Astrovioidea: A New Superorder of Paleozoic Cephalopods

F. A. Zhuravleva and L. A. Doguzhaeva

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

Received December 11, 2002

Contents

Vol. 38, Suppl. 1, 2004
The supplement is published only in English by MAIK "Nauka/Interperiodica" (Russia).
Paleontological Journal ISSN 0031-0301.

INTRODUCTION	S1
MATERIAL AND METHODS	S3
HISTORY OF THE STUDY OF PALLIOCERATIDS	S4
THE CONCH OF THE PALLIOCERATIDS: INTERNAL STRUCTURE AND MICROSTRUCTURE	S13
Septa and Septal Necks	S13
Cameral Deposits	S14
Metacameral Deposits	S17
Ectosiphonal Deposits	S17
DISCUSSION OF THE RESULTS OF THE STUDY	S18
ORIGIN OF PALLIOCERATIDS	S22
STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCE OF PALLIOCERATIDS	S24
SYSTEMATIC PALEONTOLOGY	S24
ACKNOWLEDGMENTS	S72
REFERENCES	S72

Paleontological Journal, Vol. 38, Suppl. 1, 2004, pp. S1–S73.

Abstract—A new superorder of Paleozoic ectochochlian cephalopods, Astrovioidea superordo nov., is designated. A distinctive feature of this superorder is that the soft cameral tissue enters the siphon cavity and secrets calcareous cameral deposits. This resulted in the destruction of the connecting rings that previously constituted, in conjunction with the septal necks, the compound wall of the siphon. In early (Ordovician) representatives of this superorder, the soft cameral tissue passed through the siphon to destroy, either partially or completely, the connecting rings and to progress occasionally along the internal surface of those rings that remained undestroyed as far as several chambers (the order Lituitida Starobogatov, 1983).

In later (Silurian and Devonian) astrovioids, the cameral tissue entered the siphon cavity through the septal foramen. The episeptal portion of the cameral tissue destroyed the connecting ring and moved over the septal neck to the earlier chamber to be fused with the hyposeptal portion of the cameral tissue located in this chamber. Subsequently, it gradually secreted calcareous deposits, thus squeezing the soft siphon in the septal neck. As cameral deposits accumulated, they filled the cavities of chambers and often came out from them to move toward the siphon and squeeze the soft siphon not only in the septal necks, but (in the absence of connecting rings) in the interspaces between them as well (the order Pallioceratida Marek, 1998).

A detailed examination of thin and polished sections of newly found and some previously published Silurian and Devonian pallioceratids by an optical microscope and, what is more important, by a scanning electron microscope has shown that, in those parts of the phragmocone within which cameral deposits reached into the siphon cavity, the connecting rings were completely destroyed, thus allowing direct connection between the soft cameral and soft siphonal tissues. In addition, some new taxonomically important details of the internal structure of shells have been revealed. Thus, it has been found that many taxa of this group of cephalopods formed in the siphon cavity a longitudinal layer of calcareous deposits that passed through all chambers over the epi- and hyposeptal deposits that filled the chambers. We propose the term *metacameral deposits* for these deposits. Furthermore, some pallioceratids contain calcareous deposits that in the absence of connecting rings were secreted by the siphon directly in the chamber cavity to meet the cameral deposits. These deposits will be referred to as *ectosiphonal deposits*. The microstructure of the cameral, metacameral, and ectosiphonal deposits have been examined with the aid of SEM.

These new data on the internal structure of pallioceratid shells and a detailed analysis of the literature that has been made in the light of these data allow the extension of the composition of this order and the development of a new classification. Thus, the order Pallioceratida now includes 5 families, 15 genera, and 32 species. The following new taxa have been separated: the families Flowerinidae, Ostreioceratidae, Astroviidae, and Plicatoceratidae; the genera *Astrovia* (with the type species *A. adorea* sp. nov.), *Ostreioceras* (with the type species *Sinoceras riphaeum* Zhuravleva, 1978), and *Syndikoceras* (with the type species *S. arcticum* sp. nov.); and the species *Astrovia marhoumensis* sp. nov., *Syndikoceras mutveii* sp. nov., and *Plicatoceras bublichenkoi* sp. nov. At present pallioceratids are known from the Wenlock through the Eifelian of Europe, Asia, Africa, and North America.

The fact that in the order Lituitida cameral deposits penetrated into the siphon cavity and resulted in a destruction of connecting rings during the life of the organism was convincingly shown by Sweet (1958), Flower (1978), Dzik (1984), and other authors. The superorder Astrovioidea existed from the Early Ordovician to approximately the Middle Devonian (Eifelian) and was virtually worldwide.

INTRODUCTION

Until recently the internal conch structure of longicone ectochochlian cephalopods that possess lamellar cameral deposits and constitute the family Lamellorthoceratidae Teichert, 1961 has remained virtually unknown. This usually resulted in lumping the five previously designated genera into one genus, *Arthrophyllum* Beyrich, 1850 (Babin, 1966; Bandel and Stanley, 1989; Niko, 1991; etc.). Although the majority of researchers recognized that complex lamellar cameral structures can be formed only in direct contact with soft tissue located in the chambers, they have long assigned this family to the order Orthocerida and made no attempts to revise the systematics of this order (Fisher and Teichert, 1969; Stanley and Teichert, 1976; etc.).

There is, however, another opinion about the formation of lamellar cameral deposits in these cephalopods. Bandel and Stanley (1989) believe that these complex calcareous structures formed in chambers devoid of any living soft tissue by way of gradual encrustation of calcite layers over the organic framework of thin membranes secreted by the visceral mass of the body in the process of chamber formation. Calcitic crusts formed through precipitation of calcite from extrapallial fluid, which penetrated the chamber from the siphon through an "organic tube." These authors tend to unite lamellorthoceratids and endocochlian cephalopods into a side branch (widely distributed but unbranched) of a group of cephalopods that gave rise to all modern cephalopod mollusks, except for *Nautilus*.

Dzik (1984) united lamellorthoceratids through the Early Silurian species of the type *Leurocycloceras bucheri* Flower, 1941 and further through the Early Ordovician genus *Sinoceras* into a single branch with the Early Ordovician family Lituitidae Phillips, 1848 and included them in a new suborder, Lituitina, which was designated by him. Although he considered these cephalopods to be a unique group, he did retain them in the order Orthocerida.

Only in 1998 Marek separated lamellorthoceratids from the order Orthocerida into a separate order Pallioceratida (Marek, 1998), in which he included two families: Leurocycloceratidae Sweet, 1964 and Lamellorthoceratidae Teichert, 1961. This author used the primordial presence of soft tissue in the chambers and the incompletely closed (i.e., with openings) connecting rings as distinctive characters of this order. Although Marek ranked this group as an order, he pointed to the fact that morphologically and anatomically pallioceratids differ from the other cephalopods at the subclass level, as in Nautiloidea, Actinoceratoidea, and Endoceratoidea. He believes that these two families of pallioceratids differ in the form of the cameral mantle, i.e., in leurocycloceratids the mantle was shaped like a sack (bag), whereas in lamellorthoceratids the mantle consisted of elongated, diverse, but predominantly radially arranged plates. Thus, we see that this author gave a very brief and generalized characterization of the internal structure of pallioceratids, disregarding any distinctive features.

Studying the structure of numerous shells of Ludlow orthochoanitic cephalopods of the Czech Republic, Kolebaba (1974, 1999a, 1999b) has clearly shown the chambers contain soft tissue that secreted calcareous deposits, including lamellar deposits. However, his interpretations of the structure of the siphon and the nature of the cameral tissue have been the subject of much controversy.

Detailed study of new and some earlier published materials on the shells with well-preserved internal parts in polished and thin sections through an optical microscope and, what is more important, through a scanning electron microscope allowed us to discover both the common features of their internal structure that belong to all pallioceratids and those particular, earlier unknown, structural features characteristic of each individual taxon. The most important common feature of this group of cephalopods is the destruction of connecting rings, which is caused by the soft cameral tissue that penetrates the siphon and secretes cameral deposits. At first the episeptal cameral tissue penetrates into the septal neck and, after reaching its edge, secretes calcareous deposits, which squeezed the soft siphon. Simultaneously (occasionally, slightly earlier or shortly afterward), the hyposeptal soft tissue, which is gradually mineralized, spreads from the preceding chamber to the edge of the septal neck and either merges with the episeptal soft tissue or overlaps it and the edge of the neck. In some species (e.g., *Ostreioceras riphaeum*), the soft siphon was squeezed and, occasionally, shifted dorsally (with respect to the level of the necks) in the interspaces between the necks. As the chamber cavities filled with cameral deposits, the soft cameral tissue spread from these cavities to the siphon cavity and, probably, fused into a single longitudinal layer, which secreted a longitudinal layer of metacameral deposits, which covered the cameral deposits and continued to press the soft siphon (*Flowerina shimanskyi, Syndikoceras arcticum, Plicatoceras bublichenkoi*, etc.). During this phase of ontogeny, the siphon had no hard walls. This is supported by the fact that ectosiphonal deposits developed in many taxa and grew directly through the cavity chamber toward the cameral deposits. In some genera, they penetrated deeply into the chamber cavity to come into close contact with the cameral deposits (*Astrovia adorea*); in other genera, although they only slightly penetrated into the chamber cavity, they also were fused with the cameral deposits (*Gorgonocers visendum*); in still other genera, they came into contact with the metacameral deposits that covered the cameral deposits (*Syndikoceras arcticum*). Within the same conch, the cameral, metacameral, and ectosiphonal deposits have the same microstructure, thus suggesting that they were secreted by the same siphonal and cameral tissues.

On the other hand, different species differ in morphology and microstructure of their cameral deposits. The simplest microstructure of the cameral and metacameral deposits is featured in the Wenlock species *Flowerina shimanskyi*. Its cameral and metacameral deposits consist of layers that are parallel to the depositional surfaces. Their microstructure is prismatic, and the elongated crystalline structures in the layers are oriented perpendicular to the surface of the respective layer. In Emsian *Syndikoceras arcticum*, the cameral and metacameral deposits have a complex prismatic microstructure, in which very small prisms are arranged in elongated complex structures of at least two different orders. The smallest prisms are arranged in elongated structures (rays) with featherlike longitudinal sections; these rays are, in turn, arranged in complex branches with longitudinal sections in the form of featherlike plates.

The early Eifelian *Ostreioceras riphaeum* has only cameral deposits, which consist of thin corrugated layers arranged in small transverse folds. The microstructure of these deposits is a spongy matrix with porous walls and, thus, more distinctly shows transverse features.

In the Pragian species *Astrovia adorea* and in the Eifelian species *Gorgonoceras visendum*, the cameral and ectosiphonal deposits consist of distinctive structures, virgulae, which will be described in detail below.

The cameral deposits of the Late Emsian *Plicatoceras bublichenkoi* were represented by extremely complex plate-shaped structures formed by a combination of distinctive plates-folds, which will be described in detail below. The metacameral deposits formed as corrugated longitudinal layers on the uneven surface of the cameral deposits. The microstructure of both types of deposits is a spongy matrix with porous walls, which differs, however, from that of *O. riphaeum.*

Thus, it is apparent that the internal conch structure is by itself sufficient to distinguish clearly between all of the species under study to the point that they undoubtedly belong not only to different genera but, with rare exceptions, to different families as well. At present the order Pallioceratida comprises a total of 32 species, belonging to 15 genera and 5 families. Four families, i.e., Flowerinidae, Ostreioceratidae, Astroviidae, and Plicatoceratidae, have been established for the first time. The diagnosis and exact generic composition of the fifth family, Lamellorthoceratidae Teichert, 1961, still remain unclear. A new genus, *Syndikoceras*, has been included in this family only tentatively because of the superficial similarity between the longitudinal sections of the cameral deposits of *S. arcticum* from the Emsian of Novaya Zemlya and the three shells illustrated by Mutvei in 1956 from the Eifelian of northern Africa (pl. XIII, figs. 2–4).

The internal structure of the entire conch and the microstructure of its morphological details are diverse enough both for separating four new families and for demonstrating that the order Pallioceratida was a group with a fairly branched dendrogram, in which one can easily see small branches persisting through several ages. Thus, the family Astroviidae with its distinctive microstructure of the cameral and ectosiphonal deposits, which consisted of virgulae, probably persisted through three periods and was widely distributed. Its representatives have been reported from the Ludlow of the Czech Republic (*Astrovia*? sp.), from Pragian strata of the Lower Devonian in the Kuznetsk Basin (*Astrovia adorea*), and from the Eifelian of the Middle Devonian of northern Africa (*A. marhoumensis*) and the eastern slope of the central Urals (*Gorgonoceras visendum*). Cephalopods of the family Plicatoceratidae apparently lived from the Ludlow to the end of the Early Devonian. *Plicatoceras*? sp. has been found in the Ludlow of the Czech Republic; *P. nishidae*, in the lower Lochkovian of Japan; and *P. bublichenkoi*, in the upper Emsian of the Balkhash area. The family Ostreioceratidae belongs, perhaps, to the same branch as Silurian Flowerinidae. However, the available material on pallioceratids is inadequate for a precise determination of the phylogenetic relationships between these small groups. At present Pallioceratids are certainly known from the Wenlock through the Eifelian and occur virtually worldwide. Lacking fossil material on lituitids, we could not examine the structure of their shells; therefore, our conclusions that pallioceratids descended from this Early Ordovician order have been made only on the basis of the literature. It seems that the most probable ancestors of those cephalopods that lost connecting rings were lituitids, because their connecting rings were partially disturbed during their life and, thus, the cameral deposits entered the siphon, which was primordially devoid of endosiphonal deposits. We have arrived at the idea that these unusual cephalopods should be designated as a separate superorder, Astrovioidea, under the influence of the hypothesis advanced by Dzik (1984).

MATERIAL AND METHODS

The material on which this paper is based was collected from five localities in Russia, one locality in Kazakhstan, and one locality in Ukraine. Of all the forms under study only *Ostreioceras riphaeum* Zhuravleva, 1978 is fairly abundant. The collection contains more than 300 specimens of this species most of which are fragments of phragmocones varying in length and diameter. Most of the shells display well-preserved interiors. A total of 5 thin sections and about 40 polished sections, most of which were studied with SEM, were prepared during this study. Most of the material was collected by the first author (F.A.Zh.) in 1957. In addition, we used the material collected by A.A. Pronina 1941. The remains of shells lie in compact, silicified, thick-bedded, about 1.5-m-thick (probably, lenticular) cherry red limestone uncovered in a ditch on the left bank of the Bobrovka River 400 m to the south-southwest of the cupola furnace located in the village of Pokrovskoe in the Artemovskii District of the Sverdlovsk Region. This limestone contains a rich and diverse fauna of cephalopods, which include, in addition to pallioceratids (*O. riphaeum* represented by many shells and *Gorgonoceras visendum* represented by one conch), fairly abundant and diverse orthoceratoids (21 species from 13 genera) and ammonites (11 species from 8 genera) and more uncommon nautiloids (six species from four genera) and bactritoids (at least three genera). In addition to cephalopods the limestone includes abundant shells of brachiopods, rugose corals, bivalves, gastropods, trilobites, tentaculites, and crinoids. According to Bogoslovskii (1969), the assemblage of ammonoids found in this limestone indicates their early Eifelian age. Another locality of *O. riphaeum* has been discovered in the Gorno-Altai. Five small fragments (well preserved internally) of the adapical part of a conch were donated by V.P. Udodov in 1984. He collected them from greenish gray, thinly laminated, shaly marls of the Terent'evskaya Formation, exposed on the left slope of the Sukrobu ravine, a left-bank tributary of the Sema River, downstream of the small town of Shebalino. The stratigraphic position of this formation has been determined on the basis of ammonites as the upper Emsian or lower Eifelian.

Unfortunately; the other species under study are represented only by single specimens.

The specimen of *Astrovia adorea* sp. nov. is a fragment of the adapical part of a phragmocone with a length of 25 mm and an adoral diameter of 9 mm that consists of seven chambers, which are extremely well preserved internally. It was found by G.G. Astrova in

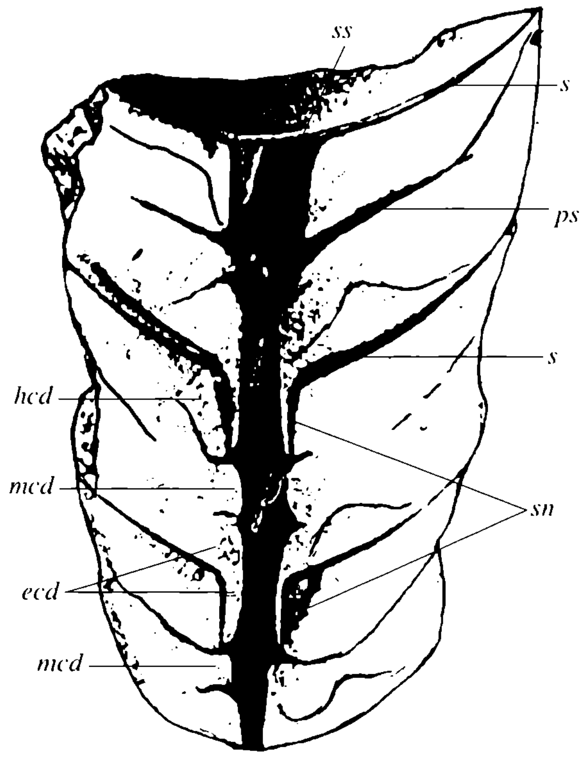


Fig. 1. *Ostreioceras? thomsoni* (Barrande, 1866); longitudinal section of three chambers filled with episeptal, mural, and hyposeptal cameral deposits; the episeptal deposits pass through the septal neck toward the hyposeptal deposits of the previous chamber; Silurian of England (Barrande, 1866, pl. 214, fig. 5). Designations: (*s*) septum, (*ps*) "pseudoseptum," (*sn*) septal neck, (*ecd*) episeptal cameral deposits, (*hcd*) hyposeptal cameral deposits, (*mcd*) mural cameral deposits, (*ss*) soft siphon.

1963 in the stratotype section of the upper Krekovo layers of the Pragian Stage that are composed of dark gray and gray laminated limestone (occasionally marly or arenaceous) and exposed in the Starogur'evskii quarry in the vicinity of the town of Gur'evsk on the southwestern margin of the Kuznetsk Basin. This limestone contains abundant faunas of corals and brachiopods.

Plicatoceras bublichenkoi sp. nov. has also been designated on the basis of a single fragment of the cast of the adapical part of a conch that is 17 mm long, 10 mm in adoral diameter, and consists of three and a half chambers. In this part the cameral deposits were already well developed and very well preserved. The specimen was found by N.L. Bublichenko in 1940 in deposits of the Kazakh Horizon, which have been assigned to the upper part of the Emsian Stage, that are exposed to the north of the Kopa Hill located northwest of the small town of Sayak in the northeastern Balkhash Region. The stratotype of the Kazakh Horizon is located in the Katan-Bulak Mountains (northern slope of the Dzungarian Alatau Range). The horizon is composed of dark gray to black calcareous tufas, interbedded with sandstones and tuffstones with minor amounts of muddy organic limestones with diverse remains of fauna and flora, including tabulate corals; bivalves; rugose corals; ammonites, i.e., *Teicherticeras* sp. and *T. (Convoluticeras)* sp.; tentaculites; bryozoans; brachiopods; trilobites; and crinoids.

The only specimen of *Syndikoceras arcticum* sp. nov. is a small fragment of a conch with a partly preserved three-layered wall and well-preserved interior. It consists of seven chambers and has a length of 40 mm and an adoral diameter of 18 mm. The specimen comes from black limestone of the Emsian Stage of Yuzhny Island of Novaya Zemlya that is exposed 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point and 36 km west-northwest of Cape Rakovyi, and was provided by G.I. Kharitonichev from his 1975 collection.

One specimen of *Flowerina shimanskyi* Zhuravleva et Kisselev is a small fragment of a cast (which is well preserved internally) which has been restudied with SEM to reveal the presence of metacameral deposits, which have not been known in species of this genus. It was found within 400 m of the lower outskirts of the village of Studenitsa on the left bank of the Studenitsa River of the Dniester River basin in the Restevskaya Subformation of the Furmanovo Formation of the Wenlock Stage of the Lower Silurian of Podolia.

The material was studied in thin sections and polished sections with an optical microscope and in polished sections with a scanning electron microscope (CamScan). All materials studied are housed at the Paleontological Institute of the Russian Academy of Sciences.

HISTORY OF THE STUDY OF PALLIOCERATIDS

In 1866 Barrande described *Orthoceras thomsoni* on the basis of a fragment of the phragmocone of a straight conch from the Silurian of Great Britain that was handed over to him by Prof. W. Thomson. A longitudinal section of this fragment, consisting of three chambers filled with cameral deposits, is seen in Fig. 1, which displays a siphon without connecting rings. The episeptal deposits pass through the septal foramen and fuse with the hyposeptal deposits of the preceding chamber at a level of the edge of the long, gradually tapering septal neck. In the absence of connecting rings, the growing cameral deposits squeezed out and deformed the soft siphon. Some lines drawn within the cameral deposits indicate that their configuration was fairly complex (Barrande, 1866, pl. 214, figs. 4, 5; here Fig. 1).

Three-quarters of a century later, Flower (1941) described from the Wenlock of Indiana a new species, *Leurocycloceras bucheri*, in which the cameral deposits pass from chamber to chamber and connecting rings and siphonal deposits are absent. In the longitudinal section the dorsal side of the holotype distinctly shows (Flower, 1941, pl. 2, fig. 4) that the episeptal deposits penetrate the septal foramen as a thin layer and fuse some distance from the edge of the septal neck with the more massive hyposeptal deposits of the preceding chamber that penetrate into the same septal foramen. It is worth noting that the hyposeptal deposits do not adjoin the septum and septal neck in the angle formed by the latter, thus leaving this angle vacant. On the ventral side the massive hyposeptal deposits almost entirely fill the cavity of the chamber, and the episeptal deposits cover with a thin layer the inside of the septal neck along more than half of its length. The surface of the ventral side of all cameral deposits is covered with a thin darker layer, which, according to Flower, can be easily taken for connecting rings, although it does not even approach the septal necks. In Flower's opinion the connecting rings either were calcified only slightly and, thus, destroyed or were completely absent. He pointed out that the internal structure of this species is of the same type as in "*Orthoceras*" *brucense*, which had been considered by him and assigned to the genus *Leurocycloceras* previously (Flower, 1939).

Flower believed that this type of internal structure of conch was characteristic of the entire genus *Leurocyclocers* Foerste, 1928, to which he assigned more than ten species from the coeval beds of North America. However, this type of structure has not been recorded in the majority of these species and, above all, in the type species, *L. raymondi* Foerste, 1928, to which a fragment of the body chamber with annulate ornamentation that strikingly differs from that of *L. bucheri* has been designated as the holotype. Thus, we believe that it is better to separate on the basis of the species *L. bucheri* a new genus, *Flowerina*, and place into it all species with this type of internal structure (Zhuravleva and Kisselev, 2001).

In the same paper Flower (1939) described from the same strata an interesting form represented by a series of dolomitic endocasts of chambers, on the surfaces of which there are impressions of the cameral mantle, as *Leurocycloceras* cf. *niagarense*. In his opinion the concentric ribs on the casts reflect the rugosity of the cameral tissue and the series of radial tubular impressions that run from the siphon to the periphery apparently reflect the system of blood vessels that penetrated this tissue.

More recently this species has been described from the Wenlock of Podolia (Balashov and Zhuravleva, 1962). In the fragment studied the cameral deposits differ from those of the holotype in being at a later stage of their growth and in that the epi- and hyposeptal deposits on the dorsal side are nearly equal to each other in volume and show a distinct "pseudoseptum." In addition, the hyposeptal deposits do not adjoin the septum and septal neck in the angle formed by the latter, thus leaving this angle vacant. On the ventral side the episeptal deposits penetrate into the septal neck deeper and are thicker than in the holotype.

A short time later, Holland (1965) designated a new species, *Leurocycloceras whitcliffense*, on the basis of disassociated endocasts of the chambers of a phragmocone from the upper part of the Ludlow of Wales and adjacent areas. These casts have previously been assigned to *Orthoceratites imbricatus* Wahlenberg or to *Orthoceras marloense* Phillips. As in the endocasts of the chambers of *L.* cf. *niagarense*, which was described by Flower, the surface of these casts bear impressions of blood vessels of the cameral tissue in the form of fairly large furrows, which radiate almost radially from the siphon to the periphery, and smaller furrows located between them.

Subsequently, Babin (1966) designated a new genus, *Murchisoniceras*, with *Orthoceras murchisoni* Barrande, 1868 from the Ludlow of the Barrandian region as its type species and assigned this genus to the family Geisonoceratidae. The longitudinal sections of phragmocones depicted by Barrande (1868, pl. 321, figs. 6, 10) show that *O. murchisoni* has no connecting rings and that the episeptal cameral deposits pass through the septal foramen into the previous chamber and fuse with its hyposeptal deposits. The structure of cameral deposits is unknown.

In 1969 Collins (1969) described a new species, *Leurocycloceras superplenum*, from the Wenlock of northern Canada. The cameral deposits of this species have complex shapes (pl. 8, figs. 9–12). In addition to the relatively thin episeptal and massive hyposeptal deposits, they apparently included mural deposits, which at a certain growth stage changed the direction of layers to move away from the episeptal deposits. The latter apparently slightly changed their structure in the larger near-siphon region. The episeptal deposits enter the septal foramen as a thin layer and continue up to the very edge of the orthochoanitic septal neck. The massive hyposeptal deposits enter the septal foramen and surround the neck and the episeptal deposits that overly the neck but do not adjoin them (Collins, 1969, text-fig. 6). The episeptal deposits frequently form a fairly wide adoral ring near the siphon (pl. 8, fig. 10). There are no vestiges of connecting rings. Collins believes that the presence of a narrow interval left uncovered between the epi- and hyposeptal deposits demonstrates that the rings were either thin and elastic or even entirely absent (Collins, 1969, text-fig. 6). In our view, this seems to be highly unlikely.

Of special interest are papers by Starobogatov (1973, 1974, 1983a, 1983b), in which he advanced his view that the origin of the class Cephalopoda is related to some as yet unknown representatives of the class Solenoconchia. In Starobogatov's last two papers on the classification system and phylogeny of cephalopod mollusks, he established a new order, Lituitiformes, on the basis of the following characters: the ectochochlian orthocones are spirally coiled apically and possess cameral deposits, the mantle complex is dimerous, the brachial support possesses numerous tentacles, the apical region of the internal sac is polyfunctional, the hydrostatic apparatus is purely liquid, the chambers are filled with the body, and the liquid of the float is located under the mantle.

Kolebaba (1974) described a new species, *Mariaceras*, from the lower Ludlow of Bohemia as a form with an orthoceroid conch the chambers of which primordially contained soft tissue ("cameral mantle") that is immediately connected with the tissue of the siphon through the opening on the dorsal side, where connecting rings were lacking. According to Kolebaba, the ventral side of this form bore siphonal deposits that formed a continuous layer on the connecting rings and septal necks (text-fig. 1). The detailed description of the type species of this genus, *M. pragense*, included illustrations of the transverse and longitudinal sections of phragmocones of different shells, which probably belong to different species. Unfortunately, in the majority of longitudinal sections, including that of the holotype (pl. 1, fig. 7), the relation between the septa and septal necks and the cameral deposits cannot be clearly seen, in particular on the ventral side. The drawing was apparently made after the sample illustrated in pl. 1, fig. 4, although the internal structure of the holotype considerably differs from this sample and is more similar to that illustrated in pl. 1, fig. 5. On the ventral side of the latter conch, the episeptal cameral deposits of neighboring chambers spread far into the septal foramen, where they apparently fuse to form a single layer, the surface of which bears a continuous black layer, which probably contains a substantial proportion of organic matter. There are no traces of connecting rings on the ventral side. On the dorsal side near the siphon, the epi- and hyposeptal deposits form thick ridges facing one another that approach one another as they grow. Well-developed casts of chambers of other shells represent the surfaces of cameral deposits (Kolebaba, 1974, pl. II, figs. 1, 3, 7–10). The adapical alveolar surface of the cast is a direct representation of the spiny surface of episeptal deposits (Kolebaba, 1974, pl. II, figs. 7, 8). The adoral surfaces of the casts of chambers show impressions representing a system of blood vessels (Kolebaba, text-figs. 9, 10). Traces of smaller vessels branch and go from the deep medial groove to the periphery. The lateral surface of the cast of two adjacent chambers also shows traces of blood vessels (Kolebaba, 1974, text-fig. 3). The above features, which are characteristic of the shells studied by Kolebaba, suggests that their chambers contain soft tissue; however, it is difficult to agree with his interpretation of the structure of the siphon.

Thus, although the number of the described species of straight ectochochlian cephalopods in which connecting rings had not been found and the episeptal cameral deposits passed through the septal foramen from one chamber to the previous chamber and united with its hyposeptal deposits was then already considerable, the internal structure of cephalopod shells with lamellar cameral deposits remained virtually unknown. As a result, many researchers placed all or almost all six genera of the family Lamellorthoceratidae Teichert, 1961 in the synonymy of one genus, *Arthrophyllum* Beyrich, 1850 and considered differences between them to be interspecific (Babin, 1966; Bandel and Stanley, 1989; Niko, 1991; etc.). Thus, it makes sense to trace in as much detail as possible the history of the study of all forms with lamellar cameral deposits and to assess the criteria used for defining separate genera of the group under consideration.

The genus *Arthrophyllum* Beyrich, 1850 was originally mistaken by its author for coral and has a long and complicated history, which was presented in considerable detail in Teichert's paper (1961). Roemer (1852), who described a small fragment of the phragmocone with lamellar deposits in chambers under the name *Arthrophyllum crassum* Beyrich, was the first to recognize this form as a cephalopod. He believed that Beyrich established the genus *Arthrophyllum* for the species *Orthoceratites crassus*, which was described by Roemer (1843). Under this name Roemer depicted two specimens. Teichert pointed out that one of them (pl. 10, fig. 6) should be considered according to the Code of Zoological Nomenclature as the holotype of *O. crassus*, i.e., the type species of the genus *Arthrophyllum*. This is a fragment of the cast of phragmocone, which is circular in cross section and consists of six chambers. A small well-preserved fragment of the wall of the conch shows transverse ornamentation of narrow curved striae. The position of the siphon is unknown. According to Teichert, the cameral deposits show a series of vertical "rays" on the cast of each chamber. Subsequently, some researchers disputed the presence of lamellar cameral deposits in this conch (Dahmer, 1939; Flower, 1955).

The available information is meager and, thus, it is impossible to get a clear idea of the holotype of the type species of the genus *Arthrophyllum*, and, therefore, the species itself and the genus as a whole. Unfortunately, the holotype cannot be restudied, since Teichert failed to find it.

Later H. Sandberger and F. Sandberger (1850–1856) described under the generic name *Orthoceras* two species of straight cephalopods from the Lower Devonian of Nassau in which chambers are filled with radial plates, which, as well as plates in chambers of *Arthrophyllum*, were treated by these authors as secondary structures. The specimens included in these species considerably differ both from *A. crassum* and from each other within each species in many characters, such as the angle of conch expansion, the shape of its cross section, the character of ornamentation, etc. (Sandberger and Sandberger, 1850–1856, pl. 18, fig. 4 and pl. 1, fig. 6). Such striking differences suggest that these forms belong not only to different species, but, perhaps, even to different genera. The final establishment of the taxonomic position of these forms requires a detailed study of their internal structure.

Two small fragments of the casts of phragmocones from the Emsian of Germany are figured in the paper by Schroeder (1888) under the name *Orthoceras planiceptatum* Sandberger. One of them shows a convex adapical surface of (probably) hyposeptal deposits consisting of numerous slender plates, converging from the periphery to the septal foramen (Schroeder, 1888, pl. 8, fig. 6c). The other fragment (Schroeder, 1888, pl. 8, fig. 6a) shows a siphon (apparently, eccentric) exposed by erosion. The tubular structure shown in the figure at the location that is characteristic of connecting rings apparently represents metacameral deposits.

Hermann (1912, pl. 22, fig. 19) presented under the name *Orthoceras* (*Arthrophyllum*) sp. a drawing of the specimen from the Lower Devonian of Germany; this specimen is a cast of one chamber, which is filled with slender closely located plates, converging toward the central septal foramen.

Liebrecht (1913, pl. 15, figs. 4a, 4b) presented drawings of two fragments of the shells of *Arthrophyllum* from the upper Lower Devonian of Germany showing lamellar cameral deposits. The second specimen shows a siphon with fairly well-defined, slightly convex segments of the siphon. Level with the septal foramen is drawn a dashed line. A section (more likely, a crack) passed near the siphon without crossing its cavities. Structures reminiscent of connecting rings apparently are the surface of cameral deposits.

Schmidt (1933) described under the name *Orthoceras* (*Arthrophyllum*) sp. interesting fragments of the casts of phragmocones from the Lower Devonian of Germany. Drawings presented in the same paper (Schmidt, 1933, pl. 5, figs. 5, 15, 16) show that the mural-episeptal cameral plates are immediately adjacent to the siphon. Hyposeptal deposits are absent. The fragment that is split along the siphon (pl. 5, fig. 15) fairly distinctly shows the absence of connecting rings. The transversely oblique structures that diverge from the siphon on a level with the chamber cavity resemble virgulae of ectosiphonal deposits (compare *Astrovia adorea*, Pl. 7, figs. 1a, 1b; Pl. 8).

Later Dahmer (1939) established a new species, *Orthoceras kahlebergense*, with the holotype *Orthoceratites crassus*, which was figured by Roemer (1843, pl. 10, fig. 10). Four specimens varying in the degree of preservation are figured under the name *O. kahlebergense*. The first specimen, which is a fragment of the cast of 11 chambers and the rear portion of the body chamber, has an elliptical cross section and nearly central siphon. The suture is straight and transverse. The cameral plates are slender, nearly straight, and closely spaced. Three other specimens are slightly compressed in a transverse direction, probably laterally, but show the oblique suture. The cameral deposits are also composed of numerous slender plates, occasionally slightly sinuous. The internal structure of shells remains unknown (Dahmer, 1939, text-figs. 7–10).

Teichert (1961) restudied many conches of cephalopods with lamellar cameral deposits from the Lower and Middle Devonian of Germany and assigned all of them to the genus *Arthrophyllum*; however, he pointed out that the species composition of this genus was then uncertain. He believed *A. kahlebergense* (Dahmer, 1939) to be the only validly described species and pointed out that the type species *A. crassum* (Roemer, 1843) and the species *O. planiseptatum* and *O. undatolineatum*, described by H. Sandberger and F. Sandberger, require careful restudy.

All these fragmentary materials were presented predominantly in the form of drawings and gave no idea of the taxonomic composition of this group of cephalopods in the Devonian of Germany.

The genus *Lamellorthoceras* was designated (Termier and Termier, 1950) on the basis of a series of specimens from the Lower and Middle Devonian of northern Africa represented predominantly by short fragments of casts of phragmocones with lamellar cameral deposits. In addition to the type species *L. vermiculare* from the Eifelian, one more species, *L. gracile*, was established from the Siegenian. Diagnosis of the genus and descriptions and comparison of species are absent. Specimens are presented in the form of rather sketchy line drawings. No holotype of the type species was designated by the authors.

Later the Termiers' materials were restudied and illustrated photographically by Teichert (1961). Among the specimens that were assigned to the type species by its authors, there are forms that markedly differ even in those few external characters that are preserved. In particular, Teichert pointed out the presence of both straight and slightly bent shells, different shapes of the plates of cameral deposits in cross sections of phragmocones (straight, sinuous, and branching), and different arrangement of plates (in certain forms, they converge at an acute angle on the ventral side). It seems that this series contains fragments of shells that belong to different species and, perhaps, even to different genera.

In order to establish characters for the genus *Lamellorthoceras*, it is necessary to reveal distinctive features of its type species; for this purpose, we will select a neotype from available specimens. The specimen from the type series of *L. vermiculare* that was depicted first contains plates in the siphon rather than in the chambers and does not belong to this group of cephalopods. The second specimen provides no information because of its poor preservation. The third specimen, depicted in pl. 135, fig. 9 (Teichert, 1961, pl. 2, fig. 1), may be selected as a neotype of the type species. This is a short fragment of phragmocone, with a partly well-preserved wall, which bears shallow transverse ornamentation on the surface that forms a ridge on one side and a sinus on the opposite side. The cross section of the adapical end of the specimen made by Teichert (1961, pl. 1, fig. 12) at an angle of 30° to the transverse plane and passing through two neighboring chambers and outside of the septal neck shows radial cameral plates that intricately branch at their distal edge. Thus, judging by the neotype, one may speculate that the conch of *L. vermiculare* bore delicate transverse ornamentation, which probably formed a ventral sinus and dorsal ridge and possessed cameral deposits in the form of radial, intricately branching structures. A longitudinal section of one of the specimens assigned by Teichert to this species is poorly preserved and falls somewhat short of the median plane; hence, the relationship between the septal necks and cameral deposits cannot be determined. Thus, the internal structure of the conch of the type species *L. vermiculare*, as well as the genus *Lamellorthoceras* as a whole, remains unknown.

In 1950 Le Maitre (1950) established a new species, *Orthoceras coralliforme*, which she subsequently assigned to the genus *Lamellorthoceras* (Le Maitre, 1952). She examined 26 specimens (fragments of casts) from the Lower and Middle Devonian of Algeria. A major portion of these specimens were casts of phragmocones in which chambers were filled with numerous longitudinal plates converging from the walls to the siphon. The longest fragment of the series consists of nine chambers. Le Maitre did not designate any holotype for this species. These conchs differ from all earlier described forms with similar cameral deposits in the larger angle of expansion, which varies from 15° to 20° and, in some specimens, attains, according to Le Maitre, even 24°–30°. This distinctive feature prompted one of the authors of this paper (F.A.Zh.) to assign the species *O. coralliforme* to a separate genus, *Coralloceras* (Balashov and Zhuravleva, 1962). Eight forms illustrated by Le Maitre under one species name differ from each other in a number of visual characters. The form that should be designated as the holotype is illustrated in pl. 8, figs. 1 and 2 and represents a fragment, which consists of six chambers, widens at an angle of 21°–22°, and has a dorsoventrally compressed elliptical cross section and nearly central siphon. The adoral end displays numerous cameral plates, arranged in separate sectors. As the plates approach the siphon, they merge. Another form (pl. 8, figs. 6–8) has a circular cross section, expands at an angle of 16°, and displays a submarginal siphon in the adapical part of the fragment. These differences alone suggest that the series of specimens examined by Le Maitre contains representatives of at least two species, perhaps, from different genera. Thus, judging from the holotype (*O. coralliforme*), it is believed that the genus *Coralloceras* is characterized by a rapidly expanding conch, which is compressed dorsoventrally in cross section and has a nearly central siphon.

Mutvei (1956) was the first to publish longitudinal medial sections that show details of the internal structure of the lamellar cameral deposits of straight conchs of cephalopods. Four specimen from the Eifelian of the northern Sahara were depicted by this author under the name "*Lamellorthoceras*" in order to show, as he believed, the variations in the deposition of calcareous material in the chambers of phragmocone after the death of the organism. Unfortunately, this well-preserved material was ignored by subsequent researchers of this group. It is worth noting, however, that a detailed interpretation of the internal structure of these forms was quite difficult before we obtained better preserved materials.

As previously mentioned, Teichert (1961), who studied many forms with lamellar cameral deposits from the Lower and Middle Devonian of Germany and the entire Termiers' collection, designated a new family Lamellorthoceratidae with two constituent genera: *Arthrophyllum* Beyrich, 1850 and *Lamellorthoceras* Termier et Termier, 1950. According to Teichert, these genera differ in the form of cameral plates, which are sinuous, distally branching, and both epi- and hyposeptal in *Lamellorthoceras* and straight and only episeptal in *Arthrophyllum*.

In 1961 F.A.Zh. described a new genus, *Gorgonoceras*, with the type species *G. visendum* from the lower Eifelian on the eastern slope of the Central Urals. As distinctive characters that differentiate it from the other genera were indicated the presence of longitudinal ornamentation consisting of slender riblets, epi- and hyposeptal cameral plates that are sinuous in the longitudinal tangential section of the specimen, and the presence of a thick mid-ventral plate that bifurcates at its distal edge. The internal structure of the conch as a whole was misinterpreted (see below).

On the basis of the study of a large (70 specimens) collection of lamellorthoceratids from the Eifelian of France, Babin (1964) arrived at a conclusion that many external characters, such as the angle of the conch expansion, the shape of the conch cross section, the degree of the conch bend, the height of chambers, the position of the siphon, and the shape of the plates of cameral deposits cannot serve as reliable characters for distinguishing genera. He believes that, judging from these characters, one will be inclined to think that in his collection there are representatives of both genera, i.e., *Arthrophyllum* and *Lamellorthoceras*. Finally, he arrived at a conclusion that there is most likely only one genus, *Arthrophyllum*, whereas *Lamellorthoceras* and *Coralloceras* are synonymous names. He retained (with certain reservations) *Gorgonoceras* as a separate genus. Later Babin (1966) described under the name *A. vermiculare* (Termier et Termier, 1950) the series of specimens from the Couvinian of France that contains both ortho- and cyrtoceraconic conchs. A cross section of one of these shells shows numerous sinuous cameral plates (Babin, 1966, pl. 15, fig. 5a). In the form described as *A. gracile*, cameral deposits are represented by a few thick plates (Babin, 1966, pl. 15, fig. 9). It is difficult to accept Babin's opinion that all shells illustrated by him belong to one genus.

Sweet (1964) included in the family Lamellorthoceratidae three genera; i.e., *Arthrophyllum, Lamellor-*

thoceras, and *Gorgonoceras*. He considered *Coralloceras* to be a synonym of *Lamellorthoceras*.

Later Stanley and Teichert (1976) designated a new genus, *Esopoceras*, with the type species *E. sinuosum* from the Emsian of the USA. In the diagnosis of the genus and in the description of the type species, these authors included all characters that they were able to observe both on the outside and in cross sections in all 13 specimens, which are represented by fragments (predominantly short) of casts of phragmocones. The structure of the siphon wall has remained unknown because of the absence of longitudinal sections. Considerable variations that were observed within both each specimen and the entire collection in the form of the cross sections of the shells, in the position of the siphon, and in the length of chambers were attributed by these authors to the variations in the degree of preservation of the material and in the position of fragments inside the phragmocone, whereas variations in the arrangement of cameral plates in the cross sections of the siphon, are attributable, in their opinion, to the varying level of the plane sections of the chamber; namely, straight and longitudinal plates appear in cross sections as radial plates, whereas curved bending plates show a bilaterally symmetrical arrangement.

Perhaps, this is a plausible explanation; however, it is very difficult to believe that one species may possess two such different forms: a conch that is circular in cross section, has a nearly central siphon and radial cameral plates, and, in addition, is dissected at two different levels (Stanley and Teichert, 1976, pl. 2, figs. 1, 4) and a laterally compressed conch that has a significantly eccentric siphon and a bilaterally symmetrical arrangement of plates that are grouped in four separate sectors (Stanley and Teichert, 1976, pl. 2, fig. 7). Stanley and Teichert (1976, p. 9) insistently called attention to the structures surrounding the siphon and directed from the siphon to the wall rather than from the wall to the siphon (Stanley and Teichert, 1976, pl. 2, figs. 4, 7). These structures apparently represent ectosiphonal deposits, which will be thoroughly discussed below.

In our opinion, the series of specimens assigned by these authors to *E. sinuosum* contains at least two different species, which, perhaps, belong to different genera. The available information is inadequate to provide a more or less clear idea of the type species *E. sinuosum* and the genus *Esopoceras*. The authors of the genus believed that such complex cameral structures could be only secreted by the cameral mantle. Thus, they considered the arrangement and form of these plates to be important for improving the taxonomy of lamellorthoceratids and emphasized that they should be studied in thin sections on the basis of well-preserved materials. They were inclined to believe that all five of the previously described genera are valid taxa.

The view of Dzik (1984) on this group of cephalopods is of special interest. He considered Devonian lamellorthoceratids, as well as some Silurian species of straight ectochochlian cephalopods with a siphon devoid of connecting rings and with simple, non-lamellar cameral deposits entering the siphon, to be remote descendants of the Ordovician family Lituitidae. One distinctive feature of lituitids is the destruction during their lifetime of connecting rings and the penetration of cameral deposits into the siphon through the openings that appeared in the connecting rings. These deposits spread along the internal surface of the intact portions of connecting rings to assume the appearance of endosiphonal deposits. Dzik unites eight genera (*Rhynchorthoceras* Remele, 1881; *Sinoceras* Shimizu et Obata, 1935; *Murchisoniceras* Babin, 1966; *Arthrophyllum* Beyrich, 1850; *Lamellorthoceras* Termier et Termier, 1950; *Gorgonoceras* Zhuravleva, 1961; *Coralloceras* Zhuravleva, 1962; and *Espoceras* Stanley et Teichert 1976) in the family Sinoceratidae Shimizu et Obata, 1935 and places this family, along with three other families (Lituitidae Phillips, 1848; Sphooceratidae, Flower, 1962 and Ophioceratidae Hyatt, 1894) in a new suborder, Lituitina, which he has separated within the order Orthocerida. Considering lituitids to be descendants of some orthoceraconic cephalopods, he propose a phylogenetic scheme in which lituitins stemmed from the genus *Rhynchorthoceras*. The apical part of the conch of this genus, in contrast to the other genera of lituitids, is not coiled in a spiral pattern, but rather merely slightly bent. In this scheme the Devonian lamellorthoceratids are shown to be descendants of lituitids, which have completed the lineage of the family Sinoceratidae. Dzik believed that in lamellorthoceratids the lamellar structure of cameral deposits could be of no taxonomic significance. A more detailed discussion of his phylogenetic scheme will be given below.

A paper on lamellorthocerids by Bandel and Stanley (1989) is at least equally interesting. They examined abundant fossil material (60 well-preserved shells) from five localities in Germany (predominantly from Lower Devonian Hunsrück slates), France, northern Africa, and the USA and extracted quite interesting and important information on the ontogeny, life-style, taphonomical environment, and diagenesis of shells of this group of cephalopods. Their studies have shown that lamellorthocerids possessed a straight longiconic conch, which was circular or laterally compressed in cross section and varied in length from 5 to more than 500 mm. The juvenile conchs, which are abundant in Hunsrück slates, measure 4–5 mm in length and have an isolated spherical initial chamber with a diameter of about 0.6 mm and a constriction at the level of the first septum. The whole conchs are about 5 mm long and consist of four chambers, including the body chamber. The last chamber is two times as long as the phragmocone; however, this proportion is reversed in adult conchs. After leaving their eggs, juvenile individuals apparently differed little from adults in appearance and body organization. The surface of the conch bears only growth lines, which form a small ventral sinus and a low, wide dorsal ridge. Bandel and Stanley believed that slender longitudinal riblets (about 6 per 1 mm) result from demineralization of a wall, when only the organic component of the wall ("skin") persists after diagenesis and develops such a wrinkled appearance. The relative length of chambers diminishes in ontogeny. The internal surface of the conch bears a ventral channel, and the dorsal side bears a row of longitudinal parallel furrows. In the view of these authors, these furrows are similar to mantle muscle scars occurring in *Spirula*, *Pseudorthoceras*, belemnoids, and aulacoceratids. The mural portions of septa are short. The suture is straight on the dorsal side and forms a low saddle on the ventral side. The siphon is fairly narrow, with its relative width decreasing adorally, and is shifted to the ventral side. These authors believed that the siphon is similar to those of Mesozoic ammonites and is composed of elastic organic tissue. In our opinion, this is not supported by the illustrations of specimens made by them. The septal necks are short, approximately 1/5 of the chamber length, and suborthochoanitic. The term "connecting rings" does not occur in their paper. They mentioned only a "true siphonal tube," which can be seen in some X-ray radiographs and in thin sections (Bandel and Stanley, 1889, pl. 8, figs. 45a, 47, 48). Unfortunately, no relationships between this structure and the septal necks can be seen in these illustrations.

The cameral deposits represent irregularly arranged longitudinal plates (flat or sinuous) that frequently branch, come from the chamber wall to converge at the siphon, and fill most of the adapical chambers. Bandel and Stanley believed that these plates were originally organic blades that were secreted by the visceral mass of the animal in the process of chamber formation. A complex arrangement of these blades into several series served to divide the chamber into compartments, to separate the cameral fluid from the siphon, and to retain gas bubbles in some places of the chamber. These blades were a matrix for mineralization. According to Bandel and Stanley, the formation of matrix began on the ventral triangular blade, which was suspended both from the adapical part of the organic siphon and from the chamber wall. This blade was an attachment membrane similar to that in the ammonite genus *Quenstedtoceras*. More slender blades, suspended from both this membrane and the siphonal tube, moved apart radially to reach the chamber wall, thus dividing the chamber into compartments filled with fluid. In addition to these blades, one or several (in larger chambers) oblique blades stretch along the entire chamber from the adapical septum on the ventral side to the adoral septum on the dorsal side. In places where the radial blades come into contact with an oblique blade, they form irregularly shaped cavities. The mineralization of this matrix began in the posterior chambers, when the phragmocone consisted of no less than 20 chambers, and the first chamber was at least 0.5–1.0 mm in diameter and advanced as the conch grew. This resulted in the gradual formation of a counterbalance to the progressively heavier soft body that, in contrast to the external (with respect to the phragmocone) rostrum characteristic of belemnoids and aulacoceratids, these authors named "internal rostrum." A series of 14 to 25 chambers remained empty between the chambers containing plates and the body chamber. Mineralization proceeded gradually and continuously by deposition of calcite on organic blades from extrapallial fluid, which percolated from the siphon through the organic tube. Mineralization occurred predominantly on the ventral side, where the matrix was immersed in fluid, whereas the chambers on the dorsal side were filled with gas. The calcitic plates that were formed by this process preserved better than the aragonitic walls of the conch. During ontogeny the number of blades that were to form plates in chambers increased. Some conchs were found buried in an oblique or, occasionally, even almost vertical position, with the apical end directed downward. However, the majority of internal rostra were redeposited and, thus, deformed and worn to variable degrees. Organic blades in plates were destroyed by diagenesis.

After studying all available materials on lamellorthoceratids, except for the genus *Gorgonoceras*, Bandel and Stanley concluded that many external and internal features of the conch are results of diagenesis rather than morphological characters and that four or five of the currently recognized genera were separated in vain. They believed that in fact there exists only one genus, *Arthrophyllum* Beyrich, 1850. In their opinion, small variations that were observed when studying the material reflect differences at the species level. These authors considered lamellorthoceratids to be a unique group in that they are similar in appearance to straight nautiloids but markedly differ from the latter in internal structure at the higher taxonomic level. Some characters, such as long muscle scars on the surface of casts, suggest that lamellorthocerids may belong to endocochlian cephalopods. These authors assumed that lamellorthoceratids were a side branch of some group that had undergone an explosively radiative evolution and gave rise to all modern cephalopods, except for *Nautilus*. *Eoteuthis elfridae* Sturmer, 1985, which is represented by an 8-cm-long specimen with arms from Hunsrück slates, is likely to be a juvenile *Arthrophyllum*. Unfortunately, none of the three longitudinal sections of phragmocones that were furnished by these authors is likely to include the septal foramen and show the relationship between the septal necks and cameral deposits. This is discussed in detail below.

Niko (1991) described a new genus, *Plicatoceras*, with the type species *P. nishidai*, from the lower Lochkovian of Japan. He placed this genus in the family Lamellorthoceratidae and all the other genera of this family in the synonymy of the genus *Arthrophyllum*. The only specimen (a fragment of a straight, smooth, 49-mm-long conch, which is laterally compressed in cross section) was examined by Niko in thin sections. In the cross section of a chamber, this specimen shows 27 to 30 platelike structures that run from the wall to converge on the siphon. The interior of each plate contains a thin dark-colored layer. The thick mid-ventral plate is thick, and its distal edge partially encloses the siphon. The longitudinal section displays very long chambers. The septa have extremely short necks on the dorsal side and are enclosed in epi- and hyposeptal cameral deposits. The latter deposits constitute very complex structures within chambers; these structures are directed at the siphon predominantly at a nearly right angle. The cameral deposits of the ventral side constitute vermiform, intricately intertwined formations, which occupy the entire cavity of the chamber. The surface of these deposits is lined with a thin black sinuous layer, which closely follows the rugged surface of these deposits. Niko mistook this layer, which represents metacameral deposits, for connecting rings.

Marek (1998) designated a new order, Pallioceratida, for which he presented the following diagnosis: "Longiconic or subcyrtoconic conchs with initially soft tissue in gas chambers. Connecting rings open rather than closed structures; thus, their internal space merged with that of chamber. Although well-developed in the adapical part, cameral deposits never fill the entire cavity of the chamber." This author believes that morphologically and, accordingly, anatomically these cephalopods differ from the other nonammonoid cephalopods at the subclass level; for example, as from Nautiloidea, Actinoceratoidea, and Endoceratoidea. Marek differentiated two groups in the order Pallioceratida: (a) cephalopods with bag-shaped cameral mantles (the family Leurocycloceratidae Sweet, 1964) and (b) cephalopods in which the cameral mantle consists of more or less elongated plates that are variously but predominantly radially arranged (the family Lamellorthoceratidae Teichert, 1961). He pointed out, however, that the diagnoses of these families may be changed after a detailed study of these cephalopods.

Subsequently, Kolebaba (1999a, 1999b) published new data on the Silurian (Ludlow) cephalopods in which chambers contained soft tissue. He examined the internal structure of conchs predominantly in longitudinal and transverse thin sections. Using the similarity in the cross section of the conch and the position of the siphon as the sole basis, Kolebaba (1999a) assigned the forms illustrated in the six plates of this paper to three species, i.e., *Plagiostomoceras pleurotomum* (Barr., 1866), *Orthoceras obelus* Barr., 1870, and *Protobactrites styloideum* (Barr., 1866). He established a new genus, *Nucleoceras*, on the basis of the second of these species. Since Kolebaba selected fragments of conchs with unknown internal structures as lectotypes for the first two species and as a holotype for the third species, the identification of conchs examined by Kolebaba as belonging to these species cannot be considered proved. Moreover, since all three species are type species of the respective genera, the taxonomic positions of these genera are also uncertain. In this case, no other species can be assigned to these three genera. Apparently, Kolebaba has to give consideration to this nomenclatural question. In this paper we only tentatively accept his choice.

Kolebaba considered the species *Protobactrites styloideus* to be a senior synonym of *Mariaceras pragense*, which had been described by him earlier, although the siphon and cameral deposits in the holotype of the latter species (Kolebaba, 1974, pl. I, fig. 7) markedly differ in structure from those of the conchs illustrated by him under the name *P. styloideum* (Kolebaba, 1999a, p. 6, text-fig. 6; pl. I, fig. 4). In the form shown in p. 6, text-fig. 6, the structures adjacent to the cameral deposits on the ventral side of the conch apparently represent ectosiphonal rather than endosiphonal deposits. The ectosiphonal deposits, which are described in detail below, do not extend beyond one chamber, in contrast to the episeptal deposits, which enter the septal foramen. On the chamber side, the boundary of these ectosiphonal deposits is poorly defined and bears little resemblance to the connecting ring. Probably, this is only the contour of the external surface of these deposits. Apparently, the same is true of the form illustrated by the photograph of a thin section and a line drawing made by Kolebaba after this photograph (1974, pl. I, fig. 4; text-fig. 1). This photograph clearly indicates that in the adoral segment only the episeptal cameral deposits enter the septal foramen, whereas the structures that this author referred to as endosiphonal deposits do not extend beyond this segment. It is possible that this conch belongs to the species designated by Kolebaba as *Protobactrites styloideum*. The presence of ectosiphonal deposits suggests that this conch belongs to the family Astroviidae. However, the final solution of this problem requires a detailed structural study of both ectosiphonal and cameral deposits.

The conchs depicted in pl. 3 under the name *Plagiostomoceras pleurotomum* are most similar in internal structure to species of the genus *Ostreioceras* and, apparently, represent a species of one more genus of the family Ostreioceratidae. As in species of the genus *Ostreioceras*, the thin layer of mural-episeptal cameral deposits enters the septal foramen and advances to meet the more massive hyposeptal deposits of the previous chamber, which enclose the edges of both the septal neck and the episeptal deposits overlying it (pl. 3, figs. 5, 6, 7).

As noted above, the genus *Nucleoceras* was established on the basis of *Orthoceras obelus* Barr., 1870, in the lectotype of which the internal structure of the conch is unknown. Plates 4, 5, and 6 present under a single generic name, *Nucleoceras*, longitudinal and transverse sections of phragmocones, which Kolebaba believed to belong to different species of this genus, i.e., *N. obelus*, *N.* sp. A, and *N.* sp. B. With allowance made for our new data, it is clear that these plates show conchs not only of different species, but of different genera and even of different families. Thus, the conch that was presented first under the name *N. obelus* in pl. 4, fig. 1 is most similar to that of the species *Plicatoceras nishidai* Niko, 1991 from the lower Lochkovian of Japan in internal structure (very short septal necks; the absence of "pseudoseptum" on the ventral side; the outline of cameral deposits in longitudinal sections; and, perhaps, the structure of cameral deposits) and, most likely, represents one of the species of the genus *Plicatoceras*, which is described below. It is quite possible that the transverse section shown in pl. 5, fig. 2 belongs to a similar conch. Furthermore, it is by no means improbable that, judging from numerous aforementioned characters (short septal necks, cameral deposits that form no "pseudoseptum," and the presence of metacameral deposits), the form illustrated in pl. 6, figs. 4–7 as *Nucleoceras*? sp. B also belongs to the family Plicatoceratidae.

Plate 4, fig. 2 displays a lateral section of two chambers of another conch that runs through the middle of the siphon. This photograph distinctly shows that, in addition to the cameral deposits, there are ectosiphonal deposits moving away from the siphon to the cavity of the chamber and toward the cameral deposits, but stopping short of reaching them. The dark sinuous layers that line the cameral deposits and were mistaken by Kolebaba for a phantom siphonal tube are the second phase of ectosiphonal deposits. The width of the soft siphon located between these layers is considerably narrower than the septal foramen. This form most likely belongs to some species of the genus *Astrovia*, which was reported earlier only from Pragian deposits of the Kuznetsk Basin and from the Eifelian of northern Africa. Nothing definite can be said of the forms that Kolebaba illustrated in the other numerous photographs apart from the fact that they belong to pallioceratids. Thus, the taxonomic position of the genus *Nucleoceras* Kolebaba, 1999, with the type species *N. obelus*, remains unclear.

The subsequent paper (Kolebaba, 1999b) described a new species under the name *Nucleoceras hollandi*, for which a conch of unknown internal structure was selected as the holotype. Kolebaba also examined a fragment of the phragmocone of another conch in longitudinal and cross sections. The longitudinal section of this fragment shows that in the adapical part on the ventral side there is a continuous, thin, black layer, which is slightly convex at the level of the chambers and lies on the uneven surface of cameral deposits, which filled the cavities of the chambers. This layer apparently consists of metacameral deposits. The structure of the chambers was not preserved. On the dorsal side the cavity of the chamber is only partially filled with cameral deposits. The epi- and hyposeptal deposits have an uneven surface and enter the cavity of the siphon only in the septal foramina. Their common surface, facing the siphon, is strongly convex toward the chamber. In the adoral part of the fragment, one of the chambers preserves a slightly convex, thin, probably uncalcified, connecting ring. The neighboring septal foramina also show remnants of rings (pl. 1, fig. 2). This part of the phragmocone apparently bore no cameral deposits. Although connecting rings have been preserved both on the ventral and dorsal sides, Kolebaba has continued to apply the term "connecting trough." In his opinion, this trough has been left by a connecting ring on the ventral side. However, it is hard to believe, since on the ventral side the cameral deposits entered the siphon through the septal foramen (with the connecting ring being destroyed by them or nonexistent) well before those on the dorsal side.

The existence of connecting rings in the adoral part of the phragmocone, where no cameral deposits had yet been developed, and the absence of any evidence of connecting rings in the adapical part of the phragmocone, where the cameral deposits were well developed, suggest that some (or even all) pallioceratids primordially evolved connecting rings; however, these rings were weak because they were composed of organic material and, thus, easily destroyed by the soft cameral tissue (cameral mantle) that approached them over the surfaces of septa and lined the walls of the chamber.

Furthermore, Kolebaba's idea of a soft cameral tissue of his "sipho-cameral mantle," which, in his view, primordially filled the entire cavity of the chamber (Kolebaba, 1999a, text-fig. 5) seems strange. For this continuous tissue, he devised a special attachment system in which "pseudosepta" are considered to be its principal component. In our opinion, Kolebaba will have to revise his views on this subject. It is worth noting, however, that Kolebaba has made a considerable contribution to the knowledge of this interesting group by adding information on its taxonomic diversity, stratigraphic range, and geographic distribution.

From the above discussion it is clear that, in the majority of collections, examined by different authors at different times, conchs of those cephalopods that lost the solid hard wall of the siphon in ontogeny and, especially, those that had lamellar cameral deposits belong to different species and, frequently, different genera. Notwithstanding all available illustrations of the surfaces of the casts and even those of their transverse sections, it is quite difficult to get some idea of the conch as a whole, much less of its internal structure, which frequently proved to be quite complex. It is now quite evident that the study of this group, as well as of other fossil nonammonoid cephalopods, requires the preparation of longitudinal medial sections (both thin and polished) of conchs that run through the cavity of the siphon. In addition, our experience tells us that the study of the microstructure of their internal details through a scanning electron microscope is necessary.

THE CONCH OF THE PALLIOCERATIDS: INTERNAL STRUCTURE AND MICROSTRUCTURE

The Wall of the Conch

None of the forms under study has an entirely preserved wall of the conch.

Ostreioceras riphaeum. The entire material representing this species experienced ferrugination. The conch has a fairly thin wall, which gives no evidence of surface ornamentation. In places the wall shows three hardly distinguishable layers, which have lost their initial microstructure: the internal and external layers are thin, and the intermediate layer is thick.

Astrovia adorea. In this form the wall of the conch is only partially preserved. The longitudinal and transverse sections show two layers on the dorsal side of the wall: (1) The internal layer is thin, black, apparently elastic, and concave at the level of an inclusion located between the layers; in longitudinal sections, it shows a crenulated surface; in thin sections, it shows a stratification in color intensity (from yellow to dark brown); in an SEM, this layer seems massive and amorphous (Pl. 7, figs. 1a–1d; Pl. 8; Pl. 9, figs. 1a, 1b). (2) The external layer is thick, light in color, and prismatic; its internal part is greater and contains elongated structures, which are aligned at right angles to the surface of the internal layer; its external part is smaller, with the structures directed backward, at obtuse angles. The prisms that constitute this layer are provided with short, pointed processes, which apparently connect them to each other. The surface of the external layer is worn down by erosion (Pl. 7, figs. 1a–1d; Pl. 8; Pl. 9, figs. 1c, 1d). Whether or not this layer belongs to this conch is open to question.

Gorgonoceras visendum. In this species the surface of the cast of the fragment has conserved only a small portion of the internal layer of the conch wall, which is folded in distinct longitudinal ridges (Pl. 14, fig. 1a).

Syndikoceras arcticum. The conch of this species has a wall consisting of three layers; the initial microstructure of them has not been preserved. The two internal layers and, perhaps, the external layer are arranged in low longitudinal ridges, which are reflected in the cast (Pl. 16, fig. 1c; Pl. 18, figs. 1a–1d). The surface of the external layer is hidden from view by rock material.

Flowerina shimanskyi and ***Plicatoceras bublichenkoi*** are represented only by fragments of casts.

Septa and Septal Necks

The septa and septal necks of the pallioceratid specimens under study are usually enclosed in the cameral deposits and have lost their initial thickness and microstructure.

Flowerina shimanskyi is represented by a sole fragment, which contains two septa enclosed in the cameral deposits; the greatest portion of these septa have been dissolved and those which penetrated into the septal neck have been deformed. The adapical septum alone has retained its complete thickness but has lost the microstructure and septal neck. In the preceding septa the necks are slightly convex. On the dorsal side they deflect from the septum at a nearly right angle, attain about 1/3 of the chamber length, and have a well-defined outwardly curved edge. On the ventral side the necks deflect from the septum at an obtuse angle and reach slightly farther than on the dorsal side, where they are partially disintegrated; however, they apparently also had an outwardly curved edge (at the level of edges they show traces of expansion). The microstructure of the necks has been lost (Pls. 1, 2).

Ostreioceras riphaeum has septa of moderate thickness with a fairly long mural portion; in places they show remains of the nacreous microstructure (Pl. 5, figs. 1c; Pl. 6, fig. 1a). The septal necks are commonly very long, gradually tapering marginally, and quite often curved outwardly or inwardly (Pl. 5, figs. 1b, 1d). In places they show remains of the nacreous microstructure (Pl. 5, fig. 1c).

Astrovia adorea has very thin septa with a short mural part; in the uncovered part the septa are divided by the median notch. In the thin section they show a fine-crystalline structure (Pl. 7, fig. 1d). Near the conch wall the septa are considerably thicker (Pl. 8; Pl. 9, figs. 1a, 1b). In an optical microscope the septal necks appear to be well-defined, short, and suborthochoanitic (Pl. 7, figs. 1a, 1b; 8). However, SEM study clearly shows that the neck with adjacent parts of the septum have no well-defined boundaries; i.e., the edge of the neck seems to merge with the cameral deposits that surround it (Pl. 10, figs. 1a, 1b; Pl. 12, fig. 1).

Gorgonoceras visendum has septa and short suborthochoanitic septal necks of moderate thickness. Their microstructure has been lost (Pl. 14, fig. 1b).

Syndikoceras arcticum. In this species the septa have a short mural part and are slightly thicker near the conch wall (Pl. 18). In places they have preserved the nacreous microstructure (Pl. 22, figs. 1b, 1c). The septal necks are short, orthochoanitic on the ventral side, and suborthochoanitic on the dorsal side. Although an optical microscope display shows a fairly well-defined edge (Pl. 17), SEM photographs invariably show that the edge of the neck merges with the cameral deposits even where it has preserved the nacreous microstructure (Pls. 19, 20; Pl. 22, fig. 1a).

Plicatoceras bublichenkoi. This species, as well as many other pallioceratids, has septa that are tightly compressed between the cameral deposits of neighboring chambers; thus, it is impossible to determine their true thickness. The mural part of the septa and the wall of the phragmocone have been destroyed (Pl. 31; Pl. 32, fig. 1a). The septal necks are short; on the ventral side, they are orthochoanitic; on the dorsal side, they are somewhat longer with a slightly tapering edge on the

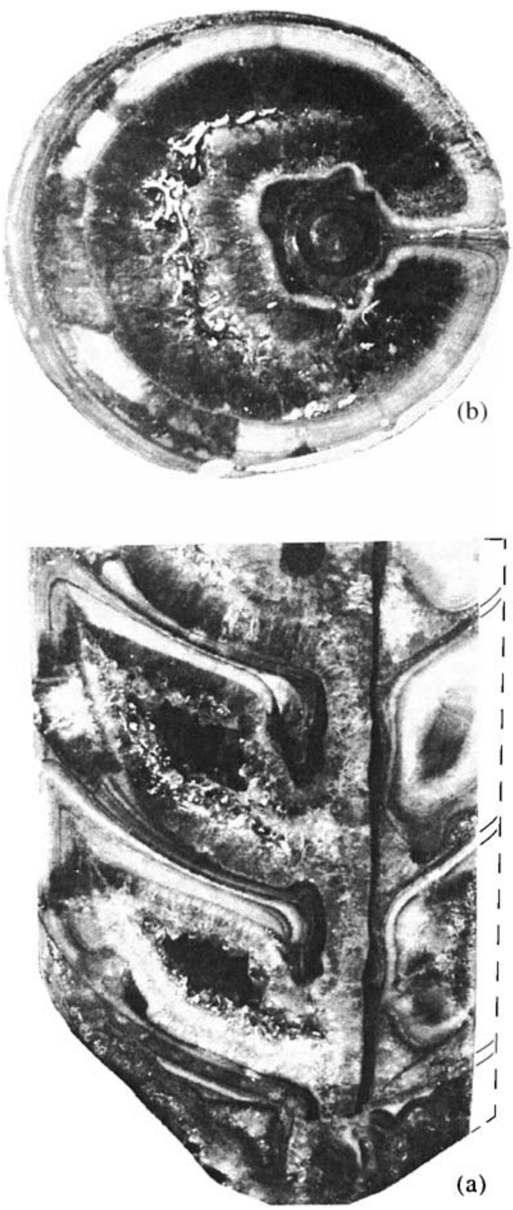


Fig. 2. *Flowerina shimanskyi* Zhuravleva et Kisselev, 2001; holotype PIN, no. 1793/1801, ×2.6; (a) longitudinal dorsoventral section: on the dorsal side the episeptal cameral deposits pass through the septal foramen and merge with the more massive hyposeptal deposits of the previous chamber; on the ventral side nearly the entire cavity of the chamber is filled with massive hyposeptal deposits; metacameral deposits are arranged in longitudinal layers throughout several chambers; (b) the cross section level with the edge of the septal neck: cameral deposits are arranged parallel to the chamber wall and, after a sharp turn to the ventral side, move to the siphon; the hyposeptal deposits surround the neck, the episeptal deposits are located inside the neck; the metacameral deposits are located on the ventral and lateral sides and inside the neck; Ukraine, Podolia, the Dniester River basin, left bank of the Studenitsa River, 400 m downstream of the downstream end of the village of Studenitsa; Lower Silurian, Wenlock, Furmanovo Formation, Restevskaya Subformation.

dorsal side. The necks proper are very slender; through an optical microscope, they are more clearly visible owing to the thin layer of cameral deposits that overlies them (Pl. 31; Pl. 32, fig. 1a). The structure of the necks has been lost.

Cameral Deposits

In most pallioceratid species under study, the cameral deposits differ both in morphology and, especially, in microstructure.

Flowerina shimanskyi. The conch of this species is characterized by epi- and hyposeptal deposits. On the dorsal side the episeptal deposits run through the septal foramen to the previous chamber and merge there with the hyposeptal deposits, which are markedly thicker than the episeptal deposits. In the angle between the septum and neck, the hyposeptal deposits do not approach either the septum or the neck. On the ventral side the episeptal deposits form a thin layer that runs through the septal neck and joins the massive hyposeptal deposits of the previous chamber, which occupy there virtually the entire cavity of the chamber, leaving little room in the adapical part of the chamber near the siphon. The cameral deposits have a prismatic microstructure in which prismatic structures are elongated and directed perpendicular to the surface of deposits. In the middle part of the massive hyposeptal deposits, the prismatic microstructure is subsequently replaced by the fine-crystalline microstructure (Pls. 1, 2). The cross section that runs through a small portion of the edge of the septal neck shows that the layers of the epi- and hyposeptal deposits, which were arranged parallel to the wall of the chamber, take a sharp turn to the siphon on the ventral side and, being immediately adjacent to each other, reach and enclose the siphon; the septal neck contains the episeptal deposits of the subsequent chamber (Fig. 2a).

Ostreioceras riphaeum forms in the chambers deposits of three kinds: hyposeptal, united mural-episeptal, and mural deposits. The mural deposits are formed through the separation of them from the episeptal deposits in the posterior part of the chamber and rapidly grow toward the siphon, thus frequently deforming and shifting it dorsally from the level of the septal neck (Pl. 3, figs. 1, 2; Pl. 4; Pl. 5, fig. 1d). The episeptal deposits form a thin layer that enters the septal neck and merge with the hyposeptal deposits of the previous chamber at the level of the edge of the septal neck. The hyposeptal deposits in turn frequently enter the septal neck, enclosing and, occasionally, turning its edge inward (Pl. 5, figs. 1b, 1d; 4). The episeptal deposits occasionally form a fairly wide and thin adoral ring around the soft siphon (Pl. 3, fig. 6). In this species the hyposeptal deposits are in contact with the mural deposits rather than with the episeptal deposits, as in most known forms. The free space that was left between the episeptal deposits and the mural deposits, which separated from them, and the cavity left by the completely destroyed soft siphon were subsequently filled with sediment. The sediment that fills this slit follows the rugosity of the underlying episeptal deposits (Pl. 3, figs. 3, 6; Pl. 4; Pl. 5, figs. 1a, 1b). This region of the body, which in the longitudinal section of the phragmocone is markedly different in color, is also typical of other species of the genus *Ostreioceras*. The internal surfaces of all cameral deposits are plicate, which is due to the rugosity of the plates from which they are composed (Pl. 3, figs. 2, 5).

The cameral deposits of *O. riphaeum* consist of thin, finely waved layers, which are thrown into transverse folds. In the thin section at high magnification, they seem to be arranged in a regular lattice, which is formed by "shivering" boundaries between the layers and small transverse structures located between these boundaries (Pl. 4). In an SEM the hyposeptal deposits show the same pattern (Pl. 5, fig. 2). At high magnification in an SEM, the folds of the episeptal deposits that lie on the septum, which preserved the initial nacreous microstructure, have the aspect of separate reticulate bushes penetrated by pores in which the transverse elements of the structure are seen somewhat more clearly (Pl. 6). This type of microstructure of cameral deposits may be named a reticulate-porous structure.

Astrovia adorea. This species has both epi- and hyposeptal cameral deposits. The episeptal deposits entered the previous chamber by several layers through the septal foramen. The first layer of the episeptal deposits entered the septal neck, got around its edge, occasionally twisted around it, and merged with the hyposeptal deposits of the previous chamber (Pl. 8; Pl. 10, fig. 1a). The next layer is darker (probably, less mineralized), runs through the septal foramen, goes around the neck, which is covered by the first layer and the hyposeptal deposits of the previous chamber, and comes in contact with its episeptal or mural-episeptal deposits (Pl. 8; fig. 3). The last thin black layer of the cameral deposits occasionally comes off from the previous layer in the form of a thin film (Pl. 8, second and fourth foramina on the dorsal side). On the ventral side the cameral deposits are more mineralized, and the boundaries between the layers can only be traced in some places.

The cameral deposits of *A. adorea* are composed of elongated undulating or sinuous structures, which run to the siphon and start from the thin initial layer that lined the wall of the chamber and septa and in which the small structural elements are perpendicular to the surface of deposits (Pl. 7, fig. 1d; Pl. 9, figs. 1a, 1b). In the longitudinal and transverse sections of the phragmocone, these structures look like feathers; three-dimensionally, they apparently represent structures in which, like needle-leaves of a shoot of spruce, smaller elements radiate from the central axis in all directions, usually at an oblique angle (Pl. 7, figs. 1a, 1d, 1c; Pl. 8; Pl. 9, figs. 1f, 1g; Pl. 10, fig. 1a; Pl. 12, fig. 1). We propose the term *virgulae* for these structures. The longitudinal axis of the virgula is apparently a tubular structure, whereas the smaller branches that diverge from it are narrow articulated tubules (Pl. 11, figs. 1a, 1b; Pl. 12, fig. 1). The neighboring virgulae have no distinct boundaries, thus suggesting that they have been formed within soft tissue rather than on the surface (Pl. 9, figs. 1f, 1g; Pls. 10, 11).

Gorgonoceras visendum. In this species, as well as in *A. adorea*, the episeptal and less massive hyposeptal cameral deposits also consist of virgulae, which on the worn surface of the cast and in the tangential section look like longitudinal sinuous plates (Pl. 14, fig. 1e). The longitudinal medial section shows septa on the dorsal side that are completely enclosed, along with their short septal necks, by the epi- and hyposeptal deposits of the two neighboring chambers. On the ventral side, where the chambers are completely filled with deposits, the boundary between the epi- and hyposeptal deposits is indiscernible (Pl. 14, fig. 1b). In the cross section the virgulae of the cameral deposits look like plates that run from the periphery to the siphon and become slightly bent to the middle of the ventral side. The ventral side of the section of the adoral end of the holotype that runs through the episeptal deposits shows a thick complex structure with a forked distal edge; this structure apparently consists of several virgulae (Pl. 14, fig. 1c). The other cross section that runs at the level of the septal neck, predominantly through the hyposeptal deposits, shows no such structures; however, it shows inside the septal neck a layer of episeptal cameral deposits, which penetrated from the next chamber. On the ventral side this layer is markedly thicker than on the lateral and dorsal sides (Pl. 14, fig. 1d). The virgulae of *G. visendum*, as well as those of *A. adorea*, consist of a tubular axis and smaller tubular articulated branches that radiate from the axis in all directions at an oblique angle (Pl. 15, fig. 1b).

Syndikoceras arcticum. The cameral deposits of this species are very complex in structure; thus, it is extremely difficult to determine the true character of their constituent structures from several sections of one small fragment. The nearly medial longitudinal section of a specimen shows that on the ventral side the deposits fill the cavity of the chamber and look like alternating light and dark structures, which are narrow and long and most of all resemble plates. The episeptal plates go away both from the walls of the chamber and from the septa to the siphon, thus forming narrow folds. They run through the septal foramen into the previous chamber and merge with its hyposeptal deposits. The hyposeptal plates first move away from the peripheral part of the septum parallel to the wall, subsequently parallel to the septum, and finally back in the septal neck, thus partially covering its edge. The plates of the dorsal side are poorly preserved; thus, only one thing is clear: the episeptal deposits run through the septal neck and merge with the hyposeptal deposits of the previous chamber (Pl. 17). In the tangential section that is parallel to and one-third of the radius away from the medial section, the cameral plates look different: those of them that run from the walls and from the peripheral parts of the septa are oriented nearly parallel to the septa and form narrow folds (Pl. 16, figs. 1e, 1f). The episeptal plates in the most concave part of the septum are short, sharp-ended, aligned perpendicular to the septum, and shaped like tongues of flame (Pl. 16, fig. 1f; Pl. 24, fig. 1b). The hyposeptal plates on the convex part of the septum are also short and converge to the center of the septum (Pl. 16, figs. 1e, 1f; Pl. 23, fig. 1a).

In the cross section of the holotype, the relatively wider and lighter plates separated by narrower dark interspaces show a featherlike structure, in which small elongated components form an acute angle to the central axis. The distal ends of these plates are pointed or forked. As the center of the ventral side is approached, the plates become increasingly undulating (Pl. 16, fig. 1g). In an SEM the cameral deposits of *S. arcticum* show a complex microstructure. The elongated sinuous and folded plates that occur in the plane of the section at different angles show a quite complex and diverse pattern. Dissected along the axis, these structures look like straight, bent, or sinuous feathers, in which the relatively smaller elongated structural components radiate at an acute angle from a central axis (Pl. 22, fig. 1e; Pl. 23, fig. 1a; Pls. 24, 25, 28). The neighboring structures are frequently merged with one another and have no clearly defined boundaries (Pl. 25). In other places there are well-defined plates separated by narrow interspaces with a less ordered arrangement of elongated components (Pl. 22, fig. 1e). In the longitudinal section of the phragmocone, the longitudinal feathers are outnumbered by complex star-shaped structures, in which long complex rays radiate from a median region with a close random arrangement of its constituents (Pl. 19–21; Pl. 22, fig. 1d; Pl. 26). Occasionally such star-shaped structures have clearly defined boundaries (Pl. 20, fig. 1d; Pl. 26). This suggests that in *S. arcticum* the cameral deposits mineralized as long branches arranged in rows resembling plates rather than as true plates. In this case the star-shaped structures may be considered to be either transverse (Pls. 19–21, 24) or oblique (Pl. 22, fig. 1d; Pl. 28) sections of branches, and the feathers may be considered to be axial or nearly axial sections of branches (Pl. 22, fig. 1e; Pls. 24, 25). These numerous closely spaced branches dissected by one plane at different angles give the impression of a random arrangement of rays (Pls. 19, 20; Pl. 22, fig. 1a). The long featherlike, seemingly intertwined branches are clearly visible in Pl. 24, fig. 1a. The rays constituting branches also have a complex microstructure, which is similar to that of the branches. They are composed of the finest prismatic crystals, which are aligned perpendicular or at oblique angles to the axis of the ray (Pls. 21, 25–27). The appearance of rays varies with the angle of the section, degree of preservation, and etching rate during preparation. The crystals constituting rays frequently merge with each other. Nevertheless, the prismatic nature of the crystals is clearly seen in many places, including interspaces between rays (Pls. 21, 25, 27, 29). In some of the interspaces between rays there are numerous pores of unknown nature.

Plicatoceras bublichenkoi. The cameral deposits represent extremely complex structures, the true shape of which is extremely difficult to determine and describe. The longitudinal sections of the holotype clearly show the initial layers on the surfaces of both septa (Pl. 30, fig. 1e; Pl. 31; Pl. 32, fig. 1c). Before the wall of the chamber was erased, it apparently was lined with a similar layer.

Approximately at the mid-length of the adoral chamber, the cross section shows about 30 plates running from the periphery to the siphon. The most simple of them are thin and long and look like folds closed at the apex. The cast of the fold resembles a black narrow irregular cavity. The wings of the fold consist of two layers: the external layer is thin and dark and the internal layer is thicker and lighter. The majority of plates formed by several folds are complex structures. In addition to the majority of long and thin plates, the dorsal and lateral sides contain meshworks of very short and thick plates. On the ventral side the plates form the most complex structure, which apparently has developed from a thin unbranched outgrowth. This structure branched out as it grew toward the siphon and, after giving rise to the thick apex, was the first to reach the siphon. There are also other complex structures, which are thick at their bases and immediately adjacent to this structure from all sides as if it were partially enclosed by them (Pl. 30, fig. 1c). All plates are thick and merged with each other at their bases but become thinner to the apex.

The cross section that runs slightly in back of the previous section through the septum shows a few unbranched episeptal plates-folds closed at the apex inside the septum and a tangled network of hyposeptal sinuous plates of the previous chamber outside of the septum (Pl. 30, fig. 1d).

The longitudinal medial section shows that the episeptal layer of cameral deposits becomes thinner, penetrates through the septal foramen into the previous chamber, and merges with its hyposeptal layer in such a way that both the septum and neck are completely enclosed in the cameral deposits. The surface of the episeptal layer in the region of the neck is darker in color, thus giving the general impression of a thick neck. The hyposeptal layer in the region of the neck is very thick and makes the angle formed by the septum and neck nearly flat (Pl. 31; Pl. 32, fig. 1a). On the dorsal side, where the deposits are at an earlier growth stage, one can clearly see that differently shaped complex structures, which are combinations of several (also complex) plates, go away from the mural, episeptal, and, apparently, hyposeptal layers of the cameral deposits nearly parallel to the septa (Pl. 30, figs. 1c, 1e; Pl. 31). On the ventral side the cameral deposits fill the entire cavity of the chamber. The plates-folds form there still more complex structures: differently shaped folds, rings, thick meshworks, etc. (Pl. 31; Pl. 32, figs. 1a, 1d).

The longitudinal tangential section, which is parallel to and approximately half a phragmocone radius away from the medial section, shows plates-folds, which are sinuous and branching, being interrupted (in places) and directed virtually toward each other, and originating from the initial epi- and hyposeptal layers of the cameral deposits. These plates-folds very clearly show two-layered walls separated by a discontinuous black median cavity. The external layer of the folds is darker than the internal layer. The folds gradually thicken apically owing to the increase in the light-colored internal layer and simultaneous decrease in interspaces between the folds. In the lateral portions of this section, which are located closer to the chamber wall, the folds form complex meshworks (Pl. 30, fig. 1e). The microstructure of the cameral deposits is shaped like a spongy matrix with porous walls (Pl. 33).

Metacameral Deposits

On the surface of the cameral deposits, which have completely filled the cavity of the chamber, the soft tissue on the ventral side of all chambers passes into a united longitudinal layer and secretes another longitudinal layer of calcareous deposits, which stretch out through the entire row of the chambers. We proposed the term metacameral deposits for these deposits (Zhuravleva and Kisselev, 2001). Among the pallioceratids under study, metacameral deposits occur in three species: ***Flowerina shimanskyi, Syndikoceras arcticum***, and ***Plicatoceras bublichenkoi.***

Flowerina shimansky. The surface of the cameral deposits bears longitudinal layers of metacameral deposits. Both metacameral and cameral deposits have a prismatic microstructure, in which elongated prismatic aggregates of crystals are aligned perpendicular to the surface of these deposits (Pls. 1, 2).

Syndikoceras arcticum. A continuous longitudinal layer of calcareous metacameral deposits formed on the surface of the cameral deposits. Similar to the cameral deposits, this layer grew toward the soft siphon, thus squeezing and shifting it dorsally. Both metacameral and cameral deposits are composed of elongated complex structures (rays), which either were aligned perpendicular to the surface of deposits or, occasionally, were shaped like spherulites (fanlike). Between the cameral and metacameral deposits there is a dark gray discontinuous layer, which is either amorphous or has a thick ill-defined structure, perhaps slightly mineralized remains of soft tissue (Pls. 19–21).

Plicatoceras bublichenkoi. The metacameral deposits are a continuous longitudinal lining that was first secreted layer by layer on the rough ventral surface of the cameral deposits (which filled the chamber and only slightly overfilled it to enter the siphon beyond the level of the septal necks) and subsequently gradually moved circularly into the lateral and dorsal sides. The microstructure of both metacameral and cameral deposits is a spongy matrix with porous walls (Pl. 31; Pl. 32, figs. 1a, 1b; Pl. 33, figs. 1a, 1b).

Ectosiphonal Deposits

Among the species under study there are species with conchs that contain, in addition to the cameral and metacameral deposits, which were secreted by the cameral tissue, calcareous deposits, which in the absence of connecting rings were secreted by the soft siphon directly into the cavity of the chamber to grow toward the chamber wall and cameral deposits. We propose the term *ectosiphonal deposits* for these deposits. They have been discovered only in three species: ***Astrovia adorea, Gorgonoceras visendum***, and ***Syndikoceras arcticum.***

Astrovia adorea. Both the ectosiphonal and cameral deposits consist of virgulae. An individual virgula is an elongated structure in which smaller tubular articulated branches, which gradually become shorter toward the apex of the virgula, diverge at an oblique angle on all sides from the central hollow tubular axis, which gradually thins toward the apex (Pl. 9, figs. 1f, 1g; Pl. 10, figs. 1a, 1c). The axis of the virgula is bent at the base. On the ventral side of the soft siphon, which had been substantially squeezed by the cameral deposits, about ten virgulae penetrated into the free portion of the cavity of each chamber, gradually thinned toward the apex, and jammed together to penetrate deep into the chamber cavity, where they entered the area between the epi- and hyposeptal cameral deposits and merged with them (Pl. 7, figs. 1a, 1b, 1d, 1f; Pl. 8; Pl. 10, figs. 1a–1c; Pl. 12, fig. 1). Subsequently, the soft siphon secreted one after another longitudinal thin black layers on the sinuous surface formed by the bases of the virgulae; the uppermost layers reached the level of the septal foramina to lie on the surface of the episeptal cameral deposits (Pl. 7, figs. 1a, 1d, 1f; Pl. 8). On the dorsal side the ectosiphonal deposits are at an earlier stage of their growth and still have to go a long way to come in contact with the cameral deposits. In this region they look like slightly elongated bodies composed of virgulae that either have already separated (Pl. 7, fig. 1b) or still remain unseparated (Pl. 7, fig. 1e; Pl. 8), with the apices facing into the chamber cavity. Small oval and rounded bodies that are located near the ends of unseparated virgulae are embryos of virgulae. In this region the free space between the incompletely formed ectosiphonal and cameral deposits and the cavity left by the collapsed soft siphon are filled with rock material (Pl. 8). The ectosiphonal deposits were secreted considerably later than the cameral deposits. As both the ectosiphonal and cameral deposits move away from their point of origin, they become increasingly darker in color. In an optical microscope the color of the layers changes from gray to black in the polished section and from light yellow to dark brown in the thin section. This probably results from increased concentrations of organic matter, which underwent silicification during the diagenesis of these layers. Thus, the uppermost thin black layers of the ectosiphonal and cameral deposits, which in places have come off from the previous layer as thin films, contain only Ca and Si (Pl. 8).

Gorgonoceras visendum. In those parts of the phragmocone that have been studied, the ectosiphonal deposits occur only on the ventral side. They penetrate only slightly into the chamber cavity. We have failed to study their microstructure but believe that they, as well as the cameral deposits, were composed of virgulae (Pl. 15).

Syndikoceras arcticum. In the longitudinal medial section of the phragmocone, the ectosiphonal deposits look like plates arranged in separate longitudinal rows (five to seven in a row), which lie on the ventral side against each chamber and occupy in the chamber cavity the portion free of the episeptal cameral deposits passing through the septal foramina. The plates are inclined adapically to the surface of the metacameral deposits. In three adapical chambers the ectosiphonal deposits are immediately adjacent to the metacameral deposits. More adorally there was an opening, which now is filled with rock material, between them and the metacameral deposits. Adorally the plates become increasingly shorter to become nearly indistinguishable against the last chamber. Unfortunately, we failed to study the microstructure of the ectosiphonal deposits in this species (Pl. 17).

DISCUSSION OF THE RESULTS OF THE STUDY

A detailed study of the literature shows that to date the internal structure of the shells of straight ectochochlian cephalopods with lamellar cameral deposits have been poorly understood. As previously mentioned, the six genera that were united by K. Teichert in 1961 into the family Lamellorthoceratidae, predominantly on the basis of the external characters of chiefly small fragments of poorly preserved shells and their transverse sections, have been treated by many authors as one genus *Arthrophyllum*. Longitudinal sections of shells, which might be useful for the acquisition of additional and more reliable information, have been made very infrequently and have often been misinterpreted.

Mutvei (1956) was the first to provide figures of four relatively well preserved conchs from the Eifelian of Northern Africa in longitudinal medial sections. Unfortunately, until recently, this material was ignored by other researchers, including the first author (F.A.Zh.). However, these sections clearly show that the cameral deposits pass, as in *Leurocycloceras bucheri*, described by Flower as early as 1941, from each chamber through the septal foramen in the previous chamber and merge with its hyposeptal deposits, thus indicating the absence of connecting rings. Study of our materials makes it possible to conclude that the four conchs depicted by Mutvei belong to two genera of different families.

The internal structure of the conch of *Gorgonoceras visendum* Zhuravleva, 1961, shown both in transverse and longitudinal sections, was misinterpreted by the author of the species. The medial section clearly shows that on the dorsal side both the septum and neck are enclosed in the cameral deposits of the two neighboring chambers, thus indicating the absence of connecting rings. On the ventral side the ectosiphonal deposits were taken for the endosiphonal deposits, although no boundaries between them and the cameral deposits can be taken for the connecting rings.

Unfortunately, none of the needed information can be extracted from the longitudinal section of a short fragment of the phragmocone of *Lamellorthoceras vermiculare* Termier et Termier that was provided by Teichert (1961, pl. II, fig. 4) because its interior has been poorly preserved.

The longitudinal sections of the shells of lamellorthoceratids presented by Bandel and Stanley (1989) cannot show the relation between the septal necks and cameral deposits. Thus, one of the best sections of the form from the Emsian of New York that is shown in pl. 4, fig. 20 is tilted at an angle to the longitudinal axis of the conch and failed to pass through the septal foramen in all chambers, except for the adapical chamber. In these chambers the interrupted structures that resemble convex connecting rings are perhaps boundaries between the cameral and ectosiphonal deposits, which have only slightly penetrated into the cavity chamber. At the same time, in the adapical chamber, where the section has passed through the septal foramen, the siphon on the ventral side is bordered by an interrupted wall, which is flat rather than convex and resembles the internal surface of the ectosiphonal deposits of *Astrovia adorea*. It is by no means improbable that this form belongs to some species of the genus *Esopoceras* Stanley et Teichert, 1976, which was described from these deposits. In the specimen from the Eifelian of Morocco, shown in pl. 4, fig. 26, the segment of the siphon is bordered by an interrupted structure, which is more likely to be remains of ectosiphonal deposits rather than a connecting ring. All the other sections shown in this paper provide no information on the internal structure of the shells. Our materials, which show that the morphology and microstructure of the cameral deposits, as well as of the newly discovered metacameral and ectosiphonal deposits, is different in different genera and families, invalidates the conclusions made by Bandel and Stanley about both the mode of formation of the lamellar cameral deposits and the internal structure of the conch. It is also impossible to share their opinion that the longitudinal fine rugosity of the conch wall results from its demineralization and contraction of its organic component. Recall that such rugosity can be seen on the cast of the fairly well preserved holotype of *Syndikoceras arcticum*, where it occurs at least in the two internal layers of its three-layered wall and, perhaps, in the external layer, which, unfortunately, is enclosed by rock material. Moreover, the assumption of these authors that lamellorthoceratids belong to the endocochlian cephalopods is refuted in our opinion by the close similarity between the internal structure of their conchs and that of ectochochlian cephalopods such as the genus *Flowerina*, which possesses an annulate conch and morphologically simple, non-lamellar cameral deposits.

Plicatoceras nishidai Niko, 1991 was fairly thoroughly illustrated by its author, including a longitudinal medial section of the adapical part of the holotype. However, the internal structure of the conch was misinterpreted by him. This section shows that on the dorsal side the septum and neck are enclosed in the cameral deposits of the two neighboring chambers, thus indicating the absence of connecting rings. On the ventral side, the rough surface of the cameral deposits filling the chamber cavity bears a united thin black longitudinal layer, which apparently consists of metacameral deposits. Niko took this layer for "shivering" connecting rings.

As previously discussed, the pallioceratids studied by Kolebaba belong to at least four different families.

Our study of the available shells, which are frequently heavily worn on the outside but usually well preserved inside, in polished sections and in thin sections with an optical microscope and, especially, with a scanning electron microscope has made it possible to reveal in great detail their internal structure and to understand to some extent certain features of the internal structure of the shells of some other, earlier known forms.

It has been found that all of the six studied species, which belong to different genera and families, have some features of the internal structure in common; namely, the absence of connecting rings, which is proved by the free passage of the episeptal cameral deposits from each chamber through the septal foramen into the previous chamber, by the amalgamation of them with the hyposeptal deposits of the previous chamber, and, especially, by the formation by the soft tissue of the siphon of ectosiphonal deposits, which grew directly into the chamber cavity toward the cameral deposits. The absence of connecting rings indicates, in turn, that the soft cameral tissue, which secreted the cameral deposits, is immediately connected with the tissue of the siphon. The closest connection apparently took place on the ventral side, in the adapical part of the chamber, where the cameral deposits were secreted and gradually reached, in the course of their growth, first the lateral sides and subsequently the dorsal side. The septal necks apparently became less mineralized and, frequently, thinner toward the edge; their edge was occasionally curved outward or inside the neck or, in other cases, was enclosed in the cameral deposits, which obscure its contours. At the same time some other structural features characteristic of each separate form were revealed, thus allowing determination of the rank and taxonomic position of each of these forms in the group under consideration.

Thus, study of the holotype of *Flowerina shimanskyi* from the Wenlock of Podolia with an SEM has shown that its structural features only partially coincide with those of the type species of this genus *F. bucheri* from the Wenlock of North America. In particular, in both species the hyposeptal deposits on the dorsal side are not adjacent to the septum and septal neck within the angle formed by the latter (Pl. 1). This feature is typical of both the holotype *F. bucheri* and the specimen of this species from the Wenlock of Podolia that was recorded earlier (Balashov and Zhuravleva, 1962, pl. 14, fig. 3). Probably, this feature is characteristic of the genus *Flowerina* as a whole, as well as the massive hyposeptal cameral deposits, the volume of which is frequently much greater than that of the episeptal deposits. In the species under consideration, the septal necks have an outwardly curved edge, at least on the dorsal side. Unfortunately, the shape of the edge in the necks of the type species is unknown. On the other hand, *F. shimanskyi* has, in addition to the cameral deposits, metacameral deposits, which have not been revealed in the type species. The cameral and metacameral deposits have the same prismatic microstructure (Pls. 1, 2).

In *Ostreioceras riphaeum* (Zhuravleva, 1978) from the Eifelian of the Central Urals, the septal necks are long, become gradually thinner and increasingly less mineralized marginally, frequently curved outward or inward, perhaps, under the pressure of the approaching cameral tissue (Pl. 5, figs. 1b, 1d). The cameral deposits in this species change their configuration in the course of growth: the mural deposits first differentiate from the continuous mural-episeptal deposits in the posterior part of the chamber and subsequently rapidly grow toward the siphon. The mural and episeptal deposits leave a free space between them. This space and the cavity left by the soft siphon are filled with sediment. This opening filled with rock material is usually clearly seen in longitudinal sections of the phragmocones, and their folded structure is better seen in the underlying episeptal deposits. The hyposeptal deposits of this form are in contact with the mural deposits rather than with the episeptal deposits, as is usually the case in other similar cephalopods. The cameral deposits of *O. riphaeum* consist of thin layers separated by a "shivering" boundary and arranged in fine rounded folds separated by acute-angled interspaces (Pl. 3, figs. 1, 3–6; Pl. 4; Pl. 5, fig. 2). In an SEM they show a reticulate-porous microstructure (Pl. 6). Metacameral deposits are absent. The shape of the cameral deposits in *O. riphaeum* is virtually the same as that in *Leurocycloceras* *superplenum* Collins, 1969 from the Eifelian of northern Canada. Notwithstanding the fact that the microstructure of the cameral deposits in this species is unknown, there is no question that it belongs to the genus *Ostreioceras*. Thus, the Eifelian genus *Ostreioceras* differs from the Wenlock genus *Flowerina* in the more complex folded cameral deposits with a reticulate-porous microstructure and distinctive morphology and the absence of metacameral deposits. These differences have served as a basis for establishing a separate family, Ostreioceratidae. It is by no means improbable that this genus includes the Silurian species described by Barrande (1866) as *Orthoceras thomsoni*, which resembles the former in the morphology of cameral deposits and in the absence of metacameral deposits.

The conch of *Astrovia adorea* with a well-preserved interior is the most interesting and informative of all forms under study. This conch has shown more clearly than all the other specimens a newly discovered feature of the internal structure of pallioceratids, ectosiphonal deposits, i.e., deposits that were secreted outward by the epithelium of the siphuncular cord in the absence of connecting rings into the chamber cavity toward the cameral deposits. Both ectosiphonal and cameral deposits are composed of distinctive tubular structures, virgulae, which serve as the central axis for other smaller articulated tubular structures that radiate from it in all directions at an oblique angle (Pl. 7, figs. 1b, 1d–1f; Pl. 9, figs. 1f, 1g; Pl. 10, figs. 1a, 1c; Pl. 11; Pl. 12, fig. 1a). The identical microstructure of the ectosiphonal and cameral deposits indicates that the cameral deposits were also secreted by the epithelium that lined the wall of the chamber and septa. At a later growth stage of the ectosiphonal deposits, the epithelium of the siphon secreted, on the surface formed by the bases of the virgulae, thin black longitudinal layers of ectosiphonal deposits, which were apparently slightly mineralized (Pl. 7, figs. 1d; Pls. 8, 10). Penetration of the ectosiphonal deposits deep into the chamber cavity suggests the absence of metacameral deposits, and their position with respect to the chamber cavity and cameral deposits indicates that they were secreted considerably later than the cameral deposits. Thus, the existence of ectosiphonal deposits is the most conclusive evidence of the absence of both connecting rings and any hard shells in the siphuncular cord and metacameral deposits. No form other than this conch has episeptal cameral deposits that pass through the septal foramen into the previous chamber as two thick layers. The first layer tuns round the septal neck and merges with the hyposeptal deposits of the previous chamber. The second layer turns round the first layer and hyposeptal deposits and comes in contact with the second layer of the episeptal deposits of the previous chamber (Pl. 7, fig. 1a; Pl. 8; fig. 3).

The wall of *A. adorea*, which has been only partially preserved, show two layers: a thin fairly elastic (apparently organic) internal layer and a thick prismatic external layer, which has been heavily worn and, perhaps, wrinkled at the surface. The assumption that the external layer belongs to this conch is open to question because of the lack of analogues in the known pallioceratids. The more so as one of the internal layers of the wall of *Gorgonoceras visendum*, which has cameral deposits consisting of virgulae identical to those of *A. adorea* (Pl. 15, fig. 1b), bears ornamentation of slender longitudinal ridges (Pl. 14, fig. 1a), which are characteristic of at least two internal layers of the three-layered wall of the conch of *Syndikoceras arcticum* (Pl. 16, figs. 1a, 1c).

As previously mentioned, in addition to the type species, the genus *Astrovia* includes the form depicted by Mutvei (1956, pl. I, fig. 4) from the Eifelian of northern Africa. This form is described here as a separate species, *A. marhoumensis* (Pl. 13, fig. 1).

We believe that on the basis of such specific features of the internal structure of the conch of *Astrovia* and *Gorgonoceras* as the quite distinctive microstructure of the cameral deposits (virgulae), the development of ectosiphonal deposits, and the absence of metacameral deposits these genera should be placed into a new family, Astroviidae, because these features clearly distinguish these genera from all know pallioceratids.

The holotype of *Syndikoceras arcticum* is the only one of the specimens under study that preserved a small fragment of the three-layered wall of the conch. The two internal layers bear distinct longitudinal ornamentation of low folds, which can be seen on the cast. As previously discussed, the presence of such ornamentation on the intact surfaces of the conch and cast refutes the assumption made by Bandel and Stanley (1989) that the longitudinal rugosity results from decalcification of the conch wall and contraction of its organic component (Pl. 16, figs. 1a, 1c; Pl. 18). In *S. arcticum* the cameral deposits appear on the surface of the cast as extremely thin convergent and divergent longitudinal plates, which are aligned at an oblique angle to the axis of the conch and ornamentation (Pl. 18, fig. 1b).

In this species the cameral deposits consist of minute prismatic crystals that are arranged in complex structures of at least two orders; these structures are so complicated that one may get only a very approximate idea of them. The small prismatic crystals are arranged in elongated structures (rays), which radiate from some central axis in all directions, frequently at an oblique angle, like needle-leaves around a shoot of spruce. These complex rays are in turn arranged in a similar manner, thus forming larger elongated structures (branches), which may be arranged in rows that resemble plates. The branches or their rows form variously shaped folds, which in the plane of the section are seen at different angles and, thus, look like quite complex combinations. The structure of the cameral and metacameral deposits is identical. Since both kinds of deposits show no clearly defined layers, it is hard to tell whether these deposits were secreted inside the cameral tissue or on the surface of the cameral tissue.

The ectosiphonal deposits, which essentially differ morphologically from those of *A. adorea*, are adjacent to the metacameral deposits at the level of the two adapical chambers; at the level of the other chambers, they are separated from the metacameral deposits by an interspace filled with rock material (Pl. 17). Unfortunately, the microstructure of these deposits remains to be investigated. The fuzzy edge of the septal necks, which are enclosed in the cameral deposits, and the presence of metacameral and, especially, ectosiphonal deposits leave no doubt of the absence of connecting rings and the existence of a direct connection between the cameral and siphonal tissues.

In addition to the type species, the genus *Syndikoceras* includes the form depicted by Mutvei (1956, pl. I, figs. 1–3) from the Eifelian of northern Africa. The morphology of the cameral deposits of these three shells is closely related to that of the type species. On the ventral side the surface of the cameral deposits is covered by a dark layer with a crenulated surface, which most likely represents metacameral deposits. The other structures that in the section of the siphon look like thin oblique plates arranged in rows against the cavities of several chambers and, occasionally, adjoin the metacameral deposits represent, in our opinion, ectosiphonal deposits. They show a striking similarity to the ectosiphonal deposits of the aforementioned *Astrovia marhoumensis*, which was depicted by Mutvei in the same plate (here Pl. 33, fig. 1). A new species, *S. mutveii*, is described here on the basis of these shells, with the conch depicted in Fig. 1 designated as the holotype. Thus, the genus *Syndikoceras* sharply differs from the other genera with the well-known internal structure of the conch in having cameral deposits with a complex prismatic microstructure and in the presence of both metacameral and ectosiphonal deposits. However, we cannot rule out the possibility that detailed study of the topotypes of *Lamellorthoceras vermiculare* may show that the genus *Syndikoceras* is a synonym of the latter. After some hesitation, we have decided to place this genus into the family Lamellorthoceratidae, notwithstanding the fact that the internal structure of the shells of the other genera of this family remains unclear.

A new species from the Emsian of the Balkhash area, the morphology of which most closely resembles that of the early Lochkovian *Plicatoceras* Niko, 1991, is described here as *P. bublichenkoi*. From the type species *P. nishidai*, it differs in the relatively short chambers, longer septal necks, and differently shaped cameral deposits. The cameral deposits of the type species represent extremely complex structures, which in the cross section are similar to those of our species and in the longitudinal medial section on the ventral side look like vermiform structures that fill the chamber cavity and form differently shaped short fenestrules and folds, which are directed at different angles to the longitudinal axis of the conch (Niko, 1991, text-fig. 1, text-figs. 4, 6). The structure and microstructure of the cameral and metacameral deposits of the type species still remain to be studied. The cameral deposits of *P. bublichenkoi* consist of plates-folds, which combine to form intricately shaped structures-plates, the exact shape of which is virtually impossible to determine. The microstructure of both the cameral and metacameral deposits (the latter form longitudinal layers on the surface of the former) is a spongy matrix with porous walls (Pl. 31; Pl. 32, figs. 1a, 1b; Pl. 33). All these characters clearly show that the genus *Plicatoceras* sharply differs from all pallioceratid genera with known internal structures; hence, it is classified as a separate family, Plicatoceratidae.

Thus, the analysis of the literature data and available fossil material using scanning electron and optical microscopes shows that among the other cephalopods the order Pallioceratida Marek represents a separate, taxonomically diverse group, which existed at least from the Wenlock through the Eifelian and had a wide geographic distribution. The characteristic feature of these cephalopods is the soft cameral tissue that penetrates into the siphon cavity and secretes there calcareous cameral deposits and the associated disintegration of thin (probably organic) connecting rings. Convincing evidence of this feature is the following structural features of the shells of these cephalopods.

(1) The episeptal cameral deposits pass from each chamber through the septal foramen into the previous chamber to merge with the hyposeptal deposits of the previous chamber; in some forms the slightly mineralized edges of the necks were often curved outward or inward from the neck, and in other forms they were obscured by the cameral deposits.

(2) The presence of a continuous longitudinal layer of metacameral deposits in the cavity of the siphon on the surface of the cameral deposits, which filled the chambers on the ventral side. The metacameral deposits were secreted by the cameral tissue, which advanced from the chambers to merge in a single longitudinal layer. Both cameral and metacameral deposits consist of the same structural elements; however, in the latter the elements are oriented at right or, more rarely, oblique angles to the surface of the cameral deposits.

(3) The formation (in many taxa) of ectosiphonal deposits that were secreted by the soft tissue of the siphon in the absence of connecting rings directly into the chamber cavity toward the cameral deposits. The secretion of the ectosiphonal deposits lags somewhat behind that of the cameral and metacameral deposits.

(4) The microstructure of the ectosiphonal deposits is identical to that of the cameral deposits, thus showing the identity of the cameral and siphonal tissues.

The order Pallioceratida includes 5 families, 15 genera, and 33 species. Of these taxa, four families, three genera, and five species are described for the first time (see SYSTEMATIC PALEONTOLOGY). On the basis of the foregoing discussion, we propose the following classification.

Phylum Mollusca

Class Cephalopoda

Superorder Astrovioidea Zhuravleva et Doguzhaeva, superordo nov.

Order Lituitida Starobogatov, 1983

Family Lituitidae Phillips, 1848

Genus *Rhynchorthoceras* Remele, 1881

Genus *Tyrioceras* Strand, 1934

Genus *Holmiceras* Hyatt, 1894

Genus *Lituites* Bertrand, 1763

Genus *Ancistroceras* Boll, 1857

Genus *Cyclolituites* Remele, 1886

Genus *Angelinoceras* Hyatt, 1894

Genus *Trilacinoceras* Sweet, 1958

Family Sinoceratidae Shimizu et Obata, 1935

Genus *Sinoceras* Shimizu et Obata, 1935

Order Pallioceratida Marek, 1998

Family Flowerinidae fam. nov.

Genus *Flowerina* Zhuravleva et Kisselev, 2001

F. bucheri (Flower, 1941)

F. brucensis (Williams, 1919)

F. shimanskyi Zhuravleva et Kisselev, 2001

F.? cf. *niagarensis* (Foerste, 1928)

F.? *etheridgii* (Blake, 1882)

F.? *whitcliffensis* (Holland, 1965)

Genus *Murchisoniceras* Babin, 1966

M. murchisoni (Barrande, 1868)

M.? sp.

Genus *Mariaceras* Kolebaba, 1974

M. pragense Kolebaba, 1974

Family Ostreioceratidae fam. nov.

Genus *Ostreioceras* gen. nov.

O. riphaeum (Zhuravleva, 1978)

O. superplenum (Collins, 1969)

O.? *thomsoni* (Barrande, 1866).

? "*Plagiostomoceras pleurotomum*" Kolebaba, 1999

Family Astroviidae fam. nov.

Genus *Astrovia* gen. nov.

A. adorea sp. nov.

A. marhoumensis sp. nov.

A. sp.

? "*Protobactrites styloideus*" Kolebaba, 1999

? "*Nucleoceras hollandi*" Kolebaba, 1999

Genus *Gorgonoceras* Zhuravleva, 1961

G. visendum Zhuravleva, 1961

Family Lamellorthoceratidae Teichert, 1961

Genus *Arthrophyllum* Beyrich, 1850

A. crassum (Roemer, 1843)

A. kahlebergense (Dahmer, 1939)

A.? *planiseptatum* (H. et F. Sandberger, 1850–1856)

A.? *undatolineatum* (H. et F. Sandberger, 1850–1856)

Genus *Lamellorthoceras* G. et H. Termier, 1950

L. vermiculare G. et H. Termier, 1950

L. gracile G. et H. Termier, 1950

Genus *Coralloceras* Zhuravleva, 1962

C. coralliforme (Le Maitre, 1950)

Genus *Esopoceras* Stanley et Teichert, 1976

E. sinuosum Stanley et Teichert, 1976

Genus *Syndikoceras* gen. nov.

S. arcticum sp. nov.

S. mutveii sp. nov.

Family Plicatoceratidae fam. nov.

Genus *Plicatoceras* Niko, 1991

P. nishidai Niko, 1991

P. bublichenkoi sp. nov.

? "*Nucleoceras obelus*" Kolebaba, 1999

? "*N.*" sp.

ORIGIN OF PALLIOCERATIDS

The results of our detailed study of the literature and fossil material show that among the ectochochlian (predominantly longicone) cephalopods there was a fairly large, taxonomically diverse, and independent branch of a high rank, which was widely distributed both stratigraphically and geographically and sharply different from all of them in the internal structure of the conch. The characteristic feature of this branch is that during the life of the animal the soft cameral tissue penetrated into the siphon cavity, destroyed the connecting rings, and secreted there calcareous deposits. In the early representatives of the branch, the cameral tissue passed through the siphon, thus either perforating or completely destroying the connecting ring and spreading over the internal surface of the remains of the connecting rings. In the later representatives, the cameral soft tissue passed through the septal neck, fused with the soft tissue of the previous chamber, and destroyed the two neighboring connecting rings: adoral and adapical. No traces of connecting rings have been revealed in the part of the phragmocone that experienced the penetration of the cameral tissue into the septal foramen and its further spreading in the space that was originally occupied by the siphon. The existence of such a branch was first proposed by Dzik (1984), who advanced the hypothesis that all known Silurian and Devonian genera with cameral deposits passing through the septal foramen from chamber to chamber originate from the Early–Middle Ordovician genus *Rhynchorthoceras* Remele, 1881 from the family Lituitidae Phillips, 1848.

In this genus and in many other lituitid genera, their connecting rings were prone to partial disintegration during the life of the animal, thus facilitating the spreading of the soft cameral tissue into the siphon. The family Lituitidae comprises genera in which the shapes of the conch vary from those with a cyrtoconic, only slightly arcuate adapical part (genus *Rhynchorthoceras*) to those with a tightly coiled apical part and short, straight adoral part (genus *Cyclolituites*). The siphon changed its initial ventral position for a nearly central position, which was only slightly displaced ventrally or dorsally. The septal necks are orthochoanitic and fairly long. The connecting rings are either thin or thicker, two-layered, and perforated or resorbing so that well-developed cameral deposits passed through these openings into the siphon and spread over the internal surface of the connecting rings, thus forming a sort of endosiphonal deposits (Sweet, 1958, p. 116, 135, pl. 20, fig. 3, text-fig. 15B; Flower, 1975, pl. 2, figs. 5, 6; pl. 3, figs. 5, 6; Dzik, 1984, pl. 39, figs. 1, 3; pl. 40, figs. 1, 2; text-fig. 50). The episeptal and hyposeptal cameral deposits in some species of such genera of this family as *Rhynchorthoceras*, *Ancistroceras*, and *Lituites* (Holm, 1885; Remele, 1890; Schindewolf, 1942; Sweet, 1958) have surfaces with closely spaced plications, which radiate from the center to the periphery, and form a crenulated "pseudoseptum" when these surfaces are in contact. Remele (1890) reported that on the surfaces of the episeptal deposits in *Lituites perfectus* and *L. lasaulxii* there are marks that resemble those in *Leurocycloceras* cf. *niagarense* Foerste, 1928, which were described and treated by Flower (1941) as marks of blood vessels of the cameral mantle. The epi- and hyposeptal cameral deposits of lituitids continue uninterruptedly from the ventral side to the lateral sides of the chamber; on the dorsal side, they leave a gap filled with vertically located plates, which are known as *vertical lamellae*. As in the other cephalopods, the cameral deposits of lituitids were first secreted in the apical part of the conch and subsequently advanced adorally.

The opinions of researchers on the origin of lituitids differ. Most of them believe that this group is a descendant of coiled forms: barrandeocerids or tarphycerids (Hyatt, 1894; Flower, in Flower and Kummel 1950; Sweet, 1958; Furnish, Glenister in Teichert *et al.*, 1964; Flower, 1975). Flower (1975) advances the hypothesis that the lituitids originated from the family Trocholitidae of the order Tarphycerida. By contrast, Schindewolf (1942) believed that lituitids are descendants of some orthoceroid cephalopods. The fact is that the conchs of the most ancient lituitids, which are attributable to the genus *Holmiceras* Hyatt, 1894 and have previously been known from the uppermost Arenig, have a coiled apical part. However, Dzik (1984) reported that he discovered a still more ancient representative of this family in which only the apical part of the conch is slightly arcuate. He described it as *Rhynchorthoceras* aff. *beyrichi* (Remele, 1880) from an erratic boulder of red limestone located in the *Paraistodus originalis* Zone (Volkhov BIIβ). From the later representatives of this genus, it differs in the relatively short septal necks and simpler edge of the aperture. Assuming that the ancestors of lituitids are among straight orthoceroid cephalopods, this author separated four families (Sinoceratidae Shimizu et Obata, 1935; Sphooceratidae Flower, 1962; Lituitidae Phillips, 1848; and Ophioceratidae Hyatt, 1894) in a new suborder, Lituitina, of the order Orthocerida. In his opinion the family Sinoceratidae comprises the following genera: *Rhynchorthoceras* Remele, 1881; *Sinoceras* Shimizu et Obata, 1935; *Murchisoniceras* Babin, 1966; *Arthrophyllum* Beyrich, 1850; *Lamellorthoceras* Termier et Termier, 1950; *Gorgonoceras* Zhuravleva, 1961; *Coralloceras* Zhuravleva, 1962; and *Esopoceras* Stanley et Teichert, 1976. In his phylogenetic scheme, he considered the genus *Rhynchorthoceras*, in which only the apical part of the conch is slightly arcuate, to be ancestral to the family. In his opinion, this genus is a direct descendant of orthoceratids, and all the other genera of sinoceratids are descendants of this genus or its closest relatives. He prefers the first assumption, which is supported by the elongation of the septal necks in those species that followed *R.* aff. *beyrichi* but preceded the genus *Sinoceras*. The latter may be considered to be a direct descendant of the genus *Rhynchorthoceras*, which became extinct in the Llandeilo. It only differs from *Rhynchorthoceras* in the straight conch with a central siphon and irregular growth lines on its surface. The stratigraphic position of the genus *Sinoceras* is uncertain; however, Dzik believes that the time of its appearance may be estimated on the basis of some specimens of *Sinoceras chinense* (Foord, 1888) that are housed at the University of Wroclaw. These specimens come from deposits of China associated with the limestones of the Baltic Sea area and contain the conodont *Dipsilodus viruensis*, which occurs from the Llandeilo to the Late Ordovician. Subsequently, this author considers the Silurian species "*Orthoceras*" *evanescens* Barrande, 1866, which is separated by a substantial gap in the Late Ordovician from the genus *Sinoceras*, and *Leurocycloceras superplenum* Collins, 1969, which he assigned to the Siegenian, although this species was described by its author from the Eifelian. The Wenlock species *L. brucense* (Williams, 1919) is shown as the nearest side branch but is placed level with the Llandovery.

The genus *Murchisoniceras* Babin, 1966, the type species of which *M. murchisoni* (Barrande, 1866) has cameral deposits similar to those of *Leurocycloceras bucheri*, has a fairly close relationship to the main lineage, which begins with *Sinoceras* and ends with "*O.*" *evanescens*. In the other species, *M. obsolescens*, from the Ludlow of Barrandian region, the internal structure of the conch is unknown and the branch is continued as far as Přídolí by the species "*O.*" *teniale* Barrande, 1866. Dzik believes that the species *Mariaceras pragense* was based on the juvenile part of the conch of some *Murchisoniceras* species. In his scheme this large branch ends with the species *Gorgonoceras* *visendum* from the lower Eifelian of the Central Urals. The genus *Sphooceras* Flower, 1962 was separated by its author into a separate family; however, Dzik places it into the family Sinoceratidae since he believes that its type species shows no evidence of decollation of the orthoceroid part of the conch and the thick, long apical chamber is the first chamber of the phragmocone. The structure that has been taken for a septum of truncation represents cameral deposits that consist of slender radial plates joined by transverse anastomoses and that resemble the cameral deposits of *Arthrophyllum* in structure. He assumes that if a conch is such that the width of its thick apical part is greater than that of the aperture of the adult conch, it may have a larva that developed outside of the egg capsule in the form of a little spiral cap. On the basis of similarity in the structure of the cameral deposits, this author believes that phylogenetically the poorly studied Devonian genera are related to the genera *Murchisoniceras* and *Sphooceras*. At the same time he emphasizes that the structure of the cameral deposits may be of no diagnostic value. Thus, our investigations refute this opinion. As previously mentioned, Marek (1998) designated a new order, Pallioceratida, in which he differentiates two groups of cephalopods that have cameral mantles: the families Leurocycloceratidae Sweet, 1964 and Lamellorthoceratidae Teichert, 1961. In the first family, the cameral mantles are shaped like bags; in the second family, they consists of elongated plates that are arranged radially or almost radially. In his opinion, the Pallioceratids existed from the Early Ordovician to the Early Carboniferous. It is not clear which Ordovician cephalopods are meant. Apparently, it is the Lituitida that he has in mind on the basis of the literature. This ordinal name is derived by this author from Latin *pallium* (mantle), thus indicating the main structural feature of the conch of these cephalopods, i.e., the primordial presence of the mantle in its chambers. In our opinion this name is an unfortunate choice since, according to our investigations, soft tissue existed in the chambers of other cephalopods, in particular, pseudorthoceratids and actinocerids, the siphon wall of which retained the connecting rings (Zhuravleva and Doguzhaeva, 1999). Moreover, it is widely believed that the cameral deposits of all ectochochlian cephalopods could only be secreted by the mantle that lined the interior surface of the chamber walls (Teichert, 1935, 1964; Flower, 1939, 1955, 1964; Starobogatov, 1973, 1974, 1983a, 1983b).

Since we have no fossil material on lituitids, we failed to study them. However, judging from the available literature on the structure of the conch in this group of cephalopods, we are inclined to agree with Dzik that they are the most probable ancestors of pallioceratids. We believe that lituitids and their descendants, pallioceratids, constitute a single branch, the rank of which corresponds to such taxa as Orthoceratoidea, Actinoceratoidea, Nautiloidea, etc.; hence, it makes sense to create a new superorder, Astrovioidea. We are inclined to believe that this superorder belongs to the subclass Orthoceroda. In order to substantiate this new superorder, however, it is necessary to find and examine using an electron microscope new well-preserved fossil material.

STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCE OF PALLIOCERATIDS

Pallioceratids existed virtually worldwide in the seas at least from the Early Silurian (Wenlock) to the Middle Devonian (Eifelian). Their conchs are known from numerous localities in Europe, Africa, Asia, and North America. Pallioceratids have been discovered in Silurian deposits of Europe: in the Wenlock and Ludlow of the Czech Republic, in the Wenlock of Ukraine, in the Ludlow of Great Britain, and in the Přídolí of Poland. In the Devonian deposits, their remains have been discovered in northern Africa (the Pragian and Eifelian of Algeria and Morocco); in Europe (the Emsian and Eifelian of Germany, the Eifelian of France, and the Emsian of Novaya Zemlya); in Asia (the Eifelian of Turkey, the eastern slope of the Central Urals, and the Gorno-Altai; the Pragian of the Kuznetsk Basin; the Emsian of Kazakhstan; and in the lower Lochkovian of Central Japan); and in North America (the Emsian of New York and Nevada and the Eifelian of northern Canada). Below, these data are listed in Tables 1 and 2.

SYSTEMATIC PALEONTOLOGY

CLASS CEPHALOPODA

Superorder Astrovioidea Zhuravleva et Doguzhaeva, superordo nov.

Diagnosis. Conch orthoceraconic, slightly curved cyrtoceraconic, and lituiticonic with narrow siphon. Soft cameral tissue destroyed connecting rings, penetrated into cavity of siphon, and secreted there calcareous deposits. In early (Ordovician) representatives, connecting rings experienced partial destruction, and calcareous deposits secreted in siphon spread along internal surface of surviving portion of siphon wall. In later (Silurian and Devonian) astrovioids, cameral tissue entered cavity of siphon through septal neck and secreted there calcareous deposits, squeezing soft siphon and completely destroying connecting rings. Cameral deposits increased in volume and, in absence of connecting rings, pressed soft siphon along its entire length to form in some taxa continuous longitudinal layer of metacameral deposits. In some taxa soft siphon secreted into cavity of chamber ectosiphonal calcareous deposits.

Composition. Orders Lituitida Starobogatov, 1983 and Pallioceratida Marek, 1998

Comparison. It differs from the other superorders in the spreading of the soft cameral tissue into the siphon cavity and in the associated destruction of the connecting rings and secretion there of calcareous cameral deposits.

Table 1. Stratigraphic occurrence of pallioceratids

Species	Silurian				Devonian				
	Lower		Upper		Lower			Middle	
	Lly	Wen	Lud	Prg	Loch	Prag	EMs	Eif	Ziv
Flowerina bucheri		+							
Flowerina brucensis		+							
Flowerina niagarensis		+							
Flowerina shimanskyi		+							
Flowerina? cf. *niagarensis*		+							
Flowerina? *etheridgii*		+							
Flowerina? *whitcliffensis*			+						
Murchisoniceras murchisoni			+						
Murchisoniceras ? sp.				+					
Mariacers pragense			+						
"*Protobactrites styloideus*"			+						
Ostreioceras? *thomsoni*			+						
"*Plagiostomoceras pleurotomum*"			+						
"*Nucleoceras obelus*"			+						
"*Nucleoceras hollandi*"			+						
Astrovia sp.			+						
Plicatoceras nishidai					+				
Astrovia adorea						+			
Lamellorthoceras gracile						+			
Arthrophyllum crassum							+	+	
Arthrophyllum kahlebergense							+		
Arthrophyllum? *Planiseptatum*							+		
Arthrophyllum? *undatolineatum*							+		
Esopoceras sinuosum							+		
Syndikoceras arcticum							+		
Coralloceras coralliforme							+	+	
Plicatoceras bublichenkoi							+		
Astrovia marhoumensis								+	
Gorgonoceras visendum								+	
Ostreioceras riphaeum								+	
Ostreioceras superplenum								+	
Lamellorthoceras vermiculare								+	
Syndikoceras mutveii								+	

O c c u r r e n c e. Lower Ordovician, Arenig–Middle Devonian, Eifelian; Europe, Asia, Africa, and North America.

Order Lituitida Starobogatov, 1983

Lituitiformes: Starobogatov, 1983, p. 5

D i a g n o s i s. Conch either lituiticonic, from nearly straight, only slightly curved in apical part to tightly coiled in apical part and straightened in adoral part, or orthoceraconic. Siphon nearly central. Septal necks orthochoanitic and long. Connecting rings resorbing or perforated. Cameral deposits enter siphon through partly or completely destroyed connecting rings and spread along internal surface of surviving portion of siphon wall.

C o m p o s i t i o n. Family Lituitidae Phillips, 1848; Sinoceratidae Shimizu et Obata, 1935.

C o m p a r i s o n. See below in Comparison section for Pallioceratida.

Table 2. Geographic occurrence of pallioceratids

Species	Europe							Northern Africa		Asia						North America		
	France	Germany	Czech Republic	Ukraine	Poland	England	Novaya Zemlya	Algeria	Morocco	Turkey	Central Urals	Kuznetsk Basin	Gorno-Altai	Kazakhstan	Japan	New York	Nevada	Northern Canada
Flowerina bucheri				+												+		
Flowerina brucensis																+		
Flowerina niagarensis																+		
Flowerina shimanskyi							+											
Flowerina? cf. *niagarensis*																+		
Flowerina? *etheridgii*						+												
Flowerina? *whitcliffensis*						+												
Murchisoniceras murchisoni	+		+															
Murcisoniceras? sp.					+													
Mariaceras pragense			+															
"*Protobactrites styloideus*"			+															
"*Plagiostomoceras pleurotomum*"			+															
"*Nucleoceras obelus*"			+															
"*Nucleoceras hollandi*"			+															
Ostreioceras riphaeum											+		+					
Ostreioceras superplenum																		+
Ostreioceras? *thomsoni*						+												
Astrovia adorea												+						
Astrovia marhoumensis								+										
Astrovia sp.			+															
Gorgonoceras visendum											+							
Arthrophyllum crassum		+																
Arthrophyllum kahlebergense		+																
Arthrophyllum? *planiseptatum*		+																
Arthrophyllum? *undatolineatum*		+							+									
Lamellorthoceras vermiculare	+	+							+									
Lamellorthoceras gracile								+	+									
Coralloceras coralliforme								+	+									
Esopoceras sinuosum																+	+	
Syndikoceras arcticum							+											
Syndikoceras mutveii								+										
Plicatoceras nishidai															+			
Plicatoceras bublichenkoi														+				

R e m a r k s. Dzik (1984) considers pallioceratids to be close to the family Sphooceratidae Flower, 1962, which comprises taxa in which the conch experienced, in the opinion of many researchers, recurring decollation (see Gnoli and Kisselev, 1994). Those parts of the conch that survived the truncation are relatively short and thick and have a central siphon with short suborthochoanitic necks and without connecting rings and endosiphonal deposits. The cameral deposits resemble those with ornamentation consisting of folds or radial striations and have been found only in the form of a thin layer on the wall of the chamber that was the nearest to the truncated chambers in the type species of the genus *Sphooceras*, *S. truncatum* (Barrande, 1860). The phylogenetic relationships between this family and the group under study remain unclear.

Occurrence. Lower Ordovician, Arenig–Upper Ordovician, Ashgill; Balto-Scandia, North America, China.

Family Lituitidae Phillips, 1848

Diagnosis. Conch only slightly curved or tightly coiled in apical part of varying size and straightened in adoral part. Initially siphon ventral and, shortly after, nearly central. Septal necks orthochoanitic and long. Connecting rings are two-layered or thin, one-layered, and partly or completely destroyed. Cameral deposits enter siphon and spread along internal surface of surviving parts of connecting rings.

Composition. Genera: *Rhynchorthoceras* Remele, 1881; *Holmiceras* Hyatt, 1894; *Ancistrocers* Boll, 1857; *Lituites* Bertrand, 1763; *Angelinoceras* Hyatt, 1894; *Cyclolituies* Remele, 1866; *Trilacinoceras* Sweet, 1958; and *Tyrioceras* Strand, 1934.

Occurrence. Lower Ordovician, Arenig–Middle Ordovician, Caradoc; Baltoscandia, North America, Poland (in erratic boulders).

Family Sinoceratidae Shimizu et Obata, 1935

Diagnosis. Conch straight and longiconic. Siphon central. Septal necks orthochoanitic and long. Connecting rings unknown. Episeptal cameral deposits enter siphon through septal foramen and fuse with hyposeptal deposits of previous chamber.

Composition. Genus *Sinoceras* Shimizu et Obata, 1935.

Comparison. It differs from the other families of the order in the straight, rapidly expanding conch with an initially central siphon.

Occurrence. Middle Ordovician; China.

Order Pallioceratida Marek, 1998

Diagnosis. Conch longiconic, orthoceraconic, or slightly curved cyrtoceraconic. Siphon usually displaced ventrally from center. Septal necks ortho- or suborthochoanitic. Connecting rings (if any) thin, probably organic, prone to complete destruction in ontogeny by cameral deposits that moved into cavity of siphon. In addition to cameral deposits, many taxa contain metacameral or ectosiphonal deposits, or both. Morphology and microstructure of deposits vary from taxon to taxon.

Composition. Families Flowerinidae fam. nov.; Ostreioceratidae fam. nov.; Astroviidae fam. nov.; Lamellorthoceratidae Teichert, 1961; and Plicatoceratidae fam. nov.

Comparison. It differs from Lituitida in having connecting rings that were completely destroyed by the movement of the soft cameral tissue into the siphonal cavity and in the formation in many taxa of metacameral and ectosiphonal deposits.

Occurrence. Lower Silurian, Wenlock–Middle Devonian, Eifelian; Japan, Kazakhstan (Balkhash area), Russia (the Central Urals, Kuznetsk Basin, Gorno-Altai, and Novaya Zemlya), Ukraine, Turkey, western and central Europe (Germany, France, Great Britain, Czech Republic, and Poland), northern Africa (Algeria and Morocco), North America (the United States and Canada).

Family Flowerinidae Zhuravleva, fam. nov.

Diagnosis. Conch orthoceraconic, laterally compressed in cross section, and either smooth or with transverse annulate ornamentation. Siphon eccentric or submarginal. Metacameral deposits present. Cameral and metacameral deposits have prismatic microstructure, in which elongated prismatic structures are aligned perpendicular to surface of deposits.

Composition. Genera *Flowerina* Zhuravleva et Kisselev, 2001; *Murchisoniceras* Babin, 1966; and *Mariaceras* Kolebaba, 1974.

Comparison. See respective Comparison sections for comparison with other families.

Occurrence. Lower Silurian, Wenlock of North America, England, and Ukraine; Upper Silurian, Ludlow of the Czech Republic, France, England; and Přídolí of Poland.

Genus *Flowerina* Zhuravleva et Kisselev, 2001

Flowerina: Zhuravleva and Kisselev, 2001, p. 24.

Type species. *Leurocycloceras bucheri* Flower, 1941; Lower Silurian, Wenlock; North America, Indiana.

Diagnosis. Conch slightly compressed laterally in cross section, with ornamentation of low oblique rings. Siphon displaced ventrally from center. Hyposeptal deposits usually more massive than episeptal deposits and not adjoining septum and neck on dorsal side in angle formed by the latter. Some species contain metacameral deposits.

Species composition. *Flowerina bucheri* (Flower, 1941) (Pl. 14, fig. 4); *F. brucensis* (Williams, 1919); *F. niagarensis* (Hall); *F. shimanskyi* Zhuravleva et Kisselev, 2001; *F.*? cf. *niagarensis* (Hall) (Flower, 1941); *F.*? *etheridgii* (Blake, 1882); and *F.*? *whitcliffensis* (Holland, 1965).

Comparison. It differs from *Murchisoniceras* and *Mariaceras* in the eccentric rather than submarginal position of the siphon in the conch.

Occurrence. Lower Silurian; North America, Ukraine, Great Britain.

***Flowerina shimanskyi* Zhuravleva et Kisselev, 2001**

Plates 1 and 2

Leurocycloceras bucheri: Kisselev *et al.*, 1987, p. 48, pl. 12, fig. 4.

Flowerina shimanskyi: Zhuravleva and Kisselev, 2001, p. 26, pl. III, fig. 2

Holotype. PIN, no. 1793/1801; Ukraine, Podolia, Dniester River basin, left bank of the Studenitsa River, 400 m downstream of the downstream end of the village of Studenitsa; Lower Silurian, Wenlock, Furmanovo Formation, Restevskaya Subformation.

Description (Fig. 2). The conch is represented by the holotype, a fragment of the cast of the adapical part of an orthoceraconic conch, which is laterally compressed in cross section with a ratio of diameters 1.03. This fragment is 30 mm long and consists of four chambers, of which only two central chambers preserved their full length; on the ventral side approximately 3 mm of the specimen are cut away. The surface of the cast is worn and has preserved no ornamentation.

The chambers are of medium length: one-half the diameter of the phragmocone.

The suture is inclined ventrally and apparently forms a shallow dorsal lobe and a deeper ventral lobe.

The septa are concave for a distance of one-half the chamber length and inclined to the ventral side; with their maximum concavity located near the siphon. The adapical septum alone preserved its full thickness (Pl. 1, fig. 1d).

The diameter of the siphon in the septal foramen is 0.15 the diameter of the phragmocone. The siphon is laterally compressed and separated from the ventral wall of the chamber by a distance of approximately 0.25–0.26 the diameter. The septal necks are about one-third the chamber length and slightly concave-convex; on the dorsal side they are deflected from the septum at a right angle and have a thick outwardly curved edge; on the ventral side they are deflected from the septum at an obtuse angle and partially disintegrated; perhaps, they also possessed an outwardly curved edge (Pl. 1, figs. 1a–1c; Pl. 2, fig. 1a).

Connecting rings are absent.

The cameral deposits are epi- and hyposeptal; the latter are especially well developed on the ventral side (Pl. 2, figs. 1a, 1b).

The metacameral deposits are arranged in longitudinal layers over the cameral deposits along the entire fragment and, like the cameral deposits, have prismatic microstructure, in which elongated crystalline structures are aligned perpendicular to the depositional surface. The cross section made level with the end of the septal neck shows that all layers of the cameral deposits that line circularly the chamber walls on the inside converge to the center of the ventral side from the right and left and, being tightly compressed to each other, make a sharp turn to the siphon. The hyposeptal deposits surround the septal neck, and the episeptal deposits of the next chamber are enclosed in the neck (Fig. 1b).

Comparison. It differs from the type species in having well-developed metacameral deposits. Comparison with other species of this genus is impossible because of lack of information on them.

Material. The holotype, which was collected by G.N. Kisselev 1963.

Family Ostreioceratidae Zhuravleva, fam. nov.

Diagnosis. Conch orthoceraconic, circular in cross section, with smooth surface. Siphon eccentric. Cameral deposits composed of thin rugulose layers, arranged in transverse folds. Microstructure of cameral deposits spongy-porous (for a detailed discussion see above). Metacameral and ectosiphonal deposits are absent.

Composition. The type genus and, perhaps, forms depicted by Kolebaba (1999a) as *Plagiostomoceras pleurotomum* in pl. 3, fig. 4 and pl. 3, figs. 5–7.

Comparison. It differs from Flowerinidae in the thinly laminated, rugulose cameral deposits with a microstructure represented by a spongy-porous structure and in the absence of metacameral deposits. See respective Comparison sections for comparison with other families.

Occurrence. Upper Silurian, Ludlow of the Czech Republic and England; Middle Devonian, Eifelian of northern Canada, Central Urals, and Gorno-Altai.

Genus *Ostreioceras* Zhuravleva, gen. nov.

Etymology. From Greek *ostreion* (conch).

Type species. *Sinoceras riphaeum* Zhuravleva, 1978; Middle Devonian, lower Eifelian; eastern slope of the Central Urals, Gorno-Altai.

Diagnosis. This genus forms, in addition to epi- and hyposeptal deposits, mural deposits that in adapical part of chamber come off from originally undivided mural-episeptal deposits. Free space between episeptal and mural deposits filled with sediment and cavity left by disintegrated soft siphon constitute characteristic features of this genus. Hyposeptal deposits in contact with mural deposits, rather than with episeptal deposits, as in other known forms.

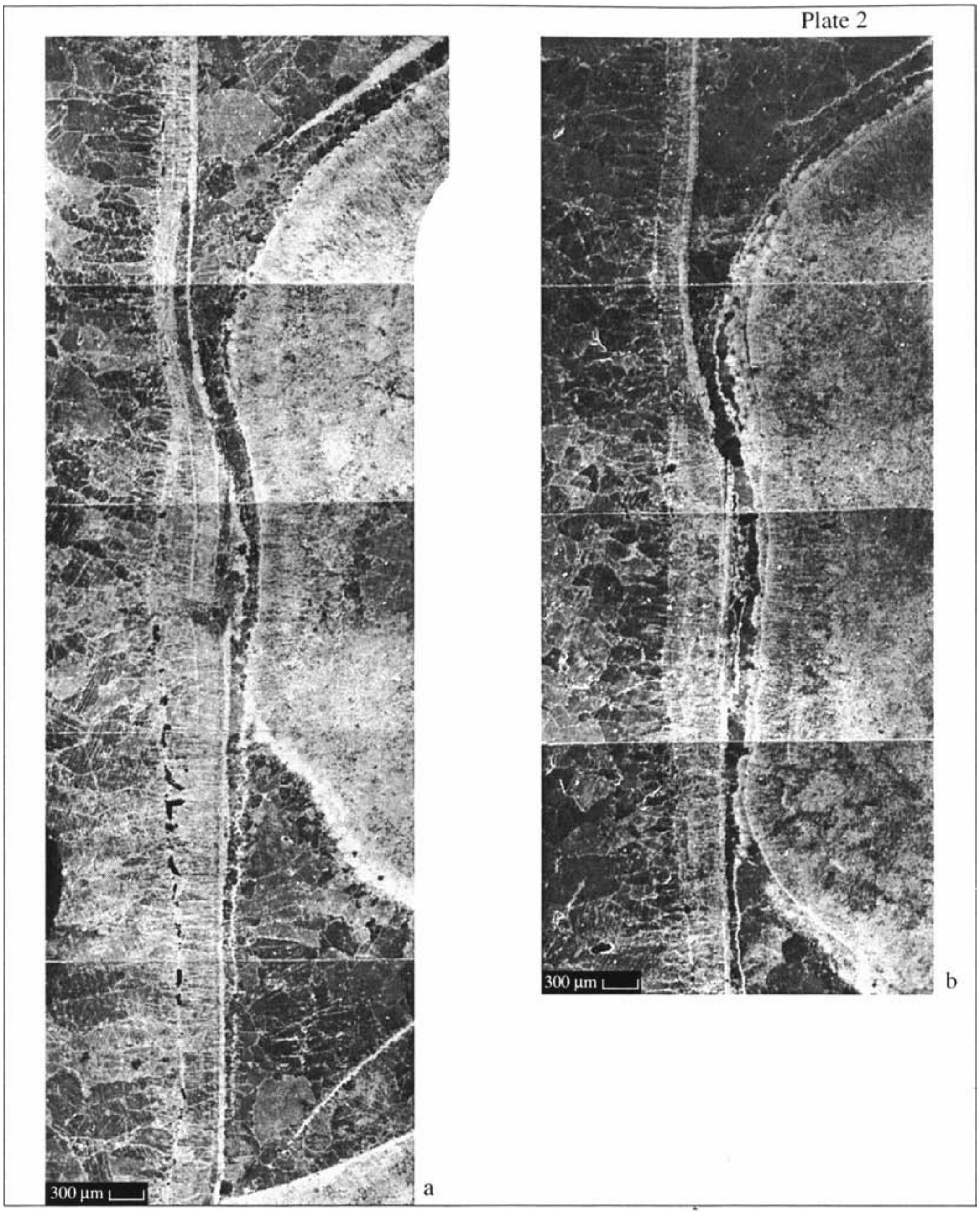
Species composition. In addition to the type species, *O. superplenum* (Collins, 1969) and *O.? thomsoni* (Barrande, 1866) and, perhaps, the form depicted by Kolebaba (1999a) in pl. 3 under the name *Plagiostomoceras pleurotomum.*

Remarks. The species *Orthoceras thomsoni*, which was described by Barrande, has been assigned (with certain reservations) to the genus *Ostreioceras* on the basis of similarity in morphology of cameral depos-

Explanation of Plate 1

Fig. 1. *Flowerina shimanskyi* Zhuravleva et Kisselev, 2001; holotype PIN, no. 1793/1801 (SEM photograph); dorsal side: (1a) a part of the adoral septum and its neck with a blunt, outwardly curved edge that are enclosed in the epi- and hyposeptal cameral deposits; the hyposeptal deposits do not cover the angle formed by the septum and neck; (1b) an enlarged detail of (1a) showing the edge of the septal neck; (1c) a part of the median neck: the dorsal side (left) showing a partially deformed septum and neck with an outwardly curved brim that also are enclosed in the cameral deposits and the ventral side (right) showing a part of the broken neck located between the hyposeptal cameral deposits (right) and two layers of metacameral deposits (left); the thickening at the level of the neck end is its recurved brim; (1d) a fragment of the adapical septum that retained the entire thickness; Ukraine, Podolia, the Dniester River basin, left bank of the Studenitsa River, 400 m downstream of the downstream end of the village of Studenitsa; Lower Silurian, Wenlock, Furmanovo Formation, Restevskaya Subformation.

Plate 2



Explanation of Plate 2

Fig. 1. *Flowerina shimanskyi* Zhuravleva et Kisselev, 2001; holotype PIN, no. 1793/1801 (SEM photograph); ventral side: (1a) a part of the adapical (full-length) chamber showing the metacameral deposits of two layers, which are swollen level with the septal neck brim (left), massive hyposeptal deposits (right); small part of a septum with a fragment of its episeptal deposits (top); and the edge of a partially disintegrated septal neck, probably with a recurved brim (center); (1b) a similar part in the next chamber: the septum and neck are also partially disintegrated; massive hyposeptal deposits have preserved the prismatic structure only in outer layers; Ukraine, Podolia, the Dniester River basin, left bank of the Studenitsa River, 400 m downstream of the downstream end of the village of Studenitsa; Lower Silurian, Wenlock, Furmanovo Formation, Restevskaya Subformation.

its; judging by the drawing, in both taxa mural deposits have come off and metacameral deposits are absent.

Occurrence. Silurian England, ?Czech Republic; Middle Devonian, Eifelian of the Central Urals, Gorno-Altai, and northern Canada.

Ostreioceras riphaeum **(Zhuravleva, 1978)**

Plates 3–6

Sinoceras riphaeum: Zhuravleva, 1978, p. 47, pl. I, figs. 3–7.

Holotype. PIN, no. 1359/523; Sverdlovskaya Region, Artemovskii district, left bank of Bobrovka

Creek, 400 m south-southwest of the cupola furnace at the village of Pokrovskoe; Middle Devonian, lowermost Eifelian.

D e s c r i p t i o n . The conch is large and expands predominantly at an angle of 3°, occasionally 2° or 4°. The length of the body chamber is about one-third of the conch length. The holotype, a fragment 290 mm long and 33 mm wide at its maximum diameter, shows a wide and deep constriction in front of the aperture on the cast of the body chamber. The largest specimen has a diameter of 53 mm and a pair of longitudinal parallel furrows on the dorsal side of the cast of the body chamber. The aperture shows no constrictions and no distinct edges.

The surface has preserved no ornamentation. The wall is thin and has lost its initial structure. Within a small portion of the wall, however, one can distinguish three layers, of which the internal and external layers are thin, and the intermediate layer is thick. The interior of the wall frequently contains cavities with granules of hematite.

The chambers vary in length from medium to very long. In fragments comparable in diameter, the length-to-width ratio of the chamber varies from 0.8 to 1.2–1.5; predominantly 0.8–1.0.

The septa with a short mural part are concave for a distance of 0.3–0.4 of the chamber length and slightly inclined to the ventral side; in places they have preserved a nacreous microstructure (Pl. 5, fig. 1c; Pl. 6, fig. 1a).

The suture is straight and inclined to the ventral side.

The diameter of the siphon in the septal foramen is 0.10–0.15 of the diameter of the phragmocone. The siphon is displaced ventrally from the center by a distance of 0.04–0.07 the diameter.

The septal necks are long (0.30–0.33 of the chamber length) and cylindrical; they were occasionally lengthened in ontogeny. In the adoral parts of large specimens, the length of the necks occasionally reaches one-half the length of the chamber or more. The necks become gradually thinner and less mineralized toward the edge; with the edge being occasionally curved outward or inward (Pl. 5, figs. 1b, 1d). In places they preserved a nacreous microstructure (Pl. 5, fig. 1c). No connecting rings have been found. The relative proportions of the volumes of the episeptal, hyposeptal, and mural deposits depend to a certain degree on the length of the chambers and apparently change in ontogeny.

The cameral deposits consist of thin rugulose layers, which are arranged in transverse folds; the latter form a finely ridged pattern on the surfaces of these deposits (Pl. 3, figs. 2, 4, 5).

C o m p a r i s o n. From *O. superplenum*, it differs in the smaller angle of the conch expansion (2°–3° instead of 5°), longer chambers (with the length-to-width ratio 1.5–0.8 instead of 0.42–0.45), and the cameral deposits in which the hyposeptal deposits are in contact only with the mural rather than episeptal deposits; the lack of adequate information on the structure of its conch makes comparison with *O.? thomsoni* (Barrande, 1866) difficult.

R e m a r k s. Several small fragments, which perhaps belong to one small conch, from the Terent'evskaya Formation of the Eifelian of the Gorno-Altai differ from the Ural forms in the slightly deeper concavity of septa (0.5–0.7 instead of 0.2–0.4 the chamber length) and in the presence of a broad adoral ring of the episeptal cameral deposits that encloses the soft siphon. Judging by these characters, they are more similar to *O. superplenum* Collins, although the other aforementioned traits indicate that they are closer to the species in question. However, we regard designation of a separate species as premature because of scarcity of adequate material.

O c c u r r e n c e. The Middle Devonian, Eifelian of the Central Urals and Gorno-Altai.

M a t e r i a l. Three hundred and fourteen specimens, predominantly fragments of phragmocones varying in length (up to 290 mm) and diameter (from 3 to 53 mm, more frequently 10 mm), were collected from the same outcrop as the holotype mainly by the first author (F.A.Zh.) in 1957 and by A.A. Pronin in 1941. The specimens from the Gorno-Altai were donated by V.P. Udodov in 1984 and originated from the outcrop on the left bank of the middle Sema River, on the left slope of the Sukrobu ravine, a left-bank tributary of the Sema River downstream from the small town of Shebalino. A total of about 40 polished sections and 5 thin sections have been made.

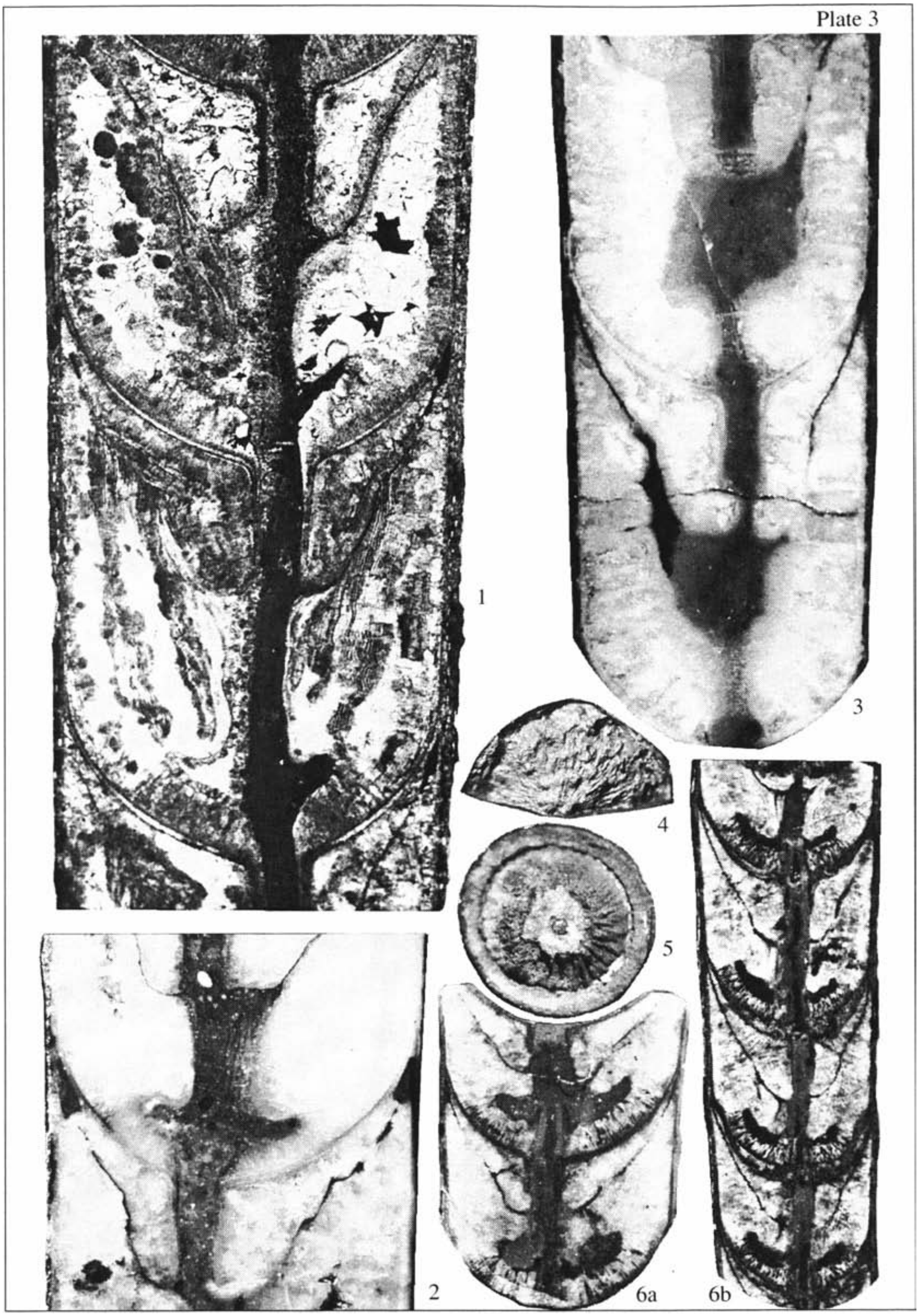
Family Astroviidae Zhuravleva, fam. nov.

D i a g n o s i s. Conch orthoceraconic or slightly curved cyrtoceraconic, slightly laterally compressed or circular in cross section. Siphon slightly displaced ventrally from center. Cameral and ectosiphonal deposits composed of virgulae (the structure of virgulae was described in detail above). Ectosiphonal deposits entering cavity of chamber and contacting cameral deposits. Metacameral deposits are absent.

C o m p o s i t i o n. Genera: *Astrovia* gen. nov. and *Gorgonoceras* Zhuravleva, 1961. In addition, this family perhaps contains forms depicted by Kolebaba under the names *Protobactrites styloideus* Kolebaba (1999a, pl. 1, fig. 4; text-figs. 7a, 7b) and *Nucleoceras hollandi* (Kolebaba, 1999b, pls. I, II).

C o m p a r i s o n. It differs from Flowerinidae in the presence of ectosiphonal deposits, the absence of metacameral deposits, and the structure of cameral deposits. From Ostreioceratidae, it differs in the presence of ectosiphonal deposits and the microstructure of cameral deposits. See respective Comparison sections for comparison with other families.

O c c u r r e n c e. Upper Silurian, Ludlow of the Czech Republic; Lower Devonian, Pragian of the Kuznetsk Basin; Middle Devonian, Eifelian of northern Africa and the Central Urals.



Genus *Astrovia* Zhuravleva, gen. nov.

Etymology. In honor of G.G. Astrova, a paleontologist and geologist.

Type species. *A. adorea* sp. nov.; Lower Devonian, Pragian Stage, upper Krekovo layers; Kuznetsk Basin.

Diagnosis. Conch orthoceraconic, slightly laterally compressed in cross section. Ectosiphonal deposits penetrate deeply into cavity of chamber. In cross section, cameral deposits show closely spaced sinuous virgulae.

Species composition. The type species, *A. marhoumensis* sp. nov., and *A.* sp., a form from the

Explanation of Plate 3

Figs. 1–6. *Ostreioceras riphaeum* (Zhuravleva, 1978); (1)–(3), and (6) longitudinal medial sections of phragmocones; (4) and (5) casts of chambers: (1) specimen PIN, no. 1359/434, thin section of two chambers, where hyposeptal, mural-episeptal, and mural cameral deposits squeeze and shift the soft siphon from the level of the septal neck to the dorsal side; the episeptal deposits run through the septal neck and merge with the hyposeptal deposits of the previous chamber, ×9; (2) specimen PIN, no. 1359/145, thin section of two incomplete chambers showing a strongly compressed and displaced siphon and the longitudinal ribbing of the internal surface of the mural deposits, which is seen on the cast of the siphon, ×6; (3) specimen PIN, no. 1359/435, thin section of two long chambers with mural and hyposeptal deposits, which strongly compress the siphon; the septal necks are long; the alternation of dark and light-colored bands in the cameral deposits shows their fine rugosity, ×9; (4) specimen PIN, no. 1359/430, an adoral radially ribbed surface of the episeptal deposits, ×2.6; (5) specimen PIN, no. 1482/321, an adapical radially ribbed surface of the hyposeptal deposits, ×3; Sverdlovskaya Region, Artemovskii district, left bank of Bobrovka Creek, 400 m south-southwest of the cupola furnace at the village of Pokrovskoe; (6) specimen PIN, no. 4720/1: (6a) a thin section of two short adapical chambers, ×10; (6b) a thin section of three and a half long chambers from the central part of the specimen: only a thin layer of episeptal cameral deposits run through the septal neck into the previous chamber and form a high adoral ring around the siphon (a ridge in cross section) that compresses the siphon; the sediment that fills the interspace between the episeptal and mural deposits shows a rugulose structure of the former, ×4.5; the interior of the siphon contains a tube of gray fine-grained material, the nature of which is uncertain; Gorno-Altai, left bank of the middle Sema River, left slope of the Sukrobu ravine, a left-bank tributary of the Sema River downstream of the small town of Shebalino; the Middle Devonian, Eifelian.

Ludlow of the Czech Republic depicted by Kolebaba (1999a, pl. 4, fig. 2).

C o m p a r i s o n. See below in Comparison section for *Gorgonoceras*.

O c c u r r e n c e. The Ludlow of the Czech Republic, the Pragian of the Kuznetsk Basin, and the Eifelian of northern Africa.

Astrovia adorea **Zhuravleva, sp. nov.**

Plates 7–11, 12, fig. 1

E t y m o l o g y. From Latin *adorea* (reward).

H o l o t y p e. PIN, no. 2218/173; Kuznetsk Basin, town of Gur'evsk, Starogur'evskii quarry; Lower Devonian, Pragian Stage, upper Krekovo layers.

D e s c r i p t i o n (Figs. 3, 4). The conch is orthoceraconic, laterally compressed in cross section with a ratio of diameters 1 : 1.07, and expanding at an angle of 7°. The holotype, a fragment of the adapical part of the phragmocone, is 25 mm long and 9 mm in diameter at the adoral end and consists of seven chambers.

Only a part of the wall has been preserved. It consists of two layers: a thin dark internal layer, which is probably organic, and thin light-colored prismatic external layer, the surface of which is worn (Pl. 7, figs. 1a, 1d; Pl. 8; Pl. 9, figs. 1a, 1b).

The internal layer in the polished section level with the "denticles" has a more intense color than in the interspaces between them; it is delineated on the outside by a thin black layer.

The thick light-colored external layer of the wall shows a prismatic microstructure. A detailed description of the wall has been provided above.

The chambers are short with a length-to-width ratio of 0.4–0.5.

The suture apparently forms a small lateral lobe.

The septa with a short mural portion are concave for a distance of 0.7 the length of the chamber and have lost their initial microstructure (Pl. 7, fig. 1d; Pl. 8).

The diameter of the siphon in the septal foramen is 0.16–0.17 the diameter of the phragmocone. The siphon is displaced ventrally from the center. The diameter of the squeezed soft siphon is 0.66–0.80 the diameter of the septal foramen. The septal necks are suborthochoanitic, with a length of 0.11–0.15 the length of the chamber. In an optical microscope they appear to be sharply defined (pl. 7, figs. 1a, 1b; pl. 8). However, an observation through an SEM reveals that the neck and the nearby septum loose their clear contours, and the edge of the neck is obscured by the surrounding cameral deposits (pl. 10, figs. 1a, 1b; pl. 12, fig. 1a).

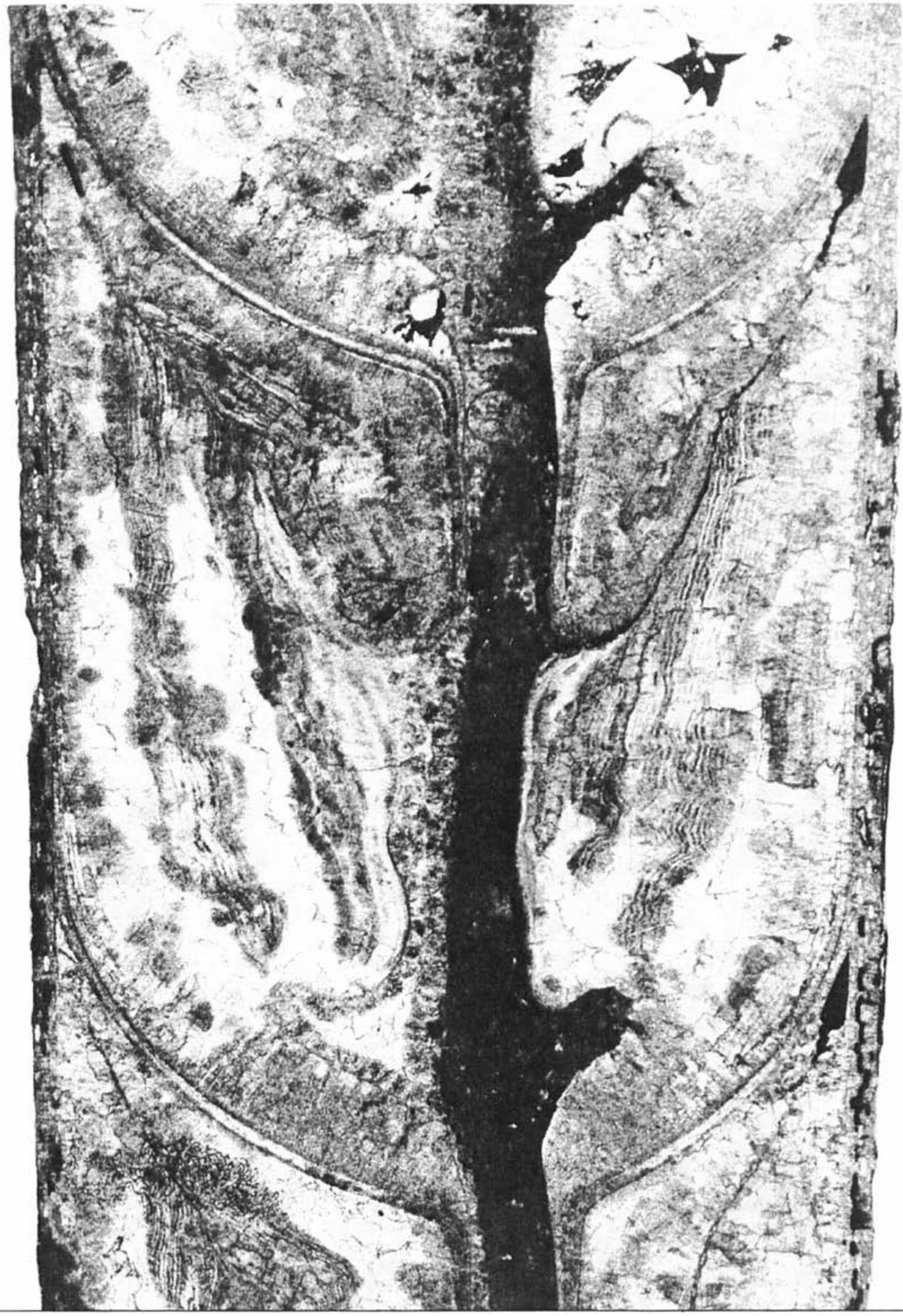
The cameral deposits are composed of elongated, undulating, and sinuous structures, i.e., virgulae, which have come off from the initial thin layer of cameral deposits that lined the wall of the chamber and septa from the outside and in which fine crystalline elements were arranged at right angles to the surface. A detailed description of the cameral deposits was given above.

The ectosiphonal deposits also consist of virgulae, which come off from the soft siphon and penetrate into the cavity of the chamber to come in contact with the epi- and hyposeptal cameral deposits. The bases of virgulae bear black, thinly laminated, longitudinal ectosiphonal deposits (Pl. 6, figs. 1a, 1d; Pl. 8; pl. 10). On the dorsal side the virgulae (Pl. 7, fig. 1e) stop short of reaching the cameral deposits, from which they are separated by a free space filled with rock material (Pl. 8). A more detailed description was given above.

The cross section of the adoral chamber contains approximately 60–70 slender, slightly undulating episeptal virgulae and 36–40 hyposeptal virgulae (Pl. 7, fig. 1c).

The longitudinal section of the specimen, in places, shows marks of blood vessels: on the ventral side they are clearly defined in the third and fifth adapical chambers where the ectosiphonal deposits adjoin the cameral deposits and one mark of the vessel is clearly seen on

Plate 4



Explanation of Plate 4

Fig. 1. *Ostreioceras riphaeum* (Zhuravleva, 1978); specimen PIN, no. 1359/434 (thin section), an enlarged detail of Pl. 3, fig. 1, long septal necks become thinner and loose their clear contours to the edge; cameral deposits consisting of thin layers are arranged in small transverse folds; sinuous surfaces of the hyposeptal and mural deposits form a "pseudoseptum" in the form of a chain; the siphon is markedly deformed and displaced dorsally; the adapical interspace between the episeptal and mural deposits is filled with rock material, ×19.2; Sverdlovskaya Region, Artemovskii district, left bank of Bobrovka Creek, 400 m south-southwest of the cupola furnace at the village of Pokrovskoe; the Middle Devonian, lower Eifelian.

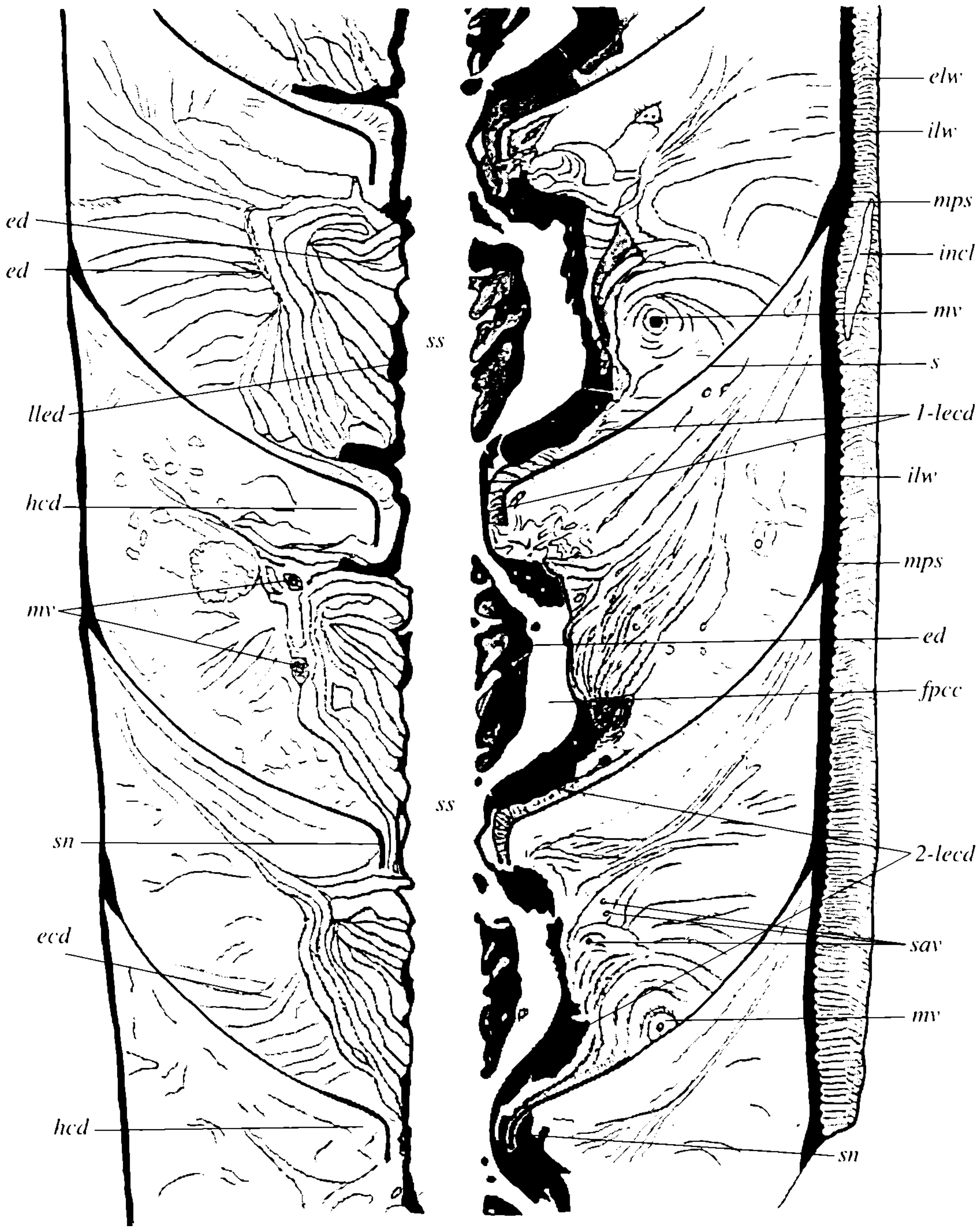


Fig. 3. *Astrovia adorea* sp. nov.: holotype PIN, no. 2218/173, ×16.6; nearly medial longitudinal section, the ventral side is on the left; Kuznetsk Basin, Gur'evsk, Starogur'evskii quarry; Lower Devonian, Pragian Stage, upper Krekovo layers. Designations for Figs. 3–5: (*elw*) external layer of the wall; (*ilw*) internal layer of the wall; (*incl*) inclusion; (*s*) septum; (*mps*) mural part of the septum; (*sn*) septal neck; (*ss*) soft siphon; (*1-lecd*) first layer of the episeptal cameral deposits; (*2-lecd*) second layer of the episeptal cameral deposits; (*hcd*) hyposeptal cameral deposits; (*ed*) ectosiphonal cameral deposits; (*lled*) longitudinal layer of ectosiphonal deposits; (*fpcc*) free part of the chamber cavity; (*mv*) marks of vessels; (*sav*) (?) section of the axes of virgulae; (*ecd*) episeptal cameral deposits.

the dorsal side in the fourth adapical chamber, where the lateral virgulae bypass the vessel (Pl. 8).

M a t e r i a l. The holotype, which was collected by G.G. Astrova in 1963.

Astrovia marhoumensis Zhuravleva, sp. nov.

Plate 8, fig. 1

E t y m o l o g y. After the populated locality of Marhouma.

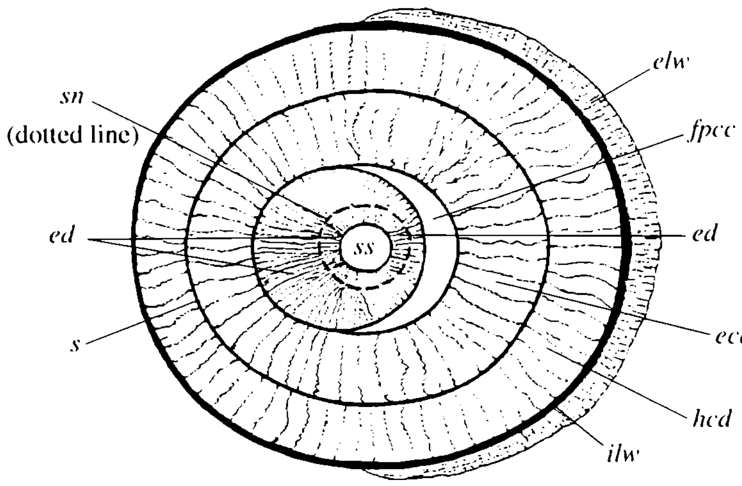


Fig. 4. *Astrovia adorea* sp. nov.; holotype PIN, no. 2218/173, ×10; schematic representation of the cross section of the third adapical chamber, the ventral side is on the left; Kuznetsk Basin, Gur'evsk, Starogur'evskii quarry; Lower Devonian, Pragian Stage, upper Krekovo layers. For designations see Fig. 3.

H o l o t y p e. The specimen illustrated by Mutvei (1956, pl. I, fig. 4) is stored at the Swedish Museum of Natural History in Stockholm; Northern Sahara; Middle Devonian, Eifelian.

D e s c r i p t i o n . The holotype is a fragment of the adapical part of an apparently fairly large orthoceraconic conch, which consists of nearly six relatively short chambers with a length-to-width ratio of 0.28–0.29. The cross section of the specimen, the structure of its wall, and the angle of conch expansion are unknown. The septa are concave for a distance of 1.10–1.12 the length of the chamber.

The diameter of the siphon in the septal foramen is 0.11 the diameter of the phragmocone. The septal necks on the ventral side are suborthochoanitic and shorter than the clinochoanitic necks on the dorsal side.

The episeptal cameral deposits enter the septal foramen as a very thin layer and beyond the edge of the septal neck merge with the thicker hyposeptal deposits of the previous chamber; this is more clearly seen on the dorsal side. Unfortunately, the structure of cameral deposits is unknown. The ectosiphonal deposits, which are probably virgulae similar to those in *A. adorea*, on the ventral side penetrate deep into the cavity of the chamber to adjoin the epi- and hyposeptal cameral deposits. Their bases are lined with a thin black longitudinal layer that stretches through the entire fragment.

On the dorsal side the ectosiphonal virgulae, which are shaped like narrow, short, slightly bent structures, come off from the soft siphon and form longitudinal rows (seven to ten in a row) against the empty cavities of the chambers. They are separated from the cameral deposits, which are located deep in the interior of the chambers, by a wide space filled with rock material.

C o m p a r i s o n. It differs from *A. adorea* in the relatively larger conch with shorter chambers, more concave septa, narrower virgulae of the ectosiphonal deposits, and the episeptal cameral deposits (in *A. adorea*, the episeptal cameral deposits pass through the septal foramen as two thick layers, the latest of which merges with the episeptal rather than with the hyposeptal layer of the previous chamber).

M a t e r i a l. The holotype, which was collected by X. Mutvei.

Genus *Gorgonoceras* Zhuravleva, 1961

Gorgonoceras: Zhuravleva, 1961, p. 93; Balashov and Zhuravleva, 1962, p. 91; Babin, 1964, p. 142; Sweet, 1964, p. K235; Stanley, Teichert, 1978, p. 83.

T y p e s p e c i e s. *G. visendum* Zhuravleva, 1961; the Middle Devonian, lower Eifelian; the eastern slope of the Central Urals.

D i a g n o s i s. Conch slightly curved cyrtoceraconic, circular in cross section. Internal layer of wall with fine longitudinal folds. Ectosiphonal deposits penetrate only slightly into cavity of chamber. In cross section cameral deposits show rare, occasionally sinuous virgulae.

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

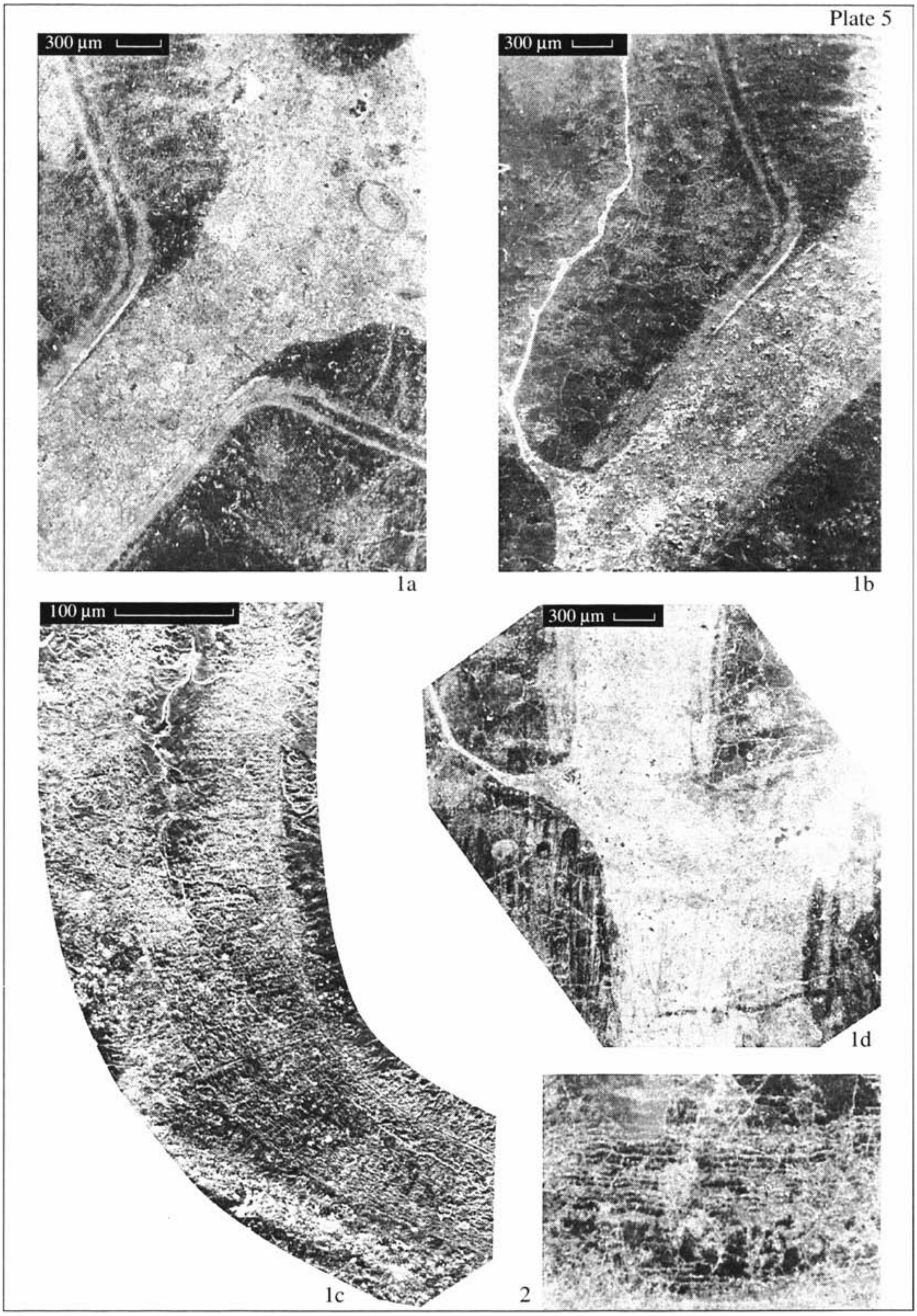
C o m p a r i s o n. It differs from *Astrovia* in the slightly curved conch that is circular in cross section and the ectosiphonal deposits that only slightly penetrate into the chamber cavity.

Gorgonoceras visendum Zhuravleva, 1961

Plate 14, fig. 1; Plate 15

Gorgonoceras visendum: Zhuravleva, 1961, p. 93, pl. 12, fig. 1; Balashov, Zhuravleva, 1962, p. 16, fig. 1; Zhuravleva, 1978, p. 83, pl. 23, fig. 4; Sweet, 1964, p. K236, fig. 167.

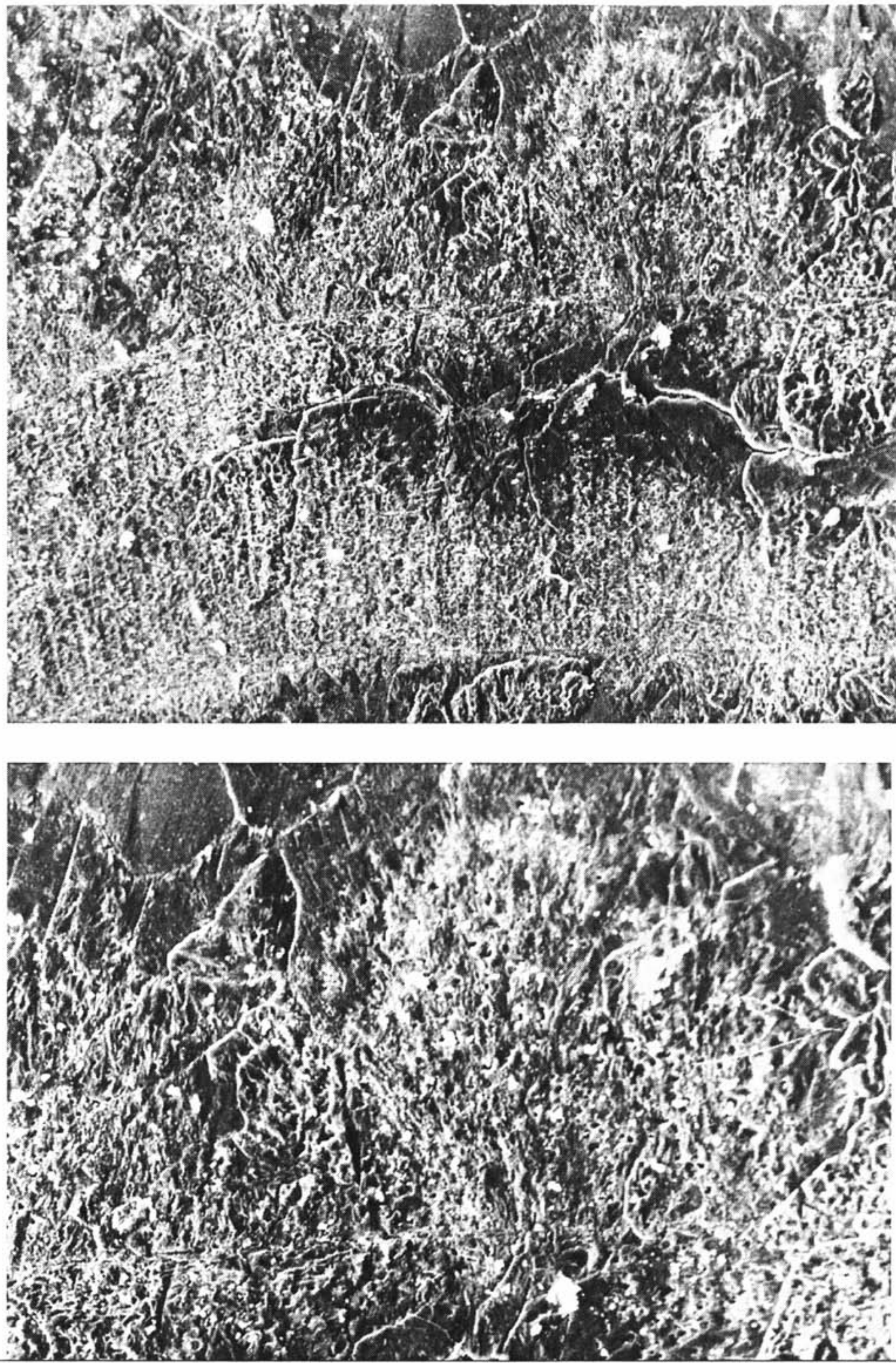
H o l o t y p e. PIN, no. 1359/505; Sverdlovskaya Region, Artemovskii district, left bank of Bobrovka



Explanation of Plate 5

Figs. 1 and 2. *Ostreioceras riphaeum* (Zhuravleva, 1978) (SEM photograph); (1) specimen PIN, no. 1359/145; longitudinal medial section of the phragmocone: (1a) episeptal deposits penetrate as a thin layer into the septal neck; (1b) epi- and hyposeptal deposits penetrate into the septal neck, the edge of which is curved outwardly; (1c) parts of the septum and septal neck that preserved a nacreous microstructure (episeptal deposits are on the left); (1d) hyposeptal and mural deposits with a longitudinally ribbed surface; the edges of the neck on the ventral and dorsal sides are curved outwardly and inwardly, respectively; (2) specimen PIN, no. 1359/235, thin sinuous layers of hyposeptal deposits, ×50; Sverdlovskaya Region, Artemovskii district, left bank of Bobrovka Creek, 400 m south-southwest of the cupola furnace at the village of Pokrovskoe; Middle Devonian, lower Eifelian.

Plate 6



1a

1b

Explanation of Plate 6

Fig. 1. *Ostreioceras riphaeum* (Zhuravleva, 1978); specimen PIN, no. 1359/145 (SEM photograph): (1a) an enlarged detail of Pl. 4, fig. 1c, a part of the septum with a nacreous microstructure (bottom) and two folds of the episeptal cameral deposits (top), ×400; (1b) an enlarged right fold of (1a) showing the microstructure (a spongy-porous structure) of the episeptal cameral deposits, ×660; Sverdlovskaya Region, Artemovskii district, left bank of Bobrovka Creek, 400 m south-southwest of the cupola furnace at the village of Pokrovskoe; the Middle Devonian, lower Eifelian.

Creek, 400 m south-southwest of the cupola furnace at the village of Pokrovskoe; Middle Devonian, lower Eifelian.

D e s c r i p t i o n (Fig. 5). The conch expands at an angle of about 4°. The holotype, a fragment of the phragmocone, is 62 mm long and 10 mm in diameter at the adoral end and has preserved within a small area a thin internal layer of the wall of the conch with narrow, low longitudinal folds: seven or eight folds per 5 mm. The worn surface of the cast shows sinuous epi- and hyposeptal cameral deposits.

The chamber is of medium length; 2.5–3.0 chambers per diameter.

The septa are concave to a depth less than the length of the chamber and inclined to the ventral side.

The suture is probably straight and inclined to the ventral side.

The diameter of the siphon in the septal foramen is 0.16–0.17 the diameter of the phragmocone. The siphon is displaced ventrally. The length of the septal necks is 0.17–0.12 the length of the chamber. The septal necks are suborthochoanitic; on the ventral side they are slightly longer than on the dorsal side.

The cameral deposits consist of virgulae. On the dorsal side the episeptal deposits along with the hyposeptal deposits, which are smaller in volume, enclose the septum and the neck and leave a fairly discernible "pseudoseptum." On the ventral side the ectosiphonal deposits overlie the cameral deposits and only slightly penetrate into the chamber cavity; the boundary between them is indiscernible. In the cross section of the specimen, the virgulae are shaped like nearly flat plates, the proximal edges of which virtually merge with each other. The section of the adoral end of the holotype shows that in the episeptal deposits on the ventral side there is a thick complex structure that is formed by several virgulae (Pl. 14, fig. 1c). Another section that was made level with the septal neck through the hyposeptal deposits shows no such structure; however, it shows that inside the septal neck there are layers of the episeptal cameral deposits, which are thicker on the ventral side. Both sections together contain 60–64 virgulae (pl. 14, fig. 1d). The virgulae of the cameral deposits of *Gorgonoceras* are similar to those of *Astrovia adorea* (pl. 15, fig. 1b).

M a t e r i a l. The holotype, which was collected by the first author (F.A.Zh.) in 1957.

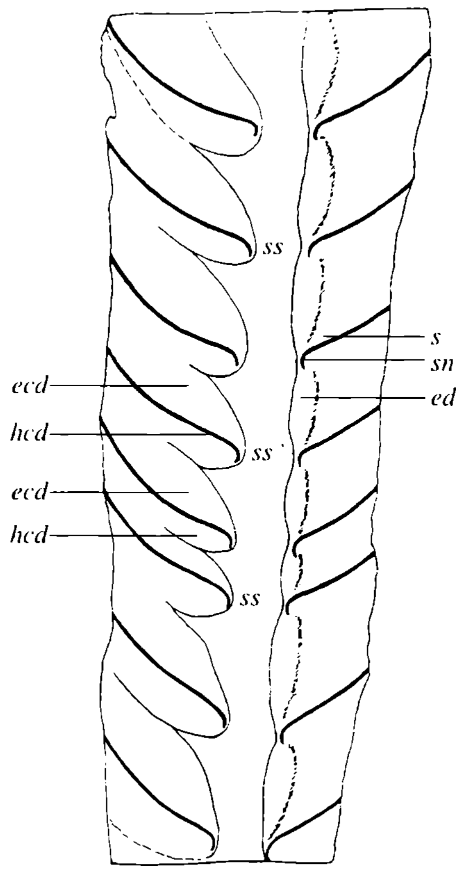


Fig. 5. *Gorgonoceras visendum* Zhuravleva, 1961; holotype PIN, no. 1359/505, ×5.1; longitudinal dorsoventral section, the ventral side is on the right; Sverdlovskaya Region, Artemovskii district, left bank of Bobrovka Creek, 400 m south-southwest of the cupola furnace at the village of Pokrovskoe; Middle Devonian, lowermost Eifelian. For designations see Fig. 3.

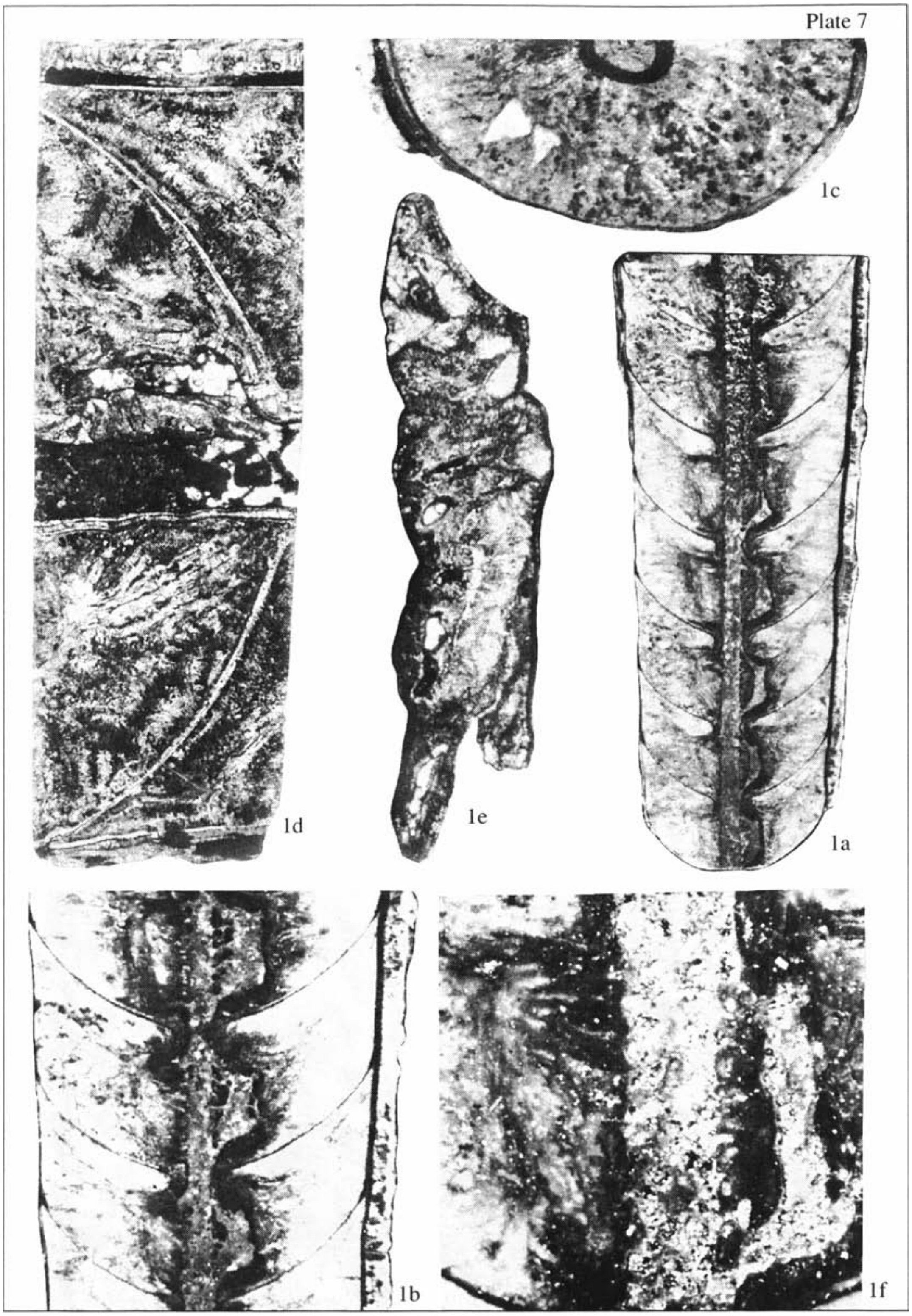
Family Lamellorthoceratidae Teichert, 1961

D i a g n o s i s. Conch orthoceraconic or slightly curved cyrtoceraconic. Cameral deposits consist of plates of complex configuration. Metacameral and ectosiphonal deposits apparently well developed. Microstructure of cameral and metacameral deposits known only in one genus, *Syndicoceras*.

C o m p o s i t i o n. Genera: *Arthrophyllum* Beyrich, 1850; *Lamellorthoceras* Termier et Termier, 1950; *Coralloceras* Zhuravleva, 1962; *Esopoceas* Stanley et Teichert, 1976; and *Syndikoceras* gen. nov.

C o m p a r i s o n. It differs from Flowerinidae and Ostreioceratidae in the cameral deposits consisting of plates that form intricately shaped folds. Comparison with Astroviidae is impossible because of lack of information on many genera from this virtually composite family.

R e m a r k s. The placement of the genus *Syndikoceras* into the family Lamellorthoceratidae was to a great extent tentative. Similarly, some characters that are typical of this genus (and apparently some other genera) have only tentatively been included in the diagnosis. In particular, the authors point out that the genus *Esopoceras* possesses deposits that grow from the siphon toward the chamber wall; these are apparently ectosiphonal deposits. There is no doubt that the majority of genera that we have placed into this family require careful restudy using new well-preserved material and a scanning electron microscope.



O c c u r r e n c e. Lower Devonian, Pragian–Middle Devonian, Eifelian; western Europe (Germany and France), northern Africa (Morocco and Algeria), Turkey, Russia (Novaya Zemlya), and North America (New York and Nevada).

Genus *Syndikoceras* Zhuravleva, gen. nov.

E t y m o l o g y. From Greek *syndikos* (defense attorney).

T y p e s p e c i e s. *S. arcticum* sp. nov.; Lower Devonian, Emsian; Novaya Zemlya.

Explanation of Plate 7

Fig. 1. *Astrovia adorea* sp. nov.; holotype PIN, no. 2218/173: (1a) a nearly medial longitudinal section of the phragmocone, the ventral side is on the left; cameral deposits pass through the septal foramen from each chamber to the previous chamber; the ectosiphonal deposits on the ventral side penetrate deep into the chamber cavity to come in contact with the cameral deposits and are separated from them by an interspace filled with rock material on the dorsal side, ×4.2; (1b) a longitudinal tangential section of three chambers showing the initial parts of the tubular virgulae of the ectosiphonal deposits that come off from the siphon into the chamber cavity, ×7; (1c) a cross section of the holotype (half) level with the septal neck: closely spaced virgulae of the cameral deposits, the episeptal virgulae are on the outside, and the hyposeptal virgulae are on the inside; the septal neck contains episeptal cameral deposits, and its ventral side (right) contains both episeptal and ectosiphonal deposits, ×8; (1d) a longitudinal section of two incomplete chambers, the ventral chamber is on the left (thin section); the dorsal side shows two layers of the wall: a thin dark internal layer and thick light-colored external layer; "featherlike" virgulae of the cameral deposits come off from both the chamber wall and the septa; on the ventral side a strand of smaller ectosiphonal virgulae is in contact with the cameral deposits; as viewed from the siphon the virgulae are lined with thin longitudinal layers of the ectosiphonal deposits; on the dorsal side the interspace between the developing ectosiphonal virgulae and cameral deposits is filled with rock, ×13.6; (1e) an enlarged detail of (1d), ectosiphonal virgulae on the dorsal side at early stages of their growth showing axial tubular parts of virgulae dissected at different angles, ×39; (1f) a longitudinal section of the second highest chamber showing tubular initial parts of the virgulae of the ectosiphonal deposits, ×18.6; Kuznetsk Basin, Gur'evsk, Starogur'evskii quarry; Lower Devonian, Pragian Stage, upper Krekovo layers.

D i a g n o s i s. Conch orthoceraconic, circular in cross section. Wall thin and three-layered: two internal layers with low, narrow longitudinal ridges, visible on cast. Surface of external layer unknown. Suture with low ventral and dorsal saddles. Septal necks orthochoanitic on ventral side and suborthochoanitic on dorsal side. Ectosiphonal deposits not penetrating into cavity of chamber, but adjoining metacameral deposits. Microstructure of metacameral and cameral deposits complex and prismatic. Microstructure of ectosiphonal deposits unknown.

S p e c i e s c o m p o s i t i o n. The type species and *S. mutveii* sp. nov.

C o m p a r i s o n. It differs from *Lamellorthoceras* in the unbranched plates of the cameral deposits; and from *Coralloceras*, in the more slowly expanding conch, which is circular in cross section. Comparison with *Arthrophyllum* and *Esopoceras* is difficult because of lack of information on the structure of the conchs of these genera.

O c c u r r e n c e. Lower Devonian, Emsian of Novaya Zemlya; Middle Devonian, Eifelian of northern Africa.

Syndikoceras arcticum Zhuravleva, sp. nov.

Plate 12, fig. 2; Plates 16–24

E t y m o l o g y. From Latin *arcticus* (northern).

H o l o t y p e. PIN, no. 3822/455; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of Yagel triangulation point, 36 km west-northwest of Cape Rakovyi; Lower Devonian. Emsian.

D e s c r i p t i o n (Figs. 6, 7). The conch expands at an angle of 4°–5°. The holotype, a fragment of the phragmocone, is 40 mm long, has an adoral diameter of 18 mm, and consists of seven chambers. The surface of the cast has preserved fragments of the intermediate and internal layers of the conch wall with low, narrow longitudinal folds, which are visible on the cast; the surface of the external layer is overlain by rock material

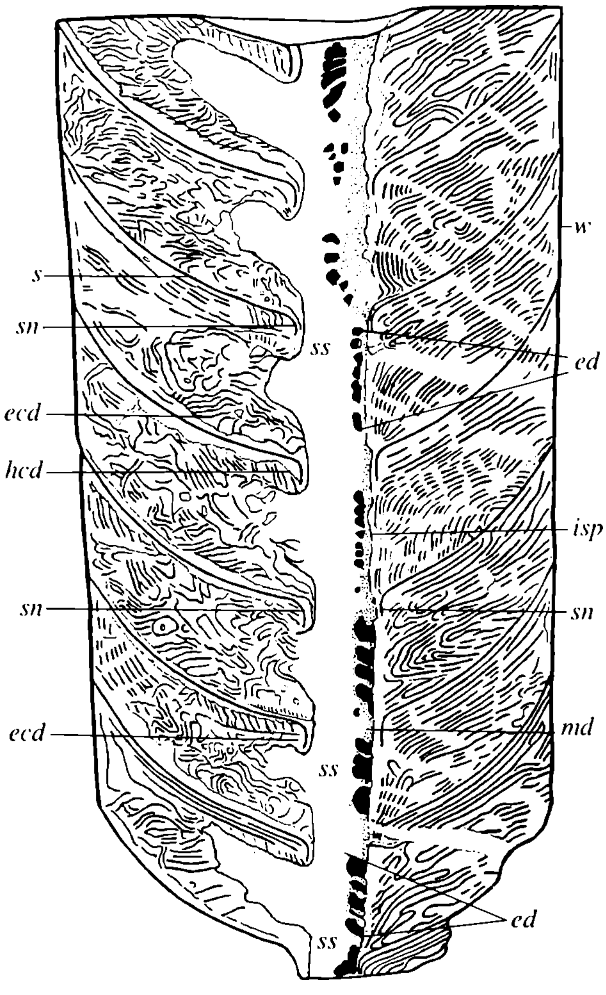


Fig. 6. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455, ×4; longitudinal dorsoventral section, the ventral side is on the right; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point, 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian. Designations: (*w*) wall; (*s*) septum; (*sn*) septal neck; (*ss*) soft siphon; (*ecd*) episeptal cameral deposits; (*hcd*) hyposeptal cameral deposits; (*md*) metacameral deposits; (*ed*) ectosiphonal deposits; (*isp*) interspace between the metacameral and ectosiphonal deposits.

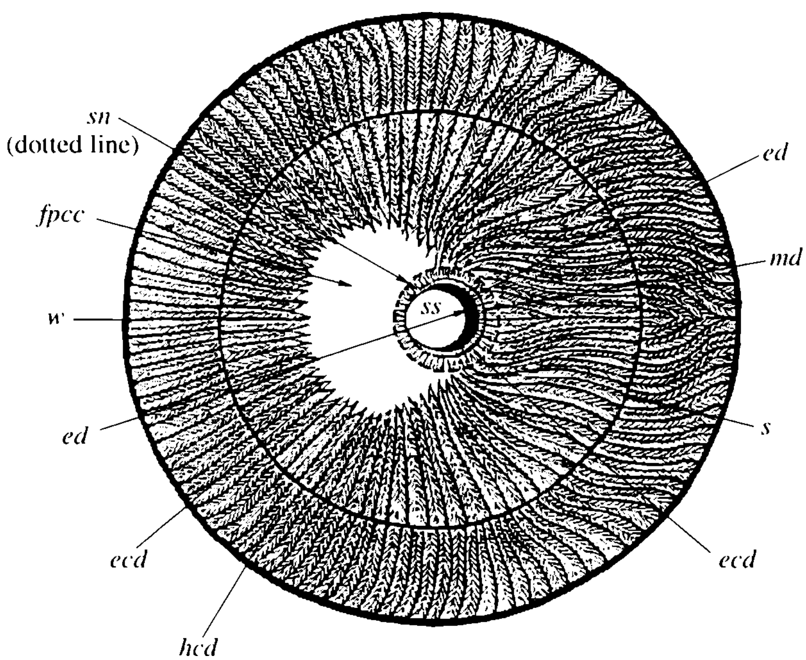


Fig. 7. *Syndikoceras arcticum* sp. nov.; H o l o t y p e. PIN, no. 3822/451, ×4.8; schematic representation of the cross section of the third adapical chamber, the ventral side is on the right; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point, 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian. Designations: (*w*) wall; (*s*) septum; (*sn*) septal neck (dotted line); (*ss*) soft siphon; (*ecd*) episeptal cameral deposits; (*hcd*) hyposeptal cameral deposits; (*md*) metacameral deposits; (*ed*) ectosiphonal deposits; (*fpcc*) free part of the chamber cavity.

(pl. 16, figs. 1a, 1c). The boundaries of the intermediate layer are best visible in the longitudinal section (Pl. 18, figs. 1b, 1c).

The chamber is short, its length-to-width ratio is 0.25–0.26.

The septa are thin, with a short mural part, concave for a distance of 1.2–1.3 the length of the chamber, and perpendicular to the axis of the conch. In places they have preserved a nacreous microstructure.

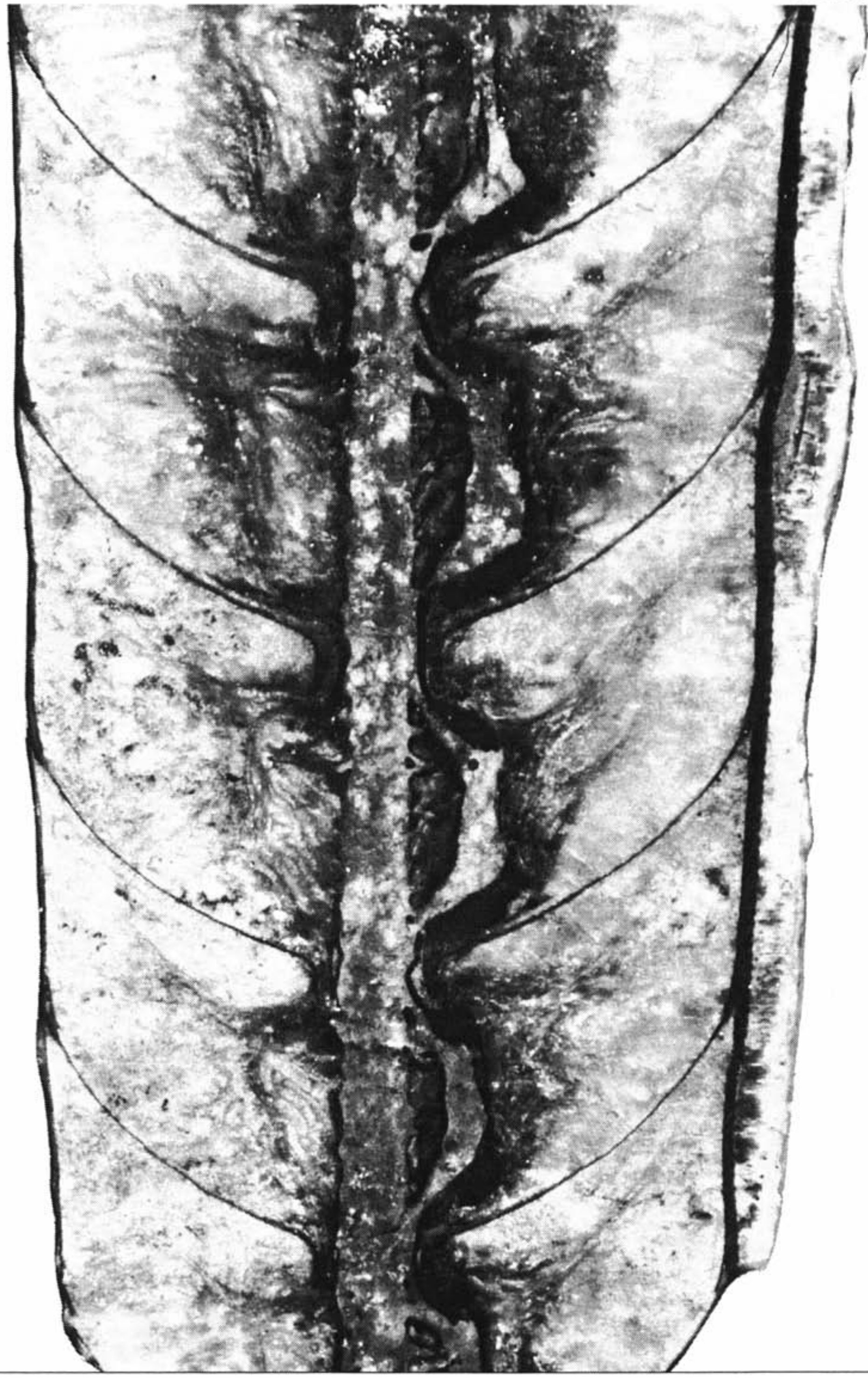
The suture apparently has a broad, low ventral saddle and higher dorsal saddle.

The diameter of the siphon in the septal foramen is 0.15–0.17 the diameter of the phragmocone. The siphon is displaced to the ventral side by a distance of 0.1 its diameter. Level with the septal foramen, the soft siphon was compressed by the episeptal deposits to 0.75–0.80 its initial thickness (Pl. 16, fig. 1d; Pl. 17).

In an optical microscope the septal necks, which are orthochoanitic on the ventral side and suborthochoanitic on the dorsal side, may appear to be fairly distinct and have a length of 0.18–0.20 the length of the chamber. However, SEM photographs show that the edges of the necks are obscured by the cameral deposits (compare Pl. 17 and Pls. 19, 20) even though the necks preserve a nacreous microstructure (Pl. 22, fig. 1a).

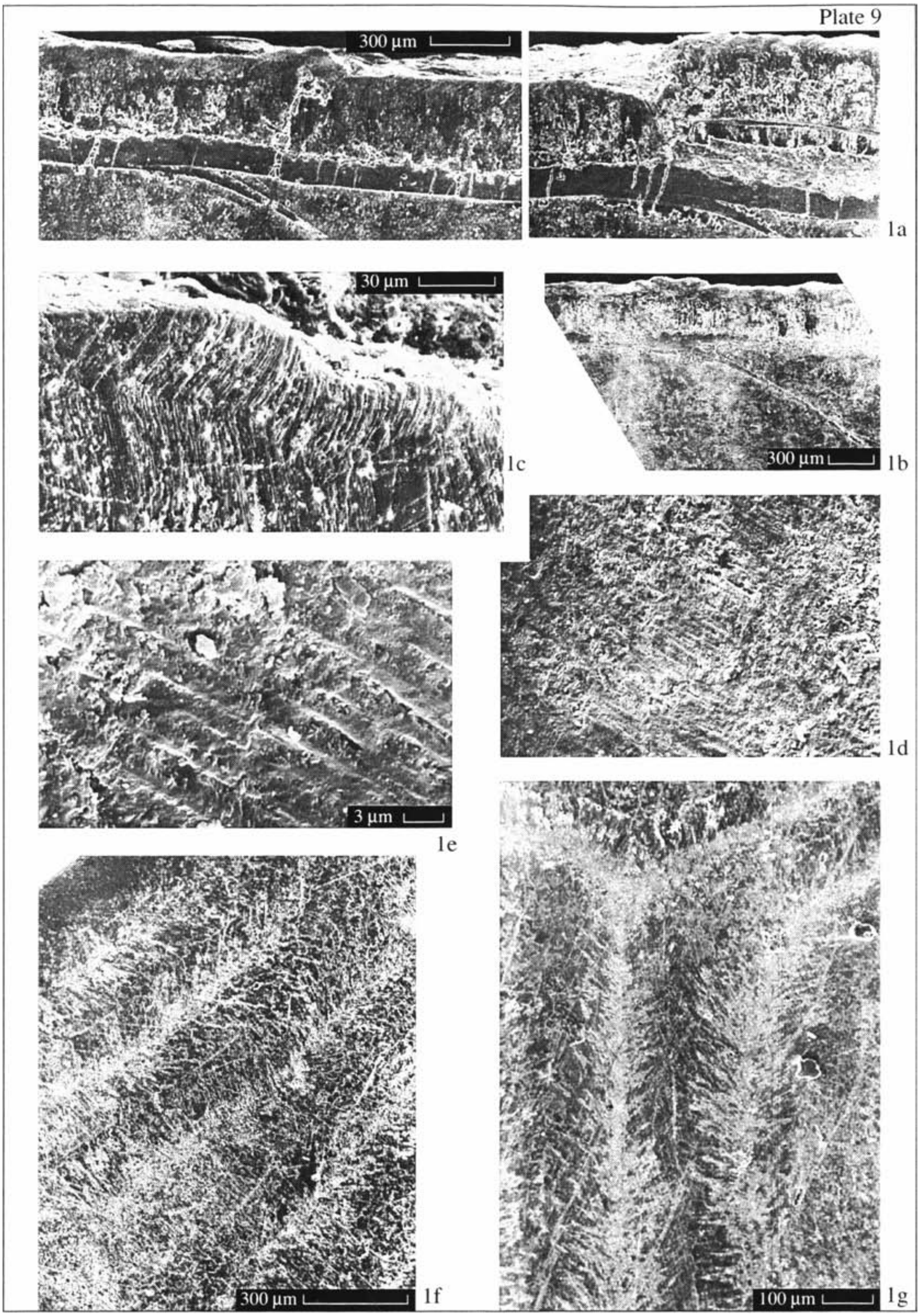
The cameral deposits consist of plates (? or branches) that form complex folds. The surface of the cast shows very thin longitudinal plates, which are arranged at an acute angle to the axis of the conch and are intricately interconnected (Pl. 18, figs. 1a, 1b). On the ventral side the deposits fill the cavity of the chamber. There, the plates are arranged predominantly parallel to the septum, thus forming narrow folds. The episeptal deposits pass through the septal neck and merge with the hyposeptal deposits of the previous chamber. The metacameral deposits lie as a single longitudinal layer on the cameral deposits; in places there are noncontinuous bands of denser (?amorphous) material between them. The ectosiphonal deposits, which in cross sections look like plates arranged in noncontinuous rows against the cavities of two or three adapical chambers, adjoin the metacameral deposits except for a small gap between them and the metacameral deposits that is located more adorally and has been filled with sediment (Pls. 17, 19–22). The metacameral and ectosiphonal deposits do not come together in this part of the phragmocone on the dorsal side (Pl. 17, fig. 3). In the cross section the cameral deposits look like nearly flat or, more ventrally, like undulating featherlike plates (Pl. 16, fig. 1g). The microstructure of the cameral and metacameral deposits is prismatic and has been discussed in detail previously in this paper (Pls. 19–29). Unfortunately, we failed to study the microstructure of the ectosiphonal deposits.

Plate 8



Explanation of Plate 8

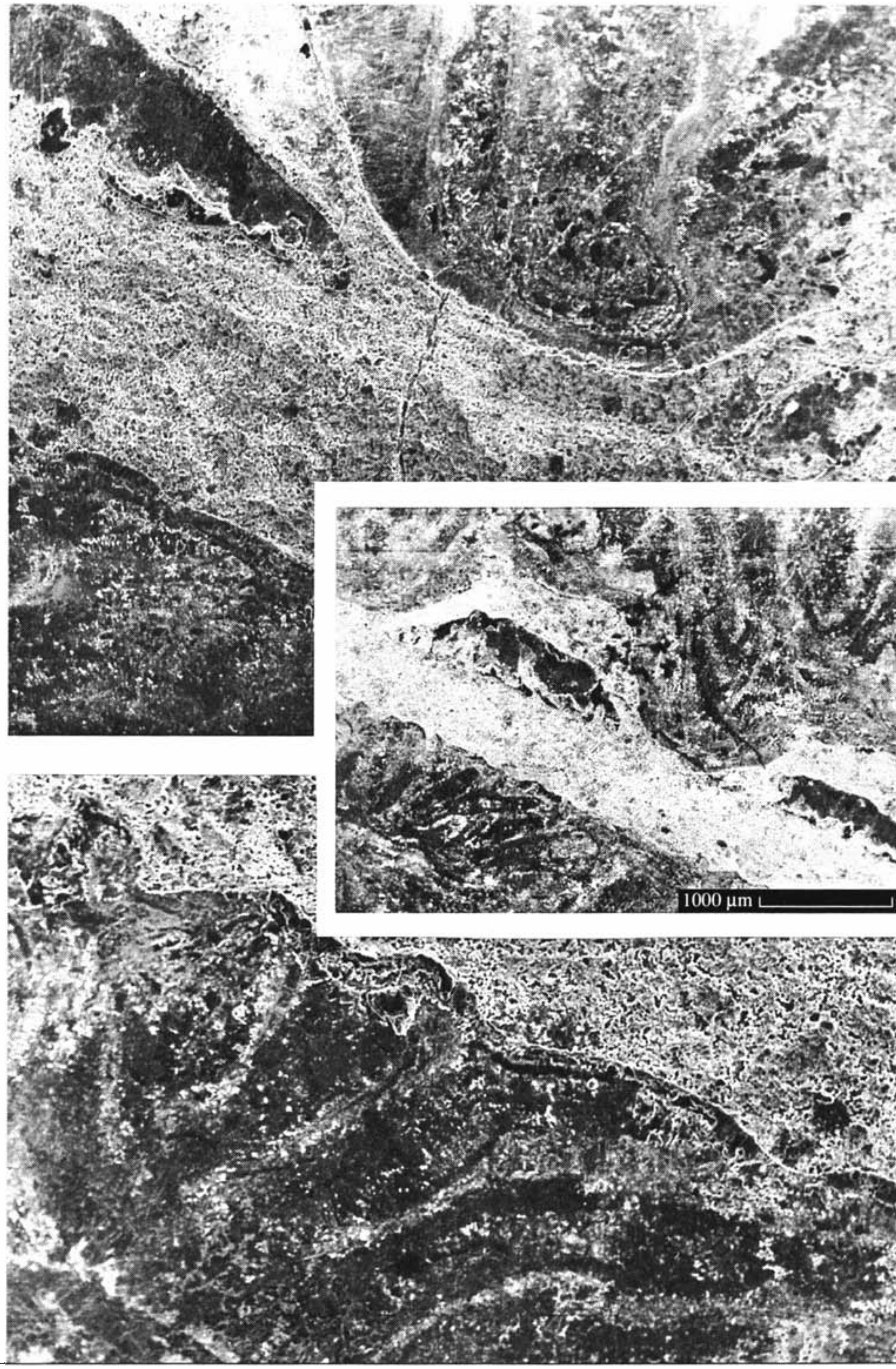
Fig. 1. *Astrovia adorea* sp. nov.; holotype PIN, no. 2218/173; an enlarged detail of Pl. 7; fig. 1a, ×14; on the dorsal side the internal dark layer of the wall level with the inclusion is curved inwardly; the first layer of the episeptal deposits turns round the septal neck and merges with the hyposeptal deposits of the previous chamber, the next, darker layer turns round this contact and merges with a like layer of the episeptal deposits of the previous chamber; level with the second and fourth adapical foramina, the last thin layer of the episeptal deposits comes off from the previous layer as a thin film; on the ventral side the virgulae of the ectosiphonal deposits come in contact with the epi- and hyposeptal cameral deposits in the chamber cavity, and on the siphon side their bases bear longitudinal layers, which were secreted later; on the dorsal side the ectosiphonal deposits are separated from the cameral deposits by an interspace filled with rock material; Kuznetsk Basin, Gur'evsk, Starogur'evskii quarry; Lower Devonian, Pragian Stage, upper Krekovo layers.



Explanation of Plate 9

Fig. 1. *Astrovia adorea* sp. nov.; holotype PIN, no. 2218/173 (SEM photograph); (1a) and (1b) a wall of two layers with an inclusion between them and the septa with short mural parts; the surface of which is covered by the first thin layer of the cameral deposits; (1c) a marginal area of the external layer of the wall with curved back constituent structures; (1d) a prismatic structure of the external layer; (e) an enlarged detail of (1d), prisms connected with slender curved processes; (1f) "featherlike" virgulae of the cameral deposits in the cross section of the chamber; and (1g) "featherlike" virgulae of the cameral deposits in the longitudinal section of the chamber; Kuznetsk Basin, Gur'evsk, Starogur'evskii quarry; Lower Devonian, Pragian Stage, upper Krekovo layers.

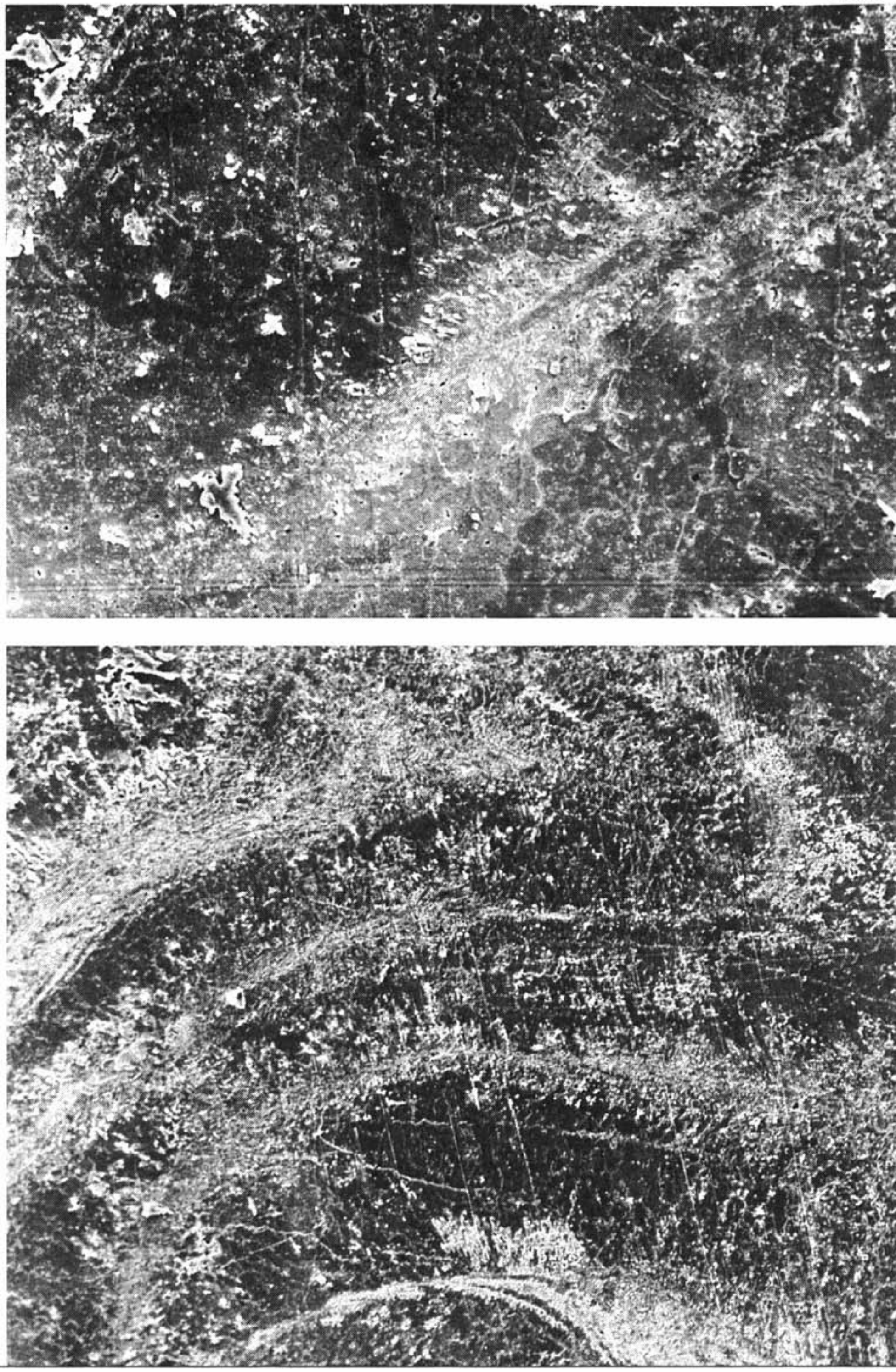
Plate 10



Explanation of Plate 10

Fig. 1. *Astrovia adorea* sp. nov.; holotype PIN, no. 2218/173 (SEM photograph); enlarged details of Pl. 8: (1a) ectosiphonal and cameral deposits in the region of the second adapical neck (the ventral side at the bottom); (1b) cameral and ectosiphonal deposits in the region of the first adapical septal neck; on the dorsal side the episeptal cameral deposits pass through the septal neck, and the layer nearest to the neck curls around it in a spiral pattern and adjoins the hyposeptal deposits of the previous chamber; the next layer of the episeptal deposits comes to an end after passing far behind to the episeptal deposits of the previous chamber; (1c) ectosiphonal deposits on the ventral side of the second lowest chamber; virgulae come off from the siphon into the chamber toward the cameral deposits; longitudinal layers of the ectosiphonal deposits lie on the bases of virgulae; Kuznetsk Basin, Gur'evsk, Starogur'evskii quarry; Lower Devonian, Pragian Stage, upper Krekovo layers.

Plate 11



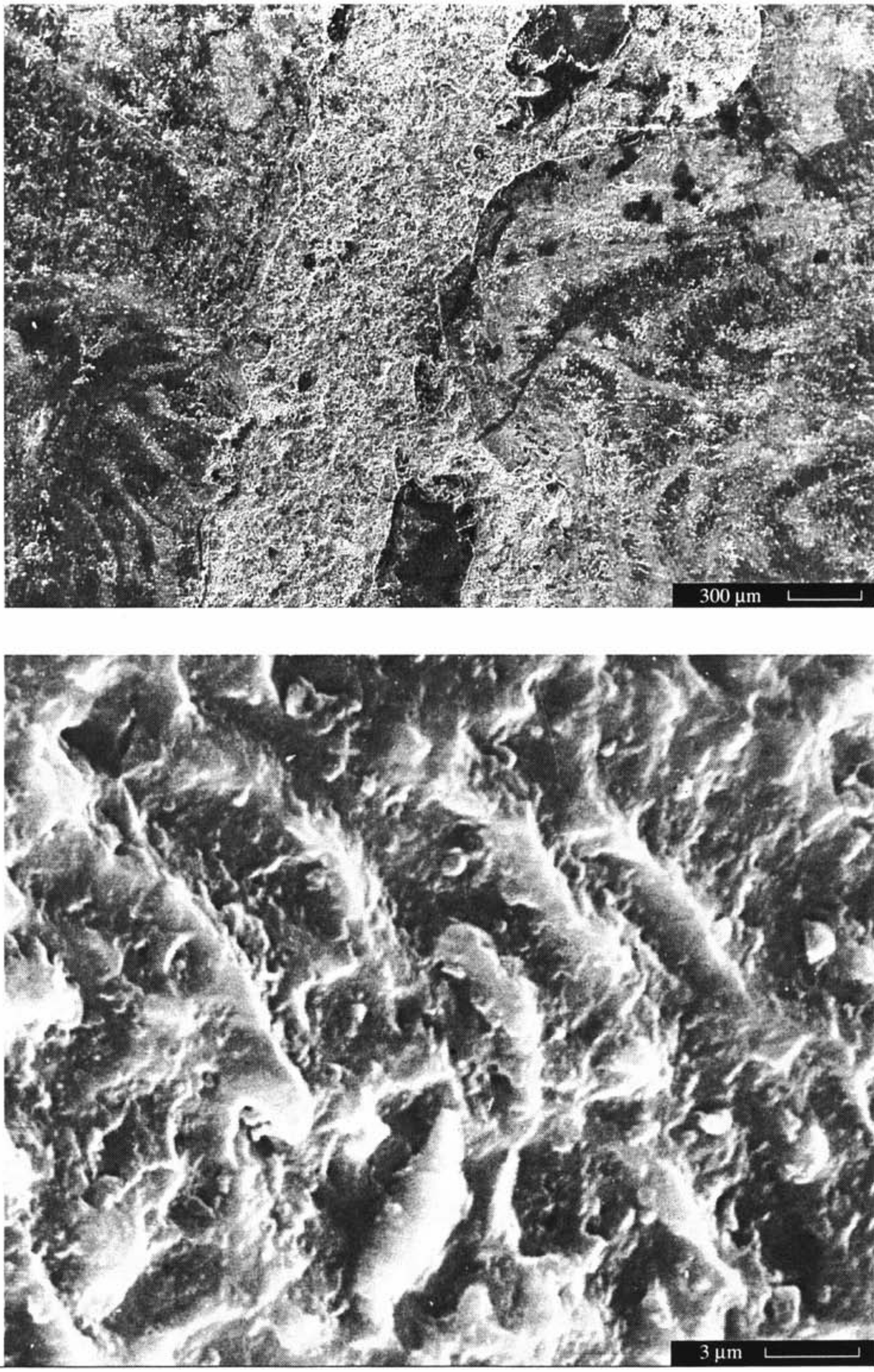
1a

1b

Explanation of Plate 11

Fig. 1. *Astrovia adorea* sp. nov.; holotype PIN, no. 2218/173 (SEM photograph): (1a) an enlarged detail of pl. 10, fig. 1c, the fourth lowest virgula of the ectosiphonal deposits showing a hollow, gradually narrowing axis and smaller virgulae that come off from it at an oblique angle; at the base the axis of the virgula is curved, ×440; (1b) sinuous virgulae of the cameral deposits; small virgulae that come off from the axis of the lowest of them are hollow articulated tubules, ×170; Kuznetsk Basin, Gur'evsk, Starogur'evskii quarry; Lower Devonian, Pragian Stage, upper Krekovo layers.

Plate 12

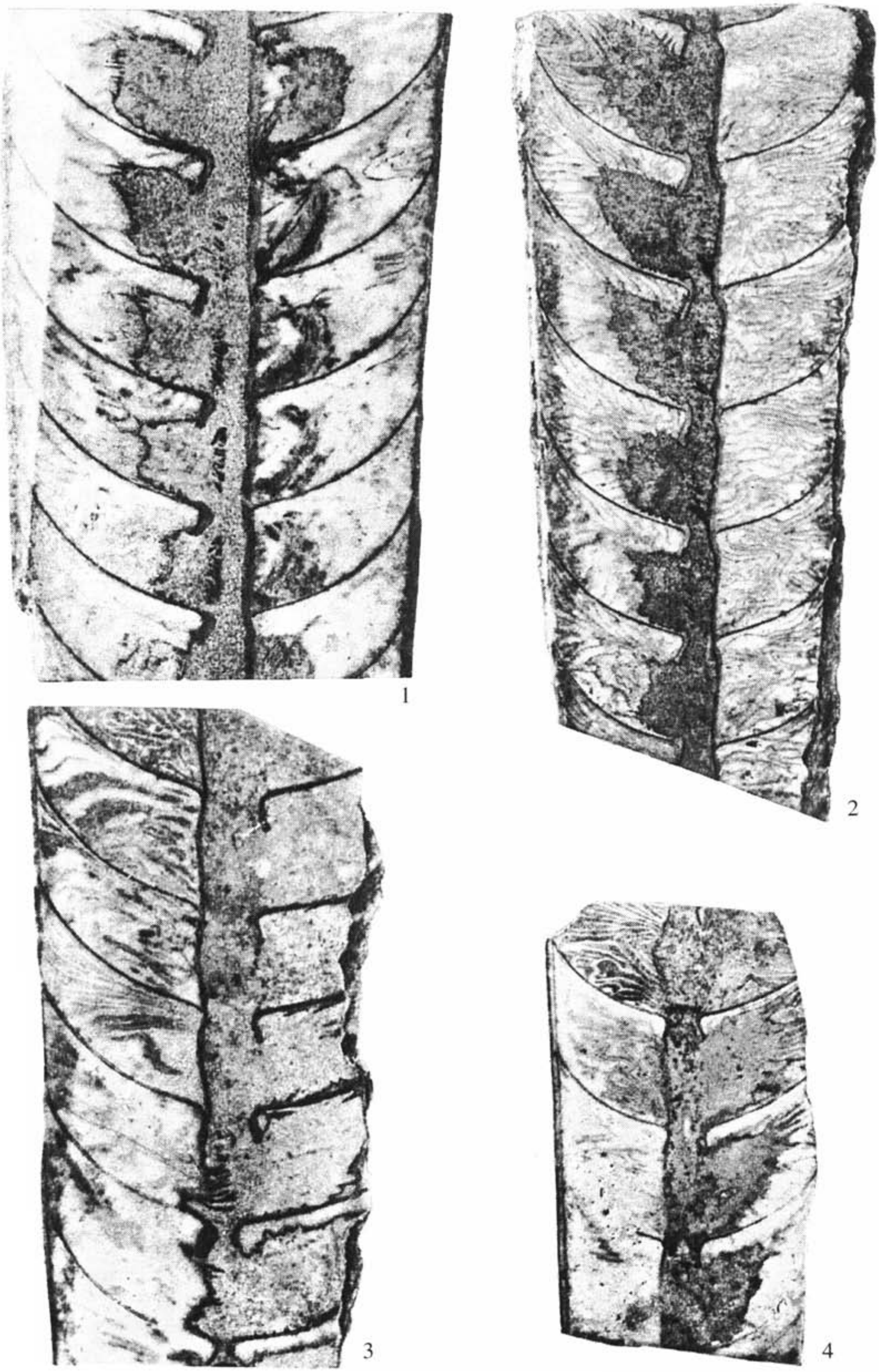


Explanation of Plate 12

Fig. 1. *Astrovia adorea* sp. nov.; holotype PIN, no. 2218/173 (SEM photograph), a longitudinal section in the region of the second adapical neck (the ventral side is at the left); thin septa with very short orthochoanitic septal necks are difficult to distinguish among sinuous cameral virgulae: ectosiphonal virgulae are located on the left, at the bottom of the septum under the hyposeptal deposits; at the right, on the dorsal side, the septum and barely perceptible neck are enveloped by sinuous virgulae of the epi- and hyposeptal deposits; Kuznetsk Basin, Gur'evsk, Starogur'evskii quarry; Lower Devonian, Pragian Stage, upper Krekovo layers.

Fig. 2. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455 (SEM photograph); considerably modified prismatic microstructure of the cameral deposits; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of Yagel triangulation point, and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.

Plate 13



Explanation of Plate 13

Fig. 1. *Astrovia marhoumensis* sp. nov.: the holotype is the specimen depicted by Mutvei (1956) in pl. 1, fig. 4 and stored at the Swedish Museum of Natural History in Stockholm; longitudinal medial section of the part of the phragmocone, the ventral side is on the right, ×2; on the ventral side the ectosiphonal deposits penetrate deep into the chamber cavity and come in contact with the epi- and hyposeptal cameral deposits; on the siphon side they bear a dark longitudinal layer of later ectosiphonal deposits; on the dorsal side the ectosiphonal deposits are at initial stages of their growth, look like thin, slightly bent transverse plates in cross section, and are arranged in longitudinal rows against the cavities of all chambers; the episeptal deposits as a very thin layer pass through the short, slightly expanding septal neck and merge with the more massive hyposeptal deposits of the previous chamber; northern Africa, northern Sahara, Marhouma; the Middle Devonian, Eifelian.

Figs. 2–4. *Syndikoceras mutveii* sp. nov.; (2) the holotype is the specimen depicted by Mutvei in pl. 1, fig. 1 and stored at the Swedish Museum of Natural History in Stockholm; longitudinal medial section of some part of the phragmocone, the ventral side is on the right, ×1.25; cameral deposits consist of thin plates that come off from the chamber wall and septa and form complex folds; on the dorsal side the episeptal deposits pass through the septal neck as a thin layer and merge with the more massive hyposeptal deposits of the previous chamber; on the ventral side the cameral deposits fill the chamber; on the siphon side they are lined with a thin dark layer, which probably consists of metacameral deposits; ectosiphonal deposits that have only preserved in several chambers look in cross section like longitudinal rows consisting of thin slightly bent transverse plates, which on the ventral side adjoin the metacameral deposits; (3) and (4) specimens depicted by Mutvei in pl. 1, figs. 2 and 3 and housed at the Swedish Museum of Natural History in Stockholm; longitudinal medial sections of phragmocones, the ventral side is on the left (fig. 3, ×2; fig. 4, ×1.4); the necks and the cameral and ectosiphonal deposits are similar to those described in the holotype; northern Africa, northern Sahara, Marhouma; the Middle Devonian, Eifelian.

Comparison. See below Comparison section for *S. mutveii*.

Material. The holotype, which was collected by G.I. Kharitonicheva in 1975.

Syndikoceras mutveii Zhuravleva, sp. nov.

Plate 13, figs. 2–4; Plate 16, figs. 2 and 3

Etymology. In honor of X. Mutvei.

Holotype. The specimen depicted by Mutvei (1956) in pl. 1, fig. 1 is stored at the Swedish Museum of Natural History in Stockholm; Northern Sahara, 30 km from Beni Abbès; Middle Devonian, Eifelian.

Description. The conch expands at an angle of about 7°–8°. The structure of the wall and its surface are unknown.

The chamber is of medium length, with a length-to-width ratio of 0.33–0.40.

The septa are concave for a distance of approximately 0.7–0.8 the length of the chamber and inclined to the ventral side. The suture is unknown.

The siphon is narrow; its diameters in the septal foramen and level with the septal necks are about 0.08–0.11 and 0.16–0.17 the diameter of the phragmocone, respectively. At this level the "segments" of the siphon are most convex. The septal necks are clinochoanitic, their length is 0.13–0.17 the length of the chamber.

The cameral deposits in the longitudinal medial section of the phragmocone look like thin, sinuous plates that come off from the wall and septa to the siphon and pass through the septal foramen. On the ventral side a thin longitudinal layer overlies the cameral deposits that fill the chamber cavity. This layer apparently consists of metacameral deposits. Only a part of the ectosiphonal deposits has been preserved in the form of small rows of thin inclined plates that adjoin the metacameral deposits against the cavities of the chambers (Pl. 13, figs. 2, 3). The microstructure of the cameral, metacameral, and ectosiphonal deposits has not been studied.

Comparison. It differs from *S. arcticum* in the greater angle of the conch expansion (7°–8° instead of 4°–5°), more narrow siphon in the septal foramen (0.08–0.11 instead of 0.15–0.17 the diameter of the phragmocone), and the clinochoanitic septal necks.

Remarks. These measurements are not quite accurate since all specimens are worn on one side.

Occurrence. Middle Devonian, Eifelian of the northern Sahara (Beni Abbès).

Material. Only three specimen depicted by Mutvei have been measured.

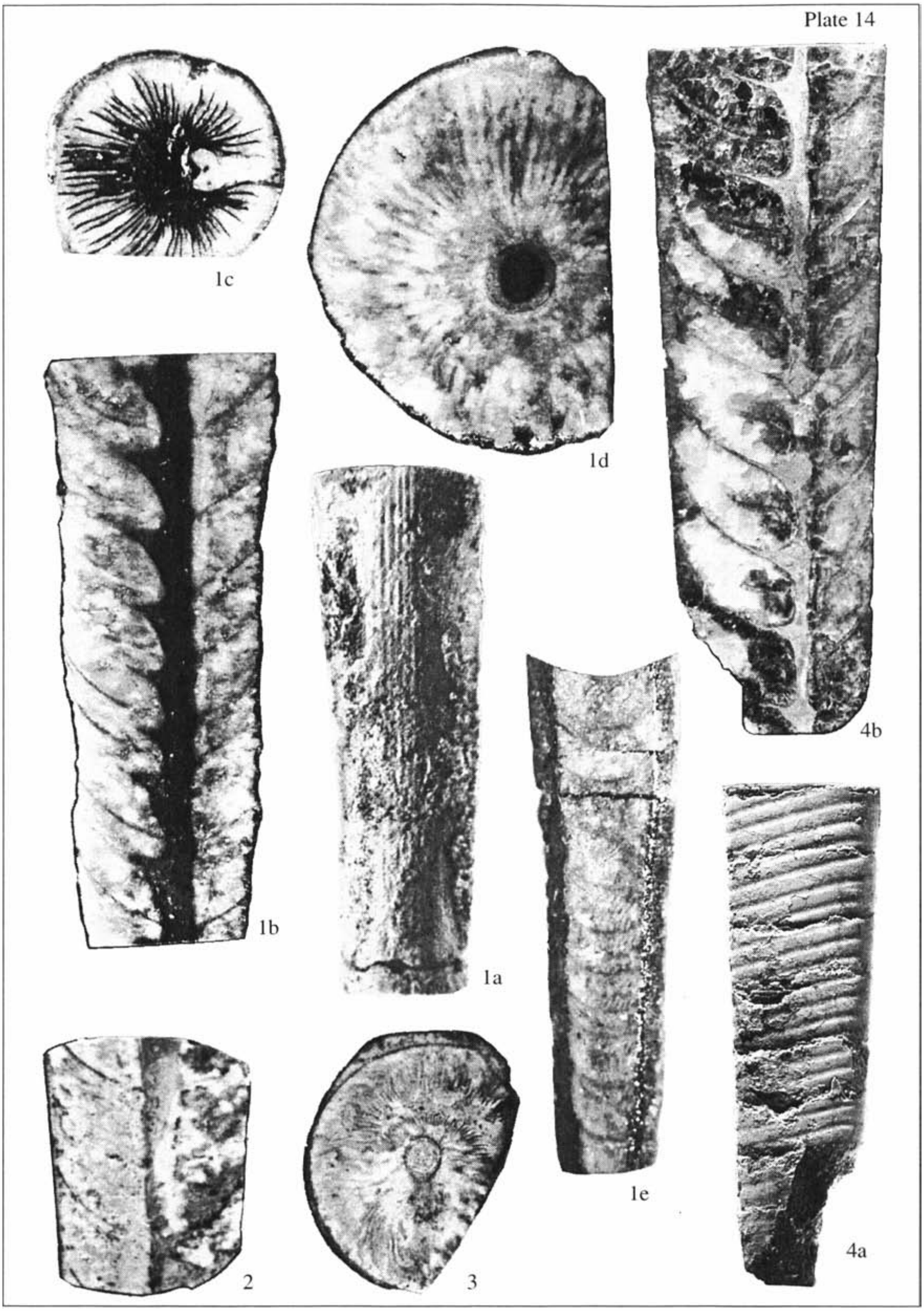
Family Plicatoceratidae Zhuravleva, fam. nov.

Diagnosis. Conch orthoceraconic. Siphon slightly displaced ventrally. Cameral deposits shaped like elongated two-layered structures, "vermiculars," forming extremely complex folds and interlacements. Laminar metacameral deposits present. Microstructure of cameral and metacameral deposits represented by spongy-porous structure. Ectosiphonal deposits unknown.

Composition. The genus *Plicatoceras* Niko, 1991. It is quite probable that this family also contains forms depicted by Kolebaba (1999a) in pl. 4, fig. 1 under the name *Nucleoceras obelus* and in pl. 6, figs. 4 and 5 under the name *N.* sp. B.

Comparison. It differs from Flowerinidae in the cameral deposits consisting of complex vermiculars, with a microstructure consisting of a spongy-porous structure; from Ostreioceratidae, in the cameral deposits composed of vermiculars and in the presence of metacameral deposits; from Astroviidae, in the cameral deposits composed of vermiculars with a microstructure represented by a spongy-porous structure rather than of virgulae and in the absence of ectosiphonal

Plate 14



Explanation of Plate 14

Fig. 1. *Gogonoceras visendum* Zhuravleva, 1961; holotype PIN, no. 1359/505; (1a) a fragment of the phragmocone that preserved an internal layer of the conch wall with fine longitudinal folds, ×2; (1b) a longitudinal medial section of the phragmocone (the ventral side is on the right); on the dorsal side the epi- and hyposeptal cameral deposits completely enclose the septa along with their short necks; on the ventral side the ectosiphonal deposits adjoin the cameral deposits and only slightly penetrate into the chamber cavity, ×4; (1c) a cross section of the adoral end below the septal neck; the cameral deposits are closely spaced, slightly undulating virgulae; a thick complex structure consisting of many virgulae is located in the middle of the ventral side, ×3; (1d) a cross section at the mid-length of the holotype through the septal neck (the ventral side is at the bottom); at this level the thick mid-ventral structure is absent; the siphon is surrounded by virgulae of the hyposeptal deposits, these are the episeptal virgulae of the previous chamber near the wall and the episeptal deposits of the next chamber in the interior of the septal neck, ×6; (1e) a tangential section showing sinuous virgulae of the epi- and hyposeptal deposits; Sverdlovskaya Region, Artemovskii district, left bank of Bobrovka Creek, 400 m south-southwest of the cupola furnace at the village of Pokrovskoe; Middle Devonian, lower Eifelian.

Figs. 2 and 3. *Syndikoceras*? *mutveii* sp. nov.; (2) specimen PIN, no. 4738/1, longitudinal medial section of four incomplete chambers (the ventral side is on the left); cameral deposits are recrystallized; the siphonal cavity shows the metacameral and ectosiphonal deposits (transverse plates in the second lowest segment), ×1.5; (3) specimen PIN, no. 4738/2, cross section level with the septal neck made at a small angle to the axis of the siphon and through the lamellar episeptal deposits (near the walls) and the hyposeptal deposits (near the siphon); cameral and, probably, metacameral deposits inside the septal neck, ×1.4; northern Africa, Algeria, 30 km from the oasis town of Beni Abbès; Middle Devonian, ?Eifelian.

Fig. 4. *Flowerina bucheri* (Flower, 1941); specimen PIN, no. 1793/1450; (4a) a cast with impressions of ornamentation of flat rings inclined to the ventral side, ×1.0; (4b) a dorsoventral section of the phragmocone (the ventral side is on the right); on the dorsal side the epi- and hyposeptal deposits of comparable volumes almost entirely enclose the septa with their necks and leave only a small free space within the angles formed by the necks; on the ventral side most of the chamber cavity is apparently occupied by the hyposeptal deposits; Ukraine, Podolia, right bank of the Dniester River near the mouth of the Studenitsa River; Lower Silurian, Wenlock, Kitaigorodskii horizon.

deposits; from Lamellorthoceratidae, in the cameral deposits composed of vermiculars rather than intricately folded plates with a complex prismatic microstructure and in the absence of ectosiphonal deposits.

Occurrence. Upper Silurian, Ludlow of the Czech Republic, Lower Devonian, lower Lochkovian of central Japan, Lower Devonian, Emsian of Kazakhstan.

Genus *Plicatoceras* Niko, 1991

Plicatoceras: Niko, 1991, p. 917.

Type species. *P. nishidai* Niko, 1991; Lower Devonian, lower Lochkovian; Central Japan.

Diagnosis. Conch slowly expanding, laterally compressed and oval in cross section. Surface smooth. Suture straight or with small lateral lobe. Septal necks orthochoanitic. Cameral deposits represented by plates-folds arranged in extremely complex structures and possessing two-layered wall and spongy-porous microstructure.

Species composition. Type species and *P. bublichenkoi* sp. nov.

Occurrence. Lower Devonian, lower Lochkovian of Central Japan and Emsian of Kazakhstan.

Plicatoceras bublichenkoi Zhuravleva, sp. nov.

Plates 30–33

Etymology. In honor of N.L. Bublichenko, a geologist and paleontologist.

Holotype. PIN, no. 4721/1; Kazakhstan, northeastern Balkhash area, north of the Kopa Hill, located north of the small town of Sayak; Lower Devonian, Emsian, Kazakh horizon.

Description (Figs. 8a–8c). The conch expands at an angle of 3°–4°. The holotype, a fragment of the cast, is 17 mm long and consists of three and a half chambers. Its adoral diameter is 10 mm. The ratio of diameters is 1.30–1.27.

The surface of the cast is nodular. The adapical end of the cast shows episeptal vermiculars that merge with each other as they approach the wall. The chamber is of medium length. The median diameter contains slightly less than two chambers. The septa are concave less than half the length of the chamber and slightly inclined to the ventral side.

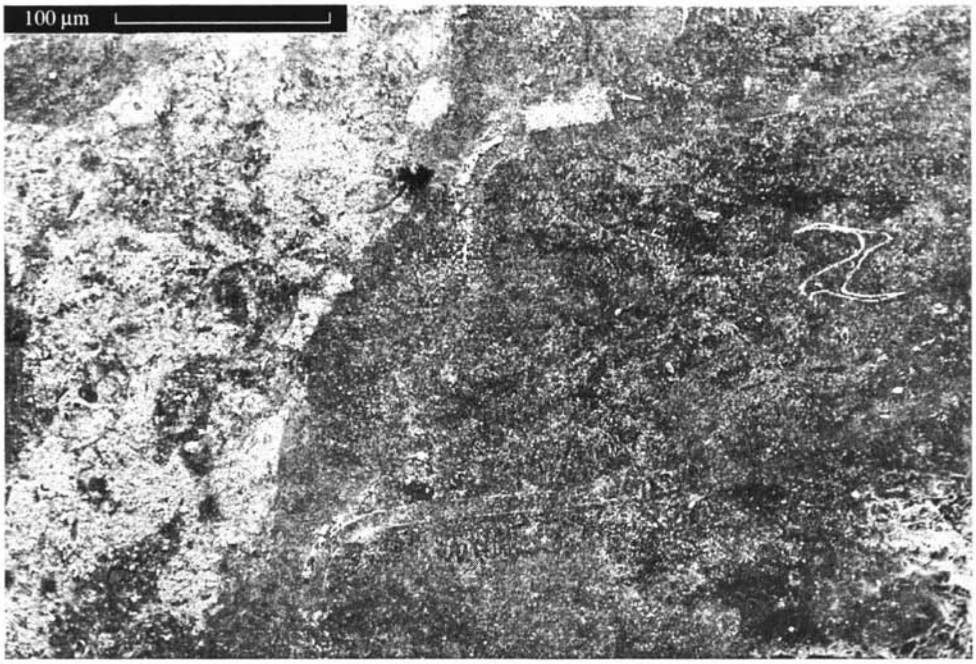
The suture is slightly inclined to the ventral side and forms a small lateral lobe.

The diameter of the siphon in the septal foramen is 0.14–0.15 the diameter of the phragmocone. The septal necks are orthochoanitic, their length is 0.2 the length of the chamber.

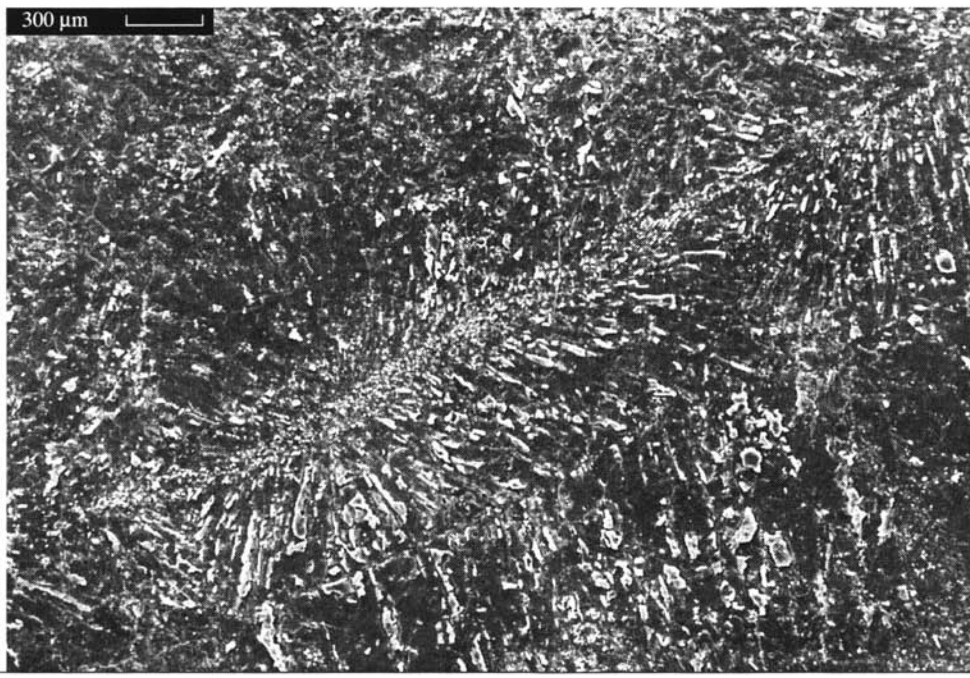
The cameral deposits consist of plates-folds that form accretions of extremely complex shapes. Their detailed description has been given above. The metacameral deposits within the region of the phragmocone that has been studied are developed only on the ventral side of the siphon; they form longitudinal sinuous layers on the surface of the cameral deposits. The microstructure of the cameral and metacameral deposits is a spongy matrix with porous walls.

Comparison. It differs from *P. nishidai* in having chambers half as long, suture inclined ventrally rather than dorsally, siphon wider in the septal foramen (0.14–0.15 instead of 0.10 the diameter of the phragmocone), and longer septal necks (0.2 instead of 0.06 the length of the chamber) and in the shape of folds and various meshes formed by the plates-folds.

Plate 15



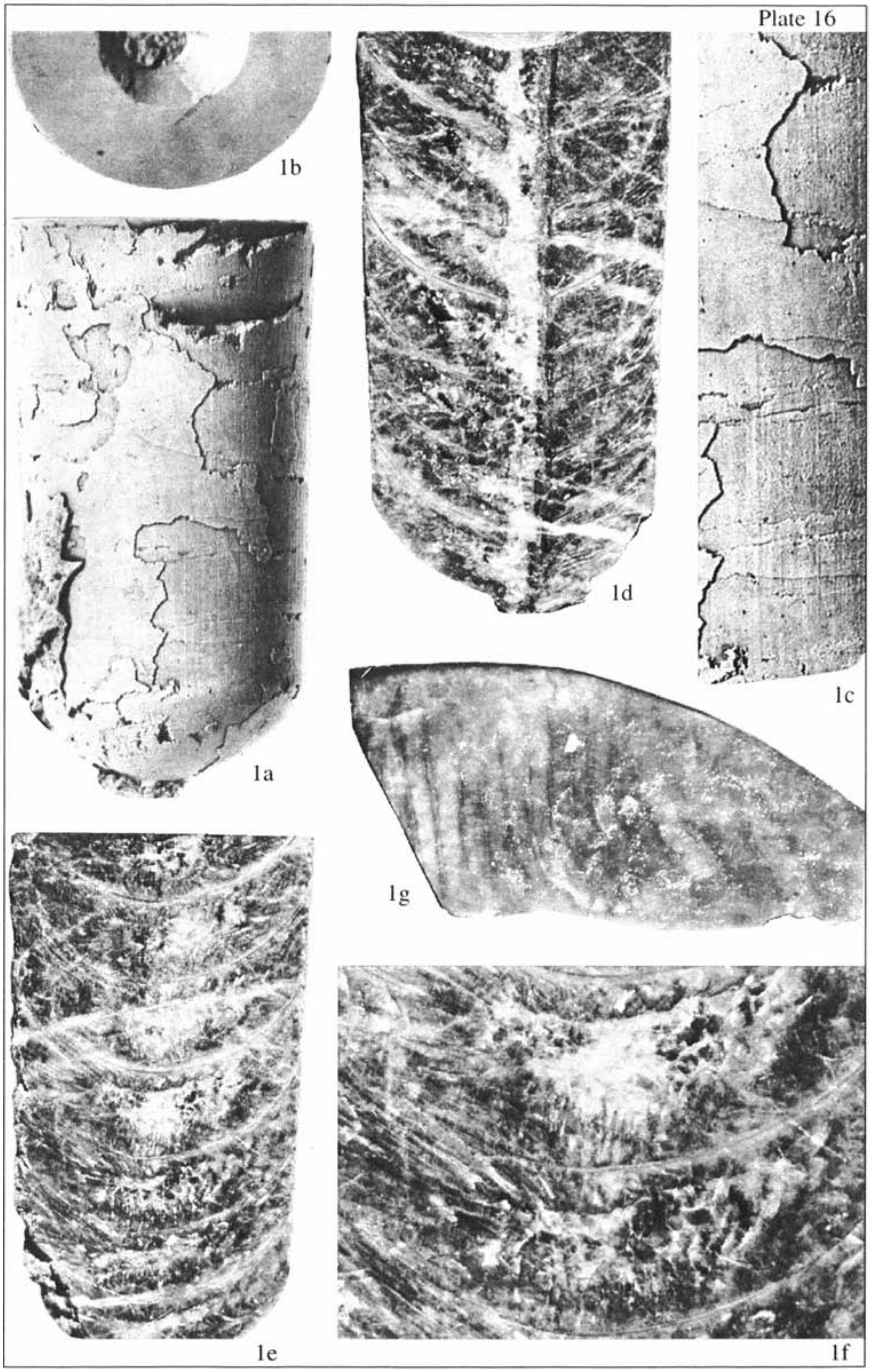
1a



1b

Explanation of Plate 15

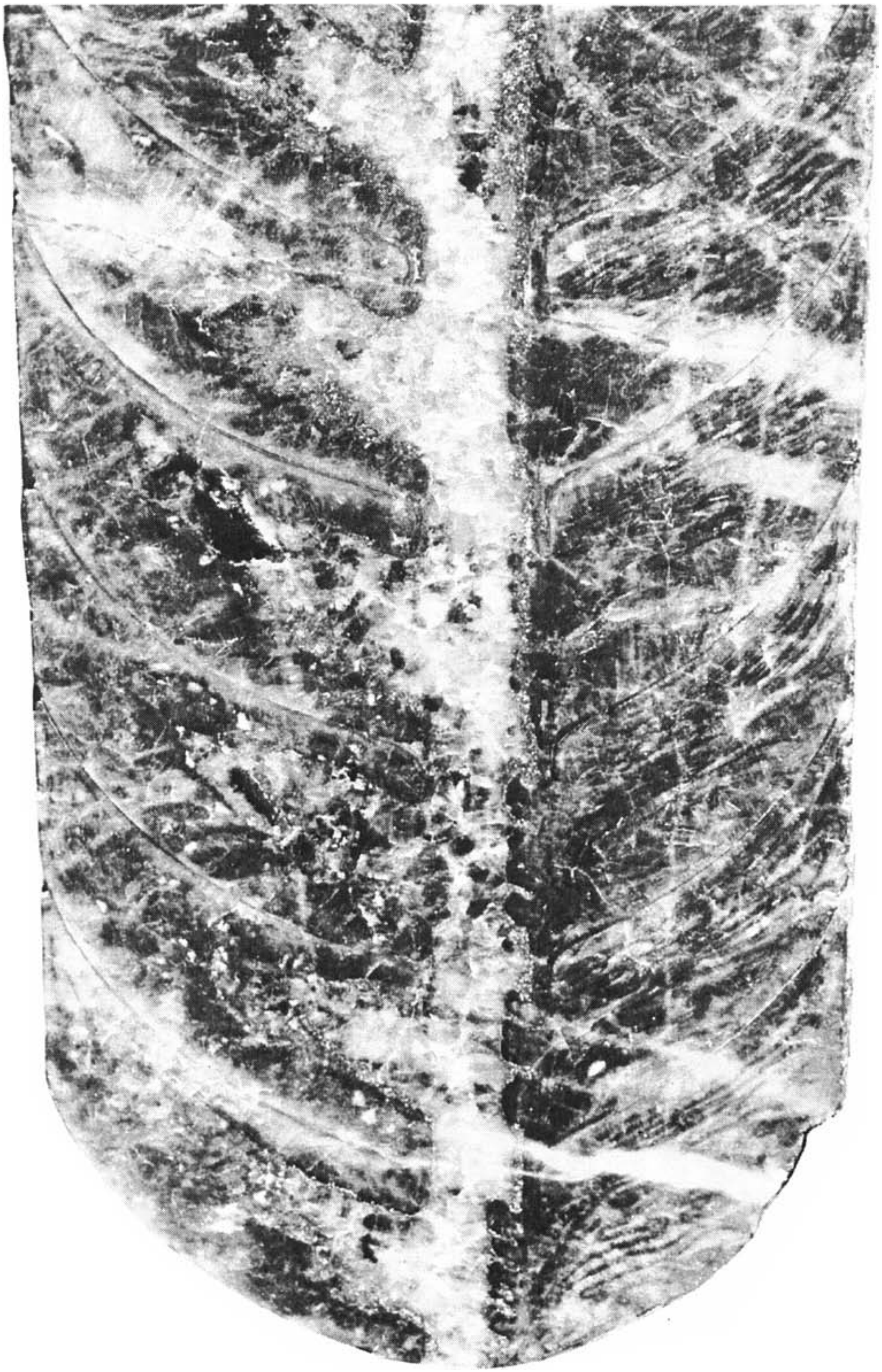
Fig. 1. *Gorgonoceras visendum* Zhuravleva, 1961; holotype PIN, no. 1359/505 (SEM photograph); (1a) ventral part of two incomplete chambers in medial section: two septa with short orthochoanitic necks among tangled virgulae of the cameral and ectosiphonal deposits; the latter adjoin the cameral deposits; (1b) two virgulae of the cameral deposits, the section of the upper virgula is made along the hollow tubular axis, and the section of the lower virgula is made near the axis; small articulated branches come off from the axes at an oblique angle; Sverdlovskaya Region, Artemovskii district, left bank of Bobrovka Creek, 400 m south-southwest of the cupola furnace at the village of Pokrovskoe; the Middle Devonian, lower Eifelian.



Explanation of Plate 16

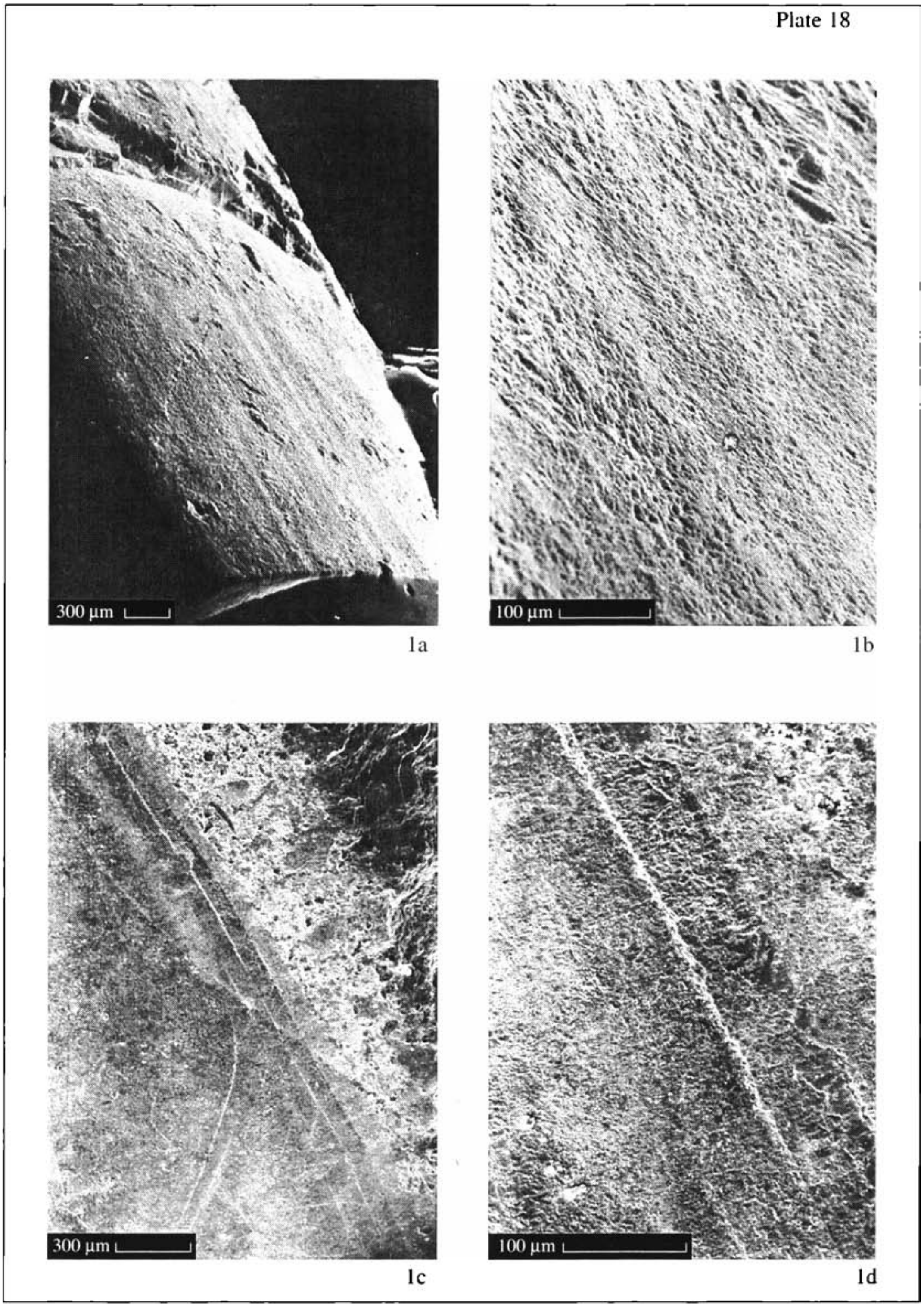
Fig. 1. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455; (1a) outward appearance, lateral side, the ventral side is on the left, ×2.4; (1b) a cross section (half), ×2.4; (1c) an enlarged detail of (1a): fragments of the conch wall showing a longitudinal ornamentation on the cast, ×5; (1d) a medial section, ventral side: lamellar cameral deposits fill the chamber; longitudinal layer of metacameral deposits overlies the cameral deposits; ectosiphonal deposits adjoin the metacameral deposits, ×2.6; (1e) tangential section showing plates of the epi- and hyposeptal deposits, which form complex folds, ×2.7; (1f) an enlarged detail of (1e), ×5.4; (1g) part of the cross section: closely spaced featherlike plates undulating ventrally (right), ×12; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of Yagel triangulation point and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.

Plate 17



Explanation of Plate 17

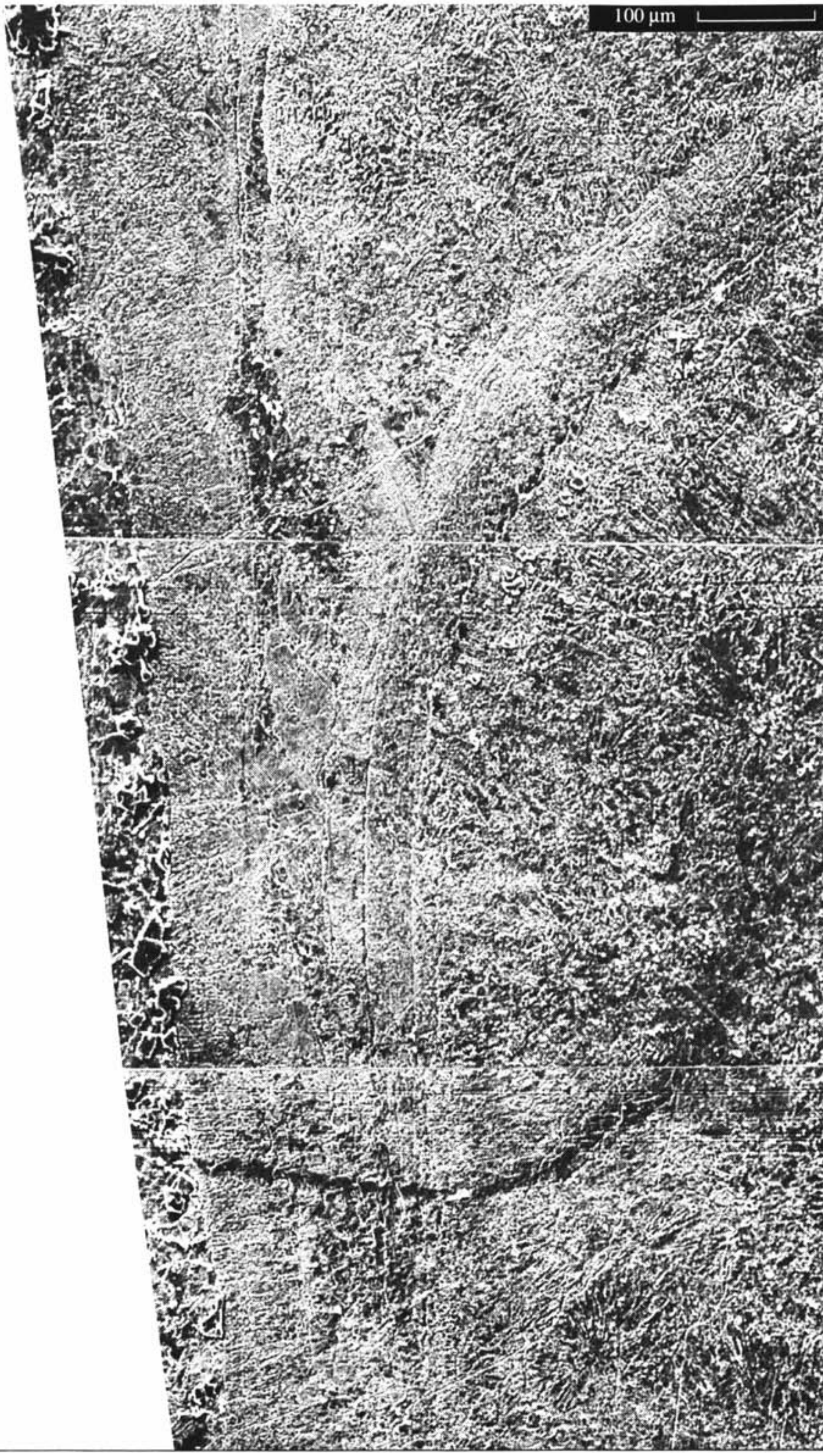
Fig. 1. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455, an enlarged detail of Pl. 16, fig. 1d: on the ventral side the cameral plates come off from the chamber wall and the septa near the walls and stretch almost parallel to the septum, thus forming narrow folds; the cameral deposits are overlain by a longitudinal layer of metacameral deposits; ectosiphonal deposits look like transverse plates arranged in longitudinal rows against each chamber; in the adapical chambers they adjoin the metacameral deposits, in the adoral chambers, they stop short of the latter; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.



Explanation of Plate 18

Fig. 1. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455 (SEM photograph); (1a) a cast of one chamber with impressions of longitudinal ornamentation; (1b) an enlarged detail of (1a) showing the surface of the cast, which consists of fine longitudinal plates aligned at a small angle to the axis of the conch; (1c) wall of the conch, which consists of three layers, and the adjacent septum with a short mural part; (1d) an enlarged detail of the wall: the boundary between the internal and intermediate layers is most clearly defined; the surface of the external layer is overlain by rock material; Novaya Zemlya, Yuzhny Island 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.

Plate 19



Explanation of Plate 19

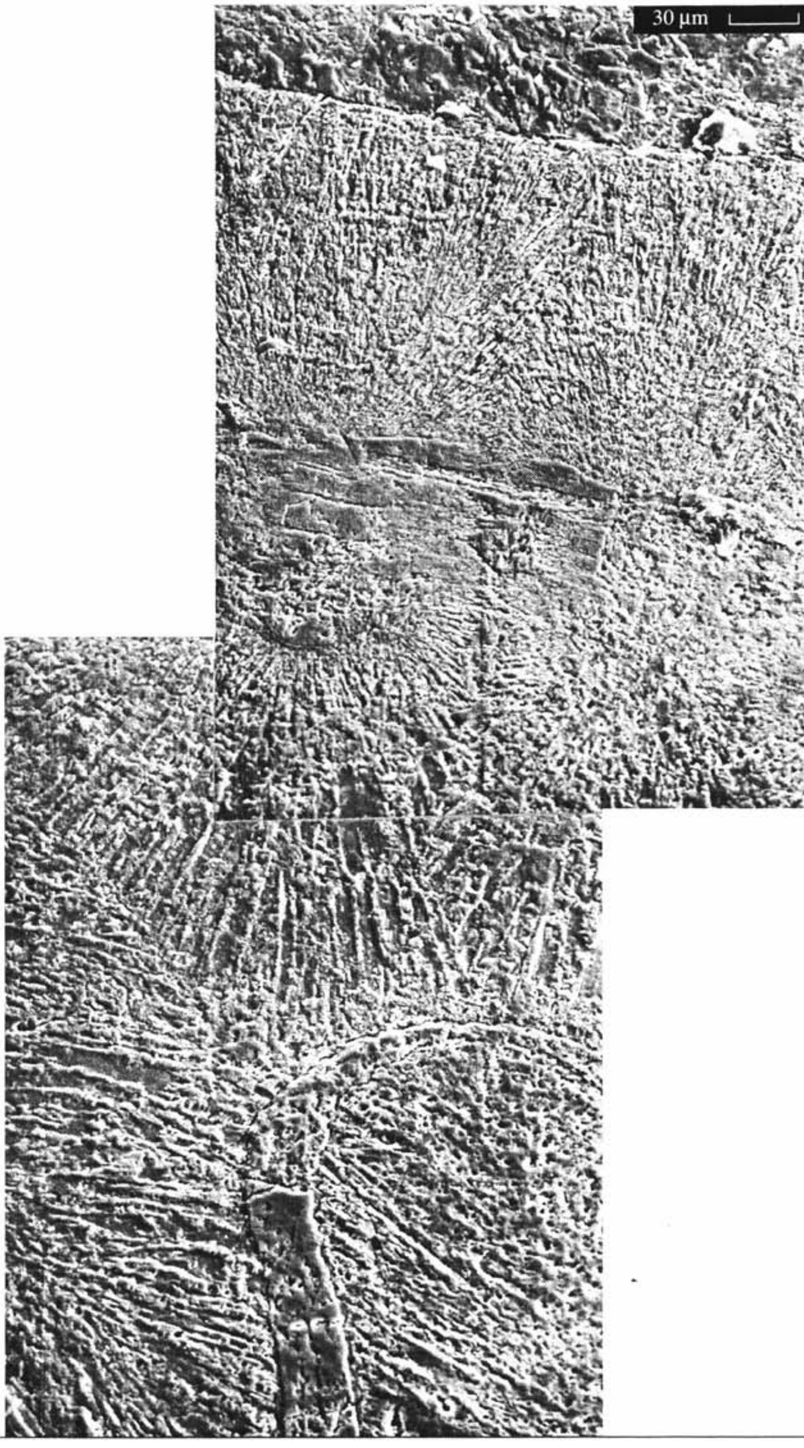
Fig. 1. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455 (SEM photograph), a longitudinal medial section in the region of the septal neck on the ventral side: the episeptal deposits pass through the septal neck and merge with the hyposeptal deposits of the previous chamber; the edge neck is poorly defined; the first layer of the episeptal deposits taper out where the septum passes into the neck; cameral deposits form complex featherlike or star-shaped structures; the metacameral deposits consist of complex elongated rays, which are arranged at a right angle to the surface of the cameral deposits; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.

Plate 20

Explanation of Plate 20

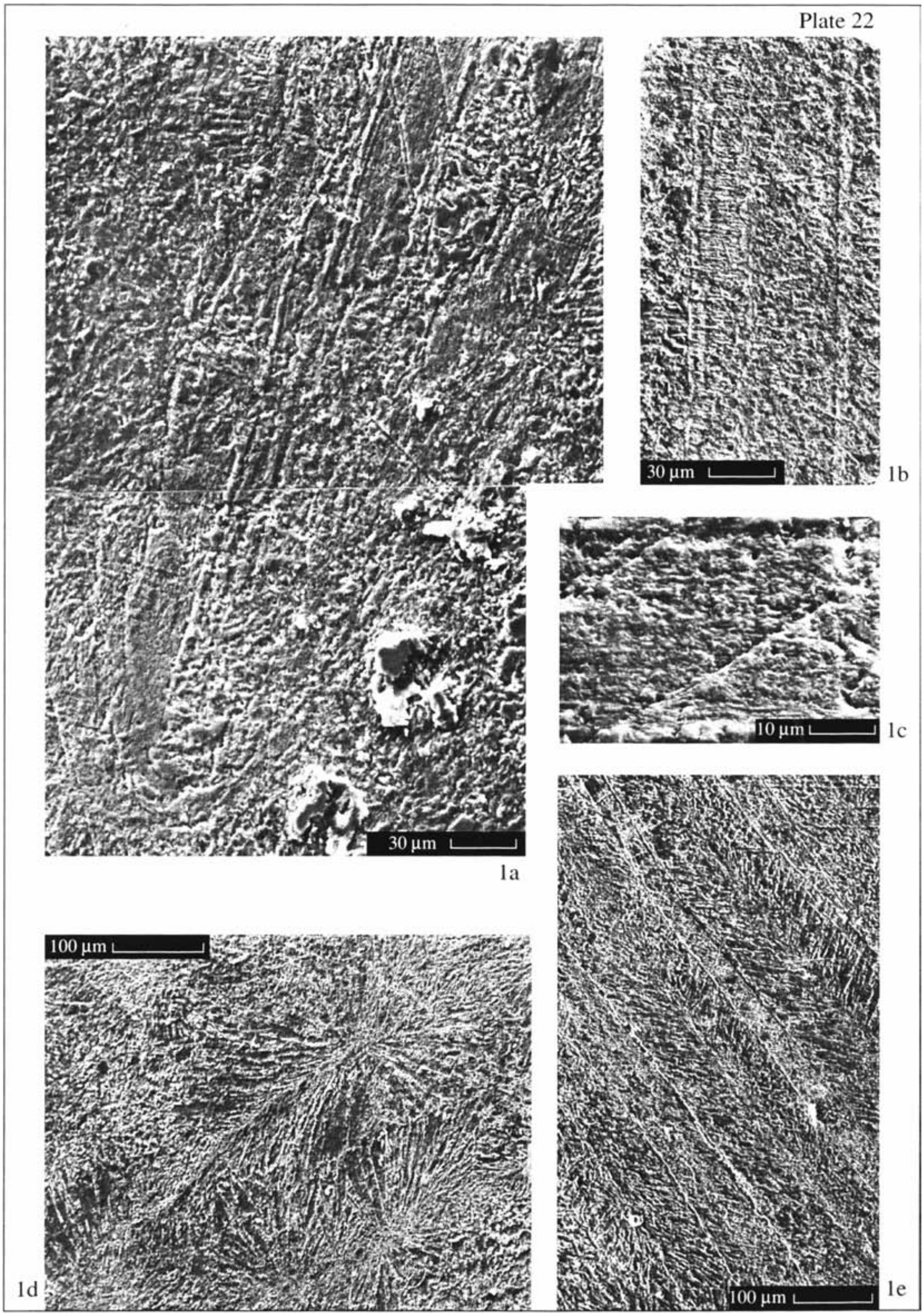
Fig. 1. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455 (SEM photograph), a longitudinal medial section in the region of the septal neck: the episeptal cameral deposits pass through the septal neck and merge with the hyposeptal deposits of the previous chamber; the edge of the neck looses its clear contours; cameral deposits form complex featherlike and star-shaped structures consisting of complex rays, which radiate from some denser regions; in the metacameral deposits the rays radiate at a right angle, more rarely radially, from the "amorphous" regions, which form a broken line between the cameral and metacameral deposits; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.

Plate 21



Explanation of Plate 21

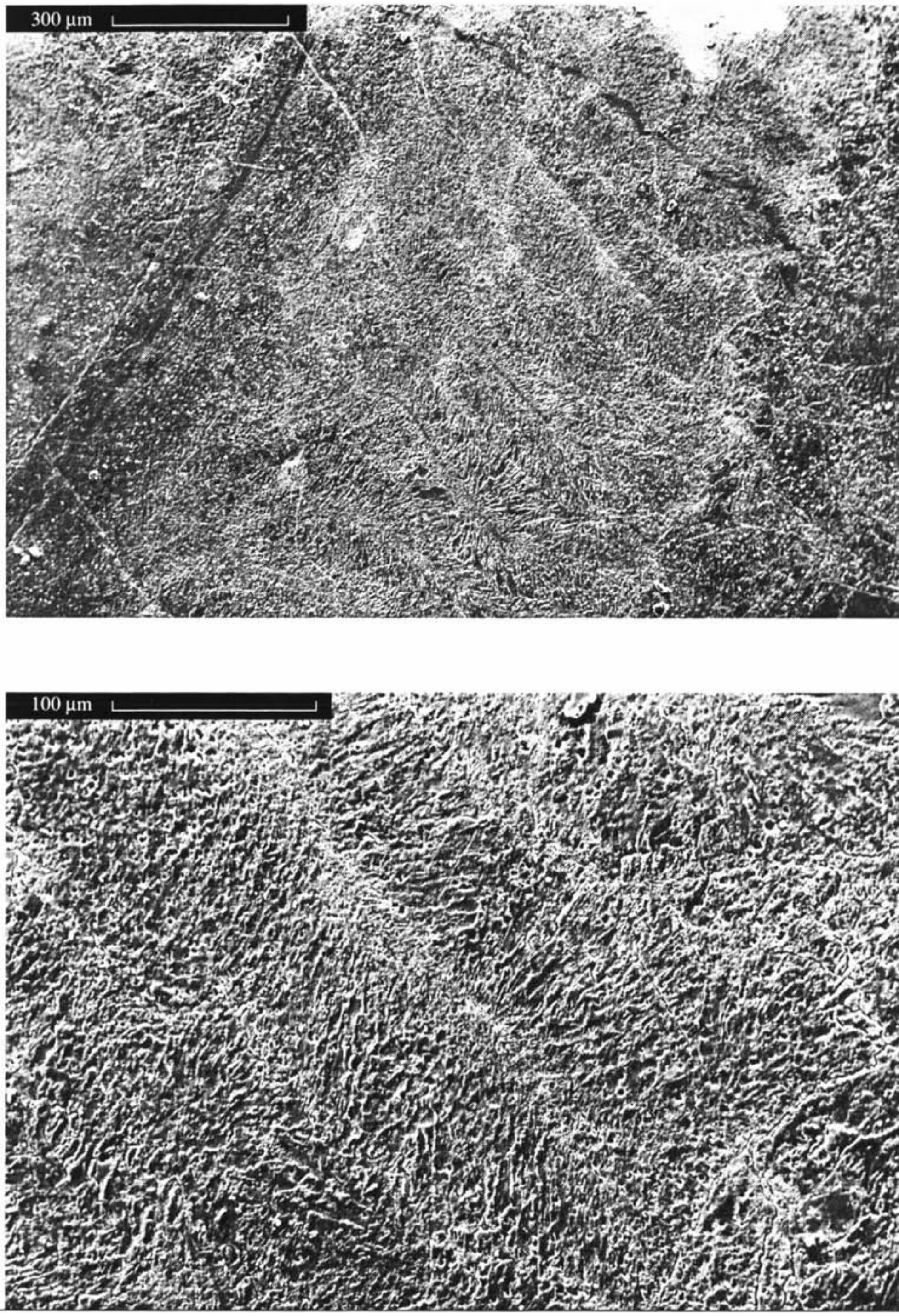
Fig. 1. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455 (SEM photograph), a part of the medial section of the chamber where the cameral and metacameral deposits consist of rays radiating from "amorphous" regions, which, perhaps, consist of like structures that are packed more tightly; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.



Explanation of Plate 22

Fig. 1. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455 (SEM photograph): (1a) a medial section level with the septal neck, in which a nacreous microstructure is partly preserved; the edge of the neck, in which the contours are obscured, and the first layer of the cameral deposits that overlies it are enclosed by the next layer of the cameral deposits that has an undulating surface; (1b) a part of the septum that partly preserved a nacreous microstructure and the first layer of the cameral deposits that overlies it and in which the structural elements are aligned perpendicular to its surface; (1c) an enlarged detail of (1a), a nacreous microstructure of the septal neck; (1d) a portion of the cameral deposits with featherlike and star-shaped arrangements of rays; (1e) well-defined featherlike plates of the cameral deposits; interspaces between them have a less regular structure; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.

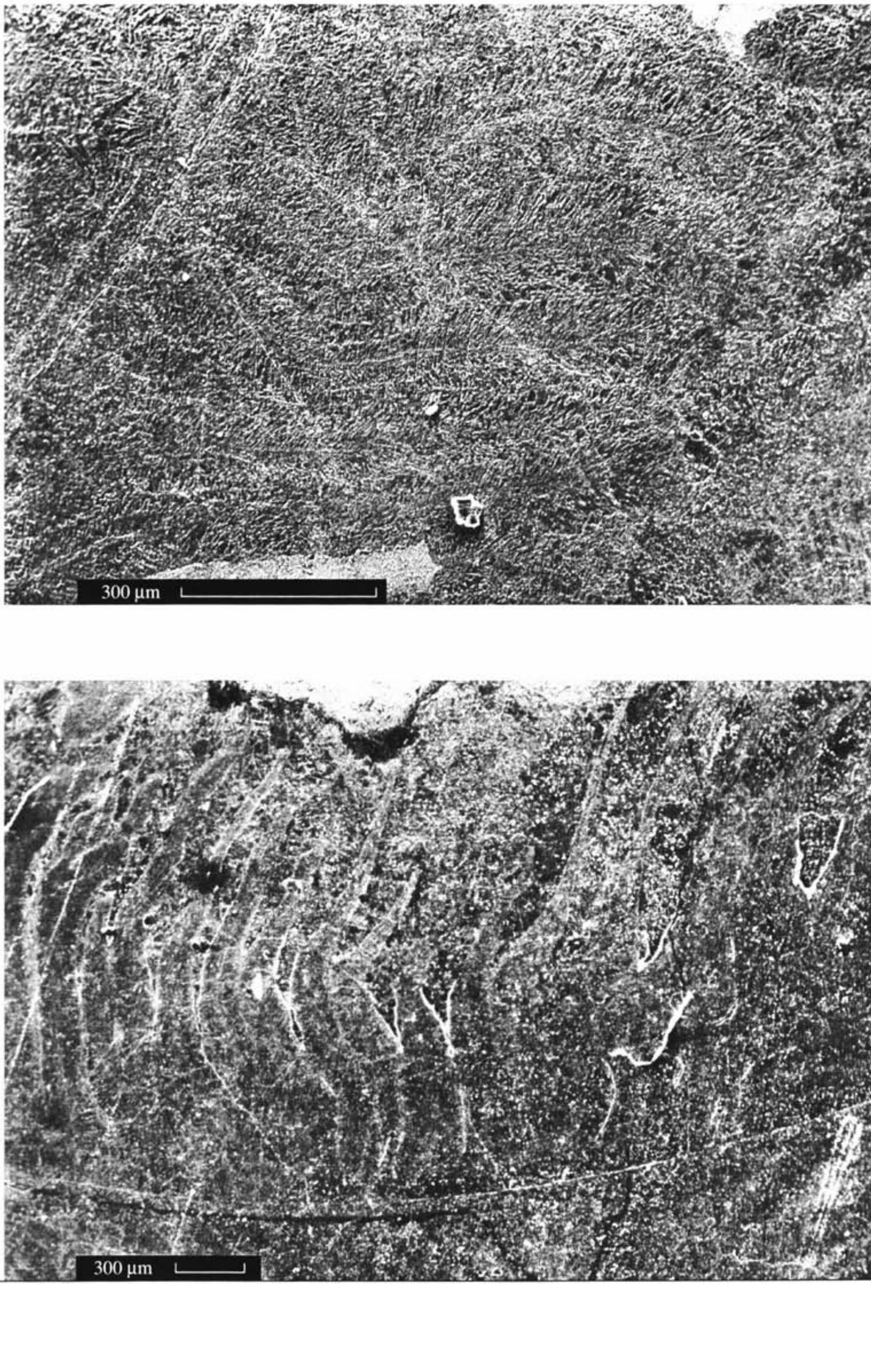
Plate 23



Explanation of Plate 23

Fig. 1. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455 (SEM photograph); (1a) hyposeptal cameral deposits in the medial section of the chamber, the septum is on the left; (1b) an enlarged detail of (1a); Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.

Plate 24



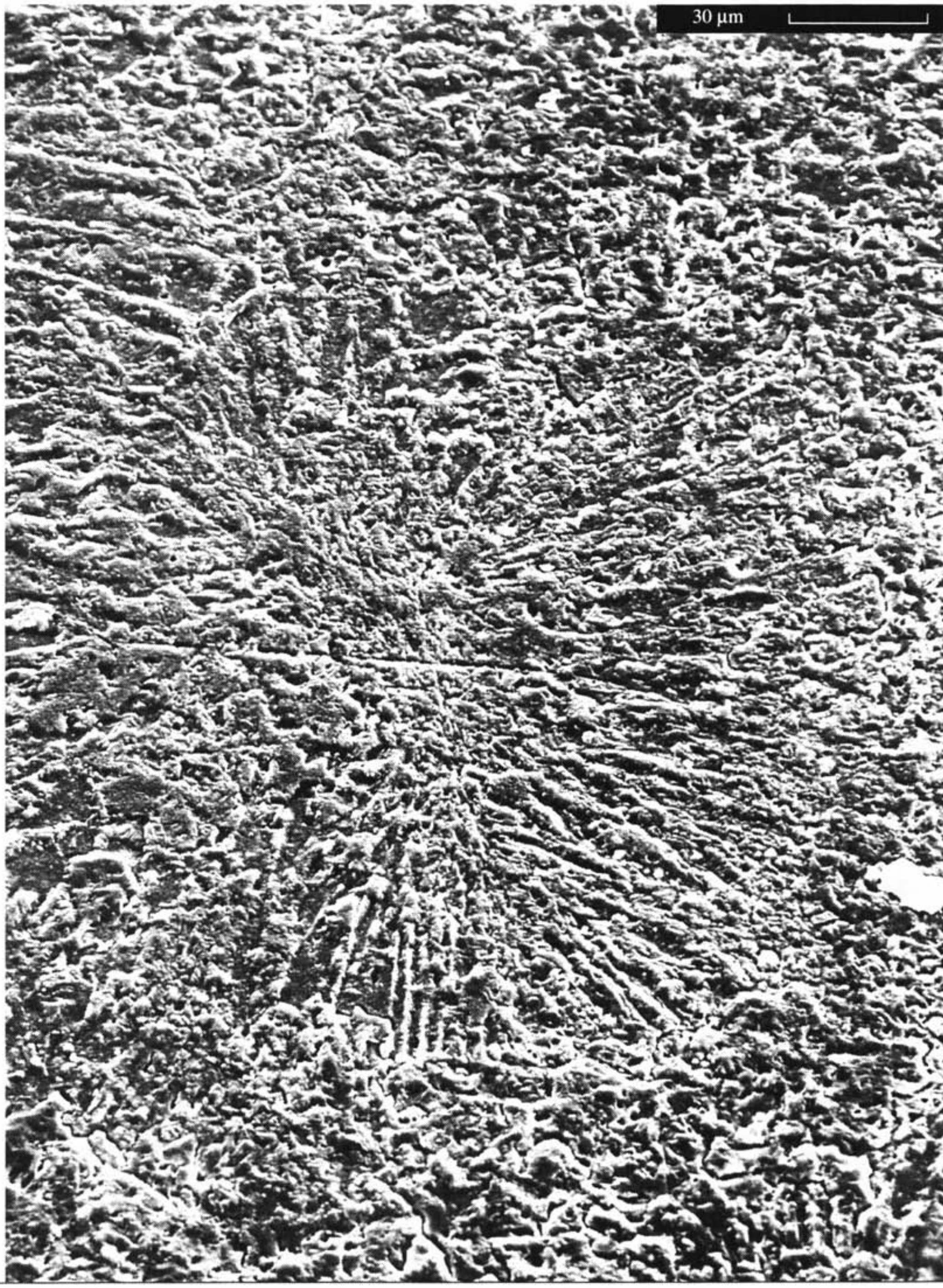
Explanation of Plate 24

Fig. 1. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455 (SEM photograph); (1a) hyposeptal cameral deposits in the medial section of the chamber, the septum is at the top left; sinuous featherlike plates are immediately adjacent to the septum; the featherlike plates of the episeptal deposits of the next chamber are behind the septum; (1b) episeptal cameral deposits in the same medial section of the chamber, the septum is at the bottom; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.

Explanation of Plate 25

Fig. 1. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455 (SEM photograph), a plate of cameral deposits in the section close to its transverse section showing a featherlike arrangement of rays, which consist of small prismatic elements; the latter apparently are arranged in rows oriented at an oblique angle to each other; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.

Plate 26



Explanation of Plate 26

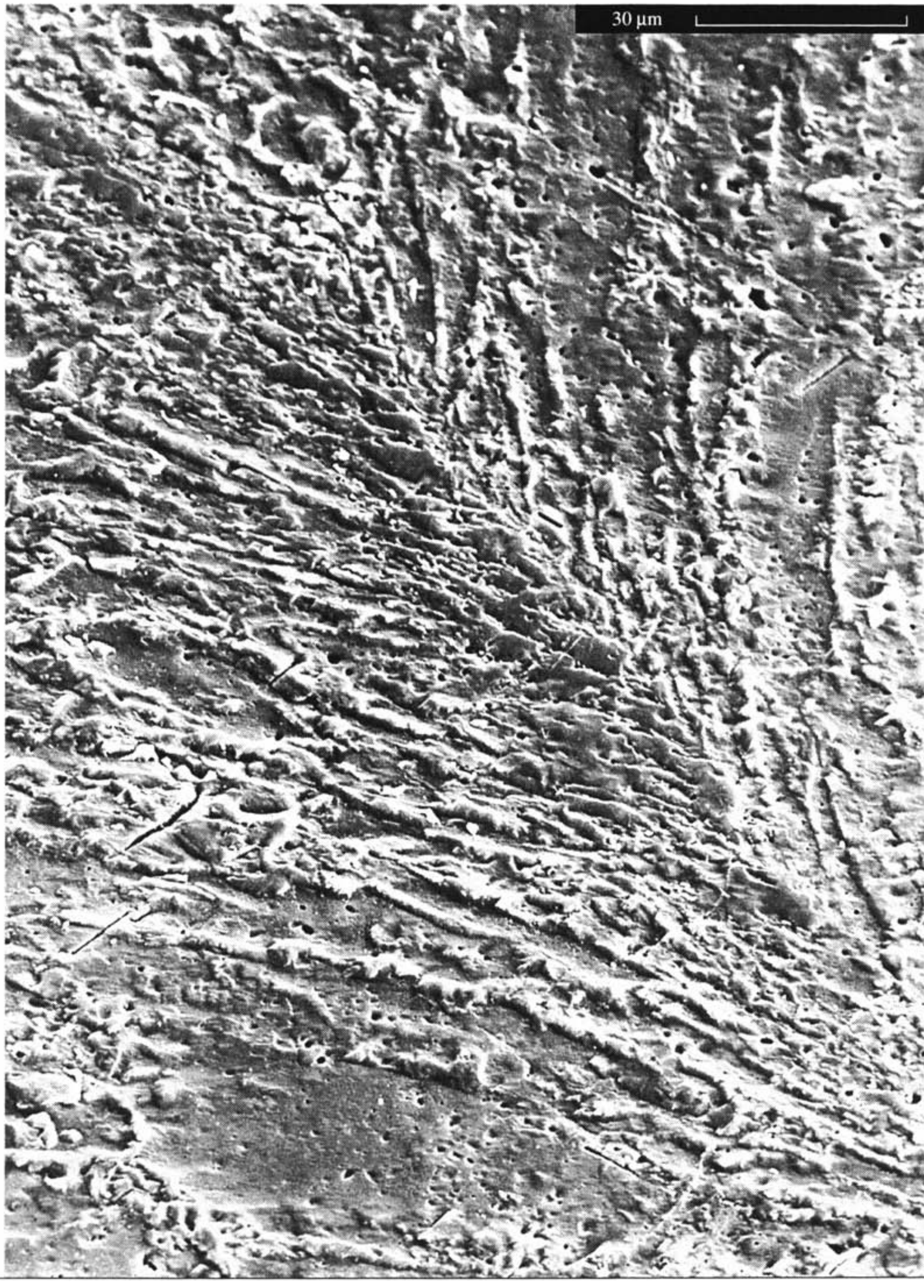
Fig. 1. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455 (SEM photograph), episeptal cameral deposits in the medial section of the chamber showing a star-shaped arrangement of rays radiating from some area with an irregular structure; in most rays the small prismatic elements have been apparently merged; however, many of them are seen between the rays; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.

Plate 27

Explanation of Plate 27

Fig. 1. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455 (SEM photograph), an enlarged detail of Pl. 26 showing rays, which apparently are rows of small prisms that are partly merged with each other; these prisms are readily visible in the interspaces between the rays in the nearly transverse section; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.

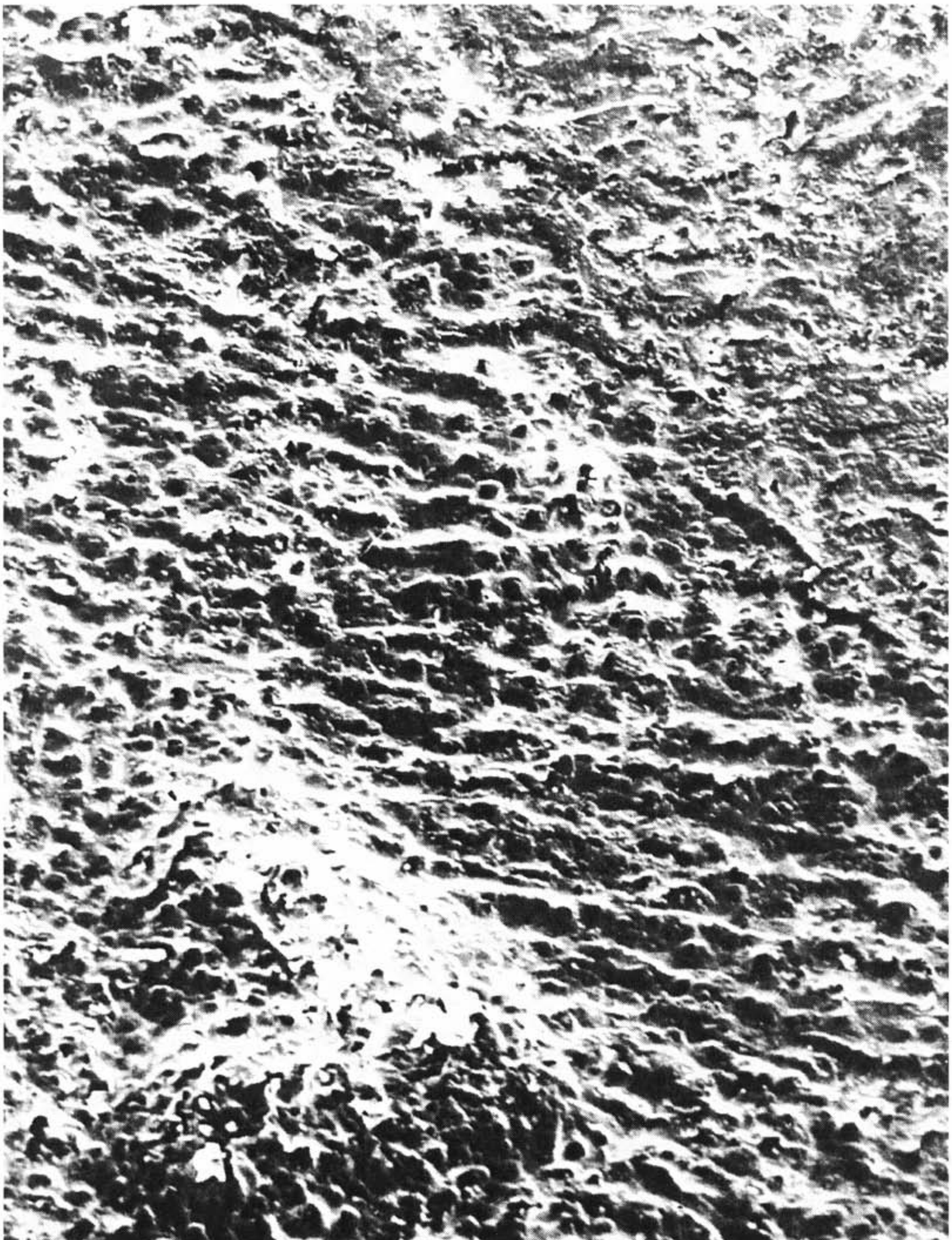
Plate 28



Explanation of Plate 28

Fig. 1. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455 (SEM photograph), a featherlike plate of the episeptal cameral deposits in an oblique section; most of the crystals forming the rays are merged with each other and are visible only occasionally; Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.

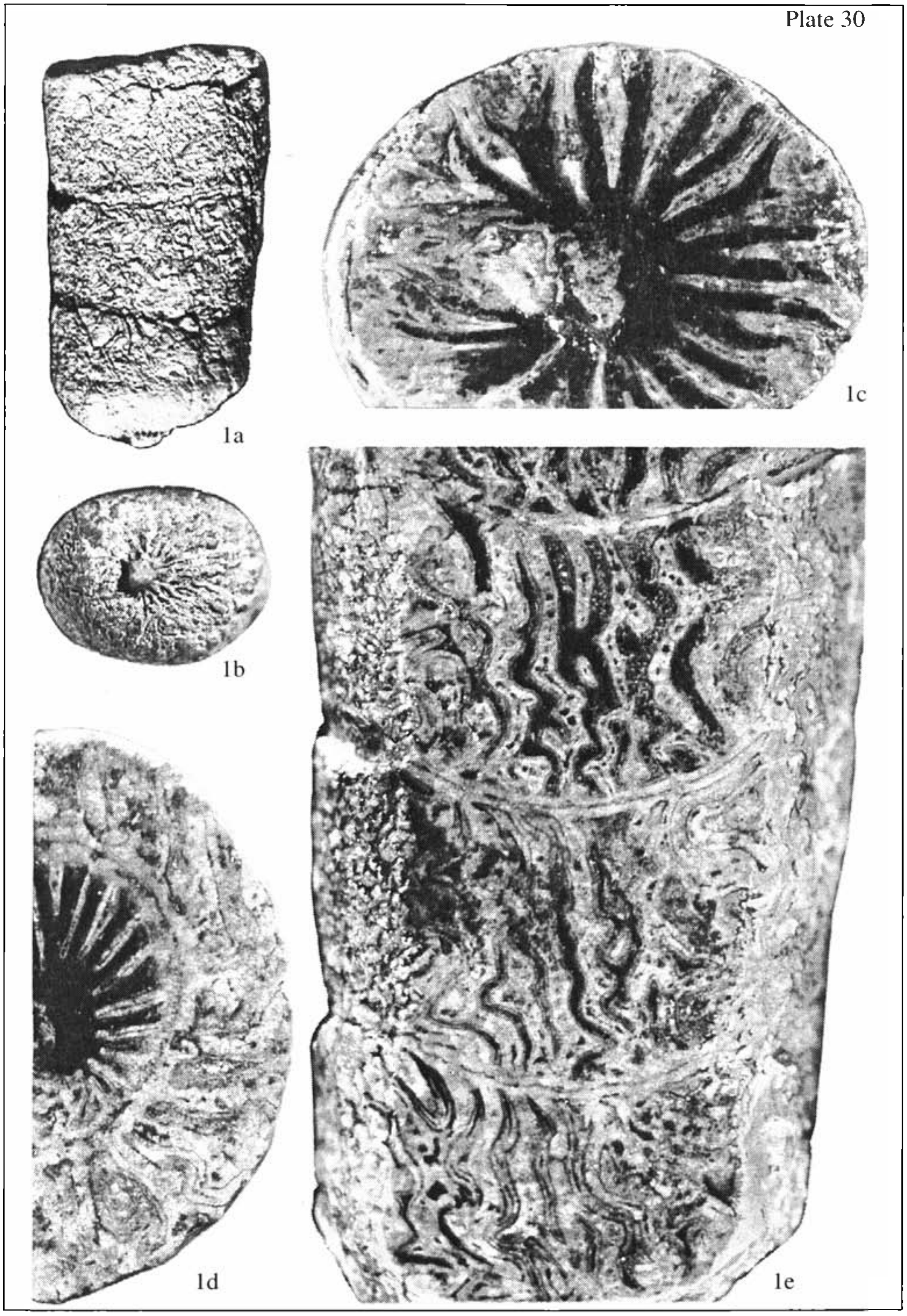
Plate 29



Explanation of Plate 29

Fig. 1. *Syndikoceras arcticum* sp. nov.; holotype PIN, no. 3822/455 (SEM photograph), a plate of the episeptal cameral deposits in the medial section of the chamber that is made at an angle to its axis; most of the crystals that form the rays are merged, but in places they are still distinguishable (the upper right angle); Novaya Zemlya, Yuzhny Island, 700 m offshore in Rakovaya Guba Bay, 1700 m south of the Yagel triangulation point and 36 km west-northwest of Cape Rakovyi; Lower Devonian, Emsian.

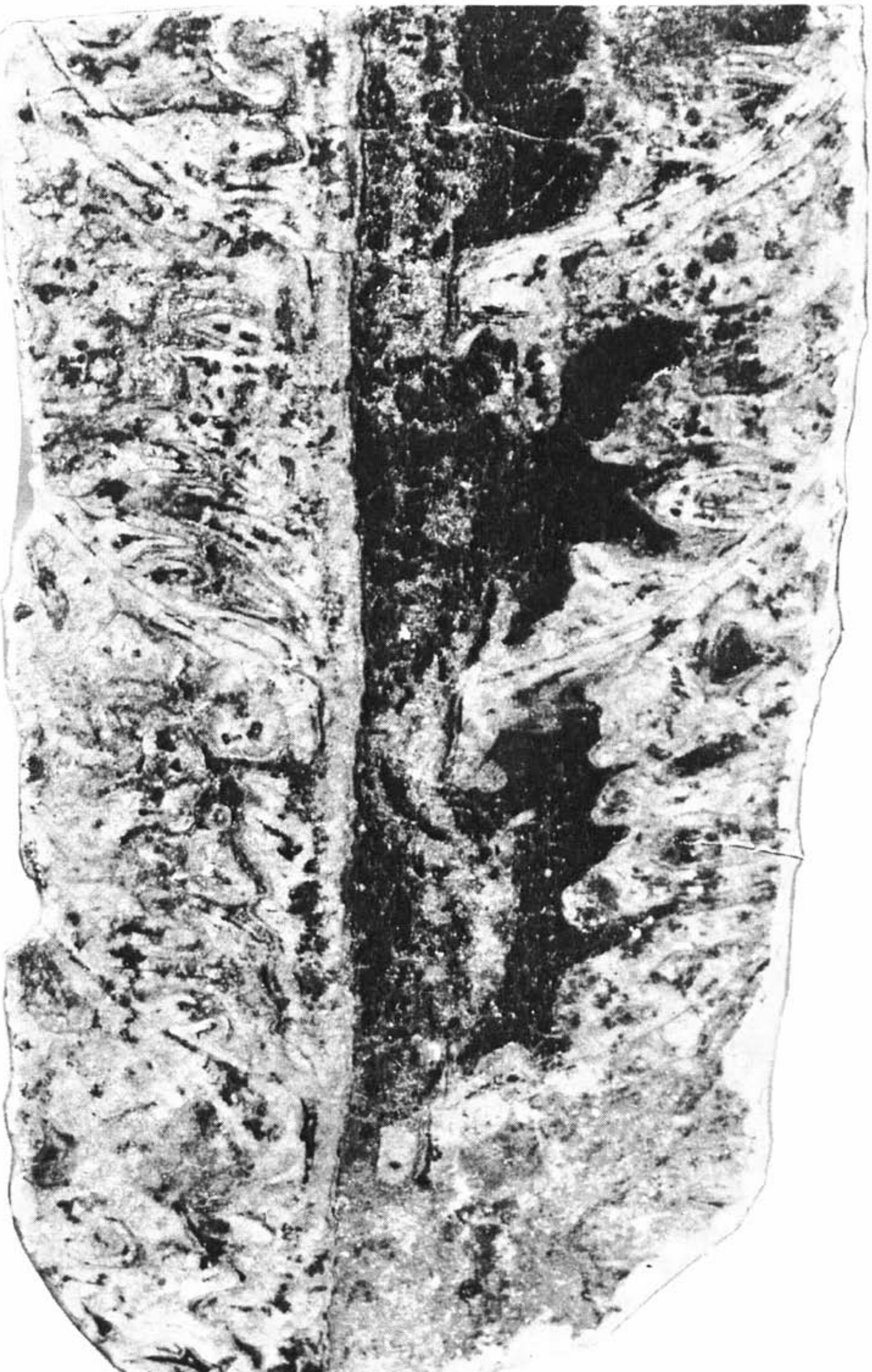
Plate 30



Explanation of Plate 30

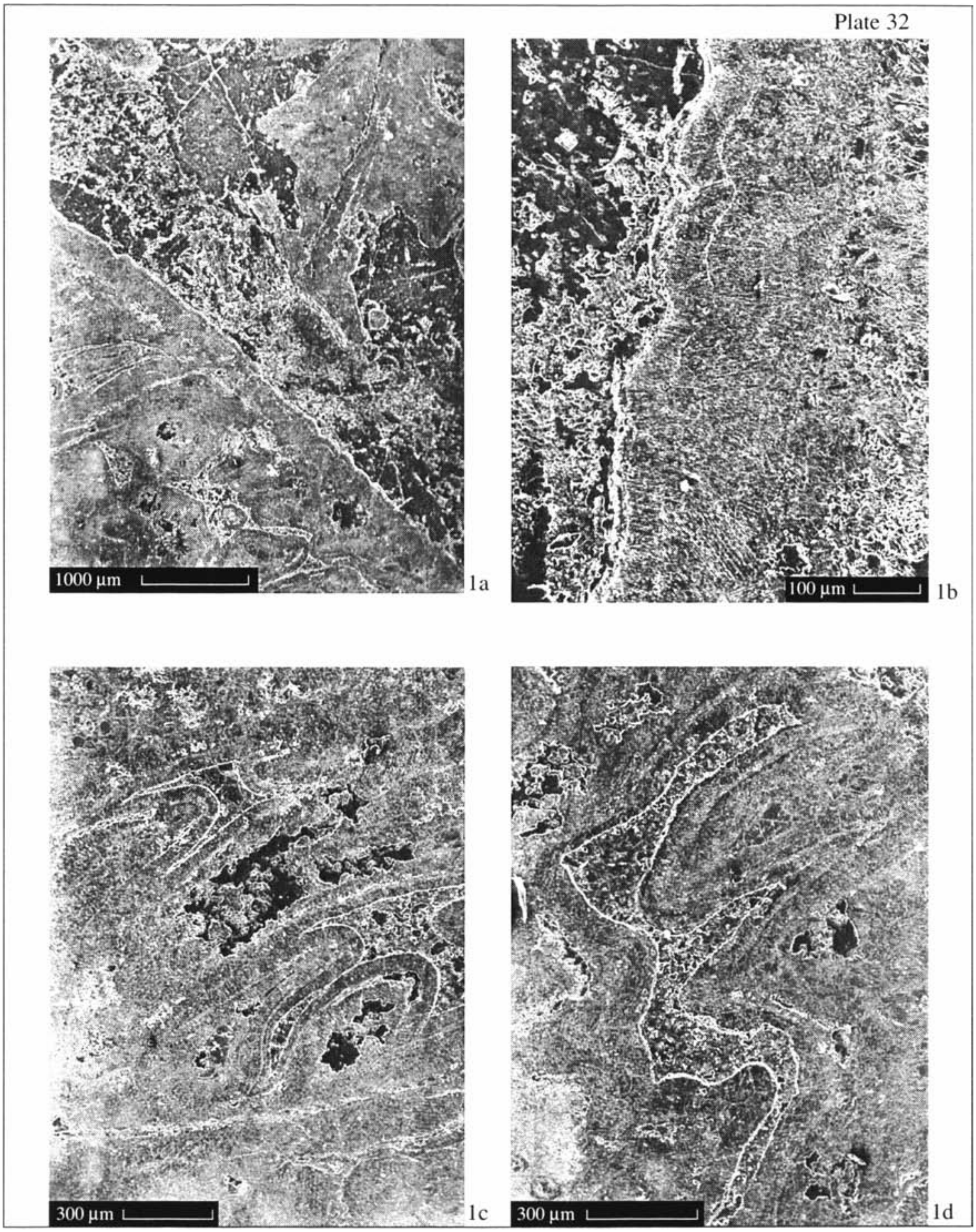
Fig. 1. *Plicatoceras bublichenkoi* sp. nov.; holotype PIN, no. 4721/1 (optical microscope photograph): (1a) a cast with a nodular surface formed by the cameral deposits (the ventral side is on the left), ×4; (1b) an adapical surface of the cast showing plates of the episeptal cameral deposits that merge with each other as they approach the siphon, ×5; (1c) a cross section of the adoral end below the septal neck: cameral deposits in the form of slightly bent folds-plates of different orders, single or combined, come off from the chamber wall to the siphon; particularly striking is the mid-ventral complex structure, the distal edge of which adjoins the siphon, ×9.5; (1d) a cross section of the adoral chamber through the septum (a half, the ventral side is at the bottom); simple plates-folds of the episeptal deposits are inside the septum, sinuous plates-folds of the mural deposits are outside the septum, ×11.5; (1e) a tangential section made parallel to the median plane, the ventral side is on the left; sinuous (occasionally branching) plates-folds stretch from the initial epi- and hyposeptal layers through the entire length of each chamber; the walls of the folds are two-layered; the walls of the folds thicken apically owing to the expansion of the internal light-colored layer, and the interspaces between them become thinner, ×9.5; Kazakhstan, northeastern Balkhash area, north of the Kopa Hill, located north-northwest of the town of Sayak; Lower Devonian, upper Emsian, Kazakh horizon.

Plate 31



Explanation of Plate 31

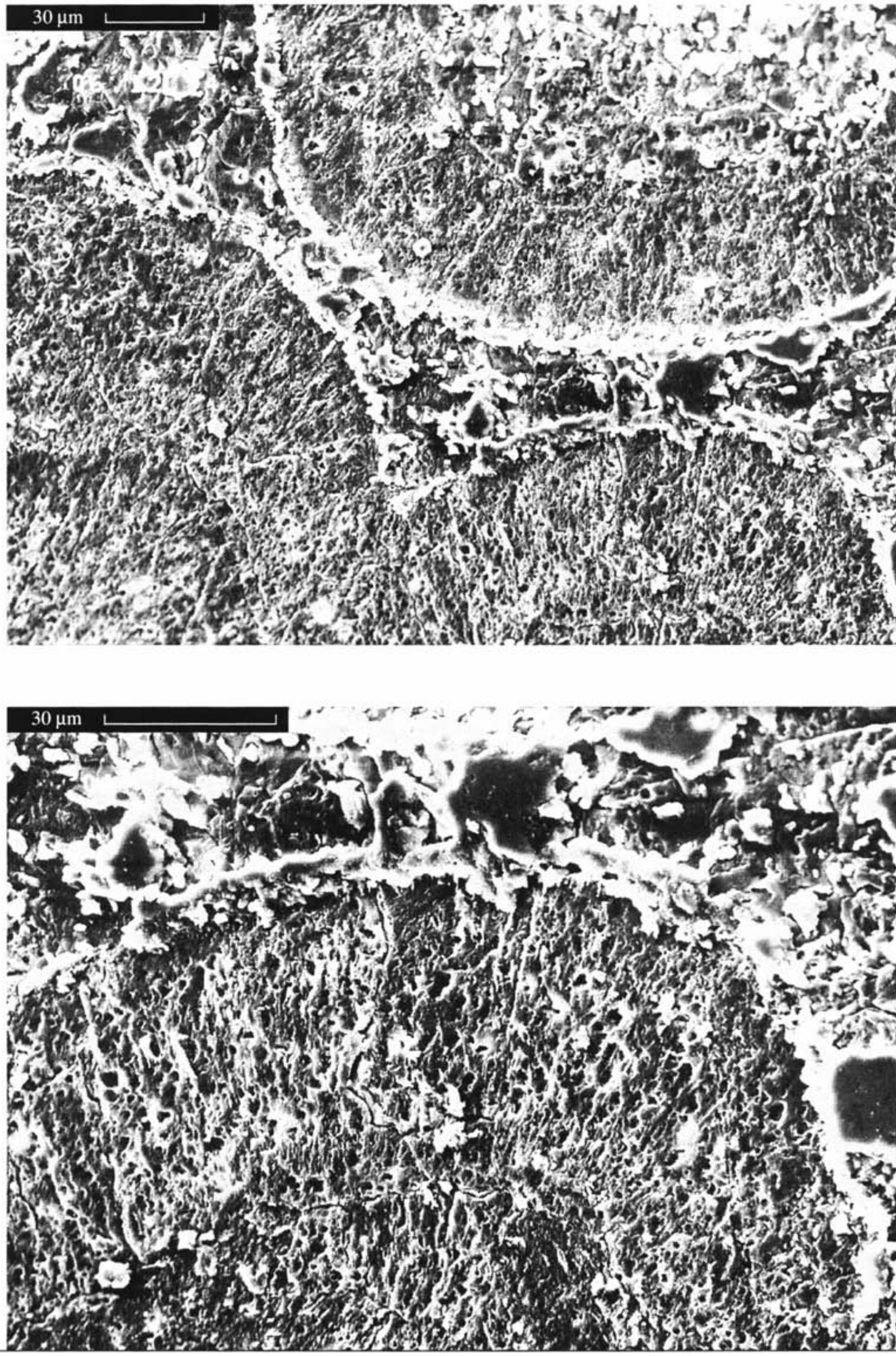
Fig. 1. *Plicatoceras bublichenkoi* sp. nov.; holotype PIN, no. 4721/1, a longitudinal medial section, the ventral side is on the left; septa and septal necks very thin; plates of the cameral deposits come off from the initial epi- and hyposeptal layers and, apparently, from the worn mural layer toward the siphon; on the dorsal side the episeptal deposits form a wide adoral ring around the siphon; on the ventral side the thin episeptal layer penetrates into the septal neck to merge with the thick hyposeptal layer; the meshes of the folds only slightly go beyond the level of the septal neck; cameral deposits are lined with a thick layer of the metacameral deposits; hyposeptal deposits are very thick on the neck both on the dorsal and ventral sides, ×155; Kazakhstan, northeastern Balkhash area, north of the Kopa Hill, located north-northwest of the town of Sayak; Lower Devonian, upper Emsian, Kazakh horizon.



Explanation of Plate 32

Fig. 1. *Plicatoceras bublichenkoi* sp. nov.; holotype PIN, no. 4721/1 (SEM photograph): (1a) a medial section in the region of the second septal neck; the septum and neck are very thin; the hyposeptal deposits on the neck are thick; the plates of the cameral deposits are complex; the metacameral deposits are lamellar; (1b) an enlarged detail of (1a), lamellar metacameral deposits; (1c) and (1d) complex structures of the episeptal deposits; at the bottom of (1c), a slender septum with a hyposeptal layer of the cameral deposits at the bottom; Kazakhstan, northeastern Balkhash area, north of the Kopa Hill, located north-northwest of the town of Sayak; Lower Devonian, upper Emsian, Kazakh horizon.

Plate 33



1a

1b

Explanation of Plate 33

Fig. 1. *Plicatoceras bublichenkoi* sp. nov.; holotype PIN, no. 4721/1 (SEM photograph): (1a) cameral deposits of the second chamber on the ventral side: the cross section of the walls of the plates shows a spongy-porous microstructure, where the slender lamellar elements of the spongy tissue are aligned perpendicular to the surface of the wall, the pores vary in size and are randomly arranged; (1b) a thin white layer on the surface of the plate apparently represents remains of the soft cameral tissue; Kazakhstan, northeastern Balkhash area, north of the Kopa Hill, located north-northwest of the town of Sayak; Lower Devonian, upper Emsian, Kazakh horizon.

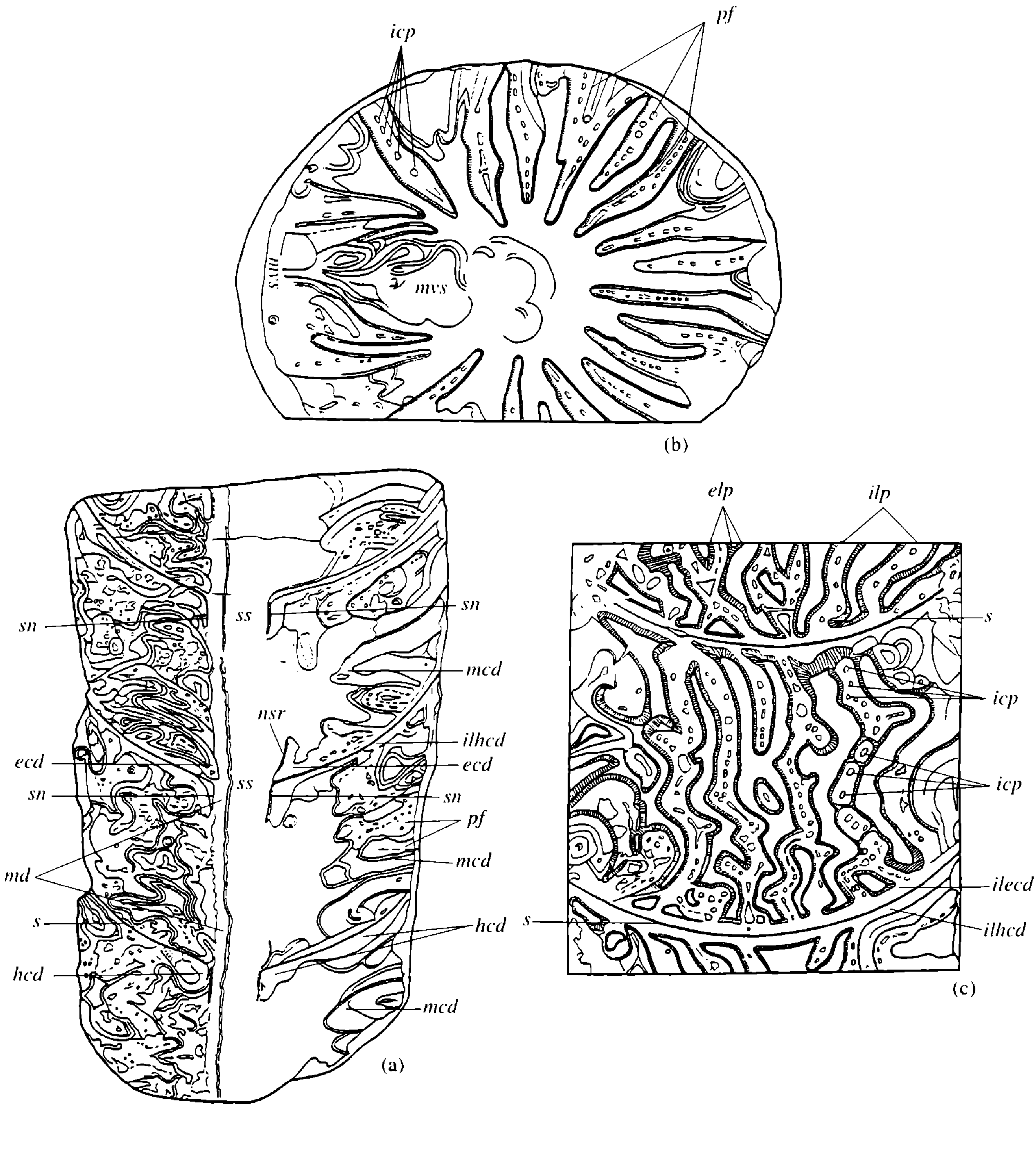


Fig. 8. *Plicatoceras bublichenkoi* sp. nov.; holotype, PIN no. 4721/1; partly schematized drawings: (a) longitudinal dorsoventral section, the ventral side is on the left, ×8; (b) cross section of the adoral end of the fragment, ×12; longitudinal tangential section of the central chamber, the ventral side is on the left, ×14; Kazakhstan, northeastern Balkhash area, north of the Kopa Hill, located north of the small town of Sayak; Lower Devonian, Emsian, Kazakh horizon. Designations: (*s*) septum; (*sn*) septal neck; (*ss*) soft siphon; (*ilecd*) initial layer of episeptal cameral deposits; (*ilhcd*) initial layer of hyposeptal cameral deposits; (*ecd*) episeptal cameral deposits; (*hcd*) hyposeptal cameral deposits; (*mcd*) mural cameral deposits; (*nsr*) near-siphon ridge (or ring); (c) (*elp*) external layer plates-folds; (*ilp*) internal layer plates-folds; (*mvs*) mid-ventral complex structure; (*icp*) irregular cavity of the plate; (*md*) metacameral deposits; (*pf*) plate-fold.

Material. The holotype, which was collected by N.L. Bublichenko in 1940.

ACKNOWLEDGMENTS

This work was supported by the International Science Foundation (grant no. M5G 000) and by the same foundation with the participation of the Government of the Russian Federation (grant M5G 300).

We are grateful to V.T. Antonova for photographic work done at the laboratory of the Paleontological Institute and to all colleagues who collected and donated the material under study.

REFERENCES

1. C. Babin, C. R. Soc. Géol. France, No. 4, 142 (1961).
2. C. Babin, Étude systématique. Essai sur la phylogénie des bivalves. Esquisse paléoécologique (Brest, 1966).
3. Z. G. Balashov and F. A. Zhuravleva, in *Fundamentals of Paleontology: Mollusks: Cephalopods* (Moscow, Akad. Nauk SSSR, 1962), pp. 82–93 [in Russian].
4. K. Bandel and G. D. Stanley, Senckenberg. Lethaea **69**, (5–6), 391 (1989).
5. J. Barrande, *Système silurien du centre de la Bohème. I partie: recherches paléontologiques, vol. 2. Classe des Mollusques. Ordre des céphalopodes* (Prague, 1865–1877).
6. J. F. Blake, *A Monograph of the British Fossil Cephalopoda: Part I. Introduction and Silurian Species* (London, 1882).
7. B. I. Bogoslovskiĭ, Tr. Paleontol. Inst. Akad. Nauk SSSR **124**, 1 (1969).
8. R. Carnall, J. W. Ewald, and J. Roth, Z. Deutsche Geol. Gesellsch. **2**, 8 (1850).
9. D. H. Collins, Bull. Geol. Soc. Canada, No. 182, 31 (1969).
10. G. Dahmer, Senckenbergiana **21**, (5–6), 338 (1939).
11. J. Dzik, Paleontol. Polon., No. 45, 1 (1984).
12. A. G. Fischer and C. Teichert, Pap. Paleontol. Contrib. Univ. Kansas, No. 37, 1 (1969).
13. R. H. Flower, Palaeontogr. Am. **2** (10), 1 (1939).
14. R. H. Flower, Am. J. Sci. **239** (7), 469 (1941).
15. R. H. Flower, Geol. Mag. **42** (2), 89 (1955).
16. R. H. Flower, Mem. New Mexico Bur. Mines Res., No. 13, 1 (1964).
17. R. H. Flower, Bull. Am. Paleontol. **67** (287), 139 (1975).
18. A. F. Foerste, Bull. J. Sci. Lab. Denis. Univ. **28** (10), 231 (1928).
19. W. M. Furnish and B. F. Glenister, in *Treatise on Invertebrate Paleontology: Part K, Mollusca 3, Cephalopoda* (Lawrence, Geol. Soc. Am., Univ. Kansas Press, 1964), pp. 343–367.
20. M. Gnoli and G. N. Kisselev, Bull. Soc. Paleontol. Italiana **33** (3), 415 (1994).
21. F. Hermann, Jahrb. Preuss. Geol. Landesanst. **33** (2), 355 (1912).
22. C. H. Holland, Palaeontology. **7** (4), 525 (1965).
23. G. Holm, Palaeontol. Abhandl. **3** (1), 1 (1885).
24. A. Hyatt, Proc. Am. Philos. Soc. **32**, 349 (1894).
25. G. N. Kisselev, N. G. Mironova, and I. N. Sinitsina, *Atlas of Silurian Mollusks of Podolia* (Leningrad, Leningr. Univ., 1987) [in Russian].
26. I. Kolebaba, Vestn. Ústředn. Ústavu Geol. **49**, 293 (1974).
27. I. Kolebaba, Acta Musei Nationalis Pragae, Ser. B, Historia Naturalis. **55** (1–2), 1 (1999a).
28. I. Kolebaba, J. Czech Geol. Soc. **44** (1–2), 131 (1999b).
29. D. Le Maitre, Bull. Soc. Géol. France, Sér. 5 **20**, 93 (1950).
30. D. Le Maitre, Paléontol., No. 12, 1 (1952).
31. F. Liebrecht, Jahrb. Preuss. Geol. Landesanst. **32** (3), 412 (1913).
32. J. Marek, Vestn. Česk. Geol. Ústavu **73** (2), 181 (1998).
33. H. Mutvei, Arkiv. Mineral. och Geol. Utgivet av Kungl. Svenska Vetenskapakad. **2** (8), 179 (1956).
34. Sh. Niko, J. Paleontol. **65** (6), 917 (1991).
35. A. Remele, *Untersuchungen über die Versteinerungens führenden Diluvialgeschiebe des norddeutschen Flachlandes mit besonderer Berücksichtigung der Mark Brandenburg* (Berlin, 1890), Stuck. 1, Lief. 3, pp. 1–108.
36. F. A. Roemer, *Die Versteinerungen des Harzgebirges* (Hannover, Hahn'sche Hofbuchhandlung, 1843).
37. F. A. Roemer, Palaeontographica. **3**, 69 (1852).
38. H. Sandberger and F. Sandberger, *Die Versteinerungen des Rheinischen Schichtensystem in Nassau* (Wiesbaden, 1850–1856), Vol. 2.
39. O. H. Schindewolf, Jenaische Z. Medizin Naturwissensch. **71**, 324 (1942).
40. H. Schmidt, Geol. Palaeontol. Abh. N.F. **19** (5), 297 (1933).
41. H. Schroeder, Jahrb. Preuss. Geol. Landesanst. 164 (1888).
42. S. Shimizu and T. Obata, J. Shanghai Sci. Inst. **2** (2), 1 (1935).
43. G. D. Stanley and C. Teichert, Univ. Kansas Paleontol. Contrib. Pap., No. 86, 1 (1976).
44. Ya. I. Starobogatov, in *Abstracts of Reports at the Session on the Scientific Results of 1972* (Leningrad, Nauka, 1973), pp. 24–25 [in Russian].
45. Ya. I. Starobogatov, Paleontol. Zh., No. 1, 3 (1974).
46. Ya. I. Starobogatov, in *Systematics and Ecology of Cephalopod Mollusks* (Leningrad, Zool. Inst. Akad. Nauk SSSR, 1983a), pp. 4–7 [in Russian].
47. Ya. I. Starobogatov, in *Systematics and Ecology of Cephalopod Mollusks* (Leningrad, Zool. Inst. Akad. Nauk SSSR, 1983b), pp. 8–12 [in Russian].
48. W. C. Sweet, Saertrykk Norsk Geol. Tidsskrift. **38** (1), 1 (1958).

49. W. C. Sweet, in *Treatise on Invertebrate Paleontology: Part K, Mollusca 3, Cephalopoda* (Lawrencee, Geol. Soc. Am., Univ. Kansas Press, 1964), pp. 216–261.

50. C. Teichert, Am. J. Sci. **29**, 1 (1935).

51. C. Teichert, Ann. Palaeontol. **47**, 93 (1961).

52. C. Teichert, in *Treatise on Invertebrate Paleontology: Part K, Mollusca 3, Cephalopoda* (Lawrence, Geol. Soc. Am., Univ. Kansas Press, 1964), pp. K190–K216.

53. G. Termier and H. Termier, Palaeontol. Marocaine. **2**, 1 (1950).

54. G. Termier and H. Termier, Soc. Géol. France, No. 15, 277 (1951).

55. M. Y. Williams, Mem. Geol. Soc. Canada **111** (1919).

56. F. A. Zhuravleva, Paleontol. Zh., No. 1, 89 (1961).

57. F. A. Zhuravleva, Tr. Paleontol. Inst. Akad. Nauk SSSR **168**, 1 (1978).

58. F. A. Zhuravleva and L. A. Doguzhaeva, in *Fossil Cephalopods: The Latest Advances in Their Study* (Moscow, Paleontol. Inst. Ross. Akad. Nauk, 1999), pp. 213–269 [in Russian].

59. F. A. Zhuravleva and G. N. Kisselev, Paleontol. Zh. **35** (4), 24 (2001) [Paleontol. J. **35** (4), 24 (2001)].