

A LATE CARBONIFEROUS ADOLESCENT CEPHALOPOD FROM TEXAS (USA), WITH A SHORT ROSTRUM AND A LONG BODY CHAMBER

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Abstract: Three longicones (Virgilian, Upper Pennsylvanian, Texas, USA) with a ventral marginal siphuncle, a shell wall with a nacreous layer, and a long body chamber were examined. The smallest is a 25 mm long adolescent, protoconch-bearing shell with a short rostrum. The rostrum has a small post-protoconch part that is about as long as the protoconch (ca 0.25 mm), and extends along about first ten camerae. The rostrum is loosely calcified and strongly pyritized, and this suggests that it originally had a combined organic and carbonate primary composition. The first septum is mineralized, with long prismatic mural parts that extend along about ten camerae and form the shell wall. At latter growth stages a nacreous layer and then an inner prismatic layer appear. The septal necks are retrochoanitic, short dorsally and long (about 1/3 camera length) ventrally. The connecting rings are thin and were probably originally organic in composition. Thin cameral deposits are distinct in the protoconch and the first two camerae. In the latter camerae the deposits are less distinct but show pyritized membranes on their surfaces.

The adolescent longicone falls within the concept of *Mutveiconites* Doguzhaeva, 2002, known from the Upper Carboniferous (Orenburgian) of south Urals, and is described as *Mutveiconites milleri* sp. n. The other two larger longicones possibly represent older growth stages of *Mutveiconites*, which is considered to be the earliest aulacocerid coleoid so far known. Also this occurrence represents the first report of this genus in North America.

Keywords: Late Carboniferous coleoid, shell morphology and ultrastructure, rostrum, evolutionary morphology, Texas

INTRODUCTION

The present study concerns the early evolution of aulacocerid coleoid cephalopods. It deals mainly with a fully preserved adolescent Late Carboniferous (Virgilian = Stephanian) longicone specimen with a short rostrum from Texas, USA. This is the second confirmed find of such a shell. The first recovery of an adolescent longicone with a short rostrum was from the Late Carboniferous (Orenburgian) in the southern Urals. These two shells belonged to two individuals that are nearly synchronous (in scale of geological time), but remarkably remote from each other in geographic space.

The adolescent longicone from Texas was recognized during examination of new material of the oldest known spirulid coleoid *Shimanskya postremus* Doguzhaeva, Mapes, Mutvei, 1999. This genus was initially referred to *Bactrites postremus* Miller, 1930 but it was separated from the bactritoids because of ultrastructural details of the shell by scanning electron microscopy study (see Doguzhaeva et al., 1999). Specimens of *Shimanskya* are known from the Virgilian deposits of Texas and Oklahoma (USA) and occur with several species of *Bactrites* (see Mapes, 1979: p. 35).

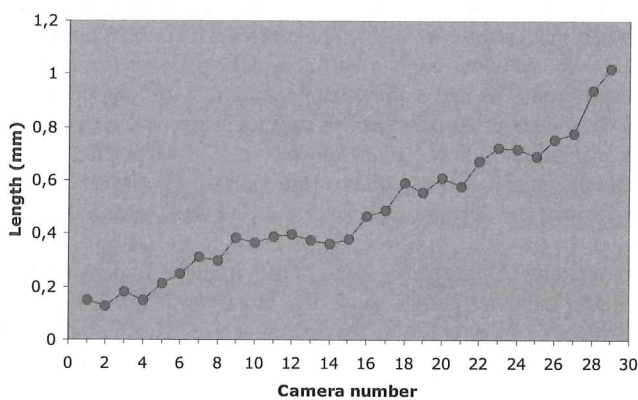
The two adolescent longicones, one from Urals and the other from Texas, with preserved initial parts of the

shell, are important because they show details of the early evolutionary stages of aulacoceratids. These details include a rarely observed combination of morphological features including: a short rostrum, a small (ca 0.3 mm) protoconch, a longiconic phragmocone with a marginal siphuncle, a shell wall with a nacreous layer and a long body chamber. The order Aulacoceratida was established by Jeletzky (1966, p. 20) who accepted Abel's (1916) and latter Schwegler's (1949) and Erben's (1964) conclusions on independent origin of aulacocerids and belemnites. A long tubular body chamber and pro-ostracum were considered to occur in aulacocerids by many authors (Mojsisovics, 1871, 1882, 1902; Gemmellaro, 1904; Wanner, 1911; Bülow, 1916; Abel, 1916; Dunbar, 1924). Naef (1922) assumed that for keeping a horizontal position, the aulacoceratids with their long slender rostrum, needed a long pro-ostracum. However, as was noticed by Bandel (1985, p. 232), there was no direct evidence for these two assumptions. No adult shell showing a morphological combination of long slender rostrum, tubular body chamber and pro-ostracum have been reported to our knowledge. Also, to our knowledge, the two Late Carboniferous adolescent shells mentioned above are the only documented coleoid longicones that have a short rostrum and a long body chamber.

MATERIAL AND STATE OF PRESERVATION

The studied material comprises three longicones from Virgilian, Upper Pennsylvanian (= Stephanian, Upper Carboniferous) beds of Texas, USA.

Specimen 1 (OUZC 5205): (Pl. 1, Figs. A, B, D, E; Pl. 3, Figs. A–F; Pl. 4, Figs. A–F; Text-fig. 1). A unique 25 mm long adolescent shell preserved inside the long body chamber of the medium-sized longiconic specimen OUZC 5206. It has a small protoconch, a short rostrum, 29 chambers in the phragmocone and a long body chamber. The body chamber is 11 mm long, which is 2/5 of shell length, and with two exceptions is filled with uniformly tan matrix identical to that seen in the body chamber of specimen 2. The conch diameter near the aperture of the body chamber is 3 mm. The phragmocone is characterized by an irregular increase in camera length (Text-fig. 1). The camerae of the phragmocone are filled with light peach-colored calcite.



Text-fig. 1 *Mutveiconites milleri* sp. n., Graphic representation of the 29 cameral length measurements showing a periodicity of the shell growth.

Specimen 2 (no. OUZC 5206): (Pl. 1, Fig. A). An incomplete shell segment 70 mm long with a 64 mm long portion of tubular body chamber and two camerae of the phragmocone. The shell diameter at the anterior broken edge is 17 mm while near the last septum the diameter is 9 mm. The body chamber, which is filled with a uniform textured matrix, also contains the adolescent longicone of specimen 1 with its initial parts preserved together with numerous undetermined pieces of organic debris and material reworked by bacteria (Pl. 4, Figs. D, E).

Specimen 3 (no. OUZC 5207): (Pl. 2, Figs. A–C). The specimen consists of a 50 mm long fragment of a longicone buried in a dense dark grey medium-sized carbonate concretion. The shell comprises eight camerae of the phragmocone and an incomplete body chamber. All but one of the camerae of the phragmocone is filled with white calcite. The camera that is the exception and the preserved apical portion of the body chamber are filled with numerous coprolites, and the interspaces between the coprolites is extensively pyritized. The maximum diameter of the shell is 9 mm, and its minimum diameter is 7 mm. This specimen is cut longitudinally through the ventral marginal siphuncle. The siphuncle is strongly pyritized inside and outside the siphuncular tube. It also has strongly pyritized layers on

the adapical septal surfaces and near the septal necks on adoral surfaces. Additionally the specimen has pyritized cameral membranes on the surface of cameral deposits. The adapical surfaces of the septa are strongly pyritized while the adoral ones are weakly and irregular pyritized mainly near the septal necks. An exception is the septum near the damaged edge of the shell, which is pyritized on both surfaces. Serious damage that was partly repaired, followed by a shell breakage, occurs at the adapical margin of the shell.

The three specimens available have a similar phragmocone structure. In all specimens the shell exhibits a slowly expanding phragmocone with moderately curved septa and a long body chamber. A narrow ventral marginal siphuncle is observed in the two larger specimens (specimens 2, 3), while in the adolescent shell (specimen 1) the siphuncle is not exposed because the section of the shell is not median. However, the siphuncle of the adolescent specimen is also considered to be marginal, because if the siphuncle had been central, it would have been visible in the longitudinal section running through the central part of the septa.

The body chamber of specimen 2, where the adolescent longicone (specimen 1) was preserved, contains a substantial amount of undetermined organic debris. EDS analyses of the sediment inside the body chamber show a content of O (24–48%), Ca (21–40%), Si (0–45%), P (0–12%), Na (0–1.6%), Al (0–1.9%), Mg (0–0.82%), Fe (0–3%), S (0–2.8%), K (0–0.8%) (C was not registered). This means that the body chamber was filled by heterogeneous material. The first two elements (O, Ca) have a more homogenous distribution in comparison with the other eight elements. In some places of the body chamber the sediment was phosphatized, in others either silicified or pyritized. This pattern of elemental distribution is possible evidence of high content in organic material during fossilization. Decay of soft body possibly occurred inside the body chamber, which influenced formation of the microenvironment that favored good preservation of the fine delicate adolescent shell within the body chamber.

The material is repositated at the Ohio University, Zoological Collections (OUZC), Athens, Ohio, USA.

GEOLOGICAL SETTING AND OCCURRENCE

The outcrop that yielded the specimens described herein is an excavated exposure in the Finis Shale Member of the Graham Formation (Lower Virgilian = Stephanian B/C). The excavation serves as the emergency spillway for Lost Creek Lake, which serves as a water supply for the community of Jacksboro, Jack County, Texas. The lake is located 3.2 km northeast of Jacksboro where Texas highway 59 crosses the northern tip of the lake. The fossiliferous outcrop is located near the dam on the southern end of the lake.

The exposure contains parts of both a transgressive and the regressive marine cycle. During the Upper Carboniferous more than 75 marine transgressive–regressive (T-R) units have been documented on the North American Mid-continent region (see Heckel 1986, 1994 for summaries). Boardman et al. (1984) analyzed the invertebrate megafauna of many of these T-R units in this region and identified and named a series of invertebrate communities that occur repeatedly in the T-R sequences.

Several marine megafaunal communities including a transgressive dysaerobic or juvenile molluscan dominated community that is separated by an unconformity from the overlying regressive mature molluscan dominated community; both communities make up the Finis Shale. This shale is capped by the Jacksboro Limestone, which has a distinct community containing phylloid algae in its upper portion (see figure 2 of Rothwell et al., 1996 for a measured section and a more complete discussion of the exposure).

The bactritoid and coleoid-bearing interval is in the regressive phase of Mature Molluscan Community. At the exposure in the spillway excavation, this community consists of approximately four meters of dark grey, when fresh and weathering, to a tan color shale, immediately above the storm deposit where shell debris and reworked phosphate concretions are concentrated (see figure 2 in Rothwell et al., 1996). The mega fauna of the bactritoid/coleoid bearing unit is dominated by cephalopods and other molluscs.

DEPOSITIONAL ENVIRONMENT

The paleoecology of the interval bearing the bactritoid/coleoid cephalopods is interpreted as being moderately deep water (more than 25 meters but probably less than 100 meters) and having a moderately well oxygenated water column with a lesser, but still oxygenated, bottom sediment. This conclusion is based in part on the overall lack of phosphate and pyrite deposition in the shale interval, which indicates that the bottom water conditions were not strongly reducing. Other supporting evidence includes the presence of an extensive benthic fauna including corals, brachiopods, and numerous different molluscs as well as complete mixing of the sediment bedding by bioturbation. However, below the water/sediment interface probably no deeper than a few centimeters, reducing conditions must have been more intense around local places where there was more organic material.

Preservation of the shelled invertebrate organisms within this community is primarily by calcium carbonate with many specimens being discrete concretions. Some original aragonite shells are preserved, especially where weathering has not appreciably altered the sediment. Some pyrite is present in freshly excavated shale micro samples, but this kind of mineralization is minor in the fossilization of the larger invertebrates. The original aragonite of the molluscan shells appears to be only partly altered to calcite.

Virtually all of the cephalopods preserved in this interval are the partial remains of shells that were partly destroyed by predators. Indeed, all the shells of some species of coiled nautiloids and ammonoids from this interval are interpreted as having been broken during the act of predation (Mapes and Chaffin, 2003). None of the bactritoids and coleoids from this interval in the Finis Shale are complete specimens, and, while they have not been studied in detail, these shells also bear the similar marks of predation that were documented on some of the cephalopods from the Finis Shale by Mapes and Chaffin (2003) including circular and oval holes produced by tooth punctures and missing shell segments produced by crushing teeth. Some specimens exhibit crushing by lithostatic pressures that occurred after burial; however, specimens excavated *in situ* are always incomplete, and because of this, the preda-

tion breakage that caused the demise of the animal can usually be separated from diagenetic crushing.

METHODS OF STUDY

Scanning electron microscopy. The initial portion of the adolescent shell as well as the shell ultrastructure was studied with scanning electron microscope (SEM) Hitachi S-4300 at the Swedish Museum of Natural History, Stockholm. The specimens were cut longitudinally, polished and etched with a water solution of 25% glutardialdehyde for 30 min. The specimens were repolished and re-etched with 5% acetic acid for 2–5 min. The etched specimens were glued to holders and coated with gold.

Energy dispersive spectrometry. EDS was used for analysis of the (a) sediment inside the body chamber of the largest shell (specimen 2) where the adolescent shell (specimen 1) was preserved, (b) the juvenile rostrum of specimen 1, (c) the shell wall, cameral deposits, septa and sediment inside the camerae and body chamber in the same specimen, and (d) the shell wall and septa in specimens 2 and 3.

Measurements of cameral length. The length of the camerae was measured on SEM images of the phragmocone, with a magnification of 40x, along the longitudinal central axis.

OBSERVATIONS ON SHELL MORPHOLOGY, ULTRASTRUCTURE AND ELEMENTAL ANALYSIS

Specimen 1 (no. OUZC 5205): (Pl. 1, Figs. A, B, D, E; Pl. 3, Figs. A–F; Pl. 4, Figs. A–F; Text-fig. 1).

The specimen is the holotype of a new species *Mutveiconites milleri* sp. n. Shell morphology and ultrastructures are described in the systematic paleontology section herein.

EDS data. EDS analyses of the rostrum show S (ca 45%) and Fe (ca 38%) in places with numerous crystals of pyrite. Beyond them, the following elements are detected: O (19–44%), Ca (0–55%), Fe (0–6.8%), Mg (0–2.3%), S (0–0.7%), Si (0–1%), Al (0–0.7%), Mn (0–0.5%), P (0–0.4%). Analyses of the chambers show peaks of Ca (33–62%), O (33–55%), Fe (0–13%), Mg (0–6%), Al (0–0.5%), P (0–0.4%), K (0–0.4%), Mn (0–0.3%), Si (0–0.2%). Spectra of the shell wall show peaks of O (29–36%), Ca (34–47%), S (0–1%), Mg (0–0.7%), K (0–0.2%). EDS analyses of the cameral deposits show O (19–50%), Ca (44–50%), Fe (0–1.7%), Mg (0–1%), S (0–0.6%), Al (0–0.4%), K (0–0.4%), P (0–0.3%). Thus, the shell wall lacks P, Fe, and Si, and in this respect, it differs from the rostrum, chambers and cameral deposits. The latter three parts of the shell seemed to contain significant amount of organic material, which is not the case with the shell wall.

Camera length periodicity. (Text-fig. 1). The septa are irregularly spaced. The first camera of the phragmocone is short; its length is equal to 3/4 protoconch length; the second camera is shorter than the first one; the third camera is longer than the preceding ones but it is still shorter than the protoconch length; the fourth camera is as long as the first one; the fifth camera is slightly longer than the third one; next

camerae show a gradual but slightly irregular increase in length. This early initial shorting between septa 2 and 3 is probably due to development of the bactritella in the egg. With the gradual septal distance lengthening beginning at the 3rd and 4th septa and the gradual lengthening of the septal spacing from that point on, the 3rd and 4th septa probably correspond to the apertural position which is also the position of the primary constriction between the 8th and 9th septum that marks the time of hatching of the animal. The measurements of the 29 camerae indicate fluctuation of shell growth with increasing and decreasing length in 6 cycles.

Specimen 2 (no. OUZC 5206): (Pl. 1, Fig. A).

Phragmocone. The preserved portion includes the last two camerae before the body chamber. The last camera is shorter than the one before the last (3 mm and 5 mm respectively); this septal approximation may indicate the terminal mature growth stage. Siphuncle is narrow, ventral, and marginal. Because of the adolescent shell (specimen 1) lies in the paramedian plane about 2 mm from the median plane of specimen 2 the siphuncle was not cut. However, it is visible on the ventral side and the oval septal foramen indicates the ventral position of the narrow siphuncle, which is exposed on the next to last septum.

Body chamber. It is long slowly expanding; the length of the preserved portion is 65 mm, the diameter near the last septum is 9 mm and "aperture" diameter is 17 mm. The body chamber is 20 times as long as the last camera of the phragmocone.

Shell ultrastructure. The shell wall consists of thick nacreous and thin inner and outer prismatic layers. Septa, which are as thick as the shell wall, are nacreous. A wrinkle layer that has delicate wrinkles oriented perpendicular to the shell axis lines the body chamber. The wrinkle layer is located between the nacreous inner layer and the prismatic outer layer. In co-occurring coleoid *Shimanskya* the wrinkle layer is between the inner and outer acicular prismatic layers of the outer shell. Interestingly, the wrinkle layer in the co-occurring bactritoids occurs on the innermost surface of the nacreous layer of the shell wall, and this characteristic difference, together with ultrastructural studies and other subtle morphological features can help identify and separate the coleoids from the bactritoids as described by Miller (1930) and Mapes (1979) that occur in the Finis Shale in Texas.

Specimen 3 (no. OUZC 5207): (Pl. 2, Figs. A-C).

Phragmocone. The slowly expanded phragmocone is a 50 mm long fragment including nine camerae. The width of the camerae is slightly larger than their length (ca 7 : 5 respectively).

Siphuncle. It is marginal and narrow. Septal necks are retrochoanitic. Their dorsal portions are about twice as long as ventral. Connecting rings are thin, non-calcified, and were probably organic. In each camera their posterior ends are attached to the inner surface of the septal necks with the aid of the annular deposits. Their anterior ends are attached to the posterior edge of each septal neck.

Septa. The septa are thin, moderately curved, and nacreous. On dorsal side, the mural parts of the septa are short, but on ventral (siphuncular) side, they are long, about 1/3 camera length.

Body chamber. Only a partly complete body chamber (maximum diameter 9 mm) is preserved. Where the shell layers are separated on the body chamber the outer surface of the nacreous layer is lined with a delicate wrinkle layer. The wrinkles are aligned perpendicular to the shell axis like the wrinkle layer of the specimen 2.

Cameral deposits. At the growth stage of the specimen, the cameral deposits are indistinct.

Cameral membranes and deposits. The membranes can be distinguished under a standard dissecting microscope because of differences in color between the white calcite filling the camerae and black or dark brown material of membranes. The membranes line the shell wall, septal surfaces and the thin, indistinct cameral deposits on the shell wall. On the adapical septal surfaces, the deposits are essentially thicker than the septa. On the adoral surfaces, they occur irregularly and do not coat the entire septal surface but are restricted to the area near septal neck.

EDS data. The analyses of the cameral membranes taken from the surfaces facing the camerae show Fe (43–67%), S (15–34%) and O (8–23%). Analyses of the cameral membranes taken from the surfaces matching the shell wall show O (22–38%), Fe (55–62%), S (6–15%), Si (1.3–3.3%). Therefore, the cameral membranes were presumably originally organic material, but diagenetically they were replaced by black pyrite and reddish marcasite.

SYSTEMATIC PALEONTOLOGY

Subclass Coleoidea Bather, 1888

Order Aulacocerida Stolley, 1919

Family Mutveiconidae Doguzhaeva, 2002

Differences. The family Mutveiconidae is erected by monotypy. A short rostrum is a characteristic feature of the family that distinguishes it from bactritoids because they lack a rostrum. Comparison with younger aulacocerids is difficult since the young growth stages are known for none of them in detail.

Genus *Mutveiconites* Doguzhaeva, 2002

Type species. *Mutveiconites mirandus* Doguzhaeva, 2002

Diagnosis: Slender longiconic orthocones with oval (in median section) protoconch; short rostrum coating protoconch and about first ten camerae, its conical post-protoconch part shorter than protoconch length, small ventral marginal siphuncle, septal necks short; camerae comparatively long; long body chamber present at least in young growth stages, shell wall of thin inner prismatic and thick nacreous layers; a gradual primary constriction is present between the eighth and ninth septum 8; there is no primary varix.

Remarks: The diagnosis was originally based on the adolescent shell described by Doguzhaeva, (2002a, Pl. 17, Figs. 1–4); adults were unknown. The family is established on the basis of the following features: longiconic phragmocone with comparatively long camerae and narrow marginal siphuncle; short rostrum coating protoconch and adult first ten camerae, its conical post- protoconch part shorter than protoconch length; long body chamber present at least in early stages of growth. In *Mutveiconites* the conotheca includes a nacreous layer that makes up the bulk of its thickness as in Bactritoidea (Doguzhaeva et al., 1996). If it was

a spirulid genus it would lack a nacreous layer like Recent *Spirula*, the Cretaceous *Adygeya* Doguzhaeva, 1996a and *Naefia* Wetzel, 1930 and the Late Carboniferous *Shimanskyia* (Doguzhaeva & al., 1999a), in all of which the shell wall consists of inner and outer acicular-prismatic plates.

The adolescent specimen from the Finis Shale under consideration fits within the diagnosis of this family. The diagnosis of the genus is the same as for the family. Therefore, there are no morphological features that would contradict with the diagnosis of the genus as well.

The two other medium-sized longicones (specimens 2 and 3) from the same locality that yielded the adolescent shell (specimen 1) described below are referred to the family and genus, with reservation. However, they are not used for the systematic description because they do not preserve the diagnostic young shell growth stages, and without these early shell growth stages, a comparison with the type genus cannot be made.

Mutveiconites milleri sp. n.

Pl. 1, Figs. A, B, D, E

Derivation of name: In honour of A. K. Miller, a famous researcher of fossil cephalopods.

Holotype. Holotype, specimen no. OUZC 5205, Ohio University Zoological Collections, Ohio University, Department of Geological Sciences, Athens, OH 45701, USA.

Type locality. The specimen was collected from the emergency spillway at Lost Creek Lake approximately 3.2 km northeast of the community of Jacksboro, Jack County, Texas. The locality is designated as TXV-200 in the Ohio University fossil collections.

Type Horizon. Upper Carboniferous, Virgilian Stage, Finis Shale Member of the Graham Formation, Texas.

Description. The holotype is a 25 mm long adolescent longiconic shell. It consists of a small hemispherical, or cup-shaped protoconch, a rostrum, in which a post-protoconch part is about as long as the protoconch, 29 camerae are present in the phragmocone and a long body chamber. The protoconch is two times broader than long; the maximum diameter is near the aperture; it is 0.50 mm and its length is 0.25 mm. There is no constriction between the protoconch and first camera of the phragmocone, which may be due to the plane of the section, or this may be a diagnostic feature that separates the coleoids from the Bactritoidea. The protoconch wall has a thin unilayered shell, possibly prismatic, that wedges out near the first septum. There is no observable closing membrane. First septum is prismatic with thick organic membranes on the surfaces; it has long mural parts and in these two respects differs from the second and all other succeeding septa. The long mural parts of the first septum form the shell wall in several (5–10) of the initial camerae before the nacreous layer appears on its inner surface. The rostrum has a 0.25 mm long post-protoconch part, which surrounds the protoconch and extends as a sheath along the first ten or so camerae. The rostrum is loosely calcified and in places strongly pyritized, presumably because of its original essentially organic composition.

The diameter of the phragmocone increases in the first two camerae, then it gradually decreases during the next 6 camerae. Between the 8th and the 9th camera the shell is at its most constricted diameter, and from this gentle constriction, the shell gradually increases towards the aperture where it achieves a maximum diameter of about 1.8 mm. The gra-

dually expanding body chamber is 11 mm long, and that is about 2/5 of the shell length. Near the last septum, the diameter is 1.7 mm, and near the aperture it is 3 mm. Its shell wall thins towards the aperture. In ontogeny the shell wall shows the following ultrastructural modifications (Pl. 4, Figs. A–D). It is prismatic until approximately 7–10th camerae then a nacreous layer appears. There is no observable primary varix; however, this may be due to the plane of the section. The nacreous layer gradually becomes thicker and starting approximately from the 20th camera, it forms the main bulk of the shell wall thickness. The inner prismatic layer appears approximately at the position of the 20th camera. The outer and inner prismatic layers are comparatively thin. The septa are thin, moderately curved, and nacreous, with the exception of the first one that is prismatic. It appears that the adapical septal surfaces were originally coated by thick organic membranes. The adoral septal surfaces lack such membranes, or they are thin. Since the section of the shell is not median a siphuncle is not exposed, however, due to indirect evidence the siphuncle must have been ventral and marginal. Thin layering of cameral deposits is present in the protoconch and in the first camera. In the protoconch they are thin near the apex (or even absent there) and become thicker toward the aperture: At a distance of half the protoconch length, they are two times and near the aperture three times thicker than the protoconch wall. The adapical surface of the first septum lacks cameral deposits. In the first camera, they also have a maximum thickness in the adoral part of the camera, where they coat the shell wall and adoral septal surface. On the shell wall, they are as thick as the shell wall but become thinner and almost wedge out on the septum towards its central part. The cameral deposits have cameral membranes lining their surfaces. The membranes occur on thin loosely calcified portion of cameral deposits along the shell wall, on septal surfaces and in the corners between the shell wall and adapical septal surfaces. These membranes may be responsible for secretion of cameral deposits.

Differences. *M. milleri* sp. n. differs from *M. mirandus* in the shape of the protoconch, which is cup-like in the former and oval in the latter (compare Pl. 1, Fig. 2; Pl. 3, Fig. 1 and Pl. 5, Figs. A, B) and by presence of cameral deposits in the protoconch and also in camerae. This can be explained by the fact that the shell of the former is at an older growth stage since it has 29 camerae, against ten camerae in the latter. Besides, in *M. milleri* sp. n. the phragmocone is less curved than in *M. mirandus* but this can be explained by the different section plane of the two shells as follows: in *M. milleri* specimen the section is not median and in *M. mirandus* specimen the section is median. Therefore, the shell in *M. milleri* sp. n. could be slightly curved.

CARBONIFEROUS PHRAGMOCONE-BEARING COLEOIDS – COMPARISON WITH HEREIN STUDIED LONGICONES

The limited data available on the initial part of the shell, phragmocone structure, and shell ultrastructure in Carboniferous phragmocone-bearing coleoids allows a systematic

comparison of the studied specimens from Texas with some of these taxa. Additionally the longicones examined are compared with Early Permian bactritoids and Mesozoic belemnoids.

List of Carboniferous phragmocone-bearing coleoids

Order Hematitida Doguzhaeva, Mapes and Mutvei, 2002 – Early Carboniferous

Family Hematitidae Gustomesov, 1976

Hematites Flower and Gordon, 1959 – Upper Mississippian, Lower Eumorphoceras Zone (= Serpukhovian), Utah, Arkansas, USA

Bactritimimus Flower and Gordon, 1959 – Upper Mississippian, Lower Eumorphoceras Zone (= Serpukhovian), Arkansas, USA

Paleoconus Flower and Gordon, 1959 – Upper Mississippian, Lower Eumorphoceras Zone (= Serpukhovian), Arkansas, USA

Order Donovaniconida Doguzhaeva, Mapes and Mutvei (in press) – Late Carboniferous

Family Donovaniconusidae Doguzhaeva, Mapes and Mutvei, 2002

Donovaniconus Doguzhaeva, Mapes and Mutvei, 2002 – Upper Pennsylvanian, Desmoinesian, Oklahoma, USA.

Order Aulacoceratida Stolley, 1919–? Devonian; Carboniferous–Jurassic

Family Mutveiconitidae Doguzhaeva, 2002

Mutveiconites Doguzhaeva, 2002 – Upper Carboniferous, Orenburgian, southern Urals, Kazakhstan; Pennsylvanian (Virgilian), Texas, USA

Order Phragmotheuthida Jeletzky in Sweet, 1964

Family Rhiphaeoteuthidae Doguzhaeva, 2002

Rhiphaeoteuthis Doguzhaeva, 2002 – Upper Carboniferous, Orenburgian, Southern Urals, Kazakhstan

Order Spirulida Pompeckj, 1912

Family Shimanskyidae Doguzhaeva, Mapes and Mutvei, 1999

Shimanskyia Doguzhaeva, Mapes and Mutvei, 1999 – Upper Pennsylvanian, Virgilian (= Stephanian); Texas, USA

Order uncertain

? *Eobelemnites* Flower, 1945 – Upper Mississippian, Chesterian, Alabama, USA

? Unnamed coleoid from Czech Republic (Košťák et al., 2002) – Early Carboniferous, Moravice Formation, Northern Moravia, Czech Republic

“*Bactrites*” *woodi* Mapes, 1979–Eudora Shale Member, Stanton Formation, Pennsylvanian, Kansas, USA. (MAPES, 1979)

Undescribed Stark coleoids (Doguzhaeva, Mapes, Mutvei and Pabian, 2002) – Upper Pennsylvanian, Missourian (= Kasimovian), Nebraska, USA

Comparison

Hematites. The similarity of this genus and the Texas longicones under examination concerns: (a) presence of a rostrum, (b) irregular mineralization of the rostrum that seemed to be of essentially organic material in both, and (c) longiconic phragmocone with comparatively long camerae and narrow marginal siphuncle with what appear to be organic connecting rings. Unlike the longicones under consideration, in *Hematites*: (a) the shell wall consists of five layers and lacks a nacreous layer; (b) the rostrum is a com-

plicated folded structure that coats the total length of the phragmocone; its post-phragmocone part is rather long as compared to the length of the body chamber, (c) the final chamber (= body chamber) is short, equal to 1.5 camera length, and (d) the protoconch and the initial part of the phragmocone are commonly truncated.

Shimanskyia. The similarity of this genus and the Texas longicones under examination concerns: (a) longiconic phragmocone with comparatively long camerae and narrow marginal siphuncle with thin and presumably organic connecting rings and septal necks that are longer on ventral side and shorter on dorsal side and (b) a long “tubular” body chamber. Unlike the longicones under examination, in *Shimanskyia* the shell wall consists of inner and outer acicular prismatic plates and lacks a nacreous layer, which is present in the Texas specimens.

Donovaniconus. The similarity of this genus and the Texas longicones under examination concerns: (a) a sheath-like rostrum (its early stage form, near the protoconch, is unknown), (b) a long body chamber, (c) a phragmocone with narrow marginal siphuncle, septal necks that are short dorsally but long ventrally and septa with comparatively long mural parts, and (d) a shell wall with a dominant nacreous layer. This genus has a moderately breviconic shell, and in this respect differs significantly from the longicones under examination.

Mutveiconites (Pl. 5, Figs. A, B). The similarity of this genus and the Texas longicones under examination concerns: (a) a longiconic phragmocone with comparatively long camerae and narrow marginal siphuncle, (b) a long slowly expanded “tubular” body chamber, (c) protoconch with its maximum diameter near the aperture, (d) the lack of a constriction between the protoconch and first camera, (e) a short rostrum coating the protoconch and about first ten camerae, its post-protoconch part is about the length of the protoconch, and in front of the protoconch it is sheath-like, (f) irregular mineralization of rostrum that is supposed to be rich in organic material, (g) no distinct primary constriction, (h) no primary varix, and (k) shell wall ultrastructure with a dominant nacreous layer.

Rhiphaeoteuthis. The similarity of this genus and the Texas longicones under examination concerns: (a) a phragmocone with narrow marginal siphuncle, septal necks that are short dorsally but long ventrally. This genus has a moderately breviconic shell, and in this respect differs significantly from the longicones under examination. Although the protoconch and early stages are unknown, a long slowly expanded body chamber at early ontogeny is possible as it was observed in undetermined juvenile shells from the same beds (see Doguzhaeva, 2002a: Pl. 15, Fig. 1; Pl. 16, Figs. 1, 6).

Hemibactrites (Bactritida): The protoconch has a primordial dome (Doguzhaeva, 1996b, c) that can be erroneously interpreted as a short rostrum because of their similar positions in the shell. However, in *Hemibactrites* the protoconch wall consists of three prismatic layers, and near the apex there is a space between the outermost layer and two other layers. This space was named a “primordial dome”. The base of the primordial dome is marked by a ring of modified micro-ornamentation on the outer surface of the protoconch. The primordial dome lacks any traces of mine-

ralization or organic filling. It looks like an originally empty space on the apex of the protoconch. Contrary to that, in the studied adolescent Texas longicone, the rostrum is loosely mineralized and has no separate layer around it. The phragmocone structure is similar in the two genera, and in both (a) the longiconic phragmocone has comparatively long camerae and a narrow marginal siphuncle, and (2) a nacreous layer is the dominant element in the ultrastructure of the shell wall. Additionally, both genera have a long "tubular" body chamber.

Conobelus, *Passaloteuthis* (Pl. 1, Fig. C) (Belemnitida). The similarities in these genera and the Texas adolescent longicones under examination concerns: (a) the long mural parts of first septum that form a shell wall in first more than 20 camerae, where conotheca proper is missing, and (b) the irregular mineralization and high content of organic material of the primordial rostrum in belemnites (Pl. 1, Fig. C) and in the juvenile rostrum of *M. milleri* sp. n. (Pl. 1, Fig. B; Pl. 3, Fig. A).

EVOLUTIONARY IMPLICATION

Nowadays, early evolution of aulacocerid coleoid cephalopods is poorly documented and, therefore, their origin is obscure. The coleoids, including the aulacocerids, evidently arose from bactritoids. Therefore, it is reasonable to assume that the "pioneers" of the aulacocerids were similar in gross morphology to bactritoids. However, for a long time, *Hematites* has been considered as an Early Carboniferous aulacocerid (Shimansky, 1960; Gordon, 1966; Gustomesov, 1976; Reitner and Engeser, 1982; Doyle, 1990; Doyle et al., 1994; Mariotti and Pignatti, 1999). The reasons for that were that this genus represented the earliest recorded cephalopod possessing a rostrum, and in chronological order, the next group having a rostrum is the aulacocerids. Besides, in both, the rostrum is a folded complex structure. Jeletzky (1966) erected the order Aulacocerida because of the pronounced morphological differences between the aulacocerids and belemnitids, such as a long body chamber, an aperture with short dorsal and ventral crests, a conotheca with growth lines, a rostrum built mainly of organic material, and prochoanitic adult septal necks. He considered the aulacocerid rostrum as analogous but not homologous to that in belemnitids. Jeletzky (1966) formally assigned *Hematites* to the order Aulacocerida, but for unknown reasons, omitted this genus in his classification. Doguzhaeva et al., (2002) restudied with the scanning electron microscope newly recovered material of *Hematites*. Their study revealed a set of features that did not fit within the diagnosis of the Aulacocerida. These features are: a short posterior "free" (post-phragmocone) part of a rostrum, short terminal (= "body") chamber, a peristome with a broad U-shaped ventral or ventro-lateral sinus, multi-layered conotheca without a nacreous layer, absence of ventral and dorsal apertural projections and growth lines, and absence of a pro-ostracum. On the basis of the differences listed above the order Hematitida Doguzhaeva, Mapes and Mutvei, 2002 was erected. Simultaneously with this, a juvenile orthoconic shell was found that shows a long body chamber, a narrow marginal siphuncle, a small protoconch, a short irregular mineralized rostrum. The post-

protoconch part of that is approximately as long as a protoconch and a shell wall has a nacreous layer. The specimen comes from the Upper Carboniferous of southern Urals, north-western Kazakhstan. This form was described as *Mutveiconites* (Doguzhaeva, 2002a). It has been considered as the earliest recorded member of the Aulacocerida. With the exception of the rostrum, it is remarkably like a bactritid shell (compare: Doguzhaeva, 2002: Pl. 1, Fig. 1 and Pl. 17, Fig. 1). The discovery of the Late Carboniferous adolescent longicone with a short rostrum from Texas, that is under examination herein, confirms the concept that the evolution of the aulacocerids started with bactritid-like forms that had a short irregularly mineralized, partly organic rostrum, which was, in its post-protoconch part, as small as a protoconch itself. From this viewpoint, the lineage of the aulacocerids is documented from the Late Carboniferous.

The striking feature of early shell ontogeny observed in the Late Carboniferous adolescent longicone from Texas, referred to the genus *Mutveiconites*, is the absence of the conotheca proper at the early growth stages. This feature has been known in some Jurassic and Cretaceous belemnites, for instance in Lower Cretaceous *Conobelus* (Doguzhaeva & al., 1999) and Lower Jurassic *Passaloteuthis* (Doguzhaeva & al., 2003), in which the long mural parts of the first septum continue along the initial portion of the phragmocone and form its shell wall. Another striking feature common for *Mutveiconites* and some belemnites is the irregular mineralization of the rostrum, in the former, and the primordial rostrum, in the latter (compare Pl. 1, Fig. B and Fig. C), indicating that both structures probably had an essentially organic composition. Further investigations are needed for discussion of these similarities.

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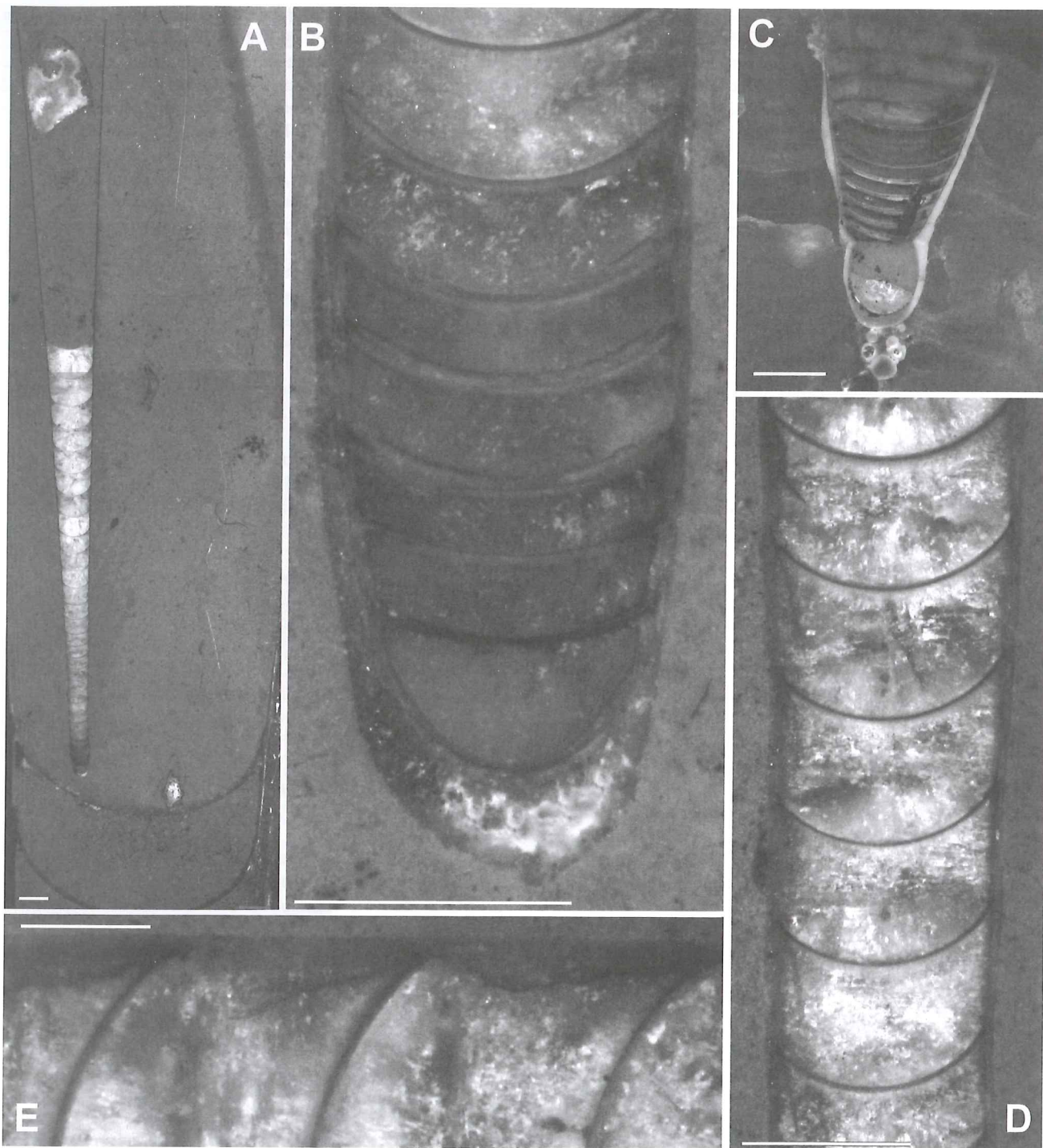


Plate 1. A–E. *Mutveiconites milleri* sp. n., Upper Carboniferous (Virgilian, = Stephanian), Texas, USA, holotype (OUZC 5205), longitudinal section. A. The adolescent longicone preserved inside the body chamber of the larger shell (OUZC 5206), showing a long body chamber and a phragmocone, scale bar is 1 mm. B. Enlarged view on the initial portion of the shell on Fig. A to show a short rostrum surrounding the protoconch and extending along the camerae, hemispherical protoconch, short irregularly spaced septa and cameral membranes on the inner surfaces of the shell; note that in the first septum the membranes are thicker than in the next septa; scale bar is 0.5 mm; D. Seven camerae of the phragmocone showing cameral membranes (left side) with their adoral ends attached to the corners between the shell wall and septa, scale bar is 0.5 mm; E. Enlarged view of the cameral membranes to show that they lie on the surface of the cameral deposits occurring along the shell wall; within the right camera the cameral membrane are coating the cameral deposits and from both ends they are attached to the septal membranes, in the next camera (to the left) the membrane is attached to the adoral septal surface but broken near its adapical end and shifted to the centre of the camera, the color photo emphasizes the presence of the cameral deposits along the shell wall, scale bar is 0.2 mm. C. *Passaloteuthis* sp. Lower Jurassic, north-western Germany. The median shell section showing a primordial rostrum exhibiting similarity with the rostrum in adolescent *M. milleri* sp. n. (compare with Fig. B). In both the apical part is loosely mineralized and evidently originally contained much organic material (for details see Doguzhaeva et al., 2002, 2003), scale bar is 0.5 mm.

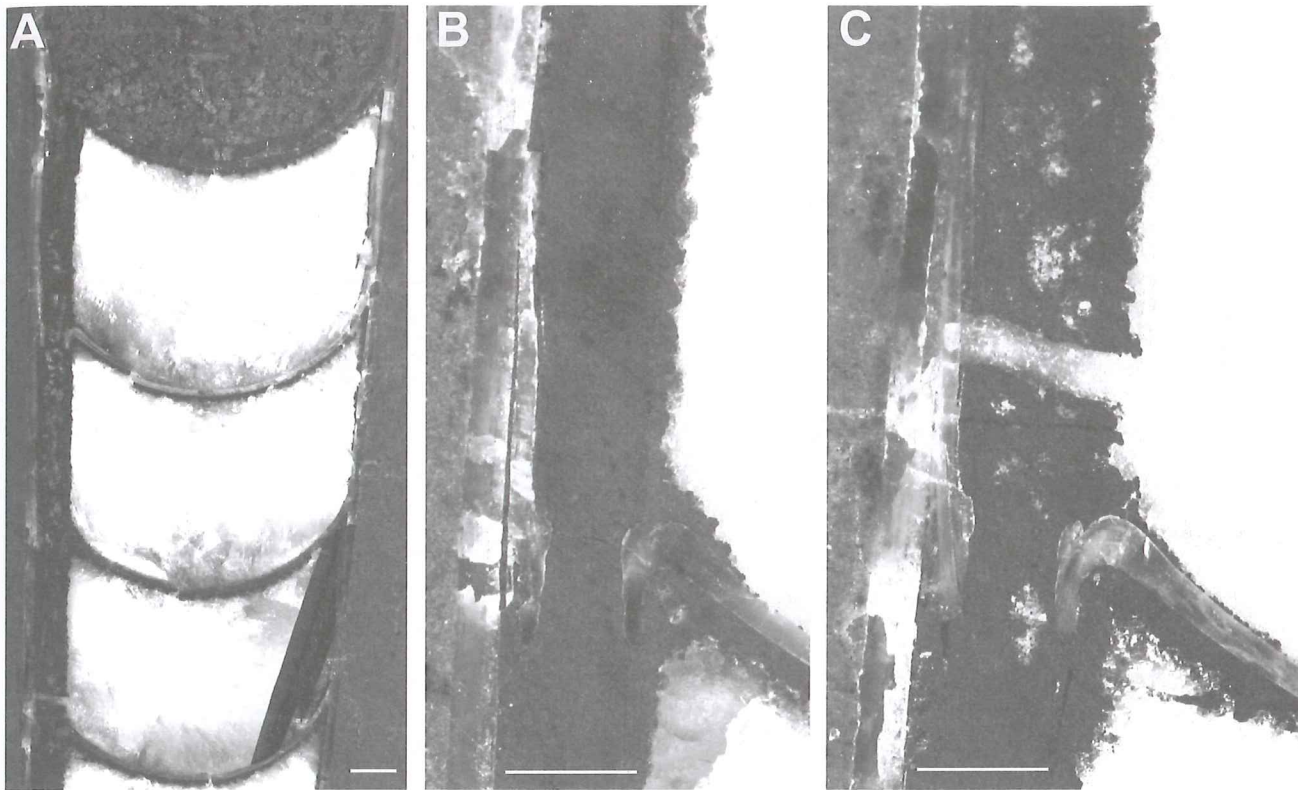


Plate 2. A–C. ? *Mutveiconites* sp., OUZC 5206, Upper Carboniferous (Virgilian = Stephanian), Texas, USA. Median shell section of medium-sized longicone showing the back part of a body chamber and last three camerae. A body chamber, a narrow marginal siphuncle and membranes on the adapical septal surfaces are strongly pyritized; camerae have no cameral deposits, scale bar is 1 mm. B, C. Enlarged view on two septal necks and connecting rings on Fig. A to show that septal necks have short dorsal portion and long ventral portion; connecting rings are thin, possibly nonmineralized, originally organic, their adapical ends are attached to the septal necks with the aid of the annular deposits inside the necks and their adoral ends are attached to the adapical tips of necks, scale bar is 0.5 mm.

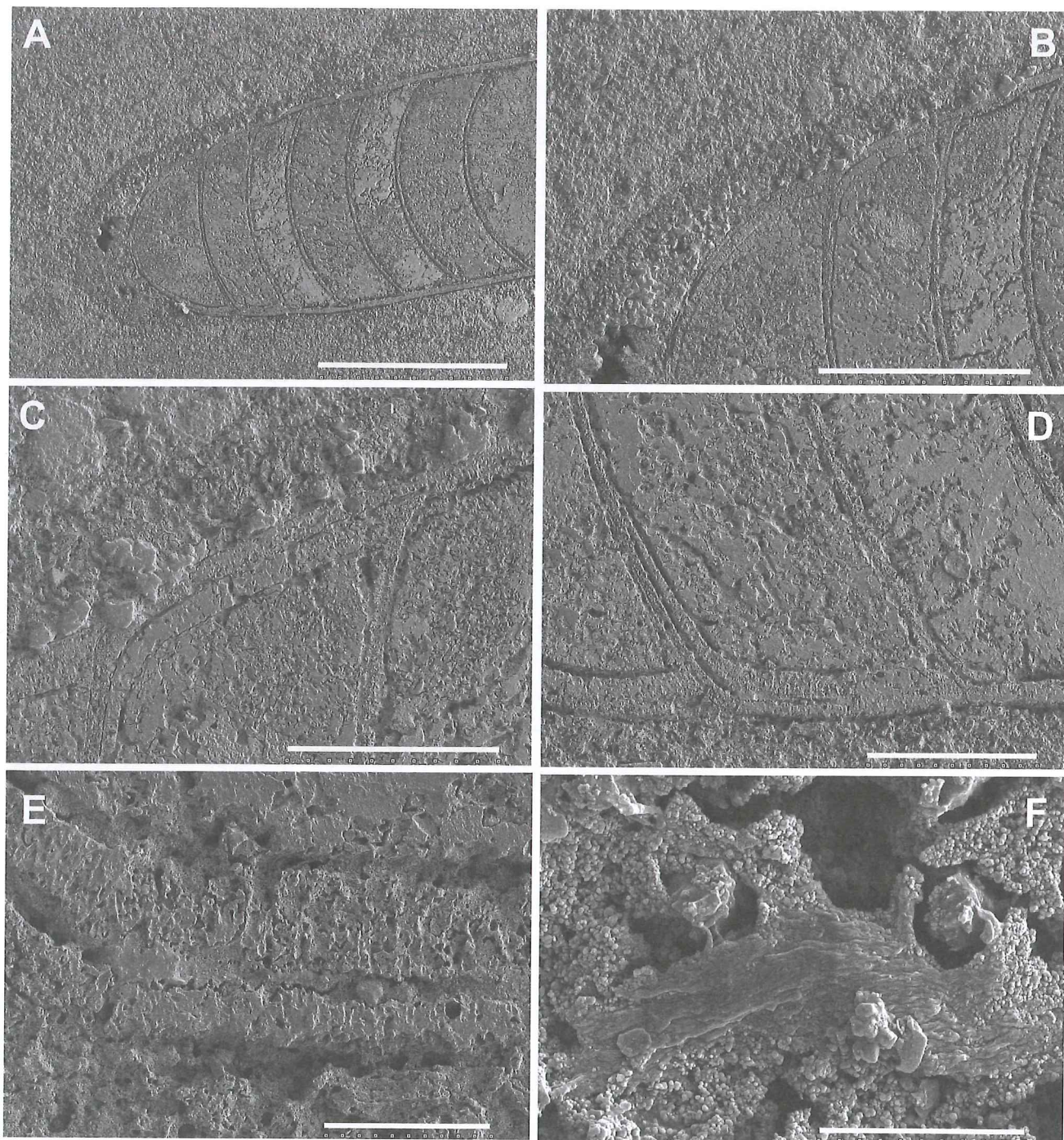


Plate 3. A–F. *Mutveiconites milleri* sp. n., Upper Carboniferous (Virgilian = Stephanian), Texas, USA, holotype (OUZC 5207), longitudinal section, SEM images. A. The initial portion of the shell to show a presence of a rostrum around the protoconch and first camerae and its length in ratio to the length of the protoconch, and camerae, scale bar is 600 μm . B. Close up of Fig. A to show irregular mineralization and strong pyritization of the rostrum, scale bar is 300 μm . C. Close up of Fig. A to show a long mural part of first septum constructing the shell wall and cameral deposits, scale bar is 120 μm . D. Close up of Fig. A to show that the cameral deposits in the protoconch and first camerae, scale bar is 120 μm . E. Enlarged view on Fig. D to show that the mural part of the first septum forms the shell wall in first camera and an interspace between them, scale bar is 30 μm . F. Enlarged view of the coprolites showing they are oval clusters composed of digested material from an unknown organism, scale bar is 3 μm .

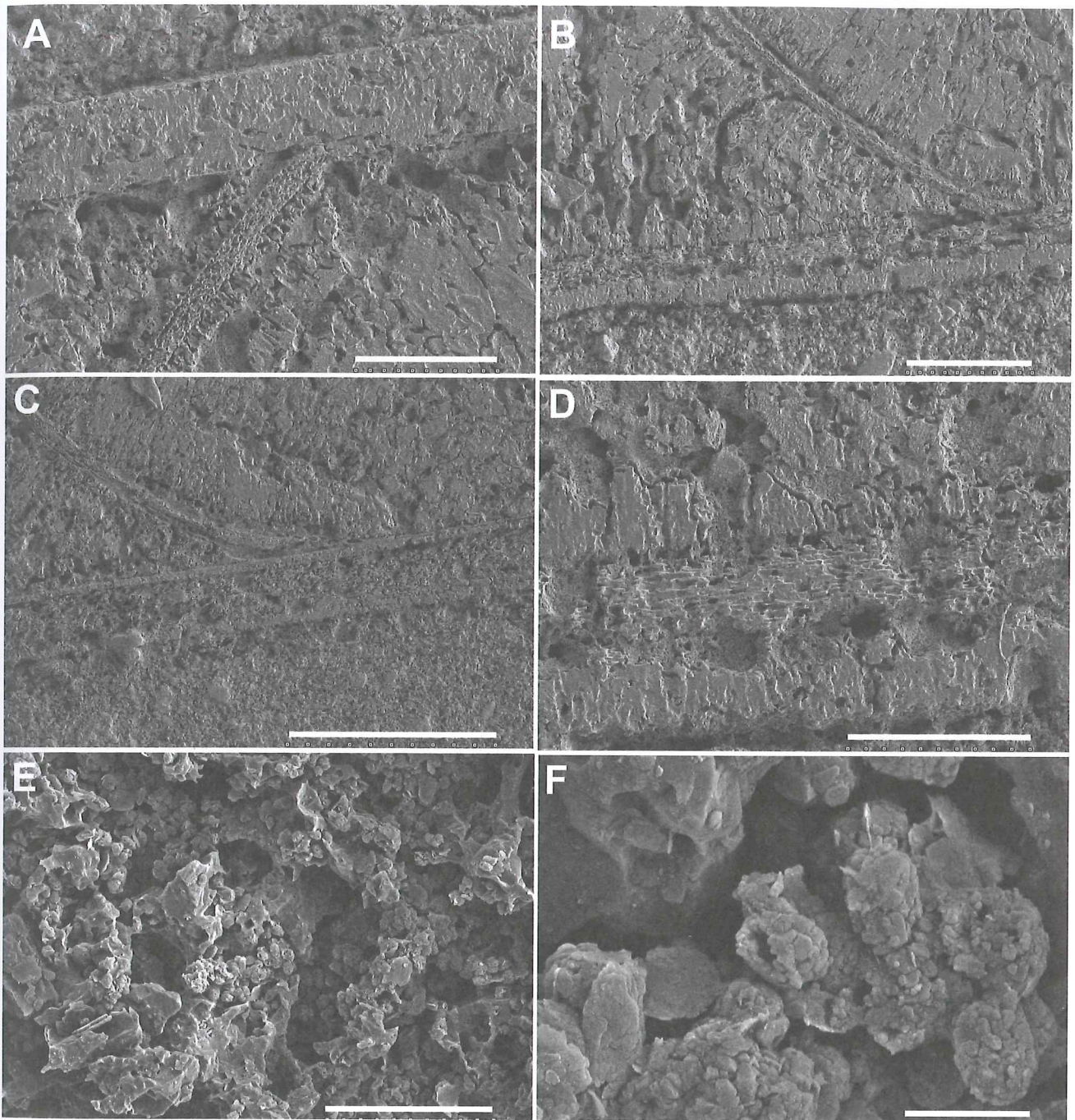


Plate 4. A–D. Shell wall ontogeny in *Mutveiconites milleri* sp. n., Upper Carboniferous (Virgilian = Stephanian), Texas, USA, holotype (OUZC 5205), longitudinal section, SEM images. A. Unilayered prismatic shell wall in first camera, scale bar is 30 μ m. B. Next growth stage, a nacreous layer is added to the outer prismatic layer, scale bar is 60 μ m. C. Next growth stage, an inner prismatic layer is added, scale bar is 120 μ m. D. Close up of Fig. C to show horizontal lamination of nacreous layer, scale bar is 30 μ m. Figs. E, F. ?*Mutveiconites* sp., OUZC 5206, Upper Carboniferous (Virgilian = Stephanian), Texas, USA. View on heterogeneous sediment in the body chamber, scale bar is 12 μ m. F. Close up of Fig. D to show microstructures evidently evidencing possible role of microorganisms (?bacteria) in reworking of the material inside the body chamber. The latter made possible fine preservation of a delicate adolescent longicone inside, scale bar is 1.2 μ m.

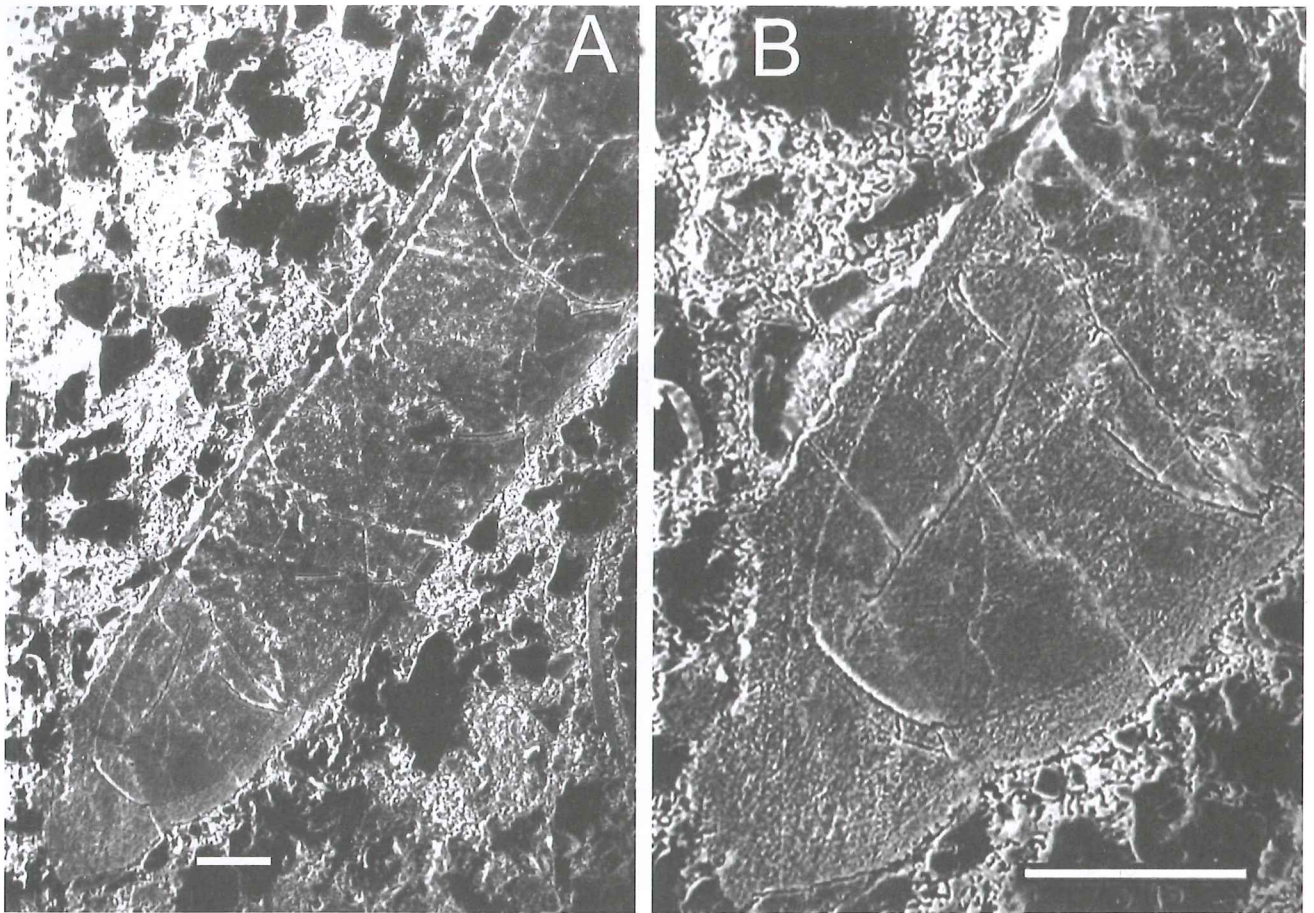


Plate 5. A–B. *Mutveiconites mirandus*, sp. PIN 3871/370, Coll. of Paleontological Inst., Russian Academy of Sci., Moscow, Upper Carboniferous, Orenburgian, south Urals, Kazakhstan (former USSR) (modified from Doguzhaeva, 2002, Pl. 17, Figs. 1–4). A. The median section of the initial portion of the shell showing a cone-like rostrum, an oval protoconch and first camerae, scale bar is 0.1 mm. B. Enlarged detail of A to show a rostrum with a short post-protoconch part and sheath-like part extending along the phragmocone, scale bar is 0.1 mm.