MIDDLE TRIASSIC PARAPOPANOCERATIDAE AND NATHORSTITIDAE (AMMONOIDEA) OF BOREAL REGION : INTERNAL STRUCTURE, ONTOGENY AND PHYLOGENETIC PATTERNS

by

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ABSTRACT

Internal structure of *Stenopopanoceras mirabile* POPOW, *Parapopanoceras* sp., *P. medium* MCLEARN, *P. janaense* (POPOW), *P. paniculatum* POPOW, *P. asseretoi* DAGYS & ERMAKOVA, *Indigirites krugi* POPOW, *Nathorstites mcconnelli* (WHITEAVES), *N. gibbosus* STOLLEY, *N. lenticularis* (WHITEAVES), *N. argatassensis* (POPOW) is described and also ontogenetic development of species *I. krugi* POPOW and *N. mcconnelli* (WHITEAVES) originating from middle triassic deposits of northern part of Middle Siberia, north-eastern part of the USSR and Svalbard is given. For the species mentioned above data is given on the position of siphuncle, shape and dimensions of protoconch, caecum, ammonitella, the angle of primary varix, structure of septal necks and the nature of their change in the course of ontogeny. Significance of these signs for taxonomy and phylogeny of triassic ammonoidea is analysed. Intergeneric difference of *Stenopopanoceras* and *Parapopanoceras* is established according to the position of siphuncle on the first whorl of the shell. On the basis of the analysis of internal structure and ontogenetic development of suture line and morphological signs *Indigirites* is considered to belong to the family Hungaritidae (subfamily Longobarditinae). Phylogenetic patterns of the ammonoidea species described are discussed.

RÉSUMÉ

On décrit la structure interne de *Stenopopanoceras mirabile* POPOW, *Parapopanoceras* sp., *P. medium* MCLEARN, *P. paniculatum* POPOW, *P. asseretoi* DAGYS & ERMAKOVA, *P. janaense* (POPOW), *Indigirites krugi* POPOW, *Nathorstites mcconnelli* (WHITEAVES), *N. gibbosus* STOLLEY, *N. lenticularis* (WHITEAVES), *N. argatassensis* (POPOW) ainsi que le développement ontogénique de *I. krugi* POPOW et de *N. mc connelli* (WHITEAVES) provenant des dépôts du Trias moyen du Nord de la Sibérie moyenne, du Nord-Est de l'URSS et du Svalbard. Pour chaque espèce des indications sont données sur la position du siphon, sur la forme et les dimensions de la protoconque, sur le caecum siphonal, sur l'ammonitella, sur les dimensions de l'angle du bourrelet primaire, sur la structure des cols septaux et sur la nature de leur modification au cours de l'ontogenèse. L'importance de ces caractères pour la systématique et la phylogénie des Ammonoidea triassiques est analysée. La différence entre les genres *Stenopopanoceras* et *Parapopanoceras* est établie en se basant sur la position du siphon sur le premier tour de la coquille. Grâce à l'analyse de la structure interne et du développement ontogénétique de la ligne de suture et des caractères morphologiques le genre *Indigirites* est attribué à la famille des Hungaritidae (sous-famille des Longobarditinae). Les relations phylogénétiques des espèces d'Ammonoidea décrites sont envisagées.

KEY-WORDS : AMMONOIDEA, CERATITIDA, *STENOPOPANOCERAS, PARAPOPANOCERAS, NATHORSTITES, INDIGIRITES*, TRIASSIC, USSR, SVALBARD.

MOTS-CLÉS : AMMONOIDEA, CERATITIDA, *STENOPOPANOCERAS, PARAPOPANOCERAS, NATHORSTITES, INDIGIRITES*, TRIAS, URSS, SVALBARD.

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I — INTRODUCTION

Ammonoidea of Parapopanoceratidae and Nathorstitidae families are abundant in middle triassic deposits of boreal paleozoogeographic region. Generic types of Parapopanoceratidae - *Stenopopanoceras* and *Parapopanoceras* are encountered in anisian deposits of North-Eastern Asia (Dagys & *alii*, 1979), Svalbard (Kortchinskaya, 1975), Eastern Greenland (Kummel, 1953), Arctic Canada and British Columbia (Tozer, 1967 ; McLearn, 1969). For the last decade *Stenopopanoceras* were identified in New Zealand (Tozer, 1971), Iran (Tozer, 1972 a) and in the Caucasus (Dagys & Ermakova, 1981). These finds prove the fact that Parapopanoceratidae were not restricted in their distribution to boreal regions only, but also could be found in Tethys and Notal regions where they, however, were of no significance in the community of ammonoidea.

Anisian deposits of North-Eastern Asia contain numerous species of *Stenopopanoceras* and *Parapopanoceras* which have, as a rule, narrow vertical range

Fig. 1 — **Location of Ammonoidea studied** : 1 - Svalbard archipelago, Edge isle ; 2 - Taimyr peninsular, Tsvetkov cape ; 3 - mouth of the Olenek River, Tumul cape ; 4 - lower course of the Olenek river, Karangati mountain ; 5 - upper course of the Kendgey river, Artist-Agatyn-Yurege creek ; 6 - Darky, the Lena's tributary ; 7 - upper course of the Olguya river, the Kolyma's tributary ; 8 - the Kegali river, the Omolon's tributary ; 9 - the Yana-Okhotskaya basin.
Lieux de récolte des Céphalopodes étudiés.

and are confined to intervals of definite age. *Stenopopanoceras* and *Parapopanoceras* studied by us originated from septarian nodules which are abundant in aleurolitic- argillaceous deposits of the anisic stage in Eastern Taimyr (cape of Tsvetkov), Oleneksky bay coast of the Laptevs sea, the Kolyma basin, the lower course of the Olenek river and the Kharaulakh range (fig. 1). In the ascensive section the Parapopanoceratidae discussed were confined to the following zonal subdivisions : *Stenopopanoceras mirabile* POPOW - *Grambergia taimyrensis* zone of lower Anisian substage, *Parapopanoceras medium* MCLEARN - *Grambergia taimyrensis* and *Lenotropites tardus* zones of Lower Anisian substage, *Parapopanoceras* sp., *P. paniculatum* POPOW and *P. janaense* (POPOW) - *Malletoptychites kotschetkovi* zone of middle Anisian substage, *P. asseretoi* DAGYS & ERMAKOVA - *Gymnotoceras rotelliforme* zone of upper Anisian substage.

Ammonoidea of genus Nathorstites are typical representatives of boreal fauna. They are abundant in upper ladinian and lower carnian deposits of North-Eastern Asia (Dagys & *alii*, 1979 ; Bychkov, 1982), Svalbard (Kortchinskaya, 1972) and Arctic Canada (Tozer, 1967). *Nathorstites* can be found also in ladinian deposits of British Columbia together with numerous Tethys ammonoidea (Tozer, 1967). They are of great importance for the stratigraphy of upper ladinian and lower carnian deposits due to narrow vertical and wide areal range of certain species. Most investigators also include *Indigirites* into the family Nathorstitidae.

Representatives of these genera were collected by us in upper ladinian argillaceous-aleurolitic rock masses of Eastern Taimyr (cape of Tsvetkov), in the mouth of the Olenek river (cape Tumul) and the Olguya river (the Kolyma basin). Besides this material the authors used, for the purpose of investigation, a few very well preserved specimens of *Nathorstites* from lower carnian deposits of Svalbard and upper ladinian deposits of the Kegali basin, which were kindly placed at our disposal by M.V. Kortchinskaya and Y.S. Repin (fig. 1). Stratigraphycally the species studied are confined to the following zones : *Indigirites krugi* POPOW - to the zone *Nathorstites lenticularis* (krugi subzone) of upper Ladinian substage ; *Nathorstites mcconnelli* (WHITEAVES), *N. lenticularis* (WHITEAVES), *N. argatassensis* (POPOW) - to the zone lenticularis of upper Ladinian substage ; *N. gibbosus* STOLLEY - to the zone *Nathorstites tenuis* of lower Carnian substage (table. 1).

Characteristic features in the development of suture line and forms of the shell *Stenopopanoceras* and *Parapopanoceras* were recently studied (Vavilov, 1978 ; Dagys, Ermakova, 1981). Some features of internal structure of Parapopanoceratidae became known due to Y.D. Zakharov's investigation (1978), who studied *P. paniculatum* POPOW.

Ontogenetic development of suture line and morphologic signs of the *Nathorstites* shell has been studied by the authors (Alekseyev, Arkadiev, Vavilov, *in*press). Peculiarities of *Nathorstites* septal neck structure were described by C. Kulicki (1979). Layers incrusting the *Nathorstites* shell at the postembryonic stage of its development were described in detail by E. Tozer (1972b). No investigation of ontogenetic development and internal structure of *Indigirites* genus has so far been made. Investigations carried out by the authors make it possible to enlarge our knowledge of the internal structure and ontogenetic development of Parapopanoceratidae and Nathorstitidae representatives and, on the basis of the data obtained, to define our notion of the status of certain genera, phylogenetic patterns and composition of families.

The collection which served as the basis for the present investigations belongs to the museum of the Leningrad Plakhanov Mining Institute (index number 312) and to the museum of All-Union Petroleum Research and Geological Prospecting Institute (index number 831).

II — TERMINOLOGY

To denote elements of the suture line of Ammonoidea the authors used the following indexing and terminology : V - ventral lobe, L - outer lateral lobe, I - inner lateral lobe, D - dorsal lobe, U (numbered) - umbilical lobes.

When describing the internal structure of shells, the authors used the terminology proposed by Drushtchic & Khiami (1969, 1970) and substantially supplemented by Y.D. Zakharov (1974, 1978).

Stage	Substage	Zone		*Stenopopanoceras mirabile* POPOW	*Parapopanoceras medium* McLEARN	*Parapopanoceras* sp.	*P. paniculatum* POPOW	*P. janaense* (POPOW)	*P. asseretoi* DAGYS & ERMAKOVA	*Indigirites krugi* POPOW	*Nathorstites mcconnelli* (WHITEAVES)	*N. lenticularis* (WHITEAVES)	*N. argatassensis* (POPOW)	*N. gibbosus* STOLLEY
				Name of species										
Karnian	Lower	*Nathorstites tenuis*												X
Ladinian	Upper	*Nathorstites lenticularis*	*Nathorstites mcconnelli*								X	X	X	
Ladinian	Upper	*Nathorstites lenticularis*	*Indigirites krugi*							X	X	X		
Ladinian	Upper	*Arctoptychites omolojensis*												
Ladinian	Lower	*Longobardites oleshkoi*												
Anisian	Upper	*Frechites humboldtensis*												
Anisian	Upper	*Gymnotoceras rotelliforme*							X					
Anisian	Middle	*Malletoptychites kotchetkovi*				X	X	X						
Anisian	Lower	*Lenotropites tardus*			X									
Anisian	Lower	*Grambergia taimyrensis*		X	X									

Table. 1 —Stratigraphical distribution of the *Stenopopanoceras, Parapopanoceras, Indigirites* and *Nathorstites*-species in the Boreal region.
Répartition stratigraphique des espèces de *Stenopopanoceras, Parapopanoceras, Indigirites* et *Nathorstites* dans la région boréale.

Abbreviations to drawings and tables

Pr - protoconch, S - siphuncle, SE - septum, PS - proseptum, SE 2 - primary septum, F - flange, Pros - prosiphon, C - caecum, NC - nepionic varix, AD - annular deposits, RSN - retrochoanitic septal neck, PSN-prochoanitic septal neck, ASN - amphichoanitic (transition) septal neck, M - cuff, BC - body chamber, SC - septal cover, SM - septal membrane, D SE - distance between septa, H Wh - height of whorl, Wh - whorl, D a - ammonitella diameter, $\propto$ - angle of primary (nepionic) varix (measurements carried out by Grandjean method), D 1 and D 2 - dimensions of protoconch in median plane, C 1 and C 2 - caecum dimensions in median plane, V and NV - ventral and near-ventral position of siphuncle, Ce - central position of siphuncle, R - retrochoanitic type, A - amphichoanitic type (transitional), P - prochoanitic type.

III — SYSTEMATIC DESCRIPTION

Order **CERATITIDA** HYATT, 1884

Suborder **Ceratitina** HYATT, 1884

Family **PARAPOPANOCERATIDAE** TOZER, 1971

Genus **Stenopopanoceras** POPOW, 1961

pl. 1, fig. 1-5

TYPE SPECIES : *S. mirabile* POPOW, 1961, Anisian, Eastern Taimyr.

ONTOGENETIC DEVELOPMENT :

Ontogenetic development of the suture line and morphological signs of *Stenopopanoceras* was studied by A.S. Dagys & S.P. Ermakova (1981). T e ne s developed due to appearance of numerous umbilical lobes in the area of umbilical seam. In the process of ontogeny lobes with even numbers (U^2, U^4 etc.) are shifted to the inner side of the whorl, while lobes with odd numbers (U^3, U^5 etc.) are shifted to the outer side of the whorl. The formula of *Stenopopanoceras*suture line is $(V_1 V_1)LU^1U^3U^3)U^5U^7 : U^6U^4U^2I (D_1D_1)$.

Information obtained from studies of individual morphogeny can be used to advantage in order to diagnos c rtain species.

INTERNAL STRUCTURE :

Internal structure of four specimens of type species has been studied. Protoconch is fine to medium (D^1 = 0.42-0.46 mm, D^2 = 0.38-0.41 mm), spherical. Caecum is rounded, of medium size (C^1 = 0.12 mm, C^2 = 0.11 mm). Primary varix was not observed. Siphuncle on the first whorl occupies ventral or near ventral position, on all successive whorls it occupies ventral position. Prochoanitic septal necks were well observed beginning with the third whorl. The length of necks of specimen N 1/312 at the beginning of the fifth whorl is 0.4 mm, the length of hydrostatic chamber being 2.5 mm. Inside its septal neck this specimen has a cuff slightly protruding backwards (fig. 2). Septal membrane connects the back side of septal neck and the sheath of siphuncle. At the point where septum bends into a septal neck there is a formation embracing the back side of septum and septal neck.

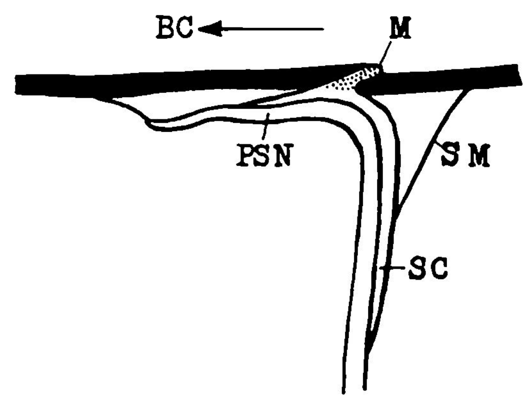


Fig. 2 — **Structure of prochoanitic septal neck of *Stenopopanoceras mirabile* POPOW.** N/312, fourth whorl (x 100). Kharaulakh range, the Kengdey river basin, Anisian, taimyrensis zone.

Structure du col septal prochoané de *Stenopopanoceras mirabile* POPOW. Quatrième tour. Chaîne de Kharaoulakhe, bassin de Kengdei, Anisien, zone à taimyrensis.

Species and number of specimen	Protoconch size, mm		Caecum size, mm		Ammonitella		Length of prosiphon	Position of siphuncle							Type of septal neck						
	D^1	D^2	C^1	C^2	D_a	a^o	mm	1	2	3	4	5	6	7	1	2	3	4	5	6	7
Stenopopanoceras mirabile POPOW N 1/312		Specimen deformed						NV	NV-V	V	V	V	.				P	P	P	–	..
Stenopopanoceras mirabile POPOW, N 2/312	0,46	0,41	0,12	0,11	.	.	–	V?	V	V	V	V	V	V	–	–		P	P	P	P
S. mirabile POPOW, N 3/312	0,42-0,43	0,38-039	–			..	–	–	..	V	V	V	V	V	–	–	P	P	P	P	P
S. mirabile POPOW, N 4/312		Specimen deformed						V	V	V	V	–	.			.		.		.	
Parapopanoceras medium McLEARN, N 6/312	0,42	0,36	..	..				Ce-NV	V	V	V	V	.	–	?	A?	P	P	P	–	–
P. medium McLEARN, N 7/312	0,36	0,35	.	.	...	–	–	Ce	NV	V	V	V	–				.	.	P	.	...
P. medium McLEARN, N 8/312	0,42	0.40	.	–	.	–	–	–		V	V	V	V	–	–	–	–	P	P	P	.
P. medium McLEARN, N 9/312	0,35	0,29	0,06-0,07	0,06-0,07		-	0,06	Ce-NV	NV-V	V	V	V	V		R	A	P	P	P	P	–
P. medium McLEARN, N 10/312	0,35	0,29	–	–			.	Ce?-NV	V	V	V					.	P	P	–	–	–
P. janaense (POPOW), N 12/312	0,50	0,42	.			–	–	NV	V	V	V	V	–	–	–	–	–	–	–	–	.
P. paniculatum POPOW, N 13/312	0,39	0,32	–		–			Ce-NV	NV-V	V	V	V	V	V	-	.	P	P	P	P	P
Parapopanoceras sp., N 14/312	0,40	0,35	–	–	–	–		Ce	NV	V	V	V	V	..	–	–	–	P	P	P	–
P. paniculatum POPOW, N 15/312	0,33	0,30		.	0,64	270		.		–	V	V	V	V	.		..	P	P	P	P
Parapopanoceras sp., N 17/312	0,26	0,25	–	–	–	–		–	–	V	V	V	V	V	.	–	..	.	P	P	P
P. asserotoi DAGYS & ERMAKOVA, N 18/312	0,38	0,31	0,08?	0,07	0,65	270	0,07	Ce	NV	V	V	V	V		R	A	?	P	P	P	–
P. asseretoi DAGYS & ERMAKOVA, N 20/312	0,33	0,32	0,10	0,09		–	0,09	Ce	NV	V	V	V	V	–	–	–	A-P	P	P	P	–
P. asseretoi DAGYS & ERMAKOVA, N 21/312	0,40	0,30	0,08	0,08	0,68	270	0,10?		NV	V	V	V	V			A	A-P	P	P	P	–
P. asseretoi DAGYS & ERMAKOVA, N 22/312	0,40	0,33	0,09	0,09	0,67	270	0,11	Ce	NV	V	V	V	V	V	R	?	A-P	P	P	P	P
P. asseretoi DAGYS & ERMAKOVA, N 23/312	0,38	0,32	–		0,65	270		Ce	NV	NV-V	V	V	V	V	?	A	A-P	P	P	P	P
Indigirites krugi POPOW, N 26/312	0,35	0,33	0,08	0,07	0,65	290	0,12	V	V	V	V	V	V	–	R	R	R	R-P	P	P	.
I. krugi POPOW, N 27/312	0,36	0,34	–	..	0,68	290	–	V	...	V	–	–	–	..	–	–	-	.		-	–
I. krugi POPOW, N 28/312	0,37	0,35	–		0,65	300	–	V	V	V	V	V	V	.	R	R	R	A	P	P	–
I. krugi POPOW, N 29/312	0,36	0,32	0,07	0,07	0,60	290	0,10	V	V	V	V	V	V		R	R	R	A	P	P	–
Nathorstites mcconnelli (WHITE.), N 30/312	0,36	0,32	–	–	0,59	270	–	V	V	V	V	V	V	V	R	R	R	A	P	P	P
N. lenticularis (WHITE.), N 31/312	0,26	0,22	–	.	0,54	270	–	V	V	V	V	V	V	.	R	R	R	R	R-A	A-P	..
N. gibbosus STOLLEY, N 32/312	0,30	0,26	.	.	0,63	270	–	–		–	V	V	–	–		..	.	A	P	–	–
N. argatassensis (POPOW), N 33/312	0,35	0,31	–	–	...	–	–	V	V	V	V	V	V	V	R	R	R	R-A	A-P	P	P
N. argatassensis (POPOW), N 34/312	0,37	0,32		.	0,66	270	.	–	V	V	V	V	–	–	R	R	R	R-A	A-P	P	–
N. mcconnelli (WHITE.), N 24/831	0,45	0,46	0,07	0,07	0,765	270	.	V	V	V	V	V	V	V	R	R	R	R	R	A-P	P
N. gibbosus STOLLEY, N 25/831	0,39	0,37	0,06	0,07	0,615	270	0,09	V	V	V	V	V	V	V	R	R	R	R	A-P	P	P

Tabl. 2 — **Characteristic signs of internal structure of middle triassic genera *Stenopopanoceras, Parapopanoceras, Indigirites* and *Nathorstites*.**

Indices caractéristiques de la structure interne des genres *Stenopopanoceras, Parapopanoceras, Indigirites* et *Nathorstites* du Trias moyen.

Thus far such formations havenot been found in mesozoic Ammonoidea. We propose to give them the name of septal covers. At the end of the fourth whorl the part of septal cover embracing septum on the back side is 0.30 mm long. Thickness of the septal cover at the point where septum bends into a septal neck is 0.02 mm.

The number of phragmocone whorls amounts to 6-
..., h ...y ..... yi g h n
whorl.

MATERIAL :

Specimen N 1/312 - Kharaulakh range, the Kengdey basin. Three specimens N 2-4/312 - Eastern Taimyr, cape of Tsvetkov.

Genus **Parapopanoceras** HAUG, 1894

pl. 2, fig. 1-7 : pl. 3, fig. 1-5 :
pl. 4, fig. 1-5 : pl. 5, fig. 1-2

TYPE SPECIES : *Popanoceras verneuili* MOJSISOVICS, 1886, Anisian, Svalbard.

ONTOGENETIC DEVELOPMENT :

Ontogenetic development of suture line and mor-
...g ... g ... b
of species (Vavilov, 1978 ; Dagys & Ermakova, 1981). Suture line develops as follows : there appear umbilical lobes in the vicinity of umbilical seam with their successive shift, that is, lobes with even numbers are shifted to the inner side of the shell, while those with odd numbers are shifted to the outer side. Suture line of *Parapopanoceras* is characterized by the presence of isolated lobes along the whole outer side of the shell's whorl. The number of lobes on the outer side of an adult shell amounts to 8-11. Suture line formula of *Parapopanoceras* is $(V_1V_1)LU^1U^3U^5U^7U^9U^{11}U^{13} : U^{12}U^{10}U^8U^6U^4U^2I(D_1D_1)$.

When diagnosing species great attention should be paid to the analysis of individual variation of the shell's shape in the process of ontogeny.

INTERNAL STRUCTURE :

Internal structure of five species of this genus has been studied - *Parapopanoceras medium* MCLEARN, *P. paniculatum* POPOW, *P. janaense* (POPOW), *P. asseretoi* DAGYS & ERMAKOVA and *Parapopanoceras* sp.

Protoconch is spherical, a little elongated along the major diameter mainly small sized (D^1 = 0.33-0.42 mm, D^2 = 0.29-0.40 mm). Specimen of *Parapopanoceras* sp. N 17/312 has a smaller protoconch (D^1 = 0.26 mm, D^2 = 0.25 mm), and specimen of *P. janaense* (POPOW) N 12/312 has a larger one (D^1 = 0.50 mm, D^2 = 0.42 mm).

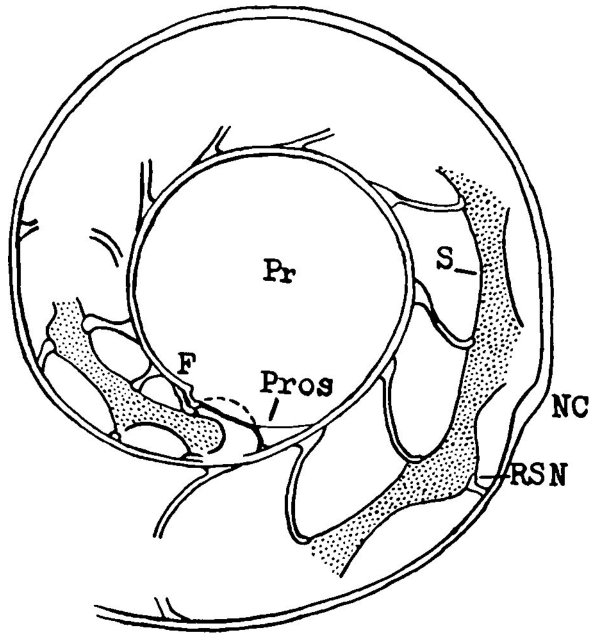


Fig. 3 — *Parapopanoceras asseretoi* DAGYS & ERMAKOVA, N 18/312.
Structure of protoconch and first whorl of phragmocone (x 100) ; Kharaulakh range, upper course of the Kengdey river, Artist-Agatyn-Yurege creek, Anisian, rotelliforme zone.
Structure de la protoconque et du premier tour du phragmocône ;chaîne de Kharaoulakhe, bassin de Kengdei, ruisseau d'Artiste-Agatyne-Juregée, Anisien, zone à rotelliforme.

Five specimens retained caecum. With *P. asseretoi* DAGYS & ERMAKOVA (specimens N 20-22/312) and *P. medium* MCLEARN (specimen N 9/312) it is spherical, small (C^1 = 0.06-0.1 mm, C^2 = 0.07-0.09 mm), located within adoral part of protoconch. Caecum of *P. asseretoi* DAGYS & ERMAKOVA (specimen N 18/312) is surrounded by a prosiphon of complicated structure (fig. 3,4). It consists of a cover surrounding caecum and two bands - a short one and a long one - connecting caecum to protoconch wall. The length of the longer prosiphon band is 0.07 mm, that of the shorter one is 0.015 mm. The colour of the cover is black, that of proseptum, primary septum, the flange and wall of protoconch is almost white. Part of the cover between the flange and prosiphon is cambered in the direction of venter, similar to protoconch wall, which is likely to result from secondary alterations when protoconch was filled with calcite. The flange is well developed, it is pulled to the centre of protoconch. Proseptum and primary septum are cambered in the direction of shell's beginning and located close to each other. They have short retrochoanitic septal necks.

Prosiphon of similar structure was previously described by Y.D. Zakharov (1971) in *Desmophyllites* aff. *siskiyonensis* ANDERSON from Campanian stage of South Sakhalin, and also by M.N. Vavilov & S.N. Alekseyev (1979) in middle triassic genus *Aristoptychites*. V.V. Drushtchic & L.A. Doguzhayeva (1981) regard the cover as a calcareous case for caecum. Probably the third constituent part of prosiphon, a cone, described by Y.D. Zakharov was also developed, but as the specimen described is poorly preserved, it was impossible to find traces of it.

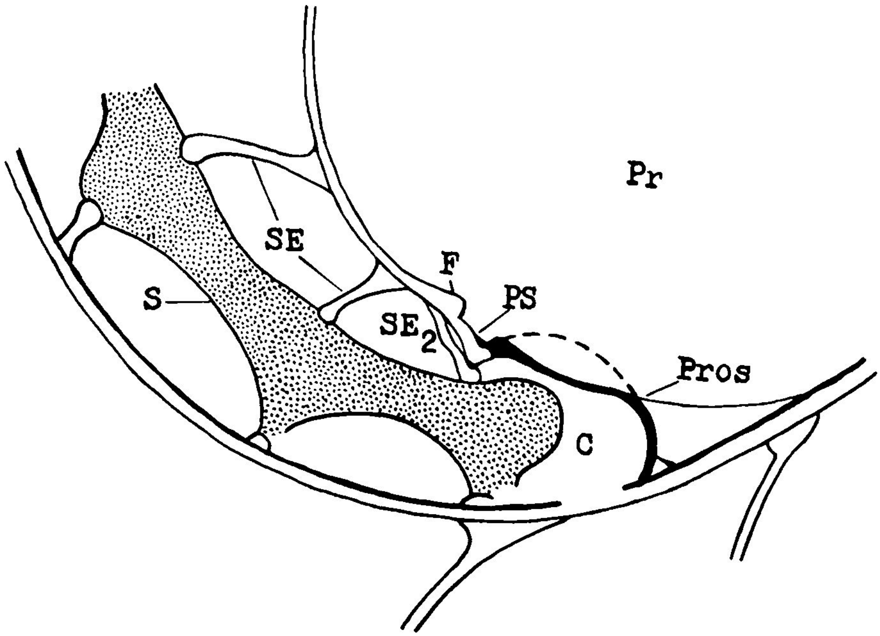


Fig. 4 — *Parapopanoceras asseretoi* DAGYS & ERMAKOVA, N 18/312.
Structure of caecum, prosiphon and first four septa (x 250). Kharaulakh range, upper course of the Kengdey river, Artist-Agatyn-Yurege creek, Anisian, rotelliforme zone.

Structure du caecum, du prosiphon et des quatre premiers septums. Chaîne de Kharaoulakhe, bassin de Kengdei, ruisseau d'Artiste-Agatyne-Juregée, Anisien, zone à rotelliforme.

Primary varix of the species studied is indistinct and seen only in thin sections. The angle of primary varix is 270°, which suggests a short body chamber of ammonitella. The range of ammonitella's diameter is 0.65-0.68 mm.

With all representatives of *Parapopanoceras* studied the siphuncle on the first whorl occupied a non-ventral position. The siphuncle of *P. paniculatum* POPOW occupied central position on the first whorl, that of *P. medium* MCLEARN - central or near-central, *P. janaense* (POPOW) - near-ventral position, *P. asseretoi* DAGYS & ERMAKOVA and *Parapopanoceras* sp. - central. With most species the siphuncle becomes ventral at the end of the second whorl, very seldom - at the beginning of the second whorl (*P. asseretoi* DAGYS & ERMAKOVA, specimen N 6/312) or on the third whorl (*P. asseretoi* DAGYS & ERMAKOVA, specimen N 23/312). At the points of its passing through septa the siphuncle often comes very close to the venter, and when passing through hydrostatic chambers it deviates, as a result the walls of siphuncle are arching. Y.D. Zakharov (1978) who studied *P. paniculatum* POPOW from anisian deposits of the Kolyma basin discovered a dorsal siphuncle in it (on the first whorl) which becomes ventral on the third whorl. Our data don't confirm it.

Septal necks of all species are short retrochoanitic on the first whorl, of transitory type (amphichoanitic) on the second, on the third they change for prochoanitic. The length of prochoanitic septal necks of some species amounts to almost one third of the length of hydrostatic chambers, while that of *P. medium* MCLEARN (specimen N 8/312) is 0.63 mm in the middle of the fifth whorl, the length of hydrostatic chamber being 2.0 mm. The length of prochoanitic septal neck of *P. paniculatum* POPOW (specimen N 15/312) at the beginning of the seventh whorl is 0.7 mm, the length of chamber being 2.3 mm. The structure of septal neck of the latter species is shown in fig. 5. On ventral and dorsal sides of the siphuncle the cuffs can be seen the length of which is 0.20-0.22 mm, on the front side of the cuffs there are annular deposits. The cuffs are located inside the septal necks. Thickness of siphuncle wall at the beginning of the seventh whorl is 0.03 mm, that of the shell wall being 0.07 mm. The colour of organic cover of the siphuncle in thin section is yellowish brown. At the point where septum bends into a septal neck a septal cover can be seen the thickness of which is up to 0.02 mm. In its structure it is similar to the one described for genus *Stenopopanoceras*. Specimen N 15/312 showed septal membranes connecting the back septal face to the siphuncle cover and membranes connecting the front septal face to septal neck. Septal membrane of the first type is often encountered among mesozoic Ammonoidea and is described by many investigators (Drushtchic, Bogoslovskaya, Doguzhayeva, 1976 ; Zakharov, 1971). Second type membrane is less often encountered. It was described by C. Kulicki (1979) who discovered it in middle triassic genus *Nathorstites* and Jurassic genus *Quenstedtoceras*. The structure of septal necks *P. asseretoi* DAGYS & ERMAKOVA species (specimen N 23/312) differs from the one described above. The cuffs of this species are protruding behind the septal necks.

In the process of ontogeny the shape of septum in median section changes but slightly. The first two septa are cambered in the direction of protoconch. The successive septa on the first three whorls look like arches slightly cambered towards aperture. On later whorls the septa are strongly arched in their central parts. Change in the shape of septum section in median plane is shown in fig. 6.

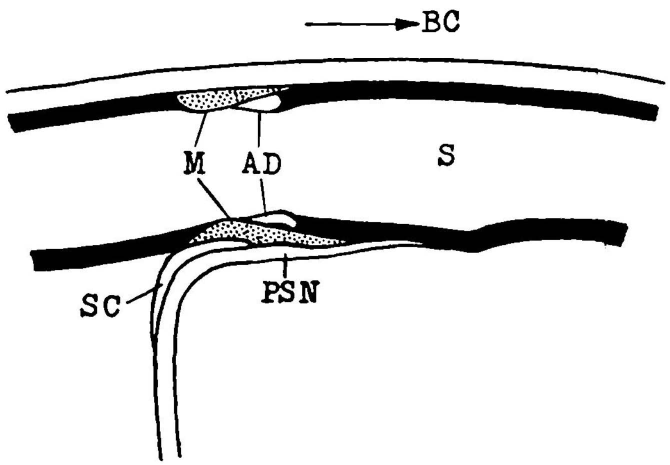


Fig. 5 — **Structure of prochoanitic septal neck of** ***Parapopanoceras paniculatum*** **POPOW**, N 15/312, beginning of seventh whorl (x 50). Eastern Taimyr, Tswetkov Cape, Anisian, kotschetkovi zone.

Structure du col septal prochoané de ***Parapopanoceras paniculatum*** **POPOW** ; début du septième tour. Taimyr oriental, cap de Zvetkov, Anisien, zone à Kotschetkovi.

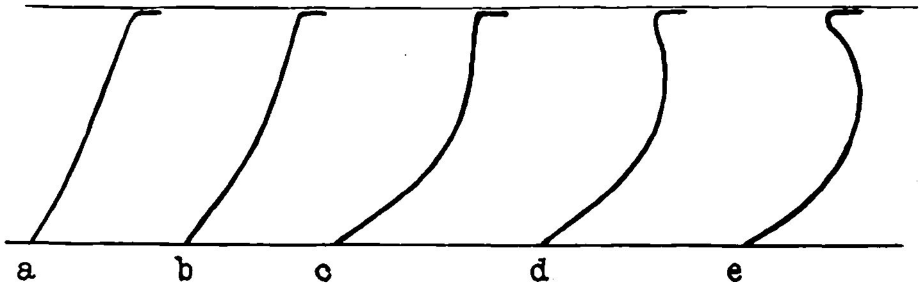
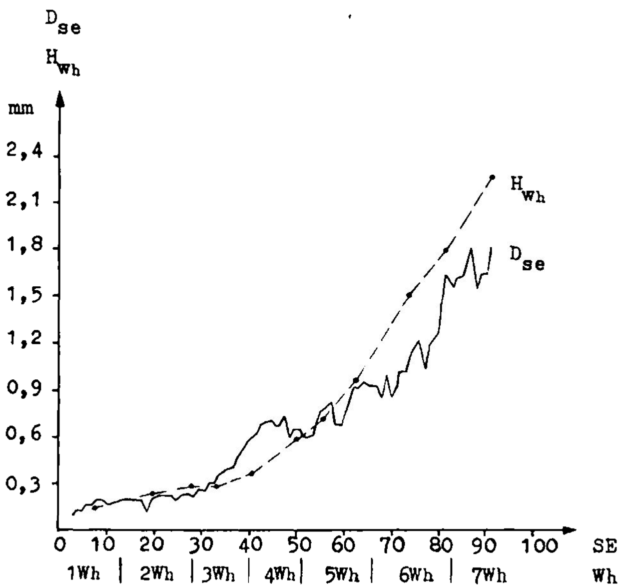


Fig. 6 — **Changing form of septal section in median plane of *Parapopanoceras paniculatum* Popow**, N 13/312 : a - end of third whorl, b - end of fourth whorl, c - end of fifth whorl, d - end of seventh whorl, e - middle of eighth whorl, last septum before body chamber. Kharaulakh range, the Kengdey basin, Artist-Agatyn-Yurege Creek, Anisian, kotschetkovi zone.

Changements de la forme de la section des septums dans le plan médian chez *Parapopanoceras paniculatum* Popow : a - fin du troisième tour ; b - fin du quatrième tour ; c - fin du cinquième tour ; d - fin du septième tour ; e - milieu du huitième tour, dernier septum avant la chambre d'habitation. Chaîne de Kharaoulakhe, bassin de Kengdei, ruisseau d'Artiste-Agatyne-Juregée, Anisien, zone à kotschetkovi.



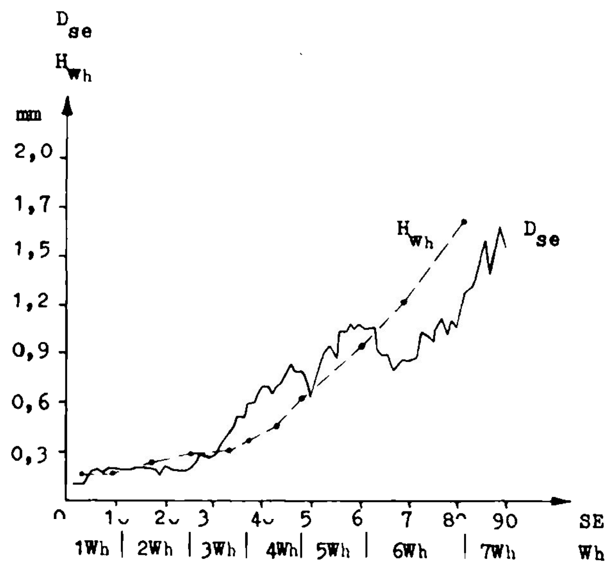


Fig. 7 — **Interdependence between the height of the shell's whorl and the length of hydrostatic chamber of *Parapopanoceras asseretoi*** Dagys & Ermakova, N 18/312. Kharaulakh range, the Kengdey basin, Artist-Agatyn-Yurege Creek, Anisian, rotelliforme zone.

Relation entre la hauteur du tour de la coquille et la longueur de la chambre hydrostatique de *Parapopanoceras asseretoi* Dagys & Ermakova. Chaîne de Kharaoulakhe, bassin de Kengdei, ruisseau d'Artiste-Agatyne-Juregée, Anisien, zone à rotelliforme.

Fig. 8 — **Interdependence between the height of the shell's whorl and the length of hydrostatic chamber of *Parapopanoceras asseretoi*** Dagys & Ermakova, N 22/312. Kharaulakh range, Artist-Agatyn-Yurege Creek, Anisian, rotelliforme zone.

Relation entre le hauteur du tour de la coquille et la longueur de la chambre hydrostatique de *Parapopanoceras asseretoi* Dagys & Ermakova. Chaîne de Kharaoulakhe, bassin de Kengdei, ruisseau d'Artiste-Agatyne-Juregée, Anisien, zone à rotelliforme.

In the process of ontogeny of *Parapopanoceras* representatives the relations of such parameters of the shell as the height of a whorl and the distance between septa change several times (fig. 7, 8). Till about the middle of the third whorl (30-33 septa) the shell of *Parapopanoceras* grows extremely slowly, the height of the whorl being about equal to the distance between septa. At the second stage (middle of the third whorl - end of the fourth whorl) the distance between septa increases and considerably exceeds the height of the whorl, consequently decreasing the number of septa per whorl (there are 10-11 septa on the fourth whorl, while the number of septa on the second whorl is 13-15). On the fourth whorl the distance between septa and the height of the whorl are about the same again, but beginning with the sixth whorl (63-66 septa) the height of the whorl becomes greater than the distance between septa. There are as many as 15-20 septa on the sixth whorl. Interdependence of these parameters is obvious : the greater is the height of the whorl, the greater is the number of septa per whorl and, respectively, the shorter is the distance between septa. Information on the number of septa per whorl of a shell of some *Parapopanoceras* species studied is given in table 3.

The number of whorls in phragmocone is normally 6-7, seldom 9 (*Parapopanoceras* sp., specimen N 17/312). The length of body chamber is 1-1.5 whorls.

MATERIAL :

10 specimens - N 5/312, 9-10/312, 18-23/312, 13/312 - Kharaulakh range, the Kengdey basin, the Artist-Agatyn-Yurage Creek. 3 specimens - N 11/312, 14/312, 16/312 - Kharaulakh range, the Darky River. 2 specimens - N 15/312, 17/312 - East Taimyr, cape of Tsvetkov. 3 specimens - N 6-8/312 - the lower course of the Olenek River, Karangati mountain. Specimen N 12/312 - the Kolyma basin, the Nyomuk River.

Species and number of specimen	Number of serta per whorl					
	1	2	3	4	5	6
Parapopanoceras asseretoi DAGYS & ERMAKOVA, N 18/312	13	15	11	11	16	17
P. asseretoi DAGYS & ERMAKOVA, N 21/312	10	13	10	10	13	15
P. asseretoi DAGYS & ERMAKOVA N 22/312	11	14	12	11	13	20
Indigirites krugi POPOW, N 28/312	9	12	12	17	17	
Nathorstites argatassensis (POPOW), N 34/312	9	10	11	12	12	17

Tabl. 3 — **Number of septa per whorl of species of *Parapopanoceras, Indigirites* and *Nathorstites*.**

Nombre de septums par tour chez les espèces des genres *Parapopanoceras, Indigirites* et *Nathorstites*.

Family **HUNGARITIDAE** Waagen, 1895

Subfamily **LONGOBARDITINAE** Spath, 1951

Genus **Indigirites** Popow, 1946

pl. 5, fig. 3,4,6

Type species : *I. krugi* Popow, 1946, Ladinian, North-East of the USSR, upper reaches of the Indigirka river.

Ontogenetic development :

Ontogenetic development of suture line and morphological signs of 2 specimens of the type species have been studied (N 25/312 and 35/312).

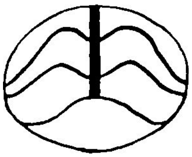


Fig. 9 — **Protoconch and first three septa of *Indigirites krugi* Popow**, N 25/312 (x 25). Mouth of the Olenek, Tumul Cape, Ladinian, lenticularis zone.

Protoconque et trois premiers septums d'*Indigirites krugi* Popow. Embouchure de l'Olenek, cap de Toumoul, Ladinien, zone à lenticularis.

Protoconch is of ellipsoidal form (fig. 9). First line is of latisellate type, second line is four-lobed -VL : ID, its outer part consisting of a shallow ventral lobe and a wide lateral lobe. The first three whorls form a semiinvolute shell with wide plano-rounded venter. Starting from the end of the first - beginning of the second whorl (H = 0.55 mm, W = 1.0 mm) small tubercles appear at the umbilical shoulder. The shell width on its first whorls exceeds the height considerably (fig. 11). With H = 0.55 mm and W = 1.0 mm (fig. 10a) the line is five-lobed - VLU^1 : ID. Lobe U^1 formed at the apex of saddle L/I is located in the vicinity of seam on the shell's outside. Ventral lobe is deepest and whole. Lobe I is on the seam. With H = 0.75 mm and W = 1.5 mm (end of the second - beginning of third whorl) lobe I is shifted to the inner side, lateral lobe becomes deepest (fig. 10b). At this stage the shell is barrel-shaped, the whorls are trapezoidal in section, the umbilicus is moderately wide and surrounded by near-umbilical frill covered with small tubercles. On the third whorl the venter tapers, keel becomes distinct on it. With H = 1.1 mm and W = 2.3 mm (third whorl) previously formed lobe U^2 can be observed in the vicinity of the seam, division of ventral lobe into two components starts at this stage (fig. 10c). With H = 1.3 mm and W = 2.8 mm (third whorl) lobe U^3 can be seen on the inner side of the whorl near the seam (fig. 10d). At this stage ventral lobe is divided into two parts by a short saddle. Lateral lobe is deepest and widest, dorsal lobe is narrow and deep. On the fourth whorl, with H = 1.6 mm and W = 3.6 mm, there appears lobe U^4 on the outer side of the shell near the seam (fig. 10e). Suture line formula at this stage is $(V_1V_1)LU^1U^2U^4 : U^3ID$. Lateral sides of the shell flatten on the fourth whorl, the whorls themselves becoming more volumetric (fig. 11). The height of whorl starts growing rapidly. With H = 2.5 mm and W = 5.0 mm (fourth whorl) denticles appear at the base of lateral and first umbilical lobes. Dorsal lobe becomes bifid (fig. 10f). Lobe U^5 originates near the seam on the outer side of the whorl. With H = 3.0 mm and W = 5.5 mm (fourth whorl) it is shifted to the inner side of the shell (fig. 10g). Main lobes and saddles acquire phylloid features, branches of ventral lobe become indented. The s lis f pp c g l concerning the seam apparently is retained at later stages of the development of shell.

An adult shell has on the fifth whorl a narrow umbilicus, wide flattened lateral sides and thin sharp venter. The shell is maximally inflated in umbilicus area. Near umbilical shoulder there are sparse tumuli from which crescentiform poorly developed low plicae radiate, these die out without reaching venter. Lateral sides are covered with very thin slightly curved lines of growth. The section of the shell on the last whorl is triangular, elongated in height. The line of the shell on its fifth whorl, with H = 17.5 mm and W = 9.5 mm, on the outer part consists of 9-10 lobes (fig. 10h). Ventral lobe is deepest, divided into two indented branches by a high median saddle. Lateral and first umbilical lobes are of almost the same depth, narrow, strongly dissected at the base and on the side walls. The other lobes are considerably shorter, indented at the base, regularly diminishing towards the seam. The main saddles are bulbous, the others are rounded. The suture line formula is $(V_1V_1)LU^1U^2U^4U^6U^8U^{10}U^{12} : U^{11}U^9U^7U^5U^3I(D_1D_1)$.

Dimensions in mm and relations. 1

	D	H	D_u	W	H/D	D_u/D	W/D
Specimen N 25/312	27?	17,5	2	9,5	0,64	0,07	0,35
Specimen N 35/312	23,5	13,5	2	9,5	0,57	0,08	0,40

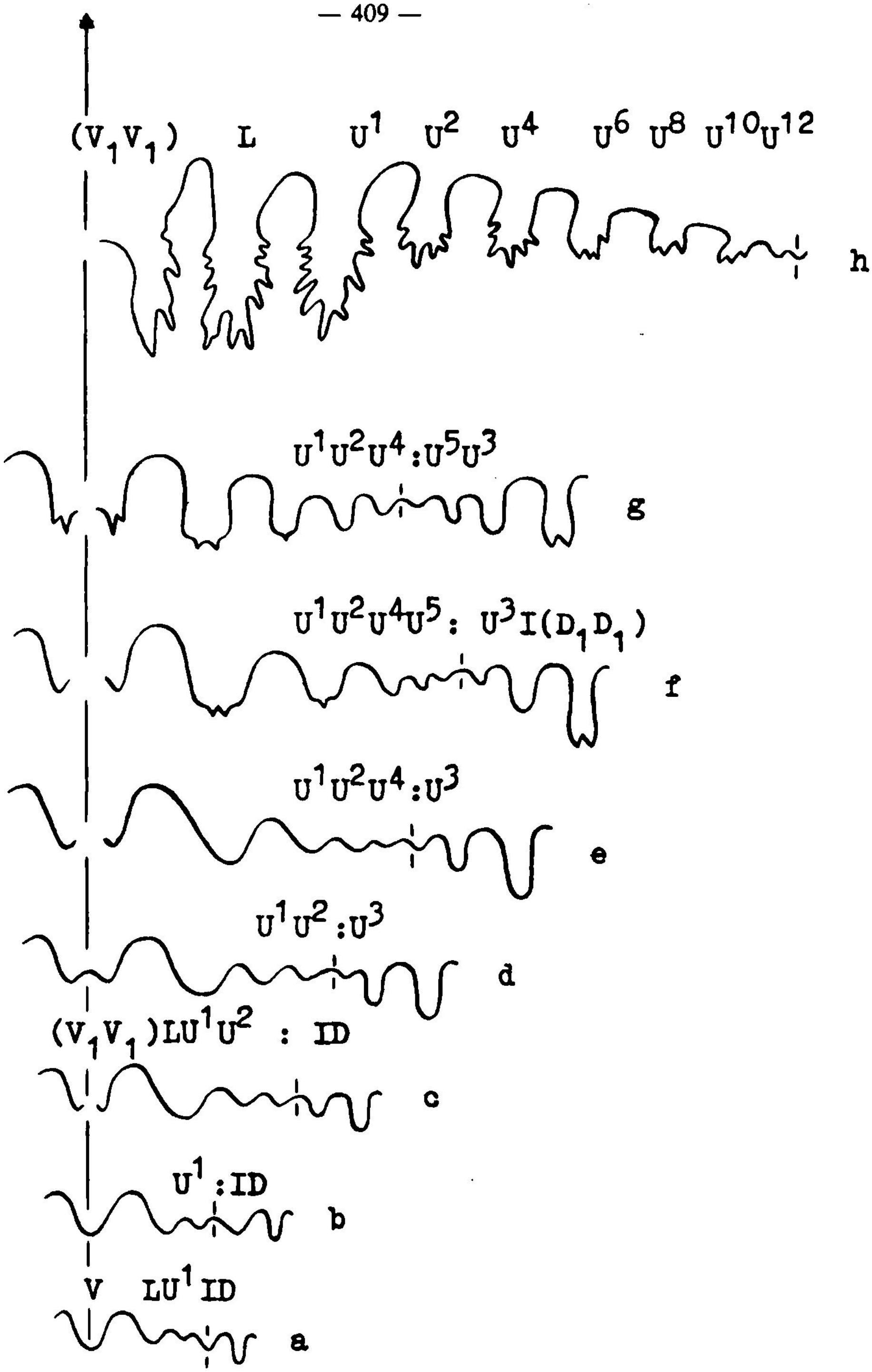


Fig. 10 — **Ontogenetic development of suture line of *Indigirites krugi* Popow**, all stages drawn from N 25/312. Tous les stades sont dessinés d'après N 25/312.
a - with H = 0.55 mm and W = 1.0 mm (end of first-beginning of second whorl) (x 17). Fin du premier tour, début du deuxième tour ; b - with H = 0.75 mm and W = 1.5 mm (end of second - beginning of third whorl) (x 12). Fin du deuxième tour, début du troisième tour ; c - with H = 1.1 mm and W = 2.3 mm (third whorl) (x 12). Troisième tour ; d - with H = 1.3 mm and W = 2.8 mm (third whorl) (x 12). Troisième tour ; e - with H = 1.6 mm and W = 3.6 mm (fourth whorl) (x 12). Quatrième tour ; f - with H = 2.5 mm and W = 5mm (fourth whorl) (x 8). Quatrième tour ; g - with H = 3.0 mm and W = 5.5 mm (fourth whorl) (x 6). Quatrième tour ; h - with H = 17.5 mm and W = 9.5 mm (fifth whorl) (x 4). Cinquième tour.
Mouth of the Olenek, Tumul Cape, Ladinian, lenticularis zone. Embouchure de l'Olenek, cap de Toumoul, Ladinien, zone à lenticularis.

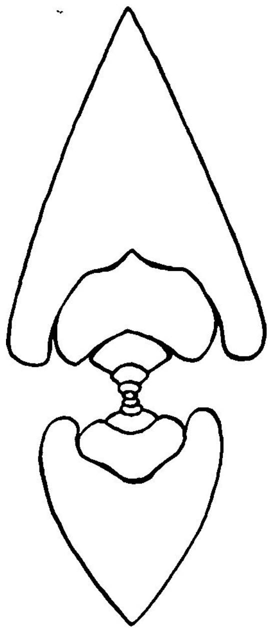


Fig. 11 — **Cross section of *Indigirites krugi* Popow shell** N 35/312 (x 3,5). Mouth of the Olenek, Tumul Cape, Ladinian, lenticularis zone.
Section transversale de la coquille d'*Indigirites krugi* Popow, spécimen N 35/312 (x 3,5). Embouchure de l'Olenek, cap de Toumoul, Ladinien, zone à lenticularis.

INTERNAL STRUCTURES :

The internal structure of four specimens of the type species of genus *Indigirites* was studied. Protoconch is small (D^1 = 0.35-0.37 mm) Caecum is small (C^1 = 0.07-0.08 mm, C^2 = 0.07 mm), almost spheroidal. The length of prosiphon is 0.1-0.12 mm. Ammonitella body chamber is short, the angle of primary varix is 290-300°. Diameter of ammonitella ranges from 0.6 to 0.68 mm. Siphuncle at all stages of ontogeny occupies ventral position. Change of retrochoanitic septal necks for prochoanitic septal necks was noted in the middle of the fourth whorl (3.5 wh.), the transition stage which is characterized by the formation of necks of transitional (amphichoanitic) type taking a little less than half a whorl. The number of whorls in phragmocone amounts to 5.

MATERIAL :

5 specimens - N 24-25/312, 27-28/312, 35/312 - the Olenek River mouth, cape Tumul. Specimen N 29/312 - East Taimyr, cape of Tsvetkov ; specimen N 26/312 - the Kolyma Basin, the Olguya River.

Family **NATHORSTITIDAE** Spath, 1951

Genus **Nathorstites** Böhm, 1903

pl. 5, fig., 5,7,8

Type species : *Popanoceras mcconnelli* Whiteaves, 1899, Carnian (?) stage of British Columbia.

Ontogenetic development :

Ontogenetic development of suture line and morphological signs of *Nathorstites* of one specimen *N. mcconnelli* (Whiteaves) - N 23/831 - was studied (fig. 12).

Earliere volutions are near-spheroidal. With H = 0.4 mm and W = 0.7 mm (fig. 12a) the line is four-lobed -VL : ID. With H = 0.5 mm and W = 0.8 mm (fig. 12b) the saddle L/I is stretched and signs of lobe U^1 become distinct on it. With H = 1.2 mm and W = 1.6 mm (fig. 12c) the line is six-lobed, on lobe U^1 shifted to the outer side, lobe U^2 is lying on the seam. Wi˙ H = ˙.˙ mm an˙ W = 2.9 mm ´fig. 12d) lobe U^2 is shifted to the outer side, lobe U^3 appears on the seam. Ventral lobe is divided into two tapered branches by a short median saddle. At the base of dorsal lobe there appear denticles. With this height of the whorl the shell is smooth with bulging lateral and wide rounded ventral sides. With H = 3.5? mm and W = 7.0 mm (fig. 12e) slight elongated tubercles appear near umbilical slope. The line at this stage is eight-lobed - $(V_1V_1)LU^1U^2U^4$: U^3ID. Further on, in the process of growth lateral sides of the shell flatten, venter tapers, slight keel appears on it. With H = 4.5 mm and W = 10.0? mm (fig. 12f) lobe U^5 appears on the seam. Ventral lobe is bifid with indented branches and is of the same depth as lateral lobe. Umbilical lobes are simple, much shorter than lateral lobe. All lobes at the base are crenulate. The saddles are wide and rounded. The line formula is $(V_1V_1)LU^1U^2U^4$: U^5U^3ID. The adult shell is involute, inflated, with rounded venter on phragmocone and slightly tapering venter on the body chamber. In the near-umbilical part of the shell slight tubercles are developed and short folds radiating from them. Section of the last whorl is low, crescentiform. Umbilicus is narrow, with steep umbilical wall.

Internal structure :

Internal structure of four species was studied by us - *N. mcconnelli* (Whiteaves), *N. gibbosus* Stolley, *N. lenticularis* (Whiteaves), *N. argatassensis* (Popow).

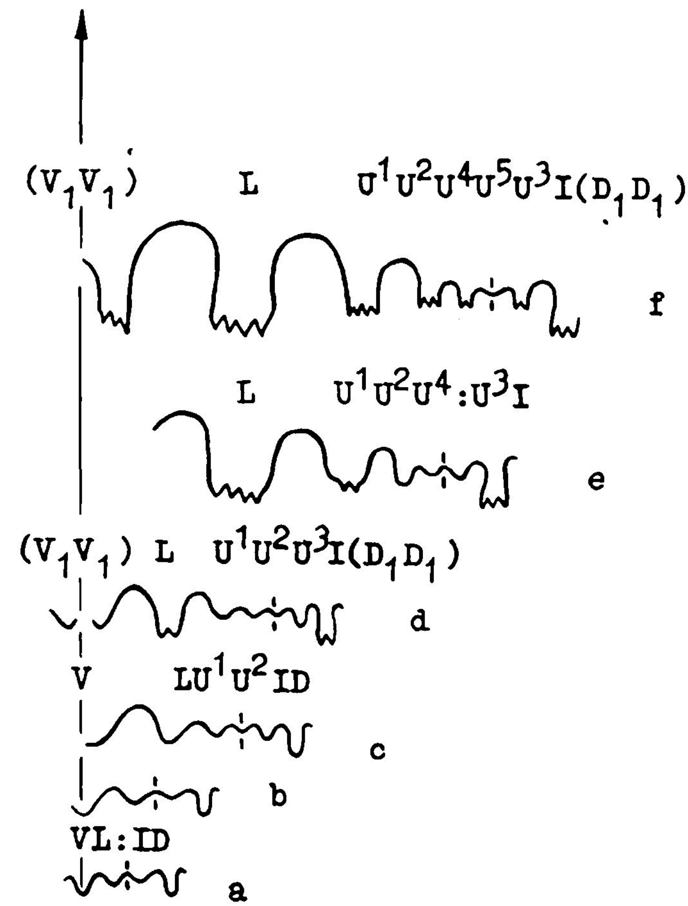


Fig. 12 — **Ontogenetic development of suture line of *Nathorstites mcconnelli* (Whiteaves)**, all stages are drawn from N 23/831 : a - with H = 0.4 mm and W = 0.7 mm (x 12.5), b - with H = 0.5 mm and W = 0.8 mm (x 12.5), c - with H = 1.2 mm and W = 1.6 mm (x 8), d - with H = 1.4 mm and W = 2.9 mm (x 8), e - with H = 3.5? mm and W = 7.0 mm (x 6), f - with H = 4.5 mm and W = 10.0? mm (x 5). Kharaulakh range, the Kengdey basin, Ladinian, lenticularis zone.

Evolution ontogénétique de la ligne de suture de *Nathorstites mcconnelli* (Whiteaves), tous les stades sont dessinés d'après N 23/831. Chaîne de Kharaoulakhe, bassin de Kengdei, Ladinien supérieur.

Protoconch is small (D^1 = 0.26-0.45 mm), near-spheroidal. Caecum is small (C^1 = 0.06-0.07 mm), spheroidal, connected to protoconch wall by prosiphon band the length of which is 0.09 mm. Ammonitella body chamber is short, its diameter ranging from 0.54 mm to 0.765 mm. The angle of primary varix is 270°. Siphuncle occupies ventral- marginal position at all stages of the development of the shell. Genus *Nathorstites* is distinguished among other ceratites for its late change of the types of septal necks. The transition stage of the species studied (transition from retrochoanitic to prochoanitic septal necks) was observed at the end of fourth, at the fifth or sixth whorls. With *N. lenticularis* (Whiteaves) (specimen N 31/312) it starts at the end of fifth-beginning of sixth whorl (fig. 13). At the beginning of the sixth whorl this specimen has retrochoanitic septal necks 0.1 mm long having at their anterior end a fold directed to the aperture mouth. In the middle of the sixth whorl prochoanitic element of the neck is distinct, its length being 0.1 mm. The length of the cuff protruding backwards is 0.09 mm. At the end of the sixth whorl the length of prochoanitic necks is already 0.32 mm, cuff length is 0.1 mm. This species has septal membranes of two types : 1. the one connecting the back septal face to the siphuncle cover and 2. the one connecting the front septal face to adoral end of the septal neck.

MATERIAL :

Specimen N 24/831 - the Omolon River Basin, the Kegali River ; N 25/831 - Svalbard Archipelago, the isle of Edge ; N 30/312 - the Yana-Okhotskaya Basin ; 4 specimens - N 31-34/312 - the Kolyma Basin, the Olguya River.

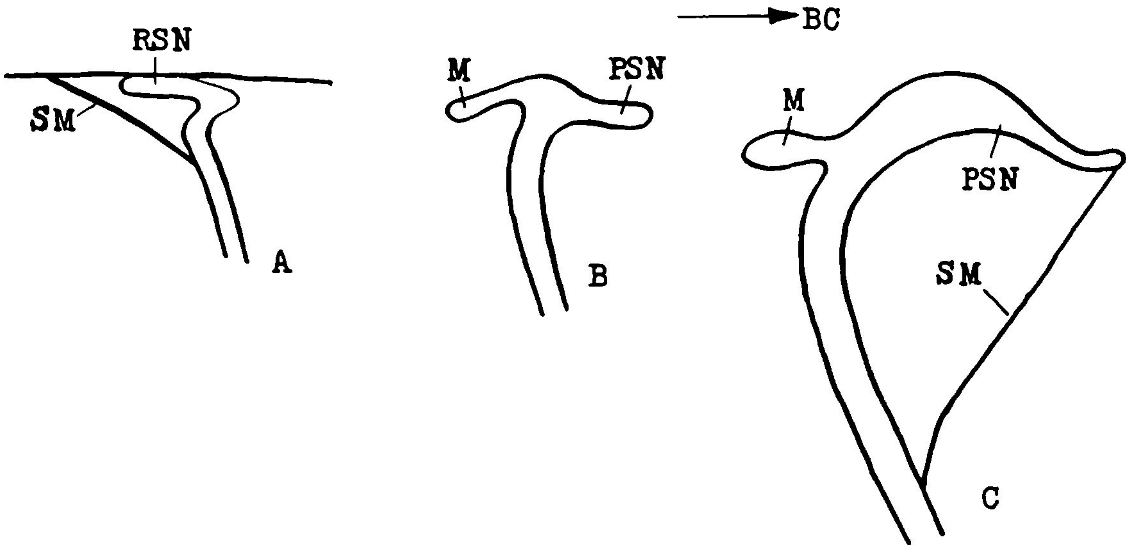


Fig. 13 — **Septal neck transition from retrochoanitic to prochoanitic type in *Nathorstites lenticularis* (WHITEAVES)** N 31/312 : A - retrochoanitic septal neck, beginning of sixth whorl (x 100), B - septal neck of amphichoanitic (transitional) type, middle of sixth whorl (x 100), C - prochoanitic septal neck, end of sixth whorl (x 100). The Kolyma basin, the Olguya River, Ladinian, lenticularis zone.

Passage du col septal rétrochoané au col septal prochoané chez *Nathorstites lenticularis* (WHITEAVES) N 31/312 : A - col septal retrochoané, début du sixième tour, B - col septal de type amphichoané (intermédiaire), fin du sixième tour. Bassin de Kolyma, fleuve Olgouya, Ladinien, zone à lenticularis.

IV — PHYLOGENETIC PATTERNS

Information that has been accumulated so far on internal structure of mesozoic Ammonoidea (Zakharov, 1978 ; Birkelund, 1981 ; Drushtchic, Doguzhayeva, 1981 and others) show that these signs can be used to advantage to define the status and phylogenetic patterns of certain taxons. The most stable and, consequently, the most important signs of internal structure are, according to the authors, the following : 1. position of siphuncle, 2. dimensions and shape of initial formations (caecum, protoconch, ammonitella), 3. angle of primary varix, 4. moment and nature of changing the types of septal necks, 5. change in the shape of septum in median section in the process of ontogeny. These signs can be applied for distinguishing categories belonging to different taxonomic units. More often than not determination of taxonomy is achieved through analysis of a whole complex of data. More seldom delineation is possible by two, even one sign. At the same time the same sign can be used to distinguish different taxons of different systematic groups of Ammonoidea.

Parapopanoceratidae are characterized by : general type of suture line development ; spheroidal, generally small protoconch and small caecum ; short ammonitella body chamber ($\alpha = 270°$) ; change in the type of septal necks at the end of second - middle of third whorl.

Stenopopanoceras and *Parapopanoceras* genera studied differ in the position of siphuncle at the initial whorls. Representatives of genus *Stenopopanoceras* have ventral and near-ventral siphuncle on the first whorl, those of *Parapopanoceras* mainly have central siphuncle.

Some investigators (Bychkov & *alii*, 1976 ; Zakharov, 1978 and others) consider *Parapopanoceras* belonging to family Megaphyllitidae. Investigations carried out by V.V. Drushtchic & L.A. Doguzhaeva (1981) showed that in such parameters of their internal structure as the position of siphuncle, diameter of ammonitella and the moment of changing septal necks genus *Megaphyllites* differs greatly from genus *Parapopanoceras*. Consequently they are not to be considered within the same family.

Early triassic genus *Prosphingites* should be regarded as ancestor to Parapopanoceratidae ; representatives of the former, apart from similar morphology of the shell, were found to have similar type of suture line development (shifting of lobes with odd numbers towards outer side in the course of ontogeny) and similar signs of internal structure (near-ventral and ventral position of siphuncle on the first whorl) (Zakharov, 1978).

Genera *Nathorstites* and *Indigirites* are also characterized by the same type of suture line development (shifting of umbilical lobes with even numbers to the outer side in the process of ontogeny), small spheroidal protoconch and caecum and ventral position of siphuncle at all stages of ontogeny. But in spite of certain similarity representatives of these genera differ in the following parameters of their internal structure : 1. Angle of primary varix (*Indigirites* - 290-300°, *Nathorstites* - 270°). 2. Moment of septal neck change (*Indigirites* - 3.5 th whorl), *Nathorstites* - 4th-6th whorl). Suture line of *Indigirites* consists of a larger number of elements and is more phylloid compared to suture line of *Nathorstites*. Up to now status of these genera was not clear. Characteristic features of *Nathorstites* - presence of enveloping layers, late moment of septal neck change - all this us believe that it is possible to isolate an independent family Nathorstitidae, which was first suggested by L. Spath (1951) and supported by many investigators (Kummel, 1957 ; Tozer, 1971 ; Kortchinskaya, 1972). *Nathorstites* differs greatly from representatives of family Megaphyllitidae (Doguzhayeva, 1973 ; Drushtchic & Dogushayeva, 1981) into which it was previously included (Popov, 1961 ; Shevyrev, 1968 ; Bychkov & *alii*, 1976). It differs both in the development of suture line and in internal structure.

Previously some investigators considered *Indigirites* to be a synonyme to *Nathorstites* (Tozer, 1961, 1971). The differences established by us suggest validity of genus *Indigirites* isolation. At present most investigators (Tozer, 1981 : Bychkov, 1982 and others) consider *Indigirites* belonging to family Nathorstitidae.

Signs of internal structure and morphological features of *Indigirites* shell are more characteristic for representatives of subfamily Longobarditinae (family Hungaritidae) than for true *Nathorstites*. Like *Indigirites, Longobardites* possess a discoid involute shell with multi-lobed strongly phylloid suture line, the same moment of septal neck change (3.5th whorl) and angle of primary varix (290°). Both genera, *Indigirites* and *Longobardites* have the same type of suture line development (Assereto, 1966).

Some common morphological features of the shell bring together genus *Indigirites* and true *Nathorstites*. These are enveloping layers, shell shape at the early stages of ontogeny, presence of near-umbilical funicle.

On the basis of investigations carried out by us obvious phylogenetic relation between ladinian genera *Indigirites* and *Nathorstites* and anisian genera *Longobardites* and *Grambergia* was established. In the process of its development this group of Ammonoidea forms phylogenetic sequence : *Grambergia -Longobardites - Indigirites - Nathorstites*. Thus, genus *Indigirites* can be regarded either as the final stage of development for Longobarditinae or as the initial stage of development for Nathorstitidae.

Internal structure of *Indigirites* and its morphology are similar to those of *Longobardites* and *Grambergia*. On the other hand, morphologically *Indigirites* is close to *Nathorstites*, but differs from it in its internal structure. Comparison of the main parameters of internal structure of *Grambergia, Longobardites, Indigirites* and *Nathorstites* is made in table 4. The authors believe that when establishing to which family *Indigirites* or *Nathorstites* belong, signs of internal structure should be the basic criterion because it is their changes in the course of onto- and phylogeny that govern morphological features of the shell. Thus, we consider *Indigirites* to belong to family Hungaritidae (subfamily Longobarditinae) and we regard it as the final stage of development of this family.

Family, genus	Position of siphuncle	Septal necks	Ammonitella		Protoconch		Caecum	
			Da	a	D^1	D^2	C^1	C^2
Hungaritidae								
Grambergia	Ventral at all stages	First 2,7 whorls are retrochoanitic the rest prochoanitic	0,91	290-300°	0,52	0,48	0,07	0,07
Longobardites	Ventral at all stages	First 3,5 whorls are retrochoanitic the rest prochoanitic	0,8-0,88	290°	0,40-0,47	0,38-0,44	0,10	0,09
Indigirites	Ventral at all stages	First 3,5 whorls are retrochoanitic, the rest prochoanitic	0,6-0,68	290-300°	0,35-0,37	0,32-0,35	0,07-0,08	0,07
Nathorstitidae								
Nathorstites	Ventral at all stages	Change of septal neck type occurs at the end of 4th, on 5th or 6th whorls	0,54-0,76	270°	0,26-0,45	0,22-0,46	0,06-0,07	0,07

Tabl. 4 — The main signs of internal structure of *Grambergia, Longobardites* and *Nathorstites*.
Principaux indices de la structure interne de *Grambergia, Longobardites, Indigirites* et *Nathorstites*.

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PLATE 1

Figs. 1-2 — *Stenopopanoceras mirabile* POPOW ; N 1/312, thin section :

1 - protoconch and 3 whorls of phragmocone (x 25)

2 - Protoconch and 1.5 whorls of phragmocone (x 50). Kharaulakh Range, Kengdey River, Anisian, taimyrensis zone.

1 - Protoconque et trois tours de phragmocône

2 - Protoconque et un tour et demi de phragmocône. Chaîne de Kharaoulakhe, ruisseau de Kengdei, Anisien, zone à taimyrensis.

Figs. 3-5 — *Stenopopanoceras mirabile* POPOW ; N 2/312.

3 - side view, life-size

4 - polished section, life-size

5 - polished section five whorls of phragmocone (x 10).

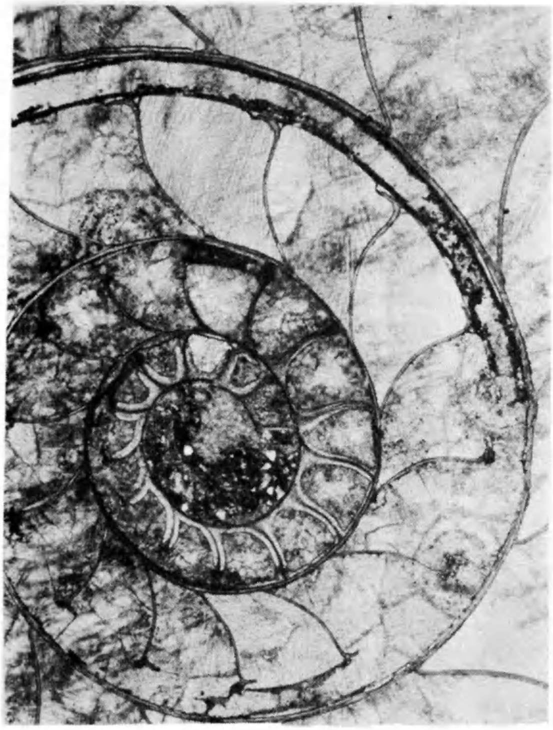
Eastern Taimyr, Cape of Tsvetkov, Anisian, taimyrensis zone.

3 - vue latérale, grandeur nature

4 - Section polie, grandeur nature

5 - Section polie, cinq tours de phragmocône (x 10)

Taimyr oriental, Cap de Zvetkov, Anisien, zone à taimyrensis.



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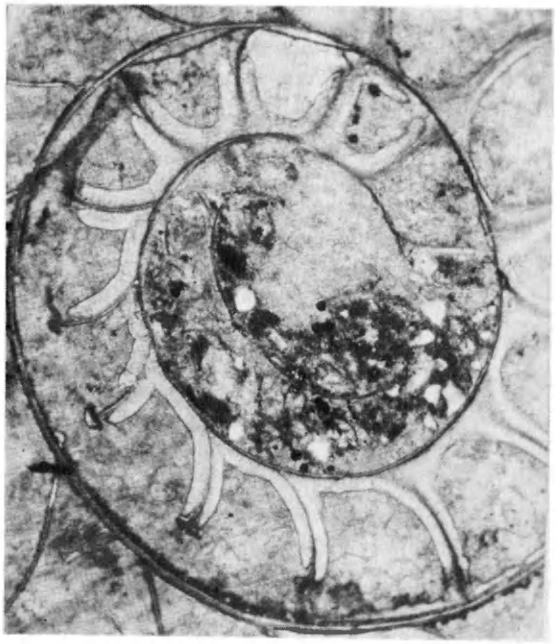

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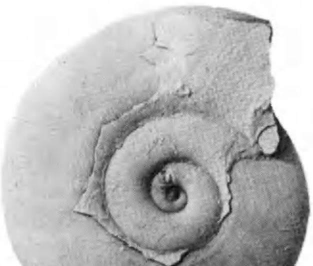

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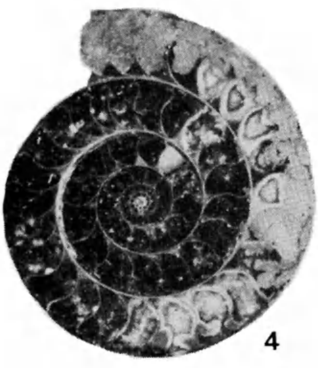

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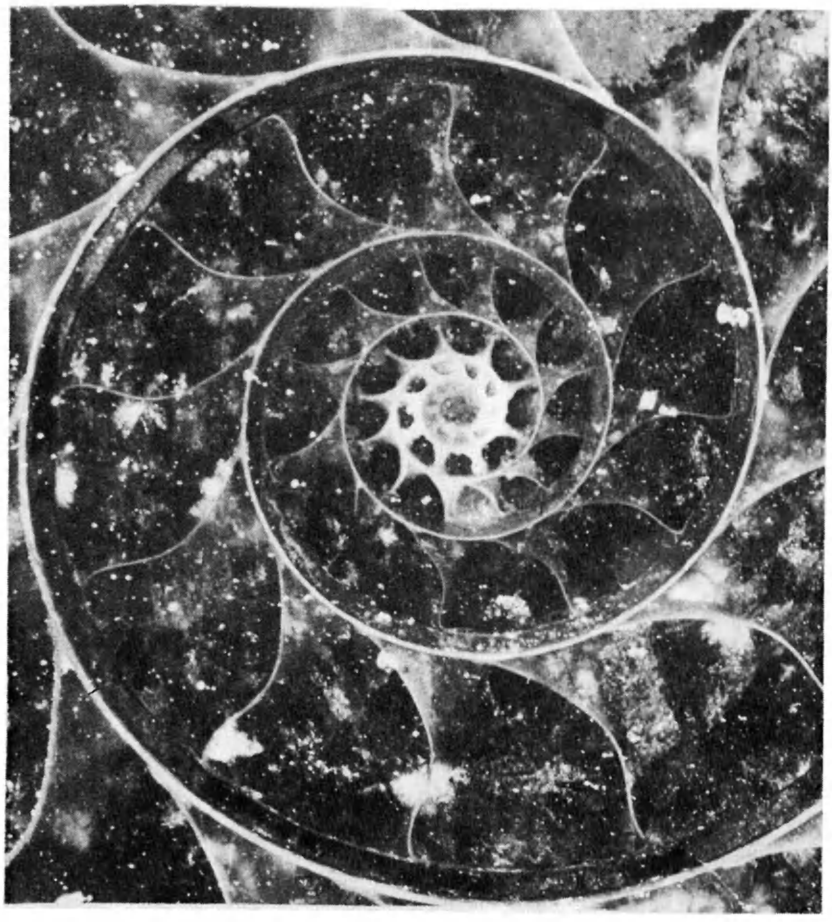

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PLATE 2

Fig. 1 — *Parapopanoceras medium* **McLearn** ; N 5/312 : a - oral view. b - side view, life-size, Kharaulakh Range, Artist-Agatyn-Yurege Creek, Anisian, tardus zone.

a - vue orale. b - vue latérale, grandeur nature. Chaîne de Kharaoulakhe, ruisseau d'Artiste-Agatyne-Juregée, Anisien, zone à tardus.

Figs. 2-3 — *Parapopanoceras medium* **McLearn**.
2 - N 6/312, polished section, protoconch and four whorls of phragmocone (x 20).
3 - N 7/312, polished section, protoconch and four whorls of phragmocone (x 20).
Lower course of the Olenek River, Karangati mountain, Anisian, taimyrensis zone.

2 - Spécimen N 6/312, section polie, protoconque et quatre tours de phragmocône.
3 - Spécimen N 7/312, section polie, protoconque et quatre tours de phragmocône.
Cours inférieur de l'Olenek, Monts de Karangati, Anisien, zone à taimyrensis.

Fig. 4 — *Parapopanoceras janaense* (**Popow**) ; N 11/312 : a - side view. b - oral view, life-size. Kharaulakh Range, Darky River, Anisian, kotschetkovi zone.

a - vue latérale. b - vue orale, grandeur nature. Chaîne de Kharaoulakhe, fleuve Darky, Anisien, zone à kotschetkovi.

Fig. 5 — *Parapopanoceras janaense* (**Popow**) ; N 12/312, polished section seven whorls of phragmocone (x 3). Kolyma River basin, Anisian, kotschetkovi zone.

Section polie sept tours de phragmocône. Bassin de la Kolyma, Anisien, zone à kotschetkovi.

Fig. 6 — *Parapopanoceras paniculatum* **Popow** : N 13/312 : a - side view. b - oral view, life-size. Kharaulakh range, Artist-Agatyn-Yurege Creek, Anisian, kotschetkovi zone.

a - vue latérale. b - vue orale, grandeur nature. Chaîne de Kharaoulakhe, ruisseau d'Artiste-Agatyne-Juregée, Anisien, zone à kotschetkovi.

Fig. 7 — *Parapopanoceras sp.* ; N 14/312, thin section, protoconch and four whorls of phragmocone (x 25). Kharaulakh range, the Darky River, Anisian, kotschetkovi zone.

Lame mince protoconque et quatre tours de phragmocône. Chaîne de Kharaoulakhe, fleuve Darky, Anisien, zone à kotschetkovi.

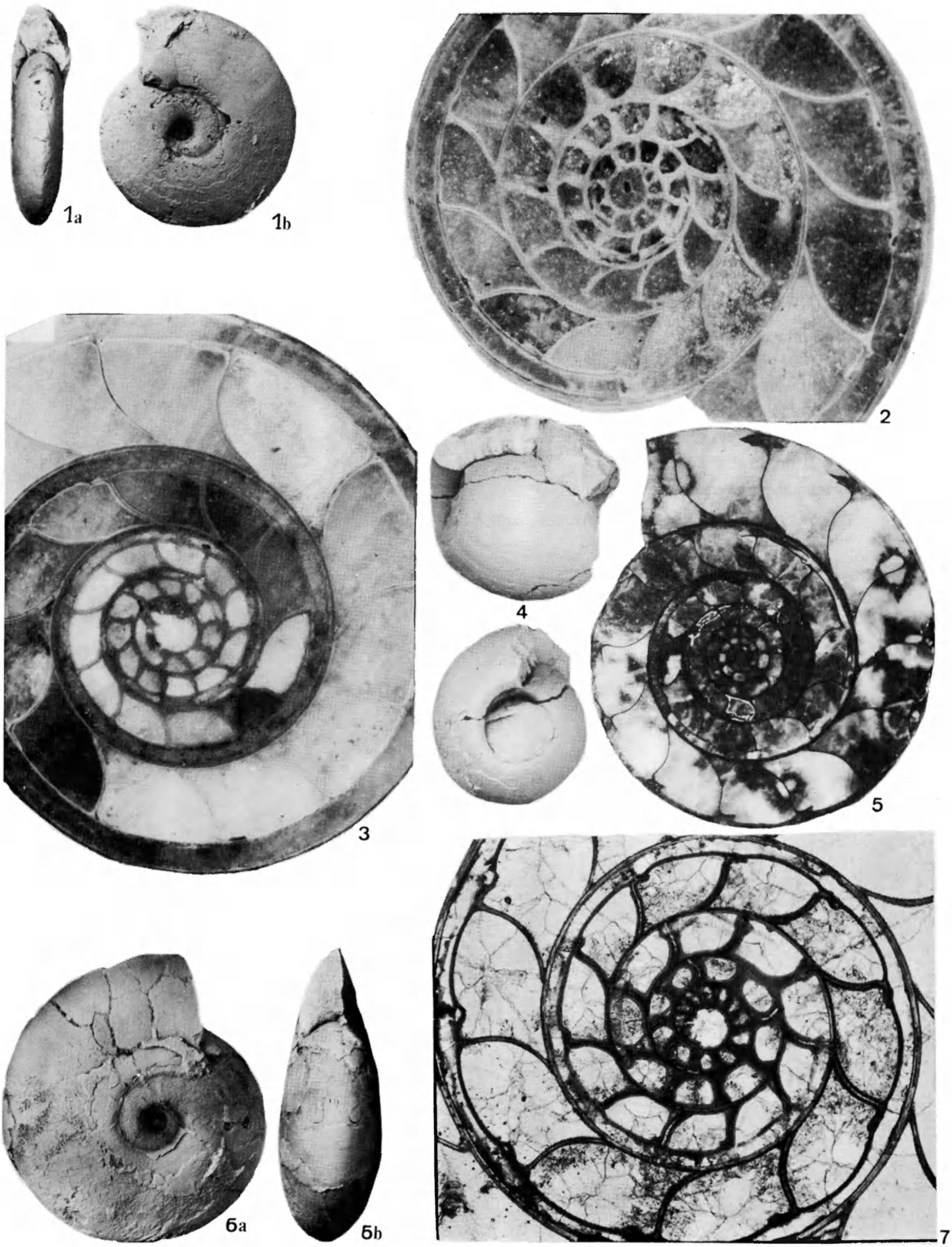
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PLATE 3

Figs. 1-5 — ***Parapopanoceras paniculatum*** **POPOW**. N 15/312, thin section.

1-4 - Prochoanitic septal necks.

1 - in the middle of sixth whorl (x 50).

2 - at the beginning of sixth whorl (x 100).

3 - at the end of fifth whorl (x 100).

4 - at the end of sixth whorl (x 50).

5 - median section of the shell (x 10).

Eastern Taimyr, cape of Tsvetkov, Anisian, kotschetkovi zone.

Lame mince

1-4 - Cols septaux prochoanés.

1 - au milieu du sixième tour.

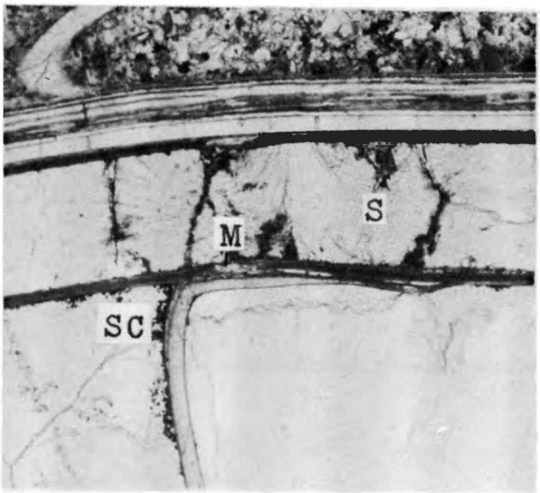
2 - au début du sixième tour.

3 - à la fin du cinquième tour.

4 - à la fin du sixième tour.

5 - section transversale de la coquille.

Taimyr oriental, cap de Zvetkov, Anisien, zone à kotschetkovi.



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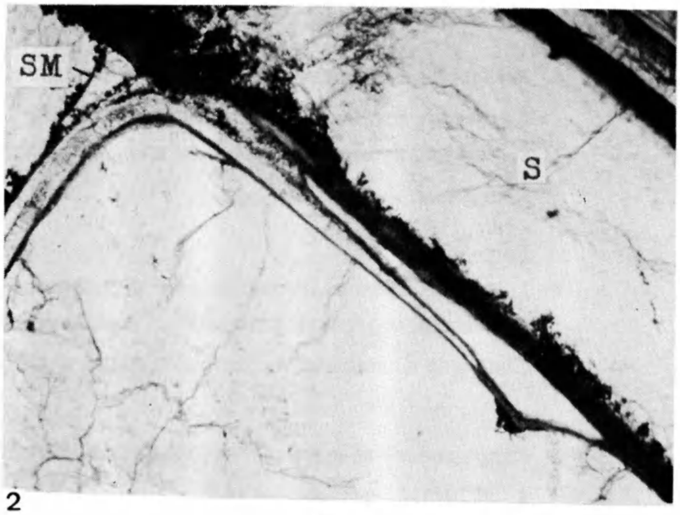

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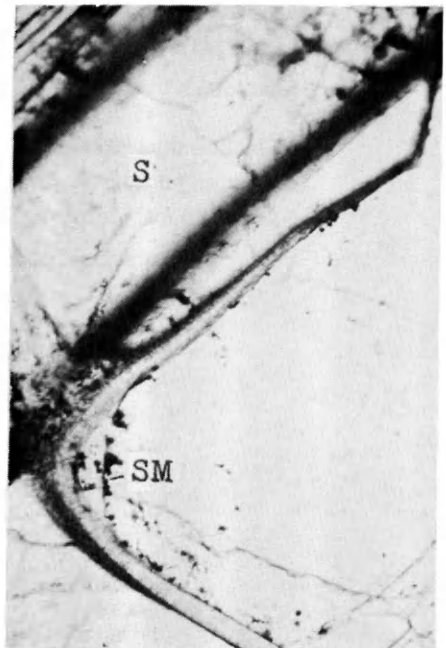

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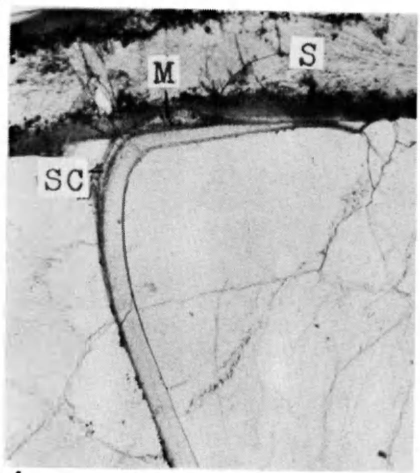

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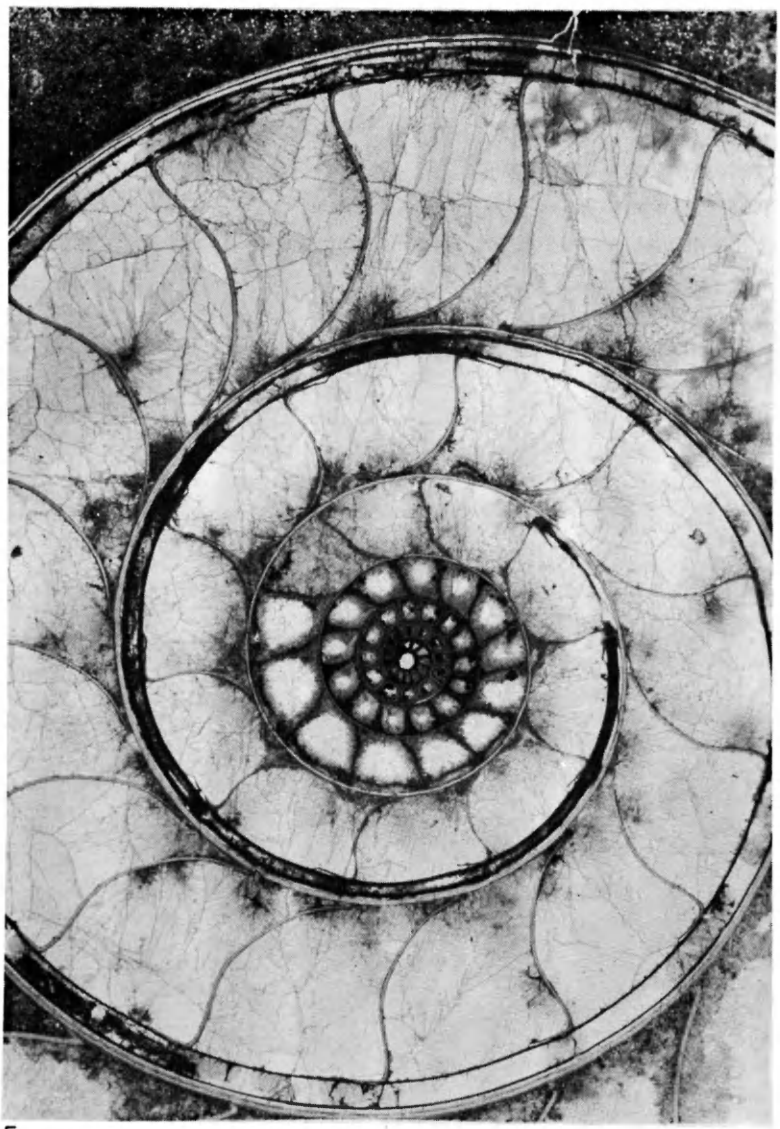

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PLATE 4

Figs. 1-2 — *Parapopanoceras asseretoi* DAGYS & ERMAKOVA. N 18/312, thin section.

1 - caecum, protoconch and first whorl of phragmocone (x 100).

2 - caecum, prosiphon, proseptum and primary septum (x 250).

Kharaulakh range, Artist-Agatyn-Yurege Creek, Anisian, rotelliforme zone.

Lame mince.

1 - caecum siphonal, protoconque et premier tour du phragmocône.

2 - caecum, prosiphon, proseptum et septum primaire.

Chaîne de Kharaoulakhe, ruisseau d'Artiste-Agatyne-Juregée, Anisien, zone à rotelliforme.

Figs. 3-5 — *Parapopanoceras asseretoi* DAGYS & ERMAKOVA.

3 - N 19/312, cross section (x 5).

4 - N 20/312, polished section, protoconch and two whorls of phragmocone (x 60).

5 - N 21/312, thin section, protoconch and three whorls of phragmocone (x 50).

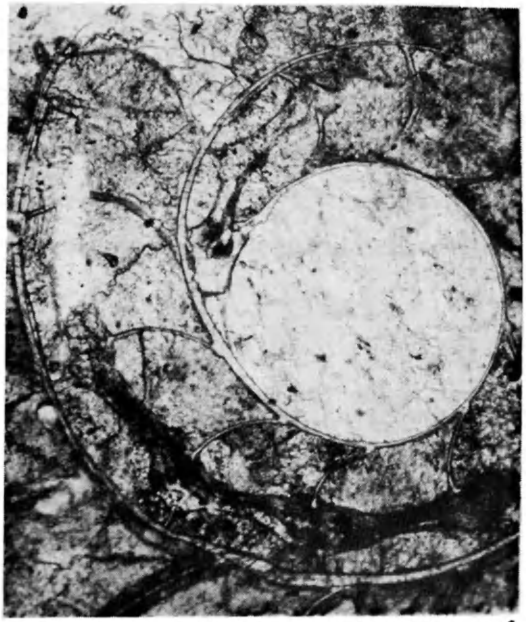
Kharaulakh range, Artist-Agatyn-Yurege Creek, Anisian, rotelliforme zone.

3 - section transversale.

4 - section polie, protoconque et deux tours de phragmocône.

5 - lame mince, protoconque et trois tours de phragmocône.

Chaîne de Kharaoulakhe, ruisseau d'Artiste-Agatyne-Juregée, Anisien, zone à rotelliforme.



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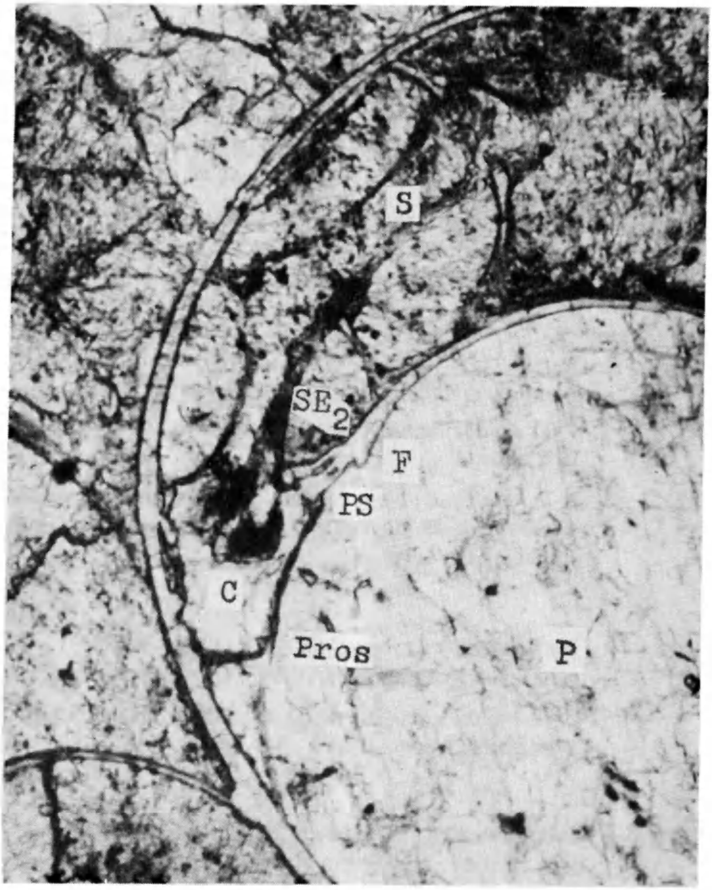

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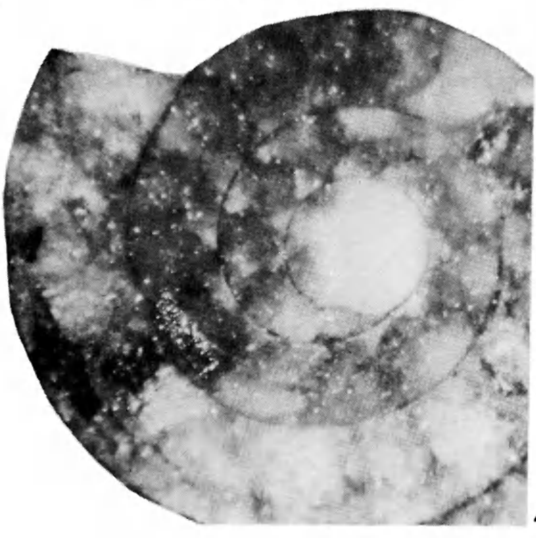

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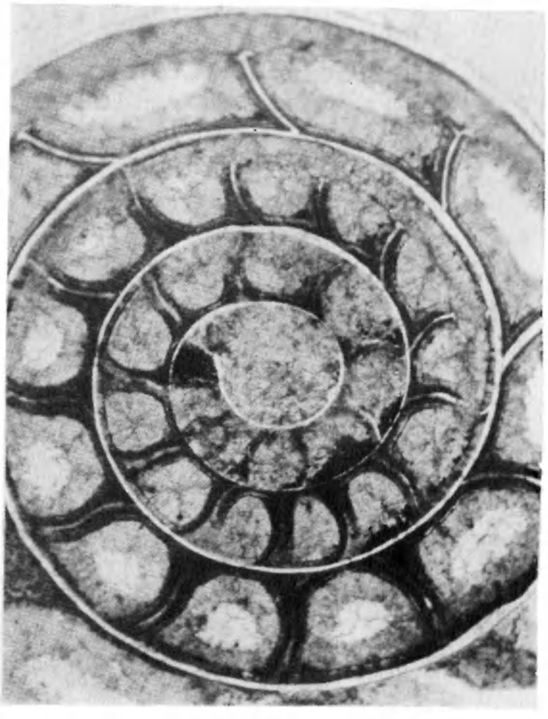

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PLATE 5

Figs. 1-2 — *Parapopanoceras asseretoi* DAGYS & ERMAKOVA, N 22/312.
1 - thin section, protoconch and three whorls of phragmocone (x 50).
2 - polished section, protoconch and 1.5 whorls of phragmocone (x 60). Kharaulakh range, Artist-Agatyn-Yurege Creek, Anisian, rotelliforme zone.

1 - lame mince, protoconque et trois tours de phragmocône.
2 - section polie, protoconque et 1,5 tour de phragmocône. Chaîne de Kharaoulakhe, ruisseau d'Artiste-Agatyne-Juregée, Anisien, zone à rotelliforme.

Figs. 3-4 — *Indigirites krugi* POPOW.
3 - N 24/312 ; a - oral view, b - side view, c - ventral (side) view, life-size.
4 - N 25/312 ; a - oral view, b - side view, life-size. The mouth of the Olenek river, cape Tumul, Ladinian, lenticularis zone.

3 - a, vue orale, b - vue latérale, c - vue du côté ventral, grandeur nature.
4 - a, vue orale, b - vue latérale, grandeur nature. Embouchure de l'Olenek, Cap de Toumoul, Ladinien, zone à lenticularis.

Fig. 5 — *Nathorstites mcconnelli* (WHITEAVES), N 23/831 : a - side view, b - ventral (side) view, life-size. Kharaulakh range, the Kengdey River, Ladinian, lenticularis zone.

a - vue latérale, b - vue du côté ventral, grandeur nature. Chaîne de Kharaoulakhe, fleuve Kengdei, Ladinien, zone à lenticularis.

Fig. 6 — *Indigirites krugi* POPOW. N 26/312, polished section, protoconch and 1.5 whorl of phragmocone (x 60). Caecum and primary constriction are seen. The Kolyma basin, the Olguya River, Ladinian, lenticularis zone.

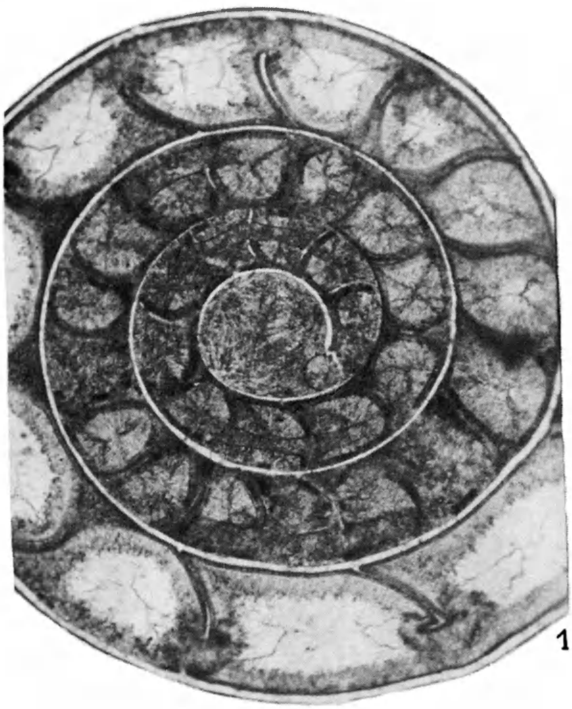
Section polie, protoconque et 1,5 tour de phragmocône (x 60). On voit le caecum et la constriction larvaire. Bassin de Kolyma, fleuve Olgouya, Ladinien, zone à lenticularis.

Fig. 7 — *Nathorstites mcconnelli* (WHITEAVES). N 24/831, polished section, 5 whorls of phragmocone (x 10). The Omolon basin, the Kegali River, Ladinian, lenticularis zone.

Section polie, cinq tours de phragmocône. Bassin d'Omolon, fleuve Kegalie, Ladinien, zone à lenticularis.

Fig. 8 — *Nathorstites gibbosus* STOLLEY. N 25/831, polished section, protoconch and two whorls of phragmocone (x 60). Caecum and primary constriction are seen. Svalbard archipelago, the isle of Edge, Carnian, tenuis zone.

Section polie, protoconque et deux tours de phragmocône. On voit le caecum siphonal et la constriction larvaire. Archipel de Svalbard, Ile d'Edg, Carnien, zone à tenuis.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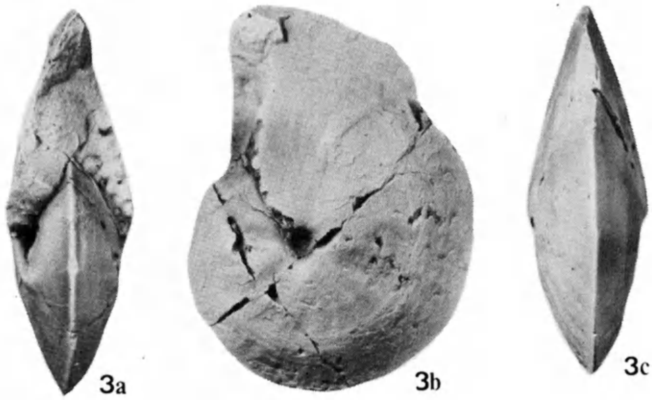
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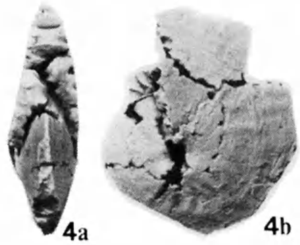
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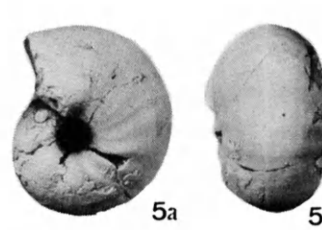
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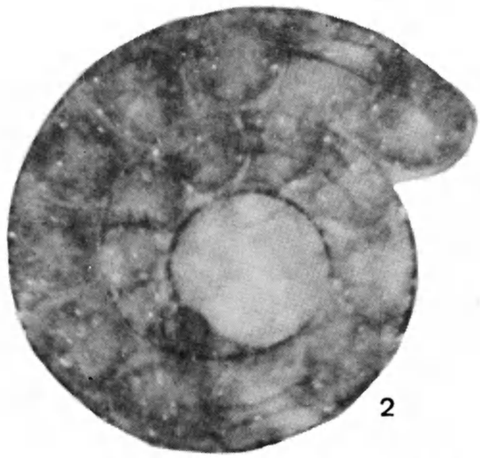
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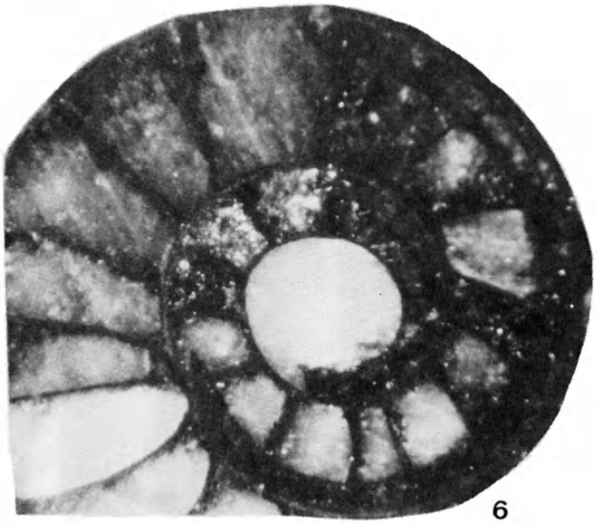
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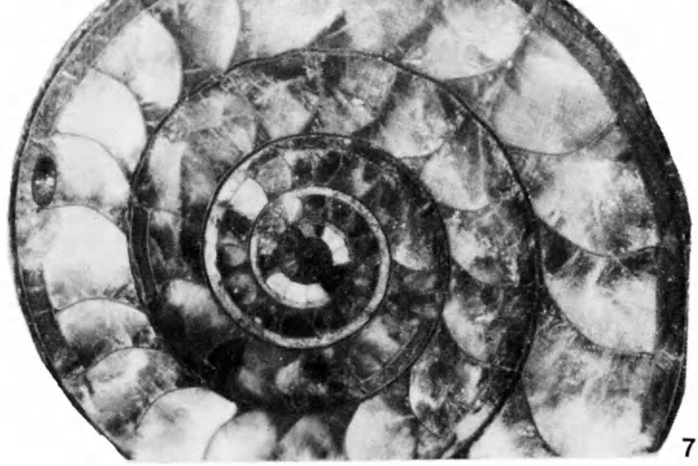
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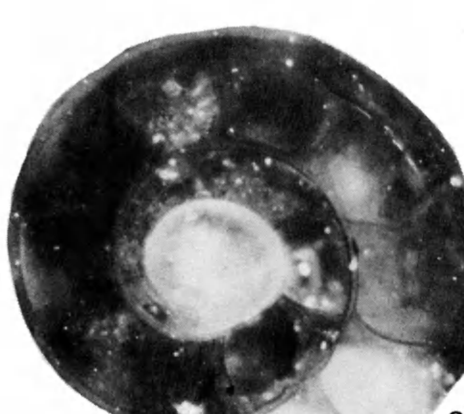
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