view,  $\times 30$ . Egor'evskii Phosphorite Mine, quarry no. 7-2bis; Upper Oxfordian, *serratatum* Zone, *serratatum* Subzone.

**Figs. 3–12.** *Exelissa (Exelissa) quinaria* (Trautschold): (3) GMM, no. 12/100, lateral to the aperture,  $\times 3$ ; (4) GMM, no. 12/97: (4a) apertural view,  $\times 3$ , and (4b) protoconch,  $\times 85$ ; (5) neotype GMM, no. 12/95,  $\times 3$ : (5a) apertural view, (5b) left of the aperture, and (5c) abapertural view; (6) GMM, no. 12/96, abapertural view,  $\times 3$ ; (7) GMM, no. 12/102, abapertural view,  $\times 3$ ; (8) GMM, no. 12/94, abapertural view,  $\times 3$ ; (9) GMM, no. 12/99, left of the aperture,  $\times 3$ ; (10) GMM, no. 12/98, protoconch,  $\times 101$ ; (11) GMM, no. 12/101, apertural view,  $\times 3$ ; (12) GMM, no. 12/131, apertural view,  $\times 3$ . Town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratatum* Zone.

**Figs. 13–15.** *Shurovites multinodosus* (Gründel): (13) GMM, no. 12/55,  $\times 3$ : (13a) apertural and (13b) abapertural views; Tyrnovo; Middle Callovian; (14) GMM, no. 12/56 (cast), lateral to the aperture,  $\times 4$ ; village of Alpat'evo; Lower Callovian, *koenigi* Zone, *curtilobus* Subzone; (15) GMM, no. 12/54, abapertural view,  $\times 3$ ; Tyrnovo; Middle Callovian.

**Fig. 16.** *Shurovites* sp. 1: GMM, no. 12/22 (cast),  $\times 4$ . village of Alpat'evo; Lower Callovian, *koenigi* Zone, *curtilobus* Subzone.

**Figs. 17–19.** *Shurovites shurovensis* sp. nov.: (17) holotype, GMM, no. 12/21,  $\times 4$ : (17a) apertural and (17b) abapertural views; (18) GMM, no. 12/125, abapertural view,  $\times 4$ ; village of Nikitino; Middle Oxfordian; (19) GMM, no. 12/133: (19a) left of the aperture,  $\times 11$ , (19b) protoconch,  $\times 88$ , and (19c) fragment of the protoconch ornamentation,  $\times 190$ ; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratatum* Zone.

folds, straight generating line); *E. (E.) dollfusi* (Choffat, 1901) [= *Melania dollfusi*] from the Senonian of Portugal (seven rows of folds); *E. (E.) formosa* (Imlay, 1941) [= *Cryptoptyxis* (?) *formosum*] from the Middle–Upper Oxfordian of the southern United States (seven rows of folds, straight generating line); *E. (E.) forojuliensis* (Pirone, 1878) [= *Cerithium forojuliensis*] from the Tithonian of Italy (five rows of folds, straight generating line); *E. (E.) grimaldi* (Guirand et Ogerien, 1865) [= *Cerithium grimaldi*] from the Lower Kimmeridgian of France (Loriol, 1887) (five rows of folds, straight generating line); *E. (E.) heliodore* (d'Orbigny, 1850 in Cottreau, 1928) [= *Cerithium heliodore*] from the Oxfordian of France (five rows of folds); *E. (E.) hohenegeri* (Zittel, 1873) [= *Cerithium hohenegeri*] from the Upper Tithonian of Czechia (five rows of folds, straight generating line); *E. (E.) normaniana* (d'Orbigny, 1850 in Cossmann, 1913) [= *Cerithium normanianum*] from the Bajocian of France (seven rows of folds, convex generating line); *E. (E.) polygona* (Fucini, 1913) [= *Tomocheilus polygonum*] from the Lower Lias of Italy (seven to nine rows of folds [= only seven are shown in the text-fig.], convex generating line); *E. (E.) prismatophora* Cossmann, 1913 from the Toarcian of France (seven rows of folds, straight generating line); *E. (E.) pupoides* (Hebert et Deslongchamps, 1860) [= *Cerithium pupoides*] from the Callovian of France (five rows of folds, slightly convex generating line); *E. (E.) pusilla* Dubar, 1948 from the Upper Pliensbachian of Morocco (seven rows of folds, convex generating line); *E. (E.) quinaria* (Trautschold, 1866); [= *Cerithium quinarium*]; *E. (E.) quinquangularis* (Hebert et Deslongchamps, 1860) [= *Cerithium quinquangularis*] from the Callovian of France (five rows of folds, slightly convex generating line); *E. (E.) specula* (Lycett, 1863) [= *Kilvertia specula*] from the Bathonian of England (six rows of folds, convex generating line); *E. (E.) spissa* Dubar, 1948 from the Upper Pliensbachian of Morocco (eight rows of folds, convex generating line); *E. (E.) strueveri* (Gemmellaro, 1878) [= *Cerithium strueveri*] from the Lower Lias of Italy (eight rows of folds, convex generating line); *E. (E.) toradoi* (Gemmellaro, 1878) [= *Cerithium toradoi*] from the Lower Lias of Italy (five to seven rows of folds, convex generating line); *E. (E.) ursicina* (Loriol, 1889) [= *Cerithium ursicinum*] from the Upper Oxfordian of France (seven rows of folds, straight generating line); *E. (E.) valanginensis* (Pčelintsev, 1965) [= *Pyraxos valanginensis*] from the Valanginian of Crimea (five rows of folds, straight generating line); *E. (E.) viriosa* (Sohl, 1965) [= *Rhabdocolpus viriosum*] from the Middle Jurassic of Utah, United States (Sohl, 1965, only figs. 1, 6) (six rows of folds, straight generating line); *E. (E.) wrighti* (Etallon, 1859) [= *Cerithium wrighti*] from the Lower Kimmeridgian of France (after Loriol, 1887) (five rows of folds, straight generating line); and ?*E. (E.) muriciformis* Gemmellaro, 1878 [= *Cerithium muriciforme*] from the Lower Lias of Italy (five or six rows of folds, ?convex generating line).

Pčelintsev (1934) mentioned the form *Exelissa* aff. *ursicina* (Loriol) from the Aalenian–Lower Bajocian of western Georgia. However, his description suggests that it is either *E. (E.) bathonica* or *E. (E.) normaniana*.

**Comparison.** The subgenus is distinguished from *Pyraxopsis* by continuous ribs and greater number of rows of folds (4–9 in contrast to 4 or 5).

**Remarks.** The species *Cerithium gemmellaro* Parona, 1883 from the Lower Lias of Italy (five or six rows of folds, pupoid shell) should be considered as an aberration, which was repeatedly reported for *E. (E.) quinaria* (Trautschold) (see Plate 4, fig. 12).

*Exelissa* (*Exelissa*) *quinaria* (Trautschold, 1866)

Plate 4, figs. 3–12

*Cerithium quinarium*: Trautschold, 1866, p. 13, pl. 2, fig. 8.

*Cryptoptyxis wrighti*: Gerasimov, 1955, p. 161, pl. 40, figs. 11 and 25.

*Cryptoptyxis quinaria*: Gerasimov, 1992, p. 85, pl. 18, figs. 1–16.

**Holotype.** Russia, Vladimir Region, Muromskii District, Ilevna River near the village of Mishino; Middle Oxfordian. The specimen is lost.

**Neotype.** GGM, no. 12/95; Moscow Region, Kolomenskii District, town of Shchurovo (Zarech'e), quarries; Middle Oxfordian, *tenuiserratum* Zone.

**Description.** The shell is 10.6–13.0 mm high. The protoconch is composed of four whorls. The first whorl is smooth and rounded, the rest of them are bicarinate. A rib runs above the suture on the last whorls. The carinae bear ribs. The number of teleoconch whorls varies from 10.3 to 12.6. The teleoconch angle is 21°–41°. The whorls are flattened. The extent of involution is 40–43%, it decreases incrementally in the last 3.0–4.0 whorls. The suture on the last whorls is shallow, resembling a small furrow. The ornamentation is composed of three strong primary ribs and one or two (rarely, three or four) secondary ribs. The first secondary rib appears on the second whorl. Initially, it is as prominent as the primary ribs, and weakens later. The third primary rib appears out of the suture in the last 3.5–4.5 whorls. The folds are prominent, orthocone, aligned into five (rarely, four or six) rows. The rows are usually straight or, occasionally, twisted counterclockwise due to shift of the folds, which is usually a quarter of whorl, or, rarely, up to a half of whorl. The rows are unsteady up to the fourth or, rarely, sixth whorl. The ribs bear large blunt tubercles. The tubercles of the upper rib are usually larger, or, rarely, equal to, the tubercles of the second primary rib. The last unaltered whorl is 31–25% as high as the shell. The shell base bears from four to six or, rarely, up to nine ribs. The aperture is oval and slightly expands through the slightly explanate margin of the outer lip. The edge of the lip is even and thin. The inner lip is thickened. A narrow, shallow but distinct groove is present at the base of the aperture. It is as deep as long, its length-to-width ratio is 1.15–1.2. The groove is present only within

the last whorl and sometimes secondarily disappears to the end of the gerontic stage.

**Ontogenetic changes.** Gerontic changes involve the stage of the modified whorl, which is approximately as long as 0.7 whorls. The stage starts from the last prominent fold. The folds disappear, being replaced by one or two successive tubercles on the upper rib. Faint ribs, which usually appear on the preceding whorl, run between two or three upper ribs of the shell base and between the ribs of the lateral surface of the whorl. The angulations of the whorl disappear, and the whorl narrows. A zone with coarse and densely spaced growth lines and lacking any other ornamentation is present just above the aperture. The zone may be completely reduced, or may become a short vermiform tube (see Pl. 4, fig. 9), but usually it is 1.0–1.5 mm wide.

**Comparison.** The species is distinguished from all other members of the subgenus by the fewer number of fold rows, or by sparse ornamentation (only two strong ribs are present on most of the teleoconch).

**Remarks.** Plate 4 displays both normal shells and rare mutations and aberrations. Common shells are shown in Pl. 4, figs. 3–5. The forms with twisted fold rows (Pl. 4, fig. 6) and hexahedral shells (Pl. 4, fig. 8) are not uncommon, usually comprising a few percent of the total number of specimens. Specimens with a tetrahedral shell (Pl. 4, fig. 11) or a shell with a vermiform last whorl (Pl. 4, fig. 9) are rare. The typical structure of the last whorl is shown in Pl. 4, fig. 5.

**Occurrence.** Middle Oxfordian, *tenuiserratum* Zone and, probably, the uppermost part of *densiplicatum* Zone of European Russia.

**Material.** Middle Oxfordian, *tenuiserratum* Zone; town of Shchurovo (Zarech'e) (22707 specimens) and refuse heaps of cement plant (303 specimens), village of Nikitino (24 specimens), village of Tyrnovo (six specimens), village of Vasil'kovo (seven specimens), village of Mikhalenino (15 specimens), town of Makar'ev (71 specimens).

#### Subgenus *Pyrazopsis* Hacobjan, 1972

*Pyrazopsis*: Hacobjan, 1972, p. 8; 1976, p. 214.

**Type species.** *Pyrazus quinquecostatus* Egojan, 1955; Upper Cenomanian of Armenia.

**Diagnosis.** Shell turriculate, with straight generating line. Protoconch unknown. Ribs between folds replaced by rows of tubercles. Folds arranged into four or five rows.

**Species composition.** Four species: type species; *E. (P.) hoeninghausi* (Keferstein, 1844) [= *Cerithium hoeninghausi*] from the Upper Cretaceous of Austria; *E. (P.) kochi* (Pálffy, 1902) [= *Cerithium kochi*] from the Upper Cretaceous of the Carpathians; and *?E. (P.) peruviana* (Olsson, 1944) [= *Pyrazus peruviana*] from the Upper Senonian of Peru.

**Comparison.** The comparison is given in the description of *Exelissa* sensu stricto

**Remarks.** Hacobjan (1972) cited more species in the composition of the taxon. I examined all of the species, except for *Cerithium pentagonatum* Schlotheim, 1820. Some of them considerably differ in morphology from true *Pyrazopsis*. These are the following species: *Murex angulatus* Solander, 1766 from the Eocene of England; *Cerithium tetragonum* Deshayes, 1837 from the Eocene of France (having four rows of folds), and *Cerithium michaillense* Pictet et Campiche, 1862 (non Pictet et Campiche, 1864). The last species probably belongs to the genus *Terebraliopsis* Cossmann, 1906. The others are morphologically similar to *Pyrazopsis*; therefore, I have to explain the reasons for their exclusion from the subgenus. *Pyrazus valanginensis* Pčelintsev, 1965 was assigned to *Exelissa* sensu stricto due to the presence of spiral ribs, but not spiral rows of tubercles. *Cerithium pyramidatum* Deshayes, 1837 from the Eocene of France is very similar to the true *Pyrazopsis*, but differs from it in the absence of characteristic modification in the last whorl and in its much larger shell. Its holotype is 55 mm high, while the type species of *Pyrazopsis* varies from 15 to 20 mm in height. *Pyrazopsis douvillei* Hacobjan, 1976 established for a form that was described by Douvillé (1904, pl. 42, figs. 5–6) from the Maastrichtian of Iran as *Pyrazus pyramidatus* insignificantly differs from the latter in ornamentation. Thus, I consider them as synonyms. *Cerithium (Pirenella?) gosauense* (Stoliczka, 1865) from the Upper Cretaceous of the Alps differs from *Pyrazopsis* in the aperture (possibly, with well-developed siphonal canal) and the folds looking like varices. All the above-mentioned species are excluded from the subgenus composition.

Pálffy (1902) described the species *E. (P.) kochi*, based primarily on the shell illustrated on pl. 25, fig. 12. Therefore, I consider this specimen as the lectotype of the species. The remaining shells illustrated belong to other species or even genera. The specimens illustrated on pl. 26, figs. 3 and 4 were regarded by the author as aberrations. In my opinion, the shell shown in fig. 1 belongs to *E. (P.) hoeninghausi* (Keferstein).

*?E. (P.) peruviana* (Olsson) is probably closely related to *Cerithium pyramidatum* Deshayes. This assumption is supported by the rather large shell size of *?E. (P.) peruviana*, which is 27 mm high, although it is incompletely preserved.

#### Genus *Shurovites* Guzhov, gen. nov.

**Etymology.** From the town of Shchurovo.

**Type species.** *S. shurovensis* sp. nov.; Middle Oxfordian, *tenuiserratum* Zone; Russia, Moscow Region, Kolomenskii District, town of Shchurovo (Zarech'e), quarries.

**Diagnosis.** Shell small, turriculate, with straight or convex generating line. Protoconch composed of 3.0–3.5 whorls. First 1.5 whorls rounded and smooth. Rounded angularity appearing on subsequent 1.5–

2.0 whorls initially observed in upper third of whorl and later descending to the middle. Carina formed in its place only in 0.4–0.7 whorl from protoconch end. Above and below carina, surface becoming even, and whorl becoming angular. Within 0.1–0.3 whorl from protoconch end, rib developed above suture. At protoconch end, external surface of whorl becoming straight, and carina descending to quarter of whorl height. Boundary between protoconch and teleoconch distinct, marked by opisthocyrt commissure and appearance of folds and strong ribs. Teleoconch whorls flattened or convex, nongradate or slightly gradate. Suture usually shallow. Ornamentation composed of three or four primary ribs and few (0–2) secondary ribs. Folds cross secondary ribs, forming tubercles. Shell base high, convex, arched or widely conical, with numerous ribs and fold ends. Aperture circular or oval, with short groove in basal area.

**Species composition.** Seven species: type species; *S. binodosus* (Gründel, 1990) [= *Exelissa binodosa*] from the Callovian of Germany; *S. comptonensis* (Hudleston, 1884) [= *Cerithium (Kilvertia) comptonensis*] from the Bajocian of England; *S. multinodosus* (Gründel, 1990) [= *Exelissa multinodosa*]; *S. unzhensis* sp. nov.; ?*S. oderinensis* (Gründel, 1999) [= *Procerithium oderinense*] from the Upper Toarcian of Germany; ?*S. solitudinis* (Douvillé, 1916) [= *Exelissa solitudinis*] from the Bathonian of Egypt; and ?*S. weldonis* (Hudleston, 1888) [= *Exelissa weldonis*] from the Bajocian of England and France.

**Comparison.** The genus differs from other members of the subfamily in the protoconch with several smooth rounded whorls and a single carina on the last whorl.

*Shurovites multinodosus* (Gründel, 1990)

Plate 4, figs. 13–15

*Exelissa multinodosa*: Gründel, 1990a, p. 768, pl. 1, fig. 6; 1999b, p. 23, pl. 5, fig. 19.

*Exelissa parva*: Gründel, 1999b, p. 23, pl. 5, figs. 13–15.

**Holotype.** Private collection of Dr. Buchholz (Stralsund); Germany, vicinity of Fonow; Lower–Middle Callovian.

**Description.** The shell is up to 9.5 mm high, with a slightly convex generating line. The protoconch is unknown. The teleoconch is composed of 8.0–10.0 flattened, nongradate or slightly gradate whorls. The teleoconch angle is 18°–26°. The extent of involution is 32%. The suture is shallow. The ornamentation is composed of four or five, rarely, six ribs. The folds are faint, their number is 15 or 16 (rarely, it varies from 14 to 19) per whorl (whorl diameter is 3 mm). The folds are opisthocline on early and middle whorls; on later whorls, they become orthocline or slightly prosocline. Large rounded tubercles appear at intersections of folds and ribs. The last whorl is 30% as high as the shell. The base of the shell bears more prominent ribs, their number is usually five, or, rarely, six or seven. The upper part of

the shell base bears the smooth ends of folds. The aperture is circular.

**Ontogenetic changes.** With shell growth, the folds are smoothed out in the lower part of the whorl and, later, in the upper part. The folds become more opisthocyrt and, within 0.3 whorl from the aperture, the distance between the folds abruptly increases. The folds are rapidly smoothed out near the aperture, only faint elevations are retained below the suture.

**Comparison.** The species differs from *S. shurovensis* and *Shurovites* sp. 1 in the less coarse ornamentation, circular tubercles, and slightly convex generating line of the shell. It is distinguished from *S. spiculus* (Lycett) by its weaker and densely spaced folds.

**Remarks.** The shells from the village of Alpat'evo differ from those from the village of Tyrnovo in the slightly gradate whorls, coarser ornamentation, and larger size. They probably represent a distinct ecological type or even a separate species. However, the material collected does not support these assumptions. Thus, I have retained the Alpat'evo form within the species discussed.

**Occurrence.** Lower Callovian, *koenigi* Zone, *curtilobus* Subzone, to the Middle Callovian of European Russia; Lower–Middle Callovian and Callovian (erratic boulders) of Germany.

**Material.** Lower Callovian, *koenigi* Zone, *curtilobus* Subzone; village of Alpat'evo (40 specimens); Middle Callovian, village of Tyrnovo (40 specimens).

*Shurovites shurovensis* Guzhov, sp. nov.

Plate 4, figs. 17–19

*Exelissa binodosa*: Gründel, 1999b, p. 22, pl. 5, fig. 16.

*Exelissa multinodosa*: Gründel, 1999b, p. 23, pl. 5, figs. 20–22.

**Etymology.** From the town of Shchurovo.

**Holotype.** GMM, no. 12/21; Ryazan Region, Spasskii District, village of Nikitino, right bank of the Oka River; Middle Oxfordian.

**Description.** The shell is up to 9.5 mm high, with straight generating line. The protoconch is composed of 3.2 whorls. The first 2.5 whorls are smooth and rounded, the last 0.5 of the whorl bears carina, which is ornamented by a rib. A faint spiral thread appears above the carina and simultaneously with it. The thread becomes a fine rib at the end of the protoconch. Another fine rib appears above the suture at 0.1–0.2 whorl from the protoconch end. The teleoconch is composed of 8.0–9.0 whorls. The teleoconch angle is 16°–27°. The early whorls are convex and then become flattened. The extent of involution is 29–34%. The suture is shallow, furrow-like. The ornamentation is composed of three robust primary ribs and a single secondary rib. The secondary rib appears on the first whorl, then becomes rather prominent, and from the fourth whorl usually weakens or even disappears (occasionally, it is constant along its whole length). The folds

are orthocline or opisthocline, their number varies from 10 to 12 per whorl (whorl diameter is 2–3 mm). Stout spinelike tubercles are formed at intersections of folds and ribs. Thus, the species is distinguished by its coarse ornamentation. The last whorl is 25–34% as high as the shell. The shell base is convex and arched, bears four or five strong ribs and folds. The aperture is circular.

**Ontogenetic changes.** Age-related changes are present in the last 0.7 whorl (or possibly more). The extent of involution decreases by 10%, the lower rib rises above the suture, and another spiral rib appears from under the suture. All ribs weaken, and the lower ends of the folds smooth out. The folds become more prosocline–prosocyrt and more widely spaced. Near the aperture, the folds are retained only in the upper part of the lateral surface of the whorl, along with two upper rows of tubercles. Age-related changes are preceded by short-term deceleration in shell growth marked by crowding folds.

**Comparison.** The species is distinguished from *Shurovites* sp. 1 by the smaller number of ribs (four versus five) and a greater distance between folds. For comparison with *S. unzhensis*, see the description of that species. Numerous forms described from the Bajocian–Oxfordian are very similar in appearance. This gives an impression of the single long-living species, starting from *S. comptonensis* (Bajocian) to *S. shurovensis* (Oxfordian of Russia). Future reexamination of these species using modern methods might reveal differences between them.

**Occurrence.** Middle Oxfordian of European Russia; Callovian of Germany (erratic boulders).

**Material.** ?Middle Oxfordian; village of Tyrnovo (one specimen); Middle Oxfordian; village of Nikitino (four specimens); Middle Oxfordian, *densiplicatum* Zone; town of Makar'ev (three specimens); Middle Oxfordian, *tenuiserratum* Zone; town of Shchurovo (Zarech'e) (four specimens).

*Shurovites unzhensis* Guzhov, sp. nov.

Plate 5, fig. 1

**Etymology.** From the Unzha River.

**Holotype.** GMM, no. 12/23; Russia, Kostroma Region, Makar'evskii District, village of Vasil'kovo, right bank of the Unzha River; Middle Oxfordian, *densiplicatum* Zone *densiplicatum* Subzone.

**Description.** The shell is up to 3.7 mm high, with straight generating line. The protoconch is composed of 3.2–3.5 whorls. The first 2.5–3.0 whorls are rounded and smooth; on the last 0.5–0.7 whorl, the carina appears. A rib appears above the suture on the 0.2–0.3 whorl. The teleoconch is composed of 5.5 whorls. The teleoconch angle is 34°–36°. The whorls are flat or slightly concave and slightly gradate. The maximum width of the whorl is at the upper rib. The extent of involution is 35%. The suture is rather deep. The ornamentation is composed of three or four strong primary

ribs and, sometimes, single strong secondary rib (appears from 0.0–0.9 whorl). The folds are orthocline, their number is 11 or 12 per whorl (in a whorl 1.8 mm in diameter). Tubercles are formed at intersections of ribs and folds crossing. The tubercles are large and rounded square in outline; on the upper rib, they are particularly large and spinelike. The last whorl is 39% as high as the shell. The shell base is convex, widely conical, and bears four ribs. The aperture is circular.

**Comparison.** The species differs from other members of the genus in its *Procerithium*-like shell, less pronounced ornamentation, and widely conical shell base.

**Remarks.** The species is convergent in shell morphology with *Procerithium russiense* (d'Orbigny) (see below). However, it is distinguished by the protoconch structure and early development of the spiral ornamentation.

**Occurrence.** Middle Oxfordian, *densiplicatum* Zone, *densiplicatum* Subzone of European Russia.

**Material.** Middle Oxfordian, *densiplicatum* Zone, *densiplicatum* Subzone; town of Makar'ev (two specimens), village of Vasil'kovo (one specimen).

*Shurovites* sp. 1

Plate 4, fig. 16

**Description.** The shell fragments attain 6 mm in height; their generating line is straight. The protoconch is unknown. Only the last 4.5 teleoconch whorls are preserved. The maximum width of the whorl is at the upper row of tubercles. The teleoconch angle is impossible to estimate precisely. The whorls are flattened. The ornamentation is composed of five strong ribs. The folds are orthocline on the early whorls, but become opisthocyrt near the aperture. The number of folds varies from 15 to 18 per whorl (in a whorl 2 mm in diameter). Large, spinelike tubercles appear at intersections of folds and ribs. The incompletely preserved base of the shell bears folds and strong ribs.

**Comparison.** Comparisons are given in the sections devoted to *Shurovites shurovensis* and *S. unzhensis*.

**Occurrence.** Lower Callovian, *koenigi* Zone, *curtilobus* Subzone of European Russia.

**Material.** Lower Callovian, *koenigi* Zone, *curtilobus* Subzone; village of Alpat'evo (two specimens).

**Genus *Cupaniella* Gemmellaro, 1911**

*Cupaniella*: Gemmellaro, 1911, p. 238; Wenz, 1940, p. 730.

**Type species.** *Cupaniella biplicata* Gemmellaro, 1911; Hettangian–Sinemurian of Italy (Sicily).

**Diagnosis.** Shell turriculate, with convex generating line. Protoconch unknown. Whorls nongradate, convex. Suture rather shallow. Ornamentation composed of three ribs, upper two positioned closely, intersected by numerous collabral folds, about 25–30 on last whorl. Last whorl narrow, strongly descending down-



1a



1b



1c



2a



2b



3



4



5



6



7



8a



8b



9



10



11



12



13



14



15



16

wards. Shell base high, cup-shaped, with numerous ribs. Aperture circular, its basal part unknown.

**Species composition.** Type species.

**Comparison.** The genus is distinguished from all other members of the subfamily by its very fine and dense collabral ornamentation.

#### Genus *Teliochilus* Cossmann, 1906

*Tomocheilus*: Gemmellaro, 1878, p. 299; Zittel, 1881–1885, p. 266.

*Exelissa* (*Teliochilus*): Cossmann, 1906, p. 43; Wenz, 1940, p. 731.

**Type species.** *Tomocheilus deslongchampsii* Gemmellaro, 1878; Hettangian–Sinemurian of Italy, Sicily.

**Diagnosis.** Shell small, ranging from low-turriculate to turriculate, with convex generating line. Whorls nongradate, convex. Suture shallow. Ornamentation composed of numerous fine ribs and several wide, rounded folds. Tubercles not present. Last whorl descending downwards, elongated anteriorly, and losing folds. Shell base high, widely conical, convex, with small ribs. Aperture circular, with thickened inner lip and rudimentary parietal canal.

**Species composition.** Four species: type species; *T. asper* (Gemmellaro, 1878) [= *Tomocheilus asper*]; *T. gradates* (Gemmellaro, 1878) [= *Tomocheilus gradates*]; and *T. semiplicatus* (Gemmellaro, 1878) [= *Tomocheilus semiplicatus*]; all from the Hettangian–Sinemurian of Italy.

**Comparison.** The genus differs from *Cupaniella* in its more distantly placed and thicker folds and wider shell. In apical view, the shell of *Teliochilus* is distinguished from *Cimoliocentrum* and *Exelissa* by the circular rather than polyhedral outline. In addition, it differs from *Cimoliocentrum* in the absence of internal folds.

#### Genus *Cimoliocentrum* Cossmann, 1909

*Centrogonia*: Cossmann, 1899, p. 5; Cossmann, 1906, p. 215.

*Cimoliocentrum*: Cossmann, 1909, p. 2; Wenz, 1939, p. 531.

**Type species.** *Centrogonia cureti* Cossmann, 1899; Barremian of France.

**Diagnosis.** Shell medium-sized, conical or turriculate, rarely, barrel-shaped, with thick walls and straight generating line. Whorls nongradate, flattened. Suture ranging from deep and angular to very shallow. Usually, whorls with few folds, aligned in regular rows, so that shell is pentahedral pyramid shaped. Rarely, whorls ornamented by coarse ribs. Spinelike tubercles formed at intersections of folds and ribs. Last whorl unknown. Shell base high, widely conical, convex. Aperture circular. Two or, rarely, one columellar fold runs inside whorls. Single internal fold present in middle of outer lip. Type species only has paired callosities on columellar side of aperture.

**Species composition.** Six species: type species; *C. archiardi* (Pirona, 1878) [= *Nerinea archiardi*] from the Tithonian of Italy (five rows of folds, convex generating line, two columellar folds and single fold on outer lip); *C. sirenum* (Oppenheim, 1889) [= *Cerithium sirenum*] from the Upper Tithonian of Italy (five rows of folds, single columellar fold, the structure of the outer lip is unknown); *C. tschani* (Ooster, 1869) [= *Nerinea (Itieria) tschani*] from the Kimmeridgian of Switzerland (five rows of folds, two columellar folds and single fold on outer lip); *C. uhligi* (Remeš, 1909) [= *Cerithium uhligi*] from the Upper Tithonian of Poland (five rows of folds, barrel-shaped shell, probably with folds); and *C. zeuschneri* (Gemmellaro, 1869) [= *Cerithium zeuschneri*] from the Tithonian of Italy (five rows of folds, convex generating line, two columellar folds).

**Comparison.** The members of this genus are distinguished from all other genera of the subfamily by their stouter, wide, barrel-shaped shell, and the presence of the folds inside the aperture.

**Remarks.** Morphological modifications of the last whorl that are characteristic of the subfamily are not observed in this genus. These were probably secondarily lost in the course of the specialization of this taxon.

#### Explanation of Plate 5

**Fig. 1.** *Shurovites unzhensis* sp. nov.: holotype GMM, no. 12/23: (1a) apertural view, ×18, (1b) abapertural view, ×18, and (1c) protoconch, ×91; village of Vasil'kovo; Middle Oxfordian, *densiplicatum* Zone, assemblage with *C. strangwaysi*.

**Figs. 2 and 3.** *Procerithium tyrnovense* sp. nov.: (2) holotype GMM, no. 12/25, ×3: (2a) apertural and (2b) abapertural views; village of Tyrnovo; Middle Callovian; (3) GMM, no. 12/121, abapertural view, ×3; Mikhailovskii Mine; Lower Callovian, *enodatum* Zone.

**Figs. 4–10.** *Procerithium russiense* (d'Orbigny): (4) GMM, no. 12/89, apertural view, ×3; village of Nikitino; Lower Oxfordian; (5) GMM, no. 12/87, abapertural view, ×3; (6) GMM, no. 12/90, abapertural view, ×3; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone; (7) GMM, no. 12/93, apertural view, ×3; village of Nikitino; Lower Oxfordian; (8) GMM, no. 12/92: (8a) protoconch and first whorls of the teleoconch, ×36, (8b) protoconch, ×79; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone; (9) GMM, no. 12/88, abapertural view, ×3; village of Nikitino; Lower Oxfordian; (10) GMM, no. 12/91, protoconch and first whorls of the teleoconch, ×34; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone.

**Figs. 11–13.** *Katosira okensis* sp. nov.: (11) holotype GMM, no. 12/24 (cast), left of the aperture, ×3; (12) GMM, no. 12/58 (cast), apertural view, ×3; village of Alpat'evo; Lower Callovian, *koenigi* Zone, *curtilobus* Subzone; (13) GMM, no. 12/57, apertural view, ×3; village of Tyrnovo; Middle Callovian.

**Figs. 14–16.** *Tyrnoviella alpatyevensis* sp. nov.: (14) GMM, no. 12/70 (cast), abapertural view, ×3; (15) GMM, no. 12/72 (cast), abapertural view, ×3; (16) holotype, GMM, no. 12/30 (cast), left of the aperture, ×3. Village of Alpat'evo; Lower Callovian, *koenigi* Zone, *curtilobus* Subzone.

### Family Procerithiidae Cossmann, 1906

**Diagnosis.** Shell medium-sized, multispiral, turriculate or high-turriculate, siphonostomatous, and anomphalous. Protoconch composed of several smooth rounded whorls. Boundary between protoconch and teleoconch coincident with opisthocyrt commissure, followed by folds. First teleoconch whorls commonly ornamented only with folds; ribs or threads forming later. Last whorl low. Shell base widely conical and convex, with threads or ribs and ends of folds. Aperture circular, with narrow angular protrusion in lower part. Above middle of base, growth lines opisthocyrt, becoming prosocyrt below.

**Generic composition.** *Katosira* Koken, 1892, *Procerithium* Cossmann, 1902, and *?Tyrnoviella* gen. nov.

**Comparison.** This family differs from the Loxonematidae in the development of the spiral ornamentation, from the Cryptaulacidae in the smooth protoconch and the teleoconch initially covered only by folds, which are later supplemented by spiral elements. All ribs of the Procerithiidae are secondary. The differences from the other families of the suborder concern the protoconch morphology.

**Occurrence.** Middle Triassic, Ladinian–Upper Cretaceous, and Cenomanian of Eurasia and America (in the Cretaceous, it probably occurred in Africa as well).

### Genus *Procerithium* Cossmann, 1902

*Procerithium*: Cossmann, 1902, p. 177 (pars); 1912b, p. 38 (pars); Gründel, 1997, p. 90; 1999b, p. 8.

*Procerithium (Procerithium)*: Cossmann, 1906, p. 23 (pars); Wenz, 1940, p. 726 (pars).

*Rhabdocolpus*: Cossmann, 1906, p. 27; Wenz, 1940, p. 727.

*Uchauxia*: Cossmann, 1906, p. 56; Wenz, 1940, p. 735.

*Mesostrombus*: Schröder, 1995, p. 35.

**Type species.** *P. quinquegranosum* Cossmann, 1902; Hettangian; France, Vendée Department, Simons-la-Vineuse.

**Diagnosis.** Shell turriculate. Protoconch composed of 3.5–4 smooth, rounded whorls. Last whorls sometimes with angulation in lower part. First whorl of protoconch almost planispiral. Teleoconch whorls nongradate or slightly gradate and flattened or gently convex. Ornamentation composed of several ribs emerging at some distance from beginning of teleoconch and densely spaced opisthocline–opisthocyrt folds, which prevail over ribs. Upper rib formed earlier than others. Tubercles at intersections of ribs and folds present. Shell base covered with spiral ribs and, in upper part, with ends of folds. Ontogenetic changes manifested as (a) frequently interrupted growth, associated with increased density and fusion between folds and appearance of commissures; and (b) folds becoming more opisthocyrt. Upper half of large whorls with clearly pronounced depression. (These ontogenetic changes occur in all species of this genus under study, but may be absent in some individuals.)

**Species composition.** Thirty-three species: type species; *P. badri* (Abbas, 1973) [= *Uchauxia badri*] from the Albian of England; *P. bajocense* (Grep-pin, 1898) [= *Pseudocerithium bajocense*] from the Upper Bajocian of France; *P. compactum* Gründel, 1999 from the Lower Aalenian, *opalinum* Zone, of Germany; *P. costellatum* (Münster, 1841–1844) [= *Cerithium costellatum*] from the Middle Jurassic of Germany; *P. crenulatum* (Eudes-Deslongchamps, 1842) [= *Fusus crenulatum*] from the Upper Lias of France; *P. emaciatum* (Haas, 1953) [= *Rhabdocolpus emaciatum*] from the Rhaetian of Peru; *P. ferea* (Dumortier, 1874) [= *Cerithium ferea*] from the Upper Toarcian, *bifrons* Zone, of France; *P. forbesianum* (d'Orbigny, 1850 in Pictet and Renevier, 1858) [= *Cerithium forbesianum*] from the Aptian of France; *P. gentili* Cossmann, 1921 [= *Procerithium (Rhabdocolpus) gentili*] from the Toarcian of Morocco; *P. granulatocostatum* (Quenstedt, 1858) [= *Cerithium granulatocostatum*] from the Upper Bathonian of Germany; *P. gratum* (Terquem, 1855) [= *Cerithium gratum*] from the Sinemurian–Pliensbachian of France; *P. ilminsterense* (Moore, 1866) (after Wilson and Crick, 1889) [= *Cerithium ilminsterense*] from the Upper Pliensbachian of England; *P. jole* (d'Orbigny, 1850 in Thevenin, 1909) [= *Cerithium jole*] from the Toarcian of France; *P. kirki* (Allison, 1955) [= *Uchauxia kirki*] from the Albian of Mexico; *P. muensteri* (Keferstein, 1841–1844) [= *Cerithium muensteri*] from the Cenomanian of Germany; *P. muricatocostatum* (Münster, 1841–1844) [= *Cerithium muricatocostatum*] from the Bajocian of Germany; *P. muricatum* (Sowerby, 1825) (after Hudleston, 1880b, 1884) [= *Turritella muricatum*] from the Bajocian–Bathonian of England; *P. nodosocostatum* (Münster, 1841–1844) [= *Cerithium nodosocostatum*] from the ?Middle Jurassic of Germany; *P. oehlerti* Cossmann, 1912 [*Procerithium (Rhabdocolpus) oehlerti*] from the Callovian of France; *P. peregrinosum* (d'Orbigny, 1842) [= *Cerithium peregrinosum*] from the Turonian of France; *P. pseudocostellatum* (d'Orbigny, 1850 in Cossmann, 1912b) [= *Cerithium pseudocostellatum*] from the Toarcian of France; *P. quadricinctum* (Münster, 1841–1844) [= *Cerithium quadricinctum*] from the Bajocian of Germany; *P. russiense* (d'Orbigny, 1850) [= *Cerithium russiense*]; *P. scalariforme* (Deshayes, 1831) [= *Melania scalariforme*] from the Bajocian of France; *P. struckmanni* (Loriol, 1874) [= *Cerithium struckmanni*] from the Upper Oxfordian of France; *P. subarmatum* (Ernst, 1923) [= *Cryptaulax subarmatum*] from the Aalenian of Germany; *P. subscalariforme* (d'Orbigny, 1850 in Grep-pin, 1898) [= *Cerithium subscalariforme*] from the Upper Bajocian of France; *P. transitorium* (Haas, 1953) [= *Protofusius transitorium*] from the Rhaetian of Peru; *P. turris* (Hudleston, 1884) [= *Cerithium turris*] from the Bajocian of England; *P. turritellae* (Haas, 1953) [= *Protofusius turritellae*] from the Rhaetian of Peru; *P. tyrnovense* sp. nov.; *P. undulatum* (Eudes-Deslongchamps, 1842) [= *Melania undulatum*] from

the Bajocian of France; and *P. wisei* (Abbas, 1973) [= *Uchauxia wisei*] from the Valanginian–Hauterivian of England.

**Comparison.** *Procerithium* differs from *Katosira* in the coarser spiral ornamentation and, often, in the slightly gradate whorls.

**Remarks.** *Rhabdocolpus* and *Uchauxia* are regarded as synonyms of *Procerithium*; for more detail, see Chapter 3.

Based on juvenile shells from the Aalenian and Pliensbachian of Germany, Schröder (1995) established the genus *Mesostrombus* and assigned it to the family Aporrhaidae. The most complete shells of this series consist of a protoconch and two teleoconch whorls and are identical in their morphological characteristics and ontogeny to the juvenile stages of *Procerithium russiense* (d'Orbigny) (see below). Therefore, I consider *Mesostrombus* to be a synonym of *Procerithium*.

*Procerithium tyrnovense* sp. nov.

Plate 5, figs. 2 and 3

**Etymology.** From the village of Tyrnovo.

**Holotype.** GMM, no. 12/25; Ryazan Region, Pronskii District, Kazach'ya River near the village of Tyrnovo; Middle Callovian.

**Description.** The shell is up to 18 mm high. The protoconch is unknown. The teleoconch consists of 11 whorls, the teleoconch angle ranges from 14° to 25°. The whorls are flattened and nongradate. The maximum whorl width is at the midheight of whorls, and the extent of involution is 35%. The suture is relatively shallow. The ornamentation is composed of six to eight ribs and widely spaced folds (11–13 per whorl in a shell of 3.5 mm in diameter). The folds are opisthocline and become opisthocyrt on the last whorls. The ribs have small tubercles. The last whorl is 26–33% of the shell height. The shell base has five or six ribs (which are identical to those on the lateral side) and the ends of folds.

**Ontogenetic changes.** In some shells, the last whorls display traces of interrupted growth.

**Comparison.** The new species differs from *P. russiense* in the nongradate whorls and the fainter, more densely spaced spiral ornamentation.

**Occurrence.** Lower and Middle Callovian of European Russia.

**Material.** Lower Callovian, *enodatum* Zone of the Mikhailovskii Mine (one specimen); Middle Callovian; village of Tyrnovo (30 specimens).

*Procerithium russiense* (d'Orbigny, 1845)

Plate 5, figs. 4–10

*Cerithium russiense*: d'Orbigny, 1845, p. 453, pl. 28, fig. 9; Hudleston, 1880b, p. 402, pl. 14, fig. 8; Loriol, 1901, p. 42, pl. 3, figs. 15 and 16; Nalivkin and Akimov, 1917, p. 95, pl. 3, fig. 18; Dykan' and Makarenko, 1990, p. 113, pl. 32, figs. 20 and 21.

*Cerithium muricatum*: Hudleston, 1880b, p. 401, pl. 14, fig. 7.

*Cerithium (Bittium) russiense*: Andreae, 1887, p. 25, pl. A, figs. 5–12.

*Procerithium (Rhabdocolpus) expulsum*: Cossmann, 1912b, p. 82, pl. 4, fig. 44.

*Procerithium (Rhabdocolpus) russiense*: Cossmann, 1912b, p. 79, pl. 4, figs. 5 and 6; Gerasimov, 1992, p. 70, pl. 19, figs. 5–11; Gerasimov et al., 1996, pl. 24, figs. 3 and 4.

*Cerithium melite*: d'Orbigny in Cottreau, 1931, p. 174, pl. 19, fig. 25.

*Procerithium russiense*: Gerasimov, 1955, p. 188, pl. 40, figs. 8–10.

*Procerithium (Rhabdocolpus) russiense*: Cossmann, 1912b, p. 79, pl. 4, figs. 5 and 6; Gerasimov, 1992, p. 70, pl. 19, figs. 5–11; Gerasimov et al., 1996, pl. 24, figs. 3 and 4.

**Holotype.** The holotype comes from the Oxfordian oolitic limestones of Ukraine: Kharkov Region, Severskii Donets River near the village of Kamenka; ?Izyum Formation, Upper Oxfordian.

**Description.** The shell is approximately 28–32 mm high. The protoconch consists of 3.5–4 whorls. The suture of the protoconch is shallow and looks like a groove. The teleoconch is composed of at least 13.5 flattened and slightly gradate whorls, its angle ranges from 20° to 27°. The maximum whorl width is at the upper rib, and the extent of involution is about 40%. The suture is deep. The ornamentation is composed of five or six (rarely, four) prominent secondary ribs. The upper rib is particularly well-developed. It appears from 0.5, 1, or 3.5 whorls (individual variation) of the teleoconch; the lower rib appears beginning from 1–4.3 whorls of the teleoconch, while the others emerge in the third whorl or even later. The early folds are opisthocline, while the late folds become opisthocyrt. A whorl 6.5–7 mm in diameter has 11 to 16 folds. The tubercles are large but blunt. The largest tubercles are located on the upper rib. The last whorl is 33% of the shell height. The shell base has 5, 6, or (rarely) 7 ribs (in the Callovian forms, 3 or 4 may occur) and ends of the folds in the upper part.

**Ontogenetic changes.** From 5.5–6 whorls, the growth lines may be broken, and the folds become opisthocyrt and more densely spaced. The first one or two breaks in the growth lines appear in the next nearest whorl or even somewhat earlier; subsequently, they are closer to each other. Thus, specimen GMM no. 12/87 has 12 breaks in a whorl of 6.7 mm in diameter. As a result, the folds become closely positioned and fused (some are possibly lost) and double and triple folds emerge. Therefore, large whorls display an increased fold density (e.g., in specimen GMM, no. 3/3, the last whorl has 1.3 times as many folds as the previous whorl). However, in some specimens, I have not registered any trace of interrupted growth even in very large whorls. In very large teleoconch whorls (later than whorl 13), the lateral surface acquires a depression in the upper half.

**Comparison.** *P. russiense* is distinguished from *P. tyrnovense* by its slightly gradate whorls and more prominent and widely spaced spiral ornamentation.

**Occurrence.** Lower Callovian, *enodatum* Zone, to the Middle Oxfordian of European Russia; Oxford-

ian of Ukraine; Lower–Middle Oxfordian of England; Middle Oxfordian–Lower Kimmeridgian of France.

**Material.** Lower Callovian, *enodatum* Zone, Mikhailovskii Mine (one specimen); Middle Callovian, village of Tyrnovo (one specimen); Upper Callovian, *athleta* Zone, *phaeinum* Subzone, village of Burdovo (two specimens); Upper Callovian, *athleta* Zone, Unzha River near the mouth of the Pezhenga River (two specimens); Upper Callovian, Stoilenskii quarry (one specimen); Upper Callovian–Lower Oxfordian, village of Nikitino (one specimen); Lower Oxfordian, village of Nikitino (187 specimens) and the Osenka River near the village of Novoselki (ten specimens); Lower–Middle Oxfordian, villages of Nikitino (nine specimens) and Chevkino (12 specimens); Middle Oxfordian, villages of Nikitino (72 specimens), Tyrnovo (21 specimens), and Mikhalenino (43 specimens), town of Makar'ev (41 specimens), Afanas'evskii quarry (one specimen), and village of Vasil'kovo (nine specimens); Middle Oxfordian, *densiplicatum* Zone, *popilaniense* Subzone, village of Vasil'kovo (11 specimens); and Middle Oxfordian, *tenuiserratum* Zone, town of Shchurovo (Zarech'e District) (87 specimens).

#### Genus *Katosira* Koken, 1892

*Katosira*: Koken, 1892a, p. 205; Koken, 1892b, p. 31; Kittl, 1894, p. 181.

*Loxonema* (*Katosira*): Cossmann, 1909, p. 27; Wenz, 1938, p. 384.

**Type species.** *Chemnitzia periniana* d'Orbigny, 1850; Lower Jurassic; France.

**Diagnosis.** Shell turriculate or high-turriculate. Protoconch composed of several rounded and smooth whorls. First whorl almost planispiral. Teleoconch whorls nongradate and flattened or convex. Several early teleoconch whorls covered with folds only; subsequently, numerous spiral threads or narrow ribs formed and intersected by densely spaced folds. Tubercles not formed. Shell base with numerous threads and ribs.

**Comparison.** This genus differs from *Procerithium* in its finer spiral ornamentation and nongradate whorls.

#### *Katosira okensis* Guzhov, sp. nov.

Plate 5, figs. 11–13

**Etymology.** From the Oka River.

**Holotype.** GMM, no. 12/24; Moscow Region, Luhovitskii District, right bank of the Oka River, village of Alpat'evo; Lower Callovian, *koenigi* Zone, *curtilobus* Subzone.

**Description.** The shell is up to 16 mm high. The protoconch is unknown. The teleoconch is composed of ten whorls, its angle ranges from 17° to 24°. The teleoconch whorls are flattened and nongradate. The maximum width is at the whorl midheight, and the extent of involution is 35%. The suture is superficial, in the shape of a groove. The ornamentation is composed of 8–10 or,

less often, of 11–13 threads and densely spaced, high, narrow folds (18–24 per whorl in a shell of 3.5 mm in diameter). The folds are opisthocline, and become opisthocyrt in the last whorls. Tubercles are absent. The last whorl is 26–33% of the shell height. The shell base has seven better developed threads and the ends of folds.

**Occurrence.** Lower Callovian, *koenigi* Zone, *curtilobus* Subzone, to the Middle Callovian of European Russia.

**Material.** Lower Callovian, *koenigi* Zone, *curtilobus* Subzone, village of Alpat'evo (38 specimens); Middle Callovian, village of Tyrnovo (17 specimens).

#### Genus *Tyrnoviella* Guzhov, gen. nov.

**Etymology.** From the village of Tyrnovo.

**Type species.** *T. alpatyevensis* sp. nov.; Lower–Middle Callovian; Russia, Moscow Region.

**Diagnosis.** Shell high-turriculate and multispiral. Teleoconch whorls slowly increasing and convex or, less often, flattened. Ornamentation composed of ribs and folds, with tubercles at their intersections. Early whorls with widely spaced and coarse folds, later becoming weaker and more densely spaced. Last whorl low. Shell base high, broadly conical, convex, with many ribs.

**Species composition.** Five species: type species; *T. gracilispira* (Cossmann, 1912) [= *Procerithium* (*Xystrella*) *gracilispira*] from the Toarcian of France; *T. praecatoria* (Eudes-Deslongchamps, 1842) [= *Cerithium praecatoria*] from the Pliensbachian of France; *T. quadriseriata* (Eudes-Deslongchamps, 1842) [= *Cerithium quadriseriata*] from the Pliensbachian of France; and ?*T. couzonensis* (Riche, 1904) (after Cossmann, 1912b) [= *Cerithium couzonensis*] from the Oxfordian of France.

**Comparison.** The new genus is distinguished from other genera by its long, narrow shell and by the pattern of changes in the collabral ornamentation.

**Remarks.** The new genus resembles the subgenus *Neocryptaulax* (Cryptaulacidae), but differs in the longer, larger shell.

#### *Tyrnoviella alpatyevensis* Guzhov, sp. nov.

Plate 5, figs. 14–16; Plate 6, figs. 1–5

**Etymology.** From the village of Alpat'evo.

**Holotype.** GMM, no. 12/30; Moscow Region, Luhovitskii District, bank of the Oka River near the village of Alpat'evo; Lower Callovian, *koenigi* Zone, *curtilobus* Subzone.

**Description.** The shell is more than 25 mm high. The teleoconch contains 13 whorls (incomplete), its angle ranges from 6.5° to 20°. The teleoconch whorls are convex, and the extent of involution is 27–41%. The maximum width is usually at the midheight of whorls; however, it is sometimes in the upper part of the whorl or closer to the suture because some spiral ribs are more

prominent than others. The ornamentation of adult whorls is composed of 6 or 7 ribs and 14–23 (rarely, up to 26) folds per whorl (4 mm in diameter). The folded whorls [for terminology, see the description of *Cryptaulax* (*Neocryptaulax*)] have orthocone folds, while subsequent whorls have opisthocyrt folds. The tubercles are large and rounded. The last whorl of the most complete fragments is 17–22% of the shell height. The shell base is covered with six to eight ribs and, in the upper part, the ends of folds. The aperture is circular and extended into the low part (broken off).

Two stages are recognized in the teleoconch ontogeny. The folded whorls occur within 4 to 7 early whorls (up to 1.3–4 mm in diameter). In this region, the folds are stout, widely spaced, and angular in the upper part. The whorls are slightly gradate because the folds are angular. The suture is deep. The maximum width of the folded whorls is always restricted to their upper part. Subsequently, the whorls more or less abruptly become reticulate-ribbed. In this region, the folds become more densely spaced and only slightly more prominent than the ribs, the suture becomes shallow, and the whorls are nongradate. In some specimens, the folds are relatively coarse up to the shell end. Little is known about the ornamentation of the early teleoconch whorls, where three ribs are observed in the lower half of the whorl. A broadly inclined (45°–55°) surface without spiral ornamentation occupies the upper 0.4 of the whorl. Below, the whorl surface is steep. It remains uncertain whether or not the ribs extend from the beginning of the teleoconch; however, the ornamentation described is observed in shells of the same diameter as the beginning of the teleoconch. Subsequently, new ribs appear: one or (?) two are on the inclined surface and three or four are on the lower surface.

**Comparison.** It is impossible to point out the differences between the new species and *T. praecatoria* because of the poor preservation of the latter. Cossmann (1912a) depicted one large and two small fragments of a subcylindrical shell that closely resembles in morphology that of *T. alpatyevensis*. Deslongchamps (1842) provided a sketchy drawing, which cannot be reliably compared with our material. The new species differs from *T. gracilispira* in the slightly convex whorls (in the latter species, they are flat) and the characteristics of the early whorls. In the specimens examined by Cossmann, the upper rib is prominent and forms thorns at the intersection with the folds. Therefore, the whorls are gradate and thorny in the upper part. *T. alpatyevensis* lacks these characters. The new species differs from *T. quadriseriata* in the larger number of ribs on the lateral side (6 or 7 in contrast to 4) and in the slightly convex whorls. It differs from *T. (?) couzonensis* in the larger number of ribs (6 or 7 in contrast to 4).

**Occurrence.** Lower Callovian, *koenigi* Zone, *curtilobus* Subzone, to the Middle Callovian of European Russia.

**Material.** Lower Callovian, *koenigi* Zone, *curtilobus* Subzone, village of Alpat'evo (92 specimens); Middle Callovian, village of Tyrnovo (18 specimens).

*Tyrnoviella* sp. 1

Plate 6, figs. 7 and 8

**Description.** The shell is up to 16 mm high (incomplete). The teleoconch is composed of more than eight whorls. The teleoconch angle ranges from 14° to 19°. Only the reticulate-ribbed whorls are known. The early whorls of some shells are slightly gradate and have relatively widely spaced folds (however, they do not increase in stoutness). The adult whorls are flattened and nongradate. The maximum width is at the midheight of whorls, and the extent of involution is 35%. The suture is relatively shallow. The ornamentation is composed of eight or nine uniform ribs and high, narrow, densely spaced folds. The folds are almost orthocone; in the last whorls, they become opisthocyrt and extend from suture to suture; a whorl 4 mm in diameter has 18–23 folds. The tubercles are small. The shell base has seven or eight ribs. The aperture is circular.

**Comparison.** This species differs from *T. alpatyevensis* in the more flattened whorls.

**Occurrence.** Middle Callovian of European Russia.

**Material.** Middle Callovian, village of Tyrnovo (14 specimens).

*Tyrnoviella* sp. 2

Plate 6, fig. 6

**Description.** The shell is 7.7 mm high (incomplete). The teleoconch includes six whorls (incomplete). The teleoconch angle is 12°. The whorls are flat. The first three whorls are folded. In the reticulate-ribbed whorls, the folds are almost as prominent as the ribs. The whorls remain gradate and become flat. The ornamentation is composed of eight ribs and 18 orthocone folds (in a whorl 2.3 mm in diameter). The shell base is not known.

**Comparison.** This species differs from *T. alpatyevensis* in its slightly gradate and flat whorls, which are covered with almost equally prominent folds and ribs, and in the orthocone folds.

**Occurrence.** Lower Callovian, *koenigi* Zone, *curtilobus* Subzone, of European Russia.

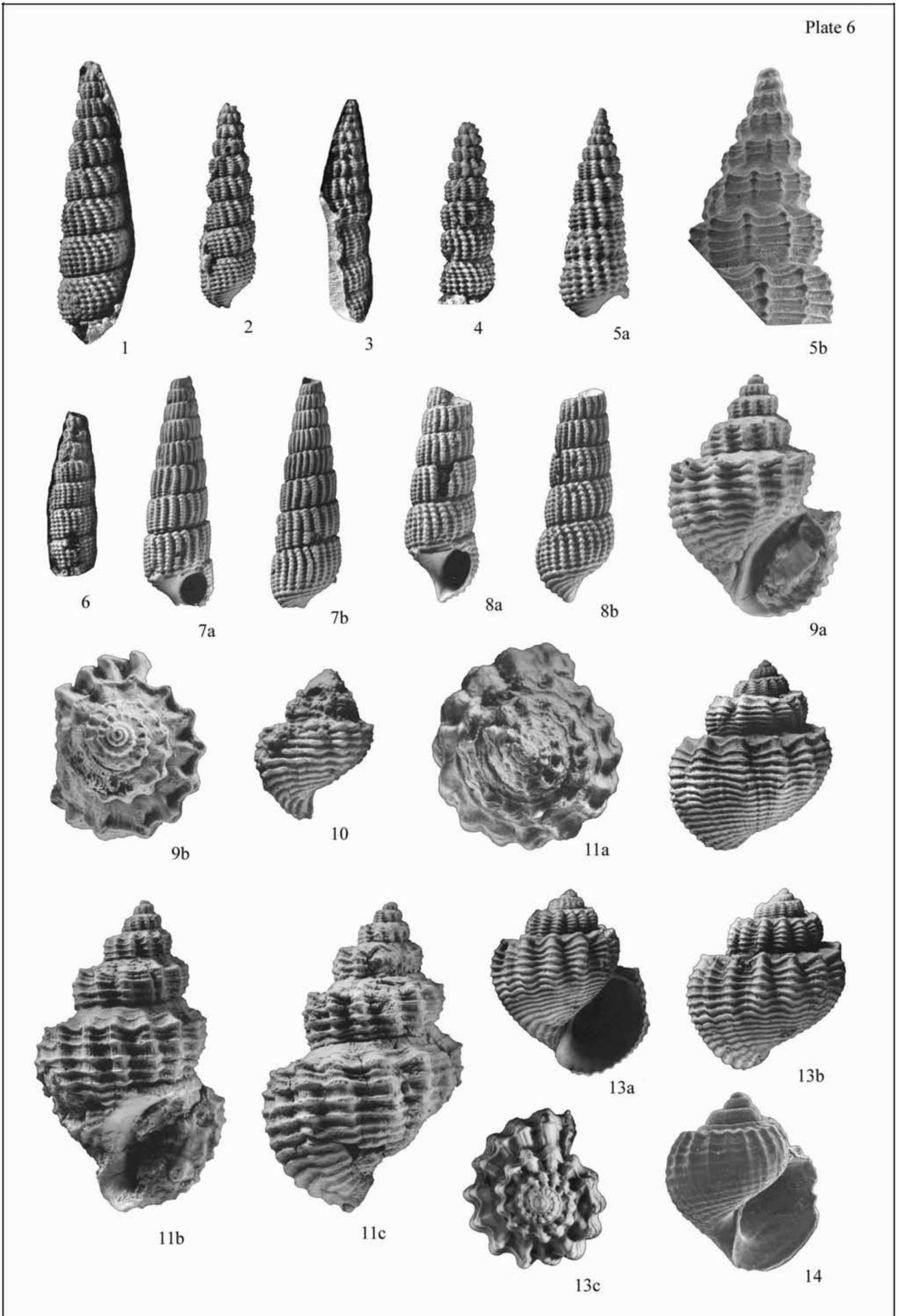
**Material.** Lower Callovian, *koenigi* Zone, *curtilobus* Subzone, village of Alpat'evo (one specimen).

Suborder Purpurinoidei Golikov et Starobogatov, 1987

Superfamily Pirpurinoidea Zittel, 1895

Family Purpurinidae Zittel, 1895

**Diagnosis.** Shell medium-sized or, rarely, large and pauci- or multispiral, ranging from turriculate to spherical, siphonostomatous, and anomphalous. Proto-



conch only described in *Purpurina* sensu stricto (see below). Teleoconch whorls gradate or prominently gradate, with angulation (carina) in upper part. Ornamentation composed of ribs or threads and folds or, rarely, of growth lines. Above carina, widely spaced ribs or threads formed; below carina, ribs numerous and usually better developed. Tubercles not formed. Aperture oval or elongated oval and rounded in lower part. Growth lines prosocline above angulation, becoming almost orthocline below angulation, and strongly curved posteriorly in lower part of shell base.

**Generic composition.** *Angularia* Koken, 1892; *Eucycloidea* Hudleston, 1888; *Moerckeia* J. Böhm, 1895; *Pseudoscalites* Kittl, 1894; *Purpurina* d'Orbigny, 1850 emend. Deslongchamps, 1860; *Tretospira* Koken, 1892; and ?*Ptychostoma* Laube, 1870.

**Remarks.** This family is similar in shell pattern to the Maturifusidae and differs from it in the slightly pronounced siphonostomatous pattern and the smooth and short protoconch with a sharp palatal carina on the last whorl.

**Occurrence.** Upper Triassic–Jurassic of Eurasia and South America.

**Genus *Purpurina* d'Orbigny, 1850 emend.  
Deslongchamps, 1860**

*Purpurina*: Deslongchamps, 1860, p. 136; Cossmann, 1913, p. 160 (pars).

*Purpurina* (*Purpurina*): Cossmann, 1906, p. 206; Wenz, 1939, p. 527.

**Type species.** *Turbo bellona* d'Orbigny, 1850; Bathonian; France.

**Diagnosis.** Shell medium-sized or large, paucior multispiral, ranging from low-turriculate to spherical. Teleoconch composed of four to seven whorls. Whorls more or less gradate, convex, and strongly involute. Suture deep. Upper part of whorls with more or less sharp angulation (carina), forming angle of about 90°. Surface above carina more or less wide, slightly sloping, and almost lacking spiral ornamentation.

Below carina, last whorl convex–conical or hemispherical, covered with densely spaced ribs, and lacking angulations. Wide, high or low, and slightly prosocline or orthocline folds extending across ribs. Toward shell end, folds becoming more rounded in outline, lower, and somewhat more smooth. Last whorl more or less high. Aperture vertically extended oval, with well-developed expansion of basal lip in shape of wide semi-circular protrusion turned downward. This expansion slightly concave (*Purpurina* sensu stricto) or flat (*Globipurpurina*). Maximum width of aperture close to its middle. From suture to lower third of surface under carina, apertural margin orthocline, becoming prosocline–prosoclyt below carina. Growth lines on lateral side slightly opisthoclyt or prosoclyt, becoming prosocline–prosoclyt in lower part.

**Composition.** Subgenera *Globipurpurina* subgen. nov. and *Purpurina*.

**Comparison.** *Purpurina* differs from the closest genus *Pseudoscalites* in its broad shell, better developed ornamentation, the aperture with the maximum width in the middle part, and the well-developed expansion of the basal lip, which is turned downward.

**Occurrence.** Lower Jurassic, Sinemurian–Upper Jurassic of Europe.

**Subgenus *Purpurina* d'Orbigny, 1850 emend. Deslongchamps, 1860**

**Type species.** *Turbo bellona* d'Orbigny, 1850; Bathonian; France.

**Diagnosis.** Shell medium-sized or large, paucior multispiral, and low-turriculate or low-conical. Protoconch not known. Teleoconch composed of four to seven whorls. Whorls strongly gradate and carinate in upper part. Maximum whorl width at carina, and extent of involution 45–50%. Wide surface observed above carina. Folds stout. Last whorl relatively high and almost conical, narrowing downward. Expansion of basal lip concave.

**Explanation of Plate 6**

**Figs. 1–5.** *Tyrnoviella alpatyevensis* sp. nov.: (1) GMM, no. 12/73 (cast), lateral to the aperture, ×3; (2) GMM, no. 12/74 (cast), abapertural view, ×3; (3) GMM, no. 12/75 (cast), lateral to the aperture, ×3; (4) GMM, no. 12/71 (cast), abapertural view, ×3; village of Alpat'evo; Lower Callovian, *koenigi* Zone, *curtilobus* Subzone; (5) GMM, no. 12/69; (5a) abapertural view, ×3, upper region of the teleoconch, ×17; village of Tymovo; Middle Callovian.

**Fig. 6.** *Tyrnoviella* sp. 2. GMM, no. 12/118 (cast), abapertural view, ×4. Village of Alpat'evo; Lower Callovian, *koenigi* Zone, *curtilobus* Subzone.

**Figs. 7 and 8.** *Tyrnoviella* sp. 1: (7) GMM, no. 12/119, ×3; (7a) apertural and (7b) abapertural views; (8) GMM, no. 12/120, ×3; (8a) apertural and (8b) abapertural views. Village of Tymovo; Middle Callovian.

**Figs. 9 and 10.** *Purpurina* (*Purpurina*) *orbignyana* Hebert et Deslongchamps: (9) PIN, no. 4863/138, ×2; (9a) apertural and (9b) abapical views; village of Gzhel'; Middle Callovian; (10) PIN, no. 4863/144, abapertural view, ×3; Moscow, Kamushki quarry; Middle Callovian.

**Fig. 11.** *Purpurina* (*Purpurina*) *serrata* (Quenstedt): PIN, no. 4863/136, ×1.5: (11a) abapical, (11b) apertural, and (11c) abapertural views. village of Gzhel'; Middle Callovian.

**Figs. 12–14.** *Purpurina* (*Globipurpurina*) *plicata* (Quenstedt): (12) PIN, no. 4863/144, abapertural view, ×3; village of Voronovo; Lower Oxfordian, *cordatum* Zone; (13) PIN, no. 4863/151, ×3; (13a) apertural, (13b) abapertural, and (13c) abapical views; Oka River between the villages of Nikitino and Chevkinno; Lower Oxfordian; and (14) GMM, no. 12/104, apertural view, ×22; Moscow, Mnevniky, Karamyshevskaya embankment; Middle Oxfordian.

**Species composition.** Nine species: type species; *P. (P.) aspera* Hudleston, 1887 [= *Purpurina aspera*] from the Bajocian of England; *P. (P.) concava* Brösamlen, 1909 [= *Purpurina concava*] from the Lower Callovian of Germany; *P. (P.) curta* Hudleston, 1887 [= *Purpurina curta*] from the Bajocian of England; *P. (P.) opalina* Brösamlen, 1909 [= *Purpurina opalina*] from the Lower Aalenian of Germany; *P. (P.) orbignyana* Hebert et Deslongchamps, 1860 [= *Purpurina orbignyana*]; *P. (P.) parvicosta* Hudleston, 1887 [= *Purpurina parvicosta*] from the Bajocian of England; and *P. (P.) serrata* (Quenstedt, 1858) [= *Turbo serratus*] and *P. (P.) suprajurensis* Etallon, 1861 [= *Purpurina suprajurensis*] from the Upper Kimmeridgian of France).

**Comparison.** This subgenus differs from the subgenus *Globipurpurina* in its longer, low-turriculate, and strongly gradate shell. In *Purpurina*, the whorls are less involute, the surface above the carina is wider, and the folds are well-developed and more prominent, in contrast to the low, rounded folds of the subgenus *Globipurpurina*.

*Purpurina (Purpurina) orbignyana* Hebert et Deslongchamps, 1860

Plate 6, figs. 9 and 10

*Purpurina orbignyana*: Hebert and Deslongchamps, 1860, p. 176, pl. 1, fig. 6; Couffon, 1919, pl. 8, fig. 7.

*Purpurina serrata*: Gerasimov, 1992, p. 63, pl. 15, figs. 10a and 11a; Gerasimov et al., 1996, pl. 22, fig. 10a (non 10b).

**Holotype.** The location is not known. France, Maine-et-Loire Department, Montreuil-Bellay; Callovian.

**Description.** The shell is up to 25 mm high. The teleoconch is composed of about four or five whorls. The teleoconch angle is 62°–64°. The maximum whorl width is at the carina, and the extent of involution is 45%. The whorl surface above the carina is slightly inclined (at an angle of 20°) and occasionally has a rib in the middle; five or six ribs occur below the carina. The folds are orthocone, 13–15 per whorl. They extend from suture to suture. The tubercles are triangular thickenings that extend along the ribs. On the carinate rib, the tubercles curve posteriorly. The last whorl is 53% of the shell height and has 11 ribs. The shell base is covered with ribs and, in the upper part, by the fold ends.

**Comparison.** *P. (P.) orbignyana* differs from *P. (P.) serrata* in its more gently sloping surface above the carina, sharper carina, and less coarse and more densely spaced ribs (see Pl. 6). The shell is smaller and shorter.

**Remarks.** Gerasimov (1992, pl. 15, figs. 10a, 10b, 11a, 11b) provided figures of three specimens: figs. 10a and 11a show the same specimen, fig. 10b shows a second specimen (*Purpurina serrata*), while fig. 11b displays a third specimen, which I have not found in the collection examined by Gerasimov.

**Occurrence.** Middle Callovian of European Russia; Callovian of France.

**Material.** Middle Callovian: village of Tymovo (one specimen), quarry between the villages of Troshkovo and Rechitsy (one specimen), and Moscow, Kamushki quarry (two specimens).

*Purpurina (Purpurina) serrata* (Quenstedt, 1858)

Plate 6, fig. 11

*Turbo serratus*: Quenstedt, 1858, p. 485, pl. 65, fig. 7.

*Purpurina serrata*: Brösamlen, 1909, p. 248, pl. 19, fig. 41; Cossmann, 1913, p. 165, pl. 8, figs. 22–24; Gerasimov, 1992, p. 63, pl. 15, fig. 10b; Gerasimov et al., 1996, pl. 22, fig. 10b (non 10a).

**Holotype.** The location is not known. Germany, Swabian Alb; Lower Callovian.

**Description.** The shell is up to 48 mm high. The teleoconch consists of about six or seven whorls. The teleoconch angle is 56°. The maximum whorl width is at the angulation or slightly lower, and the extent of involution is 45%. The surface above the carina is moderately inclined (at an angle of 40°) and has a rib in the middle. Below the carina, there are five ribs. The folds are orthocone, 15 or 16 per whorl. They extend from suture to suture and have tubercles in the shape of triangular thickenings extending along the ribs. On the carinate rib, the tubercles are not curved. The last whorl is 50% of the shell height and has 12 or 13 ribs. The shell base is covered with ribs and the ends of folds.

**Comparison.** See in the section devoted to *P. orbignyana*.

**Occurrence.** Lower Callovian of Germany; Lower–Middle Callovian of France; Middle Callovian of European Russia.

**Material.** Middle Callovian, village of Gzhel' (two specimens).

Subgenus *Globipurpurina* subgen. nov.

**Etymology.** From the Latin *globus* (sphere) and the generic name *Purpurina*.

**Type species.** *Purpurina sowerbyi* Waagen, 1866; Lower Bajocian; Germany.

**Diagnosis.** Shell medium-sized, paucispiral, and spherical. Protoconch composed of 2.5–3 whorls. Two first whorls smooth and rounded, last whorl with more or less sharp angulation in upper part. Surfaces above and below angulation horizontal and steep, respectively. Boundary between protoconch and teleoconch marked by appearance of folds. Teleoconch composed of four or five whorls. Whorls gradate and clearly narrowed toward angulation; therefore, their maximum width lower than angulation. Extent of involution 50–55%. Surface above carina from narrow to relatively broad. Folds wide, low, and semicircular. Last whorl high and hemispherical. Aperture with flattened expansion of basal lip in lower part.

**Species composition.** Fourteen species: type species; *P. (G.) clapensis* Piette et Jourdy, 1869 [= *Purpurina clapensis*] from the Bathonian of France;

*P. (G.) condensata* Hebert et Deslongchamps, 1860 [= *Purpurina condensata*] from the Callovian of France; *P. (G.) coronata* Hebert et Deslongchamps, 1860 [= *Purpurina coronata*] from the Callovian of France; *P. (G.) cottreui* Couffon, 1919 [= *Purpurina cottreui*] from the Callovian of France; *P. (G.) crispata* Cossmann, 1885 [= *Purpurina crispata*] from the Bathonian of France; *P. (G.) delphinoides* (Quenstedt, 1858) [= *Turbo delphinoides*] from the Lower Callovian of Germany; *P. (G.) ferruginea* Brösamlen, 1909 [= *Purpurina ferruginea*] from the Upper Aalenian of Germany; *P. (G.) inflata* Tawney, 1873 (after Hudleston, 1887) [= *Purpurina inflata*] from the Bajocian of England and France; *P. (G.) plicata* (Quenstedt, 1858) [= *Natica plicata*] and *P. (G.) rotunda* Hudleston, 1887 [= *Purpurina rotunda*] from the Bajocian of England; *P. (G.) tabulata* Hudleston, 1887 [= *Purpurina tabulata*] from the Bajocian of England; *P. (G.) tithonia* (Retowski, 1893) [= *Naticella* (?) *tithonia*] from the Tithonian (?Berriasian) of the Crimea; and *P. (G.) undulata* (Quenstedt, 1851) (after Brösamlen, 1909) [= *Turbo undulata*] from the Sinemurian–Pliensbachian of Germany.

**Comparison.** See the section devoted to *Purpurina* sensu stricto.

*Purpurina (Globipurpurina) plicata* (Quenstedt, 1858)

Plate 6, figs. 12–14; Plate 7, fig. 1

*Natica plicata*: Quenstedt, 1858, p. 550, pl. 72, fig. 24.

*Purpurina condensata*: Hebert and Deslongchamps, 1860, pl. 1, fig. 8b; Cossmann, 1913, p. 166, pl. 8, figs. 10–13; Gerasimov, 1992, p. 64, pl. 15, figs. 1, 2, 4–6; Gerasimov *et al.*, 1996, pl. 23, fig. 14.

*Purpurina plicata*: Brösamlen, 1909, p. 249, pl. 19, fig. 44.

**Holotype.** The location is not known. Germany, Swabian Alb; Middle–Upper Oxfordian.

**Description.** The protoconch consists of 2.5 whorls. The first whorl of the protoconch is semi-involute and projects strongly. As the shell grows, the whorls considerably increase in width; therefore, the protoconch has a concave generating line. The whorls are smooth and covered with growth lines. The upper part of the last half-whorl has a rounded angulation. The beginning of the teleoconch is marked by the appearance of folds. It consists of 4–4.5 whorls, the teleoconch angle ranges from 69° to 88°. The maximum whorl width is slightly lower than the angulation, and the extent of involution is 55%. The two last whorls are less involute; therefore, one rib becomes visible above the suture. The surface above the carina has up to three narrow threads and spiral striation; under the carina, there are six or seven ribs. Two primary ribs are present; one coincides with the carina, while the second is below it. The folds are orthocone, 13–15 per whorl. They extend from suture to suture. The intersections of ribs and folds have thickenings that extend along the ribs. The last whorl is 60–68% of the shell height and has 15–18 ribs. The shell base is covered with several ribs, while folds are usually absent.

**Occurrence.** Middle Callovian–Middle Oxfordian of European Russia; Middle–Upper Oxfordian of Germany; Lower–Middle Callovian of France.

**Material.** Middle Callovian, village of Gzhel' (one specimen); Upper Callovian–Lower Oxfordian, village of Nikitino (one specimen); Lower Oxfordian, villages of Nikitino (two specimens) and Polovchinovo (two specimens) and borehole near the village of Izvekovovo (one specimen); Lower Oxfordian, *cordatum* Zone, Sechenka River near the village of Voronovo (one specimen); and Middle Oxfordian, village of Nikitino (one specimen), Afanas'evskii quarry (one specimen), and Moscow, Mnevniky, rock dump at boreholes on the Karamyshevskaya embankment (one specimen).

*Purpurina (Globipurpurina) sp.*

Plate 11, fig. 7

The *koenigi* Zone of the Lower Callovian beds of the Nizhni Novgorod Region yielded poorly preserved *Purpurina* shells that resemble in shape those described above. However, these shells have lost most of the ornamentation and are identified on the basis of the whorl pattern and folds on the whorls. A similar shell was described from the Callovian of France and identified as *Purpurina condensata* (Hebert and Deslongchamps, 1860, pl. 1, fig. 8b). I determined this specimen as *P. (G.) plicata* (Quenstedt). However, the absence of ornamentation prevents the assignment of the *Purpurina (Globipurpurina) sp.* in question to the same species.

**Material.** Lower Callovian, *koenigi* Zone, *curtilobus* Subzone, Volga River near the village of Prosek (two specimens).

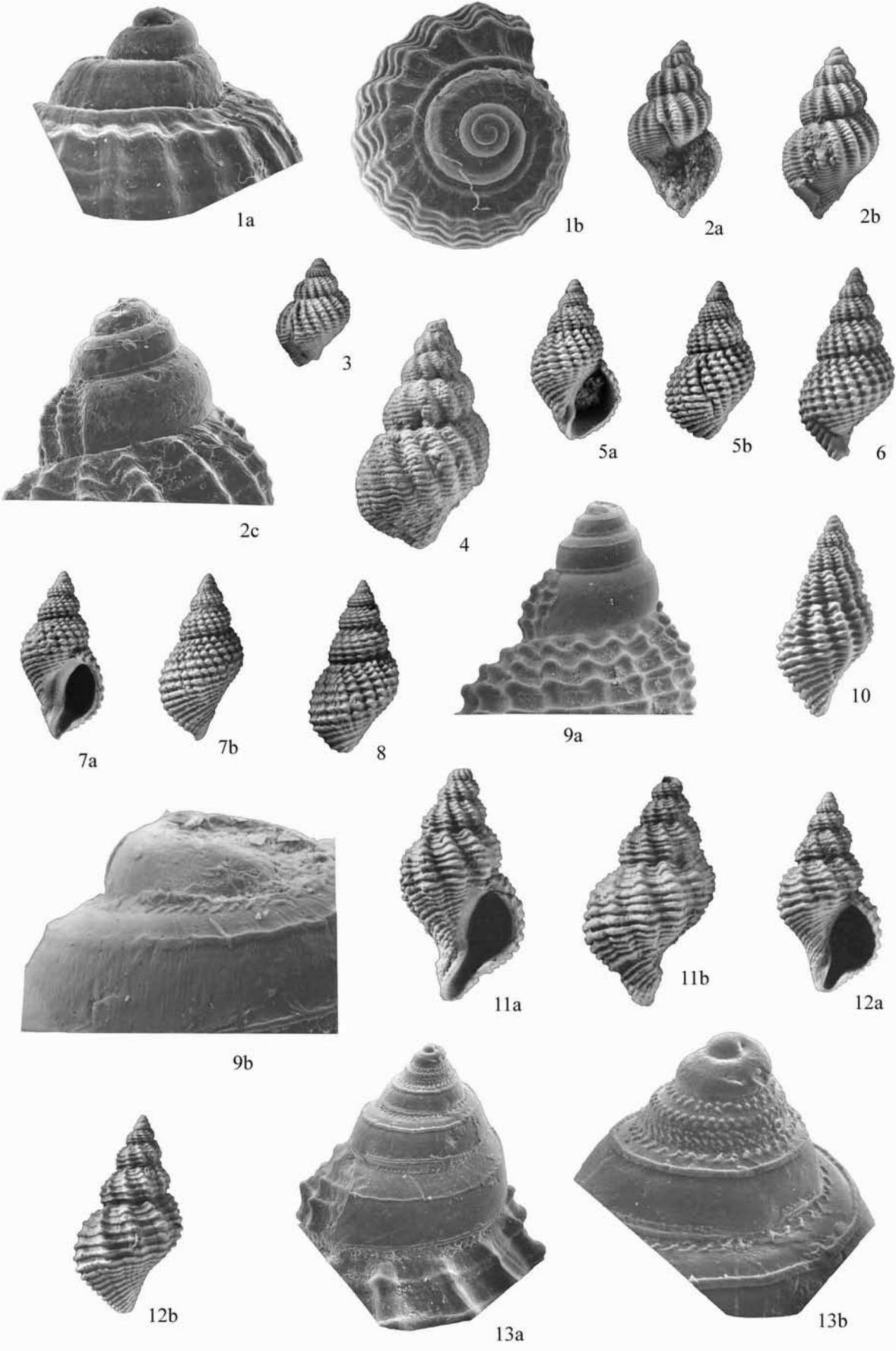
Suborder Cerithiopsodei Golikov et Starobogatov, 1987

Superfamily Cerithiopsodea H. et A. Adams, 1854

Family Cerithiopsidae H. et A. Adams, 1854

**Diagnosis.** Shell small or medium-sized, multi-spiral, turriculate, siphonostomatous, dextral, with straight generating line. Protoconch multi- or paucispiral, its first whorl often with ornamentation composed of microscopic tubercles. Subsequent whorls ranging from smooth to spirally and collabrally ornamented. Protoconch and teleoconch clearly separated by abrupt changes in ornamentation. Teleoconch whorls ranging from convex to flat, usually, reticulate-ribbed or, less often, their ornamentation composed of only stout ribs (subfamily Seilinae Golikov et Starobogatov, 1975). Aperture ranging from oval to quadrangular and having short but deep groove in lower part.

**Generic composition.** Several genera (about 12–13, in the subfamilies Cerithiopsinae and Seilinae) mostly from Cretaceous and Cenozoic. In addition, the Jurassic genera *Cosmocerithium* Cossmann, 1906 and *Novoselkella* Guzhov, 2002 and the Cretaceous genus *Prisciphora* Schröder, 1991 are included in this family. The genus *Cerithiopsidella*



Barth, 1911 has also been recorded in the Middle Jurassic (Gründel, 1977, 1980).

**Comparison.** The family Cerithiopsidae is distinguished from the Eumetulidae Golikov et Starobogotov by the protoconch, which is usually smooth or has well-developed ribs (threads). It differs from the Newtoniellidae Korobkov in the long protoconch (in the Newtoniellidae, the protoconch is compact and shaped like a little cap). It differs from the Protorculidae Bandel in the teleoconch ornamentation and in the spiral protoconch ornamentation.

**Occurrence.** Middle Jurassic, Bathonian–Recent.

### Genus *Cosmocerithium* Cossmann, 1906

*Cosmocerithium*: Cossmann, 1906, p. 26 (pars).

**Type species.** *Cerithium nysti* d'Archiac, 1843; Bathonian; France.

**Diagnosis.** Shell small or medium-sized, turriculate, with straight generating line. Protoconch composed of 4–5.5 whorls. Early 1–1.5 whorls smooth and rounded, similar to planispiral pattern. Subsequent whorl bicarinate. Last 2.5–3.5 whorls with collabral (often prevailing) and spiral ornamentation. In addition, last protoconch whorls with microsculpture consisting of tubercles or tubercle groups arranged in broken spiral rows. Whorls of protoconch convex. Early teleoconch whorls slightly convex, while later whorls often flattened and nongradate. Extent of involution approximately 40%. Ornamentation of teleoconch composed of several primary and secondary ribs. Thin, densely spaced folds extending across ribs. Shell base high, broadly conical, convex, having many ribs, and separated from lateral side by rounded angulation. Aperture rhombic or rounded rhombic, with deep, narrow groove in basal part; groove curved toward columella and varying in length. End of groove truncate, rounded rectangular. Growth lines on lateral side opisthocyrt or opisthocline–opisthocyrt, becoming prosocline–prosocyrt on shell base. Ontogenetic changes involving increase

in opisthocyrt orientation of folds and, occasionally, somewhat denser arrangement of folds.

**Species composition.** Eight species: type species; *C. brateevense* (Gerasimov, 1992) [= *Procerithium (Rhabdocolpus) brateevense*], *C. contiae* sp. nov., and *C. grandineum* (Buvignier, 1852) [= *Cerithium grandineum*] from the Lower–Middle Oxfordian of France; *C. pumilum* (Gerasimov, 1992) [= *Procerithium (Rhabdocolpus) pumilum*], *C. renardi* (Rouillier, 1849) [= *Cerithium renardi*], and *C. sanctijacobi* (Grepin, 1888) [= *Cerithium sanctijacobi*] from the Bajocian of France; and ?*C. brongniarti* (d'Archiac, 1843) [= *Cerithium brongniarti*] from the Bathonian of France.

**Comparison.** *Cosmocerithium* differs from other genera in its protoconch, which has one smooth early whorl followed by a whorl with only two ribs, and in the microsculpture on subsequent whorls. It is distinguished from many genera of the family by its more poorly developed siphonal canal.

### *Cosmocerithium renardi* (Rouillier, 1849)

Plate 9, fig. 12; Plate 10, figs. 1–4

*Cerithium renardi*: Rouillier, 1849, p. 378, pl. L, fig. 96; Lahusen, 1883, p. 37, pl. 3, fig. 7.

*Cosmocerithium renardi*: Guzhov, 2002b, p. 27, pl. 1, figs. 1–5.

**Holotype.** The holotype is lost. Moscow Region, Krasnogorskiy District, right bank of the Moskva River near the village of Gal'evo; upper Middle Oxfordian.

**Neotype.** GMM, no. 12/4; Kostroma Region, Makar'evskii District, town of Makar'ev, section Northern Makar'ev; Middle Oxfordian, *tenuiserratum* Zone.

**Description.** The shell is up to 10.5 mm high. The protoconch consists of 5.5 whorls. The first whorl is smooth, rounded, and is followed by a whorl with two ribs. Other whorls have folds, which extend to the lower rib. Initially, the folds are regularly convex and later become crescently inflated. The whorls become inflated and form concavities on the upper and lower surfaces. The folds may have tubercles just below the suture. The spiral ornamentation of two last whorls

### Explanation of Plate 7

**Fig. 1.** *Purpurina (Globipurpurina) plicata* (Quenstedt): GMM, no. 12/104: (1a) protoconch,  $\times 63$ , and (1b) abapical view,  $\times 30$ ; Moscow, Mnevniki, Karamyshevskaya embankment; Middle Oxfordian.

**Figs. 2–4.** *Maturifusus kostromensis* (Gerasimov): (2) GMM, no. 12/110: (2a) apertural,  $\times 4$ ; (2b) abapertural view,  $\times 4$ ; and (2c) protoconch,  $\times 33$ ; village of Fokino, clay quarry; Middle Callovian, *jason* Zone; (3) GMM, no. 12/124, abapertural view,  $\times 4$ ; village of Nikitino, Middle Oxfordian; (4) PIN, no. 4863/140, abapertural view,  $\times 3$ ; town of Shchelkovo; Middle Callovian.

**Figs. 5–9.** *Maturifusus keyserlingianus* (Rouillier): (5) GMM, no. 12/38,  $\times 3$ : (5a) apertural and (5b) abapertural views; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone; (6) GMM, no. 12/40, abapertural view,  $\times 3$ ; Egor'evskii Phosphorite Mine, quarry no. 7-2bis; Upper Oxfordian, *serratum* Zone, *serratum* Subzone; (7) GMM, no. 12/39,  $\times 3$ : (7a) apertural and (7b) abapertural views; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone; (8) PIN, no. 4863/141, abapertural view,  $\times 3$ ; village of Brylino (borehole); Lower Kimmeridgian, *kitchini* Zone; (9) GMM, no. 12/37: (9a) protoconch,  $\times 25$ , and (9b) fragment of the protoconch ornamentation,  $\times 160$ ; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone.

**Figs. 10–13.** *Maturifusus conspicuus* (Eichwald): (10) GMM, no. 12/41, abapertural view,  $\times 3$ ; (11) GMM, no. 12/85,  $\times 3$ : (11a) apertural and (11b) abapertural views; (12) GMM, no. 12/84,  $\times 3$ : (12a) apertural and (12b) abapertural views; (13) GMM, no. 12/112: (13a) protoconch,  $\times 42$ , and (13b) abaxial of the protoconch,  $\times 125$ . Town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone.

consists of two well-developed ribs. The last 3.5 whorls are densely covered by microscopic tubercles. The teleoconch consists of 9–11 flattened whorls. The teleoconch angle is 15°–20°. The teleoconch whorls are flat, and the extent of involution is approximately 40%. The suture is shallow. The ornamentation is composed of four primary and at most two secondary ribs. As the shell grew, the secondary ribs became as prominent as the primary ribs. The folds are slightly opisthocline–opisthocyrt or, less often, orthocline; a whorl 2–3 mm in diameter has 26–35 folds. They are usually slightly weaker than the ribs. Small rounded tubercles are formed at the intersections of folds and ribs. The last whorl is 24–28% of the shell height. The shell base has seven or eight ribs.

**Ontogenetic changes.** In some specimens, the folds become somewhat more densely spaced and more opisthocyrt with age. Sometimes, the shell end is covered with coarse growth lines. In such cases, the folds smoothen and the tubercles disappear.

**Comparison.** *C. renardi* is distinguished from *C. contiae* by the uniform spiral ornamentation in the protoconch, the greater number of spiral ornamentation (4–6 ribs in contrast to 6–7) of the teleoconch (except for the transitional forms, discussed below), the weaker folds (compared to ribs), and the flat whorls.

**Remarks.** The *tenuiserratum* Zone of the Kostroma Region yielded transitional forms intermediate between *C. renardi* and *C. contiae*. Their teleoconch is similar to that of *C. contiae*, while the protoconch resembles that of *C. renardi* (i.e., late ontogenetic stages change earlier than the early stage). These transitional forms are assigned to the species *C. renardi*. The differences from *C. pumilum* and *C. brateevense* are considered below.

**Occurrence.** Middle Oxfordian, *densiplicatum* Subzone of the *densiplicatum* Zone, to the *tenuiserratum* Zone.

**Material.** Middle Oxfordian, village of Tyrnovo (two specimens); Middle Oxfordian, *tenuiserratum* Zone, towns of Makar'ev (235 specimens) and Shchurovo (15 specimens); Middle Oxfordian, most likely *tenuiserratum* Zone, village of Mikhalenino (47 specimens).

*Cosmocerithium contiae* Guzhov, 2002

Plate 10, figs. 6–9

*Procerithium renardi*: Gerasimov, 1955, p. 189, pl. 40, figs. 2 and 3 (juv.).

*Procerithium (Rhabdocolpus) renardi*: Gerasimov, 1992, p. 71, pl. 19, figs. 1–4.

*Procerithium (Rhabdocolpus) pumilum*: Gerasimov, 1992, pl. 21, fig. 19.

*Cosmocerithium contiae*: Guzhov, 2002b, p. 28, pl. 1, figs. 6–9.

**Holotype.** GMM, no. 12/6; Russia, Moscow Region, Voskresenskii District, Egor'evskii Phosphorite Mine, quarry 7-2bis; Upper Oxfordian, *serratum* Zone, *serratum* Subzone.

**Description.** The shell is up to 10–11 mm high. The protoconch consists of 5.5 whorls. The first whorl is smooth, rounded, and followed by a whorl with two ribs. Other whorls have folds, which extend to the lower rib. Initially, the folds are regularly convex, later becoming inflated and crescent-shaped. The folds may have tubercles directly below the suture. The whorls become inflated and form concavities on the upper and lower surfaces. The spiral ornamentation of two last whorls of the protoconch changes considerably. In the middle of the whorl, two stout ribs are replaced by a series of narrow threads. The last whorl has seven ribs. The last 3.5 whorls are covered with densely spaced microscopic tubercles. The teleoconch consists of 9–11 flattened whorls. The teleoconch angle is 15°–20°. The teleoconch whorls are slightly convex, and the extent of involution is approximately 40%. The maximum width is at the midheight of the whorls. The suture is shallow. The ornamentation is composed of five primary and one or two secondary ribs. As the shell grew, the secondary ribs became as prominent as the primary ribs. The folds are slightly opisthocline–opisthocyrt. A whorl 2–3 mm in diameter has 23–35 folds. They are usually slightly more prominent than the ribs. Small rounded tubercles are formed at the intersections of the folds and the ribs. The last whorl is 24–28% of the shell height. The shell base has seven to nine ribs.

**Ontogenetic changes.** In some specimens, the folds become somewhat more densely spaced and more opisthocyrt with age. Sometimes, the shell end is covered with coarse growth lines. In this case, folds smoothen and tubercles disappear.

**Comparison.** See comparisons in the sections devoted to the other species of the genus.

**Remarks.** The collection examined by Gerasimov includes a large teleoconch fragment from the Lower Kimmeridgian all characters of which correspond to *C. renardi*. Since a large sample from the Upper Oxfordian (more than 1000 specimens) does not contain any *C. renardi*, this specimen is probably an example of *C. contiae* that displays a reversion of characters.

The Upper Kimmeridgian strata of the Ulyanovsk Region yielded a satisfactorily preserved juvenile shell, which is closely similar to *C. contiae* in the patterns of the protoconch and teleoconch. It is figured (Pl. 11, fig. 3) under the name *Cosmocerithium* sp.

**Occurrence.** Upper Oxfordian of European Russia.

**Material.** Upper Oxfordian, *serratum* Zone, *serratum* Subzone; Egor'evskii Phosphorite Mine, quarry no. 10 (one specimen) and quarry no. 7-2bis (1275 specimens).

*Cosmocerithium pumilum* (Gerasimov, 1992)

Plate 10, figs. 10–12

*Procerithium (Rhabdocolpus) pumilum*: Gerasimov, 1992, p. 74 (pars), pl. 21, figs. 15, 17, and 18.

*Cosmocerithium pumilum*: Guzhov, 2002b, p. 28, pl. 1, figs. 10–12.

**Holotype.** GGM, no. VI-222/35; Moscow, Mnevniki, riverbed of the Moskva River near the

Karamyshevskaya embankment; Upper Oxfordian, *serratum* Zone.

**Description.** Incomplete shells are up to 5 mm high. The protoconch consists of four whorls. The first whorl is smooth and circular in outline, the succeeding 0.7 of the whorl has two ribs, and the other whorls have orthocone folds. The first whorl that has folds also retains two ribs, while the succeeding whorls lack ribs. The last 2.5 whorls are densely covered with rows of microscopic tubercles and have a thickening that extends directly below the suture and has small tubercles formed by folds. The teleoconch has more than four whorls (incomplete). The teleoconch angle is 31° (early whorls). The whorls are convex, and the extent of involution is 38%. The maximum width is at the whorl midheight. The suture is superficial. From the beginning of the teleoconch, the thickening located under the suture disappears. The ornamentation is composed of four primary and four secondary ribs. The ribs are narrow and widely spaced. The folds are thin, densely spaced, and rather prominent. A whorl 1 mm in diameter has 17 folds. The folds weaken downwards and terminate short of reaching the suture. The tubercles are present on three upper ribs. The largest conical tubercles are formed on the upper rib. The shell base has six ribs; the upper rib is well-developed, while the others are weak.

**Comparison.** *C. pumilum* is distinguished from other species described here by its more convex whorls, an increase in prominence of folds and tubercles within a whorl from below upwards, and by the short protoconch.

**Occurrence.** Upper Oxfordian, *serratum* Zone, to the Lower Kimmeridgian; European Russia.

**Material.** Upper Oxfordian, *serratum* Zone, Moscow, Mnevniky, deposits from the riverbed of the Moskva River (four specimens); Lower Kimmeridgian, village of Poretzkoe (one specimen).

*Cosmocerithium brateevense* (Gerasimov, 1992)

Plate 11, figs. 1 and 2

*Procerithium (Rhabdocolpus) brateevense*: Gerasimov, 1992, p. 72, pl. 18, fig. 30; Gerasimov *et al.*, 1995, pl. 18, fig. 9.

*Cosmocerithium brateevense*: Guzhov, 2002b, p. 29, pl. 1, figs. 13 and 14.

**Holotype.** GGM, no. VI-222/38; Moscow, Brateevo, quarry; Volgian Stage, *nodiger* Zone, *mosquensis* Subzone.

**Description.** The shell is 6 mm high (incomplete). The protoconch is not known. The teleoconch is incomplete and contains 7.5 whorls. The teleoconch angle is 21.5°. The whorls are flat and slightly widened downward. The maximum whorl width is in the lower part. The suture is shallow. The ornamentation is composed of four ribs, which are supplemented by two ribs on large whorls. The ribs are uniform and regularly spaced. The folds are densely spaced, narrow, and orthocone; on the last whorls, they are opisthocline. A whorl 2 mm in diameter has 17 folds. Small circular

tubercles are formed at intersections of ribs and folds. The features of the aperture and the shell base are not known.

**Comparison.** *C. brateevense* is distinguished from other species described here by its coarser and more widely spaced spiral ornamentation and flat whorls, which expand in the lower part of the whorl.

**Occurrence.** Volgian Stage, *nodiger* Zone, *mosquensis* Subzone; European Russia.

**Material.** Upper Volgian, *nodiger* Zone, *mosquensis* Subzone; Moscow, quarry in Brateevo (three specimens) and D'yakovskoe (one specimen).

**Genus *Novoselkella* Guzhov, 2003**

*Novoselkella*: Guzhov, 2003, p. 34.

**Type species.** *N. novoselkensis* sp. nov.; Middle Oxfordian; Russia, Ryazan Region.

**Diagnosis.** Shell small, turriculate, and multi-spiral. Protoconch composed of several convex whorls covered with opisthocyrt folds and by threads in lower two-thirds of whorl. Tuberculate microsculpture also present. Boundary between protoconch and teleoconch distinct and marked by abrupt changes in ornamentation. Teleoconch whorls flattened and nongradate. Suture shallow. Ornamentation composed of many ribs and rounded folds. Shell base broadly conical, convex, with numerous ribs. Aperture oval, becoming angular in basal part. Growth lines slightly opisthocline–opisthocyrt on lateral side, becoming prosocyrt on shell base.

**Species composition.** Type species.

**Comparison.** *Novoselkella* differs from all other genera in the pattern of the shell base and ornamentation of the teleoconch. In other taxa, the base is more or less flattened; therefore, the last whorl has a basopalatal angulation. The ornamentation of the lateral side is prominent and composed of high ribs and well-pronounced narrow folds. In *Novoselkella*, the base is high and convex with a gentle transition to the lateral side of the whorl, and the ornamentation is composed of nongradate elements, i.e., both the folds and ribs are rounded. In addition, *Novoselkella* differs from all genera, except for *Cosmocerithium* and *Prisciphora*, in the complex ornamentation of the protoconch, which consists of numerous spiral and collabral elements.

**Remarks.** The distinctive features of the genus in question and its relationships are considered in detail in Chapter 3.

*Novoselkella novoselkensis* Guzhov, 2003

Plate 12, fig. 6

*Novoselkella novoselkensis*: Guzhov, 2003, p. 35, pl. 6, fig. 4.

**Holotype.** GMM, no. 12/31; Ryazan Region, Ryazanskii District, Oka River near the village of Novoselki; Middle Oxfordian.

**Description.** The shell is 4 mm high. The protoconch is incomplete and consists of three convex whorls covered with narrow, densely spaced, and prominent opisthocyrt folds and threads between them. At the boundary between the protoconch and teleoconch, the threads are replaced by better developed ribs. The teleoconch consists of four whorls (incomplete), the teleoconch angle is 18.5°. The maximum whorl width is at the midheight of whorls. The extent of involution is 42%. The ornamentation is composed of nine ribs and 19 folds (in a whorl 1.5 mm in diameter). The upper rib is slightly thicker than the others and has small tubercles. Other ribs lack tubercles and occasionally have only smooth thickenings. Five primary ribs are present. The folds are orthocline, gradually becoming weaker from above downward, and, on the last whorl, terminate short of the suture. The last whorl is 37% of the shell height. The shell base has seven ribs.

**Material.** Holotype.

#### Family Eumetulidae Golikov et Starobogatov, 1975

**Diagnosis.** Shell medium-sized, multispiral, turriculate, and siphonostomatous, with straight generating line. Shell dextral. Protoconch multi- or paucispiral, and its first whorl sometimes covered with microscopic tubercles. Subsequent whorls covered with folds and, often, with small threads. Protoconch and teleoconch usually clearly recognized by abrupt change in ornamentation. Teleoconch whorls more or less convex, with ornamentation composed of ribs and folds (usually prevailing) or only ribs. Aperture circular or oval, with groove in lower part.

**Generic composition.** In addition to *Longaevicerithium* Guzhov, 2003, about ten Cenozoic genera.

**Comparison.** The family Eumetulidae is distinguished from the Newtoniellidae Korobkov by the longer protoconch, which is covered with folds; convex whorls of the teleoconch; and the circular or oval aperture. It differs from the Protorculidae Bandel in the teleoconch ornamentation.

**Occurrence.** Upper Jurassic, Volgian–Recent.

#### Genus *Longaevicerithium* Guzhov, 2003

*Longaevicerithium*: Guzhov, 2003, p. 33.

**Type species.** *Procerithium* (*Plicacerithium*) *bitzae* Gerasimov, 1992; Upper Volgian, *subditus* Zone; Russia, Moscow Region.

**Diagnosis.** Shell medium-sized, multispiral, and high-turriculate. Protoconch consisting of several whorls covered with folds and spiral rows of microscopic tubercles. Boundary between protoconch and teleoconch easily recognized by abrupt change in ornamentation. Teleoconch whorls slow-growing, convex, and nongradate, with ornamentation composed of ribs and folds, with tubercles at intersections. Last whorl low. Shell base high, broadly conical, convex, with

numerous ribs. Aperture circular, becoming angular in lower part. Growth lines opisthocyrt on lateral side and prosocyrt on shell base.

**Species composition.** Type species.

**Comparison.** In contrast to the other genera of the family, *Longaevicerithium* has a multispiral protoconch covered with folds and spiral rows of microscopic tubercles.

#### *Longaevicerithium bitzae* (Gerasimov, 1992)

Plate 11, figs. 4–6

*Procerithium* (?) sp.: Gerasimov, 1969, p. 49, pl. 2, fig. 19.

*Procerithium* (*Plicacerithium*) *bitzae*: Gerasimov, 1992, p. 79, pl. 26, fig. 1; Gerasimov *et al.*, 1995, pl. 18, fig. 6.

*Longaevicerithium bitzae*: Guzhov, 2003, p. 33, pl. 6, figs. 1 and 2.

**Holotype.** GGM, no. IV-222/39; Moscow Region, Leninskii District, Bittsa River near the village of Saprionovo; Volgian Stage, *subditus* Zone.

**Description.** The shell is more than 19 mm high. The protoconch is incomplete, turriculate, and consists of four whorls. The whorls are convex and have densely spaced, narrow, and opisthocyrt folds. The last 2–2.5 whorls are covered with spiral rows of microscopic tubercles. The teleoconch consists of 7.5 whorls (incomplete), the teleoconch angle is 21° (one measurement). Its whorls are strongly convex, and the extent of the involution is 30%. The maximum whorl width is at the midheight of the whorl between folds or somewhat higher at the folds. The suture is relatively deep. The upper part of each whorl just below the suture forms a circular border around the preceding whorl. The ornamentation is composed of nine ribs (a whorl 1.8 mm in diameter), while the holotype has ten ribs (a whorl 5 mm in diameter). The ribs are prominent, high, and almost uniform. The folds are thick, widely spaced, high, and slightly opisthocyrt or, in the last whorls, opisthocyrt. A whorl of diameter 2–5 mm (holotype) has 14 folds. The shell base has three to eight ribs (a whorl 1.8 mm in diameter) and, in the upper part, the ends of folds.

**Occurrence.** Volgian Stage, *nikitini*–*subditus* zones of European Russia.

**Material.** Middle Volgian, *nikitini* Zone, Moscow, Kuntsevo (three specimens); Upper Volgian, *subditus* Zone, village of Saprionovo (two specimens).

#### Family Polygyrinidae Bandel, 1993

**Diagnosis.** Shell small or medium-sized, multispiral, turriculate or high-turriculate, siphonostomatous, and dextral. Protoconch turriculate, composed of convex whorls, with blunt apex and deep suture. Teleoconch whorls convex and smooth or collabrally ornamented. Aperture circular, becoming angular in basal part. Growth lines opisthocline–opisthocyrt on lateral side, becoming prosocline–prosocyrt on shell base.

**Generic composition.** *Polygyrina* Koken, 1892 and *Teutonica* Schröder, 1991.

**Comparison.** The family Polygyrinidae is distinguished from other families, except for the Protorculidae, by the smooth or collabrally ornamented teleoconch. It is distinguished from the Protorculidae by the short and blunt protoconch, which is composed of convex whorls separated from each other by deep sutures.

**Occurrence.** Upper Triassic, Carnian–Upper Jurassic, Oxfordian of Europe.

#### Genus *Teutonica* Schröder, 1991

*Teutonica*: Schröder, 1991, p. 503; 1995, p. 17; Nützel, 1998, p. 148; Gründel, 1999d, p. 40; Guzhov, 2003, p. 34.

**Type species.** *T. grammani* Schröder, 1991; Upper Bajocian; Germany.

**Diagnosis.** Shell turriculate or high-turriculate. Protoconch composed of 4–5 convex whorls; early whorls smooth, while late whorls covered with numerous collabral rows of tubercles, usually terminating short of reaching suture or folds. Row of small tubercles usually extending along suture. Teleoconch whorls convex and having inflated folds. Whorls usually covered with microscopic tubercles. Last whorl low. Shell base broadly conical, convex, and smooth. Aperture circular, becoming angular in lower part. Growth lines opisthocyrt on lateral side and prosocline on shell base.

**Species composition.** Five species: type species; *T. calloviana* Gründel, 2001; *T. clivosa* (Yamnichenko, 1958) [= *Zygopleura clivosa*] from the Upper Bajocian, *garantiana* Zone, of Ukraine; *T. rectecostata* Gründel, 1999 from the Upper Bathonian, *aspidoidea* Zone, of Germany; and *T. verrucosa* Gründel, 1999 from the Upper Bajocian-Bathonian of Poland and Germany [= *T. procera* Gründel, 1999 from the Upper Bathonian of Germany].

**Comparison.** *Teutonica* is distinguished from *Polygyrina* by the well-developed collabral ornamentation and the row of tubercles directly below the suture in the protoconch and the collabral ornamentation on the teleoconch.

#### *Teutonica calloviana* Gründel, 2001

Plate 11, fig. 8

*Teutonica calloviana*: Gründel, 2001, p. 48, pl. 1, figs. 11–14.

*Teutonica tatiana*: Guzhov, 2003, p. 34, pl. 6, fig. 3.

**Holotype.** Bundesanstalt für Geowissenschaften und Rohstoffe, Dienstbereich Berlin, no. BGR X 12323; Germany, borehole Fe Teetz; Upper Callovian, *athleta* Zone.

**Description.** The shell is 3.5 mm high. The protoconch consists of 4.5 convex whorls. The first whorl is almost planispiral, smooth, and circular in outline; later, a row of small tubercles appears directly below the suture. From the beginning of the third whorl, the protoconch is covered with densely spaced orthocline folds, which disappear on the last half-whorl. The last half-whorl is smooth and has several sharp opisthocyrt

growth lines at the end. The teleoconch consists of five whorls, its angle is 18°. The whorls are convex, with the maximum width at the midheight. The suture is shallow. The ornamentation is composed of folds, which gradually smoothen during ontogeny in the upper and lower part and transform into a row of tubercles in the middle of the whorl. The tubercles are large and semi-circular. The penultimate whorl has 12 tubercles. Large whorls have a weak spiral thickening above the suture. The last whorl is 31% of the shell height. The shell base is smooth and bordered from above by the shoulder with a weak spiral thickening.

**Comparison.** *T. calloviana* is distinguished from other species by the orthocline folds on the protoconch, which extend from suture to suture, and by the folds on the teleoconch, which are reduced to tubercles at the midheight of whorls.

**Occurrence.** Upper Callovian, *athleta* Zone, of Germany; Upper Oxfordian, *serratum* Zone, of European Russia.

**Material.** Upper Oxfordian, *serratum* Zone, *serratum* Subzone, Egor'evskii Phosphorite Mine, quarry no. 7-2bis (two specimens).

#### Superorder Bucciniformii Férussac, 1822

##### Order Bucciniformes Férussac, 1822

##### Suborder Buccinoidei Férussac, 1822

#### Family Maturifusidae Gründel, 2001

**Diagnosis.** Shell medium-sized, bucciniform or having carinate gradate whorls, siphonostomatous, and anomphalous. Protoconch whorls gradate, with two angulations or rounded; first whorl clearly projecting or planispiral. Teleoconch whorls covered with many uniform ribs (or threads) and folds. Secondary ribs usually numerous. Aperture oval or inverted teardrop-shaped, with groove in lower part; groove curved toward columella and varying in length and depth. Less often, groove replaced by angular protrusion. Outer lip thick, becoming thinner in marginal area, with even or wavy edge. Growth lines opisthocyrt above middle of shell base, becoming prosoclyrt below, and, close to columella, returning to opisthocyrt curvature. Ontogenetic changes involving weakening of folds, sometimes accompanied by increase in their density, and appearance of coarse growth lines.

**Generic composition.** *Khetella* Beisel, 1977, *Maturifusus* Szabó, 1983, and *Rhynchocerithium* Cossman, 1906.

**Comparison.** The family Maturifusidae is distinguished from other families by the fusiform or conical protoconch, which is usually composed of bicarinate whorls.

**Occurrence.** Lower Jurassic, Pliensbachian, to the Lower Cretaceous of Eurasia.

Genus *Maturifusus* Szabó, 1983

*Maturifusus*: Szabó, 1983, p. 44; Schröder, 1991, p. 40.

Type species. *M. densicostatus* Szabó, 1983; Upper Bajocian; Hungary.

**Diagnosis.** Shell paucispiral and bucciniform. Protoconch composed of 4.5–5 whorls; 1.5–2 early whorls rounded, while later whorls gradate. Last whorls with two (upper and lower) angulations with ribs. Upper angulation sharp, almost 90°, while lower angulation substantially less prominent and located at suture. First whorl of protoconch varying from semi-involute to planispiral, while subsequent whorls semi-involute. Second whorl of protoconch with tubercles. Boundary between protoconch and teleoconch marked by opisthocyrt commissure, beginning from which folds and numerous ribs developed. Teleoconch composed of 4–4.5 rounded and strongly convex whorls. Suture deep. Ornamentation composed of many ribs or threads and well-developed or, sometimes, stout opisthocyrt folds. Small tubercles formed at intersections of ribs with folds. Shell base covered with many ribs or threads and weakened ends of folds. Aperture oval or inverted teardrop-shaped, with long groove. Occasionally, lower part of aperture shaped into triangular projection, not forming clearly differentiated groove.

**Species composition.** Thirteen species: type species; *M. caseus* (Yamnichenko, 1987) [= *Fusus crassus* Yamnichenko, 1987] from the Upper Bajocian of Ukraine; *M. conspicuus* (Eichwald, 1868) [= *Murex conspicuus*]; *M. grimmensis* Gründel, 1999 from the Upper Pliensbachian of Germany; *M. keyserlingianus* (Rouillier, 1846) [= *Buccinum keyserlingianus*]; *M. kostromensis* (Gerasimov, 1955) [= *Brachytrema kostromensis*]; *M. mosquensis* sp. nov.; *M. piettei* (Hebert et Deslongchamps, 1860) [= *Fusus piettei*] from the Callovian of France; *M. piquus* (Beisel, 1983) [= *Astandes piquus*] from the Upper Kimmeridgian of northern Siberia; *M. purpuriniformis* (Conti, 1982) (juv.) [= *Brachytrema purpuriniformis*] from the Lower Bajocian, *humphriesianum* Zone, of Italy; *M. szaboi* Schröder, 1993 from the Upper Aalenian of Germany; ?*M. nassoides* (Eudes-Deslongchamps, 1842) [= *Fusus nassoides*] from the Bajocian of France; and ?*M. zeisei* (Wolleman, 1903) [= *Cerithium zeisei*] from the Aptian–Albian of Germany.

**Comparison.** *Maturifusus* is distinguished from *Khetella* by its multispiral and high protoconch and well-developed spiral ornamentation of the teleoconch. The differences from *Rhynchocerithium* are discussed in the section devoted to this genus.

**Remarks.** *Maturifusus* is morphologically similar to *Alariopsis clathrata* Gemmellaro, 1878 from the Lower Lias of Sicily, which is the type species of the genus *Alariopsis*. Thus, it is not inconceivable that *Maturifusus* is a synonym of *Alariopsis*, the resolution of this question requires the reexamination of the type material of *Alariopsis*.

*Maturifusus kostromensis* (Gerasimov, 1955)

Plate 7, figs. 2–4

?*Fusus piettei*: Hebert and Deslongchamps, 1860, p. 172, pl. 8, fig. 6 (*Fusus trigeri*, err.).

*Brachytrema kostromense*: Gerasimov, 1955, p. 196, pl. 39, fig. 17.

*Astandes kostromensis*: Gerasimov, 1992, p. 97, pl. 27, figs. 9 and 10; Gerasimov et al., 1996, pl. 22, fig. 3.

**Holotype.** The location is not known; Russia, Kostroma Region, Makar'evskii District, right bank of the Unzha River near the village of Polovchinovo; Middle Callovian.

**Description.** The shell is up to 13.5 mm high. The three last whorls of the protoconch are known. Each has two well-developed angulations. At the end of the protoconch, the angulations become rounded and lose their threads. The teleoconch consists of about four whorls, the teleoconch angle ranges from 45° to 60°. The maximum width is close to the midheight of the whorls, and the extent of involution is approximately 50%. As the shell grew, the whorls became less involute; therefore, two or three ribs emerged from under the suture. The ornamentation is composed of 12–15 threads (in a whorl 3.5–4.5 mm in diameter), five to eight of which are primary ribs. The folds range from orthocone to opisthocyrt and from thin to thick. Whorls of diameters 3.5, 4.5, and 5.5 mm have 18, 16, and 23–24 folds, respectively. On the shell base, the folds closely approach the columella. The tubercles are small and circular. The last whorls 3.5–4.5 mm in diameter have 27–29 threads, and those 5.5 mm in diameter have 30–32. The last whorl is 52–55% of the shell height. The shell base has many threads and weak folds. The aperture is oval or vertically elongated oval and has a well-developed groove.

**Comparison.** *M. kostromensis* is distinguished from other species by its narrow and densely spaced threads.

**Remarks.** The Middle Callovian beds yielded shells morphologically intermediate between *M. kostromensis* and *M. keyserlingianus*. Consequently, the latter species is most likely a descendant of the former. In the course of its formation, the folds became larger and more widely spaced, while the spiral ornamentation became coarser; as a result, the ribs became thicker and more widely spaced, and the secondary ornamentation was reduced. A further increase in the coarseness of the collabral ornamentation of *M. keyserlingianus* resulted in the appearance of *M. conspicuus*, which has especially stout folds.

**Occurrence.** Lower Callovian, *koenigi* Zone, *gowerianus* Subzone, to the Middle Oxfordian of European Russia.

**Material.** Lower Callovian, *koenigi* Zone, *gowerianus* Subzone, village of Vasil'kovo (one specimen); Lower Callovian, *koenigi* Zone, *curtilobus* Subzone, villages of Ileshevo (one specimen) and Burdovo (one specimen); Middle Callovian, *jason* Zone, village of Fokino (three specimens); Middle Callovian, Shchelk-

ovo (one specimen); and Middle Oxfordian, village of Nikitino (one specimen).

*Maturifusus keyserlingianus* (Rouillier, 1846)

Plate 7, figs. 5–9

*Buccinum keyserlingianum*: Rouillier, 1846, pl. C, fig. 5; 1847, p. 404 [non pl. G, fig. 22 (err.)]; Lahusen, 1883, p. 41, pl. 3, fig. 25; Sokolov, 1912, p. 103 (pars), pl. 2, figs. 1, 3, and 4.

*Brachytrema keyserlingiana*: Gerasimov, 1955, p. 195, pl. 39, figs. 15 and 16.

*Astandes keyserlingianus*: Gerasimov, 1992, p. 95, pl. 13, figs. 4, 7, and 13; pl. 27, figs. 1, 2, 4–6.

**Lectotype.** TsNIGRI, no. 737/1 (collection no. 10941) (Sokolov, 1912, pl. 2, fig. 3); Moscow Region, Krasnogorskii District, right bank of the Moskva River near the village of Gal'ev; Upper Oxfordian. This specimen is probably the holotype depicted by Rouillier.

**Description.** The shell is up to 13–14 mm high. The last 3.5 whorls of the protoconch with two angulations are known. At the end of the protoconch, the shoulders are not rounded. The teleoconch consists of 3.8 to 4.3 whorls, the teleoconch angle ranges from 40° to 51°. The maximum width is at the midheight of the whorls or slightly lower, and the extent of involution is 37–40%. As the shell grew, its ribs did not emerge from under the suture. The ornamentation is composed of seven ribs (in a whorl of 4.5–5 mm in diameter), including five primary ribs. The folds opisthocyrt, 16–27 per whorl; on the shell base, they closely approach the columella. The thickness and height of folds are in inverse proportion to their number. The tubercles are small and circular. On the last whorl, the ornamentation consists of 14–17 ribs (in a whorl of 4.5–5 mm in diameter). The last whorl is 53% of the height of the shell. The shell base has several ribs and weak folds. The aperture is oval or, rarely, inverted teardrop-shaped, with a wide angular protrusion or, occasionally, a groove in the lower part.

**Ontogenetic changes.** Age-related variation may manifest itself in interrupted growth. In extreme cases, the folds are considerably reduced and replaced by series of coarse growth lines.

**Comparison.** *M. keyserlingianus* and *M. conspicuus* are connected by a series of transitional forms with intermediate ornamentation. Nevertheless, *M. keyserlingianus* is regarded as an independent species due to the discovery of extinct populations (accumulations) with clearly restricted individual variation. Judging from these samples, it is possible to conclude that *M. keyserlingianus* is distinguished from *M. conspicuus* by its finer and denser ornamentation, i.e., closer positioned folds (16 and more), and, usually, oval aperture with a wide angular protrusion.

**Remarks.** The study of *M. keyserlingianus* of different age displayed evolutionary changes, which distinguish two groups (designated as  $\alpha$  and  $\beta$ ) within this species. In *M. keyserlingianus*  $\alpha$ , the sutural teleoconch

angle is substantially larger than that of the protoconch; the teleoconch consists of 3.4–4 whorls. The distance between the suture and the upper rib is approximately the same as between the latter and the next rib. The teleoconch angle usually ranges from 45° to 51° and only rarely decreases to 43°. This form occurs in the Lower and Middle Oxfordian. In *M. keyserlingianus*  $\beta$ , the teleoconch consists of more than four whorls; the sutural teleoconch angle only slightly exceeds that of the protoconch; the upper rib is located at a greater distance from the suture than from the next rib; and the teleoconch angle is usually about 40°. This form occurs in the Upper Oxfordian (*serratum* Zone).

**Occurrence.** Oxfordian–Lower Kimmeridgian of European Russia.

**Material.** Lower Oxfordian, village of Nikitino (three specimens); Middle Oxfordian: village of Nikitino (11 specimens), Afanas'evskii quarry (two specimens), villages of Tyrnovo (eight specimens), Vasil'kovo (seven specimens), and Mikhhalenino (66 specimens); Middle Oxfordian, *densiplicatum* Zone, *densiplicatum* Subzone, village of Vasil'kovo (two specimens); Middle Oxfordian, *tenuiserratum* Zone: towns of Shchurovo, Zarech'e District (25 specimens), and Makar'ev (451 specimens); Upper Oxfordian, *serratum* Zone, *serratum* Subzone, Egor'evskii Phosphorite Mine, quarry no. 7-2bis (71 specimens); and Lower Kimmeridgian, *kichini* Zone, village of Brylino, borehole no. 21 (one specimen).

*Maturifusus conspicuus* (Eichwald, 1868)

Plate 7, figs. 10–13; Plate 8, fig. 1

*Murex conspicuum*: Eichwald, 1868, p. 956, pl. 31, fig. 10.

*Astandes conspicuus*: Gerasimov, 1992, p. 97, pl. 13, figs. 3 and 6, pl. 27, figs. 3 and 7.

*Maturifusus montagi*: Gründel, 1998, p. 17, pl. 7, figs. 5–8.

**Holotype.** (?) SPbGU, no. 2/1915; Russia, Moscow Region, Krasnogorskii District, right bank of the Moskva River near the village of Gal'ev; Upper Oxfordian. Because of Eichwald's incorrect figure and serious subsequent damage (the last whorls are broken), it is impossible to identify this specimen as the holotype with certainty. No other specimens of this species are present in the collection examined by Eichwald (although the researcher indicated the presence of two shells).

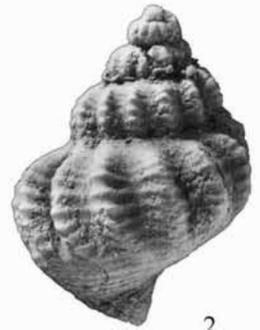
**Description.** The shell is up to 13–14 mm high. The protoconch consists of five whorls. The first whorl is circular, smooth, and semi-involute. At the end of this whorl, a weakly developed angulation emerges in its upper part; subsequently, the whorls become strongly gradate. Beginning from 1.3 whorls, a row of circular tubercles appears below the suture and is retained up to the end of the protoconch. Three additional rows of similar tubercles appear at 1.8 whorls: on the shoulder, above the suture, and in the middle between them. From 2.8 whorls, the rows of tubercles on the shoulder and above the suture are replaced by a thread. Later, the



1a



1b



2



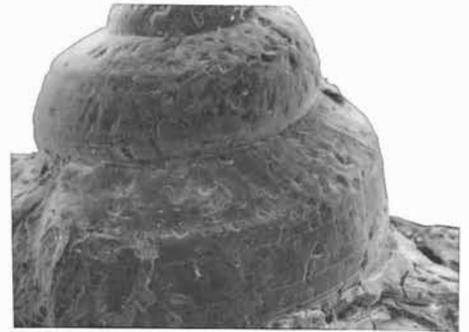
3a



3b



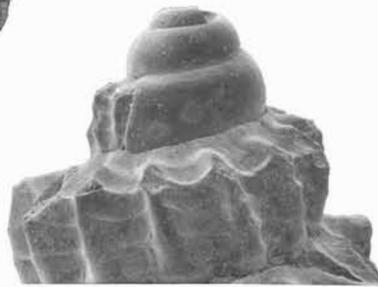
4a



4b



5a



5b



5c



6



7



8a



8b



9



10



11a



11b



12

lower angulation is formed on a level with the lower thread. The middle row of tubercles disappears beginning from the third whorl. At the end of the protoconch, the shoulders are not rounded. The teleoconch consists of 4–4.3 whorls, its angle ranges from 43° to 54°. The maximum width is close to the midheight of whorls, and the extent of involution is 41%. The ribs do not emerge from under the suture with the shell growth. The ornamentation is composed of seven to nine ribs (in a whorl 5–6 mm in diameter), including five primary ribs. The folds are opisthocyrts, 9–15 per whorl. They are thick and, on the shell base, closely approach the columella. The tubercles are circular. The last whorl has 17–21 (rarely 13) ribs (in a whorl 5–6 mm in diameter). The last whorl is 53% of the shell height. The shell base is covered with several ribs and weak folds. The aperture is inverted teardrop-shaped, with a groove in the lower part.

**Comparison.** See the sections devoted to the other species of this genus.

**Remarks.** The specimen shown in Pl. 7, fig. 12 is morphologically most similar to the presumed holotype.

**Occurrence.** Middle and Upper Oxfordian, ? Lower Kimmeridgian of European Russia; Oxfordian of Germany.

**Material.** Middle Oxfordian: villages of Nikitino (three specimens), Chevkinovo (one specimen), Vasil'kovo (two specimens), and Mikhalenino (two specimens) and town of Makar'ev (one specimen); Middle Oxfordian, *densiplicatum* Zone, town of Makar'ev (one specimen); Middle Oxfordian, *tenuiserratum* Zone, town of Shchurovo (Zarech'e District) (18 specimens); Upper Oxfordian, *serratum* Zone, *serratum* Subzone, Egor'evskii Phosphorite Mine, quarries no. 7-2bis (372 specimens) and no. 10 (two specimens).

*Maturifusus mosquensis* Guzhov, sp. nov.

Plate 8, figs. 2–4

*Khetella incerta*: Gerasimov, 1992, pl. 27, fig. 11; Gerasimov et al., 1995, pl. 18, fig. 7.

**Etymology.** From Moscow.

**Holotype.** PIN, no. 4863/139; Moscow, Kuntsevo, Suvorovskii Park, gully; Volgian Stage, *virgatus* Zone, *virgatus* Subzone.

**Description.** The shell is up to 15 mm high. The protoconch consists of 4.5 whorls. The first whorl is planispiral. The upper angulation is observed beginning from the third whorl, while before it, the whorls are rounded and smooth and, then, become gradate. The last whorl of the protoconch has a weak lower angulation. Threads extend along the angulations; on the lower angulation, the thread is usually soon after its formation replaced by a pair of narrower threads. In the last whorl of the protoconch, a series of three or four narrow, closely positioned threads emerge from under the suture. The surface between the angulations has a narrow thread and numerous spiral striae. At the end of the protoconch, the lower angulation is covered by the suture. The teleoconch consists of 3.6 whorls, its angle is impossible to estimate. The maximum width is close to the midheight of the whorls, and the extent of the involution is 40%. The ornamentation is composed of four or five ribs. The number of primary ribs is impossible to determine. The folds are stout, orthocline, and prosocline, 13–15 per whorl. The tubercles at inter sections of folds and ribs are circular. The last whorl has 14 or 15 ribs and is approximately 48% of the shell height. The shell base is covered with spiral ribs and weak folds. The aperture is almost inverted teardrop-shaped and has a groove.

**Comparison.** The new species is clearly distinguished from others by the fine spiral ornamentation of the protoconch. In addition, it differs from *M. conspicuus* in the planispiral first whorl of the protoconch, and from *M. kostromensis* and *M. keyserlingianus* in the more widely spaced collabral and spiral ornamentation.

**Occurrence.** Volgian Stage, *virgatus* (*virgatus* Subzone) and *nikitini* zones of European Russia.

**Material.** Middle Volgian, *virgatus* Zone, *virgatus* Subzone, Moscow, Kuntsevo (eight specimens, including six juveniles); Middle Volgian, *nikitini* Zone, Moscow, Kuntsevo (nine specimens, including eight juveniles.).

Explanation of Plate 8

**Fig. 1.** *Maturifusus conspicuus* (Eichwald), GMM, no. 12/86: (1a) protoconch, ×26, and (1b) fragment of the protoconch ornamentation, ×85. Egor'evskii Phosphorite Mine, quarry no. 7-2bis; Upper Oxfordian, *serratum* Zone, *serratum* Subzone.

**Figs. 2–4.** *Maturifusus mosquensis* sp. nov.: Moscow, Kuntsevo, Suvorovskii Park; Middle Volgian: (2) holotype, PIN, no. 4863/139, abapertural view, ×3; *virgatus* Zone, *virgatus* Subzone; (3) GMM, no. 12/122, ×3: (3a) apertural and (3b) abapertural views; *nikitini* Zone; (4) GMM, no. 12/106: (4a) protoconch, ×22, and (4b) fragment of the protoconch ornamentation, ×44; *virgatus* Zone, *virgatus* Subzone.

**Figs. 5–8.** *Khetella formosiformis* sp. nov.: (5) GMM, no. 12/113: (5a) abapertural view, ×3, (5b) protoconch and early whorls of the teleoconch, ×19, and (5c) protoconch, ×33; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone; (6) GMM, no. 4863/142, abapertural view, ×3; quarry between the villages of Troshkovo and Rechitsy; Middle Callovian; (7) GMM, no. 12/130, abapertural view, ×3; Afanas'evskii quarry; Middle Oxfordian; (8) holotype GMM, no. 12/26, ×3: (8a) apertural and (8b) abapertural views; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone.

**Figs. 9–12.** *Khetella formosa* (Eichwald): (9) GMM, no. 12/132, abapertural view, ×3; Egor'evskii Phosphorite Mine, quarry no. 7-2bis; Upper Oxfordian, *serratum* Zone, *serratum* Subzone; (10) GMM, no. 12/126, abapertural view, ×3; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone; (11) GMM, no. 12/109: (11a) abapertural view, ×11, (11b) protoconch, ×24; Egor'evskii Phosphorite Mine, quarry no. 7-2bis; Upper Oxfordian, *serratum* Zone, *serratum* Subzone; (12) GMM, no. 12/115, protoconch, ×20; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone.

Genus *Khetella* Beisel, 1977

*Khetella*: Beisel, 1977a, p. 146; 1983, p. 73.

*Paracerithium* (*Fossacerithium*): Gerasimov, 1992, p. 86.

Type species. *Khetella bojarkae* Beisel, 1977; Lower Kimmeridgian; Russia, Krasnoyarsk Region.

Diagnosis. Shell pauci- or multispiral, low-turriculate or low-conical, bucciniform or with gradate whorls. Protoconch composed of two smooth circular planispiral whorls and, usually, 2–2.5 angular gradate whorls with two shoulders. Occasionally, shoulders absent. Boundary between protoconch and teleoconch marked by opisthocyrt commissure and abrupt change in ornamentation (appearance of folds and ribs). Teleoconch composed of 3.5–6 whorls. Suture deep. Whorls usually gradate, with angulation in upper part, or, less often, rounded. Whorl surface above angulation gently sloping. Below angulation, last whorl rounded up to columella. Surface of whorls covered with prominent folds and numerous weak threads, usually becoming smooth with shell growth. Folds extending from suture to suture and rapidly disappearing at the base. Threads lacking tubercles. Shell base with weak spiral threads and ends of folds. Aperture ranging from oval to vertically elongated oval, with long groove or wide angular protrusion in lower part.

Ontogenetic changes. The folds become somewhat weaker with age.

Species composition. Twelve species: type species; *Kh. formosa* (Eichwald, 1868) [= *Fusus formosa*]; *Kh. formosiformis* sp. nov.; *Kh. glasunovi* sp. nov.; *Kh. gradata* sp. nov.; *Kh. hymermece*s (Cossmann, 1913) [= *Purpurina hymermece*s] from the Middle Oxfordian of France; *Kh. incerta* (d'Orbigny, 1845) [= *Buccinum incerta*]; *Kh. makaryevensis* sp. nov.; *Kh. septentrionalis* (Tullberg, 1880) [= *Buccinum septentrionalis*] from the Upper Oxfordian–Lower Kimmeridgian (Volgian? of the Novaya Zemlya); *Kh. ventrosa* Beisel, 1983 (Boreal Berriasian–Valanginian of northern Siberia); ?*Kh. brunsvicensis* (Wollemann, 1900) [= *Fusus brunsvicensis*] from the Neocomian of Holland; and ?*Kh. liasica* (Dumortier, 1874) [= *Fusus liasica*] from the Upper Toarcian, *bifrons* Zone, of France.

Comparison. *Khetella* differs from *Maturifusus* in the structural pattern of the protoconch and, usually, in the gradate whorls.

Remarks. This genus is distinguished from the convergently similar *Purpurina* (*Purpurina*) and *Pseudoscalites* by the presence of the basal protrusion.

*Khetella formosiformis* Guzhov, sp. nov.

Plate 8, figs. 5–8

*Fusus formosus*: Ilovaisky, 1903, p. 264, pl. 10, fig. 19.

*Purpurina formosa*: Gerasimov, 1955, p. 179, pl. 39, fig. 12.

*Paracerithium* (*Fossacerithium*) *formosum*: Gerasimov, 1992, p. 87 (pars), pl. 24, figs. 1 and 2; Gerasimov *et al.*, 1996, pl. 24, figs. 14 and 15.

Etymology. From the species name *Khetella formosa*.

Holotype. GMM, no. 12/26; Moscow Region, Kolomenskii District, quarry in the town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone.

Description. The shell is up to 21.5 mm high. The last 3.5 whorls of the protoconch are smooth and gently curved, changing from slightly sloping in the upper part to steep in the lower part. No angulations are formed. At the end of the protoconch, the whorl is slightly expanded. The teleoconch consists of five whorls, its angle ranges from 51° to 68°. The whorls are prominently gradate, with a gently sloping surface above the carina and conical below it. The maximum whorl width is at the shoulder, and the extent of involution is approximately 60%. The suture is deep. Four primary ribs are present, the upper rib extends along the shoulder. The ornamentation is composed of two or three narrow and widely spaced threads in the lower part of the surface above the carina and six or seven (on the third whorl of the teleoconch) well-developed threads below the carina. The folds are stout, prosocline, and angular on the carina, 13–15 per whorl. In the last whorl, the surface below the carina has 25–27 threads, some are hardly discernible. The last whorl is 55–65% of the shell height. The shell base has numerous strongly smoothed and hardly discernible threads. The aperture is vertically elongated oval, with a long, straight, narrow, shallow groove that curves toward the columella.

Comparison. The new species is distinguished from *Kh. bojarkae* and *Kh. ventrosa* by its well-developed keel-shaped angulation, well-pronounced threads above the suture, and the presence of a groove. It is distinguished from *Kh. septentrionalis* by the presence of threads and a well-developed carina, and from *Kh. incerta* by its well-developed carina. A comparison with *Kh. formosa* is given in the section devoted to this species.

Occurrence. Middle Callovian–Middle Oxfordian of European Russia.

Material. Middle Callovian, quarry between the villages of Troshkovo and Rechitsy (one specimen); Middle Oxfordian, village of Tymovo (one specimen) and Afanas'evskii quarry (one specimen); Middle Oxfordian, *tenuiserratum* Zone, town of Shchurovo (Zarech'e District) (ten specimens).

*Khetella formosa* (Eichwald, 1868)

Plate 8, figs. 9–12; Plate 9, fig. 1

?*Fusus minutus*: Rouillier, 1849, p. 377, pl. L, fig. 94.

*Fusus formosus*: Eichwald, 1868, p. 946, pl. 31, fig. 7.

*Paracerithium* (*Fossacerithium*) *formosum*: Gerasimov, 1992, p. 87 (pars), pl. 24, figs. 3 and 10.

Holotype. SPbGU, no. 2/1752; Moscow Region, Krasnogorskii District, village of Gal'ev, bank of the Moskva River; Upper Oxfordian.

**Description.** The shell is up to 20 mm high. The protoconch consists of 4.2–4.5 whorls. Two first whorls are planispiral, smooth, and gently slope in the upper part, becoming steep in the lower part. From the third whorl, the lower shoulder is formed and, then, the upper shoulder develops as well. The shoulders become angular, and the whorls become gradate. Beginning from 3.3 whorls, the upper shoulder acquires a thread. In the last half-whorl of the protoconch, the lower shoulder approaches the suture and often disappears under it. At the end of the protoconch, the whorl expands. The teleoconch consists of 3.5–4 whorls. The teleoconch angle ranges from 58° to 68°. The whorls are distinctly gradate, with a gently sloping surface above the carina and a conically narrowed surface below the carina. The maximum whorl width is at the shoulder, and the extent of involution is 58%. The suture is deep. One or two primary ribs are present. The upper rib extends along the carina. One to three narrow threads that appear late in ontogeny extend above the carina; below the carina, there are two to five threads (at the stage of a 2–2.5 whorls of the teleoconch), which are usually smooth and hardly discernible or even disappear in adult whorls. The folds are stout, prosocline, and angular on the carina; a whorl has 11–12 folds. The last whorl is 57–60% of the shell height. The shell base may be covered with very weak and smooth threads. The aperture is oval and has a long, straight, narrow, shallow groove that curves toward the columella.

**Comparison.** *Kh. formosa* is distinguished from *Kh. ventrosa* by its more widely spaced folds (11–12 in contrast to 15–17) and the presence of a groove; from *Kh. bojarkae* by the keel-shaped carina and the presence of a groove; from *Kh. makaryevensis* by gradate whorls and more widely spaced folds; from *Kh. formosiformis* by a more prominent carina, weaker threads, which are often absent in large whorls, and the presence of two angulations on the protoconch whorls; and from *Kh. septentrionalis* by a wider spire and more widely spaced folds (11–12 in contrast to 14).

**Remarks.** A shell with several well-developed ribs on the lateral side, which is characteristic of *Kh. formosiformis*, was found in the Lower Kimmeridgian of the Kostroma Region. However, this species has not been recorded above the Middle Oxfordian; therefore, we regard this specimen as either an aberrant specimen of *Kh. formosa* or one demonstrating reversion of characters. Although the scope of the species *Kh. formosa* is narrowed because of the establishment of the new species *Kh. formosiformis*, the former is represented by two morphological groups. The first (known from the Middle Oxfordian) comprises shells that have a well-developed carinate rib and one or two ribs below it, while the second (Upper Oxfordian) includes shells with the carinate rib only (moreover, this rib is weaker than in specimens from the Middle Oxfordian). If the different age of these varieties is corroborated in the future, the group from the Middle Oxfordian should be ranked as an independent species. The holotype of

*Kh. formosiformis* belongs to the Upper Oxfordian group and is identical in morphology to the shells shown in Pl. 8, figs. 9 and 11.

**Occurrence.** Middle and Upper Oxfordian and ?Lower Kimmeridgian of European Russia.

**Material.** Middle Oxfordian, village of Mikhalevino (one specimen); Middle Oxfordian, *tenuiserratum* Zone, town of Shchurovo (Zarech'e District) (seven specimens); Upper Oxfordian, *serratum* Zone, *serratum* Subzone, Egor'evskii Phosphorite Mine, quarry no. 7-2bis (nine specimens); Lower Kimmeridgian, village of Mikhalevino (one specimen).

*Khetella gradata* Guzhov, sp. nov.

Plate 9, figs. 10 and 11

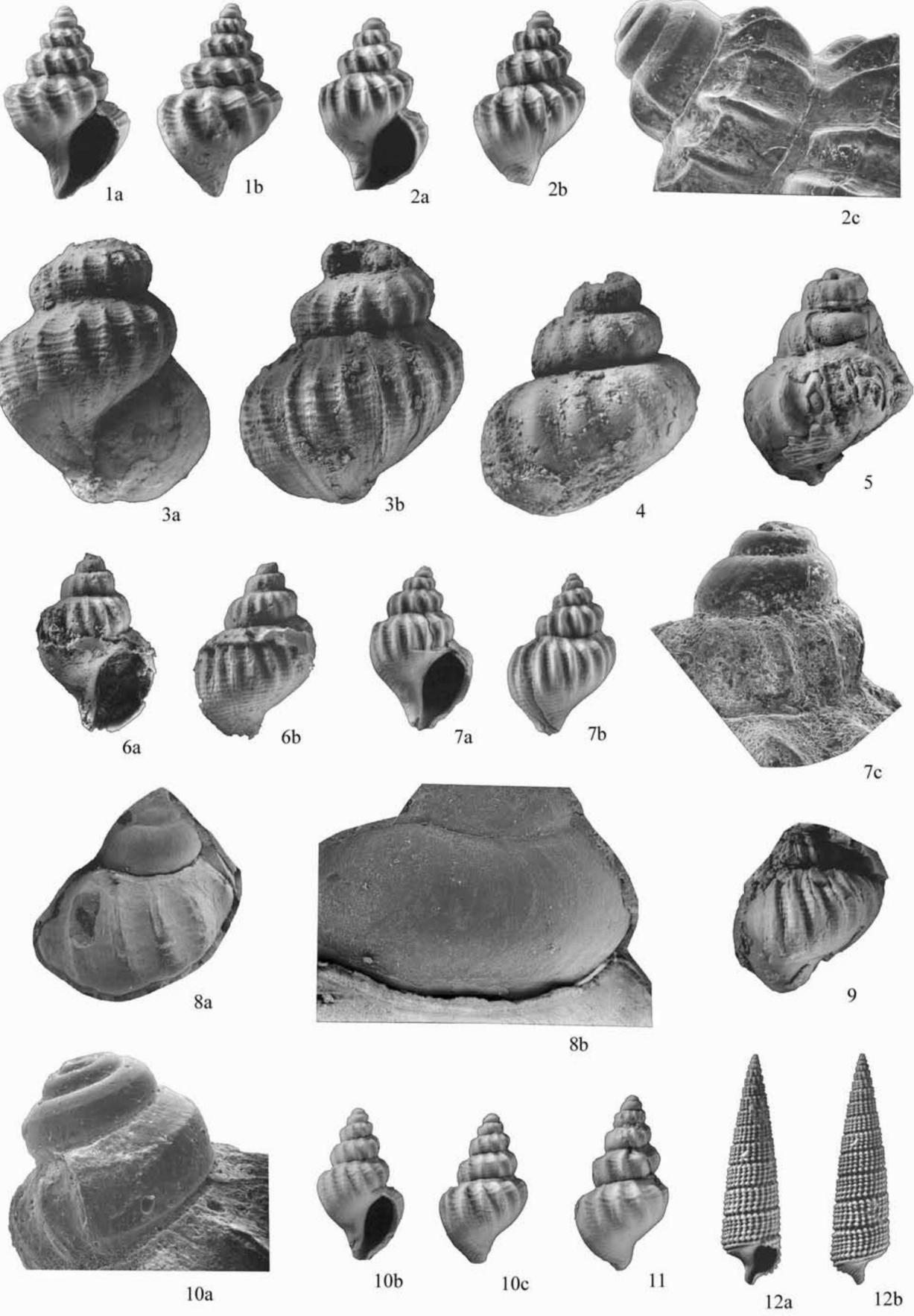
*Astandes kostromensis*: Gerasimov, 1992, pl. 27, fig. 12 (J<sub>3</sub>ox<sub>2</sub> non J<sub>2</sub>cl<sub>2</sub>).

**Etymology.** From the Latin *gradatus* (stepped).

**Holotype.** GMM, no. 12/27; Moscow Region, Kolomenskii District, quarries in the town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone.

**Description.** The shell is up to 14 mm high. The protoconch consists of 4.5 whorls, two first are planispiral. They gently slope in the upper part and become steep in the lower part. From the third whorl, both the lower and upper shoulders are clearly visible. They become angular and acquire a thread. In the last whorl, the lower angulation descends to the suture. At the end of the protoconch, the whorl expands. The teleoconch consists of 4.2 whorls. The teleoconch angle ranges from 41° to 52°. Its whorls are nongradate or slightly gradate and convex or slightly angular in the upper part. The maximum whorl width is at the angulation, and the extent of involution is 48–50%. The suture is deep. The angulation is poorly pronounced, being marked by angular folds. Threads appear from the second or third whorls; they are very weak, usually indiscernible. One or two weak and widely spaced threads are present above the angulation, and about eight (at the point of 3.5 teleoconch whorls) are below. The folds are stout, prosocline, and angular on the shoulder, each whorl has 12–13 folds. Tubercles are not formed. The last whorl is 48–52% of the shell height. The shell base has almost indiscernible threads. The aperture is vertically elongated oval, with a long, straight, narrow, shallow groove that curves toward the columella.

**Comparison.** The new species is distinguished from *Kh. bojarkae* by its well-developed groove, from other species by the poorly pronounced angulation and the narrower shell, and from *Kh. incerta* and *Kh. makaryevensis* by its more slender shell and more widely spaced and only slightly developed threads. In addition, it differs from the last species in the more widely spaced folds.



Occurrence. Middle Oxfordian, *tenuiserratum* Zone, of European Russia.

Material. Middle Oxfordian, *tenuiserratum* Zone, town of Shchurovo (Zarech'e District) (four specimens).

*Khetella incerta* (d'Orbigny, 1845)

Plate 9, figs. 2–5

*Nassa*: Fischer von Waldheim, 1837, pl. 47, figs. 4 and 5.

*Buccinum incertum*: d'Orbigny, 1845, p. 453, pl. 47, figs. 6–8.

*Turbo subpyramidalis*: Eichwald, 1868, p. 908, pl. 30, fig. 5.

*Brachitrema incerta*: Gerasimov, 1955, p. 195, pl. 39, figs. 18 and 19; 1969, p. 43, pl. 2, fig. 14.

*Khetella incerta*: Gerasimov, 1992, p. 104 (pars), pl. 27, figs. 8, 13, and 14; Gerasimov *et al.*, 1995, pl. 18, fig. 8.

Holotype. The holotype was designated by Murchison *et al.* (1845) from the Sary-gul Mountains in the Orenburg Region. The geological age of this species remains uncertain. Ilovaisky and Florensky (1941) described a section in this region. They registered the presence of the Upper Oxfordian, Upper and, possibly, Lower Kimmeridgian and the *panderi* Zone of the Volgian Stage. In addition to the list of ammonites collected, they recorded certain other fossil groups; in particular, the Upper Kimmeridgian beds yielded "abundant and diverse lamellibranchiates... and gastropods." When describing other stratigraphic intervals, these researchers did not mention gastropods. Thus, it is highly probable that the holotype of *Kh. incerta* was discovered in the Upper Kimmeridgian.

Neotype. GMM, no. 12/28; Ulyanovsk Region, Ulyanovskii District, village of Gorodishchi, right bank of the Volga River; Volgian Stage, bottom of the *klimovi* Zone.

Description. The shell is up to 35 mm long. The protoconch of typical *Kh. incerta* is not known. The

teleoconch consists of more than five whorls. The teleoconch angle ranges from 46° to 57°. Its whorls are nongradate or slightly gradate. The maximum whorl width is at the angulation, and the extent of involution is approximately 57% (in the neotype). The suture is deep. The whorls are convex or slightly angular in the upper part, while, in the lower part, they are conically narrowed. The shoulder is poorly pronounced and outlined by angular folds. The sole rib extends along the shoulder. The ribs are weak, more or less prominent, and densely cover the whorl. The last whorl has 18–22 ribs. The folds are thick, more or less prosocline, and angular on the shoulder; a whorl has 13–17 folds. Tubercles are absent. In the last whorl of the neotype, one rib is formed above the angulation and about 17 are below it (the whorl 5.4 mm in diameter). The last whorl is 50–55% of the shell height. The shell base has several weak ribs. The aperture is a vertically elongated oval, with an angular, broad, and relatively deep protrusion.

Comparison. *Kh. incerta* is distinguished from *Kh. bojarkae* by a clearly pronounced spiral ornamentation and from *Kh. makaryevensis* by its narrower shell.

Remarks. There are great difficulties with the taxonomic position of the so-called "*Khetella incerta*" described by Gerasimov from the Middle and Upper Volgian of the Russian Platform. All of these specimens and the shells examined by me in other collections are poorly preserved and mostly represented by molds with remains of the shell layer. Therefore, it is impossible to assign this material to *Khetella incerta* with certainty. Many molds are more massive than the holotype, as it is depicted by d'Orbigny (see for example, Pl. 9, fig. 4), or lack the spiral ornamentation, which is rather prominent in the holotype (see Gerasimov, 1992, pl. 27, fig. 13). In other words, they significantly differ from

Explanation of Plate 9

Fig. 1. *Khetella formosa* (Eichwald). GMM, no. 12/115, ×3: (1a) apertural and (1b) abapertural views; town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone.

Figs. 2, 4, and 5. *Khetella ? incerta* (d'Orbigny): (2) PIN, no. 4863/143: (2a) apertural view, ×4, (2b) abapertural view, ×4, (2c) protoconch, ×21; Moscow, Mnevniki, Studenyi gully; Middle Volgian, *virgatus* Zone; (4) PIN, no. 4518/617, abapertural view, ×3; Egor'evskii Phosphorite Mine, quarry no. 7-2bis; Middle Volgian, *virgatus* Zone; (5) PIN, no. 4863/147, abapertural view, ×2; Moscow, Mnevniki, Studenyi gully; Middle Volgian, *virgatus* Zone.

Fig. 3. *Khetella incerta* (d'Orbigny): (3) neotype GMM, no. 12/28, ×3: (3a) apertural and (3b) abapertural view; village of Gorodishchi; Lower Volgian; basal part of the *klimovi* Zone.

Figs. 6–9. *Khetella makaryevensis* sp. nov.: (6) holotype GMM, no. 12/29 (cast), ×3: (6a) apertural view, (6b) abapertural view; village of Ileshevo; Lower Callovian, *koenigi* Zone, *curtilobus* Subzone; (7) PIN, no. 4863/145: (7a) apertural view, ×3, (7b) abapertural view, ×3, and (7c) protoconch, ×30; Nizhni Novgorod Region, Koverminskii District, borehole no. 83 (depth of 75.5 m); Middle Oxfordian; (8) GMM, no. 12/134: (8a) general appearance, ×17, and (8b) fragment of protoconch ornamentation, ×57; town of Manturovo; Lower Callovian, *calloviense* Zone; (9) GMM, no. 12/114, abapertural view, ×3; town of Makar'ev; Middle Callovian, *jason* Zone, *medea* Subzone.

Figs. 10 and 11. *Khetella gradata* sp. nov.: (10) holotype, GMM, no. 12/27: (10a) protoconch, ×34, (10b) apertural view, ×3, and (10c) abapertural view, ×3; (11) GMM, no. 12/127, abapertural view, ×3. Town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone.

Fig. 12. *Cosmocerithium renardi* (Rouillier): GMM, no. 12/2, ×4: (12a) apertural and (12b) abapertural views. Town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone.

the type material (in the present study they are referred to as *Khetella ? incerta*). I also show a shell of "*Khetella incerta*" with a well-preserved protoconch that was depicted by Gerasimov (1992, pl. 27, fig. 14) (Pl. 9, fig. 2). Gerasimov indicated that this specimen came from the *virgatus* Zone of the Studenyi gully. However, this statement has been questioned, by myself and by some amateurs who saw the specimen, which displays a type of shell preservation that is atypical for the Volgian Stage. At the same time, it is rather similar in morphology to early *Kh. formosa* (Eichwald) (compare with the specimen shown in Pl. 9, fig. 1). However, the type of preservation of the specimen examined by Gerasimov is also atypical for the Oxfordian. Therefore, it is impossible to support or reject the dating of this specimen. Nevertheless, I have included a figure of this questionable specimen in the present study in order to familiarize researchers with this material.

**Occurrence.** Volgian Stage, *klimovi* Zone, to Boreal Berriasian, *rjasanensis* Zone, of European Russia.

**Material.** *Khetella incerta*: Lower Volgian, *klimovi* Zone (bottom); village of Gorodishchi (one specimen).

*Khetella ? incerta*: Middle Volgian, *panderi* Zone, Moscow, Mnevniki (two specimens); Middle Volgian, *virgatus* Zone, Moscow, Mnevniki (three specimens), Studenyi gully (two specimens), and Egor'evskii Phosphorite Mine, quarry no. 9-bis (one specimen); Middle Volgian, *virgatus* Zone, *virgatus* Subzone, Egor'evskii Phosphorite Mine, quarries no. 5 (one specimen) and no. 7-2bis (one specimen); Middle Volgian, *nikitini* Zone, village of Mostovo (one specimen); and Upper Volgian, *subditus* Zone, Moscow, Khoroshovo (one specimen).

*Khetella makaryevensis* Guzhov, sp. nov.

Plate 9, figs. 6–9

**Etymology.** From the town of Makar'ev.

**Holotype.** GMM, no. 12/29; Kostroma Region, Kologrivskii District, village of Ileshevo; Lower Callovian, *koenigi* Zone, *curtilobus* Subzone.

**Description.** The shell is up to 20–25 mm long. The last 2.2 whorls of the protoconch are preserved. They are smooth, rounded, with a deep suture, and have only strongly opisthocyrt growth lines. The teleoconch consists of 3.5 whorls, its angle ranges from 55° to 61°. The teleoconch whorls are convex, with a weak or almost indiscernible angulation in the upper part. The maximum whorl width is at the angulation or somewhat lower, and the extent of involution is 42–44%. The suture is deep. The surface above the angulation is very narrow and weakly inclined, while the surface under the angulation is convex. Two weak threads extend just above the angulation, and nine to ten densely spaced and barely discernible threads are below the angulation. The folds are stout, prosocline above the angulation, and almost orthocline below it. The whorl has 17–19 folds (in

a whorl 6–7 mm in diameter). Tubercles are not formed. The last whorl is 62% of the shell height. The shell base has about ten barely discernible threads and, sometimes, ends of folds. The aperture is oval, with a long, wide groove in the lower part.

**Comparison.** For comparisons, see the sections devoted to the other species of this genus. The new species is distinguished from *Kh. septentrionalis* by its weakly developed angulation, lower spire, and the presence of spiral ornamentation.

**Occurrence.** Lower Callovian, *koenigi* Zone, *curtilobus* Subzone, to the Middle Oxfordian of European Russia.

**Material.** Lower Callovian, *koenigi* Zone, *curtilobus* Subzone, village of Ileshevo (one specimen); Lower Callovian, *calloviense* Zone, town of Manturovo (two specimens); Middle Callovian, *jason* Zone, *medea* Subzone, village of Vasil'kovo (one specimen) and town of Makar'ev (four specimens); and Middle Oxfordian, borehole no. 83 (Nizhni Novgorod Region) (one specimen).

*Khetella glasunovi* Guzhov, sp. nov.

*Fusus minutus*: Trautschold, 1865, p. 17, pl. 3, fig. 13 (non *Fusus minutus* Roemer, 1836).

*Buccinum incertum*: Glazunova, 1973, pl. 43, figs. 1–7 (non *Buccinum incertum* d'Orbigny, 1845).

**Etymology.** In honor of the paleontologist A.E. Glazunova.

**Holotype.** The holotype was depicted by Glazunova (1973, pl. 43, fig. 2); Russia, Ulyanovsk Region, city of Ulyanovsk; Upper Hauterivian, *decheni* Zone.

**Description.** The shell is up to 40 mm high. The protoconch is not known. The teleoconch consists of four whorls, and its angle is approximately 50°. The teleoconch whorls are nongradate and convex. The maximum width is at the midheight of whorls. The suture is relatively deep. The shoulder is only slightly prominent and marked by weakly angular folds. The presence of the spiral ornamentation has not been mentioned. The folds are stout, prosocline, and weakly angular on the shoulder; 12–14 per whorl. The last whorl is approximately half as high as the shell. The shell base is smooth. The aperture is circular and has a straight, narrow, shallow groove that curves toward the columella.

**Comparison.** The new species is distinguished from *Kh. incerta* by the absence of spiral ornamentation, from *Kh. gradata* by the circular aperture, rounded cross section of whorls, and the absence of threads. It is distinguished from *Kh. makaryevensis* by the more widely spaced folds and the absence of threads; from *Kh. bojarkae* by the more widely spaced folds, a narrower shell, and a well-developed groove; and from *Kh. septentrionalis* by the almost completely reduced angulation (in *Kh. septentrionalis*, the angulation is well-developed).

**Occurrence.** Hauterivian of European Russia.

**Material.** Lower Hauterivian: Komi Republic, Ust'-Tsilemskii District, Pizhma River near the village of Stepanovskaya (one specimen).

**Genus *Rhynchocerithium* Cossmann, 1906**

*Rhynchocerithium*: Cossmann, 1906, p. 49; 1913, p. 155; Wenz, 1940, p. 733; Gründel, 1999b, p. 13.

**Type species.** *Cerithium fusiforme* Hebert et Deslongchamps, 1860; Callovian; France, Maine-et-Loire Department, Montreuil-Bellay.

**Diagnosis.** Shell pauci- or multispiral, turriculate or low-turriculate. Protoconch composed of 6–6.5 whorls, semi-involute from very beginning. Therefore, first whorl clearly projecting above subsequent whorls, circular in outline, and smooth. Then two carinae formed, each with rib. Lower carina much less prominent than upper. In last 1–1.5 whorls of protoconch or from beginning of teleoconch, rib formed in middle between suture and upper carina. Whorls of protoconch more or less gradate. Suture deep. Teleoconch composed of 4–7 whorls and distinguished by appearance of folds. Whorls convex and nongradate or slightly gradate. Three primary ribs present, corresponding to carinae of protoconch and rib above them. In ontogeny, upper rib usually becoming stronger, equipped with large tubercles, sometimes causing appearance of gradate whorls. Ornamentation of teleoconch composed of several ribs and well-developed narrow and densely spaced orthocline or opisthocyrt folds. Tubercles formed at intersection of ribs and folds. Last whorl relatively high, composing 35–40% of shell height. Shell base with numerous ribs and ends of folds. Aperture oval, with deep and wide canaliform groove or notch in lower part. Growth lines on lateral side ranging from slightly opisthocyrt to clearly opisthocyrt and becoming prosocyrt below.

**Species composition.** Six species: type species; *R. baeudouini* (Cossmann, 1885) [= *Cerithium baeudouini*] from the Bathonian of France; *R. douglasi* Nützel et Senowbary-Daryan, 1999 from the Norian-Rhaetian of Iran; *R. kochi* (Münster, 1841–1844) [= *Turbo kochi*] from the Pliensbachian of Germany; *R. primordiale* Cossmann, 1913 from the Toarcian of France; and *R. rozeti* (Loriol, 1872) [= *Cerithium rozeti*] from the Lower Portlandian of France.

**Comparison.** *Rhynchocerithium* is distinguished from *Maturifusus* by the presence of the third rib below the suture in some species of this genus, which may result in slightly gradate whorls; by the absence of tubercles on the protoconch; a small number of secondary ribs, which are usually rather changeable (in *Maturifusus*, the ribs of the teleoconch are uniform, and secondary ribs are usually numerous); and by the narrower and more prominent folds (in *Maturifusus*, they are wide and often semicircular).

**Remarks.** The volume and taxonomic position of the genus are only tentatively accepted. Some French

species may appear to belong to *Maturifusus*. Judging from the teleoconch structure (shell shape, general pattern and development of ornamentation), *Rhynchocerithium* is a member of the family Cryptaulacidae; however, the protoconch structure and the siphonostomatous pattern of the aperture resemble those of the family Maturifusidae.

**SUBCLASS SINISTROBRANCHIA  
MINICHEV ET STAROBOGATOV, 1979**

Superorder Architectoniciformii  
Minichev et Starobogatov, 1979

Order Epitoniiformes Minichev et Starobogatov, 1979

Suborder Epitonioides Minichev et Starobogatov, 1979

Superfamily Epitonioides Berry, 1910

**Family Epitoniidae Berry, 1910**

**Diagnosis.** Shell medium-sized or large, multispiral, ranging from low- to high-turriculate, holostomatous, with straight generating line. Protoconch usually paucispiral, smooth or covered with folds, and clearly separated from teleoconch by commissure and abrupt change in ornamentation. Teleoconch whorls usually convex, contacting (or, rarely, noncontacting), and covered with reticulate or only collabral ornamentation. Aperture oval or circular, rounded in lower part, and often with basal fold.

**Generic composition.** Many genera from the Cretaceous and Cenozoic. In addition, I have tentatively placed several Triassic genera and the Jurassic genera *Plicacerithium* Gerasimov, 1992 and *Dubariscala* gen. nov. in this family.

**Comparison.** The Epitoniidae are distinguished from the Aciridae Korobkov by its teleoconch that is ornamented with folds and the holostomatous aperture with a basopalatal angulation and from the Janthinidae Lamarck by the turriculate shell.

**Occurrence.** Upper Cretaceous–Recent.

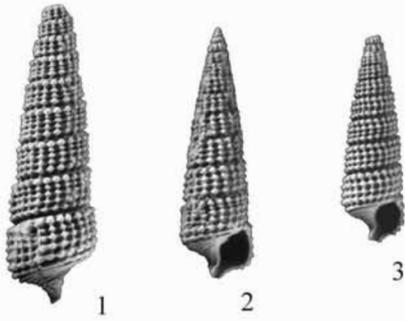
**Genus *Plicacerithium* Gerasimov, 1992**

*Procerithium* (*Plicacerithium*): Gerasimov, 1992, p. 77.

*Plicacerithium*: Guzhov, 2002, p. 18 (pars).

**Type species.** *Cerithium apicatum* Eichwald, 1868; Upper Jurassic, Upper Oxfordian; Russia, Moscow Region.

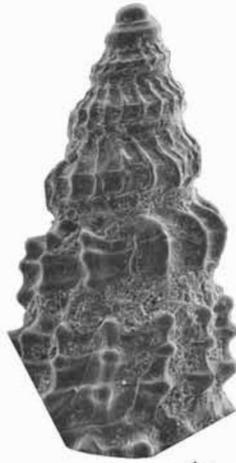
**Diagnosis.** Shell medium-sized, turriculate, and multispiral. Protoconch composed of smooth and collabraly ornamented whorls. Teleoconch whorls nongradate and flattened or convex. Suture usually shallow. Ornamentation composed of densely spaced narrow threads and stout folds extending from suture to suture. Last whorl circular in outline. Upper part of whorl occasionally with narrow gently sloping area. Shell base convex and covered with densely spaced narrow threads. Aperture not known, last whorl oval in cross section. Growth lines slightly opisthocyrt in upper part



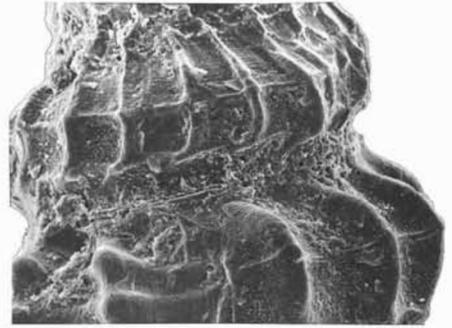
1

2

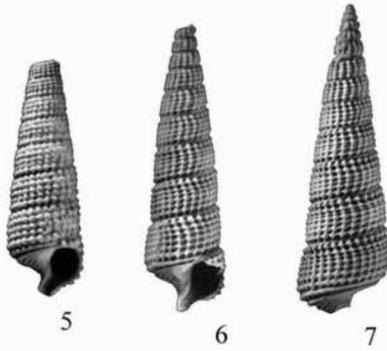
3



4a



4b



5

6

7



8a

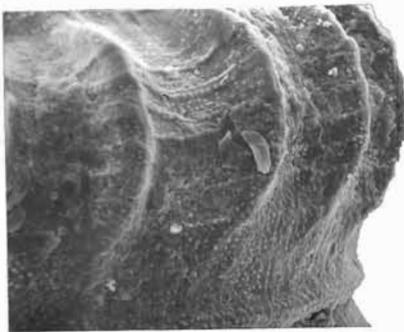
8b



9a



9b



9c



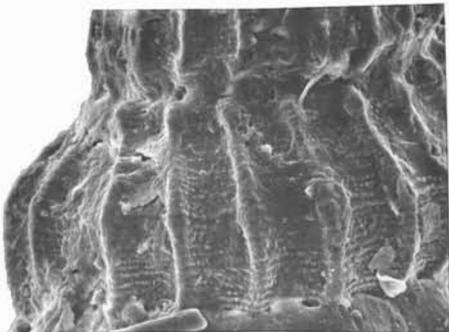
10a



10b



10c



10d



11a



11b



12

of whorl, becoming prosocyrty on shell base and slightly deviating posteriorly just under suture level.

**Species composition.** Six species: type species; *P. altum* Guzhov, 2002; *P. proundulatum* (Ammon, 1892) [= *Katosira proundulatum*] from the ?Rhaetian of Germany; *P. undulatum* (Benz, 1830–1833) [= *Melania undulatum*] from the Lias of Germany; ?*P. consobrinum* (Eichwald, 1868) [= *Cerithium consobrinum*] from the Middle Oxfordian–Lower Kimmeridgian of Crimea; and ?*P. nodulifera* (Janicke, 1966) [= *Zygopleura (Katosira) nodulifera*] from the Middle Tithonian of Germany.

**Comparison.** *Plicacerithium* is distinguished from *Proscala* by its wider shell with the convex and lower whorls and thicker folds (in *Proscala*, the whorls are flattened).

**Occurrence.** ?Triassic, Rhaetian. Lower–Upper Jurassic, Middle Tithonian.

*Plicacerithium altum* Guzhov, 2002

Plate 11, fig. 9

*Plicacerithium altum*: Guzhov, 2002a, p. 18, pl. 2, fig. 1.

**Etymology.** From the Latin *altus* (high).

**Holotype.** GMM, no. 12/10; Moscow Region, Kolomenskii District, quarry in the town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone.

**Description.** The shell is 15.7 mm high. The protoconch consists of 3.5 whorls (incomplete). The first whorl is smooth and almost planispiral, while the other 2.5 whorls are covered with high, thin, densely spaced orthocone folds. The ornamented whorls do not grow in width; therefore, the protoconch is cylindrical in shape. At the transition from the protoconch to the teleoconch, the growth of whorls abruptly changes, i.e., the teleoconch whorls rapidly increase in width. The teleoconch consists of 9.5 whorls; at the beginning, there is a strong fold (from suture to suture), which is followed by a spiral rib extending just above the suture. The whorls become inflated. From 0.2 of the first whorl, other spiral ribs appear (four or five in number). The teleoconch angle is 25°. The whorls are convex, and the extent of involution is 42%. The maximum

whorl width between folds is at the midheight of the whorl, while the maximum whorl width, including its folds, is in the upper part of the whorl. A narrow gently sloping area is located in the upper part of the whorl. The suture is shallow. The ornamentation is composed of 14 threads (in a whorl 5 mm in diameter), including five or six primary threads. The density of threads is 6–7 per mm. The folds are opisthocline, 11 per whorl (in a whorl 6 mm in diameter). As the shell grew, the number of threads gradually decreased (from 17 in the first whorl). The last whorl has 37 or 38 narrow threads (33 or 34 threads are in a whorl 6 mm in diameter). The last whorl is 33% of the shell height.

**Comparison.** *P. altum* is distinguished from *P. apicatum* by its more convex and more uniformly convex whorls and the narrower shell.

**Remarks.** I believe that *P. altum* is ancestral to *P. apicatum*. The evolutionary transformation from *P. altum* to *P. apicatum* involved the flattening of whorls and the development of finer spiral ornamentation. In addition, *P. apicatum* has a lower shell.

**Material.** Holotype.

*Plicacerithium apicatum* (Eichwald, 1868)

Plate 12, figs. 3–5

*Cerithium apicatum*: Eichwald, 1868, p. 859, pl. 29, fig. 3.

*Procerithium (Plicacerithium) apicatum*: Gerasimov, 1992, p. 77, pl. 24, figs. 11 and 12.

*Plicacerithium apicatum*: Guzhov, 2002a, p. 19, pl. 2, figs. 2–4.

**Holotype.** SPbGU, no. 2/1789, indistinct imprint of a shell (shell is not preserved); Moscow Region, Krasnogorskii District, right bank of the Moskva River near the village of Gal'evo; Upper Oxfordian.

**Description.** The shell is up to 18–20 mm high. The protoconch consists of four whorls. The first 1.5 whorls are smooth and almost planispiral (the first whorl is planispiral). Other whorls are covered with high, thin, densely spaced orthocone folds. In the last 0.2 of the protoconch whorl, the folds become opisthocyrty. Then, there is a smooth site that occupies 0.2 of the teleoconch whorl and has only growth lines and slightly prominent spiral threads. The teleoconch consists of 7.5–8 whorls. The teleoconch angle is approximately

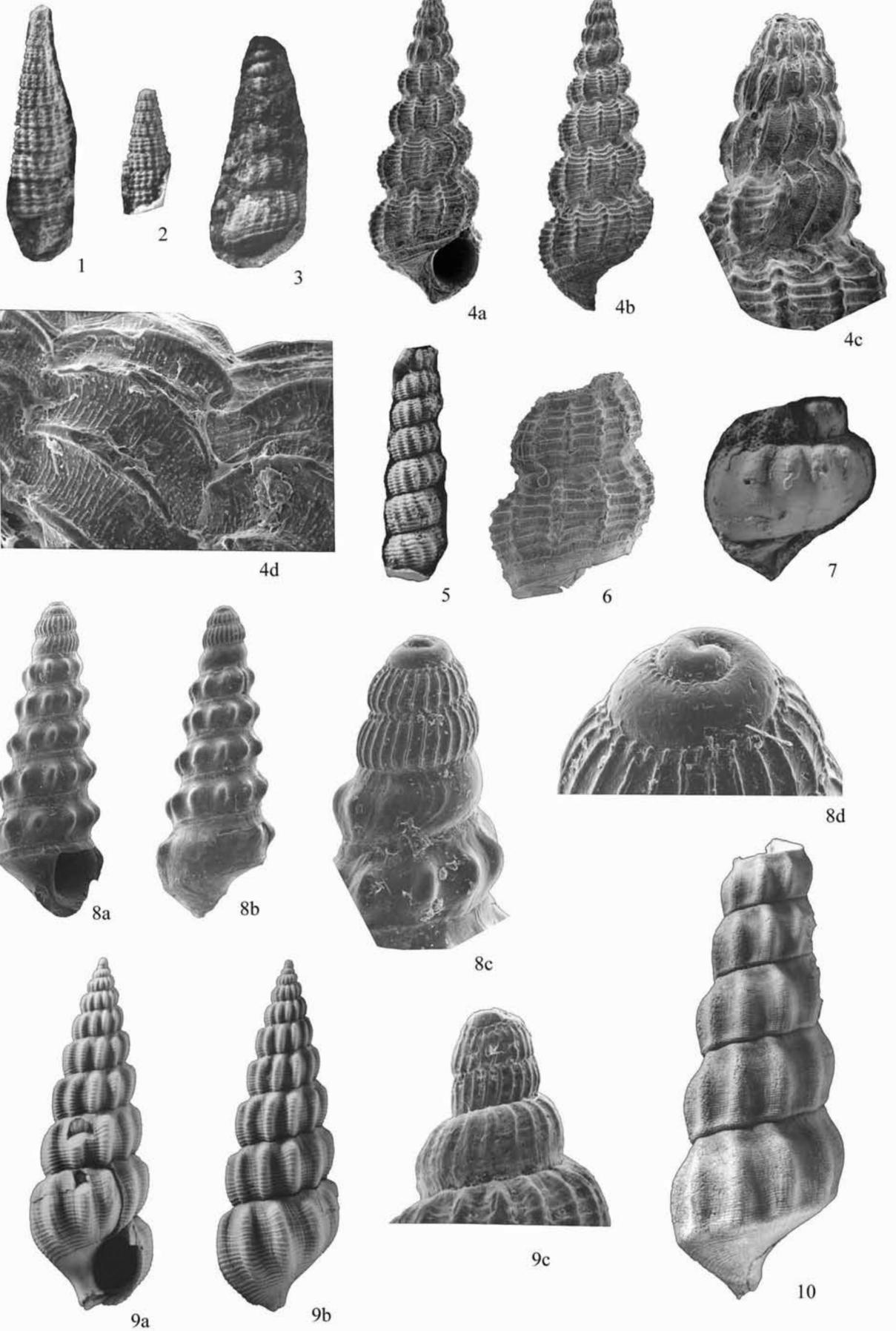
Explanation of Plate 10

**Figs. 1–4.** *Cosmocerithium renardi* (Rouillier); Middle Oxfordian, *tenuiserratum* Zone: (1) GMM, no. 12/1, abapertural view, ×4; town of Shchurovo (Zarech'e District); (2) neotype GMM, no. 12/4, apertural view, ×4; (3) GMM, no. 12/5, apertural view, ×4; town of Makar'ev; (4) GMM, no. 12/3: (4a) protoconch, ×47, (4b) microsculpture of the protoconch, ×105; town of Shchurovo (Zarech'e District).

**Fig. 5.** *Cosmocerithium ?contiae* (Rouillier); PIN, no. 4863/131, apertural view, ×4; village of Ogarkovo; Lower Kimmeridgian.

**Figs. 6–9.** *Cosmocerithium contiae* Guzhov: (6) GMM, no. 12/7, apertural view, ×4; (7) GMM, no. 12/8, abapertural view, ×4; (8) holotype GMM, no. 12/6, ×4: (8a) apertural and (8b) abapertural views; (9) GMM, no. 12/9: (9a) area left of the aperture, ×15, (9b) protoconch, ×68, and (9c) microsculpture of the protoconch, ×205. Egor'evskii Phosphorite Mine, quarry no. 7-2bis; *serratum* Zone, *serratum* Subzone.

**Figs. 10–12.** *Cosmocerithium punilum* (Gerasimov): (10) PIN, no. 4863/133: (10a) apertural view, ×29, (10b) abapertural view, ×29, (10c) protoconch, ×70, (10d) microsculpture of the protoconch, ×175; (11) PIN, no. 4863/132: (11a) abapertural view, ×28, and (11b) protoconch, ×88; Moscow, Lower Mnevniki; Upper Oxfordian, *serratum* Zone; (12) PIN, no. 4863/129, abapertural view, ×15; village of Poretskoe; Lower Kimmeridgian.



30°. The whorls are slightly convex, and the extent of involution is 42%. The maximum width is in the upper quarter of the whorl. A narrow gently sloping area is located in the upper part of the whorl. The suture is shallow. The teleoconch has six or seven threads at the beginning of the first whorl. The ornamentation is composed of 16–20 threads (in whorls 5.5–6.5 mm in diameter). The density of threads is 6–8 per mm. Initially, the folds are opisthocline–opisthocyrt and become orthocline on large whorls; whorls 5.5–6.5 mm in diameter have 11–14 folds. At the beginning of the teleoconch, folds are absent or weak, and they are formed somewhat later than threads. The last whorls have 36–39 threads. The last whorl is 36–41% of the shell height.

**Comparison.** See the section devoted to *P. altum*.

**Occurrence.** Middle–Upper Oxfordian of European Russia.

**Material.** Upper Oxfordian, *serratum* Zone, *serratum* Subzone, Egor'evskii Phosphorite Mine, quarry no. 7-2bis (seven specimens).

#### Genus *Dubariscala* Guzhov, gen. nov.

**Etymology.** In honor of the French paleontologist G. Dubar.

**Type species.** *Procerithium (Plicacerithium) korobceevense* Gerasimov, 1992; Upper Oxfordian–Lower Kimmeridgian; European Russia.

**Diagnosis.** Shell large, high-turriculate, and multispiral. Protoconch composed of smooth and collabally ornamented whorls. Teleoconch whorls nongradate and slightly convex. Suture shallow. Ornamentation composed of densely spaced narrow threads and stout folds, extending from suture to suture. Threads crossing folds without changes. Tubercles not formed. Last whorl with slightly developed basopalatal angulation, separating base from lateral side. Shell base flattened, covered with densely spaced narrow threads. Aperture not known. Whorl oval in cross section, with slightly angular flank in basal part. Growth lines

slightly opisthocyrt on lateral side, becoming prosocyrt on shell base.

**Species composition.** Type species.

**Comparison.** The new genus is particularly similar to the group *Scalaria clementina* d'Orbigny, 1842 (= "*Claviscala*") and the genus *Confusiscala* Boury, 1910 and differs from the first in the shorter and wider shell and from *Confusiscala* in the slenderer and, probably, multispiral shell, only slightly convex whorls, and shallow suture. In addition, it differs from either group in the weaker basopalatal angulation. It is distinguished from *Plicacerithium* by the presence of the basopalatal angulation, more multispiral and slender shell, and more prominent collabral ornamentation.

**Remarks.** In addition to the type species, some shells presumably belonging to this genus have been discovered in the Upper Kimmeridgian and Lower Volgian of the Volga Region; however, they are not described in the present study.

**Occurrence.** Upper Jurassic, Upper Oxfordian–Lower Volgian.

#### *Dubariscala korobceevensis* (Gerasimov, 1992)

Plate 11, fig. 10; Plate 12, figs. 1 and 2

*Procerithium (Plicacerithium) korobceevense*: Gerasimov, 1992, p. 78, pl. 24, figs. 7 and 13.

*Plicacerithium korobceevense*: Guzhov, 2002a, p. 19, pl. 2, figs. 5–7.

**Holotype.** The holotype is probably lost; Moscow Region, Voskresenskii District, Egor'evskii Phosphorite Mine, quarry no. 9; Upper Oxfordian, *serratum* Zone, *serratum* Subzone.

**Description.** The shell is up to 40–42 mm high. The protoconch consists of 2.3 whorls (incomplete). The whorls preserved are covered with high, narrow, densely spaced orthocline folds. The folds disappear before the end of the protoconch, the adjacent site is smooth and has opisthocyrt growth lines. The teleoconch consists of 16 or 17 whorls, the teleoconch angle measured at the large whorls is approximately 15°. The whorls are low and convex, and the extent of involution

#### Explanation of Plate 11

**Figs. 1 and 2.** *Cosmocerithium brateevense* (Gerasimov), Upper Volgian, *nodiger* Zone, *mosquensis* Subzone: (1) holotype GGM, no. VI-222/38 (cast), area left of the aperture,  $\times 4$ ; Moscow, Brateevo; (2) PIN, no. 4863/130 (cast),  $\times 4$ ; Moscow, D'yakovskoe.

**Fig. 3.** *Cosmocerithium* sp. PIN, no. 4863/163,  $\times 8$ ; village of Gorodishchi; Upper Kimmeridgian, *eudoxus* Zone.

**Figs. 4–6.** *Longaevicerithium bitzae* (Gerasimov): (4) GMM, no. 12/33: (4a) apertural view,  $\times 14$ , (4b) abapertural view,  $\times 14$ , (4c) protoconch,  $\times 49$ , and (4d) microsculpture of the protoconch,  $\times 145$ ; Moscow, Kuntsevo, Suvorovskii Park; Middle Volgian, *nikitini* Zone; (5) holotype GGM, no. VI-222/39 (cast), abapertural view,  $\times 2$ ; Bittsa River near the village of Sapronovo; Upper Volgian, *subdius* Zone; (6) GMM, no. 12/105, abapertural view,  $\times 23$ ; Moscow, Kuntsevo, Suvorovskii Park; Middle Volgian, *nikitini* Zone.

**Fig. 7.** *Purpurina* (*Globipurpurina*) sp. GMM, no. 12/135, abapertural view,  $\times 3$ , bank of the Volga River near the village of Prosek; Lower Callovian, *koenigi* Zone.

**Fig. 8.** *Teutonica calloviana* Gründel; GMM, no. 12/32: (8a) apertural view,  $\times 19$ , (8b) abapertural view,  $\times 19$ , (8c) protoconch,  $\times 55$ , and (8d) abapical of the protoconch,  $\times 145$ . Egor'evskii Phosphorite Mine, quarry no. 7-2bis; *serratum* Zone, *serratum* Subzone.

**Fig. 9.** *Plicacerithium altum* Guzhov, holotype, GMM, no. 12/10: (9a) apertural view,  $\times 3$ , (9b) abapertural view,  $\times 3$ , and (9c) protoconch,  $\times 49$ . Town of Shchurovo (Zarech'e District); Middle Oxfordian, *tenuiserratum* Zone.

**Fig. 10.** *Dubariscala korobceevensis* (Gerasimov): GMM, no. 12/15, abapertural view,  $\times 3$ . Egor'evskii Phosphorite Mine, quarry no. 7-2bis; *serratum* Zone, *serratum* Subzone.



1a



1b



2



3



4a



4b



5



6c



6a



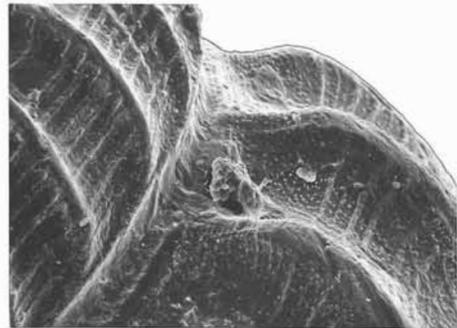
6b



6d



6e



6f

is 30–32%. The maximum whorl width is at the mid-height of whorls. The whorls are covered with numerous narrow threads, which vary in density from 5–6 to 12–13 per mm. Just above the suture, the density is at least 8.5–10 threads per mm. The last whorl (3.3 mm in diameter) has 24 threads per mm on the lateral side, and 14 or 15 threads on the base. The folds are high, opisthocyrts, and arcuate convex; 10 or 11 per whorl (in whorls 3–3.5 mm in diameter). The last whorl is 28% of the shell height (in a shell with nine teleoconch whorls).

**Occurrence.** Upper Oxfordian, *serratum* Zone, to the Upper Kimmeridgian; European Russia.

**Material.** Upper Oxfordian, *serratum* Zone, *serratum* Subzone, Egor'evskii Phosphorite Mine, quarries no. 7-2bis (four specimens) and no. 10 (one specimen); Lower Kimmeridgian, village of Mikhalenino (two specimens).

## CHAPTER 5. STRATIGRAPHIC AND FACIAL DISTRIBUTION OF JURASSIC GASTROPODS FROM EUROPEAN RUSSIA

### The Role of Gastropods in Faunal Assemblages of European Russia

Out of a total of about 38000 specimens collected (190 species), approximately 25000 (42 species) belong to the gastropod families under study. Such a high proportion indicates an important role of this group in Jurassic gastropod assemblages. The material was collected in different facies, ranging from the Lower Callovian to the Upper Volgian. Callovian and Volgian specimens come from sandy, sandy clayey, and clayey rocks, while Oxfordian and Kimmeridgian specimens have only been found in clays. Therefore, the replacement of gastropod assemblages is particularly completely studied in clayey rocks, which almost continuously spread from the Callovian to the Middle Volgian.

The stratigraphic and geographical distribution of gastropods should be considered with regard to the host rocks, because the gastropods investigated are benthic animals. Different facies of the same age differ in the taxonomic composition of gastropods and proportions of particular species; therefore, the gastropod composition in each group of rocks is considered separately. Subsequent to this, the data are summarized to get the general picture of the gastropod development in paleobasins. Below are characterized only the horizons

enclosing the species described in the present study. In addition, other gastropod groups are mentioned in the assemblages. The Jurassic zonation accepted in this study is shown in Table 4. Figure 5 shows the localities of gastropods discussed.

### Clayey Rocks

The *elatmae* Zone yielded isolated specimens of *Cryptaulax* (*Neocryptaulax*) *salebrosus* found in dark clayey nodules (village of Prosek). In addition, accumulations of indeterminable *Cryptaulax* occurred in the Mikhailovskii Mine.

Gastropod assemblages from clays of the *koenigi-jason* zones of the Bryansk (village of Fokino) and Kursk (Mikhailovskii Mine) regions are particularly thoroughly investigated. In these beds, gastropods occur in calcareous gray clays and are dominated by *Cryptaulax* (*Cryptaulax*) *protortilis* or *C. (C.) pseudoechinatus*.

The Fokino Assemblage comes from the *jason* Zone and is dominated by *C. (C.) protortilis*. *Pseudomelania laubei* Cossmann is also abundant. In the diagram, the proportion of this species is understated, because its shells are very brittle and are often broken during rock washing (Fig. 6). The assemblages from the Mikhailovskii Mine were collected in the *koenigi* and *enodatum* zones. In the *koenigi* Zone, the majority of gastropods occur within an isolated horizon, beyond which they are extremely sparse. This horizon is monospecies and consists completely of lenses filled with *C. (C.) protortilis*. To date, the rock debris and taluses of this zone have yielded only this species. In the *enodatum* Zone, gastropods are more numerous and more diverse. In the rock debris and taluses, *C. (C.) protortilis* and *C. (C.) pseudoechinatus* prevail; however, in the bedrock outcrops, only the latter species has been found. Since the study of this stratigraphic interval has been started only recently, it seems plausible that the former species will also be discovered in the future. It is not inconceivable that clays of this zone include several horizons where either of these species dominate. To date, the material collected *in situ* shows that large gastropods are dominated by *C. (C.) pseudoechinatus*, while small gastropods are dominated by *Buvignieria* sp. Among other species, *Pseudomelania laubei* is common, while such forms as *Pseudomelania extricata* Blake, *Dicroloma* sp., *Tricarilda* sp., *Sulcoactaeon* sp., and some others are scarce.

### Explanation of Plate 12

**Figs. 1 and 2.** *Dubariscala korobceevsis* (Gerasimov): (1) GMM, no. 12/14,  $\times 4$ : (1a) apertural and (1b) abapertural views; (2) GMM, no. 12/16, protoconch,  $\times 65$ . Egor'evskii Phosphorite Mine, quarry no. 7-2bis; *serratum* Zone, *serratum* Subzone.

**Figs. 3–5.** *Plicacerrithium apicatum* (Eichwald): (3) GMM, no. 12/12, abapertural view,  $\times 3$ ; village of Mikhalenino; Lower Kimmeridgian; (4) GMM, no. 12/11,  $\times 3$ : (4a) apertural and (4b) abapertural views; (5) GMM, no. 12/13, protoconch,  $\times 64$ ; Egor'evskii Phosphorite Mine, quarry no. 7-2bis; *serratum* Zone, *serratum* Subzone.

**Fig. 6.** *Novoselkella novoselkensis* Guzhov; holotype, GMM, no. 12/31: (6a) apertural view,  $\times 16$ ; (6b) abapertural view,  $\times 16$ ; (6c) protoconch, abapical view,  $\times 42$ ; (6d) protoconch, opposite side,  $\times 53$ ; (6e) elements of protoconch macroornamentation,  $\times 110$ ; and (6f) protoconch microornamentation,  $\times 210$ . Village of Novoselki; Middle Oxfordian.

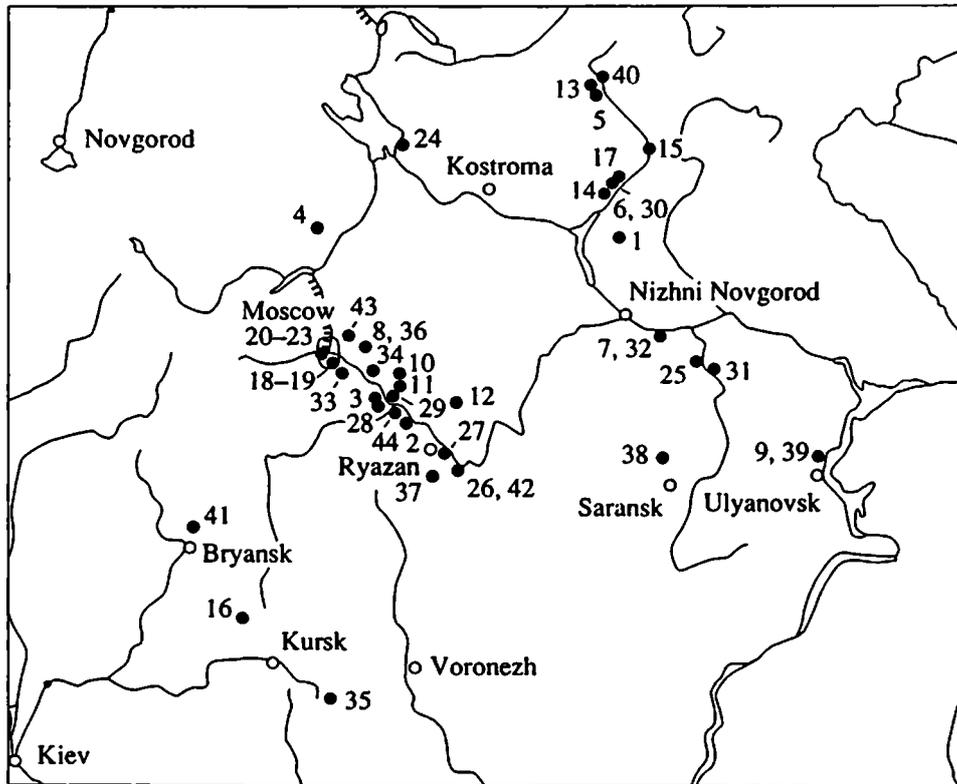


Fig. 5. Geographical position of gastropod localities: (1) borehole no. 83; (2) village of Alpat'ev; (3) Afanas'evskii quarry; (4) borehole no. 21; (5) village of Burdovo; (6) village of Vasil'kovo; (7) village of Prosek, bank of the Volga River; (8) village of Gzhel'; (9) village of Gorodishchi; (10) Egor'evskii Phosphoritic Ore Mine, quarry no. 7-2bis; (11) the same, quarry no. 10; (12) borehole near the village of Izvekovo; (13) village of Ileshevo; (14) town of Makar'ev; (15) town of Manturovo; (16) Mikhailovskii Mine; (17) village of Mikhalenino; (18) Moscow, Brateevo; (19) Moscow, D'yakovskoe; (20) Moscow, Kuntsevo; (21) Moscow, Mnevniky; (22) Moscow, Studenyi gully; (23) Moscow, Kamushki quarry; (24) village of Mostovo; (25) village of Murzitsy; (26) village of Nikitino; (27) village of Novoselki; (28) Osenka River; (29) village of Peski; (30) village of Polovchinovo; (31) village of Poretskoe; (32) village of Prosek, quarry; (33) village of Sapronovo; (34) Sechenka River; (35) Stoilenskii quarry; (36) quarry between the villages of Troshkovo and Rechitsy; (37) village of Tynovo; (38) village of Uzhovka; (39) village of Undory; (40) Unzha River near the mouth of the Pezhenga River; (41) village of Fokino; (42) village of Chevkin; (43) town of Shchelkovo; and (44) town of Shchurovo (Zarech'e District).

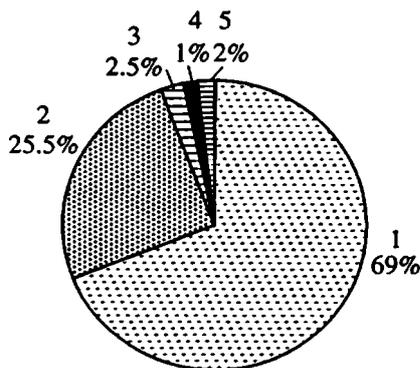


Fig. 6. Composition of the assemblage from the Jason Zone in a quarry near the village of Fokino: (1) *Cryptaulax (Cryptaulax) protortilis*, (2) *Pseudomelania laubei* Cossmann, (3) *Tornatellaea* spp., (4) *Dicroloma* spp., and (5) other genera (*Proacirsa*, *Buvignieria*, *Maturifusus*, *Tricarilda*, *Glossia*, *Bathrotomaria*, and *Eucyclus*); material: 963 specimens.

The Middle Callovian is represented by the material examined by P.A. Gerasimov from the former Kamushki quarry (Moscow), the town of Shchelkovo, and vicinity of the village of Gzhel' (moraine). The genus *Cryptaulax* is represented there by *C. (C.) protortilis*, which prevails in Gzhel' and Kamushki. This material certainly partially comes from the *coronatum* Zone (Kamushki quarry, see Gerasimov *et al.*, 1996, p. 13). Therefore, I think that *C. (C.) protortilis* dominated up to the end of the Middle Callovian. This is corroborated by the absence of *Procerithium russiense*, which apparently becomes numerous from only the Upper Callovian. Therefore, it is proposed to recognize the beds dominated by *C. (C.) protortilis* for the Lower (*koenigi-enodatum* zones) and Middle Callovian.

In the Upper Callovian, gastropod assemblages are poorly understood because specimens are rather scarce. However, in all localities with gastropods, such as quarries near the town of Mikhailov of the Ryazan Region,

temporary clay mines near the villages of Antsiferovo (Moscow Region) (Gerasimov *et al.*, 1996) and Nikitino (Ryazan Region), *Procerithium russiense* (d'Orbigny) occurs and is accompanied by infrequent *Dicroloma cochleata* (Quenstedt). Other species are scarce.

Gastropod assemblages from the Lower Oxfordian and the beginning of the Middle Oxfordian (*praecordatum*–*densiplicatum* zones and the bottom of the *popilaniense* Subzone) clearly differ from those of the Lower and Middle Callovian. In the outcrops near the villages of Nikitino, Chevkinovo, Vasil'kovo, town of Makar'ev, and other localities studied, the following picture is observed.

In the villages of Nikitino and Shatrishche, gastropods were collected in Lower Oxfordian light gray clays with pyritized fossils. *Procerithium russiense* dominates (70–80%), while the proportions of other gastropods are insignificant (Fig. 7).

In the Unzha River Basin, the same assemblage is observed in many points at the bottom of the *densiplicatum* Zone (*popilaniense* Subzone). It occurs in calcareous light gray and greenish clays of the sections near the town of Makar'ev and the villages of Vasil'kovo and Mikhalenino. The dominant species *P. russiense* composes 75–80% of the gastropod assemblage.

Thus, the composition and species proportions in the assemblages from the Lower Oxfordian and the beginning of the Middle Oxfordian have much in common with those of the Upper Callovian. Therefore, it is proposed to characterize the stratigraphic interval from the Upper Callovian to the *popilaniense* Subzone of the Middle Oxfordian as the beds dominated by *Procerithium russiense*.

Upward in the section, the dominant species *P. russiense* is replaced by *Cryptaulax* (*Cryptaulax*) *strangwaysi*, which is recorded over the rest of the *densiplicatum* Zone.

For the Unzha River, the following data were obtained.

In the town of Makar'ev, gastropods were collected from calcareous light gray and greenish clays. *C. (C.) strangwaysi* dominates (80–85%); two species, *Clathrobaculus fahrenheitii* (Rouillier) (6–8%) and *Dicroloma cochleata* (Quenstedt) (5–5.5%), are common.

In the village of Vasil'kovo, the same assemblage is characterized better than in Makar'ev. It is found in similar clays. *C. (C.) strangwaysi* clearly dominates (75%); the proportions of the other taxa from this assemblage are shown in Fig. 8.

Upward in the section, *C. (C.) strangwaysi* ceases to be the dominant species, and the leading position is occupied by *Exelissa* (*Exelissa*) *quinaria*. The assemblage dominated by this species is characteristic of the *tenuiserratum* Zone.

The sections near the towns of Shchurovo and Makar'ev are especially well-characterized.

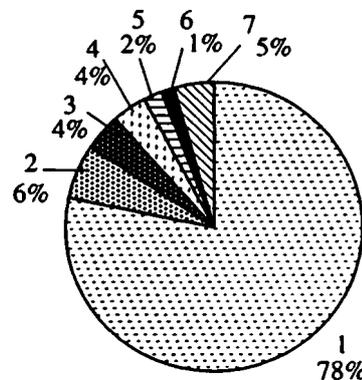


Fig. 7. Composition of the assemblage from the Lower Oxfordian of the village of Nikitino: (1) *Procerithium russiense*, (2) *Bathrotomaria muensteri* (Roem.), (3) *Dicroloma cochleata* (Quenst.), (4) *Clathrobaculus fahrenheitii* (Rouill.), (5) *Maturifusus keyserlingianus*, (6) *Cryptaulax* (*Cryptaulax*) *pseudoechinatus*, and (7) other genera (*Proacirsa*, *Tornatellaea*, *Pictavia*, *Brachytrema*, and *Eucyclus*) and other species of *Clathrobaculus*; material: 210 specimens.

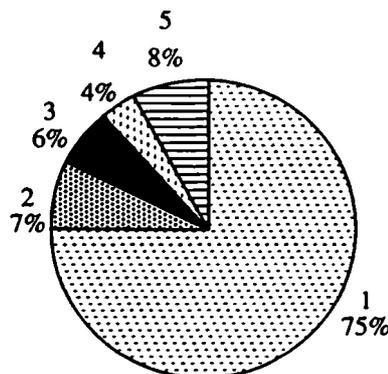


Fig. 8. Composition of the assemblage from the *densiplicatum* Zone, (*densiplicatum* Subzone) of the village of Vasil'kovo: (1) *Cryptaulax* (*Cryptaulax*) *strangwaysi*, (2) *Dicroloma cochleata* (Quenst.), (3) *Clathrobaculus* spp., (4) *Pietteia russiensis* Gerasimov, and (5) other genera (*Maturifusus*, *Buvignieria*, *Shurovites*, *Glosia*, *Parvulacraeon*, and *Tornatellaea*); material: 100 specimens.

Near the town of Shchurovo, gastropods were collected from calcareous light gray clays with numerous burrows of silt-feeders. (Different calculations have shown that *E. (E.) quinaria* dominates (80–85%), while *Dicroloma cochleata* (5.7–8%) and *C. (C.) strangwaysi* (2.5–5.3%) are also common. Summary data are present in Fig. 9.

Near the town of Makar'ev, gastropods were collected in calcareous light gray and greenish clays. *E. (E.) quinaria* dominates (57.6%), other common species are *Pictavia calypso* (d'Orbigny) (9.1%), *Tornatellaea frearsiana* (d'Orbigny) (9.1%), *Dicroloma cochleata* (6.1%), and *Bicoremytes pseudopellati* (Gerasimov) (6%).

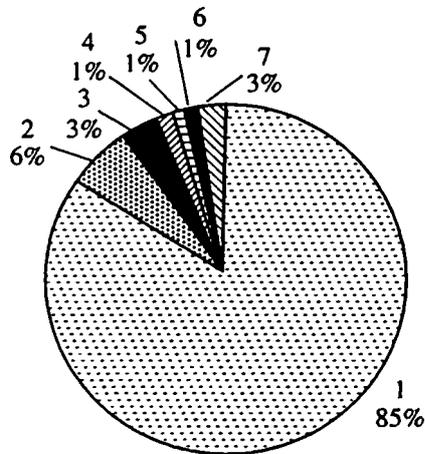


Fig. 9. Composition of the assemblage from the *tenuiserratum* Zone of the Shchurovo: (1) *Exelissa (Exelissa) quinaria*, (2) *Dicroloma cochleata*, (3) *Cryptaulax (Cryptaulax) strangwaysi*, (4) *Clathrobaculus fahrenheitii*, (5) *Pictavia calypso*, (6) *Tornatellaea frearsiana*, and (7) other genera: (*Bicorempertus*, *Pietteia*, *Maturifusus*, *Promathilda*, *Erratohilda*, *Procerithium*, and *Proacirsa*, other species of *Clathrobaculus*, and very rare *Bathrotomaria*, *Cosmocerithium*, *Khetella*, "Ueckerconulus," *Eucyclus*, *Shurovites*, and *Plicacerithium*) material: 14772 specimens.

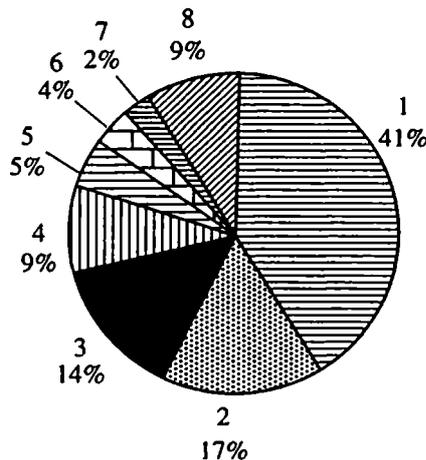


Fig. 10. Composition of the assemblage from the *serratum* Zone (*serratum* Subzone) of quarry no. 7-2bis (large gastropods): (1) *Pictavia calypso*, (2) *Maturifusus conspicuus*, (3) *Dicroloma cochleata*, (4) *Promathilda aspera*, (5) *Erratohilda* spp., (6) *Cosmocerithium contiae*, (7) *Clathrobaculus fahrenheitii*, and (8) other genera (*Dubariscala*, *Bathrotomaria*, *Khetella*, "Ueckerconulus," and *Bicorempertus*) and other species of *Promathilda*, *Maturifusus*, and *Clathrobaculus*; material: 230 specimens.

The study of outcrops and taluses near the village of Nikitino displayed a sequence of three assemblages characteristic of the Middle Oxfordian. The gastropod assemblage from the lower layers is dominated by *P. russiense* and *Clathrobaculus fahrenheitii*. These species, in particular, *P. russiense*, decrease in number upward in the section, while *C. (C.) strangwaysi*

becomes more numerous. In the taluses farther upward the section, *E. (E.) quinaria* is common. Thus, in the Kostroma Region and to the south, in the Moscow and Ryazan regions, the replacement of gastropod assemblages follows the same pattern, at least, in the Oxfordian. Therefore, I propose to recognize the beds dominated by *C. (C.) strangwaysi* in the *densiplicatum* Subzone and the beds dominated by *E. (E.) quinaria* in the *tenuiserratum* Zone.

Clayey deposits of the *alternoides* Zone of the Upper Oxfordian provided only disembodied data on gastropods, which is associated with the poor preservation of faunal remains or a lack of adequate samples. *Cryptaulax (C.) ex gr. unzhensis* and *Maturifusus conspicuus* were registered in these beds. A number of species, such as *Khetella formosa*, *Cosmocerithium contiae*, and *C. pumilum*, were dated as the Upper Oxfordian; however, they probably come from this level.

I succeeded in studying a gastropod assemblage from a bituminous layer of the *alternoides* Zone (*ilovaiskii* Subzone) near the town of Makar'ev in the Kostroma Region. This locality is characterized as follows.

Gastropods were collected in bituminous gypsum shaly clays. They are abundant but the species composition is extremely impoverished and includes almost exclusively Aporrhaidae, namely, *Dicroloma cochleata* and *Bicorempertus pseudopellati* in equal proportions. Other species are represented by small and scarce accumulations, including *Cryptaulax (C.) unzhensis* and even rarer *Cylindrobullina* sp. and *Usedomella* sp.

The gastropod composition of the *serratum* Subzone of the *serratum* Zone was studied based on specimens collected in the Egor'evskii Phosphorite Mine (Moscow Region). In these localities, gastropods were recorded in blackish gray (because of abundant organic matter) dense clays with small pyritized nodules. They were collected in quarries nos. 7-2bis and 10. Clays in quarry no. 7-2bis are rich in small bivalves, gastropods, belemnites, and scaphopods; their shells are accumulated in lenses. These beds are less pyritized than clays in quarry no. 10, which contain scarce and poorly preserved bivalves and gastropods and abundant scaphopods.

The gastropod assemblages from these beds are difficult to characterize. In addition to large forms, small gastropods (1.5–3 mm high) are also widespread. However, the collecting technique for the latter differs substantially. Therefore, the contribution of gastropods is estimated by provisional comparisons of the rock volumes processed for the collection of large and small gastropods. The composition of assemblages is determined separately for large and small gastropods.

In quarry no. 10, the amount of specimens is limited because of adverse environmental conditions (hydro-sulfide contamination). The large gastropod assemblage is dominated by *Pictavia calypso* (65.6%), while *Maturifusus conspicuus* and *Dicroloma cochleata* are common.

In quarry no. 7-2bis, the large gastropod assemblage is dominated by *Pictavia calypso* (42.6%); common species (in descending order) are *Maturifusus conspicuus*, *Dicroloma cochleata*, and *Promathilda aspera* (Rouillier). Small gastropods are dominated by small individuals of *Cosmocerithium contiae* (50–55%), *Microcerithium ostashovense* (40–45%), and juvenile *Maturifusus conspicuus* and *Promathilda aspera*. In general, *C. contiae* (50–55%) and *Microcerithium ostashovense* (44–50%) prevail, while *Maturifusus conspicuus* is less numerous (1–10%). The sample size was 3000 shells. The proportions of large gastropods are shown in Fig. 10.

All the above suggests the establishment of beds dominated by *Cosmocerithium contiae* and *Microcerithium ostashovense*.

The data on Lower Kimmeridgian gastropods are scarce. This is associated with the poor preservation of faunal remains and a small area of deposits of this age in the area investigated. Gastropods occur in black and gray clays. The collection examined by Gerasimov includes *Cosmocerithium ? contiae*, *C. pumilum*, and *Maturifusus keyserlingianus*. In gray clays of the village of Mikhalenino, I collected isolated *Dubariscala korobceevensis* and *Khetella "formosa."*

The composition of Upper Kimmeridgian gastropods was studied in the *mutabilis-eudoxus* zones (village of Murzitsy) and the upper layers of the *autissiodorensis* Zone (village of Gorodishchi). The Murzitsy Assemblage is dominated by a new species of the genus *Microcerithium*, while *Dicroloma* sp. and *Glosia* sp. are common. Other gastropods are scarce, including the genera *Maturifusus*, *Dubariscala*, *Bathrotomaria*, *Khetella*, *Quadrinervus*, and *Parvulactaeon*. In addition, Gerasimov's collection contains several pieces of rock with abundant juveniles of *Microcerithium* and *Cosmocerithium* from clays of the *eudoxus* Zone near the village of Undory. The beds dominated by *Microcerithium* sp. are tentatively recognized within the *mutabilis* Zone and the lower part of the *eudoxus* Zone. The data on gastropods from the *autissiodorensis* Zone are rather scarce. Near the village of Gorodishchi, juvenile *Maturifusus* sp., *Khetella* sp. indet., *Dubariscala korobceevensis*, *Parvulactaeon* sp., *Eucyclus* spp., *Berlieria* sp., and *Sulcoactaeon* sp. were collected. The proportions of these gastropods have not been evaluated.

Gastropods from the Lower Volgian Substage were particularly thoroughly investigated in the Gorodishchi section. In the *klimovi* Zone (beds with *Neochetoceras sterapsis*), *Quadrinervus* sp. (prevails in the collection), *Dubariscala* sp., *Khetella incerta*, *Eucyclus* spp., *Parvulactaeon* sp., and *Sulcoactaeon* sp. were collected. It is impossible to consider the structure of this assemblage, because the sample is relatively small. In the *pseudoscythica* Zone (biohorizon *Anaspidoceras neoburgense*), the mollusk association is quite different, i.e., *Cryptaulax* (*Cryptaulax*) sp. (prevails), *Crepidula* sp., *Eucyclus* cf. *jasikofianus* (d'Orbigny), *Risel-*

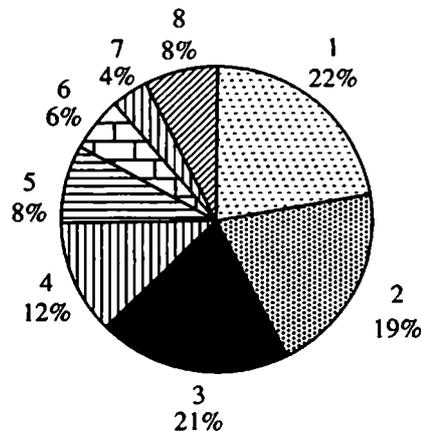


Fig. 11. Composition of the assemblage from the *virgatus* Zone (*virgatus* Subzone) of Moscow (Kuntsevo District): (1) *Infacerithium* (*Kuntseviella*) *kunceviense*, (2) *Tricarilda nikitini*, (3) *Microcerithium bicinctum*, (4) *Buvignieria choroshovensis*, (5) *Pseudomelania* spp., (6) *Parvulactaeon* spp., (7) *Ragactaeon subpellati*, and (8) other genera (*Erratohilda*, *Maturifusus*, *Proacirsa*, "*Ceritellopsis*," *Eucyclus*, *Glosia*, *Longaevicerithium*, *Emarginula*, etc.); material: 1935 specimens.

*loidea* (?) sp., *Bathrotomaria* sp. indet., *Promathilda* (?) sp. indet., and *Sulcoactaeon* sp. This material is also insufficient to consider the proportions of different species in the assemblage.

Middle and Upper Volgian deposits are mostly represented by sandy and sandy glauconitic rocks, while clays are very limited in the area of distribution. The fauna from Middle Volgian clays was investigated in the sections near the village of Gorodishchi (*panderi* Zone) and in Kuntsevo (Moscow, *virgatus* Zone).

The lower beds of the *panderi* Zone near Gorodishchi form a member of strongly calciferous clays (so-called marls) that is overlain by more or less bituminous interbedding clays. Gastropods from marls are poorly preserved, only species with large shells are observed, i.e., *Eucyclus* sp. and *Quadrinervus* sp. (other species than in the Lower Volgian Substage). In interbedding bituminous clays, gastropods are abundant and mostly represented by small shells. The assemblage is clearly dominated by *Glosia* sp. nov., while *Pseudomelania* sp. (as in the *virgatus* Zone of Kuntsevo) and *Berlieria maeotis* (Eichwald) are common. The last species is especially numerous in the most bituminous clays. In addition, isolated *Quadrinervus* sp., *Eucyclus* spp. and scarce *Tricarilda nikitini* (Gerasimov), *Maturifusus* sp., *Ragactaeon* sp., and *Parvulactaeon* spp. also occur.

In Kuntsevo, gastropods were collected in blackish gray, slightly micaceous aleuritic clays of the *virgatus* Subzone of the *virgatus* Zone. These beds are rich in small bivalves, scaphopods, and gastropods and enclose isolated small belemnites and ammonites and spines of sea urchins. Bivalves and gastropods are thin-

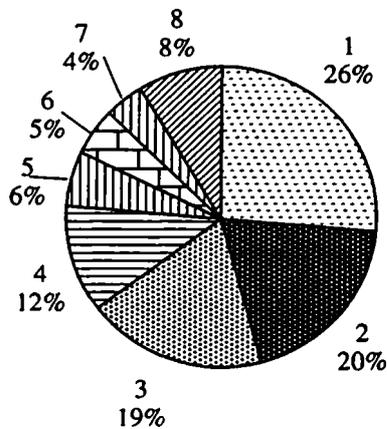


Fig. 12. Composition of the assemblage from the *koenigi* Zone (*curtilobus* Subzone) of the village of Alpat'evo: (1) *Tyrnoviella alpatyevensis*, (2) *Shurovites multinodosus*, (3) *Katosira okensis*, (4) *Eucyclus gjeliensis*, (5) *Bathrotomaria* aff. *muensteri*, (6) *Proconulus* spp., (7) *Eucyclus verrucatus* Gerasimov, and (8) other genera (*Brachytrema*, *Dicroloma*, *Bicorempterus*, *Proacirsa*, *Cryptaulax*, *Patella*, *Promathilda*, *Shurovites* (*S. sp. 1*), and *Purpurina*); material: 884 specimens.

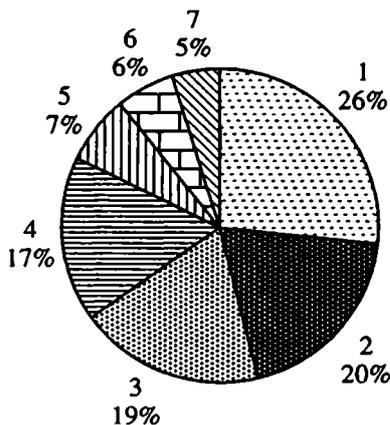


Fig. 13. Composition of the assemblage from the *koenigi* Zone (*curtilobus* Subzone) of the village of Burdovo: (1) *Bicorempterus pseudopellati*, (2) *Cryptaulax* (*Neocryptaulax*) *mutabilis*, (3) *Parvulactaeon* spp., (4) *Pseudomelania* spp., (5) *Glosia exigua*, (6) *Cryptaulax* (*Cryptaulax*) *protortilis*, and (7) other genera (*Pictavia*, *Ampullospira*, and *Maturifusus*); material: 86 specimens.

Burdovo and Ileshevo) and Oka rivers (village of Alpat'evo) I collected samples suitable for statistical analysis in the *curtilobus* Subzone of the *koenigi* Zone.

In the village of Alpat'evo, gastropods occur in a bed of ferruginous clayey and strongly aleuritic fine-medium-grained sandstone with scattered inclusions of more dense argillaceous cores. This bed is underlain by sand and gravel and overlain by interbedding sands and sandstones. *Tyrnoviella alpatyevensis* (26%), *Shurovites multinodosus* (20%), and *Katosira okensis* (19%) are most numerous, while *Eucyclus gjeliensis* Gerasimov (12%) and *Bathrotomaria* aff. *muensteri* (Roemer) (6%) are common. The structure of the assemblage is shown in Fig. 12.

In the villages of Ileshevo and Burdovo, gastropods occur in nodules of fine-medium-grained sandstone in light fine-medium-grained sand. The nodules are rich in ammonites and bivalves, while gastropods and scaphopods are less numerous. The gastropod assemblage from Burdovo is dominated by *Bicorempterus pseudopellati*, *Cryptaulax* (*Neocryptaulax*) *mutabilis*, *Parvulactaeon* spp., and *Pseudomelania* spp. In Ileshevo, the proportions of *Pseudomelania* and *Bicorempterus* decrease and the proportion of *Parvulactaeon* increases. The last genus along with *C. (N.) mutabilis* prevails in this assemblage. The structures of these assemblages are shown in Figs. 13 and 14.

Gastropod assemblages from the *calloviense* Zone were collected in the Kostroma Region. Near the town of Manturovo, gastropods were found in nodules composed of calciferous clayey sandstones. The nodules are rich in ammonites, bivalves, and scaphopods; gastropods are less numerous. Two types of nodules are present. Light and very dense nodules rich in *Pseudocadoceras* spp. are dominated by *Eucyclus* sp. and *Glosia exigua* (Gerasimov), while *Parvulactaeon* and *Pseudomelania* sp. are less numerous. The fauna from dark brachioid nodules is more diverse and dominated by *Bicorempterus pseudopellati*, while *Parvulactaeon* spp., "*Parvulactaeon*" sp., *Khetella makaryevensis* sp. nov., and some other forms are less numerous. The assemblage from the two nodule types taken together are dominated by *Eucyclus* spp. (25%), *Glosia exigua* (23%), and *Bicorempterus pseudopellati* (21%). The structure of this assemblage is shown in Fig. 15.

Near the village of Burdovo, gastropods from the *enodatum* Zone occur in yellow fine-grained sandstones enclosed in similar sands. The fauna occurs in accumulations and is represented by small bivalves and gastropods, including *Cryptaulax* (*Neocryptaulax*) *mutabilis*, *Glosia exigua*, *Parvulactaeon* spp., and "*Parvulactaeon*" sp.

The Middle Callovian assemblages from the vicinity of Makar'ev, investigated in this study, come from nodules of calciferous claystones that occur in sandy clays of the *jason* Zone (*medea* Subzone). The nodules are rich in ammonites and bivalves and additionally contain gastropods and brachiopods, which are less

walled and 3–4 mm in size, while larger specimens are scarce. Any clearly pronounced dominants are not recognized. *Infacerithium* (*Kuntseviella*) *kunzeviense* (22%), *Microcerithium binctum* (19%), and *Tricarilda nikitini* (Gerasimov) (21%) prevail, while *Buvignieria choroshovensensis* Gerasimov (12%) and *Pseudomelania* spp. are common (8%) (Fig. 11).

### Sandy and Sandy-Clayey Rocks

The earliest gastropods from the groups under study are dated Lower Callovian. On the Unzha (villages of

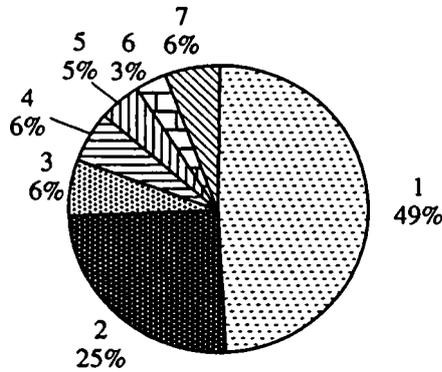


Fig. 14. Composition of the assemblage from the *koenigi* Zone (*curtilobus* Subzone) of the village of Ileshevo: (1) *Parvulactaeon* spp., (2) *Cryptaulax* (*Neocryptaulax*) *mutabilis*, (3) *Glosia exigua*, (4) *Pseudomelania* spp., (5) *Bicorempterus pseudopellati*, (6) "*Ataphrus*" sp., and (7) other genera (*Pseudomelania* (?), *Maturifusus*, *Khetella*, and *Cryptaulax* sensu stricto); material: 87 specimens.

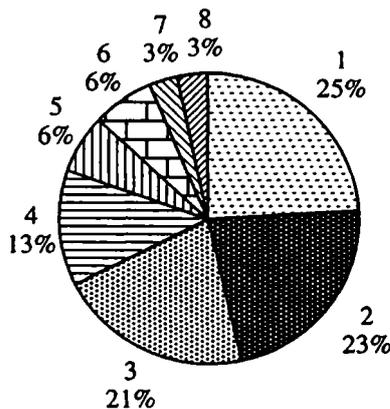


Fig. 15. Composition of the assemblage from the *calloviense* Zone of the town of Manturovo: (1) *Eucyclus* sp., (2) *Glosia exigua* (Gerasimov), (3) *Bicorempterus pseudopellati*, (4) *Parvulactaeon* spp., (6) *Pseudomelania* spp., (5) "*Parvulactaeon*" sp., (7) *Cryptaulax* (*Neocryptaulax*) *mutabilis*, and (8) *Khetella makaryevensis*; material: 62 specimens.

numerous. *Cryptaulax* (*Neocryptaulax*) *mutabilis*, *Ampullospira* spp., *Pseudomelania* sp., and *Khetella makaryevensis* predominate, while species of the genera *Parvulactaeon* and *Sulcoactaeon* are less numerous. Exact proportions of various species were not calculated because of their heterogeneous distribution and a small sample size (about 80 specimens).

In the localities examined by the author, sandy rocks disappear upward the section and are completely replaced by clayey sediments. This stratigraphic interval covers the layers from the *coronatum* Zone of the Middle Callovian to the Middle Volgian. Only some Volgian beds have yielded the species under consideration; therefore, the data on their distribution remain incomplete.

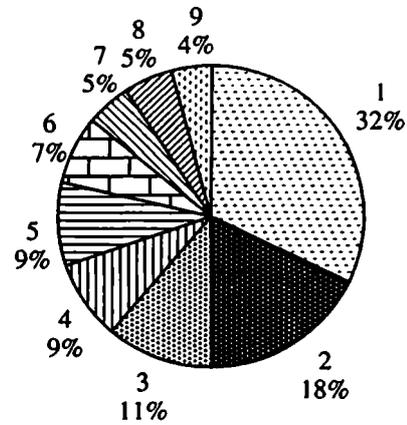


Fig. 16. Composition of the assemblage from the *nikitini* Zone of Moscow (Kuntsevo District): (1) *Infacerithium* (*Kuntseviella*) *kunceviense*, (2) "*Calliomphalus*" *bipartites*, (3) *Parvulactaeon* spp., (4) *Eucyclus jasikofianus*, (5) *Eucyclus* sp. indet., (6) *Pseudomelania* sp., (7) *Maturifusus mosquensis*, (8) other genera (*Ragactaeon*, *Tornatella*, *Sulcoactaeon*, *Neritopsis*, *Bathrotomaria*, *Longaevicerithium*, "*Proconulus*," and "*Pseudomelania*"), and (9) indeterminate gastropods; material: 233 specimens.

In quartz-glauconitic sand of the *nikitini* Zone in the Egor'evskii Phosphorite Mine (quarry no. 5), the species *Buvignieria choroshovensis*, *Infacerithium* (*Kuntseviella*) *kunceviense*, *Tricarilda nikitini*, and *Sulcoactaeon tenuistriatus* Gerasimov predominate.

In Kuntsevo (Moscow) the same zone yielded a rich gastropod assemblage, which was found in dark green quartz-glauconitic sand. *Infacerithium* (*Kuntseviella*) *kunceviense* (32%), "*Calliomphalus*" *bipartites* (Rouillier) (18%), *Parvulactaeon* spp. (11%), and *Eucyclus* sp. (18%) prevail in this assemblage (Fig. 16).

The overlying beds of the *fulgens* Zone are represented by glauconitic-quartz sediments and clearly differ in the gastropod composition. A gastropod association that comes from the greenish gray slightly clayey fine-grained glauconitic sand packed with pieces of phosphatized sandstone in Kuntsevo is better understood. It includes *Khetella* ? *incerta*, "*Calliomphalus*" *bipartites*, "*C.*" *carinatus* Gerasimov, "*C.*" *reticulatus* Gerasimov, "*C.*" *subvinealis* (Gerasimov), *Sulcoactaeon peroskianus* (d'Orbigny), *Vanicoropsis neritoides* (Trautschold), and "*Glosia*" *volgensis* (Gerasimov). In dark green glauconitic-quartz fine-grained sand of quarry no. 5 (Egor'evskii Mine), *Khetella* ? *incerta* and *Sulcoactaeon peroskianus* were recorded.

In the *subditus* Zone of Kuntsevo, the greenish brown glauconitic fine-grained sand rich in nodules composed of loose sandstone yielded *Khetella* ? *incerta*, "*Calliomphalus*" *bipartites*, "*C.*" *reticulatus*, "*C.*" *subvinealis*, *Calyptraea petasus* Gerasimov, *Sulcoactaeon peroskianus*, and *Vanicoropsis neritoides*. The greenish gray glauconitic phosphatized fine-grained sandstone (*subditus* Zone) in quarry no. 5 (Egor'evskii Mine) yielded *Bathrotomaria lopatinensis*

Gerasimov, *Eucyclus rjasanensis* Gerasimov, *Khetella ? incerta*, *Sulcoactaeon peroskianus*, and *Vanicoropsis neritoides*. In the collection from clayey-silty calcareous sandstones of the village of Eganovo (Moscow Region), *Pavulactaeon cinctus* (Rouillier), *P. sp. indet.*, and *Cryptonatica ? laevis* (Gerasimov) prevail, while *Bathrotomaria lopatinensis* Gerasimov and some species of the genus "*Calliomphalus*" ("*C. ? bipartites*", "*C. ? carinatus*", "*C. ? cf. procerus*", and "*C. ? sp. indet.*") are common. Other gastropods, including *Eucyclus spasskensis* Gerasimov, *Khetella ? incerta*, *Sulcoactaeon elongatus* (Rouillier), "*Glosia ? volgensis*" (Gerasimov), and some others, are infrequent.

In the *nodiger* Zone (*mosquensis* Subzone) of the Leninskie Gory Hills (Moscow), the gastropods, including "*Calliomphalus ? procerus*" Gerasimov, *Cryptonatica (?) laevis* (Gerasimov), *Infacerithium (Kuntseviella) kunceviense*, *Cosmocerithium brateevense*, "*Glosia ? volgensis*", and *Sulcoactaeon peroskianus*, were collected in ferruginous sandstones. The same beds in Brateevo yielded *C. brateevense*.

### Conclusions

**Clayey rocks.** In the *enodatum*–*coronatum* zones, the species *Cryptaulax (Cryptaulax) protortilis* dominates. In the case of the *coronatum* Zone, this conclusion is corroborated indirectly on the basis of specimens from Gerasimov's collection, which were dated to within the Middle Callovian (including the *coronatum* Zone). In the *enodatum* Zone, two types of assemblages are recognized; they are dominated by *C. (C.) protortilis* and *C. (C.) pseudoechinatus*, respectively. Therefore, the beds with *C. (C.) pseudoechinatus* are also recognized in the *enodatum* Zone. It is likely that, in the Upper Callovian, *C. (C.) protortilis* is gradually replaced by *Procerithium russiense*, which occurs in several localities and redeposited nodules, notwithstanding the fact that this stratigraphic interval is poorly understood. *Cryptaulax* sensu stricto has not been recorded in the Upper Callovian. *P. russiense* clearly dominates the Lower Oxfordian and the beginning of the Middle Oxfordian (*popilaniense* Subzone). Subsequently, it is replaced by *Cryptaulax (Cryptaulax) strangwaysi*, which dominates up to the end of the *densiplicatum* Zone and is replaced by *Exelissa (Exelissa) quinaria* in overlying deposits. *E. (E.) quinaria* dominates throughout the *tenuiserratum* Zone. In the *serratum* Zone, the dominant position is occupied by *Cosmocerithium contiae* and *Microcerithium ostashovense*. In clays of the *mutabilis* Zone and the lower part of the *eudoxus* Zone, beds with *Microcerithium sp.* are recognized. In the *panderi* Zone of the Volgian Stage of the Middle Volga Region, beds with *Glosia sp. nov.* are recognized. Gastropods are recorded there in more or less bituminous interbedding clays. In the *virgatus* Zone (*virgatus* Subzone) of the Moscow Region, the beds with *Microcerithium bicinctum* and *Infacerithium*

*kunceviense* are recognized. Sedimentary rocks are represented there by aleuritic clays.

**Sandy rocks.** A complete sequence of beds with gastropods has not been reconstructed (Table 3), because sandy rocks occur in only the Callovian and Volgian stages. In the Lower Callovian (*koenigi* Zone), two types of assemblages are recognized, i.e., the Alpat'ev and Burdovo assemblages. In Alpat'ev, *Tyrnoviella alpatyevensis*, *Shurovites multinodosus*, and *Katosira okensis* predominate (based on this, the beds with *T. alpatyevensis* have been recognized). This assemblage substantially differs from the Burdovo Assemblage, which is dominated by *Cryptaulax (Neocryptaulax) mutabilis*, *Sulcoactaeon spp.*, and, occasionally, *Bicorempterus pseudopellati*. It is characteristic of sections in the Kostroma Region.

Gastropod assemblages from the *calloviense* Zone of the town of Manturovo, the *enodatum* Zone of the village of Burdovo, and the *jason* Zone (*medea* Subzone) of the town of Makar'ev resemble the last assemblage. The stratigraphic ranges of these assemblages are combined in the beds with *C. (N.) mutabilis*. This species is not always the most dominant, remains one of the most numerous. It is impossible to recognize particular beds in the Volgian Stage because of a lack of adequate data. The sequence of beds with gastropods in sandy and clayey rocks is schematically shown in Table 3, and the stratigraphic ranges of individual species are shown in Table 4.

The beds characterized by particular gastropod species, which are established in the present study, are recognized on the basis of periods of maximum abundance of the species that dominate in these beds. These beds are subsidiary units that have practical significance for biostratigraphic zonation. The significance of these units is caused by the fact that they are easy to determine in field conditions. However, they are undoubtedly inferior to ammonite zones with respect to the thoroughness of zonation. In addition, it is possible to recognize an ammonite zone on the basis of a single specimen of its zonal species or, at least, other accompanying intrazonal species. On the contrary, the identification of particular beds using gastropods requires the dominant gastropod species to be ascertained, and, hence, a sample including several dozen shells must be examined. In addition, there are certain other problems. In all cases, replacement of dominant species and abrupt changes in their abundance are well-pronounced; however, there are no sections where they are distributed continuously over the whole of a layer because of the presence of biohorizons with different gastropod species. In other words, a section consists of interbedding recurrent zones (recognized by gastropods). Notwithstanding certain fluctuations of the gastropod composition over a section, the generalized pattern of the stratigraphical sequence of gastropods displays vertical replacements of dominant species in certain types of biohorizons. The recognition of particular beds considerably increases the significance of

Table 3. Stratigraphic zonation of Jurassic deposits based on gastropods.

Stage	Substage	Zone	Subzone	beds with gastropods		
				clayey rocks	sandy rocks	
Volgian	Upper Volgian					
	Middle Volgian	<i>nikitini</i>				
		<i>virgatus</i>	<i>ivanovi</i>			
			<i>virgatus</i>		beds with <i>Microcerithium bicinctum</i> and <i>Infacerithium (Kuntseviella) kunceviense</i>	
	<i>gerassimovi</i>					
	<i>panderi</i>			beds with <i>Glosia</i> sp. nov.		
Kimmeridgian	Upper Kimmeridgian	<i>autissiodorensis</i>				
		<i>eudoxus</i>				
		<i>mutabilis</i>		beds with <i>Microcerithium</i> sp.		
	Lower Kimmeridgian					
Oxfordian	Upper Oxfordian	<i>ravni</i>				
		<i>serratum</i>		beds with <i>Cosmocerithium contiae</i> and <i>Microcerithium ostashovense</i>		
		<i>alternoides</i>				
	Middle Oxfordian	<i>tenuiserratum</i>			beds with <i>Exelissa (Exelissa) quinaria</i>	
		<i>densiplicatum</i>	<i>densiplicatum</i>		beds with <i>Cryptaulax (Cryptaulax) strangwaysi</i>	
			<i>popilaniense</i>			
Lower Oxfordian	<i>cordatum</i>			beds with <i>Procerithium russiense</i>		
	<i>praecordatum</i>					
Callovian	Upper Callovian	<i>lamberti</i>				
		<i>athleta</i>				
	Middle Callovian	<i>coronatum</i>				
		<i>jason</i>	<i>jason</i>			
			<i>medea</i>			
	Lower Callovian	<i>enodatum</i>			beds with <i>Cryptaulax (Cryptaulax) protortilis</i>	
		<i>calloviensis</i>				beds with <i>Cryptaulax (Neocryptaulax) mutabilis</i>
		<i>koenigi</i>				beds with <i>Tyrnoviella alpatyevensis</i>
<i>elatmae</i>						

Table 4. Stratigraphic range and phylogenetic relationships of the species studied from central Russia

Stages	Callovian			Oxfordian			Kimmeridgian		Volgian			Boreal Berri- sian																					
	Lower	Mid- dle	Upper	Lower	Mid- dle	Upper	Lower	Upper	Lower	Middle	Upper																						
Ammonite Zone	<i>elatmae</i>	<i>koenigi</i>	<i>calloviense</i>	<i>enodatium</i>	<i>jason</i>	<i>coronatum</i>	<i>athleta</i>	<i>lamberti</i>	<i>praecordatum</i>	<i>cordatum</i>	<i>densiplicatum</i>	<i>tenuiserratum</i>	<i>alternoides</i>	<i>serratum</i>	<i>ravni</i>	<i>baylei</i>	<i>cynodoce</i>	<i>mutabilis</i>	<i>eudoxus</i>	<i>autissiodorensis</i>	<i>klimovi</i>	<i>sokolovi</i>	<i>pseudoscythica</i>	<i>panderi</i>	<i>virgatus</i>	<i>nikitini</i>	<i>fulgens</i>	<i>subditus</i>	<i>nodiger</i>	<i>rjasanensis</i>	<i>tzikwintanus</i>		
Species and subspecies																																	
<b>Cryptaulacidae</b>																																	
<i>Cryptaulax (Cryptaulax) tortilis</i>																																	
<i>Cryptaulax (Cryptaulax) pseudoechinatus</i>																																	
<i>Cryptaulax (Cryptaulax) strangwaysi</i>																																	
<i>Cryptaulax (Cryptaulax) unzhensis</i>																																	
<i>Cryptaulax (Neocryptaulax) superiostriatus</i>																																	
<i>Cryptaulax (Neocryptaulax) mutabilis</i>																																	
<i>Cryptaulax (Neocryptaulax) salebrosus</i>																																	
<i>Microcerithium ostashovense</i>																																	
<i>Microcerithium bicinctum</i>																																	
<i>Microcerithium</i> sp.																																	
<i>Infacerithium (Infacerithium) kirilli</i>																																	
<i>Infacerithium (Kuntseviella) kunceviense</i>																																	
<i>Shurovites multinodosus</i>																																	
<i>Shurovites shurovensis</i>																																	
<i>Shurovites unzhensis</i>																																	
<i>Shurovites</i> sp.																																	
<i>Exelissa (Exelissa) quinaria</i>																																	
<b>Procerithiidae</b>																																	
<i>Katosira okensis</i>																																	
<i>Procerithium tyrnovense</i>																																	
<i>Procerithium russiense</i>																																	
<i>Tyrnoviella alpatyevensis</i>																																	
<i>Tyrnoviella</i> sp. 1																																	
<i>Tyrnoviella</i> sp. 2																																	
<b>Purpurinidae</b>																																	
<i>Purpurina (Purpurina) orbignyana</i>																																	
<i>Purpurina (Purpurina) serrata</i>																																	



gastropods for biostratigraphy, since individual species substantially differ in the ranges of distribution and periods of the maximum abundance. For example, the range of *Procerithium russiense* covered the Early Callovian–Middle Oxfordian, while the maximum abundance occurred in the Early Oxfordian and the beginning of the Middle Oxfordian (*popilaniense* Time); the range of *Cryptaulax (C.) strangwaysi* included the whole of the Middle Oxfordian, while the maximum abundance was restricted to *densiplicatum* Time; etc. It is worth noting that abrupt increases in the population number of each species occur simultaneously and are equally well-pronounced over a relatively large area. In the future, it is desirable to establish a complete sequence of beds with gastropods for each group of rocks.

In summary, it should be emphasized that in sandy and clayey rocks of the Callovian–Middle Oxfordian and the Upper Oxfordian–Volgian, the beds with gastropods are established based on different criteria, i.e., in the Callovian–Middle Oxfordian, particular beds are recognized based on the dominance of larger gastropods, which are clearly visible to the naked eye. This is associated with the dispersal distribution of small gastropods, difficulties in their extraction from the host rock, or poor preservation. Therefore, it is very difficult to judge the role of small forms in the gastropod assemblages from this stratigraphic interval. On the contrary, the beds in younger deposits are established on the basis of smaller gastropod species, which are extracted by washing. In these beds, they clearly dominate quantitatively over the larger gastropod species (although certain exceptions are known).

### Ecological Features of Gastropods from European Russia

Genus *Cryptaulax*. *Cryptaulax* sensu stricto is known from the Lower Callovian to the Lower Volgian. Members of this subgenus clearly prefer a certain type of host rock. Almost all specimens (more than 99%) come from clayey deposits, where they often dominate. For example, the Lower–Middle Callovian assemblage is dominated by *C. (C.) protortilis*, and the Middle Oxfordian assemblage is dominated by *C. (C.) strangwaysi*. However, the proportion of *Cryptaulax* sensu stricto sharply decreases to a few percent in other periods (Late Callovian–Early Oxfordian and the beginning of the Middle Oxfordian, the *tenuiserratum* Zone of the Middle Oxfordian). This subgenus is absent from Kimmeridgian clays and scarce in the Upper Oxfordian, where it is represented by *C. (C.) unzhensis* in the *alternoides* Zone. The latest members of *Cryptaulax* have been registered in the *pseudoscythica* Zone of the Lower Volgian, where they occur in aleuritic clays. The sharp changes in abundance are attributable to competition with other species (in particular, the species that later occupy the dominant position in assemblages).

It is possible to consider the distribution of *Cryptaulax* sensu stricto in sandy grounds only based on the

material from the Callovian, since there are no Oxfordian and Kimmeridgian sandy rocks in the territory under study, while in the Volgian strata, this subgenus has not been recorded. Only *C. (C.) protortilis* occurs in the Callovian and is represented by very rare specimens in transitional sandy–clayey beds near the village of Alpat'ev (*koenigi* Zone) and the town of Makar'ev (*jason* Zone). Scarce specimens of this species are also present in fine–medium-grained sandstone nodules of the *koenigi* Zone near the village of Burdovo. Only nine of more than thousand Callovian shells of *Cryptaulax* sensu stricto were recorded in coarse-grained beds. Consequently, members of *Cryptaulax* sensu stricto are typical inhabitants of silty sediments in conditions of gentle water movement. They come from the strata that were formed under conditions of different oxygen content in near-bottom waters, ranging from bituminous shales (*alternoides* Zone of the town of Makar'ev) to light clays with a low content of organic matter.

Members of *Cryptaulax (Neocryptaulax)* were collected in both clayey and sandy deposits of the Lower and Middle Callovian. However, species of this subgenus differ in their distribution. In clays, the main role belongs to *C. (N.) superstriatus*. In the Callovian of the village of Fokino, this species composes several percent of the gastropod assemblage (for example, among specimens collected by Gerasimov). However, my material (about 1500 specimens) does not contain this species, which indicates that its distribution is nonuniform. The same picture is observed in clays of the *enodatum* Zone in the Mikhailovskii Mine, where other species, such as *C. (N.) mutabilis* and *C. (N.) salebrosus*, are also less numerous.

In sandy beds, the main role is played by *C. (N.) mutabilis*. It is especially numerous in sandy deposits of the Kostroma Region (*koenigi* Zone), where it is one of the most numerous species (20–25% of assemblages). This species is also common in sandy–clayey sediments of the town of Makar'ev (*jason* Zone). In clayey and strongly aleuritic fine–medium-grained sandstone near the village of Alpat'ev, *C. (N.) mutabilis* composes less than 1% of the gastropod assemblage. Another species, *C. (N.) salebrosus*, rarely but constantly occurs in sandy rocks. It is evident that *C. (N.) superstriatus* with its coarser and more widely spaced ribs and more convex whorls occurs mainly in clayey rocks (gentle water flows), while *C. (N.) mutabilis* characterized by a fine and dense ornamentation and large and flattened whorls prefers environments with more mobile water and coarse-grained substrates.

Genus *Microcerithium*. Members of this genus occur from the Lower Oxfordian to the Middle Volgian. All specimens come from clays. In the Upper Oxfordian and Middle Volgian, they occupy dominant positions in gastropod assemblages, composing 45–50 and 26%, respectively. They also occur in clays of the Upper Kimmeridgian (Middle Volga Region and Chuvashia) and the Lower Oxfordian (Moscow Region). As

regards environments, *Microcerithium* is probably restricted to silty grounds. An example is the changes in its abundance in consecutive beds of the Volgian section in Kuntsevo; it composes a quarter of the gastropod assemblage in aleuritic clays of the *virgatus* Zone and completely disappears in the overlying quartz–glaucanitic sand of the *nikitini* Zone.

**Genus *Infacerithium*.** Available material is insufficient to judge the ecology of *Infacerithium* sensu stricto. Only two specimens have been found in clays of the Upper Oxfordian (*serratum* Zone). Most of the species were described from northern Germany and Poland (Gründel, 1974b, 1999b), where they occur in clayey and aleuritic–clayey rocks. The same distribution pattern is characteristic of *Infacerithium* from the Callovian of Lithuania (Riabinin, 1912). *Infacerithium variabilis* (Morris et Lycett) was described from loose shell rocks of the Middle Bathonian of Minchinhampton. The sole species of the subgenus *Kuntseviella* is equally widespread in clayey and sandy sediments. In aleuritic clays of the *virgatus* Zone of the Kuntsevo section, it composes 21% of the gastropod assemblage, while, in the overlying quartz–glaucanitic sand of the *nikitini* Zone, its proportion is 32%.

**Genus *Shurovites*.** This genus is rare but occurs in both sandy and clayey rocks. In clayey and strongly aleuritic sandstone near the village of Alpat'ev (Koenigi Zone), *S. multinodosus* is common (20% of the gastropod assemblage), while *S. sp. 1* is rare. The Oxfordian *S. shurovensis* and *S. unzhensis* occur in clays. They are scarce but always present in assemblages (*S. unzhensis* was registered in the Middle Oxfordian of the Unzha River only).

**Genus *Exelissa*.** This genus is represented in European Russia by the single species, *E. (E.) quinaria*. At the beginning of the *tenuiserratum* phase, this species suddenly became a dominant that composed 80–90% of the gastropod assemblage; subsequently, it suddenly disappeared at the end of this phase. During the Jurassic, prior to and after the flourishing of this species, no representatives of the genus have been recorded in the former Soviet Union. Pčelintsev (1934) recorded the presence of only *Exelissa* aff. *ursicina* (Loriol) in the Aalenian–Lower Bajocian of Georgia.

**Genus *Maturifusus*.** Members of this genus occur from the Lower Callovian to the Middle Volgian in sandy and clayey rocks. In clayey rocks of the Lower and Middle Callovian, they are very scarce (isolated specimens of *M. kostromensis*). They persisted as a rare component of assemblages throughout the Early Oxfordian and most of the Middle Oxfordian (*M. keyserlingianus* and *M. conspicuus*). In the *tenuiserratum* Zone, monospecific accumulations of shells of *M. keyserlingianus* are widespread and form pockets and lenses in clays. Occasionally, such accumulations yielded from several dozen to several hundred shells, while, outside such accumulations, the shells of this species are scarce and scattered. In the Upper Oxfordian, *M. keyserling-*

*ianus* and *M. conspicuus* become rather common; at the same time, the first species comes mainly from the Middle Oxfordian, while the second is more numerous in the Upper Oxfordian. In the Upper Oxfordian, both species occur mainly in compact shell accumulations, but those composed of two species. In younger beds, members of this genus are poorly known. Only one find of *M. keyserlingianus* has been registered in the Lower Kimmeridgian, while *M. mosquensis* occurs in aleuritic clays of the *virgatus* Zone (Kuntsevo). In the Volga Region, rare members of *Maturifusus* occur in clays of the Upper Kimmeridgian (*mutabilis* and *autissiodorensis* zones) and Middle Volgian (*panderi* Zone).

Scarce specimens of *M. kostromensis* have been found in fine and medium–grained sandstones of the *koenigi* Zone of the Lower Callovian of the Kostroma Region (villages of Ileshevo, Burdovo, and Vasil'kovo). The Volgian representatives of *Maturifusus* from coarse-grained rocks are better known. The species *M. mosquensis* is common in quartz–glaucanitic sand of the *nikitini* Zone of Kuntsevo and composes about 5% of the gastropod assemblage, that is, five times higher than in the underlying clays of the *virgatus* Zone (0.95%). It is not inconceivable that a large proportion of shells determined as *Khetella ? incerta* from the Volgian beds in actuality belong to *M. mosquensis*; however, it is impossible to determine these specimens with certainty because of their poor preservation. Thus, this genus displays similar distribution patterns in both types of rocks. However, it is not improbable that many Oxfordian accumulations were formed under conditions of relatively strong water movement and, hence, display latent hiatus.

**Genus *Khetella*.** This genus is not numerous and occurs in both clayey and sandy rocks. The earliest specimens from clayey rocks were found infrequently in the *koenigi* Zone. Oxfordian–Kimmeridgian clays yielded carinate shells of *Kh. formosa* and *Kh. formosiformis* and noncarinate shells of *Kh. gradata* and *Kh. makaryevensis*. Lower Volgian clays yielded *Kh. incerta*. The noncarinate *Kh. makaryevensis* occurs in sandy rocks of the Lower and Middle Callovian. This species is rare in sandy rocks but common in transitional sandy–clayey beds (town of Makar'ev, *jason* Zone). *Kh. ? incerta* has been recorded in sandy beds of the Volgian Stage. It occurs in sands, ranging from quartz–glaucanitic (Moscow Region) to pure quartz sands (Yaroslavl Region). Thus, *Khetella* does not give preference to a particular rock type. At the same time, in the material available, the noncarinate species mainly come from sandy and sandy–clayey rocks; however, they are extremely scarce in clays, where their proportion is ten times lower than the proportion of carinate species.

**Genus *Katosira*.** The sole species *K. okensis* was collected in clayey, strongly aleuritic sandstone of the *koenigi* Zone near the village of Alpat'ev (13% of the gastropod assemblage). It is especially numerous in the

sample collected in the village of Tyrnovo. However, it is impossible to characterize the host rock of this locality, because the material was collected in fluvial sediments of a stream. Judging from the species composition of other gastropods of similar preservation, which were collected in fluvial sediments, it may be proposed that *Katosira* from Tyrnovo should be aged Middle Callovian. In outcrops of the Lower Callovian in the Kostroma Region, which are represented by medium and fine-grained sand and sandstone, this species has not been found. It is also absent from clays of the Lower and Middle Callovian.

**Genus *Procerithium*.** Two species of this genus were studied, i.e., *P. tyrnovense* (Lower–Middle Callovian) and *P. russiense* (Lower Callovian–Middle Oxfordian). *P. russiense* is mainly recorded in clays. In Lower and Middle Callovian clays, it is extremely scarce (one specimen), while it considerably increases in number since the Upper Callovian. In the Lower Oxfordian and the beginning of the Middle Oxfordian, it becomes dominant and composes at least 75–80% of the gastropod assemblage. It decreases in number in the assemblage with *C. strangwaysi*, and composes several hundredths percent in the assemblage with *E. quinaria*. *P. russiense* rarely occurs in coarse sediments (specimens were collected in a calciferous aleuritic–sandy nodule). In Ukraine, this species was found in limestones of the Izyum Formation. Almost all shells of *P. tyrnovense* come from fluvial sediments of the stream near the village of Tyrnovo (Middle Callovian), and only one shell has been found in the clay of the *enodatum* Zone.

**Genus *Purpurina*.** Shells of *Purpurina* sensu stricto are very scarce, and most of them have not been found in situ. The collection studied by Gerasimov from the former Kamushki quarry (Moscow) contains two shells of *P. (P.) orbignyana* from the sandy–clayey oolitic marl of the Middle Callovian. I have found *P. (P.) serrata* in the clayey, strongly aleuritic sandstone of the *koenigi* Zone near the village of Alpat'evo. Members of *P. (Globipurpurina)* are also scarce. Most of them were collected in clays of the Lower and Middle Oxfordian. I have several shell molds assigned to this subgenus and described above as *Purpurina (Globipurpurina)* sp. They come from calcareous aleuritic fine-grained sandstones of the *koenigi* Zone. Isolated shells of *P. (G.) condensata* (this species is not described in Chapter 4) have been collected in the *koenigi* Zone near the village of Alpat'evo and in the shell rock of the Mikhailovskii Mine of the same age.

**Genus *Cosmocerithium*.** This genus was found in European Russia in the Middle Oxfordian to the Upper Volgian of both clayey and sandy rocks. Middle Oxfordian clays yielded a subspecies of *C. renardi*. Its shells display two distribution patterns, i.e., in accumulations and as scattered isolated shells. The latter case is extremely scarcely observed; for example, in the assemblage with *E. quinaria* from quarries of the town

of Shchurovo, isolated shells of this form compose several thousandths of one percent. The bulk of material comes from accumulations, which occasionally include up to several thousand of shells (usually several hundred). These accumulations are formed together with *M. keyserlingianus* or, sometimes, by the latter species alone. In the *tenuiserratum* Zone of the Moscow and Ryazan regions, such accumulations are rarely observed, while, in the Kostroma Region, they are rather common.

The distribution of *C. renardi* in clays of the *alternoides* Zone is poorly understood. The species *C. conitiae* is known from clays of the *serratum* Zone, where it occurs in accumulations and as individual scattered shells. These accumulations also include *Maturifusus conspicuus* and *M. keyserlingianus*. Cases of isolated scattered shells are also common and play an important role in the gastropod assemblage. The role of *C. pumilum* in clays of the Upper Oxfordian remains uncertain and is probably rather changeable. This species is only known from clays of Mnevnik (Moscow), while, in the thoroughly studied outcrop in quarry no. 7-2bis of the Egor'evskii Mine, it has not been found (among several thousand shells collected by the author, K.M. Shapovalov, and V.R. Lyapin). Individual shells of *Cosmocerithium* have also been found in Lower and Upper Kimmeridgian clays.

The Volgian material is represented by *C. braeevense* and is entirely confined to sandy deposits, while clays have not yielded any specimens. This species rarely occurs in nodules of fine–medium-grained ferruginous sandstones from the *nodiger* Zone (*mosquensis* Subzone).

**Genera *Plicacerithium* and *Dubariscula*.** These genera are represented by scarce species found in clays of the Middle Oxfordian–Upper Kimmeridgian. The Middle Oxfordian beds yielded scarce *P. altum* and *P. apicatum*, while the Upper Oxfordian beds yielded somewhat more numerous *P. apicatum* and *D. korobceevensis*. In the Lower Kimmeridgian clay near the village of Mikhalenino (Kostroma Region), *D. korobceevensis* has been found. This species also occurs in Upper Kimmeridgian clays (*eudoxus* and *autissiodorensis* zones). The latest shells of *Dubariscula* come from clays of the *klimovi* Zone.

**Genus *Tyrnoviella*.** This genus occurs in the Lower and Middle Callovian. *T. alpatyevensis* has only been found near the village of Alpat'evo, where it occurs in clayey, strongly aleuritic sandstone of the *koenigi* Zone. It is one of the main species of the gastropod assemblage (29%). Similar to *Katosira okensis*, it is absent from other outcrops of parental rocks of the Callovian.

**Genus *Longaevicerithium*.** The sole species *L. bitzae* occurs rarely in sandy and clayey sediments, including the medium-grained sandstone of the *subditus* Zone, medium-grained quartz–glauconitic sand of the *nikitini* Zone, and aleuritic clays of the *virgatus* Zone.

Genus *Teutonica*. The sole species *T. calloviana* occurs extremely scarcely in clays of the *serratum* Zone.

Genus *Novoselkella*. *N. novoselkensis* is extremely scarce in Middle Oxfordian clays.

### *Morphoecological Gastropod Groups*

Gastropod associations from clayey rocks are dominated by several species in the following order: *Cryptaulax (C.) protortilis* → *Procerithium russiense* → *Cryptaulax (C.) strangwaysi* → *Exelissa (E.) quinaria* → ... *Cosmocerithium contiae* and *Microcerithium ostashovense* → ... *Microcerithium* sp. → ... *Microcerithium bicinctum*. All of these species have a turriculate multispiral shell covered with spiral and col-labral ornamentation. At the same time, they vary widely in size from 4–5 mm in *Microcerithium* to 30 mm in *Procerithium*. It is particularly surprising that the majority of species are similar in whorl shape and the fine elements of surface ornamentation. *C. (C.) protortilis* displays flattened and slightly gradate whorls with three or four ribs (hereinafter, only well-pro-nounced elements of ornamentation are taken into account). Later, *P. russiense* becomes dominant; it has flattened and slightly gradate whorls ornamented with four or five (rarely three) spiral ribs. *C. (C.) strangwaysi*, which has flattened nongradate whorls with three or, less often, two ribs, appears in the Middle Oxfordian. *M. ostashovense* has flattened nongradate whorls with three ribs, while *Cosmocerithium contiae* has slightly convex whorls with five or six spiral ribs. *E. (E.) quinaria* is distinguished by the development of rows of stout folds and the modified last whorl and has flattened nongradate whorls and only two well-pro-nounced ribs. *M. bicinctum* is distinguished by the reduced ornamentation and has slightly convex whorls, which are slightly gradate because of the presence of a stout rib in the upper part. Thus, most of the dominants are characterized by flattened whorls and many stout folds. They usually have several stout ribs, the upper of which is especially well-developed and has the largest tubercles. Therefore, a projection is formed in the upper part of the whorls, that may or may not protrude beyond the outline of the preceding whorl. Consequently, the optimal morphology of dominant species is as follows: a turriculate shell with flattened and slightly gradate whorls (because of the stout upper rib), which are covered by a dense cancellate ornamentation. This ornamentation is particularly well-pronounced in *P. russiense* and *C. (C.) protortilis* β.

The relationship between such morphology and successful development of species is illustrated by the following examples. In the Early and Middle Callovian, the shell of *P. russiense* is covered with a relatively coarse ribbing with three ribs, while, in the period of the maximum abundance (Early Oxfordian to the beginning of the Middle Oxfordian), it is represented by shells with four and five ribs. In the Early and Mid-

dle Callovian, not only *C. (C.) protortilis* but also *C. (C.) pseudoechinatus* occurred in clays. The latter species has convex nongradate whorls with very thick ribs and folds and spiny tubercles; it displays a limited range, although, in some localities, it is as numerous as the former species. Its ornamentation became less prominent with time, the third rib appeared, and the whorls were flattened. This modified appearance is characteristic of the majority of shells of *C. (C.) strangwaysi*, which was a dominant in the early half of the Middle Oxfordian. *C. (C.) protortilis* changed similarly. In the Early Oxfordian and at the beginning of the Middle Oxfordian, the majority of its shells had three ribs, i.e., two stout and one weak in the middle. At the end of the Middle Callovian, it is represented by shells with four stout ribs. In the Middle Oxfordian, *Cosmocerithium renardi* had flattened whorls with four or five ribs. In the course of its subsequent evolution, the ribs became more densely spaced (five or six), while the folds became weaker (species *C. contiae*).

This set of characters probably allowed these gastropods to be more competitive than other species that occupy the same position in the trophic structure of the community. All dominant species were most likely elements of the infauna as evidenced by the similarity in shell morphology with many extant burrowing forms, except for *E. (E.) quinaria*. If this is the case, it may be assumed that the same mode of life was characteristic of *E. (E.) quinaria*, notwithstanding the specific age-related reorganization of its shell. Thus, it turns out that at least 80% of individuals composing the gastropod community were substrate-feeders. If the assumption of their burrowing mode of life is erroneous, their trophic relationships remain uncertain. They could feed on algae (or their remains), benthic foraminifers, detritus, etc. The living Cerithioidei feed mainly on detritus or are filter-feeders. They also feed on bacteria and diatoms (Tsikhon-Lukanina, 1987).

Sandy rocks are dominated by members of *Cryptaulax (Neocryptaulax)* and *Tyrnoviella*. Notwithstanding different taxonomic position, both genera display the same pattern of ontogenetic changes. Several early whorls of the teleoconch are covered with ribs and widely spaced and stout variciform folds; later, the folds become weaker and more densely spaced, the ornamentation becomes almost reticular and finer, and the whorls become flattened. This is only well-pro-nounced in very long shells of *Tyrnoviella*. It is unlikely that these genera led a burrowing mode of life. Taking into account considerable near-bottom water flows, it is possible to propose that the adapical part of the shell leaned against the substrate. The well-developed folds in this part allowed a firm attachment of the shell under conditions of water flows, while the anterior part with more finely ornamented and flattened whorls shows a weaker resistance than in the case of well-developed variciform folds. However, variciform folds are not observed in all shells of the two genera; thus, this question requires further study on the basis of more representative materials.

Thus, a review of dominant species in each group of rocks shows that they have considerable morphological similarity, which is associated with similar adaptations of different species to similar environmental factors.

*List of Localities of Jurassic Gastropods Studied*

The list includes only those gastropod localities where the material examined in the present study was collected (Fig. 5).

(1) **Borehole no. 83.** Nizhni Novgorod Region, Koveminskii District, borehole no. 83 (depth of 75.5 m).

(2) **Alpat'evo.** Moscow Region, Lukhovitskii District, village of Alpat'evo, right bank of the Oka River.

(3) **Afnas'evskii quarry.** Moscow Region, Kolomenskii District, village of Ratchino, Afnas'evskii quarry.

(4) **Brylino.** Tver Region, Kashinskii District, borehole no. 21 (TUTsR) near the village of Brylino.

(5) **Burdovo.** Kostroma Region, Kologrivskii District, right bank, downstream from the village of Burdovo.

(6) **Vasil'kovo.** Kostroma Region, Makar'evskii District, village of Vasil'kovo, right bank of the Unzha River.

(7) **Volga River near Prosek.** Nizhni Novgorod Region, Lyskovskii District, left bank of the Volga River near the village of Prosek.

(8) **Gzhel'.** Moscow Region, Ramenskii District, village of Gzhel'.

(9) **Gorodishchi.** Ulyanovsk Region, Ulyanovskii District, village of Gorodishchi, right bank of the Volga River.

(10) **Egor'evskii Phosphorite Mine, quarry no. 7-2bis.** Moscow Region, Voskresenskii District, Egor'evskii Phosphorite Mine, quarry no. 7-2bis, 5 km north of the village of Ostashovo.

(11) **Egor'evskii Phosphorite Mine, quarry no. 10.** Moscow Region, Voskresenskii District, Egor'evskii Phosphorite Mine, quarry no. 10 near the village of Novoherkasskoe.

(12) **Izvekovo.** Ryazan Region, Tumskoii District, borehole near the village of Izvekovo.

(13) **Ileshevo.** Kostroma Region, Kologrivskii District, village of Ileshevo, gully.

(14) **Makar'ev.** Kostroma Region, Makar'evskii District, town of Makar'ev, right bank of the Unzha River, section "Northern Makar'ev."

(15) **Manturovo.** Kostroma Region, Manturovskii District, town of Manturovo, right bank of the Unzha River downstream from the railroad bridge.

(16) **Mikhailovskii Mine.** Kursk Region, Zheleznogorskii District, Mikhailovskii Mine.

(17) **Mikhalenino.** Kostroma Region, Makar'evskii District, village of Mikhalenino, right bank of the Unzha River.

(18) **Moscow, Brateevo,** right bank of the Moskva River.

(19) **Moscow, D'yakovskoe,** right bank of the Moskva River.

(20) **Moscow, Kuntsevo,** Suvorovskii Park, gully.

(21) **Moscow, Mnevnikii,** rock dump on the Karamyshevskaya embankment.

(22) **Moscow, Mnevnikii,** left bank of the Moskva River, Studenyi gully.

(23) **Moscow, Fili,** Kamushki quarry.

(24) **Mostovo.** Yaroslavl Region, Rybinskii District, Rybinskoe Water Reservoir, village of Mostovo.

(25) **Murzitsy.** Nizhni Novgorod Region, Sechenovskii District, village of Murzitsy, quarry.

(26) **Nikitino.** Ryazan Region, Spasskii District, village of Nikitino, right bank of the Oka River, 0.2–1 km downstream from the village.

(27) **Novoselki.** Ryazan Region, Ryazanskii District, village of Novoselki, right bank of the Oka River.

(28) **Osenka River near Novoselki.** Moscow Region, Kolomenskii District, bank of the Osenka River near the village of Novoselki.

(29) **Peski.** Moscow Region, Kolomenskii District, village of Peski, quarry.

(30) **Polovchinovo.** Kostroma Region, Makar'evskii District, right bank of the Unzha River near the village of Polovchinovo.

(31) **Poretzkoe.** Chuvashia, Sura River, village of Poretzkoe.

(32) **Prosek.** Nizhni Novgorod Region, Lyskovskii District, quarry near the village of Prosek.

(33) **Sapronovo.** Moscow Region, Leninskii District, Bittsa River near the village of Sapronovo.

(34) **Sechenka River near Voronovo.** Moscow Region, Ramenskii District, bank of the Sechenka River near the village of Voronovo.

(35) **Stoilenskii quarry.** Voronezh Region, Staroskol'skii District, village of Stoilo, Stoilenskii quarry.

(36) **Quarry between Troshkovo and Rechitsy.** Moscow Region, Ramenskii District, vicinity of the village of Gzhel'.

(37) **Tyrnovo.** Ryazan Region, Pronskii District, village of Tyrnovo, Kazach'ya River (alluvium).

(38) **Uzhovka.** Nizhni Novgorod Region, Pochinkovskii District, quarry near the village of Uzhovka.

(39) **Undory.** Ulyanovsk Region, Ulyanovskii District, village of Undory, right bank of the Volga River.

(40) **Unzha River at the mouth of the Pezhenga River.** Kostroma Region, Kologrivskii District, left bank of the Unzha River, 0.5 km downstream from the mouth of the Pezhenga River.

(41) **Fokino.** Bryansk Region, Dyat'kovskii District, village of Fokino, clay quarry.

(42) **Chevkino.** Ryazan Region, Spasskii District, village of Chevkino, right bank of the Oka River.

(43) **Shchelkovo.** Moscow Region, Shchelkovskii District, town of Shchelkovo, dolomitic quarry.

(44) **Shchurovo (Zarech'e District).** Moscow Region, Kolomenskii District, town of Shchurovo (Zarech'e District), quarries.

Table 5. List of localities arranged according to the geological age of gastropods studied

Age	Locality
Lower Callovian	
<i>elatmae</i> Zone	villages of Prosek and Uzhovka
<i>koenigi</i> Zone	villages of Alpat'evo, Burdovo, Vasil'kovo, Ileshevo, and Prosek
<i>calloviense</i> Zone	Town of Manturovo
<i>enodatum</i> Zone	village of Burdovo and Mikhailovskii Mine
Middle Callovian	
Nonstratified	villages of Gzhel' (in moraine), Moscow, Kamushki quarry, village of Tyrnovo, town of Shchelkovo
<i>jason</i> Zone	villages of Vasil'kovo, Mikhalenino, and Fokino and town of Makar'ev
Upper Callovian	
Nonstratified	village of Nikitino and Stoilenskii quarry
<i>athleta</i> Zone	village of Burdovo, Unzha River at the mouth of the Pezhenga River (in moraine)
Lower Oxfordian	
Nonstratified	villages of Izvekovo, Nikitino, Peski, Polovchinovo, and Chevkinov
<i>cordatum</i> Zone	Sechenka River near village of Voronovo
Middle Oxfordian	
Nonstratified	borehole no. 83, Afanas'evskii quarry, villages of Vasil'kovo, Mikhalenino, Nikitino, Novoselki, Tyrnovo, Chevkinov and towns of Makar'ev and Shchurovo, and Stoilenskii quarry
<i>densiplicatum</i> Zone	villages of Vasil'kovo, Mikhalenino, and Nikitino
<i>tenuiserratum</i> Zone	villages of Vasil'kovo, Mikhalenino, Nikitino, and Tyrnovo and towns of Makar'ev and Shchurovo
Upper Oxfordian	
<i>alternoides</i> Zone	Town of Makar'ev
<i>serratum</i> Zone	Egor'evskii Phosphorite Mine, quarries nos. 7-2bis and 10
Lower Kimmeridgian	
Nonstratified	villages of Mikhalenino and Poretskoe
<i>kichini</i> Zone	village of Brylino
Upper Kimmeridgian	
<i>autissiodirensis</i> Zone	village of Undory
<i>eudoxus</i> Zone	villages of Undory and Muriztsy
<i>mutabilis</i> Zone	villages of Undory and Muriztsy
Volgian Stage	
Lower Volgian Substage	
<i>klimovi</i> Zone	village of Gorodishchi
Middle Volgian Substage	
<i>panderi</i> Zone	village of Gorodishchi; Moscow, District Mnevnik; and Studenyi gully
<i>virgatus</i> Zone	Egor'evskii Phosphorite Mine, quarries nos. 5, 7-2bis and 9-bis and Moscow, Kuntsevo and Mnevnik districts
<i>nikitini</i> Zone	Moscow, Kuntsevo District, and village of Mostovo
Upper Volgian Substage	
<i>subditus</i> Zone	Moscow, Khoroshovo District, and village of Saponovo
<i>nodiger</i> Zone	Moscow, Brateevo and D'yakovskoe districts

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