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A Revision of the Nathorstitidae (Ammonoidea) from Northeastern Asia

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Abstract—The systematics of the Nathorstitidae from the Ladinian and Lower Carnian of Northeastern Asia is revised. The morphogenesis of the major shell structures is studied and trends in the morphological evolution within this group are revealed. A new family Tsvetkovitidae is established. Five genera and eight species are described.

INTRODUCTION

The paper deals with paleontological evidence for the new zonal scheme of the Ladinian of Northeastern Asia (Dagys and Konstantinov, 1992, 1995). Detailed biostratigraphy of this level in the Boreal Province is based on the Nathorstitidae, a group with a relatively uniform morphology of the adult conch and suture, and hence, with a controversial taxonomy. The revision of this group undertaken here is based on the type material previously described from northeastern Asia (Popow, 1946, 1961; Vavilov and Korchinskaja, 1973; Archipov, 1974), our own collection (over 800 specimens) which includes the topotypes of most endemic species, the Canadian type material described by Tozer (1994) and the material from Spitsbergen and Medvezhii Island (Weitschat and Lehman, 1983).

The revision allowed us to synonymize old species and genera, to emend their diagnoses, including combining of characters and establishing the pattern of morphogenesis of each character; to reveal major trends in the morphological evolution of the Nathorstitidae; and to reconstruct the phylogeny of this group of ammonoids. The taxa assigned to the Nathorstitacea include two groups of strictly boreal genera. The first is represented by the family Tsvetkovitidae composed of the taxa with a prolonged ophioconic stage with ornamented conch and usually with a compressed oxyconic conch in the adults. This family includes three chronologically succeeding genera: *Intornites* (Anisian), *Eonathorstites* (Ladinian, *oleshkoi* Zone), and *Tsvetkovites* (*constantis* and *neraensis* zones). The second group represented by the family Nathorstitidae s. str. possesses a subsphaeroconic conch and more primitive suture lacking pseudoadventive elements and is certainly a descendant of the Tsvetkovitidae. The Nathorstitidae includes three succeeding genera: *Indigirites* (*krugi* Zone), *Nathorstities* (*maclearni-lindstromi* zones), and *Stolleyites* (*tenuis* Zone).

The type material is housed in the Monograph Department of the Central Siberian Geological Museum in the Joint Institute of Geology, Geophysics, and Mineralogy, Siberian Division of the Russian Academy of Sciences (OIGGiM), nos. 811 and 994.

Abbreviations: D—whorl diameter, WH—whorl height, WW—whorl width, UW—umbilical width.

SYSTEMATIC PALEONTOLOGY

Superfamily Nathorstitaceae Spath, 1951

Family Tsvetkovitidae Dagys and Konstantinov, fam. nov.

Diagnosis. Juvenile conch evolute, ophioconic, with keel and lateral ribs, or nodes. Adult conch involute, oxyconic, with acute venter and flattened or concave flanks. Suture with pseudoadventive elements; lobes strongly denticulated.

Composition. Genera *Intornites* Assereto, 1966; *Tsvetkovites* Vavilov et Korchinskaja, 1973; and *Eonathorstites* Tozer, 1994.

Comparison. This family differs from the Nathorstitidae in the prolonged ophioconic stage with a ventral keel, oxyconic adult conch and in a more strongly denticulated suture with pseudoadventive elements. It is distinguished from the Longobarditidae in the conch shape at juvenile and adolescent stages and in the shell ornament.

Genus *Eonathorstites* Tozer, 1994

Longobardites: Archipov, 1874, p. 237 (pars); Arkadiev and Vavilov, 1989, p. 67 (pars).

Intornites: Konstantinov, 1991, p. 74 (pars).

Eonathorstites: Tozer, 1994, p. 137.

Type species. *Eonathorstites dieneri* Tozer, 1994; Ladinian, *poseidon* Zone; Canada, British Columbia.

Diagnosis. In juveniles conch evolute, with slightly overlapping transversely oval or round whorls, later in ontogeny conch becomes involute, flattened, with completely overlapping spear-shaped whorls. Venter possesses keel when the shape is changed to oxycone, in adults venter acute. Umbilicus very narrow. Ornament composed of radial ribs, plications, and biconvex striae. Suture with numerous, strongly denticulated lobes. External and first three lateral saddles phylloid, with acute apices, other saddles oval.

Species composition. Two species *E. dieneri* Tozer, 1994 and *E. oleshkoi* (Archipov, 1974), Ladinian of British Columbia (*poseidon* Zone) and northern Siberia (*oleshkoi* Zone).

Comparison. This genus differs from the genus *Intornites* in a greater number of more strongly denticulated lobes at similar growth stages and in the acute saddle apices.

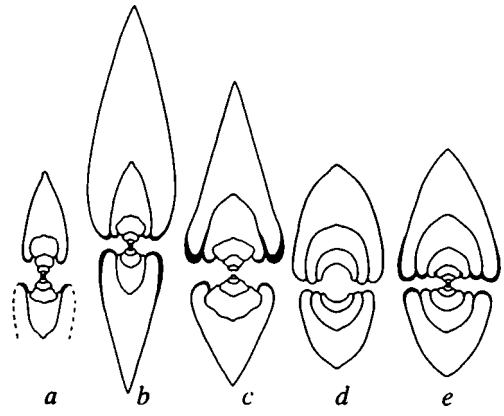


Fig. 1. Whorl cross sections, ×1: (*a*) *Eonathorstites oleshkoi* (Archipov); specimen no. 286/811; Laptev Sea, Ulakhan-Crest Cape; *oleshkoi* Zone; (*b*) *Tsvetkovites constantis* (Archipov); specimen no. 1/994; Kharaulakh Range, Nyakuchan River; *constantis* Zone; (*c*) *Ts. neraensis* (Popow); specimen no. 39/994; Laptev Sea, Ulakhan-Crest Cape; *neraensis* Zone; (*d, e*) *Indigirites krugi* Popow; (*d*) specimen no. 55/994; Indigirka River, Turakh-Yuryakh Creek; *krugi* zone; (*e*) specimen no. 62/994; Lena River, Taas-Aryy Island; *krugi* Zone.

***Eonathorstites oleshkoi* (Archipov, 1974)**

Plate 4, figs. 6–8

Longobardites oleshkoi: Archipov, 1974, p. 239, pl. 11, figs. 1 and 2.

Intornites oleshkoi: Konstantinov, 1991, p. 78, pl. 21, figs. 7–11; pl. 22, fig. 1.

Longobardites nevadanus: Arkadiev and Vavilov, 1989, p. 53, pl. 1, fig. 1.

Longobardites ex gr. *nevadanus*: Arkadiev and Vavilov, 1989, pl. 1, fig. 1.

Holotype. Geological Museum, Yakutsk State University (YaTGU), no. 14/2-49; Omoloi River; Ladinian *oleshkoi* Zone.

Conch shape. (Fig. 1*a*). At the first 4.5–5 whorls the conch is evolute and ophioconic, with weakly overlapping transversely-oval whorls. At whorls 6–7 the conch is oxyconic, involute, flattened, with very narrow umbilicus and spear-shaped whorls. The venter is acute, the flanks are weakly convex.

Dimensions in mm and ratios (%):

Specimen no.	D	WH	WW	UW	WH/D	WW/D	UW/D
288/811	6	2.2	3.3	2.3	37	55	38
292/811	10.5	4.8	3.9	3.8	46	37	36
305/811	26.1	15.8	7.5	3.3	59	29	13
312/811	39	25	12	3.5	64	31	9

Ornamentation. At whorls 2–5 flanks possess weakly sigmoidal ribs. At whorl 6 they become weaker and are replaced by the plications and biconvex growth striae. The inner whorls (from the 3 to 5.5) possess a keel.

Suture (Fig. 2*a*). There are ten lobes between the external saddle and the umbilical seam. The ventral, lateral and three successive umbilical lobes possess large median denticles and smaller lateral denticles which rise onto the sides of the saddle.

Comparison. This species differs from *E. dieneri* in the early appearance of the ventral keel, more developed ornamentation, and in the larger size.

Remarks. Vavilov (see Arkadiev and Vavilov, 1989; Korchinskaja *et al.*, 1989) considered *E. oleshkoi* (Archipov) as a synonym of *Intornites nevadanus* (Hyatt et Smith). However, these species occur in different stratigraphic levels, and *E. oleshkoi* has a more complex suture.

Occurrence. Ladinian, *oleshkoi* Zone, northern Siberia.

Material. 142 specimens: Olenek Gulf, Tumul Cape—five specimens; village of Ystannakh-Khocho—40 specimens, Ulakhan-Crest Cape—33 specimens; Stan-Khaya-Yurege Creek—8 specimens; lower course of the Lena River, Chekurovskii Cape—54 specimens; Kharaulakh Range, Nyakuchan River—two specimens.

Genus *Tsvetkovites* Vavilov et Korchinskaja, 1973

Indigirites: Popow, 1946, p. 53 (pars); 1961, p. 99 (pars); Arkadiev and Vavilov, 1984, p. 408 (pars); 1989, p. 56 (pars).

Tsvetkovites: Vavilov and Korchinskaja, 1973, p. 125; Weitschat and Lehman, 1983, p. 47.

Suordachites: Archipov, 1974, p. 241.

Type species. *Ts. dolioliformis* Vavilov et Korchinskaja, 1973 (=*Indigirites neraensis* Popow, 1946); Ladinian, *neraensis* Zone, Eastern Taimyr.

Diagnosis. At early stages conch cadiconic, with slightly overlapping whorls pentagonal in cross

Plate 4


1a


1b


1c


2a


2b


2c


3a


3b


3c


4a


4b


5a


5b


5c


6a


6b


7a


7b


7c


8c


8b


9a


9b


10a


10b

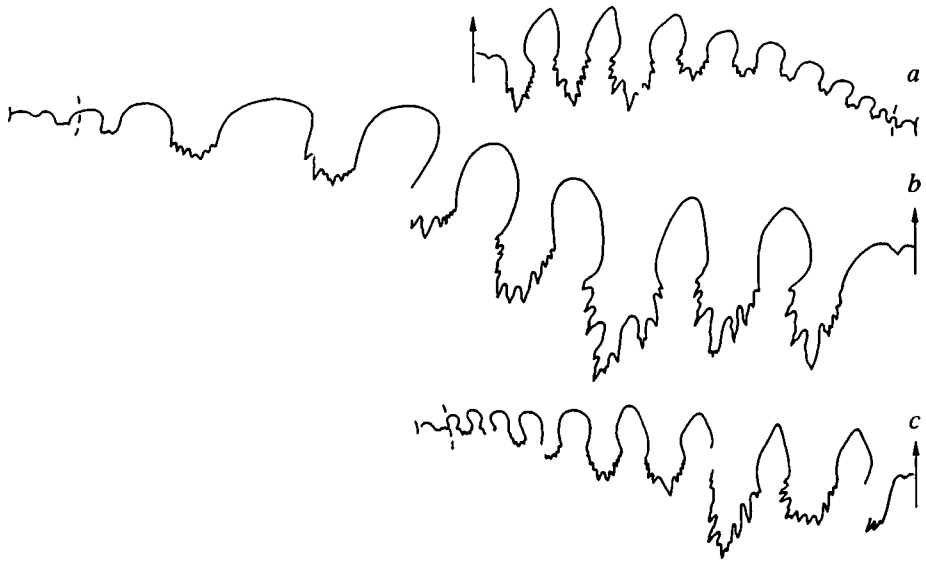


Fig. 2. Sutures of the Tsvetkovitidae: (*a*) *Eonathorstites oleshkoi* (Archipov); specimen no. 312/811, at WW = 12 mm; WH = 25 mm; Laptev Sea, Ulakhan-Crest Cape; *oleshkoi* Zone; (*b*) *Tsvetkovites constantis* (Archipov); specimen no. 10/994 at WW = 24 mm, WH = 50 mm; Kharaulakh Range, Nyakuchan River; *constantis* Zone; (*c*) *Ts. neraensis* (Popow), specimen no. 36/994 at WH = 50 mm; Laptev Sea, Tumul Cape; *neraensis* Zone.

section. Venter carinate, with keel. Umbilical margin with nodes and plications. Adult conch oxyconic, involute, from flattened to medium thickness, with completely overlapping spear-shaped whorls. Venter acute, flanks flattened or concave, with radial biconvex plications and striae. Between external saddle and seam there are nine strongly denticulated lobes. Ventral and first two or three lateral saddles with prominently acute apices.

Species composition. Five species: *Ts. neraensis* (Popow, 1946), *Ts. constantis* (Archipov, 1974), *Ts. varius* Weitschat et Lehman, 1983, *Ts. freboldi* (Tozer, 1994), and *Ts.? stolley* (Tozer, 1994) from the Ladinian of Northeastern Asia (*constantis* and *neraensis* zones), Spitsbergen (*varius* Zone), and from British Columbia (*poseidon* Zone).

Comparison. This genus differs from the genera *Eonathorstites* and *Intornites* in the inflated cadiconic conch at early stages.

Remarks. The type species *Ts. dolioliformis* was described based on the juvenile specimens with few weakly serrated lobes. Hence, the genus *Tsvetkovites* was considered as a synonym of either the genus *Nathorstites* (Shevyrev, 1986) or Indigirites (Bychkov, 1982; Tozer, 1994). The study of the topotypes of *Ts. dolioliformis* and of the species previously described as *Indigirites neraensis* (Popow, 1946) undoubtedly indicates that these two species should be considered as one species, differing at early stages from the typical form of *Indigirites*. Hence, the genus *Suordachites* Archipov, 1974 with the type species *I. neraensis* is considered a junior synonym of the genus *Tsvetkovites*.

***Tsvetkovites constantis* (Archipov, 1974)**

Plate 4, figs. 4 and 5

Longobardites constantis: Archipov, 1974, p. 240, pl. 11, fig. 3.

Indigirites constantis: Arkadiev and Vavilov, 1989, p. 56, pl. 1, figs. 5–10.

Explanation of Plate 4

In all figures a—lateral view, b—apertural view, c—ventral view; sizes are natural.

Figs. 1–3. *Tsvetkovites neraensis* (Popow); (1) specimen no. 36/994; Laptev sea, Tumul Cape; *neraensis* Zone; (2) specimen no. 32/994; (3) specimen no. 35/994; Eastern Taimyr, Tsvetkov Cape; *neraensis* Zone.

Figs. 4 and 5. *Tsvetkovites constantis* (Archipov); (4) specimen no. 2/994; (5) specimen no. 4/994; Kharaulakh Range, Nyakuchan River; *constantis* Zone.

Figs. 6–8. *Eonathorstites oleshkoi* (Archipov); (6) specimen no. 312/811, (8) specimen no. 303/811, Laptev Sea, Ulakhan Crest Cape; *oleshkoi* Zone, (7) specimen no. 308/811, Lena River, Chekurovskii Cape; *oleshkoi* Zone.

Figs. 9 and 10. *Indigirites krugi* Popow; (9) specimen no. 53/994; (10) specimen no. 52/994; Indigirka River, Turakh-Yuryakh Creek; *krugi* Zone.

Holotype. Geological Museum, Yakutsk State University (YaTGU), no. 14/2-50; Kular Range, Tuona Creek; Ladinian, *constantis* Zone.

Conch shape. (Fig. 1*b*). The conch at first four whorls is evolute, strongly inflated, with slightly overlapping oval and pentagonal whorls moderately increasing in height. The adult conchs are involute and compressed. The whorls are spear-shaped, completely overlap, and have their maximum width in the umbilical part. The venter is acute, the flanks are weakly convex. The umbilicus is very narrow and deep.

Dimensions in mm and ratios (%):

Specimen no.	D	WH	WW	UW	WH/D	WW/D	UW/D
1/994	50	30	10.8	1.25	60	22	2.5
10/994	83.2	52	25	–	63	30	–
16/994	24	14.3	–	2.3	60	–	10

Ornamentation. The umbilical shoulder of the third and fourth whorls possesses sparse (four per half-whorl) rounded nodes which become indistinct at the end of the fifth whorl and are replaced by the umbilical plications and fine biconvex growth striae. The venter of the fourth and fifth whorl possesses a keel.

Suture. (Fig. 2*b*). The ventral, lateral and two next umbilical lobes possess large median denticles and small lateral denticles reaching half the height of the saddle. The firth umbilical lobe is wider and deeper than the lateral from the beginning of the sixth whorl.

Comparison. This species differs from *Ts. freboldi* in the more strongly developed ventral keel and in the more developed phylloid appearance of the external and first lateral saddle.

Occurrence. Ladinian, *constantis* Zone, northern Siberia.

Material. 85 specimens: Kharaulakh Range, Ukta River—1 specimen; Nyakuchan River—25 specimens; right bank of the Indigirka River, near the village of Oimyakon, Turakh-Yuryakh Creek—45 specimens; region of the middle course of the Kolyma River (Zyryanka River)—4 specimens; northern Okhotsk Region, Vtoraya Sentyabr'skaya River—10 specimens.

Tsvetkovites neraensis (Popow, 1946)

Plate 4, figs. 1–3

Indigirites neraensis: Popow, 1946, p. 54, pl. 1, fig. 4; 1961, p. 100, pl. 23, fig. 3.

Tsvetkovites dolioliformis: Vavilov and Korchinskaja, 1973, p. 126, text-figs. 1*a*–1*d*.

Indigirites krugi: Bychkov, 1982, p. 35, pl. 2, fig. 8; Arkadiev and Vavilov, 1984, p. 408, pl. 5, figs. 3 and 4; 1989, pl. 2, figs. 1–3.

Holotype. TsNIGR Museum, no. 3/6397; Indigirka River Basin, Nera River; Ladinian, *neraensis* Zone.

Conch shape. (Fig. 1*c*). In the first 5.5 whorls the conch is evolute, strongly inflated, cadiconic, with whorls moderately increasing in height. At whorls 4–5.5 the cross section is pentagonal, with a carinate venter. The adult conch is involute, with the spear-shaped whorls rapidly increasing in height. The venter is acute, the flanks are flattened, or slightly concave. The umbilical margin is rounded. The umbilicus is very narrow.

Dimensions in mm and ratios (%):

Specimen no.	D	WH	WW	UW	WH/D	WW/D	UW/D
29/994	12.7	5.6	7.5	3.2	44	59	25
41/994	29.3	16.3	14.2	4	56	48	14
43/994	21.8	12.5	12	1.8	57	55	8
47/994	51.6	30.5	15	3	59	29	6

Ornamentation. At the forth and fifth whorls the umbilical rim possesses small nodes (10–12 per half-whorl). Later in ontogeny the nodes are replaced by the umbilical plications and biconvex striae. The venter of each of the fifth and sixth whorls possesses a keel.

Suture. The suture (Fig. 2*c*) closely resembles the suture of *Ts. constantis*.

Comparison. Ladinian, *neraensis* Zone of northern Siberia.

Material. Over 300 specimens: Cape Tsvetkov—253 specimens; Olenek Gulf, Cape Tumul—5 specimens, Cape Ulakhan-Crest—10 specimens, lower course of the Lena River, Taas-Aryy Island—1 specimen; Kharaulakh Range, Ukta River—1 specimen; Nyakuchan River—22 specimens; right bank of the Indigirka River, near the village of Oimyakon, Turakh-Yuryakh Creek—6 specimens; northern Okhotsk Region, Vtoraya Sentyabr'skaya River—8 specimens.

Family Nathorstitidae Spath, 1951

Diagnosis. Conch involute, semi-pachyconic, or subsphaeroconic, with subacute venter and convex flanks. Suture lacking pseudoadventive elements. Lobes denticulated only at their bases.

Composition. Genera *Nathorstites* Böhm, 1903; *Indigirites* Popow, 1946; *Stolleyites* Archipov, 1974.

Comparison. For characters distinguishing the Nathorstitidae from the Tsvetkovitidae see the description of the latter family.

Genus *Indigirites* Popow, 1946

Indigirites: Popow, 1946, p. 53 (pars); 1961, p. 99 (pars); Weitschat and Lehman, 1983, p. 49.

Nathorstites: McLearn, 1947, p. 16 (pars).

Type species. *I. krugi* Popow, 1946; Ladinian, *krugi* Zone, Indigirka River, near the village of Oimyakon.

Diagnosis. At early stages conch sphaeroconic, or pachyconic, at later stages moderately inflated and discoconic. Whorls helmet-shaped in cross section, with subacute venter. Flanks possess plications inflated close to the umbilicus and strongly bent backward at mid-flank. Between external saddle and seam there are eight denticulated lobes, with lateral lobe the deepest. Ventral and first lateral saddles with acute apices.

Species composition. Four species: *I. krugi* Popow, 1946; *I. tzaregradskii* Popow, 1946; *I. tozeri* Weitschat et Lehman, 1983; and *I.? argatassensis* Popow, 1961; Ladinian of northern Siberia (*krugi* Zone), Spitsbergen (*tozeri* Zone); and British Columbia (*medinae* Zone).

Comparison. This genus differs from the genus *Nathorstites* in the absence of the umbilical depression, in the ornament and in the more complex suture.

Indigirites krugi Popow, 1946

Plate 4, figs. 9 and 10; Plate 5, figs. 1 and 2

Indigirites krugi: Popow, 1946, p. 53, pl. 11, fig. 11; 1961, p. 99, pl. 23, fig. 5; Vavilov and Korchinskaja, 1974, p. 127, text-figs. 3a, 3b, and 4a; Bychkov, 1982, p. 35, pl. 2, figs. 7, 9, and 10.

Indigirites boehmi: Tozer, 1994, p. 139, pl. 76, figs. 1–17, text-figs. 59a–59d.

Holotype. TsNIGR Museum, no. 2/6397; right bank of the Indigirka River, Turakh-Yuryakh Creek; Ladinian, *krugi* Zone.

Conch shape (Figs. 1*d* and 1*e*). At the first 3.5 whorls the conch is strongly inflated, cadiconic, with slightly, or moderately overlapping spear-shaped whorls. The adult conch is discoidal, involute, varying from moderately thick to inflated, with completely overlapping whorls. The whorls are helmet-shaped (5–6 whorls) and rounded-triangular (7–7.5 whorls). The venter is subacute, the flanks are convex. The umbilicus is very narrow.

Dimensions in mm and ratios (%):

Specimen no.	D	WH	WW	UW	WH/D	WW/D	UW/D
65/994	18.5	9.8	11.3	2.7	53	61	14
54/994	35.2	20	18.3	3.2	57	52	9
52/994	50.2	29.5	22	3.4	59	44	7

Ornamentation. The flanks possess radial plications (6–8 per half-whorl). At mid-flank the plications are strongly bent backward, become weaker and give rise to striae.

Suture (Fig. 3*a*). The suture is denticulated as strongly as *Ts. neraensis*.

Comparison. This species differs from *I. tzaregradskii* in the rounded triangular outline of the cross section of the last whorl. It is distinguished from *I. argatassensis* in the strongly denticulated lobes. *I. krugi* resembles the coarsely ornamented varieties of *I. tozeri*. However, the inner whorls of the latter species have not been studied.

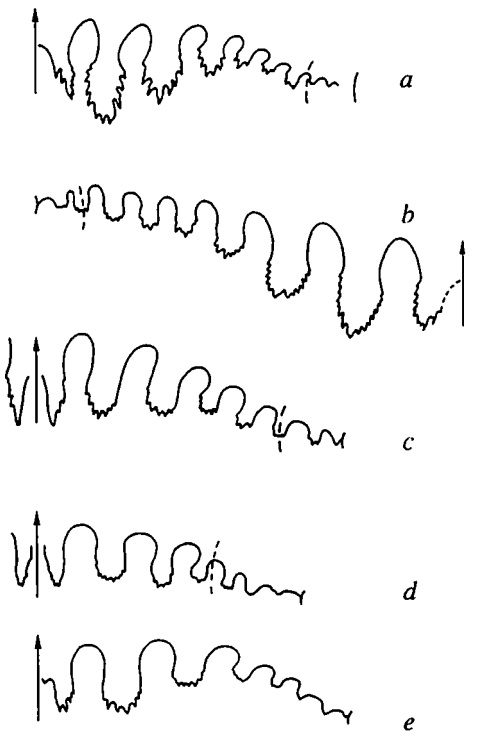


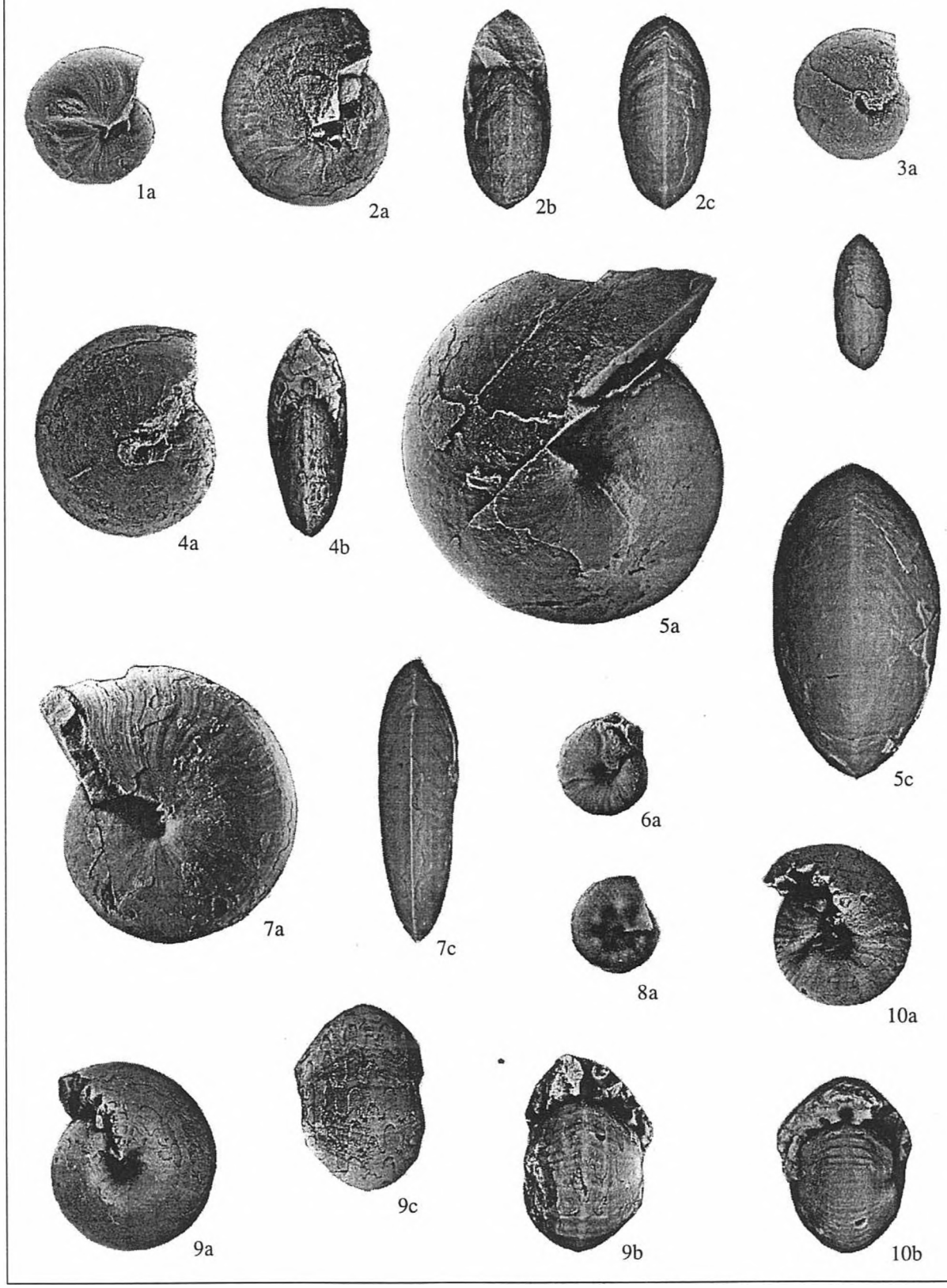
Fig. 3. Sutures of Nathorstitidae: (*a*) *Indigirites krugi* Popow: specimen no. 52/994 at WW = 17.5 mm and WH = 15 mm: Indigirka River, Turakh-Yuryakh Creek; *krugi* Zone: (*b*) *Nathorstites maclearni* Tozer, specimen no. 77/994 at WW = 15.8 mm and WH = 21.6 mm; Dzhugadzhak. *maclearni* Zone, (*c*) *N. mcconnelli* (Whiteaves); specimen no. 86/994, at WW = 16.6 mm and WH = 15.5 mm. Dzhugadzhak River, *mcconnelli* Zone; (*d*) *N. lindstroemi* (Böhm), specimen no. 97/994 at WW = 16.7 mm, WH = 10.5 mm; Dzhugadzhak River; *lindstroemi* Zone; (*e*) *Stolleyites tenuis* (Stolley); specimen no. 99/994 at WW = 9 mm and WH = 13.7 mm; Pravaya Vtoraya Sentyabr'skaya River: *tenuis* Zone.

Remarks. The adult whorls of *Indigirites boehmi* cannot be distinguished from those of *I. krugi*. If the inner whorls of these two species are found to be similar they should be synonymized.

Occurrence. Ladinian, *krugi* Zone of northern Siberia; *medinae* Zone of British Columbia.

Material. 144 specimens: Cape Tsvetkov—3 specimens; Olenek Gulf, village of Ystannakh-Khocho—12 specimens; Cape Ulakhan-Crest—10 specimens; Stan-Khaya-Yurege Creek—5 specimens; lower course of the Lena River, Taas-Aryy—14 specimens; Kharaulakh Range, Ukta River—1 specimen; Ol'khovyi Creek—4 specimens, Nyakuchan River—14 specimens; lower course of the Yana River, Baky River—8 specimens; Beta Creek—10 specimens; right bank of the Indigirka River, near the village of Oimyakon, Turakh-Yuryakh Creek—57 specimens; northern

Plate 5



Okhotsk Region, Levaya Vtoraya Sentyabr'skaya River—6 specimens.

Genus *Nathorstites* Böhm, 1903

Popanoceras: Whiteaves, 1899, p. 183 (pars).

Nathorstites: Böhm, 1903, p. 61; Smith, 1927, p. 67; Frebold, 1929, p. 305 (pars); McLearn, 1947, p. 16 (pars); Popov, 1961, p. 101; Tozer, 1961, p. 90 (pars); Korchinskaja, 1972, p. 65 (pars); Bychkov, 1982, p. 26 (pars).

Paraindigirites: Popow, 1946, p. 55; 1961, p. 100.

Metasphingites: Popow, 1961, p. 60 (pars).

Type species. *Popanoceras mcconnelli* Whiteaves, 1889; Ladinian, *sutherlandi* Zone; British Columbia.

Diagnosis. At early stages conch evolute, strongly inflated, in adults involute, from discoidal to thickly sphaeroconic, with completely overlapping longitudinally oval whorls. Venter subacute. Flanks convex, with umbilical depression. Umbilicus narrow. Living chamber comprises over one whorl. Ornamentation consists of fine growth lines which form projections on venter. Between external saddle and seam there are seven to eight lobes arranged in a single row or forming arc. Lobes denticulated only at their bases. Saddles rounded.

Species composition. Four species: *N. mcconnelli* (Whiteaves, 1889); *N. lindstroemi* Böhm, 1903; *N. sublenticularis* Popow, 1961; and *N. maclearni* Tozer, 1994; Ladinian of Northeastern Asia (*maclearni*, *mcconnelli*, and *lindstroemi* zones) and synchronous strata of Spitsbergen, Canada, and Alaska.

Comparison. The characters distinguishing this genus from *Indigirites* are listed above. *Nathorstites* differs from the genus *Stolleyites* in the absence of umbilical nodes in adults.

Nathorstites maclearni Tozer, 1994

Plate 5, figs. 3 and 4

Nathorstites maclearni: Tozer, 1994, p. 140, pl. 81, figs. 1–8, text-figs. 64a–64c.

Holotype. GSC 28606; British Columbia, Liard River; Ladinian, *maclearni* Zone.

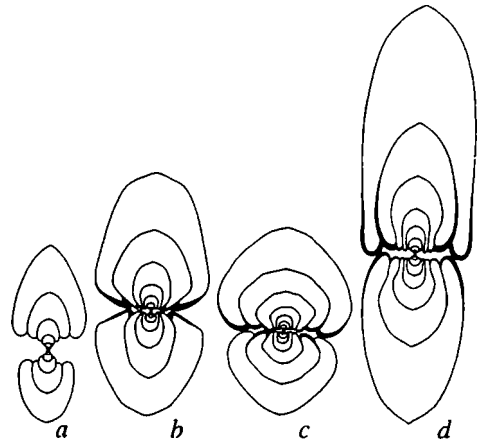


Fig. 4. Cross sections of the *Nathorstites* and *Stolleyites* conchs, ×2/3: (*a*) *Nathorstites maclearni* Tozer; specimen no. 71/994; Dzhugadzhak River, *maclearni* Zone; (*b*) *N. maclearni* (Whiteaves); specimen no. 79/994; Pravaya Vtoraya Sentyabr'skaya River; *mcconnelli* Zone; (*c*) *N. lindstroemi* (Böhm); specimen no. 91/994; Dzhugadzhak River; *lindstroemi* Zone; (*d*) *Stolleyites tenuis* (Stolley); specimen no. 98/994; Pravaya Vtoraya Sentyabr'skaya River; *tenuis* Zone.

Conch shape. (Fig. 4*a*). The first 3.5 whorls moderately overlap, are transversely oval and rounded in cross section. At whorls 4–7 the conch is discoconic, involute, compressed and moderately thick, with completely overlapping, slowly expanding whorls. The whorl cross sections vary from longitudinally oval to helmet-shaped. The venter is subacute, the umbilicus is narrow and deep.

Dimensions in mm and ratios (%):

Specimen no.	D	WH	WW	UW	WH/D	WW/D	UW/D
72/994	21	12.7	9.6	1.9	60	46	9
75/994	23.2	13.7	12.2	2.3	59	53	10
73/994	33	17	12.4	1.9	52	38	6

Ornamentation. Flanks possess faint radial plications and fine growth striae, slightly bent backward at conch diameter less than 10 mm. Later in

Explanation of Plate 5

In all figures a—lateral view, b—apertural view, c—ventral view; sizes are natural.

Figs. 1 and 2. *Indigirites krugi* Popow; (1) specimen no. 67/994; Lena River, Taas Crest Creek; *krugi* Zone; (2) specimen no. 60/994; Lena River, Taas-Crest Island; *krugi* Zone.

Figs. 3 and 4. *Nathorstites maclearni* Tozer; (3) specimen no. 72/994, (4) specimen no. 73/994; region of the middle course of the Kolyma River, Dzhugadzhak River; *maclearni* Zone.

Figs. 5 and 6. *Nathorstites mcconnelli* (Whiteaves); (5) specimen no. 80/994; (6) specimen no. 78/994; northern Okhotsk Region; Pravaya Vtoraya Sentyabr'skaya River; *mcconnelli* Zone.

Figs. 7 and 8. *Stolleyites tenuis* (Stolley); (7) specimen no. 99/994; (8) specimen no. 100/994; northern Okhotsk Region, Pravaya Vtoraya Sentyabr'skaya River; *tenuis* Zone.

Figs. 9 and 10. *Nathorstites lindstroemi* Böhm; (9) specimen no. 93/994; (10) specimen 92/994; region of the middle course of the Kolyma River, Dzhugadzhak River; *tenuis* Zone.

ontogeny the striae become less bent and are almost radial.

Suture. (Fig. 3*b*). All lobes are denticulated. The denticles in ventral, lateral and first umbilical lobes rise to the saddle sides. The external and two successive saddles are weakly phylloid.

Comparison. This species is distinguished from *N. sublenticularis* in the subacute venter.

Remarks. The species under description is tentatively referred to the genus *Nathorstites* since it lacks an umbilical depression. The suture and whorl shape of *N. maclearni* are close to those of the genus *Indigirites*.

Occurrence. Ladinian, *maclearni* Zone of northern Siberia and British Columbia.

Material. 33 specimens: Cape Tsvetkov—8 specimens; region of the middle course of the Kolyma River, Dzhugadzhak River—14 specimens; northern Okhotsk Region, Levaya Vtoraya Sentyabr'skaya River—11 specimens.

***Nathorstites mcconnelli* (Whiteaves, 1889)**

Plate 5, figs. 5 and 6

Popanoceras mcconnelli: Whiteaves, 1889, p. 138, pl. 18, figs. 2, 2a, and 2b.

Popanoceras mcconnelli var. lenticulare: Whiteaves, 1889, p. 140, pl. 18, figs. 3 and 3a.

Nathorstites mcconnelli: McLearn, 1947, p. 16, pl. 8, figs. 7 and 8; Tozer, 1961, p. 91, pl. 22, figs. 7 and 8; 1972, p. 638, pl. 124, figs. 1–7; pl. 125, figs. 1–4; Bychkov *et al.*, 1976, p. 139, pl. 29, figs. 3–5; Bychkov, 1982, p. 26, pl. 1, figs. 7–11, pl. 2, figs. 1–4; Tozer, 1994, p. 141, pl. 86, figs. 1–7; pl. 87, figs. 1–8; text-figs. 69, 70a, and 70b.

Nathorstites lenticularis: McLearn, 1947, pl. 8, figs. 4 and 5; Popow, 1961, p. 102, pl. 23, fig. 1; Bychkov *et al.*, 1976, p. 140, pl. 30, figs. 2 and 3; Bychkov, 1982, p. 28, pl. 3, figs. 1 and 2; pl. 4, figs. 2–5.

Nathorstites strongulatus: Korchinskaja, 1972, p. 69, pl. 2, figs. 10–12.

Nathorstites vosnessenskyi: Bychkov, 1982, p. 32, pl. 4, figs. 6–9.

Holotype. GSC 4716; British Columbia; Liard River; Ladinian, *sutherlandi* Zone.

Conch shape (Fig. 4*b*). In the first 3.4 whorls the conch is evolute, with circular and transversely-oval whorls, at whorls 4–5 the shapes vary from pachyconic to subsphaeroconic, with completely involute whorls. The whorls are longitudinally oval in cross section. The flanks are convex. Dorsad of the mid-flank they flatten and form the umbilical depression. In adults (6–9.5 whorls) the conch is discoidal, involute and vary from inflated to moderately inflated. The venter is subacute, the flanks are convex. The umbilicus is very narrow.

Dimensions in mm and ratios (%):

Specimen no.	D	WH	WW	UW	WH/D	WW/D	UW/D
78/994	14.4	8.2	7.2	1.6	57	50	12
86/994	30.5	16.7	18.3	1.9	55	60	6
81/994	57	32.4	38.5	2	57	68	4

Ornamentation. The shell surface possesses sygmoidal striae which form shallow sinuses across the ventral shoulder and close to the umbilicus, and a projection on the venter.

Suture (Fig. 3*c*). The ventral lobe is the deepest, the lateral lobe is slightly shallower, whereas other lobes decrease in size toward the umbilical seam. Only the lobe bases are denticulated. The saddles are rounded at their tops.

Comparison. This species differs from *N. lindstroemi* in the more strongly bent growth striae, in the more rapidly expanding whorls, and in the shallower umbilical depression.

Occurrence. Ladinian, *mcconnelli* Zone of northern Siberia; *sutherlandi* Zone of Canada.

Material. 124 specimens: region of the middle course of the Kolyma River: River Dzhugadzhak—40 specimens, Zyryanka River—4 specimens; northern Okhotsk Region, Pravaya Vtoraya Sentyabr'skaya River—76 specimens; Zhakan Creek—4 specimens.

***Nathorstites lindstroemi* Böhm, 1903**

Plate 5, figs. 9 and 10

Nathorstites lindströmi: Böhm, 1903, p. 64, pl. 7, figs. 17, 18, 25–27, 33, 34, 37–39; Popow, 1961, pl. 23, fig. 2; Bychkov *et al.*, 1976, p. 140, p. 30, fig. 7; Bychkov, 1982, pl. 2, figs. 5 and 6.

Nathorstites mojsvari: Böhm, 1903, p. 65, pl. 7, figs. 15, 16, 19-21, 28-30, 32, 35, and 36.

Nathorstites mojsvari var. *applanata*: Böhm, 1903, p. 66, pl. 7, figs. 22, 23, and 31.

Nathorstites mcconnelli: Tozer, 1961, p. 91, pl. 22, figs. 5 and 6; Korchinskaja, 1972, p. 68, pl. 2, figs. 8 and 9, text-fig. 5.

Metasphingites superus: Popow, 1961, p. 61, pl. 13, fig. 6.

Lectotype. Specimen figured by Böhm (1903, pl. 7, figs. 37–39); designated here; Spitsbergen, Medvezhii Island; Ladinian, *lindstroemi* Zone.

Conch shape (Fig. 4*c*). At the first 3 whorls the conch is evolute, strongly inflated, with slightly overlapping transversely oval whorls. In adults (6–11) the conch is strongly inflated, subsphaeroconic, involute, with slowly expanding whorls. Dorsad of the midflank the flanks flatten to form an umbilical depression. The venter is carinate. The umbilicus is very narrow.

Dimensions in mm and ratios (%):

Specimen no.	D	WH	WW	UW	WH/D	WW/D	UW/D
95/994	21.5	12.1	15.5	1.4	56	72	6.5
91/994	29.4	15.8	21.2	1.3	54	72	4
93/994	31	17.7	27	1.3	57	87	4

Ornamentation. The conch possess almost radial growth lines. Some specimens possess sparse and irregular swellings on the raised umbilical rim.

Suture (Fig. 3*d*). Close to that of *N. mcconnelli*.

Comparison. The characters that distinguish this species from *N. mcconnelli* are listed above. From other *Nathorstites* species differs in the inflated conch and almost straight growth lines.

Occurrence. Ladinian, *lindstroemi* Zone of northern Siberia (Medvezhii and Spitsbergen islands) and northern Canada.

Material. 32 specimens: region of the middle course of the Kolyma River: Dzhugadzhak River—20 specimens, Zyryanka River—6 specimens; northern Okhotsk Region, Pravaya Vtoraya Sentyabr'skaya River—4 specimens, Zhakan River—2 specimens.

Genus *Stolleyites* Archipov, 1974

Stolleyites: Archipov, 1974, p. 243; Tozer, 1994, p. 142.

Nathorstites (pars): Stolley, 1911, p. 116; Frebold, 1929, p. 395; Korchinskaja, 1972, p. 65; Bychkov, 1982, p. 26.

Type species. *Nathorstites tenuis* Stolley, 1911 (=*N. gibbosus* Stolley, 1911), Carnian, *tenuis* Zone; Spitsbergen.

Diagnosis. The conch shape and its changes throughout ontogeny are similar to those of the genus *Nathorstites*. Umbilical depression occurs in juveniles. At adolescent and adult stages conch possesses regular umbilical nodes which become weaker on the living chamber. Suture with seven–eight lobes, denticulated only at their bases and forming arc. Saddles rounded at their tops. Living chamber more than one whorl.

Species composition. Two species: *S. tenuis* (Stolley, 1911) and *S. planus* (Frebold, 1929) from the Carnian (*tenuis* Zone) of Spitsbergen, northern Siberia, Arctic Canada, and British Columbia.

Comparison. Differs from the genus *Nathorstites* in prominent umbilical nodes.

Remarks. Umbilical nodes are present in some *Nathorstites* species (e.g., in the middle growth stages of N. lindstroemi). However they are irregular and weak.

Stolleyites tenuis (Stolley, 1911)

Plate 5, figs. 7 and 8

Nathorstites lenticularis: Böhm, 1903, p. 61, pl. 7, figs. 6–8, 13, and 14; Korchinskaja, 1972, p. 67, pl. 1, figs. 1, 2, 6–8, and 12; pl. 2, fig. 6.

Nathorstites tenuis: Stolley, 1911, p. 116, pl. 9, figs. 3 and 4; Frebold, 1929, pl. 2, figs. 9–12; Korchinskaja, 1972, p. 68, pl. 1, fig. 13; pl. 2, figs. 1–5; Bychkov *et al.*, 1976, p. 141, pl. 30, fig. 4; Bychkov, 1982, p. 31, pl. 1, figs. 3–6.

Nathorstites gibbosus: Stolley, 1911, p. 120, pl. 9, figs. 1 and 2; Frebold, 1929, p. 305, pl. 2, figs. 4–8; Korchinskaja, 1972, p. 66, pl. 1, figs. 3–5, 9–11; pl. 2, fig. 7; Bychkov, 1982, p. 34, pl. 1, figs. 1 and 2; pl. 4, figs. 10–12.

Stolleyites intermedius: Tozer, 1994 p. 142, pl. 68, fig. 9.

Holotype. Specimen figured by Stolley (1911, pl. 9, fig. 3); Spitsbergen, Carnian, *tenuis* Zone.

Conch shape (Fig. 4*d*). The conch at the first 4 whorls evolute, strongly inflated, with slightly overlapping transversely oval whorls. Adult conchs varies from discoidal to subsphaeroconic and involute. The venter is subacute. The flanks possess a small umbilical depression. The umbilicus is almost closed.

Dimensions in mm and ratios (%):

Specimen no.	D	WH	WW	UW	WH/D	WW/D	UW/D
98/994	65.4	38.6	20.8	1.1	59	32	2
99/994	45.4	26.8	13.3	1.9	59	29	4

Ornamentation. At early stages conch possesses radial plications When the shell grows the plications become redundant and are replaced by the thin striae.

Suture (Fig. 3*e*). The ventral, lateral, and first umbilical lobe are denticulated at their bases. The next lobes are considerably smaller, with very weak denticulation or smooth.

Comparison. This species differs from *S. planus* in the more weakly developed umbilical depression and smaller umbilical plications in adult.

Occurrence. Carnian, *tenuis* Zone of northern Siberia, Spitsbergen, and Arctic Canada.

Material. 60 specimens: region of the middle course of the Kolyma River, Zyryanka River—8 specimens; northern Okhotsk Region, Pravaya Vtoraya Sentyabr'skaya River—40 specimens, Zhakan Creek—12 specimens.

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