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Adolescent Bactritoid, Orthoceroid, Ammonoid and Coleoid Shells from the Upper Carboniferous and Lower Permian of the South Urals

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17 Plates

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Contents

Schalen jugendlicher Bactritoideen, Orthoceren, Ammonoideen und Coleoideen aus dem Oberkarbon und Oberperm des südlichen Ural

Zusammenfassung

Gut erhaltene Schalen jugendlicher Bactritoideen, Orthoceren, Ammonoideen und Coleoideen aus dem Orenburgium (Oberkarbon) und Artinskium (Oberperm) des südlichen Ural wurden mit Hilfe des Rasterelektronenmikroskops untersucht. Abgesehen von der allgemeinen Morphologie wurde die Ultrastruktur des Protokonchs und der ersten Kammern des Phragmokons studiert. Es zeigte sich ein frühontogenetischer Unterschied zwischen Ammonoideen und Bactritoideen. Im Gegensatz zu den Ammonoideen fehlt letzeren eine primäre Varix, die Schichten der Schalenwand befinden sich immer neben der ersten Einschnürung. Weiters zeigt der Protokonch bei manchen Bactritoideen eine primordiale Aufwölbung und in den Kammern Ablagerungen, die bei Ammoniten unbekannt sind. Das unterstützt die Auffassung, die Bactritoideen nicht als ein Taxon der Ammonoidea, sondern als eigene Unterklasse Bactritoidea zu klassifizieren.

Durch ihre gute Erhaltung zeigen die Orenburgischen und Artinskischen Ammoniten die aufeinanderfolgenden Stadien der frühontogenetischen Schalenentwicklung beginnend beim Stadium vor dem Schlüpfen. Das Verhältnis zwischen der Entstehung des ersten Septums und der ersten Varix konnte gefunden werden. Im Moment des Schlüpfens wird die Mündung der Ammonitella mit einer primären Perlmutter-Varix verstärkt, die sich 360° vom Proseptum entfernt befindet, das den Protokonch vom Rest der Schale trennt.

Die untersuchten orenburgischen Orthoceren mit gut erhaltenem Apex haben ein becherförmiges Primordium mit einer Cicatrix und einem blasenartigen Caecum. Der Mündungsrand des Primordiums ist durch die Verkleinerung des Öffnungswinkels und einen Skulpturwechsel

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ringsum gekennzeichnet. Längsschnitte zeigen, dass das erste Septum längs des Primordialrandes befestigt ist. Die Perlmutterschicht der Schale erscheint nahe dem ersten Septum. Die Schale ist längs der Cicatrix dünn, unregelmäßig calcifiziert und enthält viel organische Substanz.

Zwei orenburgische, oberflächlich belemnitenartige brevikone Phragmokone ohne eine Spur von Rostrum oder scheidenartiger Struktur wurden zusammen mit den Bactriten, Orthoceren und Ammoniten gefunden. Das einzige Kennzeichen, das sie von Belemnitenphragmokonen unterscheidet, ist ein betont weiter und seichter Ventrallobus. Dies tritt bei Phragmoteuthiden auf, doch ist das Proostracum noch unbekannt.

Ein einziges orenburgisches longikones Exemplar mit kurzem Rostrum um den eiförmigen Protokonch, zehn Kammern des Phragmokons und einer langen Wohnkammer wurde zusammen mit den anderen Cephalopoden gefunden. Der postalveolare Teil des Rostrums ist kürzer als der Protokonch. Diese Form wird zu den Aulacocerida gestellt. Folgende neue Taxa werden auf der Grundlage jugendlicher Gehäuse beschrieben: Artinskische Bactriten: *Chuvashovia curvata* gen. et sp. nov., *Simobactrites kuzinae* gen. et sp. nov., *Linibactrites solidus* gen. et sp. nov., *Uralobactrites uralicus* gen. et sp. nov.und der aulacoceride *Mutveiconites mirandus* gen. et sp. nov.

Abstract

Well preserved adolescent shells of bactritoids, orthoceroids, ammonoids and coleoids from the Orenburgian (Late Carboniferous) and Artinskian (Early Permian) of the South Urals were studied with the SEM. In addition to general morphology, the shell wall ultrastructure of the protoconch and first camerae of the phragmocone was examined. This showed that early shell ontogeny differs in bactritoids and ammonoids. Unlike ammonoids, bactritoids lack a primary varix and the layers of the shell wall are continuous near the primary constriction. Besides, in some bactritoids the protoconch exhibits the primordial dome and cameral deposits which are unknown in ammonoids. This supports the idea that the bactritoids should be ranked as a separate subclass Bactritoidea rather than as a subdivision of Ammonoidea. Well preserved Orenburgian and Artinskian ammonoids exhibit the successive stages of early shell ontogeny starting with the pre-hatching ones. The interrelation of the formation of the first septum and the primary varix was traced. At the moment of hatching the aperture of the ammonitella became firmly strengthened by a nacreous primary varix situated at 360 degrees from the proseptum which separates the protoconch from the rest of the shell.

The Orenburgian orthocerids examined with a well preserved apex show a cup-like primordium bearing a cicatrix and containing a bubble-like caecum. The apertural margin of the primordium is marked by a decrease of the expansion angle and a change of the sculpture around it. Longitudinal sections show that the first septum is attached along the margin of the primordium. The nacreous layer of the shell wall appears near the first septum. The shell wall of the cicatrix is thin and irregularly calcified, with much organic matter.

Two Orenburgian breviconic phragmocones which appear superficially belemnitid, but have no traces of rostrum or sheath-like structures, were found in association with the bactritoids, ammonoids and orthoceroids. The only feature which distinguishes them from belemnitid phragmocones is a pronounced wide and shallow ventral lobe. This form is assigned to Phragmoteuthida although the pro-ostracum is still unknown.

A single Orenburgian tiny longicone with a short rostrum surrounding the egg-shaped protoconch, ten camerae of the phragmocone, and a long living chamber was found in association with the other cephalopods. The postalveolar part of the rostrum is shorter than the protoconch. The form is referred to the Order Aulacocerida.

The following new taxa are described on the basis of adolescent shells: the Artinskian bactritids *Chuvashovia curvata* gen. et sp. nov., *Simobactrites kuzinae* gen. et sp. nov., *Linibactrites solidus* gen. et sp. nov., *Uralobactrites uralicus* gen. et sp. nov., and the Orenburgian bactritid *Ovobactrites antonovae* gen. et sp. nov.; the orthocerid *Aidaroceras politum* gen. et sp. nov., the phragmoteuthid *Rhiphaeoteuthis margaritae* gen. et sp. nov., and the aulacocerid *Mutveiconites mirandus* gen. et sp. nov.

1. Introduction

The paper deals with SEM studies of well preserved Late Carboniferous and Early Permian adolescent orthocones and ammonoid shells from several localities of the South Urals discovered in the 1930s by V.E. RUZHENCEV. The non-ammonoid cephalopod fauna from these localities was mainly described by V.N. SHIMANSKY (1954, 1968) and RUZHENCEV & SHIMANSKY (1954). SEM studies of the exceptionally well-preserved Artinskian juvenile bactritoids of the South Urals have revealed several previously unknown characters of their protoconch and apical portions the phragmocone that facilitated scrutiny of the early shell ontogeny in bactritoids, ammonoids, orthoceroids, belemnoids and spirulids (DOGUZHAEVA, 1996a–c, 1999; DOGUZHAEVA et al., 1999b). To emphasize the principal differences in the early ontogeny of bactritoids and ammonoids the term "bactritella" (DOGUZHAEVA, 1996a) was introduced by analogy with "ammonitella" (DRUSCHITC & KHIAMI, 1970).

SCHINDEWOLF (1959, p. 975), describing the Lower Mississippian *Bactrites* with the protoconch preserved, stated that

> *"... the comparison of a large number of protoconch and early stages of suture lines proved the constancy of the different developmental types and confirmed the author's view of their phylogenetical significance. Beginning from the very early stages, our goniatites are different and determinable (of course not specifically, but as far as the larger evolutionary branches are concerned to which they belong). ARKELL and SPATH thus were incorrect when they designated the fundamental differences as 'unimportant and variable features.'"*

At the time when this was written the overall morphology of the protoconch and first chambers of the phragmocone had been studied in a large number of bactritoids and some other Palaeozoic orthoconic cephalopods.

However, mainly because of poor preservation, the shell ultrastructure at early ontogenetic stages was still inadequately known. Among orthoconic forms the shell ultrastructure had been mainly studied in Pennsylvanian (Upper Carboniferous) ortho- and pseudorthocerids of the Buckhorn Asphalt of the USA (ERBEN et al., 1969; RISTEDT, 1971; MUTVEI, 1972; BLIND, 1988; TANABE & UCHIYAMA, 1997). The shell ultrastructure of the Palaeozoic orthoceroids and ammonoids is better known than that of bactritoids.

2. Material Examined and Method of Study

2.1. Upper Carboniferous Shells

The Late Carboniferous shells examined come from the Orenburgian beds exposed near the villages Ilyinskiy, Nikolskiy and Creek Aidaralash, on the west slope of the South Urals (RUZHENCEV, 1950; BOGOSLOVSKAYA et al., 1995). This material was collected by RUZHENCEV and his wife, the geologist I.V. KHVOROVA in the 1950s and 1960s. RUZHENCEV labelled the samples containing the accumulations of juvenile orthocones and ammonoids as "ecological". These samples include numerous well preserved fragments of terrestrial plants indicating near-shore burial of the cephalopods. Good condition of preservation and abundance of cephalopod shells in the Upper Carboniferous as well as in the Lower Permian in the west slope of the South Urals were partly explained as a result of intensive deposition of sediment in a lagoon-like shallow sea and absence of appreciable postmortal drift of the cephalopods (RUZHENCEV, 1950; MAKSIMOVA & OSIPOVA, 1950). Additional support for this idea came from a comparatively large number of ammonoid beaks, usually preserved separately from the shells but also within living chambers and often in pairs. They were found within living chambers of adolescent shells of the goniatites *Prothalassoceras, Gleboceras, Aristoceras, Eoasianites* and the prolecanitid *Uddenites* (DOGUZHAEVA, 1999).

The samples studied represent broken pieces of flattened argillite concretions 100–250 mm long. They were sliced up, the exposed surfaces were polished and examined with the SEM to search for shells with the apical portions preserved. Orthocones showing the position of the siphuncle were studied in more detail. Altogether more than 200 conchs were studied.

2.2. Lower Permian Shells

The Lower Permian (Artinskian) sample was collected by B.I. CHUVASHOV (Institute of Geology and Geochemistry of the Urals branch of the Russian Academy of Sciences, Ekaterinburg) in the Sim River basin in the 1960s. It is a slab of soft organic limestone 100 mm long. The sample yielded around 100 juvenile shells, some of them with the protoconch preserved. A large number of shells was studied with the SEM. Shell wall ultrastructure was examined with the aid of fractured shells. Some of the shells were cut longitudinally.

The material is stored at the Paleontological Institute of the Russian Academy of Sciences under the number 3871.

3. Shell Morphology and Ultrastructure of Late Palaeozoic Adolescent Cephalopods from the South Urals

3.1. Bactritoids

Protoconch

The diameter of the protoconch ranges from 0.27 mm to 1 mm. The following size cathegories have been used: the small-sized protoconchs have diameters around 0.3–0.4 mm, medium-sized ones 0.4 mm–0.5 mm, and large-sized ones more than 0.5 mm. Being generally subspherical, the protoconchs are globular (Pl. 1, Fig. 1; Pl. 4, Fig. 10), slightly asymmetrical (Pl. 1, Figs. 10, 11; Pl. 2, Figs. 1, 3), hemispherical (Pl. 4, Figs. 1, 9), depressed (Pl. 4, Figs. 4, 5, 7, 8; Pl. 6, Figs. 1, 2), elongated (Pl. 5, Figs. 3, 4, 6, 7; Pl. 7, Figs. 4, 7) or even almost cup-like (Pl. 8, Figs. 1, 4, 6). They are separated from the phragmocone by the constriction near the first septum which is either distinct (Pl. 1, Figs. 10, 11; Pl. 2, Figs. 1–3; Pl. 4, Figs. 1–2, 4–8, 10; Pl. 5, Figs. 3–8; Pl. 6, Figs. 1, 2; Pl. 7, Figs. 1, 4, 7), moderately developed (Pl. 1, Figs. 1, 8, 9), or weak (Pl. 4, Figs. 9, 11; Pl. 6, Figs. 7, 9; Pl. 8, Figs. 2, 4, 6). They are smooth (Pl. 4, Figs. 6, 10; Pl. 6, Fig. 9; Pl. 8, Figs. 4, 6), with wrinkles around the smooth apex (Pl. 1, Figs. 8, 9; Pl. 4, Figs. 11–13), sculptured with reticulated ornament (Pl. 2, Figs. 1–6, 8–12; Pl. 5, Fig. 2; Pl. 8, Figs. 1, 3) or bear thin longitudinal ribs (Pl. 4, Fig. 9). In some cases smooth shells show wrinkles near the constriction between the protoconch and phragmocone (Pl. 5, Figs. 5, 7, 8). Several shells showed an apical boss-like primordial dome visible from the outside due to a small change of the shell curvature near the apex and the ring of modified sculpture around it (Pl. 1, Fig. 10; Pl. 2, Figs. 10; Pl. 4, Figs. 2; Pl. 5, Fig. 2; Pl. 8, Figs. 4, 6); its length is about 0.1 of the protoconch length. In smooth shells the primordial dome is also smooth but surrounded by a narrow ring of delicate ribs around its base. In sculptured shells there is a ring of modified sculpture around the primordial dome. The primordial dome is the weakest part of the protoconch as it is formed only by the outermost sub-layer of the shell wall which is easily destroyed. That is why a large number of protoconchs show circular apical spots and broken shell wall around them (Pl. 1, Figs. 6, 8, 11, 12; Pl. 4, Fig. 9). In sculptured forms the spot is surrounded by a ring of modified sculpture (Pl. 2, Figs. 11, 12; Pl. 4, Fig. 9), and in smooth shells the spot is surrounded by wrinkles (Pl. 1, Figs. 8, 9; Pl. 4, Figs. 11–13). A cicatrix is absent from all shells examined. The inner surface of the protoconch shows a ripple pattern (Pl. 2, Fig. 3), or tubercular ornamentation (Pl. 2, Fig. 13). The inner surface of the protoconch is coated by cameral deposits (Pl. 1, Figs. 1–4; Pl. 5, Fig. 6; Pl. 6, Figs. 3–8; Pl. 7, Figs. 1–8).

Phragmocone

The first camera of the phragmocone varies in length being comparatively long when it is about as long as the protoconch (Pl. 1, Figs. 1–3; Pl. 8, Figs. 2, 4) or even longer (Pl. 4, Figs. 4, 5), of medium length when it is a bit shorter than the protoconch (Pl. 4, Figs. 7, 8; Pl. 5, Fig. 4; Pl. 6, Figs. 1, 2, 6, 7; Pl. 7, Figs. 4, 7), or short when it is approximately equal to ⅓ of the protoconch length or less (Pl. 2, Figs. 1, 3; Pl. 4, Figs. 1, 2, 6; Pl. 5, Figs. 7, 8). The phragmocone is usually swollen approximately between the second and fifth septa, then becomes narrower and forms a primary constriction which is more or less pronounced (Pl. 1, Fig. 1; Pl. 2, Figs. 1–5; Pl. 4, Fig. 6; Pl. 6, Figs. 1, 2; Pl. 8, Figs. 1, 3). In sculptured shells the ornament becomes smooth towards the primary constriction and disappears immediately in front of it (Pl. 2, Figs. 1–5; Pl. 8, Figs. 1, 3). After the primary constriction the shell expands slowly or rather quickly (Pl. 2, Fig. 1; Pl. 8, Fig. 1), or even becomes narrower at some distance (Pl. 5, Fig. 3; Pl. 6, Fig. 1; Pl. 7, Fig. 6). The shell is cyrtoconic (Pl. 1, Fig. 1), or longiconic (Pl. 5, Fig. 3).

Shell Wall Ultrastructure

The protoconch has a prismatic shell wall consisting of three sub-layers. The outer sub-layer is the thinnest; it bears sculpture in sculptured forms. The three sub-layers maintain approximately constant thicknesses throughout the protoconch, except that near the first septum the two inner sub-layers either wedge out or the boundary between them and the outer sub-layer becomes indistinct. Near the apex the outer sub-layer separates from the other two sub-layers and forms the primordial dome (Pl. 3, Figs. 2, 3). The shell wall of the initial portion of the phragmocone, approximately up to the level of the third or fourth septum, is prismatic; at this level a nacreous layer appears. It gradually gets thicker and does not form a primary varix. The shell wall of the bactritella grades into the shell wall of juvenile post-hatching shell. From the 12–15th camera the nacreous layer forms the main portion of the shell wall, the outer prismatic layer becoming proportionally thinner (Pl. 1, Figs. 6, 7; Pl. 3, Figs. 1–4).

Attachment Scars

Dorsal unpaired elongated scars (Pl. 4, Figs. 1–3, 8; Pl. 5, Figs. 1, 2) were observed in *Hemibactrites* sp. on the inner surface of the protoconch and the earliest camerae. They seem to be areas of attachement of soft tissue to the shell. In the protoconch a single dorsal scar with rough relief lies close to the first septum. In Devonian *Bactritites ausavensis* dorsal paired scars were observed at later ontogenetic stages (ERBEN, 1960). In bactritoids the dorsal unpaired scars of early ontogenetic stages seemed to be replaced by paired ones at later stages of growth.

Siphuncle

The siphuncle begins with a comparatively large bubble-like caecum about half as long as the protoconch (Pl. 1, Figs. 10, 11); a prosiphon was not observed. In the first camerae the siphuncle is submarginal (Pl. 1, Figs. 1–4, 10, 11; Pl. 6, Figs. 6–8), but soon becomes marginal. In the swollen first three–four camerae the siphuncle does not follow the curvature of the shell but is straight, so there is some interspace between the shell wall and the siphuncle. In the first camerae the septal necks are short retrochoanitic, at later sages they are proportionally longer.

Septa and Sutures

The first septum is prismatic and its mural part is as long as the camera (Pl. 1–4; Pl. 5, Fig. 6; Pl. 6, Figs. 1–8; Pl. 7, Figs. 1, 2, 4, 6, 7, 8). It has a septal foramen (Pl. 1, Figs. 1–3; Pl. 6, Figs. 1–3, 5–8) so that the siphuncle passes through it in the protoconch. There is no organic closing membrane. The fourth septum observed shows a neckal lobe.The subsequent septa are nacreous. The sutures are straight with the exception of forms assigned to parabactritids (Pl. 8, Figs. 5, 7); in them the third or fourth sutures form a deep and wide ventral lobe (Pl. 8, Figs. 1, 2, 4).

Living Chamber

The living chamber is comparatively long; in the specimen illustrated on Pl. 1, Fig. 1 the preserved portion of it is about as long as the ten preceeding camerae plus protoconch.

Bactritella

The embryonic shell of bactritoids consists of the protoconch and living chamber separated by the first septum. The living chamber occupies the initial portion of the phragmocone up to the primary constriction which is situated at the place where approximately the fifth septum will be later attached (DOGUZHAEVA, 1996a). In forms with a sculptured initial portion of the shell the aperture of the bactritella is marked by the disappearance of sculpture (Pl. 2, Figs. 1–5). In parabactritids the position of the apertural margin of the bactritella is marked by the increase of the expansion angle (Pl. 8, Figs. 1, 5). At the bactritella stage the siphuncle is represented by a bubble-like caecum which must have been used in the regulation of buoyancy.

3.2. Ammonoids

The ammonoids examined represent different ontogenetic stages of shell formation. The earliest stage is represented by a partly formed ammonitella (Pl. 9, Fig. 4 and Pl. 10, Figs. 1, 2). The median section of the shell illustrated on Pl. 10, Figs. 1, 2 shows that the innermost portion of the protoconch was not yet fully calcified, proseptum and primary varix are still absent but the apertural margin comes at 360 degrees from the proseptum, the approximate length of the ammonitella in Late Carboniferous and Permian goniatites. The apertural curvature of the shell wall shows the initial stage of formation of the primary constriction (Pl. 10, Fig. 2). The shell wall here becomes thinner forwards. The next stage of ammonitella formation is illustrated on Pl. 10, Fig. 6: the protoconch is fully calcified, the proseptum is already formed and the primary varix is present but is still thin and seems not yet completed. The primary varix at this stage is illustrated on Pl. 9, Figs. 5, 6. The photos show the first appearance of the nacreous layer on the inner surface of the prismatic layer, the latter becomes thinner forwards. At the next stage (Pl. 10, Figs. 3–5) the shell has two septa, a well marked primary constriction and a fully secreted nacreous primary varix. The latter appears at a short distance in front of the primary constriction, quickly grows in thickness and together with the shell wall wedges out abruptly (Pl. 10, Figs. 4, 5). At this stage the post-hatching shell wall is still missing.

The early post-hatching stage of shell formation is documented on Pl.11, Figs. 1, 2. The only detail in which this Late Palaeozoic shell differs from Mesozoic ammonoids is a comparatively long anterior portion of the shell wall formed only by the prismatic layer (Pl. 11, Figs. 1, 2). This probably means that at early post-hatching stages the zones of secretion of the prismatic and nacreous layers were located farther apart than in younger ammonoids. In goniatites the ammonitella is involute (Pl. 9, Fig. 2), or evolute (Pl. 9, Fig. 3). In sculptured shells the beginning of the post-hatching stage is marked by the sudden appearance of ribs (Pl. 9, Fig. 2). As in goniatitids, in prolecanitids the primary varix is situated at the same distance from the proseptum which is around 360 degrees (Pl. 10, Fig. 7), and their post-hatching shell wall consists of the thin outer prismatic, thick nacreous and thin inner prismatic layers. When the next whorl is formed this set of layers is added to by a thin prismatic dorsal wall of the new whorl (Pl. 10, Fig. 8). The diameter of the ammonitellae is about 0.45–0.9 mm, and the diameter of the protoconch is 0.3 mm–0.5 mm.

3.3. Orthocerids

A single Late Carboniferous orthocerid taxon was found, described as *Aidaroceras politum* gen. et sp. nov. (Pl. 12, Figs. 1–10), showing the apical shell and position of the siphuncle. It is represented by ten conchs with well preserved shell matter. They were studied from the outside with the SEM and then cut longitudinally to study the internal shell structure (Pl. 12, Figs. 1–7). For shell morphology and ultrastructure see the section on Systematic Palaeontology.

3.4. Phragmoteuthids

A single Late Carboniferous phragmoteuthid taxon described as *Rhiphaeoteuthis margaritae* gen. et sp. nov. (Pl. 12, Figs. 1–10) was found. It is represented by two adolescent phragmocones in a good state of preservation (Pl. 13, Figs. 1–4). The larger shell exhibits the structure of the siphuncle through the thin, transparent conotheca. The smaller shell was cut longitudinally to study the siphuncle in section. Besides, a large number of presumably embryonic shells (Pl. 14, Figs. 1–6; Pl. 15, Figs. 1–6; Pl. 16, Figs. 1–7) are referred to the same group, although it is not excluded that some of them belonged to the parabactritids. For shell morphology and ultrastructure see the section on Systematic Palaeontology.

3.5. Aulacocerids

A single tiny longicone described as *Mutveiconites mirandus* gen. et sp. nov. showing a short rostrum was found among the Late Carboniferous adolescent shells (Pl. 17, Figs. 1–4). It is in a good state of preservation for detailed study. For shell morphology and ultrastructure see the section on Systematic Palaeontology.

4. Systematic Palaeontology

Subclass: Bactritoidea SHIMANSKY, 1951
Order: Bactritida SHIMANSKY, 1951
Family: Bactritidae HYATT, 1884
Genus: *Chuvashovia* gen. nov.

Derivation of name: In honour of Prof. B.I. CHUVASHOV who found the slab of organic limestone with the adolescent orthocones and ammonoids in the Sim River Basin.

Type species: *Chuvashovia curvata* sp. nov.

Type locality: Sim River Basin, South Urals, some 5 km from the village Sim along the Ufa–Cheljabinsk road.

Horizon: Lower Permian, Artinskian.

Diagnosis: Shell slender, first exogastrically cyrtoconic, later longiconic; protoconch spherical; maximum diameter of protoconch is between the middle part of its length and the first septum; its transverse diameter about the same as that of the first camera and slightly less than that of the second camera; with distinct constriction near the first septum, but not at succeeding septa; shell expands until fourth–fifth camera then gently narrows up about to 10th–11th camerae, then slowly expands again. Surface smooth, or with faint radial wrinkles around apex; siphuncle small marginal; necks orthochoanitic; camerae moderately long; septa shallow. Mural and hyposeptal cameral deposits present in protoconch and early camerae.

Range and distribution: Permian, Artinskian of the South Urals.

Remarks: The description is based on the adolescent shell; adult growth stages are unknown.

Chuvashovia curvata sp. nov.

(Pl. 1, Figs. 1–7)

Derivation of name: From Latin, curvatus, referring to the curved adolescent shell.

Holotype: 3871/301, in the Paleontological Institute of the Russian Academy of Sciences.

Type locality: The same as for the genus.

Description: The holotype is a juvenile shell 5 mm long, and comprises the protoconch, 10 camerae and a living chamber that is as long as the phragmocone and protoconch together at 0.6 mm. Shell slender, first exogastrically cyrtoconic, later longiconic. Surface smooth, or with faint radial wrinkles around the apex. Protoconch spherical, transverse diameter 0.3 mm, about the same as that of the first camera and slightly less than that of the second camera. The shell has a distinct constriction between the protoconch and first camera, but no constrictions between succeeding camerae. Phragmocone is moderately swollen for the first six camerae, it then narrows to the 10th camera and then expands slowly. Camerae moderately deep and long; shell diameter approximately equal to the length of two camerae. Siphuncle small, sub-marginal in the first three–four camerae, later marginal. Necks orthochoanitic, of medium length, about ¼–⅓ of camera length. The first septum shows a comparatively large siphuncular foramen, equal to slightly less than ⅓ shell diameter near the first suture. Mural and hyposeptal cameral deposits present in protoconch and first camerae. In the protoconch and first camerae they fill the whole space between the shell wall and the siphuncle on ventral side.

Genus: *Simobactrites* gen. nov.

Derivation of name: From the Sim River, where the specimen was found.

Type species: *Simobactrites kuzinae* sp. nov.

Type locality: Sim River Basin, South Urals, some 5 km from the village Sim along the Ufa – Cheljabinsk road.

Horizon: Lower Permian, Artinskian.

Diagnosis: Slender orthocone with globular protoconch and deep constriction between it and the first camera; maximum diameter of protoconch in middle part of its length; no constrictions at succeeding sutures; first camera narrow, looks like neck between protoconch and swollen second camera; shell narrows towards fourth camera; its diameter less than diameter of protoconch; later shell sub-cylindrical. Surface smooth, or with wrinkles around smooth apex.

Simobactrites kuzinae sp. nov.

(Pl. 4, Figs. 6, 10)

Derivation of name: In honour of L.F. KUZINA, Russian expert on Lower Carboniferous ammonoids.

Holotype: 3871/329, in the Paleontological Institute of the Russian Academy of Sciences.

Type locality: The same as for the genus.

Description: The holotype is a juvenile orthocone, about 4 mm long, with small marginal siphuncle. It comprises a globular protoconch with deep constriction between it and the first camera, five camerae and beginning of the living chamber. The protoconch is globular and comparatively large, the maximum diameter is in the middle part of the length of the protoconch and is about 0.5 mm. The first camera is narrow, long, slightly less than ½ of the longitudinal diameter of the protoconch, and looks like a neck between the protoconch and the swollen second camera which has a diameter approximately equal to the maximum diameter of the protoconch. The shell narrows towards the fourth camera where the diameter is less than that of the protoconch; the later shell is sub-cylindrical and its diameter is still less than that of the protoconch. Surface smooth, or with wrinkles around smooth apex. No constrictions at succeeding sutures. Camerae are comparatively long; the length of 1.5 camerae corresponds to the shell diameter.

Remarks: The holotype was previously illustrated, unnamed, with a note that it probably represented a new genus (DOGUZHAEVA, 1996c, Fig. 1).

Genus: *Linibactrites*

Derivation of name: From Latin, linum, thread, in referance to the thread-like longitudinal ribs on the adolescent shell.

Type species: *Linibactrites solidus* sp. nov.

Type locality: Sim River Basin, South Urals, some 5 km from the village Sim along the Ufa–Cheljabinsk road.

Horizon: Lower Permian, Artinskian.

Diagnosis: Orthocones with numerous longitudinal thread-like ribs on the surface and hemi-spherical protoconch with maximum diameter and faint constriction near the first suture; no constrictions at succeeding sutures.

Linibactrites solidus gen. et sp. nov.

(Pl. 4, Fig. 9)

Derivation of name: From Latin, solidus, in reference to the absence of the constriction between the protoconch and the first camera of the phragmocone.

Holotype: 3871/330, in the Paleontological Institute of the Russian Academy of Sciences.

Type locality: The same as for the genus.

Description: Orthocones with numerous longitudinal thread-like ribs on the surface. Hemispherical protoconch with maximum diameter and faint constriction near the first suture; no constrictions at succeeding sutures. The maximum diameter of the protoconch is 0.6 mm and its length is 0.4 mm; the ratio of protoconch width to length is about 1.4. The primordial dome is distinct and surrounded by a narrow smooth ring, after which the ribs begin.

Remarks: The holotype was previously illustrated unnamed with a note that it probably represented a new genus (DOGUZHAEVA, 1996c, Fig. 12).

Genus: *Uralobactrites*

(Pl. 4, Figs. 4, 5, 7, 8)

Derivation of name: From the Urals, where the specimen was found.

Type species: *Uralobactrites uralicus* sp. nov.

Type locality: Sim River Basin, South Urals, some 5 km from the village Sim along the Ufa – Cheljabinsk road.

Horizon: Lower Permian, Artinskian.

Diagnosis: Longicones with small depressed protoconch, distinct constrictions at first to fifth sutures; sutures straight; surface smooth with undulations near first to fifth sutures.

Uralobactrites uralicus gen. et sp. nov.

(Pl. 4, Figs. 4, 5, 7, 8; Pl. 6, Figs. 1–5)

Derivation of name: The same as for the genus.

Holotype: 3871/327, in the Paleontological Institute of the Russian Academy of Sciences.

Type locality: The same as for the genus.

Description: The holotype is a portion of a juvenile longicone 1.5 mm long, and comprises a small hemispherical protoconch, three camerae and approximately half of the living chamber. The surface is smooth. The maximum diameter of the protoconch is 0.3 mm and its length is 0.2 mm; the ratio between them is 1.5. Distinct constrictions at first to the fifth sutures are seen as undulations on the outer surface; sutures straight; surface smooth. The holotype shows small unpaired dorsal attachment scars on the inner surface of the protoconch and first camera. Paratypes (Pl. 4, Figs. 4, 5; Pl. 6, Figs. 1–5) show even smaller and more depressed protoconchs with a maximum diameter of 0.27 mm; the ratio between the maximum transverse diameter and length of the protoconch in specimens 3871/224, 225 is 2.5–3.

Genus: *Ovobactrites*

Derivation of name: From Latin, ovum, the egg, in referance to the egg-like shape of the protoconch.

Type species: *Ovobactrites antonovae* sp. nov.

Type locality: Sim River Basin, South Urals, some 5 km from the village Sim along the Ufa–Cheljabinsk road.

Horizon: Lower Permian, Artinskian.

Diagnosis: Shell with large elongated protoconch; distinct constriction between protoconch and first camera with thin and short longitudinal wrinkles on outer surface; first camera deep and rounded, its diameter less than the diameter of protoconch, and its length less than the length of the protoconch; constrictions at second and third sutures well pronounced on outer surface; no constrictions at succeeding sutures.

Ovobactrites antonovae sp. nov.

(Pl. 5, Figs. 3–8; Pl. 7, Figs. 1–8)

Derivation of name: In honour of V.T. ANTONOVA, well-known photographer of fossils, Paleontological Institute of the Russian Academy of Sciences.

Holotype: 3871/334, in the Paleontological Institute of the Russian Academy of Sciences.

Type locality: The same as for the genus.

Description: The holotype is a 6 mm long portion of the juvenile smooth longicone and comprises the protoconch, about ten camerae and part of the living chamber; it is 0.4 mm in maximum diameter. The protoconch is large, elongated, elliptical in median section; its maximum diameter is in the middle of the protoconch and is about 0.8 mm mm; the length is about 1 mm. The constriction between the protoconch and the first camera is distinct and bears short, thin longitudinal wrinkles on the outer surface. The first camera is comparatively deep and rounded; its diameter is less than that of the protoconch, and its length is less than the length of the protoconch. The constrictions at the second and third sutures are also well pronounced on the outer surface; but are absent at the succeeding sutures. The primary constriction of the shell is situated at a distance equal to slightly more than three lengths of the protoconch from its apex. Here the diameter of the shell is less than the diameter of the protoconch. Then the shell diameter gradually increases. Mural and episeptal cameral deposits are present. In the protoconch they form a prismatic layer which is four to five times as thick as the shell wall. In the first camera, cameral deposits coat the adoral surface of the first septum and the shell wall; similarly in the second and succeeding camerae. Cameral deposits could easily be erroneously taken for the shell wall in case of poor preservation. Hyposeptal cameral deposits are absent.

Subclass: Orthoceratoidea KHUN, 1940
Order: Orthocerida KHUN, 1940
Family: Orthoceratidae MCCOY, 1844
Genus: *Aidaroceras* gen. nov.

Derivation of name: The genus is named for the Creek Aidaralash where the described form comes from.

Type species: *Aidaroceras politum* sp. nov.

Type locality: Aidaralash Creek, northwestern Kazakhstan, about 50 km southeast from the town Aqtobe.

Horizon: Upper Carboniferous, Orenburgian.

Diagnosis: Subcylindrical orthocones with circular cross section, wide-conical apex formed by short rounded primordium and long rapidly expanded first camera of phragmocone. Surface with faint square pattern with dominant longitudinal thread-like ribs and minor transverse lyrae. Siphuncle small, central or slightly eccentric. Necks short, slightly cyrtochoanitic; connecting rings thin, faintly expanded in camerae. No endosiphuncular and cameral deposits. Camerae long. Sutures straight, transverse.

Remarks: The description is based on the adolescent shell, adult growth stages are unknown.

Aidaroceras politum gen. et sp. nov.

(Pl. 12, Figs. 1–7, 9, 10)

Derivation of name: From Latin, politus, beautiful, in reference to delicate sculpture of adolescent shell.

Holotype: 3871/358, in the Paleontological Institute of the Russian Academy of Sciences.

Type locality: The same as for the genus.

Description: The holotype is a 1.5 mm long portion of juvenile subcylindrical orthocone with a wide and high conical apex and a faint square-like sculpture formed by thread-like longitudinal and cross ribs. It is 0.7 mm in maximum diameter and comprises a short and wide primordium, two long camerae and a bottom part of the living chamber. The conical portion includes the primordium and first camera of the phragmocone, the former being about 5.5 times shorter than the latter. The cross section is circular.

The primordium bears a deep and long cicatrix and radial ridges and folds; it is laterally compressed so that its apex is wide and rounded from the lateral view and more acute from the ventral side. The cicatrix represents a narrow dorso-ventral depression which is longer on the ventral side where it ends, forming a wide groove here. The shell wall of the primordium is formed by a combination of transversed concentric ribs and longitudinal rods consisting of small-sized isometric elements. The apertural edge of the primordium is marked by the appearance of longitudinal, thread-like ribs on the surface and coincides with the first suture. The ribs are of two kinds: one continues along the shell, the other disappears at the first growth line. Three or four short ribs alternate with each long rib. The portion of the shell between the appearance and disappearance of the short ribs corresponds to the length of the first camera. The short ribs disappear, the first growth lines appear and the expansion angle gets smaller at the second septum. The minor transverse lirae appear later. The level of the third septum is marked on the surface by the crowding of three growth lines which look like transverse lirae; they are more pronounced in relief than the previous ones. Thus, four growth stages can be established in this form:

1) the boundary between the first and second stages is marked by the appearance of thread-like longitudinal ribs,
2) the boundary between the second and third stages is marked by the disappearance of short ribs and the appearance of growth lines,
3) the boundary between the third and fourth stages is marked by crowding of growth lines and the appearance of transverse lirae.

The siphuncle is small, central or slightly eccentric; its diameter is about 1/7–1/8 of the shell diameter. It starts in the primordium with a large rounded caecum which touches the cicatrix. The caecum is surrounded by a weakly calcified continuation of the first septal neck. Connecting rings are thin, probably organic, slightly expanding within the camerae. The second and third necks are slightly cyrtochoanitic, short, equal to 1/6–1/7 of camera length. Camerae are long; the ratio between the length and maximum width is about 2 in the first camera and 1.7 in the second one. Along the first camera the shell diameter gradually increases but along the second camera it gets smaller, resulting in a weak constriction at the last third of the second camera. Later the shell diameter slowly increases again.

The shell wall is weakest along the cicatrix where it is irregularly calcified and seems to contain much organic matter. Around the cicatrix it is two to three times thicker than the first septum. Immediately after the cicatrix the shell wall becomes much thicker and consists of outer prismatic and nacreous layers; the latter first appears in the first camera of the phragmocone. Cameral or endosiphuncular deposits are not developed.

Remarks: The description is based on juvenile and adolescent shells having up to ten camerae and being 10–12 mm long. Adult stages are unknown.

Subclass: Coleoidea BATHER, 1888
Order: Phragmoteuthida JELETZKY in SWEET, 1964
Family: Rhiphaeoteuthidae fam. nov.

Type genus: *Rhiphaeoteuthis* gen. nov.

Diagnosis: Small straight breviconic belemnite-like phragmocones with short camerae and small marginal siphuncle, wide mural rings and sutures possessing shallow ventral and omnilateral lobes. Septal necks short, cyrtochoanitic dorsally and long holochoanitic ventrally. Surface smooth. Shell wall as thin as septa.

Living chamber present in juvenile shells but absent in adoloscent ones. Rostrum absent at all growth stages.

Range and distribution: Upper Carboniferous – Lower Permian; South Urals.

Remarks: MOJSISOVICS (1882) erected the genus *Phragmoteuthis* and the family Phragmoteuthidae to express the idea first introduced by SUESS (1865) on the isolated taxonomic position of this genus possessing a teuthid-like pro-ostracum and belemnoid-like phragmocone. JELETZKY endorsed the conclusions of SUESS (1865) and MOJSISOVICS (1882) and raised the rank of the group to an order (JELETZKY in SWEET, 1964). The Upper Permian–Lower Jurassic order Phragmoteuthida includes the family Phragmoteuthidae MOJSISOVICS, 1882 with the genera *Phragmoteuthis* MOJSISOVICS, 1882, *Permoteuthis* ROSENKRANZ, 1946 and an unnamed form from the Lower Jurassic of England described and figured by HUXLEY (1864, p. 14, Pl. 1, Fig. 4, 4a) and restudied by JELETZKY (1966, p. 38, 39). The phragomoteuthids were previously known from East Greenland, Great Britain, southern and central Europe.

According to JELETZKY (1966, p. 31) the phragmoteuthids are characterized by the following features:

1) large tripartite, fanlike pro-ostracum forming the longest portion of the shell and attached to about three-quarters of the circumference of the phragmocone,
2) comparatively small breviconic phragmocone with short camerae and superficially belemnitid-like siphuncle,
3) rostrum absent, or forming a thin, *Belemnotheutis*-like investment of the apical part of the phragmocone,
4) belemnite-like arm hooks,
5) ink bag,
6) beaks resembling those of Recent teuthids, and
7) presence of muscular mantle.

The phragmocone structure of the phragmoteuthids was described in Jurassic specimens from Dorset by DONOVAN (1977) and from Germany by RIEGRAF (1982).

Although the pro-ostracum is still unknown in *Rhiphaeoteuthis*, the new family is assigned to the Order Phragmoteuthida because of the belemnoid-like phragmocone and absence of a rostrum. Besides, its shell wall is as thin as the septa, similar to the conotheca in belemnoids but unlike bactritoids and other ectocochleates.

The Early Permian *Belemnomimus* SHIMANSKY, 1954 is included in the family Rhiphaeoteuthidae because of its belemnoid-like breviconic phragmocone with short camerae and similar siphuncular structures which are here figured in median section for the first time (Pl. 13, Figs. 5, 6). SHIMANSKY (1954) assigned the genus to the Parabactritidae but he emphasized the great similarity of the phragmocone structure in this genus to that of Jurassic and Cretaceous belemnites (SHIMANSKY, 1954, p. 91). The Pennsylvanian *Bactrites nevadensis* YOUNGQUIST (HANSMAN, 1964), like *Rhiphaeoteuthis margaritae* gen. et sp. nov., has slightly curved dorsal septal necks. It is possible that this genus also belongs to the Phragmoteuthida.

Genus: *Rhiphaeoteuthis* gen. nov.

Derivation of name: From Rhiphaeus (Greek) – the ancient name of the Urals.

Type species: *Rhiphaeoteuthis margaritae* sp. nov.

Type locality: South Urals, North Kasakhstan, some 200 km N from Aqtobe, Aidaralash Creek.

Horizon: Upper Carboniferous, Orenburgian.

Diagnosis: Small, straight slightly compressed breviconic belemnite-like phragmocones, angle of expansion around 30 degrees, smooth surface, oval cross section that is narrower dorsally than ventrally, small marginal siphuncle, siphuncular foramen 1/8–1/11 shell diameter, foramen oval in cross section; septal necks short cyrtochoanitic dorsally and long holochoanitic ventrally, segments swollen dorsally and flattened ventrally; camerae short, around 1/10 of shell diameter; wide mural rings about 1/3–1/2 chamber length; sutures with shallow ventral and omnilateral lobes; shell wall thin as septa; living chamber and rostrum absent at adolescent stages.

Remarks: The description is based on two specimens, one of which was cut longitudinally. The shape of the septal necks was observed on the external surface of the holotype and in median section of the paratype; the latter shows the septal neck structure in more detail; connecting rings are not preserved.

Five juvenile breviconic phragmocones are assigned to the genus because of the following features: the angle of expansion is large, about 30 degrees; camerae short, about 1/10 shell diameter, small siphuncle, cyrtochoanitic septal necks, shell wall thin as septa. However. in juvenile conchs the siphuncle is still submarginal and the septal necks are cyrtochoanitic on the ventral side as well; the living chamber is present. The assignment of these juvenile forms to the genus shows that in *Rhiphaeoteuthis* a living chamber was present in early growth stages but a rostrum was missing; the first chamber is short and cup-like; the apex rounded; the living chamber was broad, a little longer dorsally than ventrally and formed the largest portion of the shell; a primary constriction is present, after which the angle of expansion increases.

These juvenile shells were preserved together with adolescent shells of bactritoids, orthoceroids, ammonoids and *Rhiphaeoteuthis*. They differ significantly from all other orthocones found together with them in having a large angle of expansion, very short chambers, and a conotheca as thin as the septa. Other juvenile breviconic shells belonged to parabactritids; they were recognized by their hemispherical first chambers, and the third or fourth suture lines with deep and wide ventral lobes.

Rhiphaeoteuthis margaritae sp. nov.

(Pl. 13, Figs. 1–4)

Derivation of name: In honour of Margarita F. BOGOSLOVSKAYA, Russian expert in Late Carboniferous–Permian ammonoids and the biostratigraphy of the South Urals.

Holotype: 3871/361, in the Paleontological Institute of the Russian Academy of Sciences.

Type locality: The same as for the genus.

Description: Small, a few centimetres in length at the adult stage, straight, slightly compressed breviconic phragmocones with angle of expansion around 30 degrees, smooth surface, oval cross section that is narrower dorsally than ventrally, small marginal siphuncle, approximately 1/10 of shell diameter, oval in cross section; septal necks short, cyrtochoanitic dorsally and long holochoanitic ventrally; camerae short, around 1/10 of shell diameter; wide mural rings about 1/3–1/2 of chamber length; suture line with shallow ventral and omnilateral lobes; shell wall thin as septa; living chamber and rostrum absent in the adult.

The holotype is a 15 mm long portion of the phragmocone comprising 19 camerae; it is 6 mm in maximum diameter and 2 mm in minimum diameter. The phragmocone is breviconic with straight ventral, lateral and dorsal sides; angle of expansion about 30 degrees; the cross section is oval, narrower dorsally, wider on presumed ventral side where the siphuncle is located. There is no evidence for a rostrum. The surface is smooth with weak undulations between the mural rings. Sutures show shallow ventral and omnilateral lobes. Camerae are short and wide. The siphuncle is extremely marginal, small near the septal foramen and expanding within the camerae. Near the adapical edge the diameter of the septal neck is approximately 1.3 times larger than near the septal foramen. The septal foramen is oval. The ratio of the diameter of the septal foramen to the diameter of the camera is about 1 : 9–1 : 11. Septal necks are long on the ventral side. The ratio of length between the neck and the camera is about 1 : 3–1 : 2. Connecting rings are not preserved. Mural rings are wide, about $^1/_3$–$^1/_2$ the camera length. Under the light microscope the mural rings have a dark-brown colour that seems to indicate a high content of organic matter; towards the dorsal side the conotheca also becomes brownish and the boundaries between the mural rings and the conotheca is indistinct. Near the mural rings the camerae are slightly swollen, giving an erroneous impression that the phragmocone is sculptured by weakly developed rings. The shell wall is preserved as a thin transparent layer showing in a few places the lustre of the next nacreous layer. The most adoral camera preserved is about 0.3 mm long on the ventral side. The longest camera is the 14th which is 1.2 mm long. The last camera is about half the length of the previous 18th one.

The paratype is a median section of a smaller fragment of the phragmocone; its length is 5.4 mm, maximum diameter 4 mm and minimum 1.8 mm. It has eight camerae, the most adoral camera preserved is 0.3 mm long along the shell axis, and the last one is 0.5 mm long, about $^1/_{10}$ of the diameter. The diameter of the septal foramen is about $^1/_9$–$^1/_{11}$ of the camera diameter. Connecting rings are not preserved; they seemed to have been organic. In the median section septal necks are short, cyrtochoanitic dorsally and long holochoanitic ventrally. On the ventral side the septal necks lie on the shell wall. The mural rings consist of a well developed preseptal varix and the mural part of septum; both seem to have high organic content. A similar structure of the mural rings, formed by preseptal rings preceding the septum secretion and mural parts of the septum, has been observed in the Aptian spirulids *Adygeya adygensis* and *Naefia kabanovi* and in Recent *Spirula* (DOGUZHAEVA, 1996, Text-Fig. 3A–C, Pl. 2, Fig. 1; Pl. 3, Fig. 1; Pl. 8, Fig. 3). In *Spirula* the mural rings preceded the formation of the new septum and also show much organic matter.

Order: Aulacocerida STOLLEY, 1919
Family: Mutveiconitidae fam nov.

Type genus: *Mutveiconites* gen. nov.

Diagnosis: Slender longiconic orthocones with oval protoconch; short rostrum coating protoconch and about first ten camerae, its conical post-protoconch part shorter than protoconch length, small marginal siphuncle, septal necks short; camerae comparatively long; long living chamber present at least in young stages; shell wall of thin inner prismatic and thick nacreous layers; no distinct primary constriction, no primary varix.

Range and distribution: Lower Carboniferous, Orenburgian of the South Urals.

Remarks: The description is based on the adolescent shell; adults are unknown. The family is established on the basis of the following features:

1) longiconic phragmocone with comparatively long camerae and narrow marginal siphuncle;
2) short rostrum coating protoconch and about first ten camerae, its conical post-protoconch part shorter than protoconch length;
3) long living chamber present at least in early stages of growth.

It is yet unknown if *Mutveiconites* had a closing membrane to the protoconch like belemnoids, or a caecum like *Groenlandibelus* (JELETZKY, 1966, Pl. 20, Figs. 1A, B). In *Mutveiconites* the conotheca includes a nacreous layer which makes up the bulk of its thickness. If it was a spirulid genus it would lack a nacreous layer like Recent *Spirula*, the Early Cretaceous *Adygeya* and *Naefia* (DOGUZHAEVA, 1996d) and the Early Carboniferous *Shimanskya* (DOGUZHAEVA et al., 1999a), in all of which the shell wall consists of inner and outer acicular-prismatic plates only.

Genus: *Mutveiconites* gen. nov.

Derivation of name: In honour of H. MUTVEI, to whom I am grateful for long-time collaboration on ultrastructural studies of cephalopods.

Type species: *Mutveiconites mirandus* sp. nov.

Type locality: Some 50 km southeast from the town of Aqtobe, Aidaralash Creek, northwestern Kazakhstan, South Urals.

Horizon: Upper Carboniferous, Orenburgian.

Diagnosis: The same as for the family.

***Mutveiconites mirandus* sp. nov.**
(Pl. 17, Figs. 1–4)

Derivation of name: From Latin, mirandus, striking, in reference to some unusual features of this form.

Holotype: 3871/370, in the Paleontological Institute of the Russian Academy of Sciences.

Type locality: The same as for the genus.

Description: The holotype is a 3 mm long juvenile shell, a slightly exogastric cyrtocone at the beginning, becoming longiconic. It consists of a small elongate protoconch, about ten camerae of the phragmocone and a long living chamber. There is a short, pointed boss-like rostrum surrounding the protoconch and extending along the camerae, but absent at the living chamber. The maximum diameter of the protoconch is 0.3 mm. The siphuncle is small and marginal, presumably ventral. The diameter of the siphuncle is about $^1/_6$–$^1/_7$ of the shell diameter. Septal necks are short retrochoanitic. Connecting rings are not preserved. Camerae are comparatively long; the length of a camera is about $^7/_{10}$ of its maximum diameter. The living chamber is approximately 1.3 times the length of the phragmocone. The rostrum has no distinct growth lines but a slightly separated layer can be distinguished along the periphery. The shell wall of the protoconch is prismatic. The shell wall of the living chamber consists of a thick nacreous and thin inner prismatic layer.

5. Phylogenetic Implications

The bactritoids, a comparatively small (less than 50 genera) but persistent (?Middle Ordovician, Silurian–Triassic) group of cephalopods with a wide geographical distribution, have a special place in phylogenetic discussions: they are assumed to have given rise to two large groups of cephalopods: Ammonoidea and Coleoidea. A. HYATT (1883) was the first to consider them as the ancestors of the ammonoids. HYATT and many other cephalopod specialists after him (BRANCO, 1885; CLARKE, 1893, 1894; SCHINDEWOLF, 1933, 1959; BOHMERS, 1936; MILLER, 1938; SHIMANSKY, 1954, 1958, 1962; SHIMANSKY & ZHURAVLEVA, 1961; ERBEN, 1960, 1962, 1964, 1965; HOUSE, 1996) shared the opinion that early shell ontogeny is of great importance for the consideration of cephalopod phylogeny. The bactritoids were ranked, either as the most primitive ammonoids (SMITH, 1903; SCHINDEWOLF, 1933, 1934, 1959; HOUSE, 1988, 1996; LANDMAN et al., 1996), as orthocerids with a marginal siphuncle (THOMAS, 1928; SPATH, 1936; MILLER & YOUNGQUIST, 1949; DOYLE & al., 1994), or as an intermediate group between the orthocerids and ammonoids of equal rank with the latter (SHIMANSKY, 1954, 1962; MAPES, 1979; TEICHERT, 1988). In the Treatise on Invertebrate Paleontology ERBEN classified them as the order Bactritoidea. According to R.C. MOORE (1964, p. K491, footnote), ERBEN was persuaded to do this by C. TEICHERT who thought that the bactritids had an intermediate position between Orthocerida and Ammonoidea and should be ranked on a level with the nautiloid orders. ERBEN himself would have preferred to classify the bactritids as a suborder of the Ammonoidea.

If we consider the relationship of bactritoids and ammonoids in the light of a gradual increase in shell coiling, we can hardly find any important new proofs or disproofs of the widely held view of bactritoids as primitive ammonoids. In the morphological sequence of gradually more and more strongly coiled Lower Devonian shells (ERBEN, 1964, Abb. 8.; HOUSE, 1996, Fig. 6, 7; TEICHERT, 1988, Fig. 4) it is practically impossible to find a hiatus (if there is one) between the two groups. As a result, it becomes a question

> “ ... *of convention whether to include them in the nautiloids, or to unite them with the goniatites* ... ” (SCHINDEWOLF, 1959, p. 974).

However, if we discuss the bactritoid-ammonoid relationship from the point of view of their early shell wall ultrastructure, the supposed hiatus between the two groups could be probably found.

The universal characters of the early shell ontogeny of ammonoids, namely: the primary constriction, the primary varix, and the discontinuity of the shell wall layers near the primary varix are known from the work of many people (see BIRKELUND, 1981). The layers forming the first whorl up to the adoral end of the primary varix do not continue into the following portion of the shell wall; the outer prismatic and nacreous layers which form the shell wall anterior to the primary varix first appear on the inner surface of the primary varix near its anterior end (ERBEN et al., 1969; BIRKELUND & HANSEN, 1974; DRUSCHITC & DOGUZHAEVA, 1974, 1981; DRUSCHITC et al., 1976).

This discontinuity is known in many Mesozoic ammonoids (see BIRKELUND, 1981) and also in Early Permian juvenile goniatites and in the prolecanitid *Agathiceras* (DOGUZHAEVA, 1996c, Figs. 14–16; herein Pl. 10, Fig. 7; Pl. 11, Fig. 1, 2). The discontinuity probably indicates a change in the mode of shell secretion between the embryonic and postembryonic stages. Although the discontinuity in the shell wall layers is not yet demonstrated in Devonian ammonoids, the primary varix is known in many goniatites (BOGOSLOVSKIY, 1969, 1971; HOUSE, 1965, 1996) and clymeniids (BOGOSLOVSKIY, 1976, 1981). The universal character of changes of the shell wall near the primary constriction seems to be connected with the common embryonic strategy that supported the integrity of the Ammonoidea during their existence over about 400 my.

The Late Carboniferous–Early Permian bactritoids of the South Urals, which are so far the only known forms with the shell matter preserved, revealed the following non-ammonoid characters of their juvenile shell:

1) the absence of a primary varix;
2) the absence of the discontinuity of shell wall layers near the primary constriction;
3) constant thickness of the shell wall along the protoconch;
4) the presence of internal deposits.

Thus, the bactritoids have none of the characteristic features of the embryonic shell of ammonoids, and can hardly be assigned to the Ammonoidea. They rather represent a distinct taxon of the same rank. The bactritoids are widely believed to have given rise to the coleoids (SCHINDEWOLF, 1933; ERBEN, 1964; JELETZKY, 1966, DONOVAN, 1977). FLOWER and GORDON (1959) suggested that at least some of the Parabactritidae may have close affinities with belemnoids. However, when Early Devonian coleoids were discovered (with the aid of X-ray photographs from the Hunsrück Slates taken by W. STÜRMER) (BANDEL, REITNER & STÜRMER, 1983) R. H. FLOWER (1988) questioned this idea. Concerning the origin of aulacocerids and belemnoids, the idea is based on the similarity of their subspherical protoconch and orthoconic phragmocone, with small marginal siphuncle, to those of the bactritoids. Moreover in all these groups the protoconch has a prismatic shell wall and lacks a cicatrix; the nacreous layer, where it is present, appears at the initial portions of the phragmocone and a primary varix is missing. The primordial rostrum of belemnoids and the primordial dome in bactritoids seem to be comparable structures (DOGUZHAEVA, 1996b; DOGUZHAEVA et al., 1999c).

Thus, there are no obstacles to believing that the bactritoids and belemnoids have a common origin. In the Eocene spirulid *Belemnosis*, as in Recent *Spirula*, the protoconch is also egg-shaped with a prismatic wall; it has no cicatrix, nor primordial rostrum or primordial dome (DOGUZHAEVA, 2000).

The hypothesis of the origin of the phragmoteuthids – the probable ancestors of Recent teuthids – from the bactritoids is based on the assumption that the

> “ ... *body chamber of Pseudobactrites bicarinatus* FERRONNIERE *(*SHIMANSKY*, 1962, p. 230, Fig. 1b) with its deep ventral sinus flanked by spikelike protuberance seems to be a better prototype of the phragmoteuthid proostracum. The presence of large sinuses (ventral, dorsal, lateral) in the peristome of the Pseudobactritidae (= Bojobactritidae) certainly suggests a strong development of the funnel and strong differentiation of the head part of the body, features one could expect in ancestors of the coleoid cephalopods* ... ” (JELETZKY, 1966, p. 36).

SHIMANSKY (1962, p.230) thought that the soft body of the bactritid animal probably protruded somewhat beyond the living chamber, being partly supported by the protuberances of the peristome. Phragmoteuthid phragmocones are belemnoid-like (see JELETZKY, 1966; DONOVAN, 1977; RIEGRAF, 1982) but the apical portions of the phragmocones are not known.

The idea of the origin of Jurassic–Recent teuthids from the phragmoteuthids is founded on the similarity of the gladii in the former and the pro-ostracum in the latter (NAEF, 1922; JELETZKY, 1966; DONOVAN, 1977).

The Late Carboniferous specimens described herein as *Rhiphaeoteuthis margaritae* gen. et sp. nov. diminish the gap between the Early Carboniferous *Eobelemnites caneyensis* FLOWER, 1945 and Late Permian–Early Jurassic phragmoteuthids, and show the early appearance of the phragmoteuthids.

The bactritoids are considered to be an offspring of either the orthocerids (TEICHERT, 1988), or sphaerorthocerids (RISTEDT, 1968, 1981). RISTEDT believes that bactritoids must have originated from the sphaerorthocerids because of the subspherical protoconchs in both groups. Thus, that author gives priority to the shape of the protoconch and puts the position of the siphuncle in second place. However, one can expect another scenario of development. If one accepts the Middle Ordovician *Eobactrites* SCHINDEWOLF as a bactritid (ERBEN, 1964) rather than an ellesmerocerid (SWEET, 1958), the marginal siphuncle of this form could have been inherited from ellesmerocerid ancestors. The roots of the bactritoids must then be sought among the Late Cambrian ellesmeroceroids with marginal siphuncles. The shape of the protoconch in ellesmeroceratids is still unknown; however, it cannot be excluded that some of them had a subspherical protoconch lacking a cicatrix. In orthocerids, with central siphuncle, the protoconch is cup-shaped and bears a cicatrix. A nacreous layer appears in the shell wall, a short distance from the apex. The primary varix is absent. The cicatrix is known to be present in *Nautilus* (ARNOLD, 1988), orthocerids (RISTEDT, 1971; BLIND, 1988) and actinocerids (SCHINDEWOLF, 1944; RISTEDT, 1971; DOGUZHAEVA et al., 1999c).

The Late Carboniferous orthocerid *Aidaroceras politum* gen. et sp. nov. shows a short limpet-like primordium and a long first camera of the phragmocone; the first septum is calcareous and perforated, so that the siphuncle begins as a bubble-like caecum in the primordium. The primordial dome in bactritids could be a structure comparable with the first septum of the orthocerid, with the only difference that the first septum is perforated in the described orthocerid while the basis of the primordium dome in bactritids has no perforation. According to this view the bactritids exhibit the primitive ancestral feature which is missing in orthocerids. Besides, in comparison with the orthoceroids, the first appearance of the nacreous layer in the bacritoid shell was retarded: it appears approximately in the fourth camera immediately before the primary constriction instead of in the apical part of the shell in orthocerids.

Thus, the shell wall of the protoconch and the initial portion of the phragmocone is prismatic in bactritoids, ammonoids and belemnoids, but this is not the case with *Nautilus* and orthoceroids (RISTEDT, 1971). In the latter the nacreous layer first appears near the apex of the protoconch. These morphological characters, namely, the presence or absence of a cicatrix and a nacreous layer in the protoconch, evidently indicate different embryonic strategies in bactritoids, ammonoids and belemnoids, on the one hand, and orthoceroids, actinoceroids and nautiloids, on the other.

Acknowledgements

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Plate 1

Chuvashovia curvata **gen et sp. nov.**
3871/311.
Median shell section, siphuncle to the right.

Fig. 1: Protoconch, first camerae and living chamber.
Scale bar: 1 mm.
Fig. 2: Enlarged initial portion.
Scale bar: 0.3 mm.
Fig. 3: Cameral deposits lining the protoconch and first camerae.
Scale bar: 0.1 mm.
Fig. 4: Prismatic mural and hyposeptal cameral deposits.
Scale bar: 0.03 mm.
Fig. 5: Orthochoanitic septal necks.
Scale bar: 0.1 mm.
Fig. 6: Shell wall formed by thin nacreous and thick outer prismatic layers, approximately 6^{th} camera.
Scale bar: 0.03 mm.
Fig. 7: Nacreous and outer prismatic shell wall layers of equal thickness at the end of the shell.
Scale bar: 0.01 mm.

“Bactrites” **sp.**

Fig. 8: 3871/312.
Protoconch with thin radial ribs surrounding the smooth apex.
Magnification ×80
Fig. 9: 3871/312.
Protoconch with thin radial ribs surrounding the smooth apex.
Magnification ×130
Fig. 10: 3871/313.
Median section of shell showing comparatively large bubble-like caecum in the protoconch and submarginal siphuncle in the first camerae.
Scale bar: 0.3 mm.
Fig. 11: 3871/313.
Median section of shell showing comparatively large bubble-like caecum in the protoconch and submarginal siphuncle in the first camerae.
Scale bar: 0.3 mm.

River Sim; Artinskian.

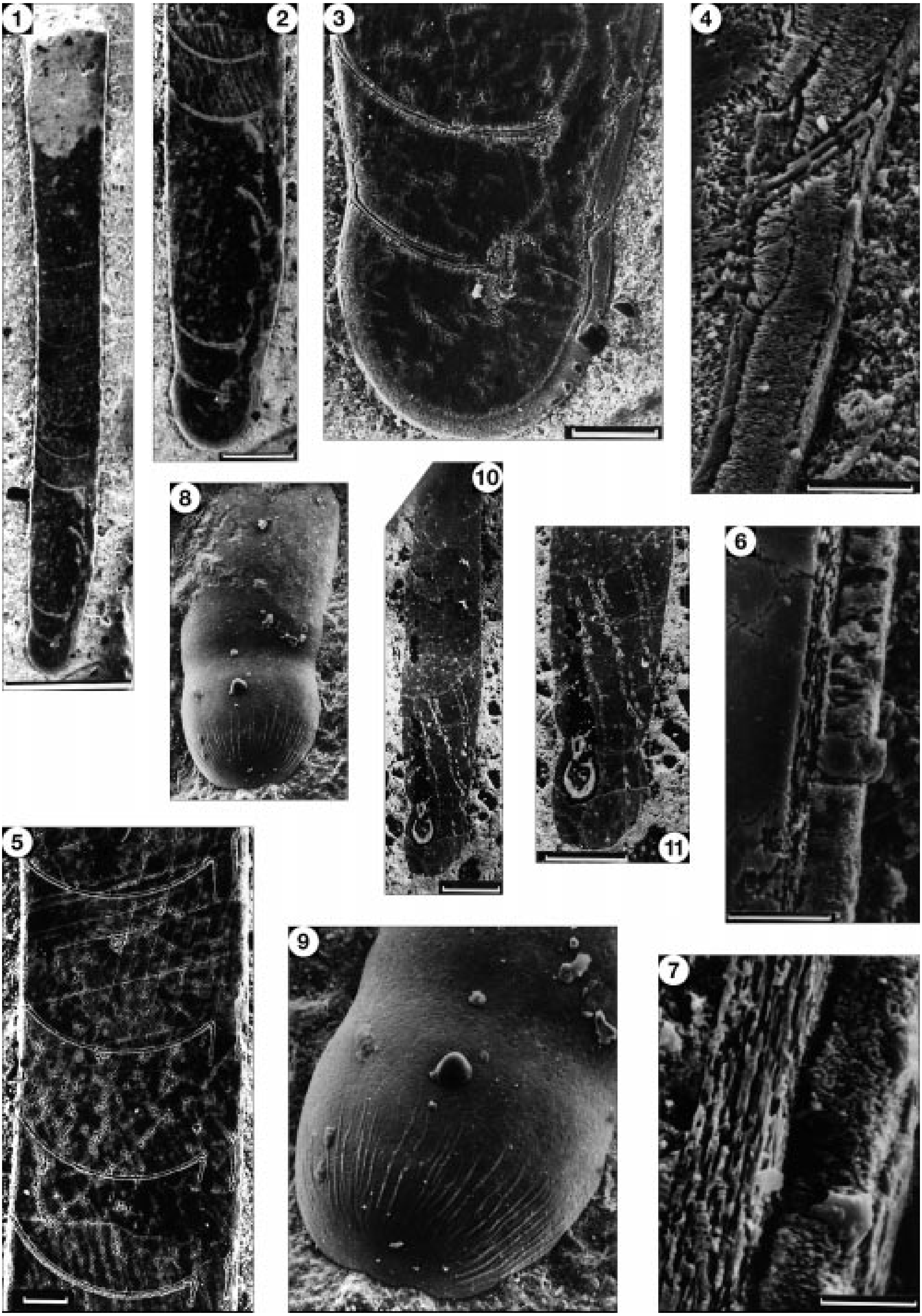
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Plate 2

***Hemibactrites* sp.**

Figs. 1,3: 3871/314.
Lateral view showing the asymmetry of the adolescent shell, the flat right side is dorsal.
Scale bar: 0.3 mm.

Figs. 2,4–9: 3871/315:
Fig. 2: Ventral view, the shell appears symmetrical.
Scale bar: 0.3 mm.
Fig. 4: Embryonic reticulated sculpture disappears near the primary constriction.
Scale bar: 0.3 mm.
Fig. 5: Embryonic reticulated sculpture disappears near the primary constriction.
Scale bar: 0.1 mm.
Fig. 6: Three prismatic layers of the protoconch shell wall.
Scale bar: 0.1 mm.
Fig. 7: Prismatic first septum and semi-lunar shape of nets of the embryonic reticulated sculpture.
Scale bar: 0.03 mm.
Fig. 8: Enlarged detail of Fig. 6 to show thin outer layer turning over near the apex of the protoconch to form a primordial dome (destroyed in the specimen).
Scale bar: 0.1 mm.
Fig. 9: Shell wall of the protoconch: two inner layers of equal thickness and thin outer layer (enlarged detail of Fig. 6).
Scale bar: 0.01 mm.

Fig. 10: 3871/316.
The protoconch showing the primordial dome.
Scale bar: 0.3 mm.

Figs. 11–12: 3871/317.
Apical part of the protoconch showing the site of the primordial dome marked by a ring of modified sculpture.
Fig. 11: Scale bar: 0.3 mm.
Fig. 12: Scale bar: 0.1 mm.

Fig. 13: 3871/318.
Inner surface of the protoconch with tubercles.
Scale bar: 0.01 mm.

River Sim, Artinskian.

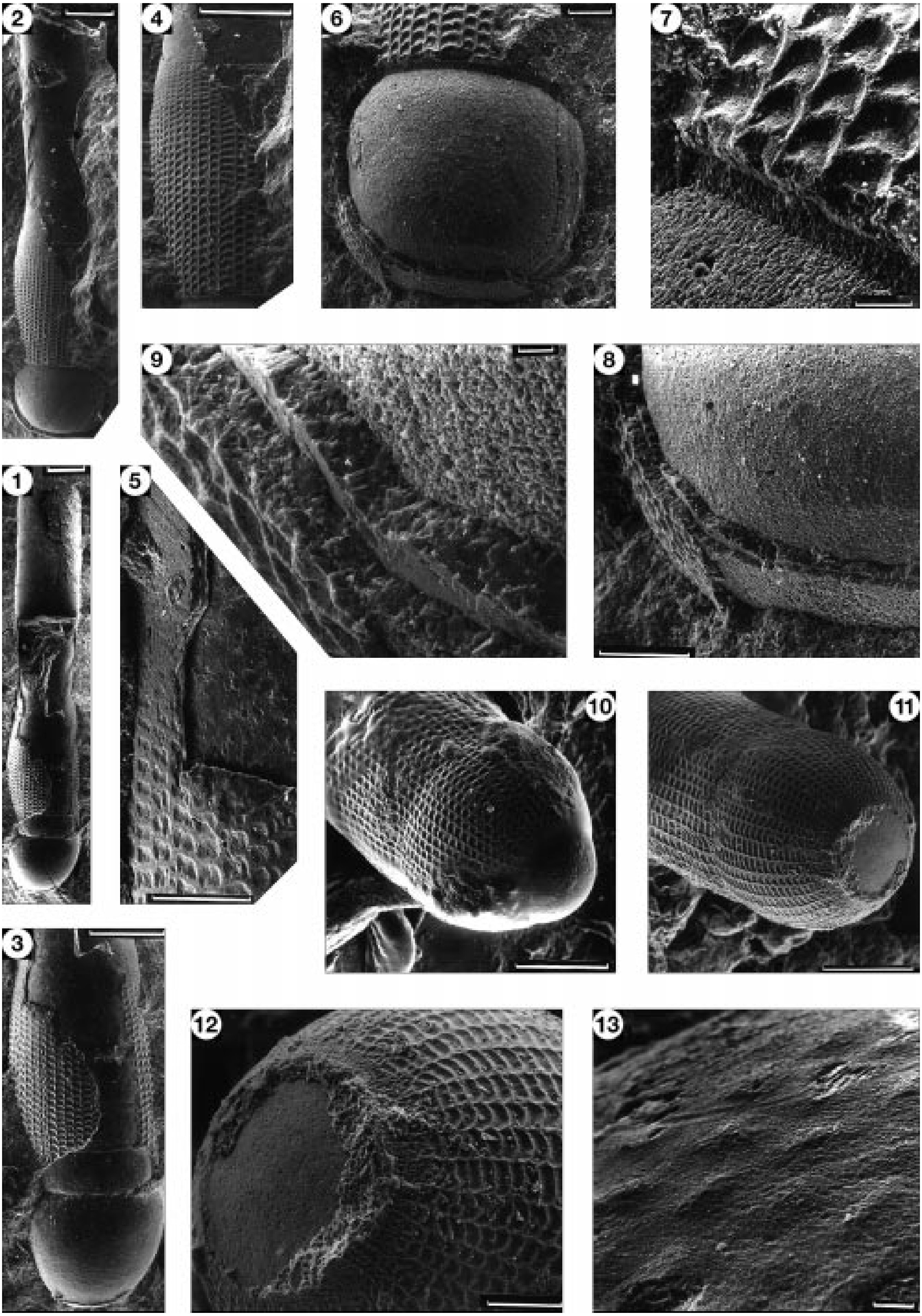
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Plate 3

Hemibactrites **sp.**
Median section, shell wall ultrastructure.

Fig. 1: 3871/319.
The appearance of a nacreous layer in the shell wall near the primary constriction, the outer prismatic layer is on the left.
Scale bar: 0.1 mm.

Figs. 2,3: 3871/320.
Primordial dome.
Fig. 2: The angle between the outer and inner layers near the point of their divergence.
Magnification ×750.
Fig. 3: The cavity of the primordial dome is not filled by shell matter.
Magnification ×350.

Fig. 4: 3871/321.
Appearance of nacreous layer, the outer prismatic layer is on the right; the inner surface of the shell seems to be coated by a set of large crystals of cameral deposits (note similar lining in Fig. 1).
Scale bar: 0.1 mm.

Fig. 5: 3871/322.
Thin outer prismatic and thick nacreous layers of the shell wall approximately in 20th chamber.
Scale bar: 0.1 mm.

River Sim, Artinskian.

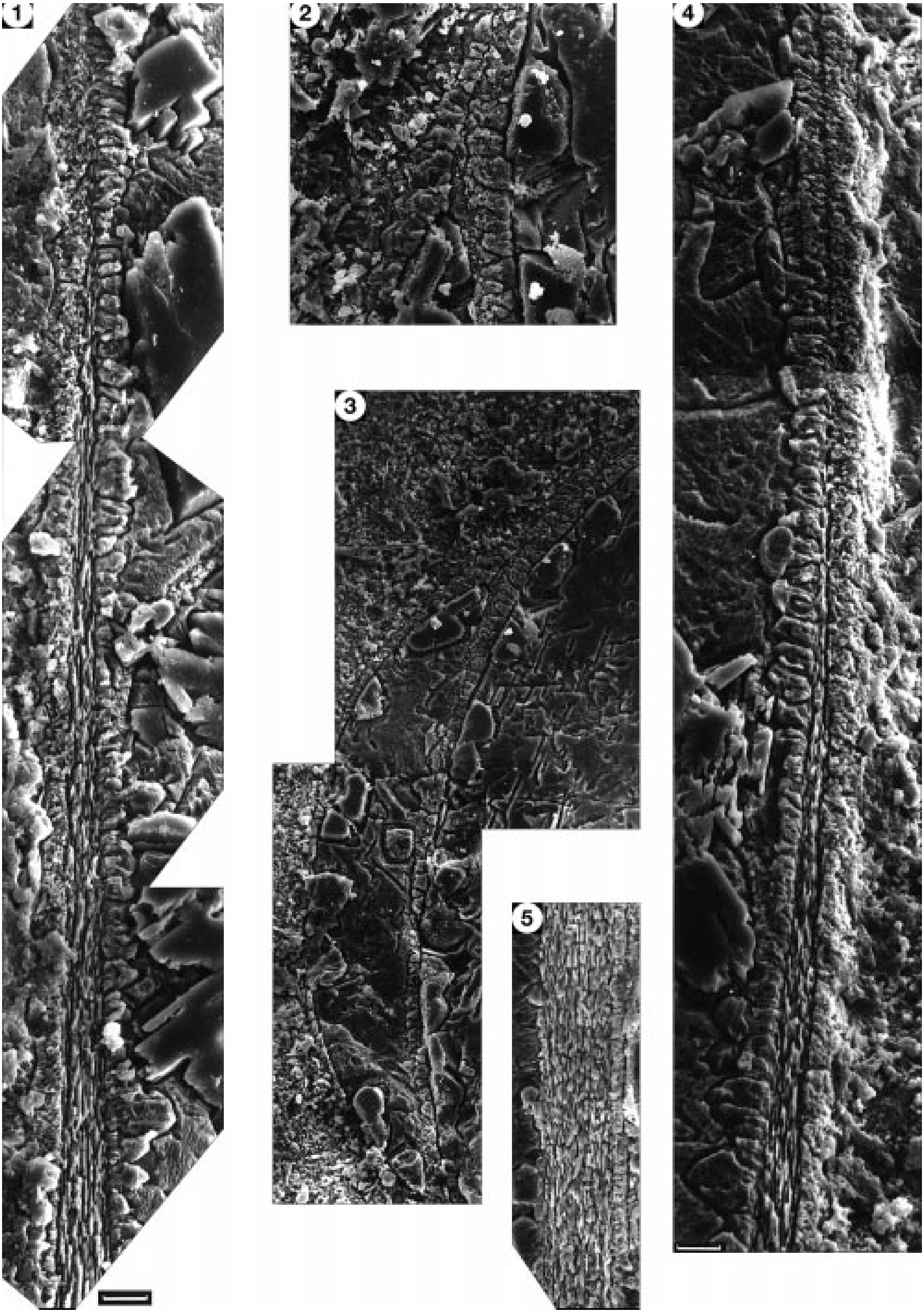
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Plate 4

Figs. 1–3: ***Hemibactrites* sp.**
3871/323.
Unpaired dorsal attachment scars on protoconch and first five camerae, on Fig. 2 the primordial dome is partly exposed.
Scale bars: Figs. 1,2: 0.3 mm; Fig. 3: 0.1 mm.

Figs. 4,5,7,8: ***Uralobactrites uralicus* gen. et sp. nov.**
3871/324, 325, 327.
Shape of protoconch and first camerae; unpaired dorsal attachment scars are visible on Fig. 8.
Scale bars: Fig. 4: 0.3 mm; Fig. 5: 0.1 mm; Fig. 7: 0.3 mm; Fig. 8: 0.1 mm.

Figs. 6,10: ***Simobactrites kuzinae* gen. et sp. nov.**
3871/326, 229.
Variations in the shape of the protoconch and first chambers (on Fig. 10 note the marginal position of the siphuncle visible in last septum).
Scale bars: 0.3 mm.

Fig. 9: ***Linibactrites solidus* gen. et sp. nov.**
3871/330.
Shell shows a weak constriction between hemispherical protoconch, with rounded spot at the site of the broken primordial dome, and first camera; note the ring around the primordial dome.
Scale bar: 0.1 mm.

Figs. 11–13: ***Chuvashovia* sp.**
3871/331.
Shell with rounded sub-spherical protoconch; the apex is smooth and surrounded by longitudinal wrinkles.
Scale bars: Fig. 11: 0.3 mm; Fig. 12: 0.1 mm; Fig. 13: 0.01 mm.

River Sim, Artinskian.

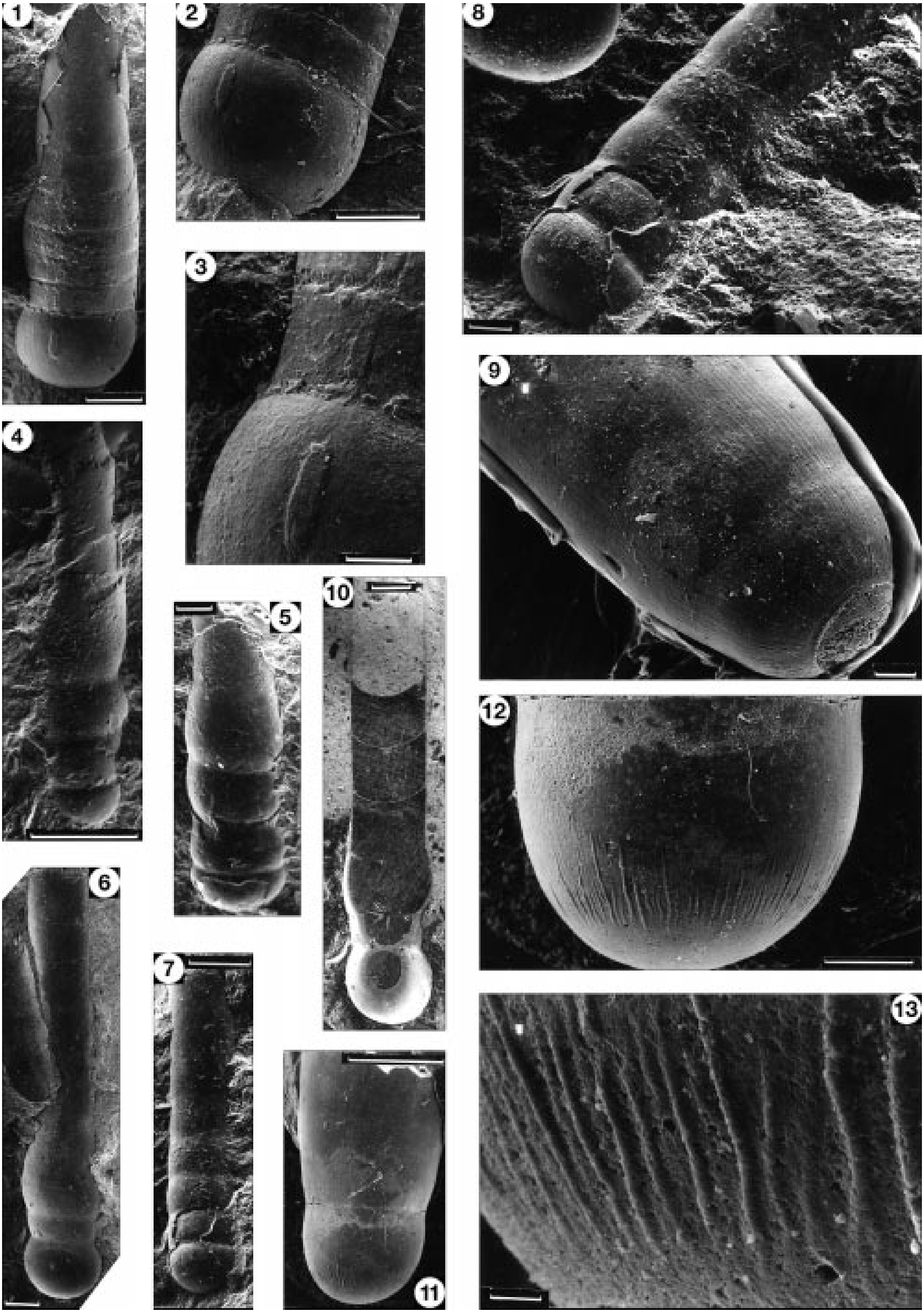
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Plate 5

Fig. 1: ***Uralobactrites* sp.**
3871/332.
Suture line of 2nd septum (protoconch is in the right bottom corner) showing dorsal (?) lobe and indistinct attachment scar.
Scale bar: 0.03 mm.

Fig. 2: ***Hemibactrites* sp.**
3871/333.
Protoconch showing the primordial dome (left side), rippled inner surface and attachment scar (partly coated by the shell wall).
Scale bar: 0.1 mm.

Figs. 3–5: ***Ovobactrites antonovae* gen. et sp. nov.**
3871/334.
Fig. 3: General view of adolescent shell with distinctly separated oval protoconch (lower right corner), distinct constrictions around the first few septa, narrowing of the shell near the primary constriction and slowly expanding shell tube after that.
Scale bar: 1 mm.
Fig. 4: Protoconch and adjoining portion of the phragmocone.
Scale bar: 0.3 mm.
Fig. 5: Short wrinkles at the constriction between the protoconch and the first camera, similar to the wrinkles around the apex of the protoconch in some other shells (compare with Pl. 4, Fig. 12).
Scale bar: 0.03 mm.

Fig. 6: ***Ovobactrites antonovae* gen. et sp. nov.**
3871/335.
Longitudinal shell section showing comparatively thick lining of cameral deposits on the inner surface of the protoconch, adoral surface of the first septum, and the shell wall of the phragmocone.
Scale bar: 0.1 mm.

Figs. 7,8: ***Ovobactrites antonovae* gen. et sp. nov.**
3871/336.
Strongly elongated protoconch showing wrinkles at the constriction between the protoconch and the first camera.
Scale bar: 0.1 mm.

River Sim, Artinskian.

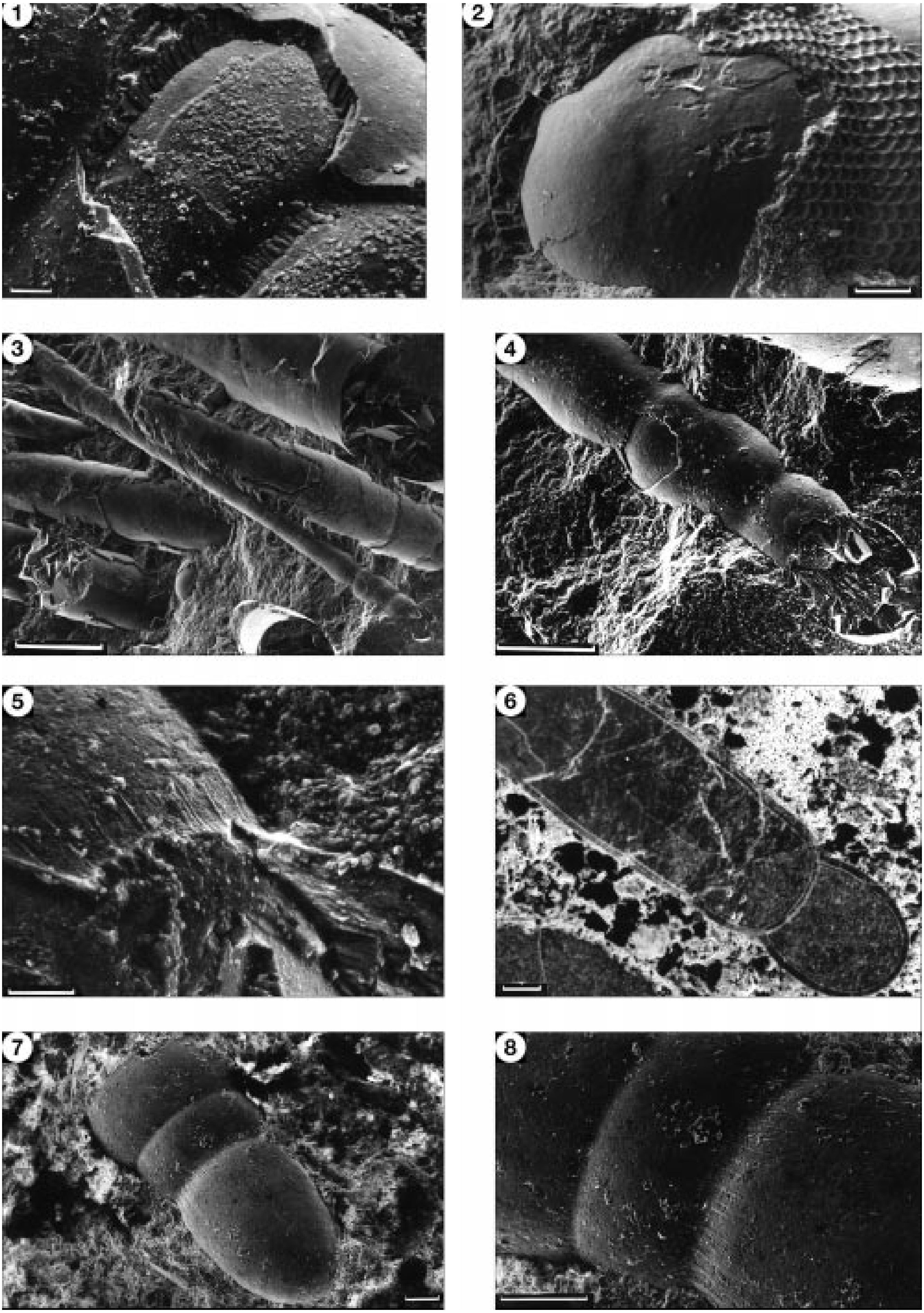
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Plate 6

Figs. 1–5: ***Uralobactrites* sp.**
3871/337.
Longitudinal shell section.
Fig. 1: General view of shell with comparatively low protoconch, narrow first and strongly swollen second camerae.
Scale bar: 0.3 mm.
Fig. 2: Submarginal siphuncle in the first camerae.
Scale bar: 0.3 mm.
Fig. 3: First septal neck with small tongue-like adapical appendix.
Scale bar: 0.1 mm.
Figs. 4,5: Cameral deposits lining protoconch, first camera and adapical surface of second septum.
Scale bars: Fig. 4: 0.1 mm; Fig. 5: 0.03 mm.

Figs. 6–8: ***“Bactrites”* sp.**
3871/338.
Longitudinal shell section showing sub-spherical, weakly separated protoconch (siphuncle to the left); cameral deposits line the shell wall and the adapical surface of the first septum.
Scale bars: Fig. 6: 0.3 mm; Fig. 7: 0.1 mm; Fig. 8: 0.03 mm.

Fig. 9: ***Chuvashovia* sp.**
3871/339.
Smooth, sub-spherical, weakly separated protoconch and first camerae; similar to *Simobactrites kuzinae* gen. et sp. nov. (Fig. 6); however, the first camera is not cylindrical and the second one is not much swollen.
Scale bar: 0.3 mm.

River Sim, Artinskian.

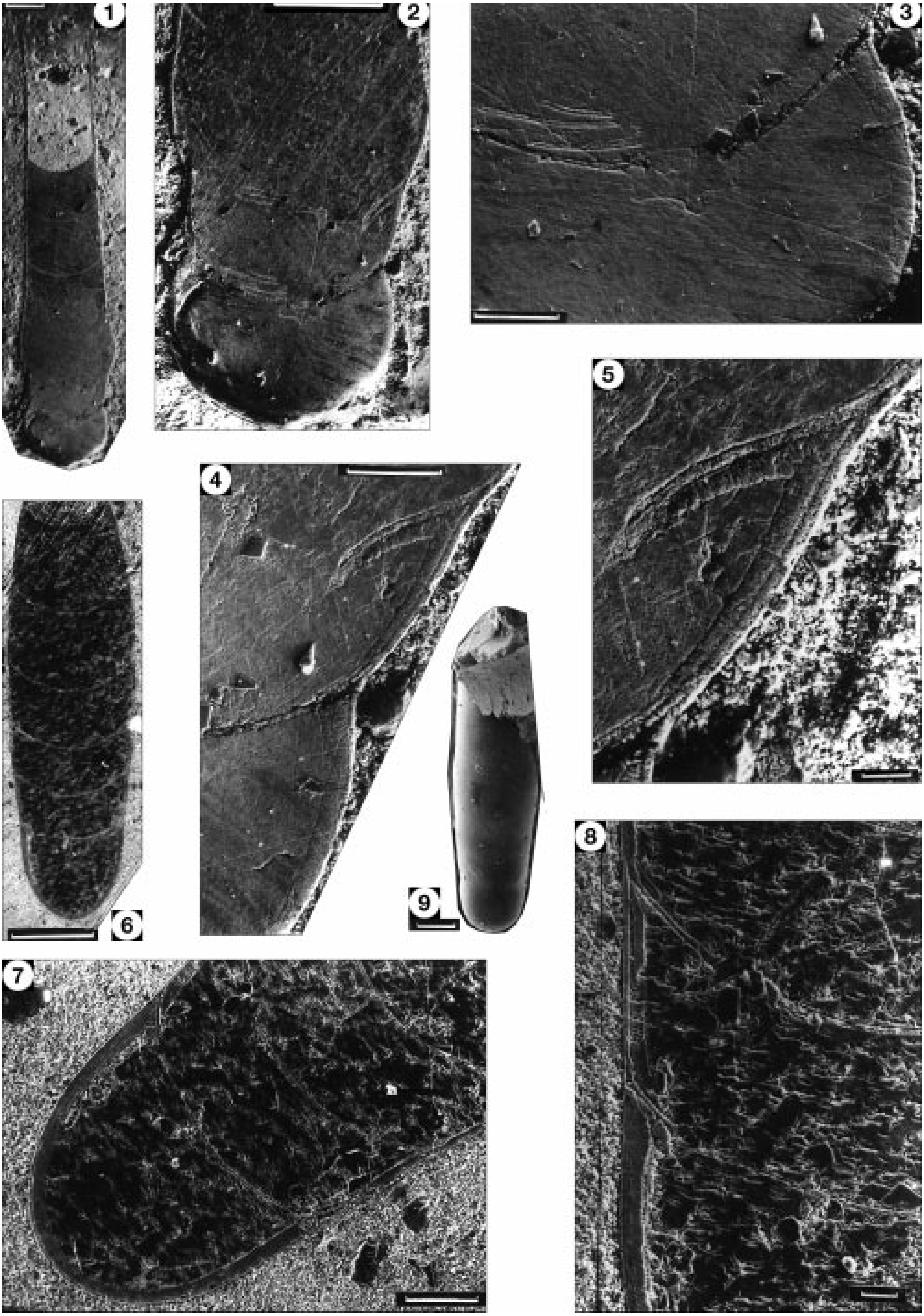
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Plate 7

Ovobactrites antonovae **gen. et sp. nov.**

Figs. 1–3: 3871/340.
Longitudinal section of shell showing cameral deposits which are five times as thick as the shell wall of the protoconch (Fig. 3) or the first septum (Fig. 2).
Scale bars: Figs. 1,3: 0.1 mm; Fig. 2: 0.03 mm.

Figs. 4,5: 3871/341.
Longitudinal section of shell with elongated protoconch, long first camera, thick mural and episeptal cameral deposits; the shell wall is thin (Fig. 5).
Scale bars: Fig. 4: 0.1 mm; Fig. 5: 0.01 mm.

Figs. 6–8: 3871/342.
Longitudinal section of the shell similar to the two previous ones; in shells of this type (Figs. 1, 4, 6) if the protoconch is broken the first camera could be erroneously taken for the protoconch and the cameral deposits for the shell wall.
Scale bars: Fig. 6: 0.3 mm; Fig. 7: 0.1 mm; Fig. 8: 0.01 mm.

Creek Aidaralash; Orenburgian.

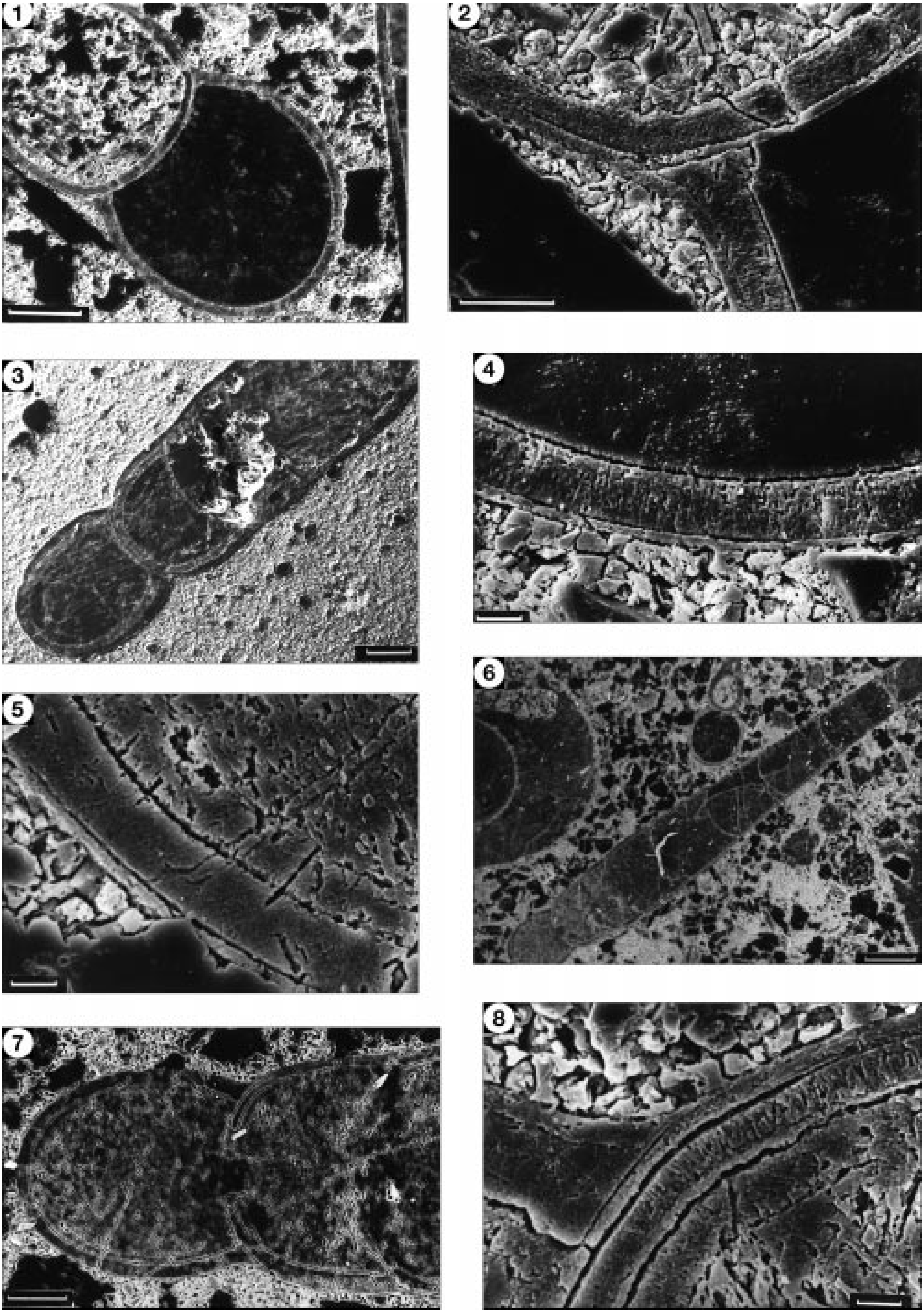
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Plate 8

Fig. 1: ***Hemibactrites* sp. (top; 3871/343) and *"Parabactrites"* sp. (bottom; 3871/244).**
General view of two shells.
Scale bar: 0.3 mm.

Fig. 2: ***"Parabactrites"* sp.**
The cup-like protoconch is shorter than the first camera, the first three sutures are straight, the fourth and fifth ones show pronounced wide and deep ventral lobes.
Scale bar: 0.3 mm.

Fig. 3: ***Hemibactrites* sp.**
The primary constriction in *Hemibactrites* sp. is more distinct than in *"Parabactrites"* sp.
Scale bar: 0.3 mm.

Figs. 4,6: ***"Parabactrites"* sp.**
3871/345.
Fig. 4: Ventro-lateral view showing short protoconch with primordial dome and the third suture line with deep ventral lobe.
Scale bar: 0.1 mm.
Fig. 6: Enlarged detail to show the primordial dome.
Scale bar: 0.1 mm.

Figs. 5,7: ***"Parabactrites"* sp.**
3871/346.
Lateral view of the shell with broken protoconch, all the septa with the exception of the first are inclined.
Scale bars: Fig. 5: 0.3 mm; Fig. 7: 0.1 mm.

Fig. 8: ***"Parabactrites"* sp.**
3871/347.
Fragment of brevicone with 10 camerae preserved.
Scale bar: 1 mm.

River Sim; Artinskian.

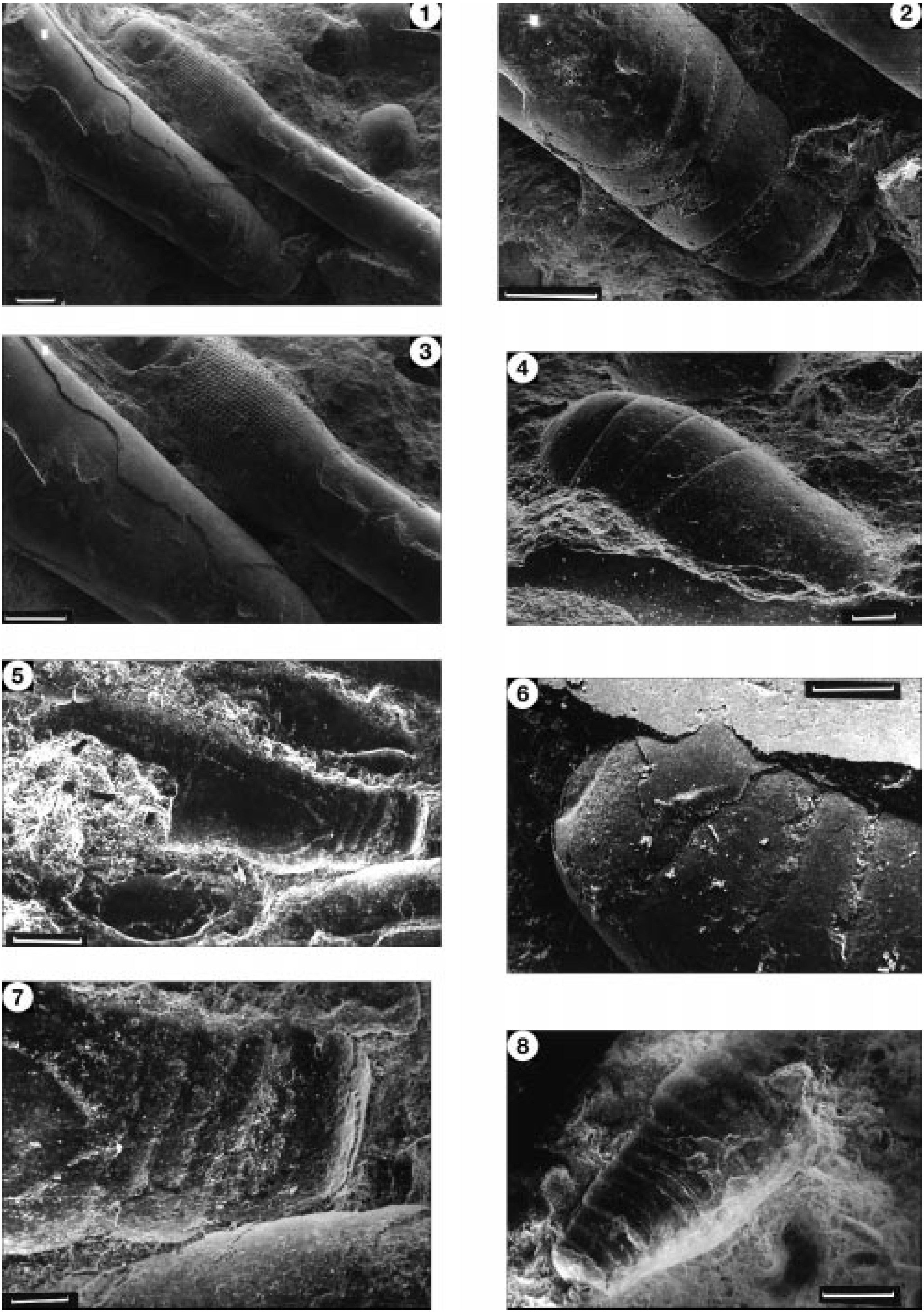
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Plate 9

Fig. 1: **Adolescent goniatitid.**
3871/348.
Median section of protoconch and first one and a half whorls; the first chamber is very short, all the others are long; the primary constriction is at an angle of 360 degrees from the first septum.
Scale bar: 0.1 mm.

Fig. 2: **Paragastrioceratidae.**
3871/349.
Adolescent shell consisting of smooth involute ammonitella and ribbed post-hatching shell.
Scale bar: 0.3 mm.

Fig. 3: **Adolescent shell of goniatite with evolute ammonitella.**
3871/350.
The primary constriction is at an angle of 360 degrees from the first septum.
Scale bar: 0.3 mm.

Fig. 4: **Non-fully grown ammonitella.**
3871/351.
External view.
Scale bar: 0.1 mm.

Figs. 5,6: **Late embryonic stage of shell formation.**
3871/352.
The primary varix is not completed.
Scale bars: Fig. 5: 0.1 mm; Fig. 6: 0.01 mm.

Figs 1,2: River Sim; Artinskian; Figs. 3,4: Creek Aidaralash; Orenburgian

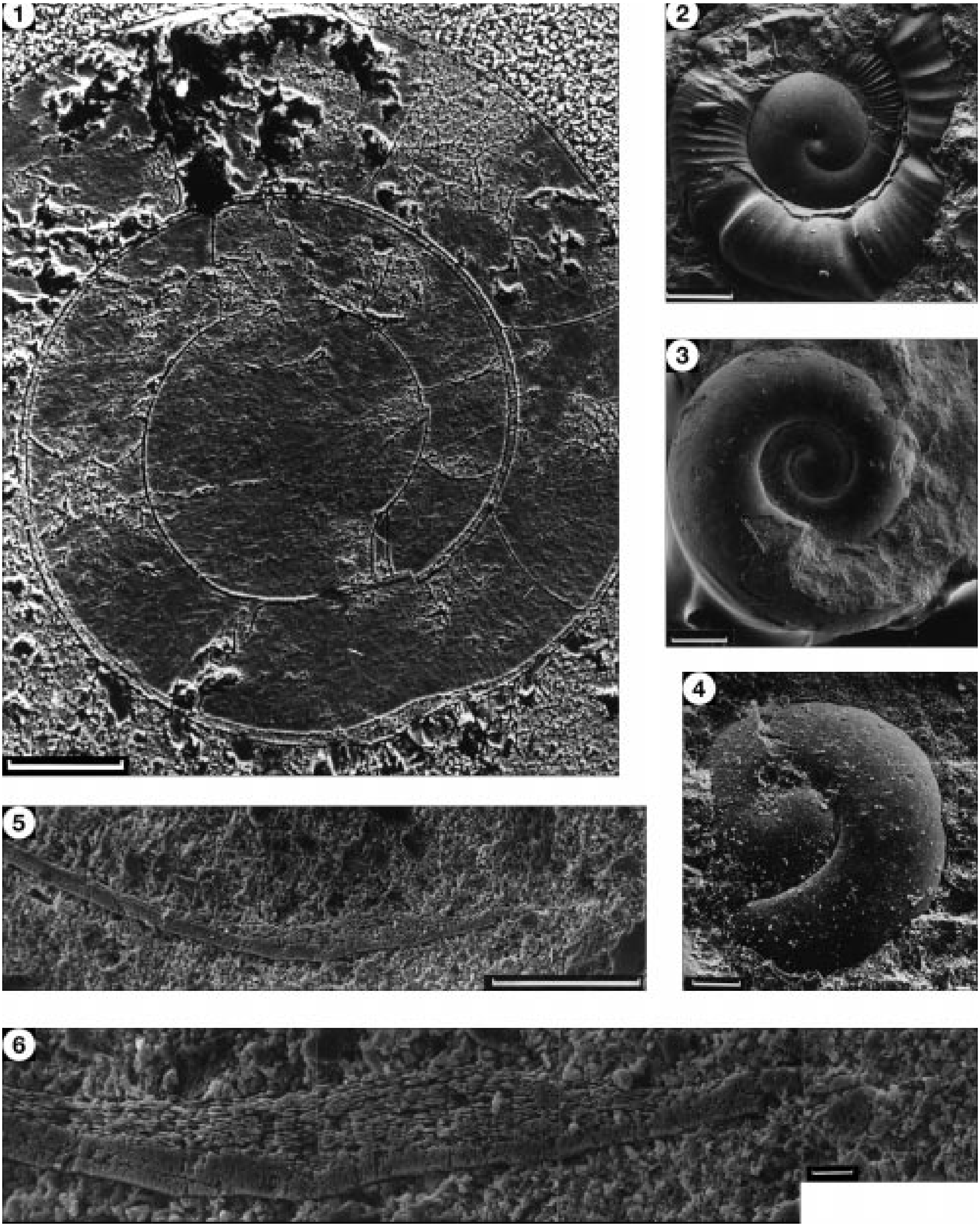

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Plate 10

Figs. 1,2: **Ammonitella, not yet fully secreted.**
3871/353.
Embryonic stage of shell formation: the proseptum and primary varix are missing and inner portion of the protoconch is not fully calcified resulting in postmortal plastic deformation of its innermost portion.
Scale bars: Fig. 1: 0.1 mm; Fig. 2: 0.03 mm.

Figs. 3–5: **Fully secreted ammonitella with two septa, primary constriction and primary varix showing well preserved nacreous ultrastructure.**
3871/354.
No posthatching shell wall yet.
Scale bars: Fig. 3: 0.1 mm; Fig. 4: 0.03 mm; Fig. 5: 0.01 mm.

Fig. 6: **Ammonitella with proseptum and primary varix.**
3871/355.
Primary constriction is at an angle of 360 degrees to the first septum.
Scale bar: 0.1 mm.

Figs. 7–8: ***Agathiceras* sp.**
3871/356.
Fig. 7: Adolescent shell, primary constriction is at an angle of 360 degrees to the first septum, primary varix is distinct.
Scale bar: 0.1 mm.
Fig. 8: 3rd whorl, shell wall formed by thin inner and outer prismatic layers and thick central nacreous layer; a very thin prismatic layer coating the outer prismatic layer represents the dorsal wall of the fourth whorl.
Scale bar: 0.01 mm.

River Sim; Artinskian.

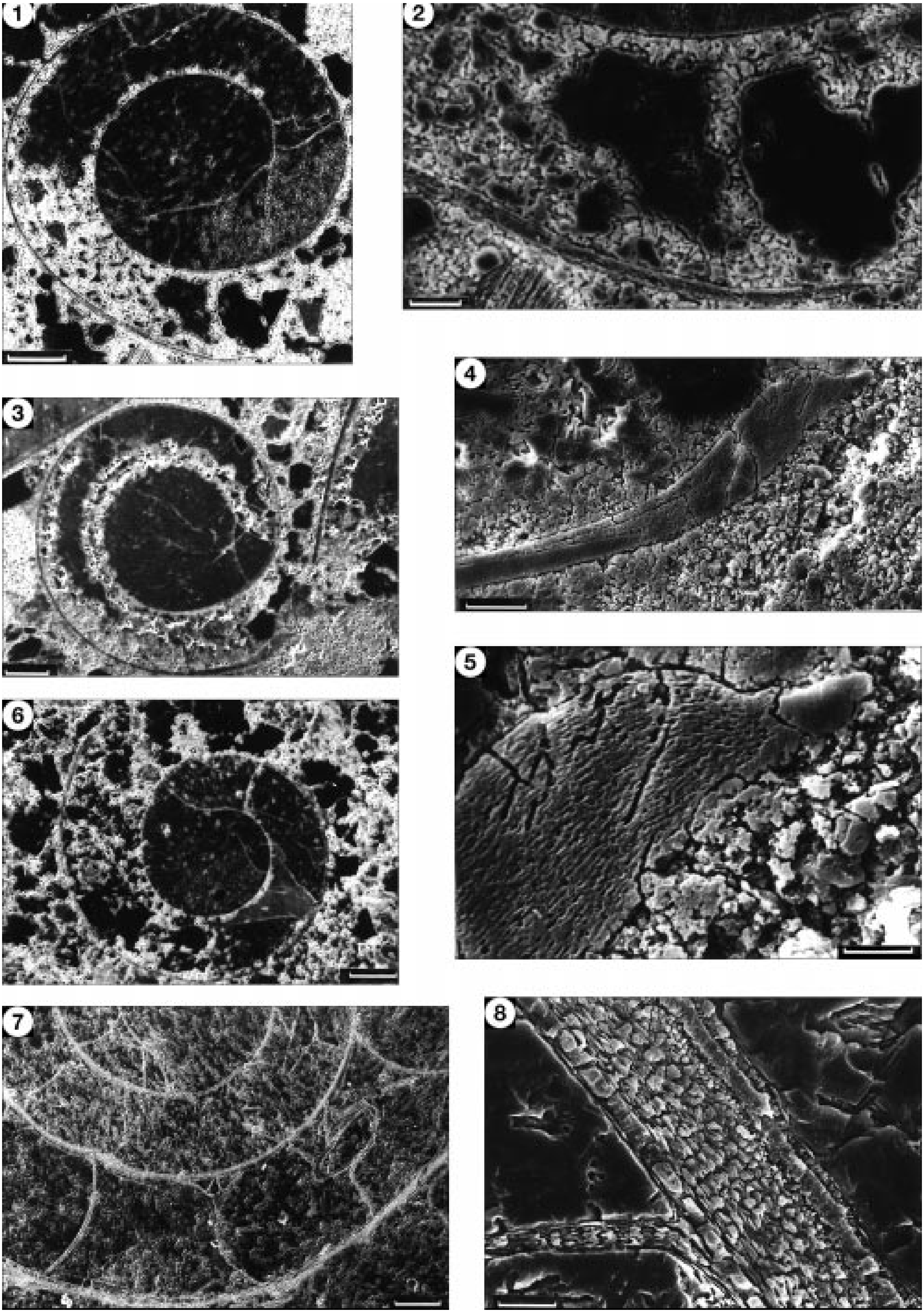
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Plate 11

Early posthatching stage of an ammonoid shell (3871/357).

Fig. 1: Median section of the shell.
Early posthatching stage with the four first septa formed.
Scale bar: 0.3 mm.

Fig. 2: Shell wall ultrastructure near the primary constriction.
The prismatic wall of the ammonitella gets thinner towards the primary constriction and disappears at the adoral end of the primary varix, the nacreous layer appears and at a short distance from this place it forms the primary varix; the post-hatching shell wall appears at the adoral part of the varix on its inner surface, the outer prismatic layer of the postembryonic shell differs from the prismatic layer of the embryonic shell in having more regular prismatic crystals, the length of which is about the same as the thickness of this layer (in the embryonic shell the prismatic crystals are shorter than the wall thickness; compare left and right parts of picture); near the shell aperture the prismatic layer is longer than the nacreous layer and becomes thinner in this direction (top of the right picture).
Scale bar: 0.03 mm

River Sim; Artinskian.

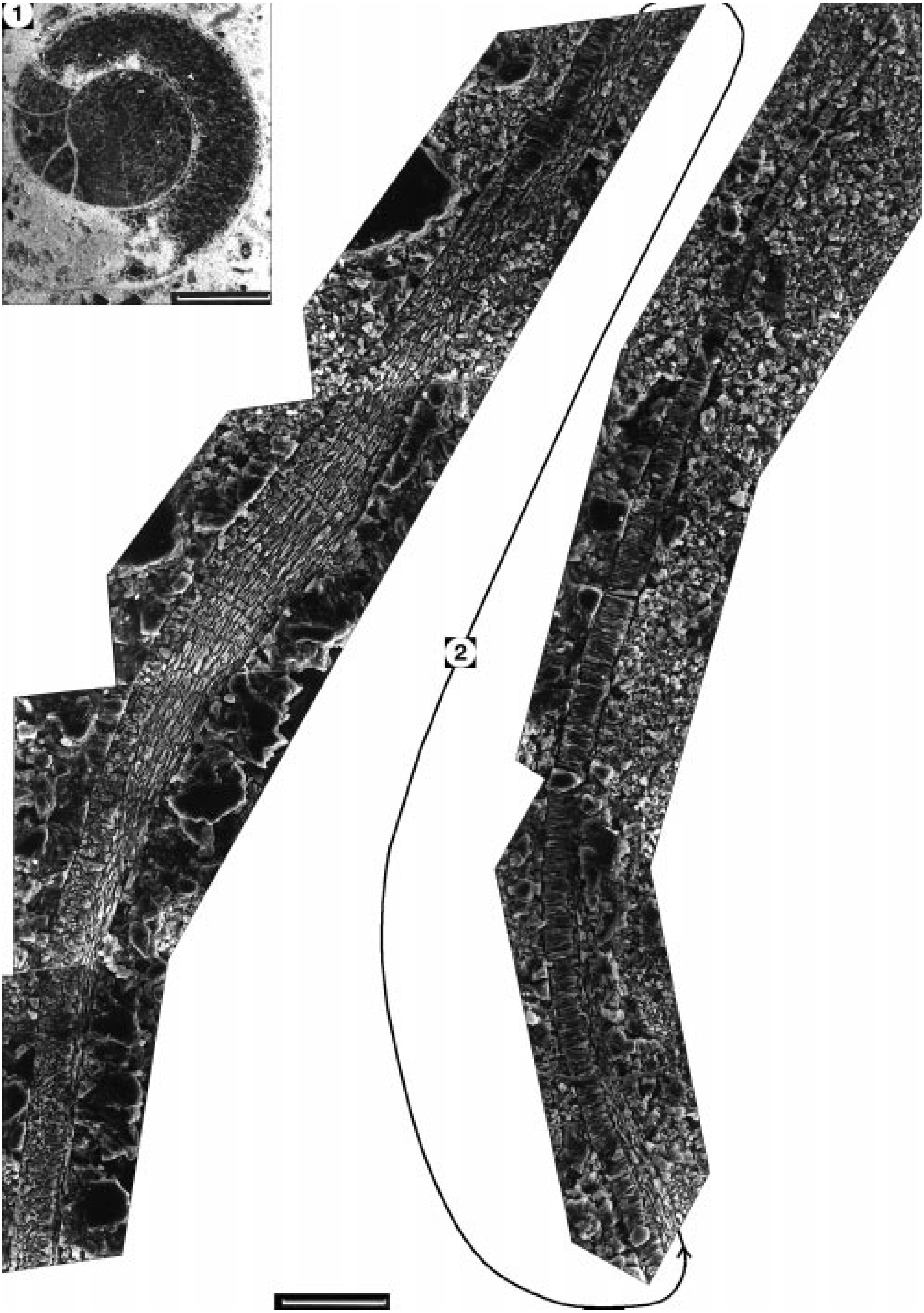
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Plate 12

Aidaroceras politum **gen. et sp. nov.**

Figs. 1–7: 3871/358.

Fig. 1: Ventral side of apical portion of adolescent shell.
Scale bar: 0.3 mm.

Fig. 2: Enlarged apex with primordium and cicatrix.
Scale bar: 0.1 mm.

Fig. 3: Cup-like primordium with ridges and folds on the surface is bordered by thin longitudinal ribs and wrinkles of the next, slowly expanding portion of the shell; the third portion exhibits growth lines and a smaller angle of expansion.
Scale bar: 0.1 mm.

Fig. 4: The primordium shows a combination of longitudinal and transverse rods, in the cicatrix the transverse rods are more distinct than the longitudinal ones.
Scale bar: 0.03 mm.

Fig. 5: Median section showing short primordium, two long camerae, small central siphuncle and part of living chamber.
Scale bar: 0.3 mm.

Fig. 6: Enlarged detail, orthochoanitic septal necks; cameral deposits are absent.
Scale bar: 0.1 mm.

Fig. 7: The caecum seems to be completely closed by the first septal neck and it is attached to the cicatrix.
Scale bar: 0.1 mm.

Fig. 8: 3871/359.
Median section; the shell is slightly curved, siphuncle central, no cameral deposits.
Scale bar: 0.1 mm.

Figs. 9,10: 3871/360.
Dorso-ventral section of shell.

Fig. 9: Short primordium with large caecum and long first camera with small central siphuncle; the first septum is attached near the border of the primordium, the second septum is attached at the border of the second portion of the shell (compare with Fig. 3).
Scale bar: 0.03 mm.

Fig. 10: Shell wall of primordium: weakly calcified cicatrix (right bottom corner) and comparatively thick wall of the rest of the shell; the first septum seems to be nacreous.
Scale bar: 0.1 mm.

Creek Aidaralash; Orenburgian.

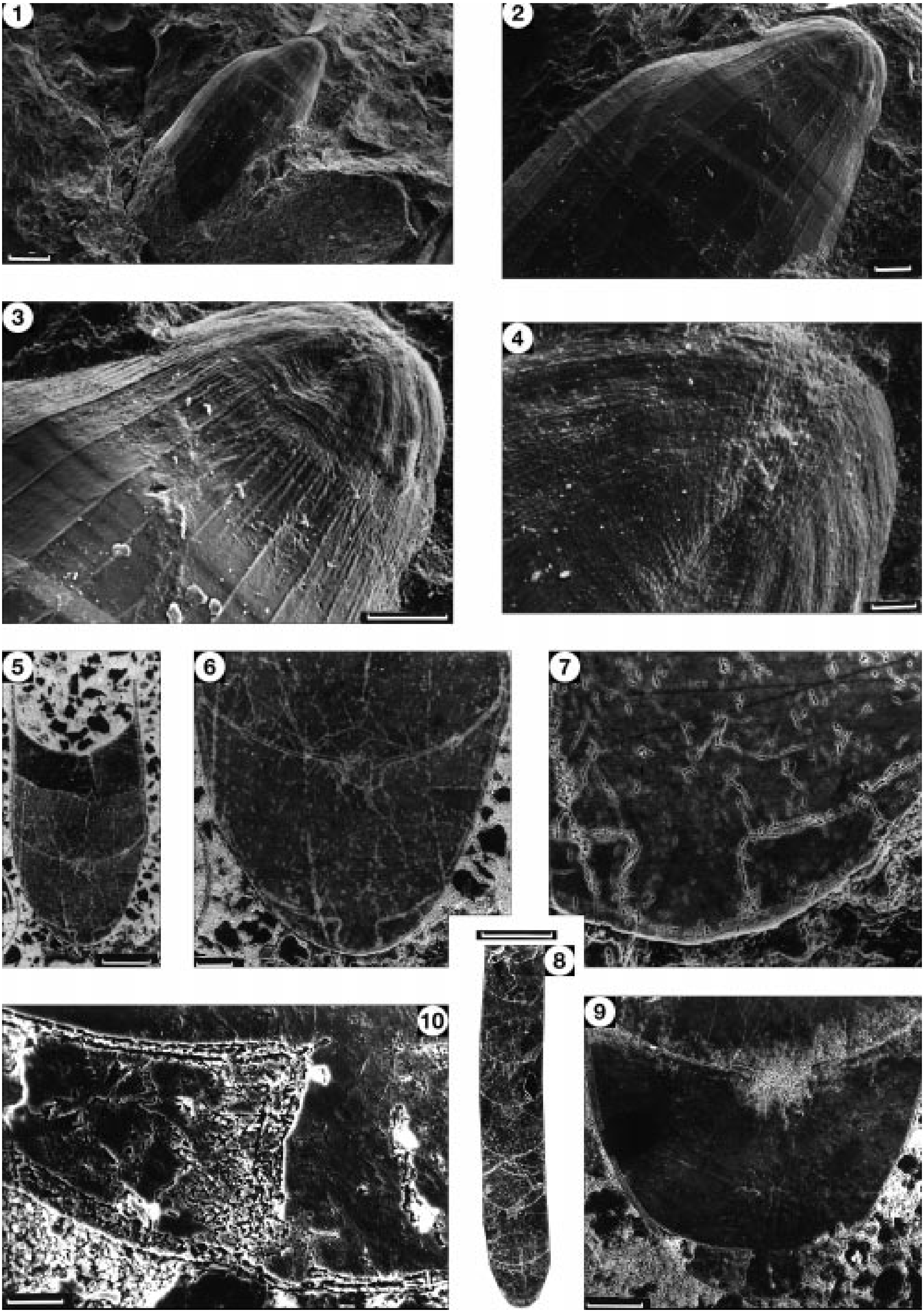
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Plate 13

Figs. 1–4: ***Rhiphaeoteuthis margaritae* gen. et sp. nov.**
3871/361; holotype.
Fig. 1: Siphuncular, presumably ventral side with wide, shallow ventral lobe, long cyrtochoanitic septal necks and wide Mural rings.
×9.5.
Fig. 2: Lateral side, wide mural rings with weak lateral lobes.
×8.5.
Fig. 3: Oval cross section showing narrower dorsal side (top) and septum; septal foramen is oval (bottom).
×9.5.
Fig. 4: Dorso-lateral side of the shell showing distinct last mural ring and probably non-fully calcified shell wall of the last camera; the phragmocone is surrounded by seed scales of terrestrial plants which are black.
×5.5.

Figs. 5, 6: ***Belemnitomimus palaeozoicus*.**
3871/362.
Fig. 5: Dorso-ventral shell section (siphuncle to the right).
Scale bar: 0.1 mm.
Fig. 6: The 5th and 6th cyrtochoanitic septal necks on the dorsal side of the siphuncle.
Scale bar: 0.1 mm.

Figs 1–4: Creek Aidaralash, Orenburgian; Figs. 5,6: River Tabantal; Asselian.

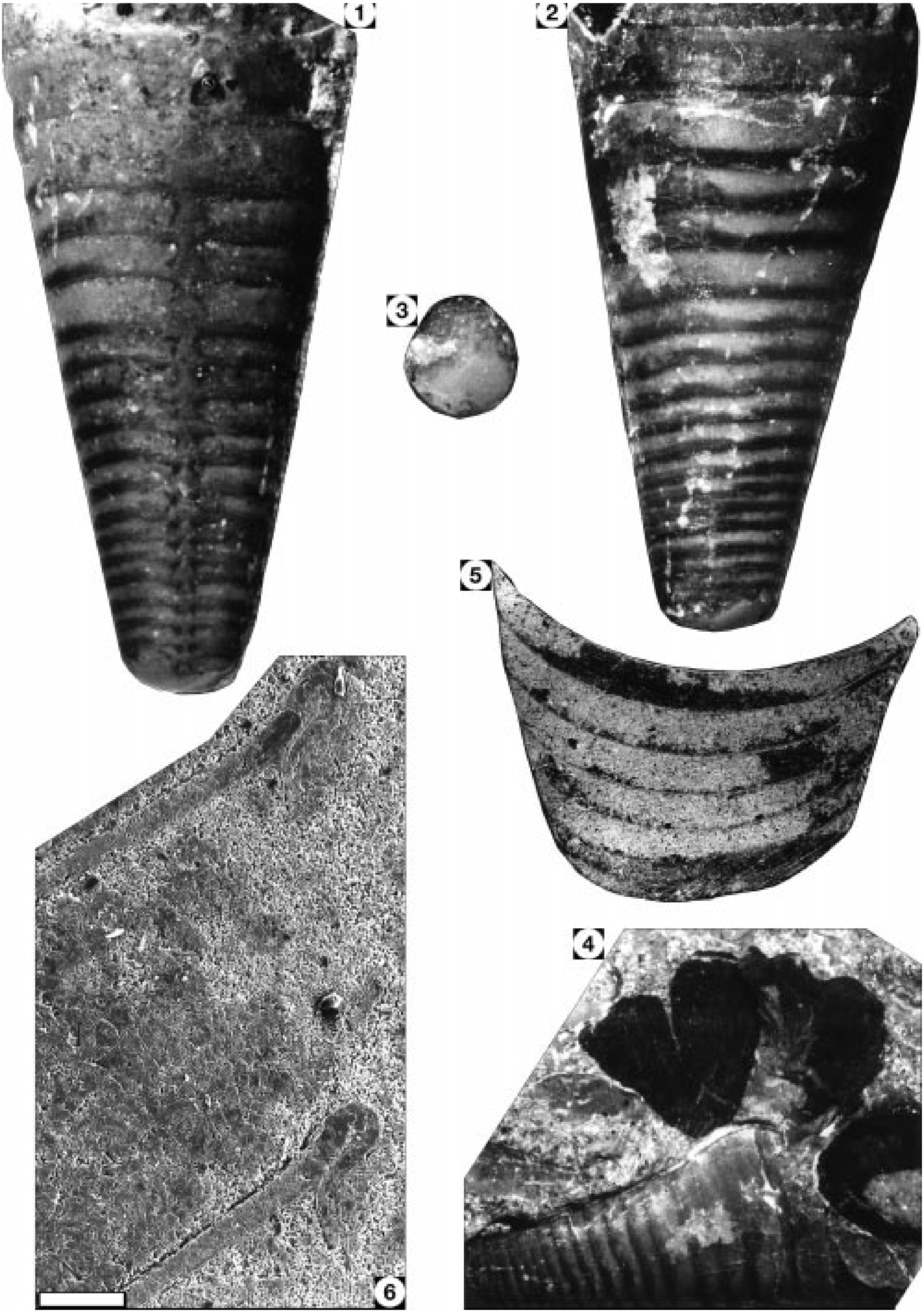
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Plate 14

Fig. 1: **Longitudinal section of embryonic breviconic ?parabactritoid shell.**
3871/363.
Compare with Pl. 8, Figs. 2,6; unilayered prismatic wall gets narrower towards the aperture, giving an impression that the real marginal edge is preserved.
Scale bar: 0.1 mm.

Fig. 2: **Longitudinal section of ammonitella and embryonic breviconic shell probably belonging to phragmoteuthids.**
Scale bar: 0.3 mm.

Fig. 3: **Enlarged phragmoteuthoid shell showing short cup-like protoconch, two camerae and living chamber.**
The siphuncle is sub-marginal, the septal neck of the second septum is short and orthochoanitic, on the ventral side camerae are longer than on dorsal side; unilayered prismatic wall gets narrower towards the aperture and wedges out after the primary constriction.
Scale bar: 0.3 mm.

Fig. 4: **Long mural part of 3rd septum.**
Scale bar: 0.01 mm.

Fig. 5: **Enlarged detail of Fig. 3**
to show thin prismatic shell wall and short orthochoanitic septal neck.
Scale bar: 0.03 mm.

Fig. 6: **Outer prismatic and nacreous layers of the shell wall at a later ontogenetic stage of the breviconic shell.**
Scale bar: 0.01 mm.

Creek Aidaralash, Orenburgian.

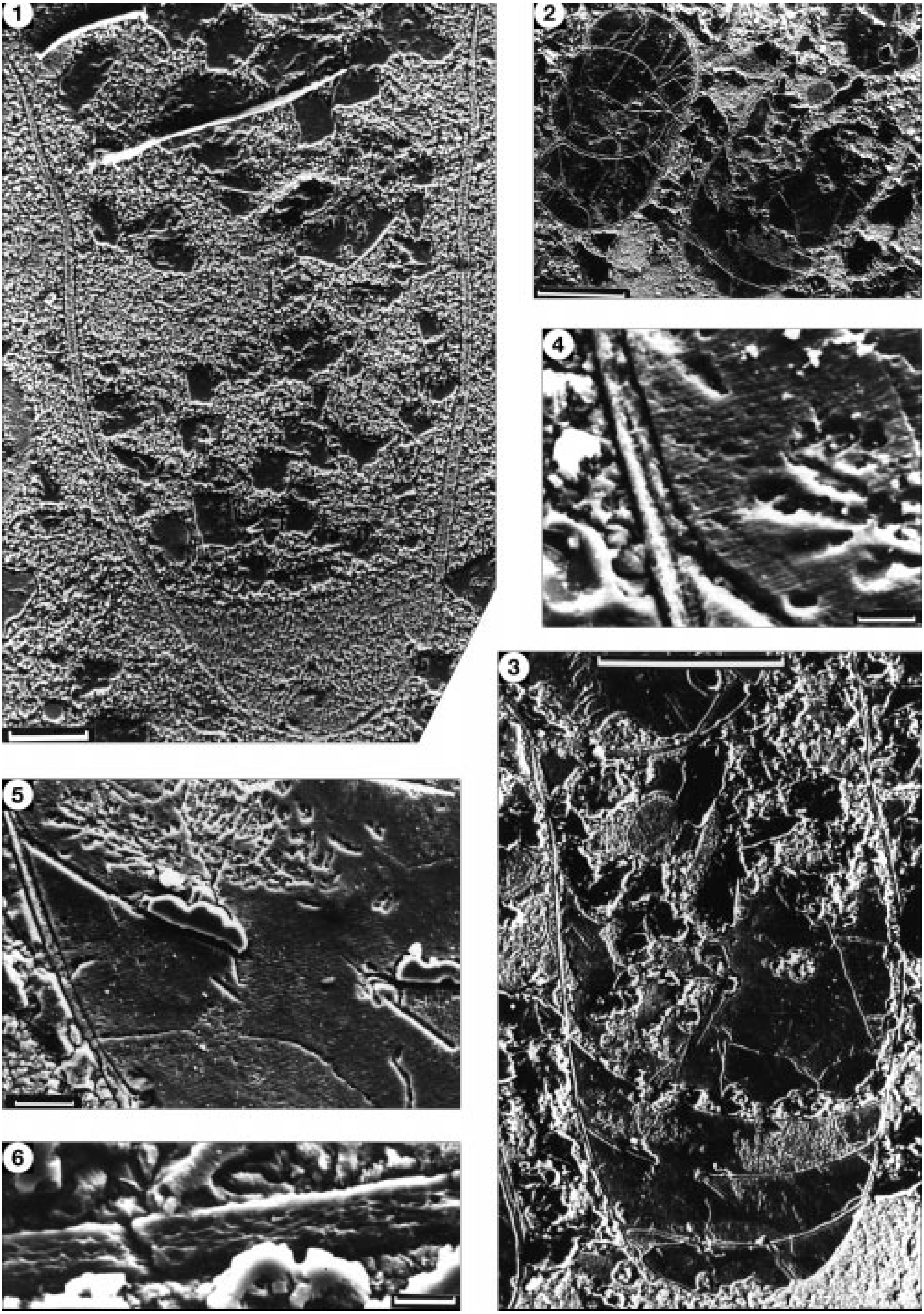
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Plate 15

Figs. 1–5: **Longitudinal sections of breviconic juvenile shells probably belonging to phragmoteuthoids.**
3871/365.
Fig. 1: Juvenile shell with cup-like protoconch, five septa and long living chamber, the primary constriction is distinct, fourth septum with wide and deep ventral lobe.
Scale bar: 0.3 mm.
Fig. 2: Prismatic shell wall near the apertural margin.
Scale bar: 0.03 mm.
Fig. 3: Prismatic shell wall of the phragmocone.
Scale bar: 0.1 mm.
Fig. 4: Enlarged phragmocone showing that the apex is not broken; the shell wall is very thin, unilayered.
Scale bar: 0.1 mm.
Fig. 5: Weakly crystallized apex showing thin inner and outer lamellae and comparatively thick, irregularly crystallized layer between them.
Scale bar: 0.01 mm.

Fig. 6: **Apical portion of juvenile, probably phragmoteuthoid shell**
consisting of cup-like protoconch, two camerae and living chamber; the shell wall is very thin.
3871/366.
Scale bar: 0.1 mm.

Creek Aidaralash, Orenburgian.

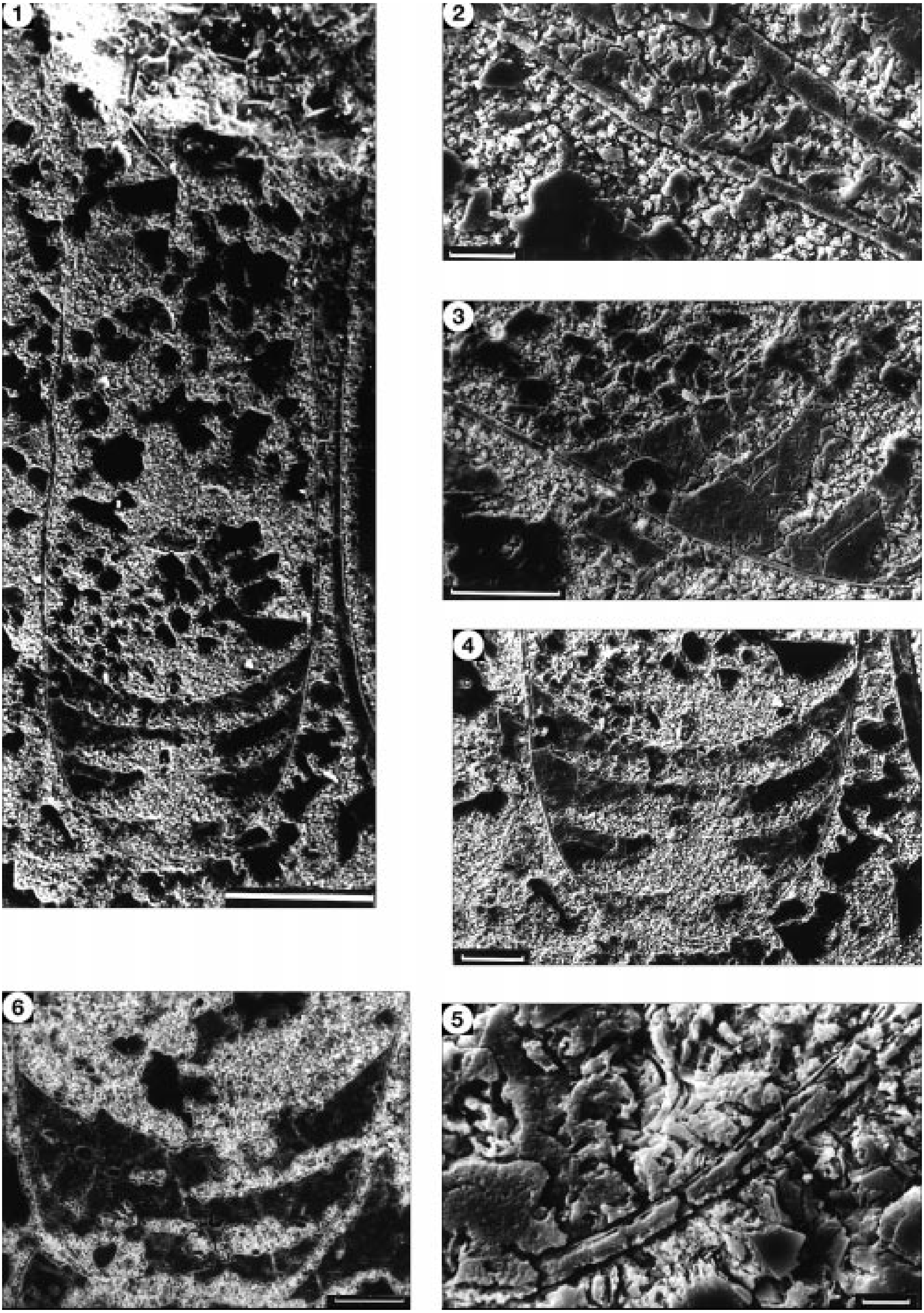
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Plate 16

Figs. 1–4: **Longitudinal sections of "embryonic" brevicones which probably belonged to phragmoteuthoids, with cup-like protoconch and very thin unilayered shell wall.**
3871/367.
Fig. 1: Protoconch, two camerae and long living chamber; margin is rather fully preserved.
Scale bar: 0.3 mm.
Fig. 2: Thin prismatic shell wall and long mural part of 3rd septum.
Scale bar: 0.03 mm.
Fig. 3: Protoconch and two camerae to show that the apex is well preserved; represents a real protoconch.
Scale bar: 0.1 mm.
Fig. 4: 1st camera with poorly preserved, short orthochoanitic septal neck and thin prismatic shell wall.
Scale bar: 0.03 mm.

Fig. 5: **Ammonitella and breviconic "embryonic" shell.**
3871/368.
Scale bar: 0.3 mm.

Fig. 6: **Thin unilayered shell wall and inclined last septum of brevicone.**
3871/368.
Scale bar: 0.3 mm.

Fig. 7: **Breviconic "embryonic" shell with cup-like protoconch, two camerae and long living chamber.**
3871/369.
Scale bar: 0.1 mm.

Creek Aidaralash, Orenburgian.

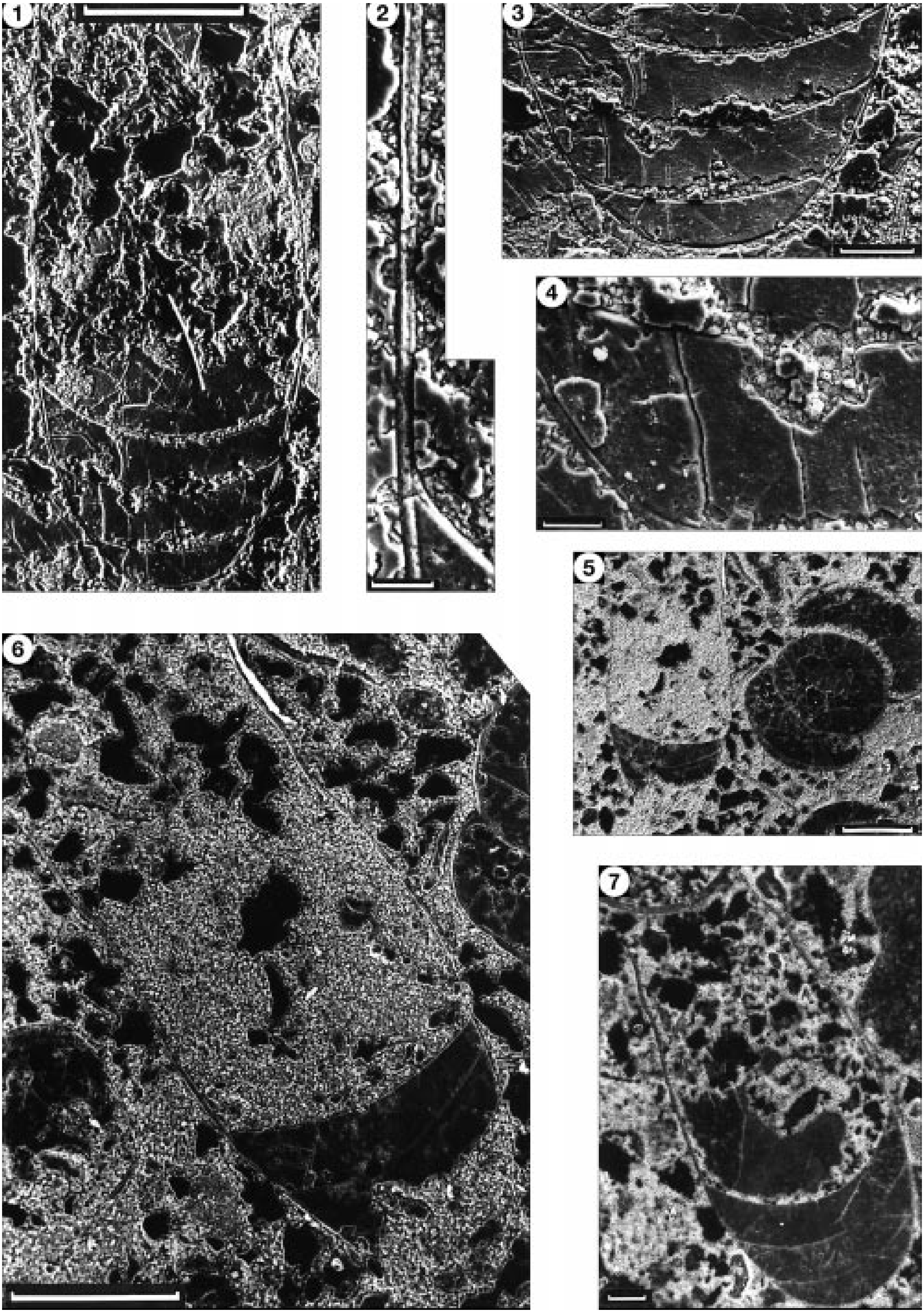
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Plate 17

Mutveiconites mirandus **gen. et sp. nov.**

Figs. 1–4: 3871/370.
Longitudinal section of the juvenile rostrum-bearing longicone with egg-like protoconch, ten camerae and long living chamber.
Fig. 1: General view.
Scale bar: 0.3 mm.
Fig. 2: Enlarged protoconch and first five or six camerae, the last septum shows traces of the septal neck indicating a marginal siphuncle (top side of the shell).
Scale bar: 0.1 mm.
Fig. 3: Rostrum showing no growth lines and irregular ultrastructure.
Scale bar: 0.1 mm.
Fig. 4: Ventral shell wall of living chamber formed by thick nacreous and thin inner prismatic layers.
Scale bar: 0.01 mm.

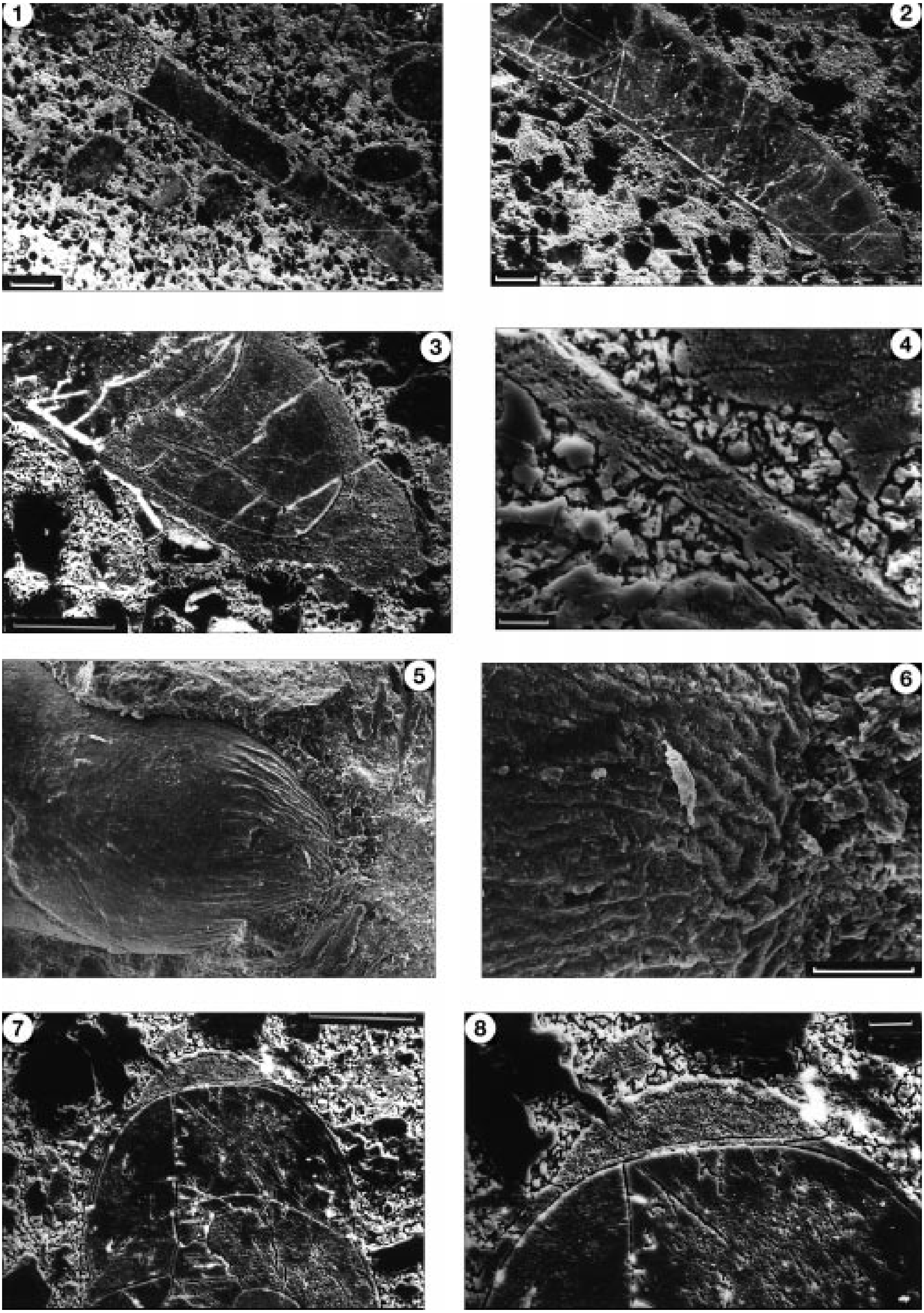
Fig. 5: 3871/371.
Elongated, asymmetrical, distinctly separated protoconch of an orthocone of unknown affinity, with deep wrinkles around apex and half of protoconch.
Scale bar: 0.1 mm.

Fig. 6: 3871/371.
Deep curved wrinkles on the apex of Fig. 5.
Scale bar: 0.01.

Fig. 7: 3871/372.
Longitudinal section of adolescent longicone bearing a hemi-spherical protoconch and short rostrum-like structure.
Scale bar: 0.1 mm.

Fig. 8: 3871/372.
Enlarged detail of Fig. 7.
Scale bar: 0.03 mm.

Creek Aidaralash, Orenburgian.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