AN EARLY CRETACEOUS ORTHOCERID CEPHALOPOD FROM NORTH-WESTERN CAUCASUS

by L. A. DOGUZHAEVA

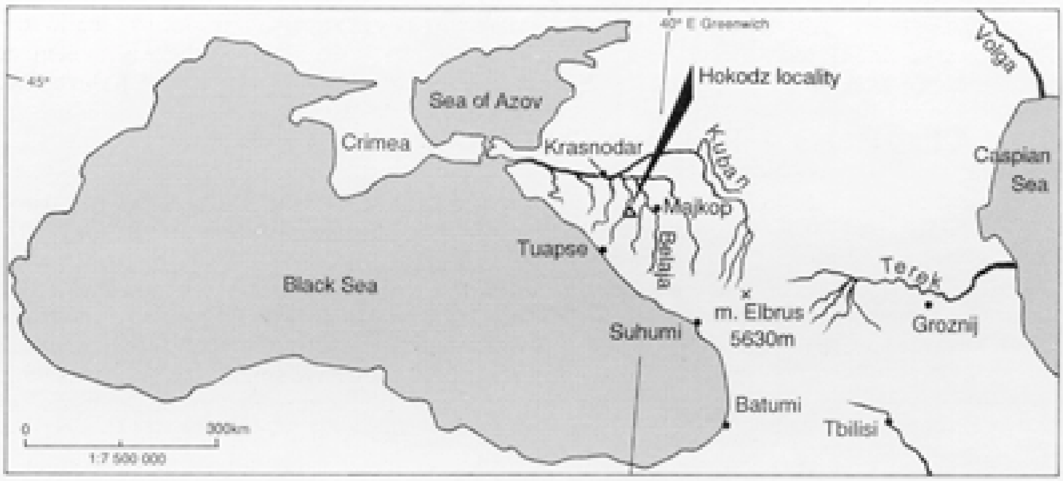
ABSTRACT. An orthocerid cephalopod is reported for the first time from the Lower Cretaceous deposits of the Caucasus. Discovery of this mollusc, *Zhuravlevia insperata* gen. et sp. nov., in such young beds shows that evolution of the orthocerid branch within the cephalopods was not terminated in the Late Triassic, as was formerly believed, but continued for a further 90–95 Ma, at least until the late Aptian (Clansenian). *Z. insperata* was found in association with numerous and diverse Aptian ammonites, rare belemnites, and a single phragmocone-bearing coleoid *Naefia*, characterized by the absence of the guard, all comprising the cephalopod fauna of the shallow Aptian sea in the Hokodz River Basin. SEM studies of *Z. insperata* and *Naefia* recovered from the same Aptian concretions have shown that the former possesses lamellar nacreous ultrastructure of the septa common for cephalopods with an external shell, while the latter possesses granular nacreous ultrastructure of the septa common for cephalopods with an internal shell. The ultrastructure of the septal neck of *Z. insperata* is closely similar to that of previously studied Carboniferous orthocerids from the Buckhorn Asphalt, hitherto the only orthocerids studied with well preserved primary ultrastructure.

IN the process of splitting numerous Aptian concretions collected by the author in the Hokodz River Basin (Text-fig. 1), a small fragment of a 13 mm long subcylindrical orthocone, with four chambers preserved, was noticed on a freshly broken surface. It could easily have been mistaken for an aulacocerid or belemnite if it were not for the septa at both ends of the orthocone distinctly displaying the central position of the siphuncle (Pl. 1, figs 1–3). Closer examination revealed additional morphological features supporting its classification as an orthocerid: (1) the thickness of the shell wall and septa are greater than in belemnites from the same nodules; (2) the outer surface of the shell exhibits fine growth lines common in orthocerids but uncommon in belemnites; (3) the septa are oblique, being attached to the shell wall closer to the aperture on one side (assumed dorsal) than on the other (assumed ventral) side, as known in other orthocerids (Zhuravleva 1978, pl. 6, fig. 7).

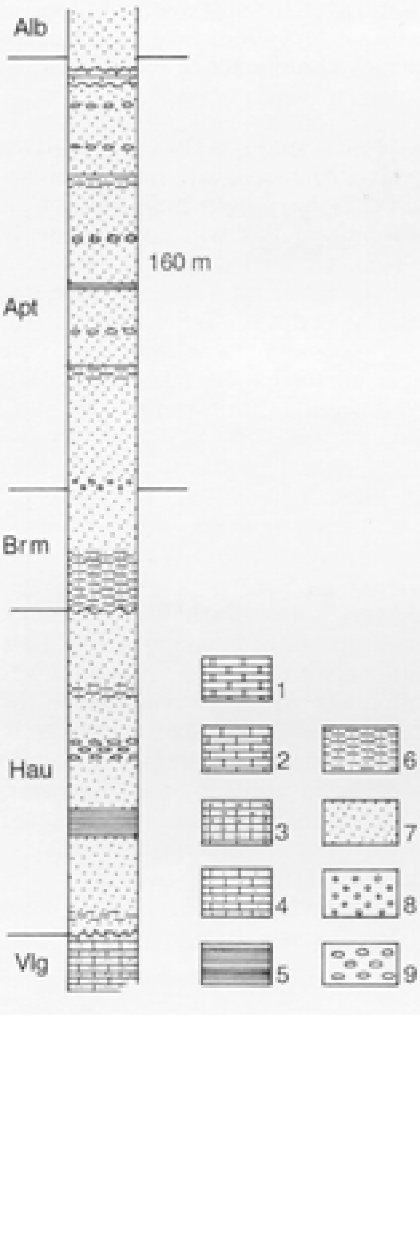
Ultrastructural studies of the orthocone demonstrated that the shell wall, septa, and septal necks are similar to those of Carboniferous orthocerids (Erben *et al.* 1969; Ristedt 1971; Mutvei 1972; Blind 1988). However, while the ultrastructure of the shell wall and septa in orthocerids is the same as in other ectocochleate cephalopods, that of the septal neck is of the type found only in orthocerids (Pl. 2).

Thus there is no doubt that this orthocone from the Aptian Stage is an orthocerid cephalopod. This find is surprising as orthocerids have not previously been found in beds younger than Late Triassic. The orthocerids first appeared in the Ordovician and the acme of their development was in the Devonian. After that time they gradually declined until only three genera remained in the Triassic (Jeletzky and Zapfe 1967; Schastlivceva 1988; Bizzarini and Gnoli 1991). However, during that period they had an extensive geographical distribution. For example, about forty species of the single genus *Trematoceras* are known from Upper Triassic beds in the Eastern Alps, the Himalayas, Timor, New Zealand, and North America. In the former USSR, orthocerids have been reported from Lower and Middle Triassic deposits of the Maritime Territory, Eastern Siberia, Mangyshlak, Verkhoyanye, and North Caucasus (Schastlivceva 1988). In this last region, two species of *Paratrematoceras* were found in Middle Triassic deposits from a section in the Tkhach River Basin (Schastlivceva 1988). No orthocerids have yet been reported from Jurassic strata.

[Palaeontology, Vol. 37, Part 4, 1994, pp. 889–899, 2 pls]



TEXT-FIG. 1. Generalized locality map showing the approximate position of the Hokodz locality.



TEXT-FIG. 2. Stratigraphical position of the horizon with *Zhuravlevia insperata* gen. et sp. nov. Adapted from Druschitc and Mikhailova (1966), with an upwards revision of the Aptian-Albian boundary. 1, dolomitic limestone; 2, limestone; 3, argillaceous limestone; 4, arenitic limestone; 5, clay; 6, siltstone; 7, sandstone; 8, conglomerate; 9, concretions.

The presence of an orthocerid in the Lower Cretaceous is unexpected. Its occurrence in such young deposits could not have been the result of reworking from older strata as there is no evidence of stratal disturbance. In the Mesozoic of the northwestern Caucasus, there is a layer-cake stratigraphy (Mitin 1965). Middle Triassic beds (which have yielded orthocerids) are overlain by the Upper Triassic, on which rest Jurassic strata. The latter are overlain by the Lower Cretaceous, all six stages of which are recognized. Further evidence that the orthocone under discussion has not been reworked is the nature of preservation of the shell material, which is the same in both the orthocone and the associated ammonites: partly phosphatized shells of a brown colour with weakly recrystallized ultrastructure. Thus, the conclusion is that this orthocerid actually inhabited the Aptian sea of the north-western Caucasus. Why then, have orthocerids never been reported from this area which has been so thoroughly studied for over a hundred years? Three reasons can be considered: (1) they were not as common in life as the ammonites or belemnites; (2) their shells are slender orthocones of small diameter, even at adult stages; (3) they have small, straight shells which are rarely preserved in their entirety. The large hiatus in the orthocerid record in the north-western Caucasus, corresponding to the interval between the Anisian and Aptian stages, could be explained by the rarity or absence of favourable conditions for burial and fossilization of marine fauna.

GEOLOGICAL SETTING

In the north-western Caucasus, the Lower Cretaceous is widespread, extending in a narrow belt in an east-west direction. It is composed mainly of sandstones, clays, and siltstones, with marls and limestones at the base (Luppov 1952; Egoian 1965; Druschitc and Mikhailova 1966). In this region, the deposits encompass six stages, with a total thickness of about 600 m (Mitin 1965; Egoian 1965). The Aptian comprises clays, sandstones, and siltstones with a high concentration of glauconite and numerous sideritic concretions. Its total thickness is about 160 m (Text-fig. 2), and ammonoids are common which makes it possible to trace the zones here (Text-fig. 3). The

Albian	Lower substage	Zone of *Douvilleiceras mammilatum* Zone of *Leymeriella tardefurcata*
Aptian	Clansenian Substage	Zone of *Diadochoceras nodosocostatum* and *Acanthohoplites bigoureti*
	Gargasian Substage	Zone of *Parahoplites melchioris* and *Colombiceras tobleri* Zone of *Epicheloniceras tschernyschewi* and *Colombiceras crassicostatum*
	Bedulian Substage	Zone of *Deshayesites deshayesi* Zone of *Deshayesites weissi* and *Procheloniceras albrechtiaustriae*
Barremian	Upper substage	'Zone' of *Heteroceras astierianum*

TEXT-FIG. 3. Ammonoid zones of the Aptian of north-western Caucasus (after Egoian 1969).

sandstone–siltstone sediments are poorly graded and the abundance of quartz gravel and carbonized wood indicates the existence of a shallow-water continental sea during this time (Mitin 1965). As evidenced through spore and pollen analysis, the profusion of Gleicheniaceae (40 per cent) and Pinaceae (34 per cent) is an indication that deposition occurred during a temperate climate regime (Rimsha and Serdjukova 1965).

The uppermost Aptian (Clansenian) of the Hokodz River Basin, from which the orthocone under discussion was collected, contains numerous sideritic concretions with well-preserved gastropods, bivalves, and carbonized wood and pine cones, together with an extremely rich ammonite assemblage. The most common ammonite genera, comprising about 100 species, are: *Euphylloceras*, *Phyllopachyceras*, *Tetragonites*, *Ptychoceras*, *Melchiorites*, *Diadochoceras*, *Acanthohoplites*, and *Hypacanthoplites* (Pl. 1, fig. 6). Some species found in this section occur frequently in the Clansenian stratotype in southwestern France. However, many others are endemic (Egoian 1965, 1969). Only two belemnite genera, *Mesohibolites* and *Neohibolites*, are known from this section, and are rare. Recently, three incomplete coleoid phragmocones identified as *Naefia* (Pl. 1, figs 4–5) have been found here by the author (paper in preparation).

SYSTEMATIC PALAEONTOLOGY

Order ORTHOCERIDA Kuhn, 1940
Superfamily ORTHOCERATACEAE M'Coy, 1844
Family GEISONOCERATIDAE Zhuravleva, 1959
Genus ZHURAVLEVIA gen. nov.

Derivation of name. Named in honour of F. A. Zhuravleva, in recognition of her major contribution to our knowledge of ancient cephalopods.

Type species. *Zhuravlevia insperata* sp. nov.

Type locality. Hokodz River Basin, north-western Caucasus.

Horizon. Lower Cretaceous, Upper Aptian (Clansenian).

Diagnosis. Small, slender orthoconic shell, circular in cross-section, gradually increasing in diameter towards the aperture. Sutures slightly oblique. Siphuncle central and narrow; necks short and suborthochoanitic; connecting rings thin and expanding slightly within the camerae. Camerae long. Surface with fine growth lines.

Comparisons. Differs from Ordovician to Devonian *Geisonoceras* Hyatt, 1884 and Lower Triassic *Pseudotemperoceras* Schastlivceva, 1986 in having a central siphuncle and longer camerae (1·50–1·70 of shell diameter compared with 0·40–0·45 for *Geisonoceras* and 0·25–0·30 for *Pseudotemperoceras*).

EXPLANATION OF PLATE 1

Figs 1–3. *Zhuravlevia insperata* gen. et sp. nov.; 3871/123 PIN. 1, outer surface of orthocone with visible growth lines; ×6. 2, fifth septum from body chamber with central opening for siphuncle; ×7·5. 3, medial section of orthoconch showing central position of siphuncle; ×7·5.

Figs 4–5. *Naefia* sp.; 3871/124 PIN. 4, lateral view with marginal siphuncle on left; ×6. 5, medial section showing position of siphuncle and structure of septal necks; ×8.

Fig. 6. Piece of concretion with ammonite shells; a, *Diadochoceras*; b, *Ptychoceras*; c, *Melchiorites*; d, *Euphylloceras*; ×1. All specimens from the Clansenian, Aptian; Hokodz River basin, NW Caucasus, Russia.

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Remarks. The new genus is based on a single specimen representing the part of the phragmocone that adjoins the body chamber. Siphonal and cameral deposits were not formed in the fragment recovered. Therefore the new genus is assigned provisionally to the family Geisonoceratidae, primarily on the basis of the configuration of the septal necks, position of siphuncle, and resemblance to the genus *Pseudotemperoceras*. *Zhuravlevia* is similar to the latter in shell morphology and in the absence of siphonal and cameral deposits in the camerae adjoining its body chamber. However, Schastlivceva (1988) considered the inclusion of *Pseudotemperoceras* within the geisonoceratids as tentative, because of the significant stratigraphical gap between the occurrence of it and other geisonoceratids previously discovered (middle Ordovician-Lower Triassic). For the same reason, the assignment of *Zhuravlevia* to the geisonoceratids is also tentative.

Zhuralevia insperata sp. nov.

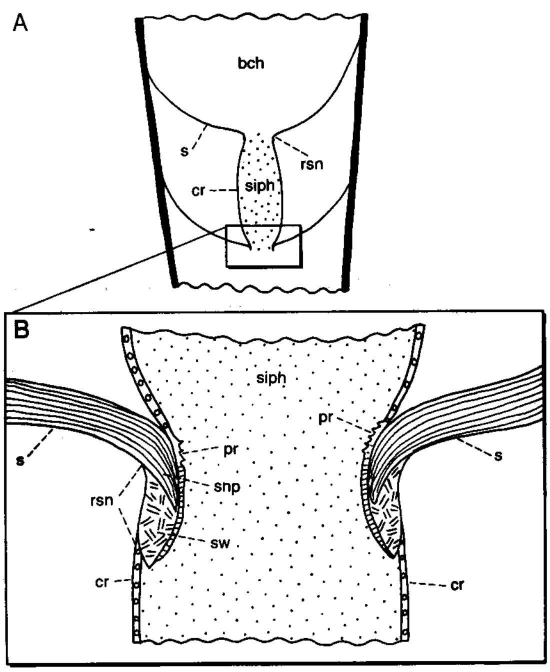
Plate 1, figures 1–3; Text-figure 4

Derivation of name. From Latin *insperata* – unexpected, alluding to its unusually high stratigraphical position.

Holotype. 3871/123, Palaeontological Institute, Russian Academy of Science, Moscow.

Type locality. Hokodz River Basin, northwestern Caucasus.

Diagnosis. Small, slender orthoconic shell, circular in cross-section. Available fragment of the phragmocone is 13 mm in length and 6 mm in maximum diameter. Angle of expansion 5 to 6°. Surface with fine, indistinct transverse growth lines. Length of camerae 1·5 to 1·7 their diameter. Suture oblique. Siphuncle central and narrow, length about 1·7 the diameter of the phragmocone. Connecting rings thin, slightly expanding within the camerae (Text-fig. 4A–B). Length to width ratio of segments is about 3·5. Diameter of the septal foramen is 0·5 the diameter of the segment. Necks suborthochoanitic, very short, about 1·13 the length of the camerae. Siphonal and cameral deposits unknown.



TEXT-FIG. 4. Schematic medial sections of a chamber in *Zhuravlevia insperata* gen. et sp. nov. A, position and shape of siphonal segment. B, structure of septal neck, consisting of septal neck proper and additional swollen part, with thin connecting ring adjoined to the latter. Legend: bch, body chamber; cr, connecting ring; pr, prismatic layer; rsn, retrochoanotic septal neck; s, septum; siph, siphuncle; snp, septal neck proper; sw, swollen additional part of the septal neck.

ULTRASTRUCTURE OF THE SHELL

Shell ultrastructure in *Z. insperata* has been studied to obtain additional criteria elucidating the classification of this form within the cephalopods. Based upon morphological characters alone, placement of this orthoconic cephalopod within the orthocerids or in some unknown coleoid group with a central siphuncle is uncertain. Therefore details concerning the ultrastructure of the specimen have been compared with available data on the orthocerids and for undetermined fossil coleoids from the same concretions.

Modern knowledge of the ultrastructure of the orthocerid shell is based upon studies of material from the Pennsylvanian (Upper Carboniferous) Buckhorn Asphalt of the USA (Erben *et al.* 1969; Ristedt 1971; Mutvei 1972; Blind 1988). The Buckhorn Asphalt provides the only locality where orthocerids with a well-preserved primary shell ultrastructure have been collected. The shell wall in these orthocerids is composed of the outer prismatic, nacreous, and inner prismatic layers. The septa consist primarily of a nacreous layer with a spherulitic-prismatic layer along the periphery. A prismatic layer forms a prominent ridge around the entrance to the septal neck. Nacreous ultrastructure on the concave adoral face of the septum is modified by the presence of fairly thick conchiolin membranes, whereas in the largest remaining portion of the septum these membranes are thin and regularly spaced. The septal necks consist solely of a continuation of the nacreous layer forming the septa. The inner surface of the most proximal portion of the neck is covered by a thin prismatic layer. The distally swollen region of the neck is distinctly separated from the proximal part, which has a strongly modified ultrastructure. According to Mutvei (1972), the conchiolin membranes of the septal necks continue to the structurally modified part, but the nacreous lamellae are replaced by prismatic lamellae. Blind (1988) described the swollen portion of the septal neck as spherulitic and assumed that the siphuncular epithelium bordered by spherulitic prisms was anchored to the septal neck after deposition of the outer connecting ring. The connecting ring consists of two layers: the outer of uncalcified conchiolin and the inner prismatic (Mutvei 1972). The conchiolin layer of the connecting ring occasionally contains dispersed spherulites (Blind 1988).

In the four chambers immediately preceding the body chamber, the siphuncle was covered only by the outer conchiolin layer, and the inner prismatic layer appeared at the fifth chamber (Blind 1988). Therefore, secretion was retarded.

Preservation of the Caucasian Aptian orthoconic shell is sufficient to allow study with the SEM. However, the level of detail observed in the material examined from the Buckhorn Asphalt was not obtained in the Aptian material. As in the orthocerids from the Buckhorn, the shell wall consists of three layers. The nacreous layer is the thickest portion of the wall, while the prismatic layers are comparatively thin. Septa are one-third the thickness of the shell wall, and consist primarily of the nacreous layer (Pl. 2, fig. 3). The narrow adapical portion of the septum differs from the remaining part in the presence of fairly thick conchiolin membranes. The nacreous layer possesses a columnar type structure common for the septa of the ectocochleate cephalopods.

The septal necks are separated into two regions by a distinct boundary (Pl. 2, figs 2–4; Text-fig. 4B). The septum passes into the septal neck proper which, consequently, is nacreous. The septal neck proper then decreases in thickness in the adapical direction. The adapical region adjoining the septal neck proper from outside is larger and usually swollen (Pl. 2, figs 2–4; Text-fig. 4B). Unlike the septal neck proper, the swollen part does not pass into the septum. The inner surface of the septal neck appears to be invested by a thin prismatic layer (Text-fig. 4B).

Connecting rings are not preserved except for the small parts adjoining the septal necks, but they are indicated by the shape of the segments of the siphuncle within the chambers (Pl. 2, figs 2, 4; Text-fig. 4B).

From this discussion, it is clear that the shell ultrastructure of *Z. insperata* is similar to that of the Pennsylvanian orthocerids. The unique structure described here in the septal necks is known only in the orthocerids. Ultrastructural studies of the coleoid *Naefia* from the same Aptian concretions (Pl. 2, fig. 5) show that the septa are composed of granular crystallites (Pl. 2, fig. 5). Intralamellar organic membranes which subdivide the septal nacre into thin mineral lamellae in the ectocochleate cephalopods are absent here, while the nacreous layer of the shell wall is not modified and shows lamellar ultrastructure. The same difference between the septal nacre and shell wall nacre is well known in other coleoids (Mutvei 1970, 1984; Dauphin and Kelle 1982; Hewitt *et al.* 1991). In contrast, in *Z. insperata* the nacre of the septa and of the shell wall is of the same type, resembling in this respect other ectocochleate cephalopods. Thus, the septal ultrastructure in *Z. insperata* convincingly supports its belonging to the ectocochleate cephalopods and the ultrastructure of the septal necks confirms its placement in the orthocerids.

PHYLOGENETIC IMPLICATION

The Aptian orthocerid described above as *Zhuravlevia insperata* shows that the evolution of the order Orthocerida was not terminated in the Late Triassic as previously believed, but continued at least 90–95 Ma longer, to almost the middle of the Cretaceous.

Teichert (1988) combined the Orthocerida with the Plectronocerida (Upper Cambrian), Yanhecerida (Upper Cambrian), (?) Protactinocerida (Upper Cambrian), Ellesmerocerida (Upper Cambrian-Ordovician), Ascocerida (Middle Ordovician-Upper Silurian) into the subclass Orthoceratoidea Kuhn 1940. Teichert considered that this subclass was the central cephalopod stock, giving rise to all other cephalopods. The Orthocerida had a range of about 360 Ma, which is the longest among cephalopods.

The Aptian orthocerid shows that, together with Nautiloidea and Ammonoidea, the Orthoceratoidea crossed the Triassic–Jurassic boundary, although all of these groups were close to extinction. For the evolutionary pattern of the subclass Orthoceratoidea in post-Triassic time, one can use the term 'outage', introduced by Teichert (1988). Teichert used this to describe the crises which 'may occur during a prolonged interval during which the group virtually or completely disappears from the paleontological record... the group became so restricted in taxonomic scope and in habitat that fossil representatives are great rarities or have not yet been identified at all' (Teichert 1988, p. 70).

The shell morphology in *Z. insperata* exemplifies the strong morphological conservatism showed by the orthocerids during their evolution. The comparison of the septal neck ultrastructure in *Z. insperata* with that in Carboniferous orthocerids gives further indication of high morphological (ultrastructural) stability as a characteristic of the orthocerids. Unfortunately, absence of ultrastructural data for other orthocerids does not allow wider comparison. My attempts to study shell ultrastructure in Triassic orthocerids and pseudoorthocerids (described by Schastlivceva 1988) have not yet yielded results because of poor preservation of shell material. Preservation of the shell matter unfit for SEM studies can also be the reason for the lack of the ultrastructural information on orthocerids of other ages.

The fact that *Z. insperata* possesses a simple shell morphology gives additional confirmation to the idea that times of crisis for the cephalopods, such as at the Triassic–Jurassic boundary, were passed through by comparatively simply organized forms. However, the morphological features

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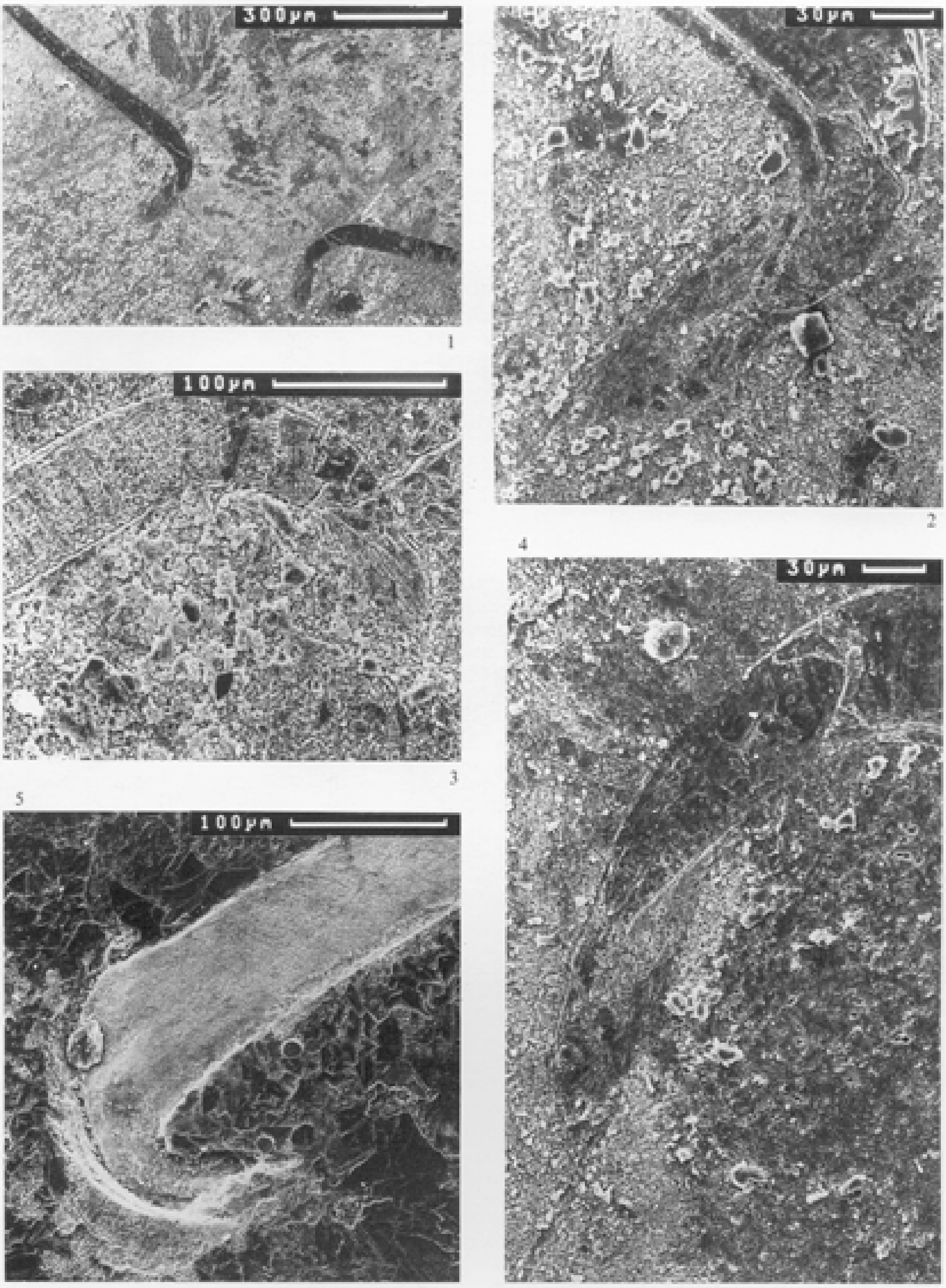
EXPLANATION OF PLATE 2

Figs 1–4. *Zhuravlevia insperata* gen. et sp. nov.; 3871/123 PIN; scanning electron micrographs of etched medial section of orthoconch. 1, general view of retrochoanitic septal neck; × 55. 2, enlarged left portion of septal neck shown in fig. 1, showing that it consists of the septal neck proper and an additional swollen part; × 325. 3, nacreous lamellar ultrastructure and columnar type of septum near septal neck; × 265. 4, right portion of septal neck, consisted also of the septal neck proper and an additional swollen part; thin connecting ring adjoining septal neck is distinctly visible in lower left corner; × 325.

Fig. 5. *Naefia* sp.; 3871/124 PIN; scanning electron micrograph of etched medial section of septum and retrochoanitic septal neck, showing differences in septum ultrastructure and septal neck structure compared with *Z. insperata*; × 240.

Both specimens from the Clansenian, Aptian; Hokodz River Basin, NW Caucasus, Russia.

PLATE 2



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that made for survival are not yet adequately known. In this connection, the small size of the shell at adult ontogenetic stages in *Z. insperata*, indicated by the short last chamber of the phragmocone before the body chamber, is worth noticing. It is obvious that, if the Aptian orthocerids had medium-to-large-sized shells, they would have been found earlier, because the cephalopod assemblage in the Hokodz river locality is rich in taxonomic variety and number. So, the small size of the shells must have been a characteristic feature of these orthocerids.

Acknowledgements. I am indebted to Dr F. A. Zhuravleva (Palaeontological Institute, Moscow) and Professor C. H. Holland (Trinity College, Dublin) for valuable discussions in Moscow. For constructive comments and help in the translation of the manuscript, I am pleased to thank Dr L. F. Kusina (Palaeontological Institute, Moscow), Dr M. R. Milligan (Mote Marine Laboratory, Sarasota), and C. H. Holland. I also thank V. T. Antonova (Palaeontological Institute, Moscow) for the photography and B. Lindsten (Swedish Museum of Natural History, Stockholm) who prepared the text-figures.

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Typescript received 19 April 1993
Revised typescript received 23 December 1993