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Orthocerid and Ammonoid Shell Structure: Its Bearing on Cephalopod Classification

By

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Abstract SEM observations on orthocerid and ammonoid shell structure are described. The systematic position of the orthocerid cephalopods, all of which in the past had often been referred to the Nautiloidea, is discussed. "Orthocerida" with a cap-shaped first chamber are referred to the superorder Pseudorthoceratoidea (subclass Nautilomorphi). "Orthocerida" with an ammonoid type of early ontogenesis are named Michelinoceratoidea (subclass Coleoidea). Trematoceratidae n. fam. is described.

Introduction

The cephalopods with a calcified chambered shell (orthocerids, nautiloids, ammonoids, and belemnoids) were abundant marine invertebrates during the Paleozoic and Mesozoic. Among the living cephalopods, they are represented as a matter of fact only by *Nautilus*, *Spirula*, and *Sepia*. But phylogenetic connections among the cephalopod groups mentioned above are not fully investigated now because of a lack of complete data on the early ontogeny and shell microstructure and embryonic shell morphology of some fossil representatives, particularly orthocerids. Corresponding information on ammonoids has been suggested by numerous workers (Birkelund, 1967, 1980; Erben, Flajs & Siehl, 1969; Druschits, Doguzhaeva & Mikhailova, 1978; Kulicki, 1979; Kulicki & Doguzhaeva, 1994; Tanabe *et al.*, 1980, 1993; Druschits & Doguzhaeva, 1981; Zakharov & Grabovskaya, 1984; Zakharov, 1986, 1989; Zakharov *et al.*, 1987; Landman & Bandel, 1985; Landman, 1988; Landman *et al.*, in press; Doguzhaeva & Mutvei, 1986a, b, 1989; and many others). But some rarely preserved ammonoid structures need to be discussed further. Data on orthocerid embryonic shells are represented only in the works of the following authors: Clarke (1893), Schindewolf (1933, 1935, 1944), Bohmers (1936), Shimansky (1948, 1954, 1962a), Balashov (1957), Mutvei (1957), Zhuravleva (1959), Shimansky & Zhuravleva (1961), Ristedt (1968), Barskov (1972, 1989), and Blind (1987). The shell microstructure of some Paleozoic orthocerids ("*Orthoceras*" sp., *Pseudorthoceras* sp., *Kingoceras* sp.) was recently investigated by BLIND (1987, 1988a, b).

A comparative study of the structure, development, and morphological relationships of *Nautilus*, *Sepia*, *Spirula*, and *Belemnoteuthis* shells was made by BANDEL and BOLETZKY (1979) and BANDEL and KULICKI (1988).

The significance of some observations on fossil and recent cephalopods (including data on morphology and anatomy of their soft parts and radula elements) for the major classification of the Cephalopoda was recently discussed by FLOWER and KUMMEL (1950), MOORE *et al.* (1952), SHIMANSKY and ZHURAVLEVA (1961), SHIMANSKY (1962b), MUTVEI (1964), TEICHERT and MOORE (1964), LEHMANN (1967, 1981, 1990), TEICHERT (1988), ZEISS (1969), ZHURAVLEVA (1972), STAROBOGATOV (1976, 1983), DZIK (1984), BERTHOLD and ENGESER (1987), ENGESER and BANDEL (1988), BARSKOV (1989), ENGESER (1990), DOGUZHAEVA (1991), and some others.

This paper is a first attempt to show the significance of the cephalopod shell structure features for higher systematics. The studies were conducted using SEM. After polishing, the specimens were treated in 1% HCl. The surface of the ammonitella shells and protoconchs from the Lower Permian of South Urals was treated in 2% acetric acid for 1.0–1.5 minutes.

Shell Microstructure of Triassic Orthocerids

Previous studies on the shell microstructure of the "Orthocerida" are based, as was mentioned above, on Paleozoic material (RISTEDT, 1971; BLIND, 1981, 1987, 1988a, b).

In this paper, I investigated the shell microstructure of Triassic orthocerids based on exceptionally well-preserved specimens of *Trematoceras* sp. cf. *T. campanile* (MOJSISOVICS) from the uppermost Lower Triassic strata (upper Olenekian, *Olenikites spiniplicatus* Zone) exposed in the Olenek River, Arctic Siberia. They were viewed under SEM and ordinary microscope (in thin sections).

My observations indicate that the outer shell wall of Triassic Trematoceras consists of three calcareous layers: (1) an outer prismatic layer, (2) a central nacreous layer, and (3) an inner prismatic layer (Plate 1, fig. 1; Fig. 1). The following microstructural description and measurements were made at a stage of about 10 mm in phragmocone diameter. The outer prismatic layer (Plate 1, figs. 1, 2) is represented by small elongate prisms oriented at an acute angle to the wall surface. Its thickness is 10 μm. The central nacreous layer, 70 μm thick, partly recrystallized, consists of numerous, very delicate lamellae that are arranged in series of rows (Plate 1, fig. 2). The inner layer, 10 μm thick, is composed of short, irregularly oriented prisms (Plate 1, fig. 1).

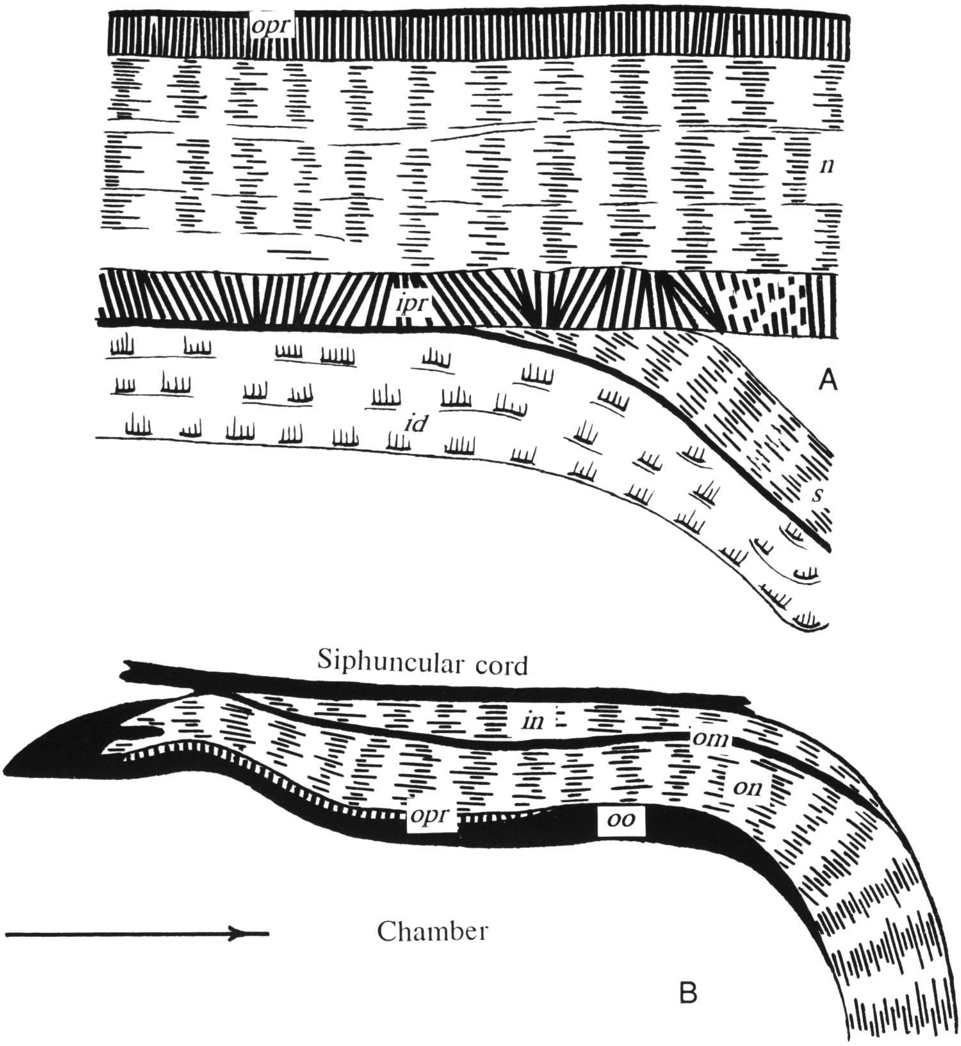

Fig. 1. Shell structure in *Trematoceras* sp. cf. *T. campanile* (MOJSISOVICS). A, Shell wall and septum structure, opr: outer prismatic layer, n: nacreous layer, ipr: inner prismatic layer, id: intracameral deposits; B, Septal neck structure, oo: outer organic layer, opr: outer prismatic layer, on: outer nacreous sub-layer of the nacreous layer, in: inner nacreous sub-layer of the nacreous layer with organic membrane (om) between them. An arrow indicates the adoral direction.

The septa in their central parts usually consist of a single (nacreous) layer (Plate 1, fig. 3; Plate 2, figs. 1, 5, 6). The thickness of the septa in these places reaches 30 μm. In Plate 2, fig. 2, within the nacreous layer, one can recognize the organic membrane (om) and prismatic sublayer (pr).

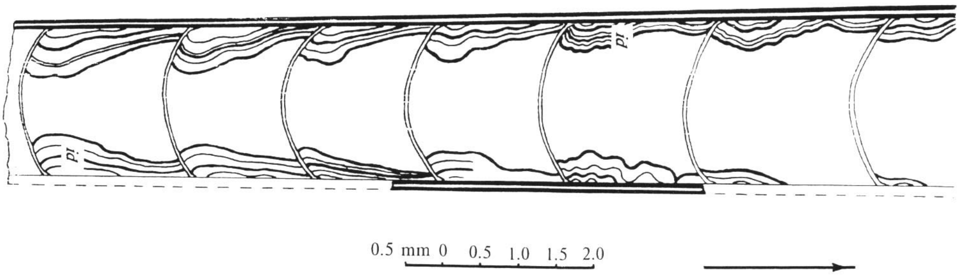

Fig. 2. Phragmocone of *Trematoceras* sp. cf. *T. campanile* (MOJSISOVICS) with seven chambers, as well as the corresponding intracameral deposits (id). NSM PM15980.

Within the septal necks of Triassic *Trematoceras*, four organic and calcareous layers and sublayers are recognized: 1) the outer organic layer (8 μm thick), 2) the outer prismatic layer (1 μm), 3) the outer nacreous sublayer of the nacreous layer (28 μm thick), which is separated from the outer prismatic layer by a conspicuous organic membrane, and 4) the inner nacreous sublayer of the nacreous layer (9 μm thick), which is separated from the outer nacreous sublayer by another conspicuous organic membrane (Plate 2, figs. 3, 4; Fig. 1). The inner prismatic layer that was encountered in Paleozoic "*Orthoceras*", *Pseudorthoceras*, and *Kionoceras* seems to be missing in Triassic orthocerids.

The cameral deposits (Plate 1, fig. 2; Fig. 2) which were presumably secreted during the animal's lifetime, occur on all sides of the camerae, showing bilaterally symmetrical distributions. The amount of the deposits within each camera tends to decrease toward to the aperture, and this observation seems to support the previous interpretation that a living orthocerid had a nektobentic mode of life while maintaining its shell in a horizontal position (BLIND, 1991).

Some Rarely Preserved Structures in Ammonoids

Adventitious layers of the septa: Ammonoidea are usually characterized by single-layered (nacreous) septa. But it is very likely that some rare, well-preserved Mesozoic ammonoids retain a composite structure in their septa (BIRKELUND, 1967; BIRKELUND& HANSEN, 1968; TANABE *et al.*, 1982). Additional calcareous elements of the septa were also recognized in Late Cretaceous *Zelandites japonicus* MATSUMOTO from the Maastrichtian of the Naiba River in Sakhalin Island (ZAKHAROV & GRABOVSKAYA, 1984). The first additional lens-formed layer was recognized in the central part of the distal surface of the septa in the outer (IV–VI) whorls of the shell (Plate 5, figs. 1–3). It covers about 60% of the septal surface. It is made up of calcareous material showing the prismatic structure; hence it was called a prismatic layer. It consists of tall prisms oriented at a right angle to the septal surface and located just on the prolongation of the lamellar rows of the nacreous layer. The maximum thickness of this layer at the end of the fifth whorl is 20 μm making up about 30% of the total thickness of the septum.

There is another adventitious calcareous layer on the distal surface of the *Zelandites* septa (distal nacreous layer) (Plate 5, figs. 2, 3). It is represented by short lenses overlying the prismatic layer, showing a prominent relief on the septal surface. At the end of the fifth whorl, the lenses measure 80 μm in length and 10 μm in thickness, about 14% of the total thickness of the septum.

The adventitious structural elements of the septum also have been discovered in some Triassic ammonoids (ZAKHAROV, 1986). The septa of *Prosphingites czekanovskii* MOJSISOVICS from the upper Olenekian (Lower Triassic) in the Olenek River are generally nacreous. But within the seventh whorl of the shell, there are lens-shaped prismatic layers about 110 μm in length and 8 μm thick that have been discovered at the place of transition to the septal necks (proximal side) (Plate 5, figs. 4, 5). A similar prismatic layer on the proximal side of the septa has also been recognized in Anisian *Parapopanoceras* and *Stenopopanoceras* from Arctic Siberia (ARKADIEV & VAVILOV, 1984) both of which are direct descendants of *Prosphingites.* ARKADIEV and VAVILOV (1984) called this prismatic septal layer a septal cover, without any microstructural description.

The nacreous layer of septa in the majority of ammonoid groups and the proximal nacreous layer in Cretaceous *Zelandites* seem to be homologous with that in Recent *Nautilus.* The prismatic layer in Cretaceous *Hypophylloceras* (*Neophylloceras*) can be correlated with the semi-prismatic layer of the septa in Recent *Nautilus.* The lenses of the distal nacreous layer in *Zelandites* do not have any homologies in recent cephalopods. Taking into account the small size of these structures, which have a prominent relief on the distal surface of the septum, they seem to be connected with attachment muscles.

The nature of the septal prismatic cover (septal prismatic zone of TANABE *et al.*, 1982; element of associated structures of TANABE *et al.*, pers. com.) in Triassic *Prosphingites*, *Parapopanoceras*, *Stenopopanoceras* and Jurassic *Eleganticeras* is not clear. It is very difficult to decide whether the septal prismatic cover is homologous with the spherulitic-prismatic layer in the septum of Recent *Nautilus.* This question cannot be resolved without special investigation. At the same time this structure differs from the cuff and auxiliary deposit (DRUSCHITS & DOGUZHAEVA, 1981) and by its position on both the septum and septal neck.

In my opinion (ZAKHAROV, 1984b), ontogenetic acceleration in ammonoid evolution is reflected, as a rule, in changes in both morphology and microstructure of the shell; the latter seems to be evident in change on a cytological level.

Caecum veins: Both the caecum and prosiphon, which were originally made of organic material are commonly observed in all ammonoids, some orthocerids, *Spirula* and *Groenlandibelus*, whereas they are absent in nautilid and belemnitid cephalopods. Detailed investigations indicate that the caecum of some ammonoids has a complicated structure (ZAKHAROV, 1972, 1984a; ZAKHAROV & GRABOVSKAYA, 1984; TANABE *et al.*, 1980; DRUSCHITS & DOGUZHAEVA, 1981; LANDMAN & BANDEL, 1985) including caecum veins (Plate 6, figs. 1–4), which were usually connected with a prosiphon and a pore system (Plate 6, figs. 1, 2). The caecum veins were recognized on the surface of the inner cover of the caecum in Permian *Neopronorites* from South Urals. The pores in the inner caecum covering (folded membrane) have been discovered in Permian Artioceras from South Urals (Plate 6, fig. 6).

Wrinkle layer: This cephalopod (ammonoid) feature may be an important systematic characteristic, but there are questions about its original microstructure. The wrinkle layer has been reliably established only in the dorsal wall (Plate 3, figs. 2–6; Plate 4, figs. 1–6), where it can be easily recognized because of its original sharp-edged ridges in transversal section and its position between the outer prismatic layer of the previous whorl and the inner prismatic layer. In *Zelandites* (ZAKHAROV & GRABOVSKAYA, 1984) and *Phyllocladiscites* (DOGUZHAEVA & MUTVEI, 1986b) the latter consists of two modifications (sub-layers) in median section: an outer sub-layer and an inner sub-layer. In the outer sub-layer of the inner prismatic layer, the crystallites are rather irregular, small, more or less isometric; the inner sub-layer is composed of coarse, more or less vertical prisms and has a greater thickness than the wrinkle layer or outer sub-layer (Plate 3, figs. 1–6; Plate 4, figs. 3, 5, 6). In some places the sub-layers have a sharp boundary between them (Plate 4, fig. 6). The wrinkle layer seems to be originally organic. According to ZAKHAROV and GRABOVSKAYA (1984), in Late Cretaceous *Zelandites* from Sakhalin Island the dark brown wrinkle layer has aconspicuous lamellar structure (it consists of, apparently, conchiolin membranes and diagenetically altered fragments) (Plate 2, fig. 1). (More or less similar structures were discovered by VOSS-FOUCART and GREGOIRE (1971) in conchiolin matrices of some fossil cephalopods). The latter does not agree with previous observations on Triassic *Megaphyllites* from the Caucasus (DOGUZHAEVA, 1981; DOGUZHAEVA & MUTVEI, 1986b). Its wrinkle layer with prismatic structure (DOGUZHAEVA & MUTVEI, 1986b) seems to be significantly altered diagenetically.

Conclusion

Several outstanding points of view on the systematic position of orthocerid cephalopods can be distinguished (Table 1). The recent data on early ontogenesis show that Orthocerida are clearly polyphyletic (not a natural unit) (RISTEDT, 1968; ENGESER, 1990). One stock of this group, pseudorthocerid cephalopods—superorder Pseudorthoceratoidea BARSKOV, characterized by a nautiloid type of early ontogenesis (nauta and seminauta types in the sense of SHIMANSKY (1962a), "B1" and "B2" modes of RISTEDT (1968), and the first structural type in the sense of BARSKOV (1989) must be naturally retained within the subclass Nautilomorphi AGASSIZ. Another orthocerid stock with ammonoid type of early ontogenesis (nautella type in the sense of SHIMANSKY (1962a), "A" mode of RISTEDT (1968) and the second structural type in BARSKOV (1989), which I suggest naming Michelinoceratoidea FLOWER, which must be excluded from the Nautilomorphi into the subclass Coleoidea BATHER.

At present we have information on shell microstructure only for orthcerids with a cap-shaped first chamber (nautiloid type of early ontogenesis): "*Orthoceras*" sp., *Pseudorthoceras* sp., *Kinoceras* sp., and *Trematoceras* sp.). BLIND's (1988 b) "*Orthoceras*" sp. from the Buckhorn-Asphalt of Oklahoma is indeed characterized by the cap-shaped first chamber. However it does not agree with data on *Orthoceras* from the type region for the type species of this genus (BALASHOV (1957) reported a spherical first chamber for *Orthoceras* sp. from the Ordovician of Estonia). The truth is that the early ontogenetical stage in the typical Orthoceratinae is still poorly known; at present it is difficult to determine their systematic position.

As already mentioned, Paleozoic and early Mesozoic orthocerids with a large embryonic shell and a cap-shaped first chamber, as well as Recent Nautilus (subclass Nautilomorphi) have triple- or double-layered septal necks, which is in contrast to single layered septal necks in most ammonoids (subclass Coleoidea), characterized by a small embryonic shell and a spherical protoconch and some other features. It can be generally accepted that there is a connection between the type of early ontogenesis and the character of shell microstructure in the Cephalopoda. Data on orthocerid shell structure seem to be important for higher systematics.

In contrast to the Paleozoic Pseudorthoceratoidea, the septal necks for the early Mesozoic ones (*Trematoceras*) are characterized by lacking the inner prismatic layer and reduction of the outer prismatic layer. These features can be considered as diagnostic ones at a family level.

Systematic Palaeontology

Class Cephalopoda CUVIER, 1797

Subclass Nautilomorphi AGASSIZ, 1847

Superorder Pseudorthoceratoidea BARSKOV, 1963

Diagnosis: Orthocerids with large embryonic shell, cap-shaped first chamber, nautiloid type of shell structure in early ontogenesis, triple- or double-layered septal necks in adult stage. A siphuncle is subcentral or central in position, with

Table 1. Major classifications

BATHER in FLOWER & KUMMEL (1950), SHIMANSKY (1962a)	MOORE, LALICKER & FISCHER (1952)	SHIMANSKY (1962), KRYMGOLZ (1958)	TEICHERT & MOORE (1964)
Order Nautiloidea	Subclass Nautiloidea: Ellesmeroceratida, Endoceratida, Actinoceratida, Michelinoceratida, Ascoceratida, Oncoceratida, Discosorida, Nautilida	Subclass Ectocochlia: Nautiloidea (Volborthellida, Ellesmeroceratida, Tarphyceratida, Orthocerida, Ascoceratida, Discosorida, Oncoceratida, Nautilida), Endoceratoidea, Actinoceratoidea, Bactritoidea, Ammonoidea	Subclass Nautiloidea: Ellesmerocerida, Orthocerida, Ascocerida, Tarphycerida, Barrandeocerida, Oncocerida, Discosorida, Nautilida
			Subclass Endoceratoidea
			Subclass Actinoceratoidea
			Subclass Bactritoidea
Order Ammonoidea	Subclass Ammonoidea		Subclass Ammonoidea
Order Coleoidea	Subclass Dibranchia	Subclass Endocochlia: Decapoda, Octopoda	Subclass Coleoidea

of the class Cepholopoda.

<table>
<tr><th>MUTVEI (1964)</th><th>LEHMANN (1967)</th><th>TEICHERT (1967, 1988)</th><th>ZEISS (1969)</th></tr>
<tr><td rowspan="2">Subclass? Orthoceratomorphi</td><td rowspan="4">Subclass Lateradulata</td><td>Subclass Orthoceratoidea: Ellesmerocerida, Orthocerida, Ascocerida</td><td rowspan="4">Subclass Nautiloidea: Ectocochlia (Nautilida)</td></tr>
<tr><td>Subclass Actinoceratoidea</td></tr>
<tr><td>Subclass? Oncoceratomorphi</td><td>Subclass Endoceratoidea</td></tr>
<tr><td>Subclass? Nautilomorphi</td><td>Subclass Nautiloidea (Discosorida, Oncocerida, Tarphycerida, Nautilida)</td></tr>
<tr><td>Subclass? Ammonoidea</td><td rowspan="3">Subclass Angusteradulata</td><td>Subclass Bactritoidea</td><td rowspan="3">Subclass Coleoidea: Eucochlia (Orthocerida, Actinocerida Endocerida, Bactritida, Ammonitida), Endocochlia (Aulacocerida, Fragmoteuthida, Belemnitida, Teuthida, Octopodida, Sepiida)</td></tr>
<tr><td rowspan="2">Subclass? Coleoidea</td><td>Subclass Ammonoidea</td></tr>
<tr><td>Subclass Coleoidea</td></tr>
</table>

Table 1.

ZHURAVLEVA (1972)	STAROBOGATOV (1976)	STAROBOGATOV (1983)	DZIK (1984)
Subclass Nautiloda: Nautiloidea (Plectronoceratida, Discosorida, Oncoceratida, Tarphyceratida, Nautilida)	Subclass Actinoceratea: Ellesmeroceratida, Endoceratida, Actinoceratida, Orthoceratida, Pseudorthoceratida, Ascoceratida, Plectronoceratida, Discosorida, Oncoceratida, Intejoceratida, Dissidoceratida Subclass Nautilea: Tarphyceratida, Nautilida	Subclass Actinocerationes: Tarphyceratiformii, Oncoceratiformii Actinoceratiformii Subclass Endocerationes: Orthoceratiformii, Endoceratiformii Subclass Nautiliones: Barrandeocratiformes, Nautiliformes	Subclass Nautiloidea: Endoceratida, Tarphyceratida, Orthoceratida, Discosorida, Oncoceratida, Nautilida
Subclass Orthoceroda: Orthoceratoidea, Endoceratoidea, Actinoceratoidea, Bactritoidea, Ammonoidea, Coleoidea	Subclass Ammonea Subclass Teuthea	Subclass Bactritiones: Bactritiformii, Ceratitiformii Subclass Ostopodiones: Sepiiformii, Octopodiformii	

(continued).

ENGESER & BANDEL (1988)	ENGESER (1990)	DOGUZHAEVA (1991)	This paper
Subclass Nautiloidea	Subclass Nautiloidea: ? Ellesmerocerida, Endocerida, Actinocerida, Tarphycerida, "Orthocerida"		Subclass Nautilomorphi (or Nautiloda): Endoceratoidea, Actinoceratoidea, Pseudorthoceratoidea, Nautiloidea
Subclass Coleoidea: Ammonoidea, Belemnoidea, Vampyromorphoidea, Decapoda	Subclass Neocephalopoda: "Orthocerida", Ascocerida, Bactritida, Ammonoidea, Ascocerida, Coleoidea	Subclass Orthoceroda: Ellesmeroceratoidea, Endoceratoidea, Actinoceratoidea, Orthoceratoidea, Bactritoceratoidea, Ammonoidea, (including Octopodida)	Subclass Coleoidea: Michelinoceratoidea, Ascoceratoidea, Bactritoidea, Ammonoidea, Belemnoidea, Vampyromorphoidea, Decapodoidea

various kinds of intracameral deposits.

Composition: One order: Pseudorthocerida BARSKOV (Pseudorthoceratidae FLOWER and CASTER, Kionoceratidae HYATT, Trematoceratidae, fam. n., Pseudactinoceratidae SCHINDEWOLF, ?Proteoceratidae FLOWER, ?Groenlandoceratidae SHIMIZU and OBATA, ?Paraphragmitidae FLOWER, Clinoceratidae FLOWER.

Distribution: Ordovician-Triassic.

Family Trematoceratidae, new family

Diagnosis: Pseudorthocerids with a central siphuncle and intermediate nautiloid-ammonoid structural type of septal neck, characterized by lacking the inner prismatic layer and reduction of the outer prismatic layer.

Subclass Coleoidea BATHER, 1888

Superorder Michelinoceratoidea FLOWER, 1945

Diagnosis: Orthocerids tending to have a small embryonic shell, isolated spherical protoconch, central or subcentral siphuncle, narrow radula (no more than 9 teeth in every transverse row), and not over 10 arms.

Composition: One? order: Michelinocerida FLOWER (Michelinoceratinae FLOWER, ?Orthoceratinae M'COY, Sphaerorthoceratinae RISTEDT, Shikhanoceratidae SHIMANSKY, ?Geisonoceratidae ZHURAVLEVA, ?Sactorthoceratidae FLOWER, ?Lamellorthoceratidae TEICHERT.

Remarks: Now we have more complete information (including data on a soft body and jaw apparatus) (ZEISS, 1969; MEHL, 1984) on Michelinoceratinae than on a Orthoceratinae. Because of a contradictory point of view on early ontogenesis of Orthoceratinae (SCHINDEWOLF, 1933; BALASHOV, 1957; BLIND, 1988b), we can not reliably include it in the coleoid orthocerid group.

Distribution: Ordovician-Permian.

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Explanation of Plates

Plate 1

Figs. 1–3. Shell wall structures in adult *Trematoceras* sp. cf. *T. campanile* (MOJSISOVICS) from the upper Olenekian (*Olenikites spiniplicatus* Zone) in the Olenek River, Mengilyakh Spring, Arctic Siberia. Y. D. ZAKHAROV coll. in 1967.

Fig. 1. Three layers of the shell wall: the outer prismatic layer (opr), the nacreous layer (n), and the inner prismatic layer (ipr). At the lower part of the picture, one can see the intracameral deposits (id) of the shell wall and septum (s). An arrow indicates the adoral direction. ×439. Specimen 1123 (DVGI 900/802) from loc. 221.

Fig. 2. The outer prismatic (opr) and the nacreous (n) layer of the shell wall. ×1422. Specimen 1124 (DVGI 33/802) from loc. 221.

Fig. 3. The nacreous layer (n) of the shell wall. ×715. Specimen 1085 (DVGI 901/802) from loc. 221.

Plate 2

Figs. 1–6. Septum and shell wall structures in adult *Trematoceras* sp. cf. *T. campanile* (MOJSISOVICS). Arrows indicate the adoral direction.

Fig. 1. The nacreous layer (n) in the central portion of the septum. ×1580. Specimen 1085 (DVGI 903/802) from loc. 221.

Fig. 2. The nacreous layer (nac) with a conspicuous organic mebrane (om) and a prismatic sublayer (pr) of secondary(?) origin in the central part of the septum. ×2380. Specimen 1195 (DVGI 904/802) from loc. 221.

Fig. 3. Septal neck. ×476. Specimen 1085 (DVGI 903/802) from loc. 221.

Fig. 4. Part of Fig. 3, showing the outer organic layer (oo), the outer prismatic layer (opr), the outer nacreous sublayer of the nacreous layer (on), and the inner nacreous sublayer of the nacreous layer (in) with organic membranes (om), ×1580.

Fig. 5. The nacreous layer (n) of the shell wall. ×2380. Specimen 1195 (DVGI 903/802) from loc. 221.

Fig. 6. The nacreous layer (n) in the central part of septum. ×794. Specimen 1195 (DVGI 903/802) from loc. 221.

Plate 3

Figs. 1–6. Wrinkle layer and its position in the shell wall of *Zelandites japonicus* MATSUMOTO from the Lower Krasnoyarka Suite (lower Maastrichtian) of the Naiba River, Sakhalin Island. Y. D. ZAKHAROV and V. S. GRABOVSKAYA coll. in 1976.

Fig. 1. Median section of the shell wall in the 2nd–3rd whorls without a wrinkle layer. ×1580. ipr: inner prismatic layer, n: nacreous layer, opr: outer prismatic layer in the 2nd whorl, o.ipr, i.ipr: outer and inner sub-layers of the inner prismatic layer in the 3rd whorl.

Fig. 2. Median section of the shell wall at the beginning of the 3rd and 4th whorls to show the appearence of the wrinkle layer. ×1422. ipr: inner prismatic layer, n: nacreous layer, opr: outer prismatic layer in the 3rd whorl, wr: wrinkle layer, o.ipr, i.ipr: outer and inner sub-layers of the inner prismatic layer in the 4th whorl.

Fig. 3. Median section of the shell wall and septum in the 3rd and 4th whorls to show the outer prismatic layer with distinct transverse undulations in the 3rd whorl. ×1580. The designation of the layers as in Fig. 2.

Fig. 4. Median section of the shell wall at the end of the 3rd and 4th whorls. ×790. The designation of the layers as in Fig. 2.
Fig. 5. Median section of the shell wall at the middle of the 3th and 4th whorls. ×1580. The designation of the layers as in Fig. 2.
Fig. 6. Median section of the shell wall at the end of the 3rd and 4th whorls. ×948. The designation of the layers as in Fig. 2.

Plate 4

Figs. 1–6. Structure and position of the wrinkle layer in the shell wall in the 4th and 5th whorls of *Zelandites japonicus* MATSUMOTO from the Lower Krasnoyarka Suite (lower Maastrichtian) of the Naiba River, Sakhalin Island. Y. D. ZAKHAROV and V. S. GRABOVSKAYA coll. in 1976. Specimen 5 (DVGI 952) from loc. 12.
Fig. 1. The lamellar structure of the dark brown wrinkle layer. ×5000. n: nacreous layer, opr: outer prismatic layer in the 4th whorl, wr: wrinkle layer, o.ipr: outer sub-layer of the inner prismatic layer in the 5th whorl.
Fig. 2. The configuration of the sharp-edged ridge of the wrinkle layer. ×5000. Adoral direction is from right to left.
Fig. 3. The thick inner sub-layer of the inner prismatic layer. ×812. Designation of the layers as in Fig. 1.
Fig. 4. The undetermined structure of the wrinkle layer between its ridges. ×1422. ipr: inner prismatic layer, n: nacreous layer, opr: outer prismatic layer in the 4th whorl, wr: wrinkle layer, o.ipr: outer sub-layer of the inner prismatic layer in the 5th whorl.
Fig. 5. Median section of the shell wall. ×1160. Designation of the layers as in Fig. 1.
Fig. 6. The existence of the boundary between the outer and inner sub-layers of the inner prismatic layer in the 6th whorl. ×237. Ipr: inner prismatic layer, n: nacreous layer, opr: outer prismatic layer, o.ipr and i.ipr: outer and inner prismatic sub-layers of the inner prismatic layer in the 6th whorl.

Plate 5

Figs. 1–8. Median section of the septa to show the presence of the adventitious calcareous layers in some Triassic and Cretaceous ammonoids.
Fig. 1. *Zelandites japonicus* MATSUMOTO, 60th septum, NSM PM15979, the proximal nacreous (pn) and prismatic (pr) layers. ×474. Sakhalin Island, Naiba River; Lower Krasnoyarka Suite (lower Maastrichtian). Y. D. ZAKHAROV and V. S. GRABOVSKAYA coll. in 1976 (specimen 5 from loc. 12).
Fig. 2. *Zelandites japonicus* MATSUMOTO, 62nd septum consisting of the proximal nacreous (pn), prismatic (pr), and distal nacreous (dn) layers. ×396. Same specimen as in Fig. 1.
Fig. 3. *Zelandites japonicus* MATSUMOTO, 59th septum consisting of the proximal nacreous, prismatic and distal nacreous layers. ×396. Designation of the layers as in 2. Same specimen as in Fig. 1.
Fig. 4. *Prosphingites czekanovskii* MOJSISOVICS, 7th whorl, septal neck, DVGI 353/802, the septal prismatic cover (sp) and nacreous layer (n). ×790. The arrow indicates the adoral direction. Arctic Siberia, Olenek River, Mengilyakh Creek; Olenekian, *Olenikites spiniplicatus* Zone. Y. D. ZAKHAROV coll. in 1967 (specimen 22 from loc. 221).
Fig. 5. Part of Fig. 4 (septal bend). ×2370.
Fig. 6. *Gymnotoceras reteliforme* (MEEK), DVGI 5/816. Median section of the septal neck to show the absence of the adventitious prismatic elements in this ammonoid. ×237. Taimyr, Keshin Spring; Anisian. M. N. VAVILOV coll., apparently, in 1980.

Figs. 7, 8. Parts of Fig. 6. The outer nacreous sub-layer (on) (=the cuff accordng to DRUSCHITS and DOGUZHAEVA's (1987) terminology) and the inner nacreous sub-layer (in) of the nacreous layer. ×474 (7), ×790 (8).

Plate 6

Figs. 1–6. Caecum veins and pore system in Paleozoic ammonoids.

Figs. 1, 2. *Neopronorites skvorzovi* (TCHERNOW), DVGI 45/811, prosiphon (p) and caecum veins (cv) on the surface of the inner cover of the caecum. ×230 (1 and 2). South Urals, Aktasty River; Artinskian. Y. D. ZAKHAROV coll. in 1975 (specimen 6 from loc. 306).

Figs. 3, 4. Same specimen as in Figs. 1, 2. Caecum veins on the surface of the inner cover of the caecum. ×1400 (3), ×1900 (4).

Fig. 5. *Artioceras rhipaeum* (RUZHENCEV), DVGI 47/811, inner surface of the inner caecum covering (folded membrane). ×750. South Urals, Aktasty River; Artinskian. Y. D. ZAKHAROV coll. in 1975 (specimen 1 from loc. 307).

Fig. 6. *Neopronorittes skvorzovi* (TCHERNOW), DVGI 45/811, inner surface of the inner caecum covering (folded membrane) to show pores. ×2800. South Urals, Aktasty River; Artinskian. Y. D. ZAKHAROV coll. in 1975 (specimen 6 from loc. 306).

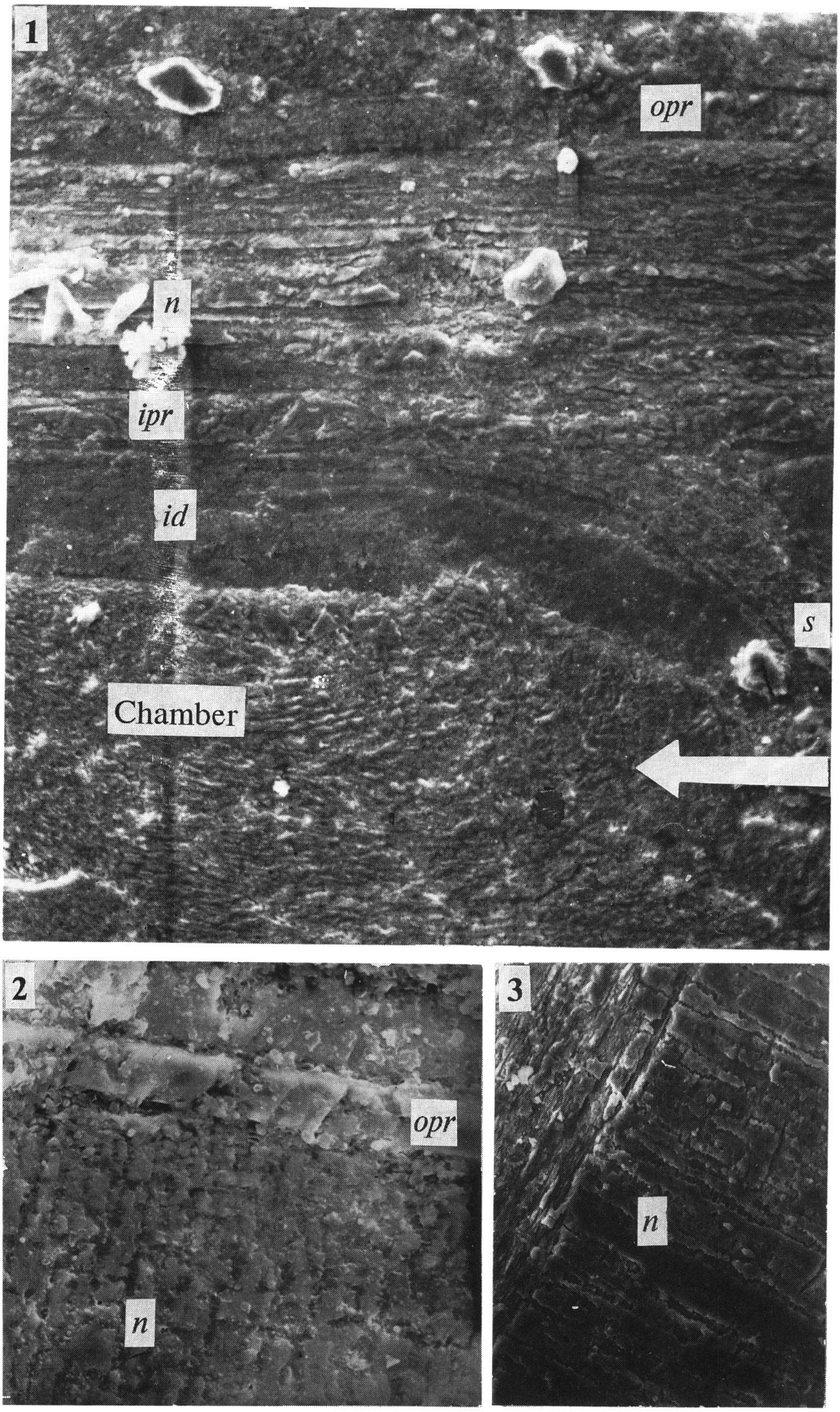

Plate 1

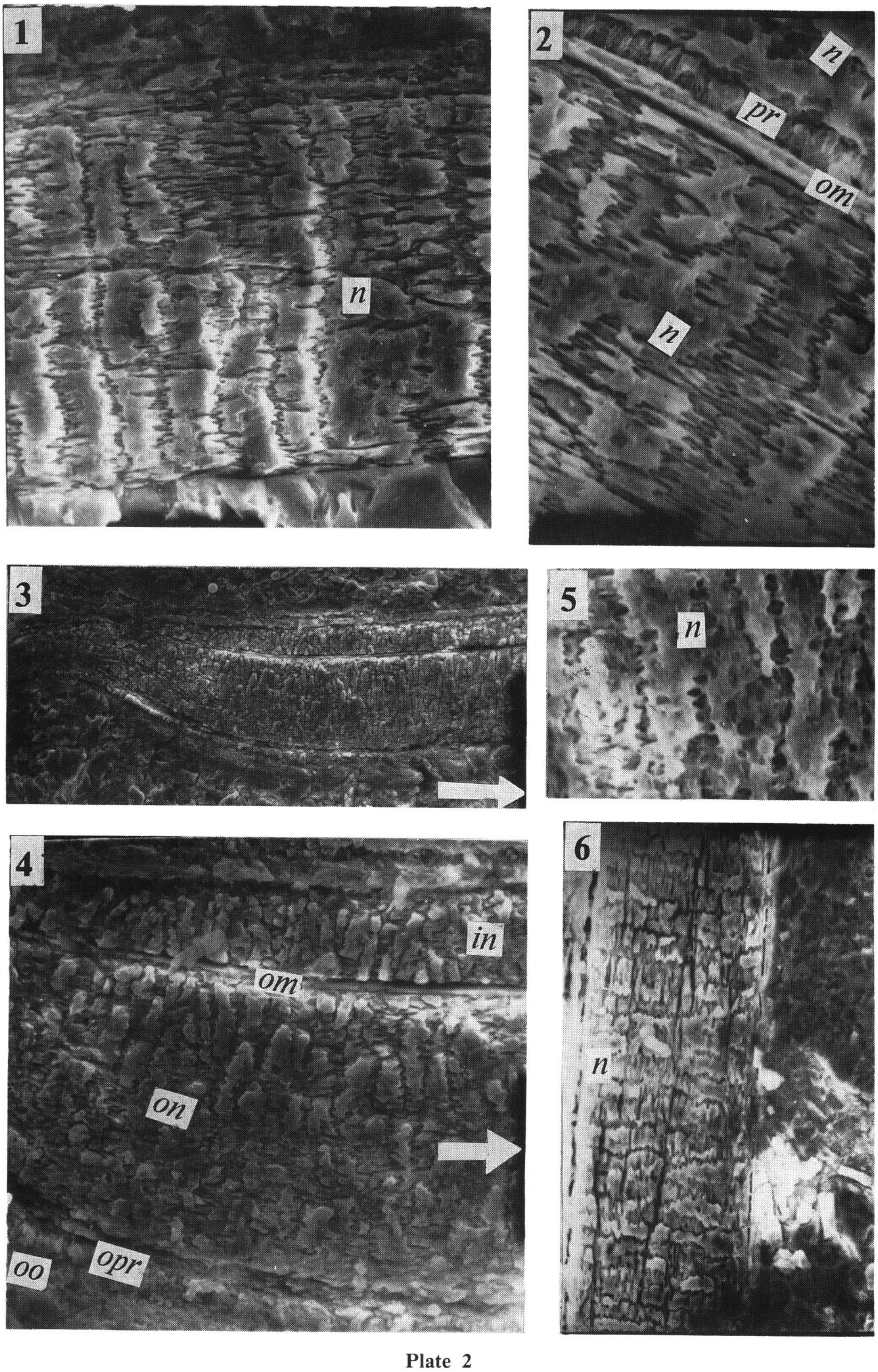

Plate 2

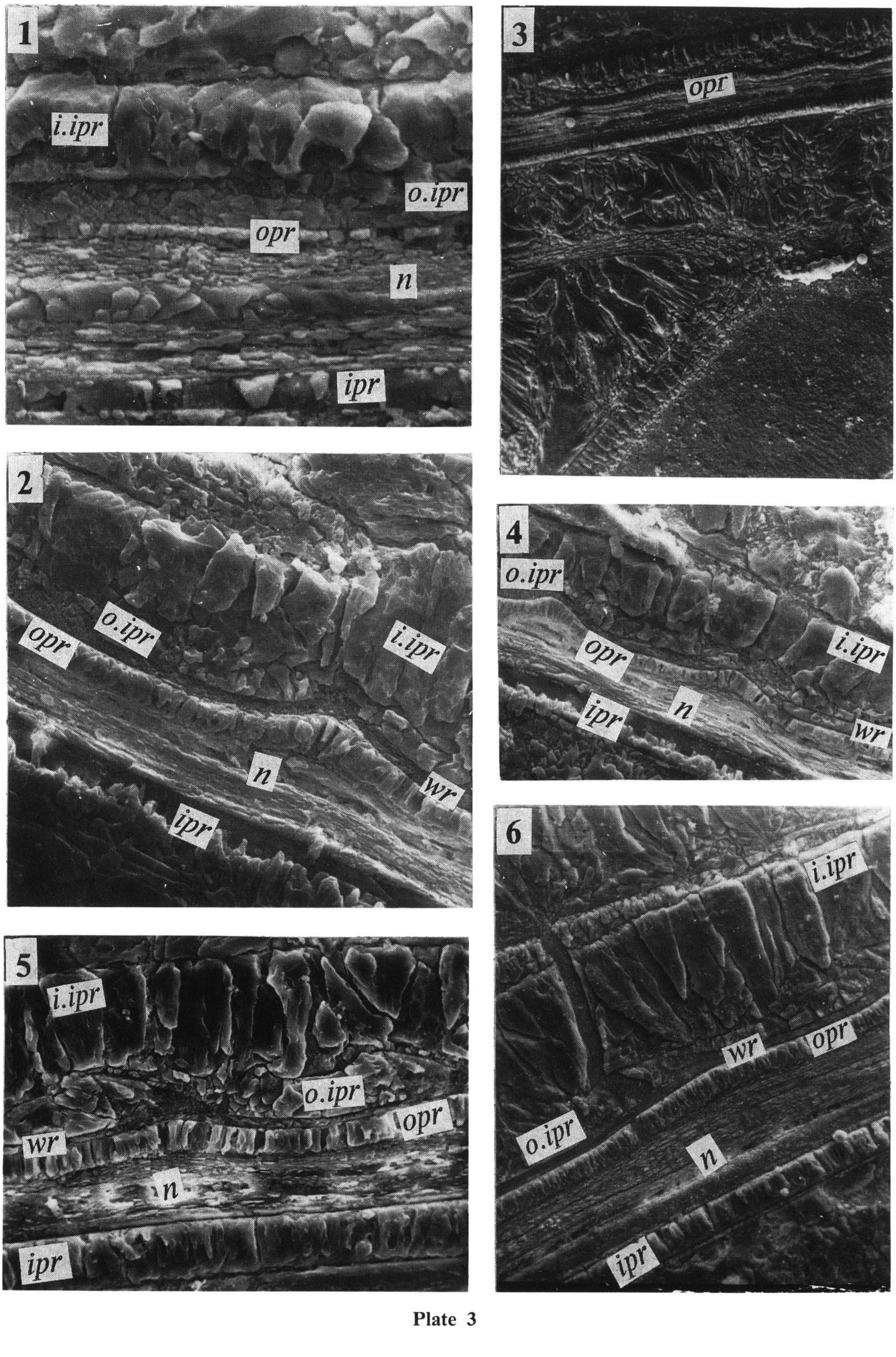
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Plate 3

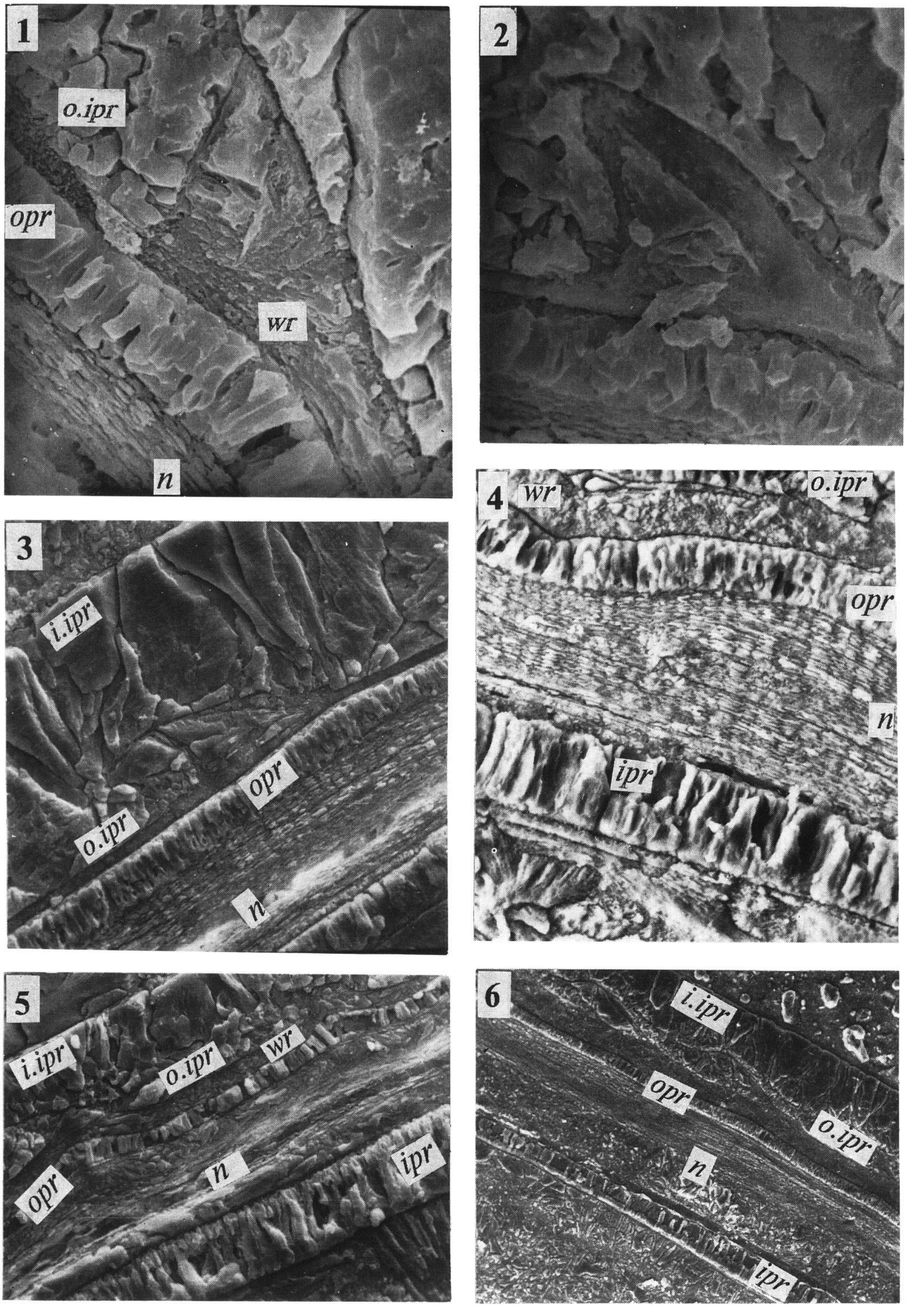
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Plate 4

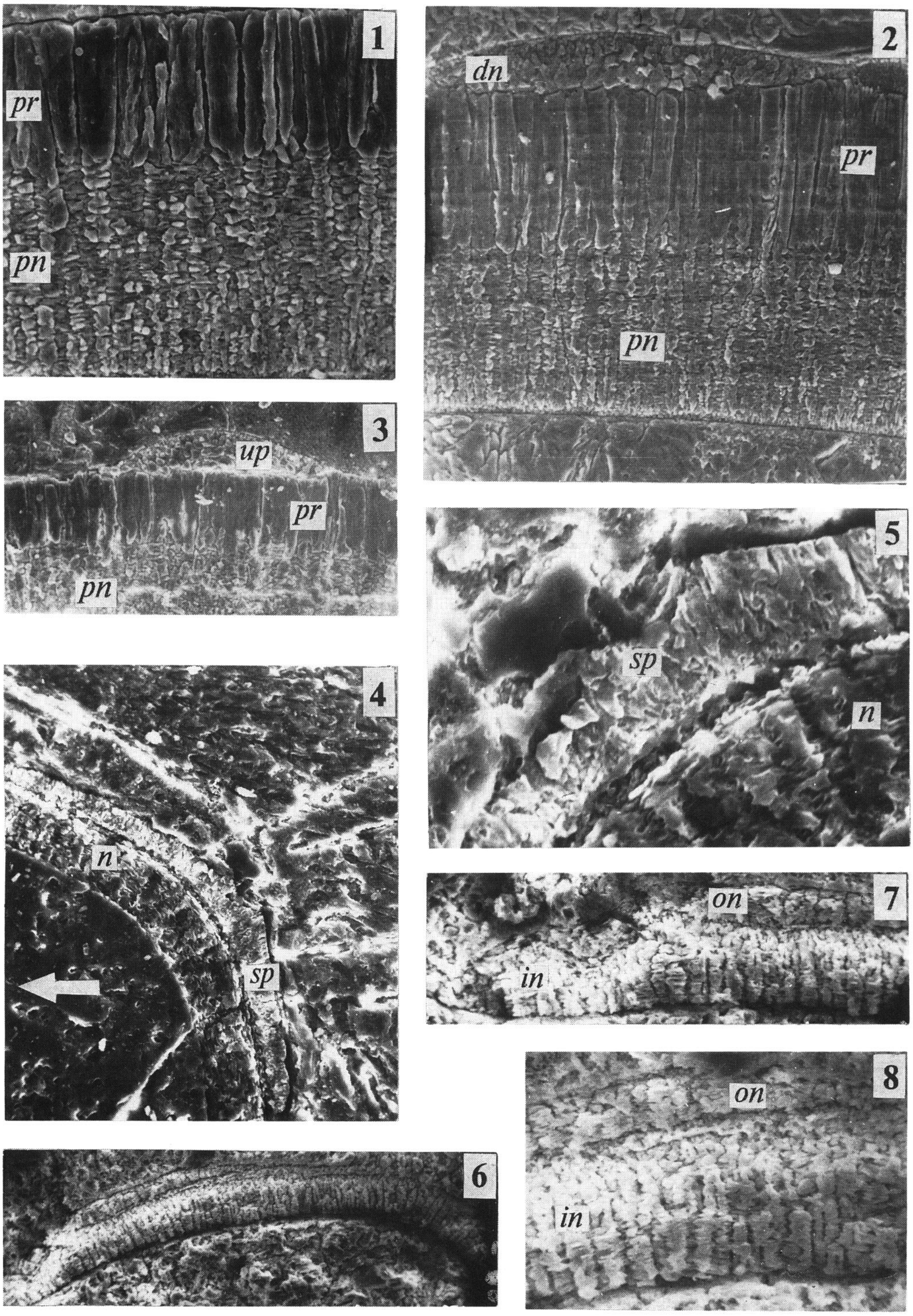

Plate 5

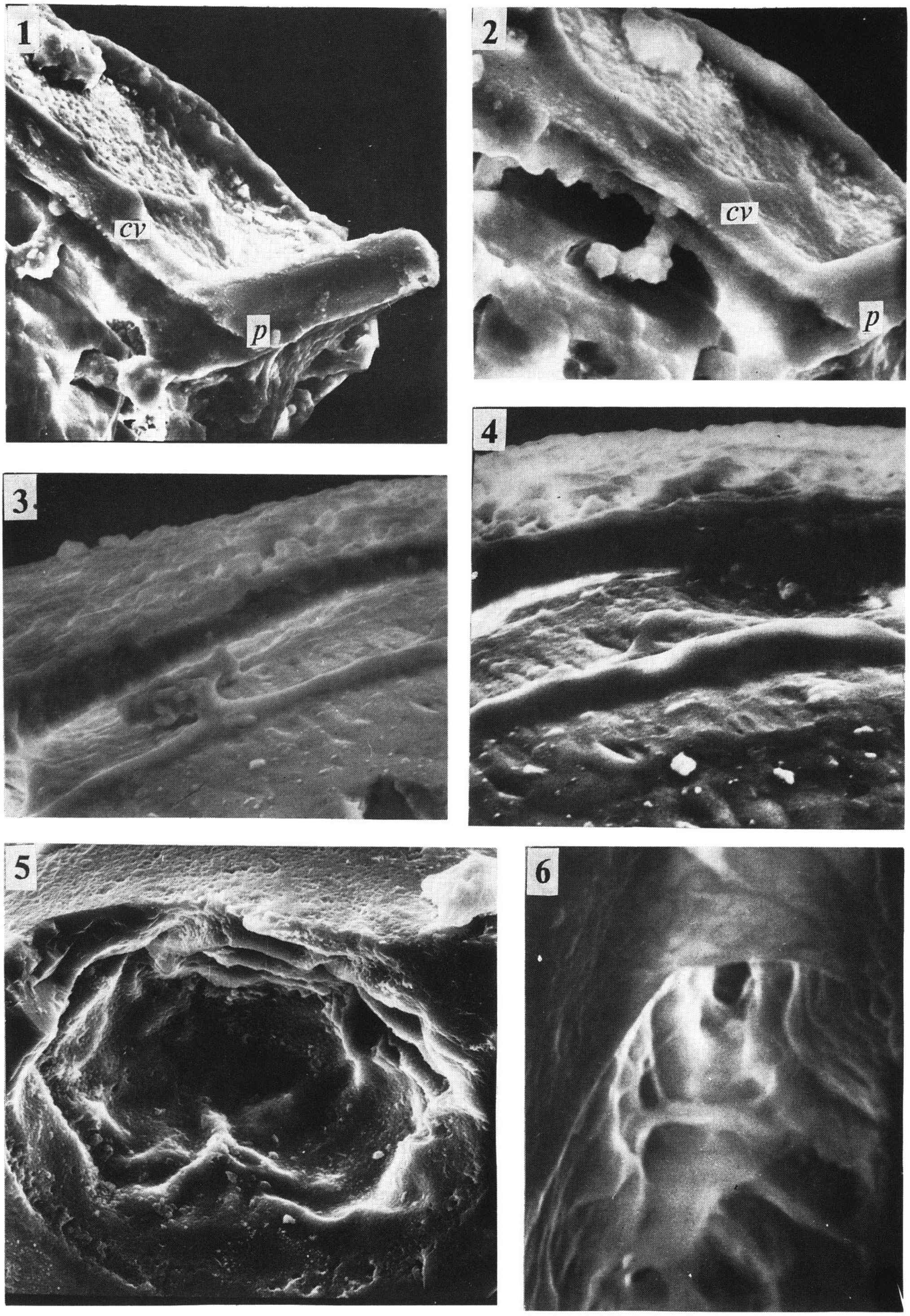

Plate 6