Early Devonian fishes from coastal De Long Strait, central Chukotka, Arctic Russia

Elga MARK-KURIK
Institute of Geology at Tallinn University of Technology
Ehitajate tee 5, 19086 Tallinn (Estonia)
kurik@gi.ee

Alain BLIECK
Université Lille1 : Sciences de la Terre, UMR 8217 du CNRS "Géosystèmes"
F-59655 Villeneuve d'Ascq cedex (France)
alain.blieck@univ-lille1.fr

Carole J. BURROW
Queensland Museum, Geosciences
122 Gerler Road, Hendra Qld 4011 (Australia)
carole.burrow@gmail.com

Susan TURNER
Queensland Museum, Ancient Environments
122 Gerler Road Hendra Queensland Qld 4011 (Australia)
paleodeadfish@yahoo.com

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ABSTRACT
Calcareous and sandy deposits from the basal members of the Enmakaj and Pil'hikaj formations in coastal exposures along the De Long Strait in central Chukotka, Arctic far-eastern Russia, have yielded two assemblages of fossil fish comprising heterostracan plate fragments, turiniid and other thelodont scales, acanthodian scales and a partial tooth, typical of the Old Red Sandstone facies. Exceptional are acanthothoracid placoderm platelets characteristic of marine facies. In addition a sarcopterygian fragment have been found in Member 1 of the Enmakaj Formation. Some scale surfaces show an unusual, scoured preservation. A Lochkovian age, and most probably basal Lochkovian, is supported for the Enmakaj assemblage, and a somewhat later Lochkovian age is supposed for the Pil'hikaj assemblage. The palaeobiogeographic affinities of these assemblages based on the heterostracans and thelodonts are with other Lochkovian occurrences in Arctic regions such as Severnaya Zemlya, Spitsbergen and the northern and north-eastern Old Red Sandstone Continent in general.

KEY WORDS
Fish assemblages,
biostratigraphy,
Devonian (Lochkovian),
Russian Far East,
Chukchi A. R.,
palaeobiogeography,
heterostracan,
thelodont,
placoderm,
acanthodian,
sarcopterygian.

RÉSUMÉ

Poissons du Dévonien inférieur de la côte du Détroit de De Long, péninsule des Tchouktches, Russie arctique.

Des sédiments calcaro-gréseux des membres inférieurs des formations d'Enmakaj et de Pil'hikaj, le long de la côte du Détroit de De Long, dans la partie centrale de la péninsule des Tchouktches, dans l'Extrême-Orient arctique russe, ont livré deux assemblages de poissons fossiles comprenant des fragments de plaques d'hétérostracés, des écailles de thélodontes turiniides et autres, des écailles et une dent incomplète d'acanthodiens, typiques du faciès des Vieux Grès Rouges. La présence de plaquettes de placodermes acanthothoracides, caractéristiques de faciès marins, est exceptionnelle. Des restes de sarcoptérygiens ont également été trouvés dans le Membre 1 de la Formation d'Enmakaj. L'état de conservation de la surface de certaines écailles est inhabituel et comme « décapé ». Un âge lochkovien, et très probablement lochkovien basal est proposé pour l'assemblage de la Formation d'Enmakaj, et un âge lochkovien un peu plus récent pour l'assemblage de la Formation de Pil'hikaj. Leurs affinités paléobiogéographiques, d'après les hétérostracés et les thélodontes, sont à rechercher du côté d'autres localités lochkoviennes des régions arctiques tels que la Terre du Nord (Severnaya Zemlya), le Spitsberg et les marges nord et nord-est du Continent des Vieux Grès Rouges en général.

MOTS CLÉS
Assemblages ichtyens, biostratigraphie, Dévonien (Lochkovien), Extrême-Orient russe, région autonome des Tchouktches, paléobiogéographie, hétérostracés, thélodontes, placodermes, acanthodiens, sarcoptérygiens.

INTRODUCTION

Limited and rarely described Devonian deposits occur in the far north-east of the Russian Arctic, in the northern part of the Chukchi Autonomous Okrug (district) on the southern coast of the De Long Strait (Proliv Longa in Russian), to the SSW of Wrangel Island (note that the name of the strait must be written "De Long Strait" because it has been named after the American explorer George Washington De Long; see Anon. 2010). The outcrop area is located between the mouth of the River Pegdymel' in the west and Cape Shmidt (Mys Shmidta in Russian, named after the Academician Otto Schmidt) to the east, i.e. between longitudes 174°E and *c.* 180°E (Fig. 1, upper map). Structurally it belongs to the northernmost part of the Kuyul tectonic division at the northern edge of the Chukotka Fold Belt (Bychkov & Gorodinsky 1992: fig. 1; Natal'in *et al.* 1999: figs 1, 7), which is a component of the Arctic Alaska – Chukotka Terrane (Till *et al.* 2010).

A review of earlier investigations of the studied area and a detailed description of the Devonian section were given by Rogozov & Vasil'eva (1968). These authors first identified the occurrence of the Lower Devonian rocks in the area and subdivided the strata into formations based on lithology and fauna (Rogozov & Vasil'eva 1968: 152, fig.). The Devonian section Poberezh'e ('the Coast') is 4.5 km long, starting at the longitude of Cape Enmakaj (Enmykaj) and almost reaching the Pil'hikaj (Pilzykej) lagoon to the west. The Devonian rocks crop out along Tonnel'nyj Brook, and separate exposures also occur in the upstream part of the River Kuul' (Fig. 1, lower map). The Lower Devonian of the Coast section is subdivided into a lower, Enmakaj Formation and an upper, Pil'hikaj Formation, which are succeeded by the Middle Devonian Long Formation and the Upper Devonian Pegdymel' Formation. The latter formation is exposed in the basin of the River Pegdymel'.

The De Long Strait coastal area is significant because it has yielded Lower Devonian fishes from three levels, which also contain representatives

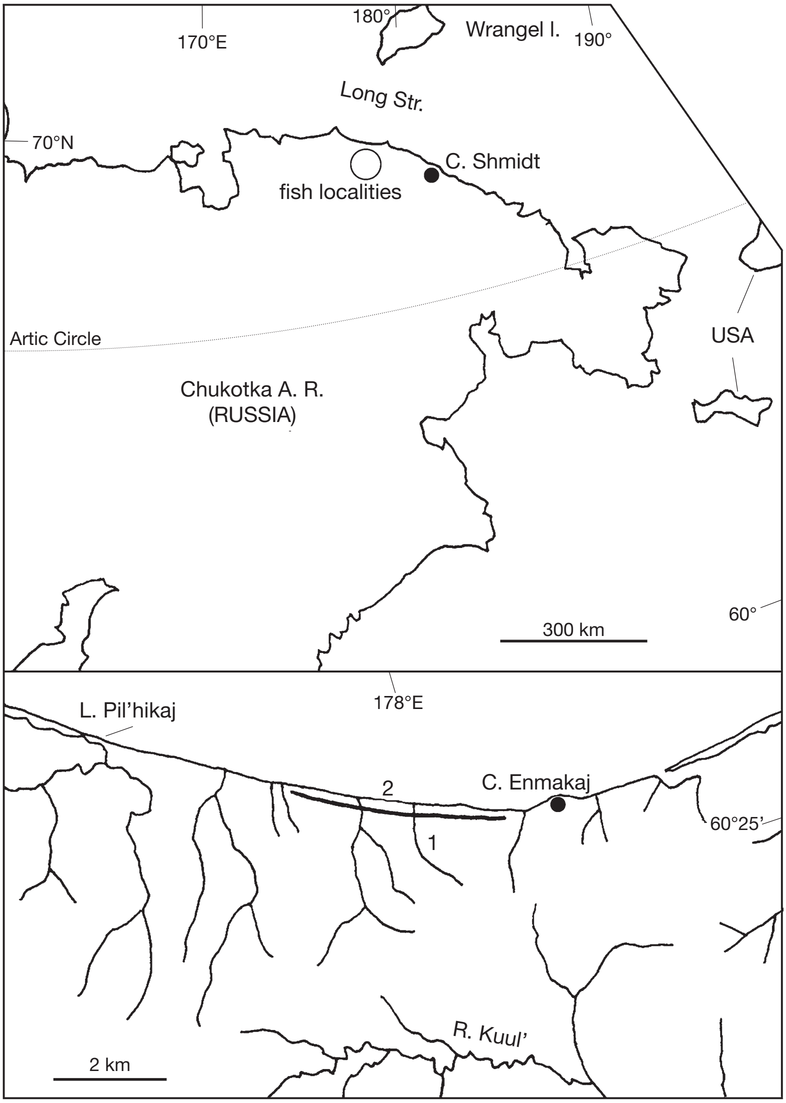

Fig. 1. — Maps indicating the position of the Lower Devonian fish localities at the southern coast of the De Long Strait, Chukchi Autonomous Okrug (A. R.), Arctic far-eastern Russia. **1**, Tonnel'nyj Brook; **2**, the Coast (Poberezh'e) section. Abbreviations: **C**, cape; **L**, lagoon.

of shelly faunas (brachiopods, corals, crinoids, tentaculites, ostracodes). The fossil fishes were collected by Y. Rogozov's team in 1967 from two localities in the Coast and Tonnel'nyj Brook sections (Fig. 1). Cherkesova (1973) mentioned two fish remains discovered in the Lower Devonian Pil'hikaj Formation of the De Long Strait area, identified as belonging to "Heterostraci Pteraspidae" and "Arctolepidida" (placoderm) that supported the Early Devonian age of the samples. The latter specimen, however, also appears to be a fragment of a heterostracan, and is fully described in the present paper (see below). Novitskaya (1986, 2004) described a pteraspid dorsal shield, found in Tonnel'nyj Brook (the "Heterostraci Pteraspidae" of Cherkesova 1973) as Pteraspidiformes indet. 1 (Novitskaya 1986: 119, pl. XXIV: 1, 2), later being as an erratum Pteraspidiformes indet. 2 (Novitskaya 2004: 170). She (Novitskaya 1986: 125) also mentioned that, in the shape and depth of the pineal notch, the plate resembles that of *Podolaspis* Zych, 1931. In the same study Novitskaya, based on pteraspids, made a first biostratigraphic assessment that the deposits were Lochkovian (Early Devonian) in age.

Additionally, Cherkesova (1973) mentioned a sarcopterygian "*Porolepis* sp." in the underlying Enmakaj Formation. She (Cherkesova 1973: 279, table and abstract) gave a detailed subdivision of the lower part of the Enmakaj Formation. Invertebrates and *Porolepis* appeared to be numerous in an interval from the Member IV to the lower part of the Member VIII. Below it there were three members (I-III): the Member II contained flora (*Taeniocrada decheniana* (Göppert, 1847), cf. *Cooksonia* Lang, 1937, *Psilophytites* sp.), the Member III yielded brachiopods etc. The Enmakaj fish assemblage, described by us, comes probably from the interval of the Member IV to lower part of the Member VIII. It evidently corresponds to the upper part of the Lower Member (1) of Rogozov & Vasil'eva (1968).

A preliminary identification, including that of five different Early Devonian representatives of agnathans (heterostracans) and fishes which remained unpublished at that time, was given by the senior author (EMK) in 1976. The late Dr Svetlana Cherkesova (Institute of Arctic Geology, Leningrad now St Petersburg) gave information (pers. comm. to EMK 2002) on the stratigraphic range of the samples and the dating of the formations (Fig. 2), however, considering the age of the Pil'hikaj Formation as Pragian-Emsian, based on invertebrate data. She was in the field together with the team of Y. Rogozov and identified all the brachiopods listed in Rogozov & Vasil'eva (1968).

A full assemblage of fish specimens from two members (Fig. 2) will be described in this paper. Of the fish groups A. Blieck described Pteraspidomophi, S. Turner Thelodonti, C. J. Burrow Acanthodii, E. Mark-Kurik Placodermi and Sarcopterygii. Paleobiogeographic interpretation was given by AB, CJB and ST.

GEOLOGICAL SETTING AND STRATIGRAPHY

The general description of the Lower Devonian Enmakaj and Pil'hikaj formations comes from Rogozov & Vasil'eva (1968: 153-154; translated and slightly modified by EMK).

The Enmakaj Formation is 270 m thick with dominant sandstones. Characteristic for the formation are thin bedded sandstones, with an occurrence of cavernous leached sandstone with fossils and a thin macro-intercalation of sandstone and clayey shale. Such rock units reach a thickness of 10-15 m, with sandstone beds of 3-5 cm thick, and clayey shale layers of 1-1.5 cm. The formation is subdivided into three members:

– the Lower Member (1) consists mainly of sandstone with thin layers of argillite and clayey shale. In the upper part of the member, thin beds of fossil-bearing sandstone, siltstone, clayey shale and rarely limestone (as lenses or nodules) are intercalated. Fossils comprise brachiopods *Atrypinella* sp., *Cyrtina* sp., ostracodes, crinoids, plant and fish remains (described below);

– the Middle Member (2) is a sandstone and shale unit with well-marked intercalation of thick and thin platy sandstone and clayey shale. This sandstone reveals ripple marks and trace fossils in a more clayey facies;

– the Upper Member (3) is mainly a shale and limestone unit with siltstone interbeds. At the base of the unit there is a limestone with corals: *Spongophyllum* sp., *Pseudoamplexus* sp., *Hexagonaria* sp., *Grypophyllum* sp., *Acanthophyllum* cf. *mansfieldense* (Duncan, 1898), and brachiopods: *Atrypinella* ex gr. *barba* Khodalevich, 1939, "*Camarotoechia*" cf. *haraganensis* Amsden, 1958, *Dubularia* ex gr. *thetis* (Barrande, 1879), *Carinatina* ex gr. *comata* (Barrande, 1879), *Cyrtina* sp. (ex gr. *dalmani* Amsden, 1958) and *Howellella* sp. Leached sandstones, occurring in the upper part of the member, contain brachiopods: *Parachonetes*? sp., "*Stegorhynchus*" ex gr. *nympha* (Barrande, 1879), *Dentatrypa* sp. and *Carinatina* sp. Tentaculites, ostracodes, trilobites, bryozoans and other fossils have also been noted in all the above rocks.

Series	Stage	Formation & thickness	Member & thickness	Lithology	Invertebrates	Fishes and **sample numbers**
UPPER DEVONIAN		Pegdymel' 80-100 m		sandstone	foraminifers	
MIDDLE DEVONIAN		Long 560 m		sandstone shale limestone (rare)	brachiopods	
LOWER DEVONIAN	Emsian, Pragian to Lochkovian (upper? part)	Pil'hikaj 432 m	Upper **(6)** 167.8 m	sandstone siltstone		
			Middle **(5)** 136.7 m	sandstone siltstone	brachiopods	fish remains (indet.)
			Lower **(4)** 127.5 m	siltstone sandstone	brachiopods corals crinoids	heterostracans **74** **?73-4 (74-3)**
	Lochkovian	Enmakaj *c.* 260 m	Upper **(3)** 35.1 m	shale limestone sandstone	corals brachiopods tentaculites ostracodes	
			Middle **(2)** 116 m	sandstone shale	trace fossils	
			Lower **(1)** 107.7 m	sandstone	brachiopods ostracodes crinoids	heterostracans thelodonts acanthodians placoderm sarcopterygian **73**

Fig. 2. — Devonian of the De Long Strait area (Chukchi A. R.), Arctic far-eastern Russia: local stratigraphical units, their thickness, general lithology and fossil content.

The boundary between the Enmakaj Formation and the overlying Pil'hikaj Formation may be defined in two different ways, either at the base of the siltstone-sandstone member overlying Member 3, or within the leached sandstone beds in the upper part of the Enmakaj Formation.

The Pil'hikaj Formation conformably overlies the Enmakaj Formation. The Pil'hikaj Formation, with siltstones predominant, is 432 m thick. Characteristic for the formation is the occurrence of siltstone with calcite concretions containing fossils (fishes, etc.) and micro-intercalation of thin layers (a few millimeters in thickness) of sandstone, siltstone, clayey shale and limestone. In the formation three members are established:

– the Lower Member (4) is a siltstone-sandstone unit with 20-30 cm thick, clayey shale interbeds and rare syngenetic calcite concretions. This unit often contains brachiopods of the family Pygnacidae, *Carinatina* ex gr. *comata*, *Stegorhynchus* ex gr.

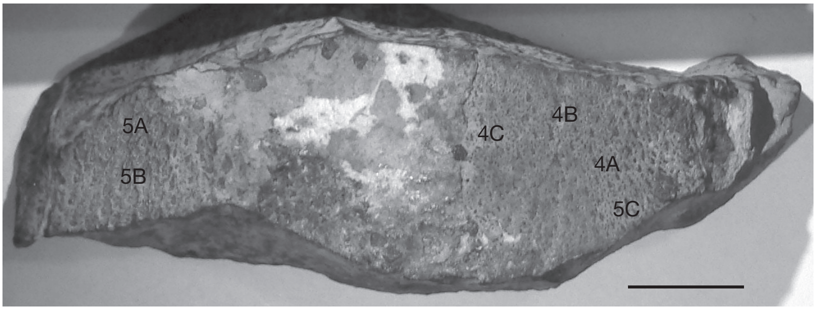

Fig. 3. — Heterostraci: Traquairaspididae? indet., specimen PIN 3845/4, sample 74-3, Poberezh'e (Coast) section, Chukotka, Arctic far-eastern Russia; Lower Member (4) of Pil'hikaj Formation, Lochkovian. Natural external mould of a fragment of plate of the head carapace. **4A**-**C**, **5A**-**C**, refer to details of ornamentation on Figures 4 and 5 respectively.

nympha, *Clorindina* sp. and fish remains. In the shales, rare tabulate and rugose corals, crinoids and other invertebrates have been found. The member has a bed of large sandstone-siltstone concretions (from 80 cm to 1-1.2 m in diameter) of early diagenetic origin;
– the Middle Member (5) consists of sandstone and siltstone with interbeds of clayey shale and calcite concretions, that include brachiopods and fish remains;
– the Upper Member (6) is a sandstone-siltstone unit with clayey shale interbeds. The stratified sandstone of this unit is well sorted.

MATERIAL AND METHODS

The fish specimens at our disposal are mostly tiny fragments or small isolated skeletal elements. They came from two levels:
– a) a grey calcareous siltstone sample from outcrop no. 73 of the Lower Member (1) of the Enmakaj Formation at the Tonnel'nyj (Tunnel'nyj) Brook, which yielded, after treatment with dilute acetic acid, several plate fragments (the largest one is 13 mm long) and acanthodian and thelodont scales. The fish remains are pyritized and etched, in several cases quite strongly; for instance, the thelodont and acanthodian scale crowns and even the bony bases were affected (Figs 7, 9). The specimens with collection numbers of the Institute of Geology, Tallinn University of Technology (TUT, specimens GIT 580-1 to 27), were obtained from rock pieces of a siltstone sample taken in the field for the study of brachiopods and given to us by S. Cherkesova;
– b) material of the Lower Member (4) of the Pil'hikaj Formation, from the Coast (Poberezh'e) locality, consists of a 7 cm long sample (no. 74-3) of grey, strongly cemented calcareous siltstone with fine cracks filled with calcite. On its surface the sample has an impression of heterostracan ornament. A bone fragment (about 5 cm long) with a double number 73-4 (74-3) from Tonnel'nyj Brook could come either from the Enmakaj Formation or, more probably, from the base of the Pil'hikaj Formation (based on information supplied by S. Cherkesova). The fragment was from the contact between two different rocks: grey siltstone and clayey shale. Because the siltstone had a carbonate cement, the ornament could be cleaned using dilute acetic acid. Both of these macroremains plus a small fragment are housed in the Palaeontological Museum, Russian Academy of Sciences, Moscow (collection no. with prefix PIN).

We have not seen the fish remains from a third level, in the Middle Member (5) of the Pil'hikaj Formation (Fig. 2), mentioned by Rogozov & Vasil'eva (1968).

Some macrospecimens were whitened with ammonium chlorite. All were photographed, using a digital camera Nikon D 200 or one attached

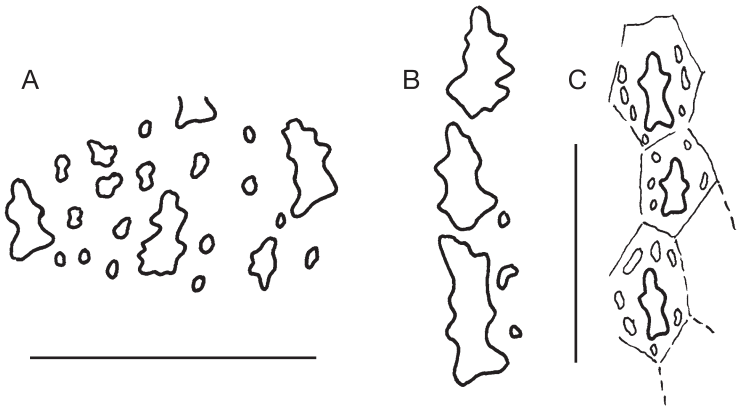

Fig. 4. — Details of superficial ornamentation of specimen PIN 3845/4. **A**, **B**, **C**, refer to the three areas indicated on Figure 3[4A, 4B, 4C].

to a (binocular) microscope Nikon AZ 100. Microremains were studied and photographed with the Zeiss Scanning Electron Microscope (SEM) EVO-MA15 in the Centre of Materials Research, Faculty of Chemical and Materials Science, Tallinn University of Technology (GIT specimens).

SYSTEMATIC PALAEONTOLOGY

Phylum CHORDATA Haeckel, 1874
Subphylum VERTEBRATA Lamarck, 1801
†Class PTERASPIDOMORPHI Goodrich, 1909
Subclass HETEROSTRACI Lankester, 1868
Order TRAQUAIRASPIDIFORMES
Tarlo, 1962
Family Traquairaspididae Kiaer, 1932

Traquairaspididae? gen. et sp. indet.
(Figs 3-5, 6A-C)

"Arctolepidida" – Cherkesova 1973: 276-279, table.

Material. — Specimens PIN 3845/2 to 3845/4: fragments of a large plate of the head carapace (PIN 3845/4), of a probable dorsal spine (PIN 3845/3), and of another element of the carapace (PIN 3845/2); microremain GIT 580-5.

Localities and stratigraphic horizons. — PIN 3845/4 is from locality (sample) 74-3, the Coast (Poberezh'e) section, south of De Long Strait, Chukotka, far-eastern Russia; Lower Member (4) of Pil'hikaj Formation, Lochkovian (upper? part). PIN 3845/3 and 3845/2 are from locality 73-4 (74-3), Tonnel'nyj Brook, same horizon as PIN 3845/4. Specimen (microremain) GIT 580-5 is from locality 73, Tonnel'nyj Brook, Lower Member (1) of Enmakaj Formation, Lochkovian.

Description

Specimen PIN 3845/4

This specimen is mostly preserved as a natural, external mould of a large fragment of a plate from the head carapace of a heterostracan (Fig. 3). Owing to the alignment of superficial ornamentation of oak-leaf-like tubercles, the antero-posterior axis of the plate is orientated up-down on Figure 3, by comparison to some specimens figured and described by Dineley & Loeffler (1976: pl. 1: 1-3, pl. 4: 1, 3) where the narrower extremity of tubercles is orientated frontward. So, the minimum width of the plate is evaluated at *c.* 6 cm, with a preserved length of 22 mm. It does not show any plate or field boundary. The ornamentation is made of series of alternating tubercles, with bigger tubercles surrounded by fields of smaller ones (Figs 4; 5A-C). Bigger tubercles are oak-leaf-shaped, triangular with rounded lateral expansions. They are 1.5 to 2 mm long (Figs 4; 5A-C). In most cases no boundary is seen on either side of these tubercles, except in a small area (Fig. 4C) where polygonal boundaries (either pentagonal or hexagonal) seem to surround some tubercles in a tessellated-like pattern. Each tessera would thus be made of a bigger central tubercle with smaller outer tubercles, with a total length of *c.* 1.5 mm.

PIN 3845/4 has an ornamentation (or "exoskeletal ultrasculpture" *sensu* Märss 2006) which looks very like that of some traquairaspid heterostracans figured and described by Dineley & Loeffler (1976): ?*Traquairaspis retusa* Dineley & Loeffler, 1976 (Dineley & Loeffler 1976: pl. 1: 1; fig. 5), Traquairaspididae indet. Type 2 (Dineley & Loeffler 1976: pl. 4, 1 and fig. 16). So, PIN 3845/4 does probably correspond to a fragment of a dorsal shield of a traquairaspid, and more precisely to its anterior part because the alignments of tubercles diverge rearward.

The central part of PIN 3845/4 shows a series of small (< 1 mm long) triangular tubercles with only one expansion on both sides, that are surrounded by a single row of much smaller tubercles, each set of bigger and smaller tubercles being limited by a polygonal, either pentagonal or hexagonal, boundary which mimics *c.* 1.5 mm long tesserae (Fig. 4C). This pattern is reminiscent of *Lepidaspis serrata* Dineley & Loeffler, 1976 (figs 73-76 and pls 29, 32). However, no tessera of *Lepidaspis* Dineley & Loeffler, 1976 shows additional smaller tubercles, peripheral to the main central one (Dineley & Loeffler 1976: figs 73-75, pl. 32, 5-8) – except the tessera in their plate 32, 6 which bears a small lateral tubercle beside the main central denticulated one. So, PIN 3845/4 is probably not from *Lepidaspis*.

Specimen PIN 3845/3

This specimen is a 52 mm long fragment of a probable dorsal spine of a heterostracan. It is 23 mm wide at its (proximal) wider extremity, and 16 mm wide at its (distal) narrower extremity (Fig. 5D). It is laterally flattened and symmetrical. The narrower extremity is broken and thus shows a natural transverse section of the bone: its histology is typical of a heterostracan with a central cancellous, honeycomb-like layer where the cancellae have a mean width of 0.5 mm, while the outer layer, below the external tuberculated surface, is reticulated (with smaller cavities). The wider extremity of PIN 3845/3 is broken as well, and shows the same histological structure.

The external ornamentation of its distal part, where the matrix has been removed, shows parallel rows of alternating, narrow, long tubercles (Fig. 5D) interspersed with much smaller tubercles (Fig. 5E, F). The bigger tubercles are 1 to 3 mm long × 0.5 mm wide. They sometimes show a median longitudinal faint ridge (carina or crest) (Fig. 5F), and all have small lateral denticulated expansions that are always simple, rather sharp, and never subdivided (bifid). The smaller intermediate tubercles are very small, elongate, sharp and arranged as 1, 2 or 3 rows between the bigger tubercles (Fig. 5E, F). No boundary of tessellated-like units is visible on this part of the specimen.

This ornamentation is very like the one of several traquairaspid taxa described by Dineley & Loeffler (1976), but different from each of them in its detailed features. The Traquairaspididae indet. Type 3 of Dineley & Loeffler (1976: pl. 4: 3, fig. 17) has bigger elongate and smaller intermediate tubercles, but the latter are relatively longer than on PIN 3845/3, and they are organised as "long, narrow […] twig-like ridges" (Dineley & Loeffler 1976: 40) unlike those of PIN 3845/3. The Traquairaspididae indet. Type 4 of Dineley & Loeffler (1976: pl. 4: 4, fig. 18) also has intercalated smaller tubercles, but the bigger ones are much bigger (1.5 to 8 mm long × 0.8 mm wide), "round crested" and "commonly kinked, unbranched" (Dineley & Loeffler 1976: 41) unlike those of PIN 3845/3.

PIN 3845/3 has the same shape as a specimen from the Lower Devonian of Spitsbergen which is the dorsal spine of a heterostracan, and was identified as *Weigeltaspis heintzi* Tarlo, 1964 by Blieck (1983: pl. VI: 2-5; based upon the holotype preserved in the Palaeontological Museum of Oslo, Norway – specimen PMO D 2440/2441, and its probable counterpart preserved in the Muséum national d'Histoire naturelle, Paris – specimen MNHN.F.SVD900). However, specimen PIN 3845/3 is broken in its proximal part and is not preserved attached to its dorsal plate. The holotype of *W. heintzi* (Tarlo 1964: pl. IV: 6-7; 1965: pl. IV: 2; Blieck 1983: pl. VI: 5) bears a series of *c.* 2 mm long, elongate tubercles with lateral bifid denticulations, but without intermediate smaller tubercles, unlike PIN 3845/3.

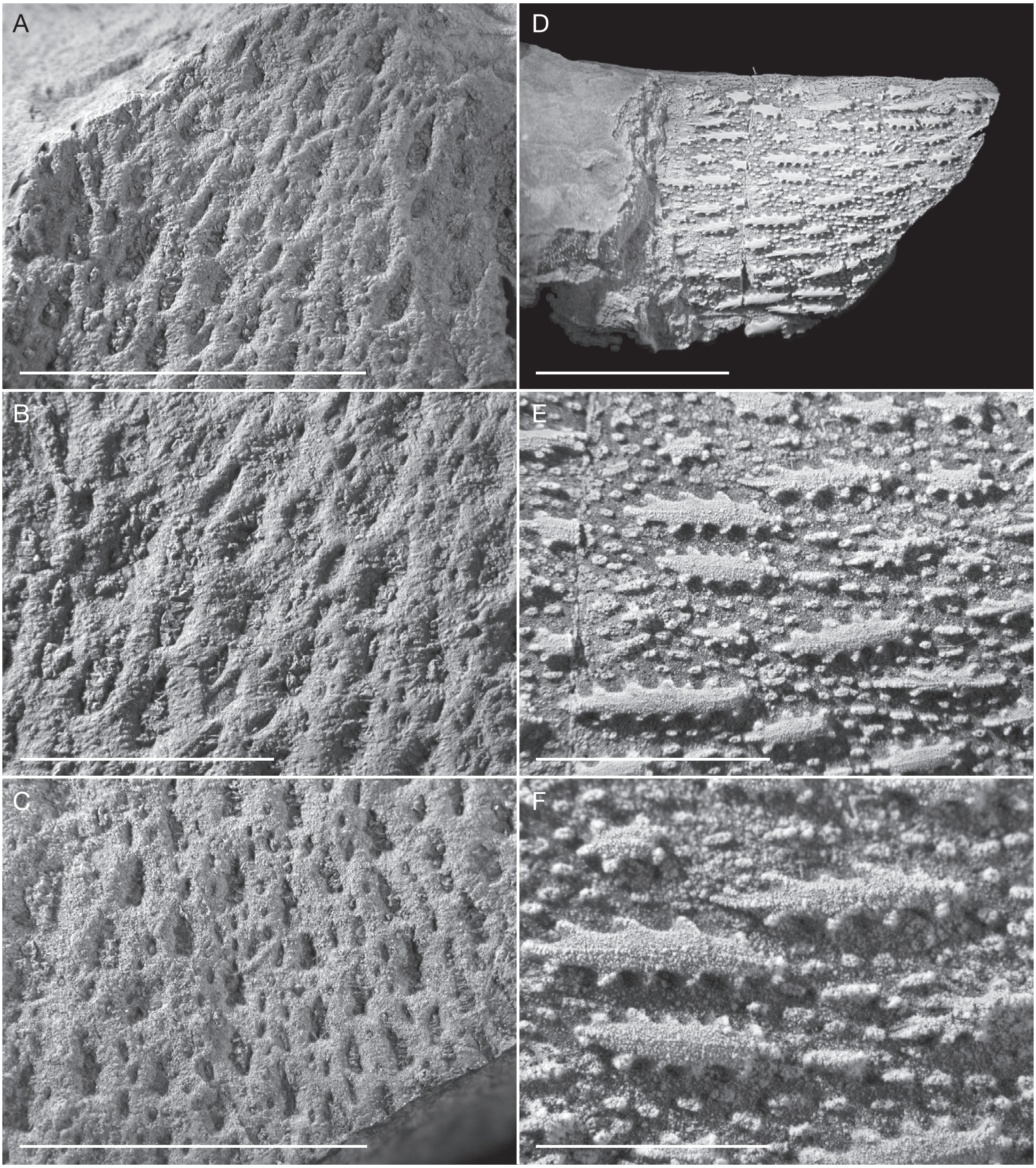

FIG. 5. — Heterostraci: Traquairaspididae? indet.: **A**-**C**, specimen PIN 3845/4 (same as Figures 3 and 4), sample 74-3, Poberezh'e (Coast) section, Chukotka, Arctic far-eastern Russia; Lower (4) Member of Pil'hikaj Formation, Lochkovian; details of superficial ornamentation of areas 5A, B, C as indicated on Fig. 3; **D**-**F**, specimen PIN 3845/3, sample 73-4 (74-3), Tonnel'nyj Brook, Chukotka, Arctic far-eastern Russia; Lower Member (4) of Pil'hikaj Formation, Lochkovian; distal end of specimen (**D**) with details of ornamentation (**E**, **F**). Scale bars: A, C, D, 1 cm; B, E, 0.5 cm; F, 0,25 cm.

Specimen GIT 580-5

This is a 15 mm long fragment of a dermal bony plate with elongate, sharp (higher than wide) tubercles (Fig. 6A, B). These tubercles show simple lateral denticulations. No intercalated smaller tubercles and no tessellated-like pattern are visible on this specimen. Tarrant (1991: 402) gives a diagnosis of the order Traquairaspidiformes (family Traquairaspididae of Dineley & Loeffler 1976) where the ornamentation of dorsal shields is "often of elevated, laterally serrated tubercles, commonly with narrow interstitial tubercles or ridges". Commonly does not mean always, so our specimen GIT 580-5 could be a traquairaspid. Being stratigraphically older than the specimens PIN 3845/2-4, the specimen 580-5 might represent a distinct taxon, but this cannot be demonstrated based upon such poorly preserved material.

Specimen PIN 3845/2

This specimen is probably a fragment from a plate, rather than a tessera, because its edges are broken (Fig. 6C). It shows two rather big, round-topped, *c.* 1.5 mm long tubercles with lateral simple or bifid denticulations. It shows no interstitial smaller tubercles, but a few small tubercles are visible on what is probably the outer edge of the specimen (upper part on Fig. 6C).

Discussion

This material has been provisionally determined as "traquairaspid", "*Traquairaspis* sp. indet." or "*Lepidaspis*" on the handwritten labels and notes preserved with it. These variations reflect the uncertainty regarding its taxonomic status. As described above, this heterostracan material is consigned to what is usually understood as traquairaspids (order Traquairaspidiformes or family Traquairaspididae, depending of authors' opinion). However, few articulated traquairaspids are known, and it is difficult to determine such fragmentary remains as the ones figured here (Figs 3-5; 6A-C). Rare exceptions are the specimens from the Lower Devonian of the Canadian Arctic, where most described species of Traquairaspididae (*sensu* Dineley & Loeffler 1976) have a fused dorsal shield enclosing orbital and branchial openings, and comprising rostral, pineal, orbital and median dorsal fields (see e.g., ?*Traquairaspis mackensiensis* Dineley & Loeffler, 1976 [Dineley & Loeffler 1976: pl. 3: 1]). These taxa were not included in Tarrant's (1991) revision of the traquairaspids based on Anglo-Welsh material. His order Traquairaspidiformes is subdivided into two families: Phialaspididae White, 1946, and Traquairaspididae Kiaer, 1932, the latter being based upon the original material from the Upper Silurian of Scotland, *Traquairaspis campbelli* (Traquair, 1913) (Kiaer 1932). Tarrant (1991: 402) diagnosed the family Phialaspididae as having dorsal shields, which usually comprise separate plates with a vaulted dorsal disc usually bearing a thick median dorsal spine (called a vane by Tarrant). So, if our specimen PIN 3845/3 (Fig. 5D-F) corresponds to the same taxon as PIN 3845/4 (Figs 3; 4; 5A-C), it might be referable to the taxon Tarrant (1991) called Phialaspididae, and Blieck (1983: pl. VI: 2-5) called *Weigeltaspis* Brotzen,1933, following Tarlo (1965: 20) who considered *Weigeltaspis* to be characterized by a "dorsal median plate long and narrow, with prominent median ridge in posterior half of plate". This material was attributed to the Traquairaspidiformes by Blieck (1983: 89) by comparison with *Traquairaspis symondsi* (Lankester, 1868) (*in* Dineley 1964: fig. 5), the type species of *Phialaspis* Wills, 1936 *in* Tarrant (1991: 403), and thus of the family Phialaspididae *sensu* Tarrant (1991). The second specimen of *Weigeltaspis heintzi* figured by Tarlo (1965: fig. 2C) shows a ?branchial plate, a dorsal disc and a field of tesserae, features that persuaded Tarlo to classify *Weigeltaspis* among his Psammosteiformes.

The small area with a tessellated-like pattern on PIN 3845/4 (Fig. 4C) recalls the ornament of *Lepidaspis*, but this latter genus was considered an agnathan vertebrate of uncertain affinities by its authors (Dineley & Loeffler 1976: 175 *et seq.*). All this seems to be very confusing. A revision of all material that has been called "traquairaspids" is needed. A conservative opinion is kept here, and the material from Chukotka is provisionally attributed to Traquairaspididae? indet. based upon

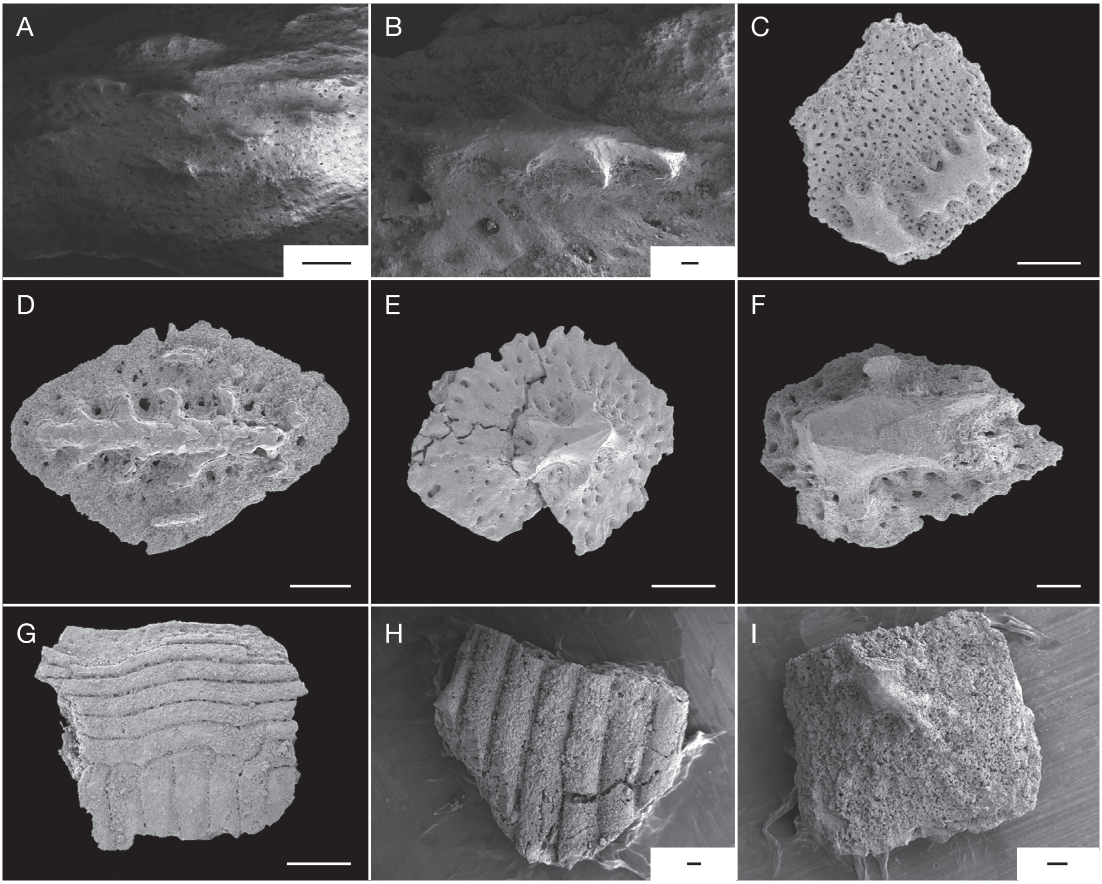

FIG. 6. — Heterostracan microremains from the Lower Devonian of Chukotka, Arctic far-eastern Russia: **A**, **B**, Traquairaspididae? gen. et sp. indet., specimen GIT 580-5, from locality (sample) 73, Tonnel'nyj Brook, Lower Member (1) of Enmakaj Formation, Lochkovian; **C**, Traquairaspididae? gen. et sp. indet., specimen PIN 3845/2, locality 73-4 (74-3), Tonnel'nyj Brook, Lower Member (4) of Pil'hikaj Formation, Lochkovian; **D**, *Lepidaspis*? sp., tessera, specimen GIT 580-2, locality 73, same origin as specimen 580-5 (**A**, **B**); **E**, **F**, *Oniscolepis*? sp., tesserae, specimens GIT 580-1 (**E**) and 580-3 (**F**), locality 73, same origin as specimen 580-5 (**A**, **B**); **G**, **H**, Poraspididae gen. et sp. indet., fragments of a scale (**G**) and of a plate (**H**), specimens GIT 580-4 (**G**) and 580-7 (**H**), locality 73, same origin as specimen 580-5 (**A**, **B**); **I**, Heterostraci? indet., tessera (platelet), specimen GIT 580-8, locality 73, same origin as specimen 580-5 (**A**, **B**). Scale bars: A, C, 1 mm; B, 100 μm; D, 300 μm; E, G, 500 μm; F, H, I, 200 μm.

its dermal ornamentation (exoskeletal ultrasculpture) of oak-leaf-like tubercles with mostly no tessellated pattern of the plates. Well developed dorsal structures such as a dorsal spine on Devonian agnathans is classically interpreted as an adaptation to Old Red Sandstone or Old Red Sandstone-like water environments, which occur by convergence in different higher taxa such as the heterostracans, osteostracans, galeaspids and pituriaspids (Janvier 1996: fig. 7.10.G).

Order CYATHASPIDIFORMES Berg, 1937
Family PORASPIDIDAE Kiaer, 1932

Poraspididae gen. et sp. indet.
(Fig. 6G, H)

MATERIAL. — Specimens GIT 580-4, 6 and 7 of the Institute of Geology, Tallinn University of Technology, Estonia: fragments of a flank scale (GIT 580-4) and of undetermined plates (GIT 580-6 and 7).

Locality and stratigraphic horizon. — Locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

Description

This material is represented by three small fragmentary remains of dermal bony elements. The specimen GIT 580-4 (Fig. 6G) is from a flank scale of a poraspidid heterostracan similar to the scales figured, for example, by Blieck (1982: pl. VIII: 2, 4: *Poraspis rostrata* Kiaer & Heintz, 1935). It bears six flat dentine ridges per mm as in various *Poraspis* Kiaer, 1930 species from the Lochkovian of Spitsbergen (Blieck & Heintz 1983: table 1). The specimen GIT 580-7 (Fig. 6H) has more vaulted (convex) and wider (2/mm) dentine ridges. It probably also comes from a poraspidid plate.

Incerti ordinis
Family Oniscolepididae
Märss & Karatajūtė-Talimaa, 2009
Genus *Oniscolepis* Pander, 1856

Oniscolepis? sp.
(Fig. 6E, F)

Material. — Specimens GIT 580-1 and 580-3: isolated tesserae with a central tubercle.

Locality and stratigraphic horizon. — Locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

Description

These are two small bony elements, partly fractured, but corresponding to isolated tesserae. Specimen GIT 580-1 (Fig. 6E) is *c.* 1.8 mm long, with a single central, denticulated tubercle which shows a thin longitudinal crest. Specimen GIT 580-3 (Fig. 6F) is *c.* 1.5 mm long with a single central, bigger, denticulated tubercle. Both tesserae have a very thin base which corresponds to the cancellous layer with rather wide chambers. They may be compared to "juvenile scales" of *Strosipherus* Pander, 1856 (*sensu* Karatajūtė-Talimaa & Märss 2008), recently synonymized with *Oniscolepis* by Märss & Karatajūtė-Talimaa (2009: fig. 4A). Both specimens can also be compared with broken portions of the superficial layer of traquairaspid elements (e.g., Fig. 4C), but in traquairaspids the base is usually much thicker than in GIT 580-1 and 3. So, affinities with *Oniscolepis* (senior synonym of *Strosipherus*) seem more likely.

Discussion

Strosipherus and *Oniscolepis*, now synonymized under the name *Oniscolepis* (Märss & Karatajūtė-Talimaa 2009), are representatives of tessellated heterostracans, the taxonomic status of which is still uncertain (see the discussion/comparison section in Märss & Karatajūtė-Talimaa [2009: 58-60]; see also Elliott & Loeffler [1989]). The family Oniscolepididae Märss & Karatajūtė-Talimaa, 2009, including *Oniscolepis* and *Kallostrakon* Lankester, 1870, is considered by Märss & Karatajūtė-Talimaa (2009) as belonging to the eriptychiid heterostracans (order Eriptychiida Ørvig, 1958; see also Obruchev 1964]; Eriptychiiformes Tarlo, 1962). However, the phylogenetic relationships of eriptychiids to heterostracans are still in debate. Eriptychiids proper (family Eriptychiidae Tarlo, 1962) are either considered as the sister-group of Heterostraci (e.g., Janvier 1996), or as an order of the subclass Heterostraci (e.g., Märss 1986; Märss & Karatajūtė-Talimaa 2009). So, the phylogenetic relationships of oniscolepidids, eriptychiids and heterostracans may be considered as unsolved, and we keep here Oniscolepididae at an uncertain ordinal rank within heterostracans.

The occurrence of oniscolepidid remains in the Lochkovian of Chukotka, if confirmed, would fit the presently known stratigraphical distribution of Oniscolepididae, which ranges from the Upper Silurian (Pridoli) to Lower Devonian (Lochkovian) (Märss & Karatajūtė-Talimaa 2009).

Incerti ordinis
Incertae familiae

Genus *Lepidaspis* Dineley & Loeffler, 1976

Remarks

Dineley & Loeffler (1976) have not precisely classified *Lepidaspis* among vertebrates, keeping this genus as *incertae sedis*. They, however, noticed affinities with Pteraspidomorphi, that is, Thelodonti and

Heterostraci (Dineley & Loeffler 1976: 190). Based upon detailed superficial ornament pattern, Blieck (1982: 47) classified *Lepidaspis* as "Heterostraci incerti ordinis et incertae familiae", an opinion which has not been retained in the Paleobiology Database (Hendy 2012) where *Lepidaspis* is classified among the family Corvaspididae "according to Blieck *et al.* 2002". The latter assertion is wrong: Blieck *et al.* (2002) did not include *Lepidaspis* among Corvaspididae, and we keep here *Lepidaspis* as an undetermined heterostracan (following Blieck 1982).

Lepidaspis? sp. (Fig. 6D)

MATERIAL. — Specimen GIT 580-2: isolated tessera.

LOCALITY AND STRATIGRAPHIC HORIZON. — Same as specimens GIT 580-1, 3, 4, 6 and 7: locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

DESCRIPTION

The specimen is a diamond-shaped, 1.7 mm long tessera with a single central, narrow, elongate tubercle (*c.* 1.4 mm long). This tubercle has denticulated edges. Each denticulation is simple (undivided). Additionally, on each side of this central tubercle occurs a much smaller narrow tubercle (Fig. 6D). The base of the tessera is perforated by small foramina of the underlying (probably reticulated) layer. This tessera compares well with those of *Lepidaspis serrata* Dineley & Loeffler (1976: figs 74, 76, pl. 32: 6, 7), and especially with the tessera in their plate 32: 6, which bears a small lateral tubercle beside the main central denticulated one. However, because we have here a single tessera, it is difficult to compare with the great variability of shapes observed on *Lepidaspis serrata* tesserae (Dineley & Loeffler 1976), and so only tentatively assign GIT 580-2 to *Lepidaspis*.

HETEROSTRACI? indet. (Fig. 6I)

MATERIAL. — Specimen GIT 580-8: isolated tessera or platelet.

LOCALITY AND STRATIGRAPHIC HORIZON. — Same as specimens GIT n° 580-1, 2, 3, 4, 6 and 7: locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

DESCRIPTION

This specimen is an isolated square-shaped element (either a tessera or platelet), partially broken, and with an altered surface. It bears a single, probably central, star-shaped tubercle (Fig. 6I). Because it is larger (*c.* 3.2 mm long for its preserved part) than all other tesserae that have been prepared from sample 73 of the Coast section, we suggest that it might correspond to a different taxon. Furthermore, with such a small sample (a single specimen), no thin section has been made, and thus its histology is not confirmed as being of a heterostracan.

†Subclass THELODONTI Jaekel, 1911

REMARKS

Following Märss *et al.* (2007), we shall place the higher taxon as a Subclass equivalent to Heterostraci in the Class Pteraspidomorphi, although the full analysis of phylogenetic characters of this latter "clade" is as yet wanting and the interrelationships between the subclasses should be explored more fully.

Order THELODONTIFORMES Kiaer, 1932

REMARKS

As there were only a few specimens retrieved from the sample 73 of the Lower Member (1) of the Enmakaj Formation, it is difficult to determine the species of thelodont. All, however, have typical thelodontiform histology with a single or few pulp openings in the base.

Family TURINIIDAE Obruchev, 1964

REMARKS

Several turiniid taxa have been described (e.g., Märss *et al.* 2007) but variation of scale form is not precisely known. Some of the scales from Chukotka are tentatively referred to three of the current turiniid species.

Genus *Turinia* Traquair, 1896

Remarks

As there is only one articulated specimen of the type species *Turinia pagei*, from the Lower Devonian (lower Lochkovian) Lower Garvock Group of Scotland, and rare other patches of scales, we still cannot determine the full extent of variation in this taxon. The range of scales apparent on the macrofossils does not "match" the wealth of variation presented by isolated scales in beds of the same age (e.g., Gross 1967; Ørvig 1969a; Turner 1973: figs 8a, b, e, g, pl. 2; 1982: pl. 97; Karatajūtė-Talimaa 1978; Märss & Ritchie 1998: fig. 49). This is one of the taxonomic problems to be accounted for when examining an assemblage of few scales.

Six of the scales, described below, would seem to be referable to one of the principal genera known in the Devonian, *Turinia*, by their platform-like crown with rounded undulating ridges or posterior extending lappets. The turiniid scales are of different age classes exhibiting from relatively shallow bases to deeper bases with small pulp openings of more mature ones (Märss *et al.* 2007).

Turinia pagei (Powrie, 1870) ?
(Fig. 7A, B)

Material. — Specimens GIT 580-16 and 580-19: scales (the second one lost).

Locality and stratigraphic horizon. — Locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

Description

Specimen GIT 580-19 (Fig. 7A) is a mature scale seen here in antero-lateral view, with a high simple elliptical crown, pointed posterior, and a flat topped rounded anterior. There are possible minor ridges on the posterior otherwise smooth neck. The condition of the scale surface, however, is poorly preserved (see Taphonomy discussion below). The deep base has an anterior extension of the base, which might have projected into a longer root. Scale GIT 580-16, seen in lateral view (Fig. 7B), is more typical of a head to cephalopectoral scale with a series of rounded undulations around the gently rounded crown. The upper surface is smooth. The base is not larger than the crown but extends slightly anteriorward; it too exhibits slight scalloping in its basal growth around a medium-sized central pulp cavity.

These scales are typical of many turiniid head or cephalopectoral scales and are tentatively placed in *T. pagei*. Alternatively they might belong to *Turinia composita* Karatajūtė-Talimaa, 2002 or *Turinia polita* Karatajūtė-Talimaa, 1978 (see below).

Turinia sp. cf. ***T. composita***
Karatajūtė-Talimaa, 2002
(Fig. 7C, D)

Material. — Specimens GIT n° 580-10 and 580-11: scales.

Locality and stratigraphic horizon. — Locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

Description

The scale GIT 580-10 (Fig. 7C) is wide and rhombic with the crown not quite as wide as the base. The anterior rim of the crown is gently scalloped into three sections. The large flat median part of the crown has two lateral lappet areas which expand posteriorly so that the crown ends in at least five points. A smaller extension to the lower left might be an artifact or a further lower lappet on that side. The posterior parts are not well preserved but probably extended well beyond the mid-posterior point of the crown. There is a wide shallow grooved neck separating the crown from the relatively shallow base. As the basal view is not available the pulp opening type is unknown. The base is slightly thickened anteriorly into a short downwards-projecting narrow spur, which is broken off at the tip. Specimen GIT 580-11 (Fig. 7D) is generally similar although wider across the scale than in 580-10. The projections extend from the median part of the crown as well as being placed on a short narrow lateral lappet or ridge on both

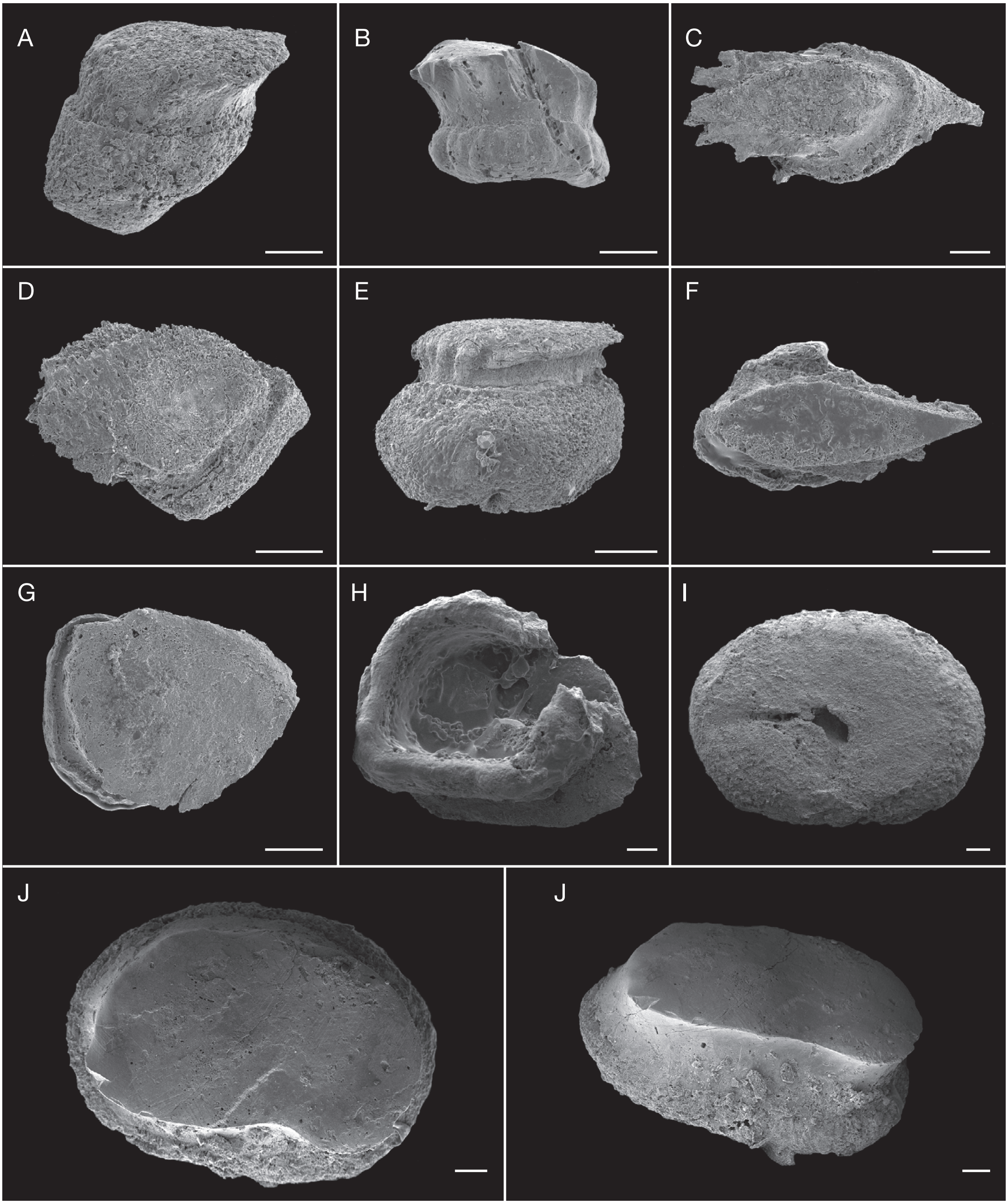

Fig. 7. — Thelodont scales from the Lower Devonian of Chukotka, Arctic far-eastern Russia: **A**, **B**, *Turinia pagei* (Powrie, 1870) ?, specimens GIT 580-19 (**A** in antero-lateral view) and 580-16 (**B** in lateral view); **C**, **D**, *Turinia* sp. cf. *T. composita* Karatajūtė-Talimaa, 2002, specimens GIT 580-10 (**C** in crown view) and 580-11 (**D** in latero-crown view); **E**, *Turinia* sp. cf. *T. polita* Karatajūtė-Talimaa, 1978, specimen GIT 580-17 in lateral view; **F**, *Turinia* sp., specimen GIT 580-12 in crown view; **G**, **H**, *Nikolivia*? sp. cf. *N. gutta* Karatajūtė-Talimaa, 1978, specimen GIT 580-13 in crown (**G**) and basal (**H**) views; **I**-**K**, *Nikolivia*? sp., specimen GIT 580-9 in basal (**I**), crown (**J**) and latero-crown (**K**) views. All specimens from locality (sample) 73, Tonnel'nyj Brook, Lower Member (1) of Enmakaj Formation, Lochkovian. Scale bars: A-C, F, G, 200 µm; D, 250 µm; E, 300 µm; H-K, 100 µm.

sides. The extended parts are better preserved and number 9 or 10 with the posterior mid-point. The neck is wider and the base slightly shallower; it extends anteriorly into a short projection. As with the other scale, the basal view is not available and so the pulp opening type is unknown. Within the neck as seen in the lower right of Fig. 7D there are exposed parts of three fine concentric ridges, which might be evidence of growth lines within the basal tissue (cf. Märss *et al.* 2007).

These two scales with their wide laterally expanded crown with several separate posterior points are comparable with the body scales of *Turinia composita* (Karatajūtė-Talimaa 2002: fig. 1G, H) and to some extent with some of *Turinia barentsia* Blom & Goujet, 2002 (Blom & Goujet 2002: pl. 2). As with the other scales, the surface is severely scoured or etched and opening of dentine and bony aspidine structure can be seen.

Turinia **sp. cf.** ***T. polita***
Karatajūtė-Talimaa, 1978
(Fig. 7E)

MATERIAL. — Specimen GIT 580-17: scale.

LOCALITY AND STRATIGRAPHIC HORIZON. — Locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

DESCRIPTION
From the lateral view of this scale, the flat crown can be seen well with the anterodorsal crown rim gently scalloped. The crown is smaller than the base with a vertical neck and thin groove around the rim. The base is deep and rounded with a small central to offset pulp opening, typical of an older scale where the pulp is overgrown.

This is a possible head or cephalopectoral scale and seems most comparable with those of *Turinia polita*. This latter taxon is found in Lochkovian assemblages alongside *Turinia pagei* in some parts of the Old Red Sandstone Continent (e.g., in Britain: Karatajūtė-Talimaa 1978; Talimaa 2000; ST pers. obs.) whereas in other places seems to appear a little later in the Lochkovian (e.g., Blom & Goujet 2002).

Turinia sp.
(Fig. 7F)

MATERIAL. — Specimen GIT 580-12: broken scale.

LOCALITY AND STRATIGRAPHIC HORIZON. — Locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

DESCRIPTION
This relatively large scale, seen in dorsal crown view, is broken on either side of the crown. All that remains is the wide and flat elliptical mid-section of the crown and the anterior parts of two lateral segments, which may or may not have been separated from the mid-section by a deep channel on the one side. The remnants of an expanding lateral lappet are left mid-scale on the other side. The neck is trough-like and the base apparently not deep.

This specimen shows a typical turiniid body scale configuration, resembling the type species. It also resembles the mid-section of body scales of other turiniid taxa such as *Turinia barentsia* from the Ben Nevis Formation, Red Bay Group of Spitsbergen (Blom & Goujet 2002), and *Turinia composita,* but with the poor state of preservation, this taxon is left in open nomenclature.

Family NIKOLIVIIDAE Karatajūtė-Talimaa, 1978 ?
Genus *Nikolivia* Karatajūtė-Talimaa, 1978 ?

Nikolivia? **sp. cf.** ***N. gutta***
Karatajūtė-Talimaa, 1978
(Fig. 7G, H)

MATERIAL. — Specimen GIT 580-13: scale.

LOCALITY AND STRATIGRAPHIC HORIZON. — Locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

DESCRIPTION
GIT 580-13 has a flat simple slightly subtriangular crown with a slight scalloping of anterior rim (Fig. 7G) and a shallow neck that merges with the rounded base that almost matches the crown in size. The ventral view shows the wide open, thelodontid

type narrow base, which is a relatively thickened torus around a very large pulp cavity with some dental tubule openings within (Fig. 7H).

Based on published occurrences, there are no exactly similar scales to this one from the Chukotka material or elsewhere. However, it is a placoid thelodont scale rather than a simple shark scale based on its rounded base and simple crown. It is not identical to but is generally comparable with those of *Nikolivia gutta*, known from several Lower Devonian (Lochkovian) assemblages, but shares the large open pulp cavity and smooth subrounded crown shape (cf. Turner 1973: pl. 1; Karatajūtė-Talimaa 1978). The range of variation of another rounded nikoliviid scale with a large rounded base, *Nikolivia aligera Karatajūtė-Talimaa, 2002* (Karatajūtė-Talimaa 2002: fig. 6) also from Arctic Russia, might also encompass this scale. Within the postulated scale range of yet another taxon, *Nikolivia balabayi* Karatajūtė-Talimaa, 1978 (Karatajūtė-Talimaa 1978: fig. 29; see also Märss *et al.* 2007: fig. 128) from the Lower Devonian Czortkow Stage of Podolia (Ukraine), there are some smooth scales of a similar nature but they are more elongate.

Nikolivia? sp.
(Fig. 7I-K)

MATERIAL. — Specimen GIT 580-9: scale.

LOCALITY AND STRATIGRAPHIC HORIZON. — Locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

DESCRIPTION

This is an unusual ovoid scale with a wide base, wider than the high, extremely flat and almost featureless crown (Fig. 7J, K). There is a slight asymmetry to the crown with some curvature to one side. The base is also apparently not deep but it is overgrown with a small central pulp hole, denoting a mature state (Fig. 7I). There is a lateral groove to one side leading to the scale rim.

The wide shape of this scale is unlike any *Turinia* or *Nikolivia* taxon seen elsewhere. It might be a pathological scale or broken with the crown top sheared off, and/or from the crown flatness it might be a ventral scale on the body. Some cephalopectoral scales of *Turinia antarctica* Turner & Young, 1992 (Turner & Young 1992: figs 4c, l, n, 5m, 7a) show flat tops to the crowns that suggest this explanation. The presence of a groove on the base for a large canal is uncommon, and combined with the slight depression to the side of the scale, might indicate that this is a specialized scale associated with a pore-canal or lateral line (see Märss *et al.* 2007). There is a possibility that this is a new form but until further material showing the variation is found, the identification of the taxon for this scale is tentative at best.

COMMENTS ON DISTRIBUTION OF THELODONTS

In general the majority of scales are typical of Lower Devonian assemblages around the Old Red Sandstone Continent, with *Turinia* and *Nikolivia* type scales. The turiniid scales fall within the variation range of the type species and co-occuring taxa such as *Turinia composita*, *T. barentsia* and *T. polita*, all found in the British, Baltic to Arctic localities. As so few scales were recovered from locality 73, Tonnel'nyj Brook, Chukotka and possibly the smallest scales were lost, the absence of such expected key taxa as *Boreania minima* Karatajūtė-Talimaa, 1985, which typically occur in the earliest Lochkovian (e.g., Talimaa 2000) is not surprising.

Based on published occurrences, there are no identical scales to the two nikoliviid-like scales in the new material from Chukotka. However, they are generally comparable with *Nikolivia gutta* known from the Lochkovian of Britain, the Baltic and Spitsbergen and perhaps others from Arctic Russia and Podolia (Ukraine).

Superclass GNATHOSTOMATA
Gegenbaur, 1874
†Class PLACODERMI M'Coy, 1848
Order ACANTHOTHORACI Stensiö, 1944
Family PALAEACANTHASPIDIDAE Stensiö, 1944

Palaeacanthaspididae gen. et sp. indet.
(Fig. 8)

MATERIAL. — Specimens GIT 580-22 to 580-25: isolated skeletal elements and fragments of bony plates with "star-shaped" tubercles.

Locality and stratigraphic horizon. — Locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

Description

Four microremains from the Enmakaj Formation belong to placoderms. The best-preserved specimen (Fig. 8A; GIT 580-22) is an isolated spindle-like skeletal element, twice longer than wide. It has a slightly oval central tubercle, placed asymmetrically, and around it smaller asymmetrical tubercles, forming three rows, except at one of the sides. At the opposite side the tubercles are partly laterally compressed and lamellar. Tubercles have narrow smooth ridges, which are most numerous on the central tubercle (up to 13). The ridges end at the sharp tips of tubercles. The second remain (Fig. 8B; GIT 580-25) is rather fragmentary and shows spongy bone with four broken tubercles on it. Ornament of the tubercles is rougher than that of the previous specimen. The ridges are in cross section less sharp in comparison with those of the specimen GIT 580-22. One of the ridges bifurcates at its proximal end. Apices of the tubercles were differently directed. The specimen could be a fragment of a larger spindle-like element.

Two remaining specimens of poor preservation show ornament of different type. The specimen GIT 580-23 (Fig. 8C) is probably a fragment of an exoskeletal plate with a slightly concave margin (?). It is covered with small stellate flat round or elongated tubercles. Number of short ridges varies from 7 to 10. Most of the tubercles are clearly separated from one another. The specimen GIT 580-24 (Fig. 8D) is a fragment, in which the ornament resembles somewhat that of the specimen 580-23 but is rougher. Stellate tubercles are closely backed. Short ridges end with minute rounded swellings. The specimens may belong to different forms.

Comparison and stratigraphical distribution

Identification of the Lower Devonian placoderm microremains is complicated as in many cases the ornament of the carapace plates is not figured in details. However, there are exceptions, concerning acanthothoracids (also called as palaeacanthaspids or radotinids according to their earliest known representatives *Palaeacanthaspis* Brotzen, 1934 and *Radotina Gross, 1950*). Ørvig's (1975) paper on the acanthothoracid *Romundina* Ørvig, 1975 from Arctic Canada, Prince of Wales Island, shows ornament at high magnification. Characteristics of *Romundina* tubercles are ridges, bearing rows of tiny nodules. Still, not all ridges have necessarily the nodules. Long & Young (1988) have figured similar ornament in the Emsian acanthothoracid *Murrindalaspis Long, 1984* (New South Wales, Australia), carrying even finer nodules along ridges. In one of the scales (Long & Young 1988: fig. 9B) the ends of ridges are truncated. The *Romundina* type of ornament is recognized in several acanthothoracid tubercles from the Lochkovian-Pragian of southeastern Australia (Basden *et al.* 2000). Some acanthothoracids possess the radotinid type of ornament, consisting of conical stellate tubercles with 4-12 ridges. The latter ones bear rows of small round nodules. This kind of ornament occurs in a Pragian radotinid from the Armorican Massif, France (Goujet 1976).

Tubercles similar to those of the above radotinid, i.e. acanthothoracids, can be seen in some Lochkovian buchanosteids from Australia (Basden *et al.* 2000: fig. 3). On the other hand, these early buchanosteids resemble in their ornament that of the scales of the Emsian buchanosteid *Uralosteus* Mark-Kurik & Young, 2003 (Mark-Kurik & Young 2003). Buchanosteids, namely *Buchanosteus* sp., are described from the Lochkovian of Guangxi, South China (Wang *et al.* 1998). However, buchanosteid arthrodires are much more common in the Emsian of many other regions (Mark-Kurik 2004: table 1).

According to our interpretation these few placoderm remains from the Chukotka Enmakaj assemblage belong probably all to acanthothoracids. Acanthothoracids are particularly characteristic of the Lochkovian. They are reported from Australia, North America and numerous regions of Eurasia, including the present day Arctic. Goujet (1998) mentioned that on the Prince of Wales Island, the Canadian Arctic, at least three different forms of these placoderms, one of them being *Romundina*, occur in the Lochkovian. In this region acanthothoracids can also be met together with actinolepid arthrodires.

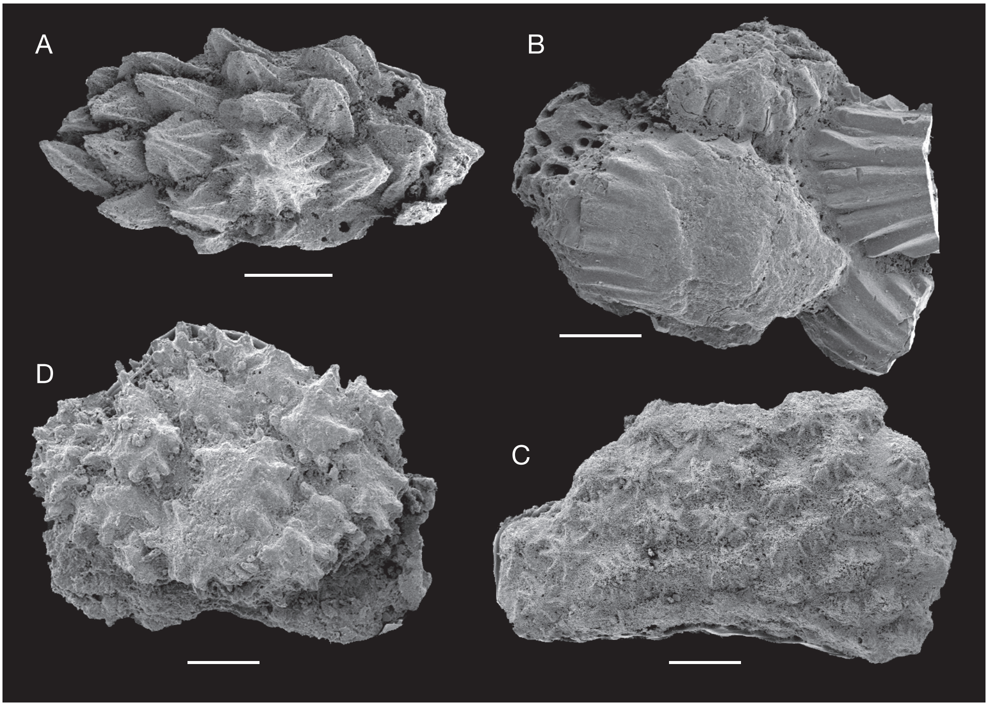

Fig. 8. — Acanthothoraci: Palaeacanthaspididae gen. et sp. indet.: **A**, specimen GIT-580-22; **B**, specimen GIT 580-25; **C**, specimen 580-23; **D**, specimen 580-24. All specimens from locality (sample) 73, Tonnel'nyj Brook, Lower Member (1) of Enmakaj Formation, Lochkovian. Scale bars: A, C, 500 μm; B, 400 μm; D, 200 μm.

In result of the reassessment of the paper by Mark-Kurik (1974) it can be said that two different acanthothoracids (one of them probably *Romundina*) come from the Pshenitsyn Formation of Kotelnyj Island, New Siberian Archipelago, Russia. Four trunk armour plates of latter material, i.e. MD, left ADL, right complex plate (AL + Sp + AVL) (Mark-Kurik 1974: fig. 1), and another complex plate (Mark-Kurik 1974: pl. II, fig.1) belong to a smaller acanthothoracid. The figures 1 to 7 of the same paper (Mark-Kurik 1974) show ornament of a larger acanthothoracid. The Pshenitsyn Formation is dated by Cherkesova (1988) as Lochkovian. The left ADL plate (Mark-Kurik 1974: figs 1-9, pl. II: 7) was erroneously identified as the equivalent plate of an arctolepid(?) arthrodire. This misinterpreation was repeated in the figure 5.3 of the paper of Blieck & Janvier (1993).

In the Lower Devonian of the Tajmyr Peninsula, westwards of the New Siberian Islands, acanthothoracids occur on four levels of the Lochkovian Ust'-Tareya Regional Stage (Mark-Kurik 1994). Three levels are in the Uryum Beds, the fourth one belonging to the upper part of the Tolbat Beds (Mark-Kurik 1994: fig. 48). Acanthothoracid skull roof and trunk armour plates from Tajmyr were compared with those found in the northern part of the Siberian Platform (Norilsk area, Kureika and Koldy River outcrops) and the Timan-Pechora province (Vozej and Lekejyaga drill cores), NE of European Russia (Mark-Kurik 1994: figs 49, 50). According to Goujet (pers. comm. to EMK 1999) some of these acanthothoracids are evidently not *Romundina* species (e.g., those in Mark-Kurik 1994: fig. 49A from the Tareya River, and fig. 49B from the Koldy River). Goujet considered them to be similar to a new acanthothoracid from the Jauf Formation of Saudi Arabia. This acanthothoracid is now published under the name *Arabosteus variabilis* (Olive *et al.* 2011), and is dated as Pragian-early Emsian. In the

Timan-Pechora province Goujet (1997) reported the presence of two forms, resembling the Saudi Arabia acanthothoracid, occurring together with a third one, practically undistinguishable from *Romundina*. In addition to acanthothoracids the actinolepid arthrodires have been found in the Lochkovian and Pragian of above province. Tsyganko *et al.* (2000) mentioned also the occurrences of radotinids in the Lochkovian Ovinparma Regional Stage of the same province. It can be concluded that acanthothoracids are more common in the Lochkovian than in the Pragian and Emsian.

Clade TELEOSTOMI Bonaparte, 1837
†Class ACANTHODII Owen, 1846
Order ISCHNACANTHIFORMES Berg, 1940 ?
Family ISCHNACANTHIDAE Woodward, 1891 ?
Genus *Garralepis* Burrow, 2002

Garralepis sp.
(Fig. 9A, B)

MATERIAL. — Specimen GIT 580-21: scale.

LOCALITY AND STRATIGRAPHIC HORIZON. — Locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

DESCRIPTION

The one scale GIT 580-21 has a kite-shaped crown 0.9 mm long with smooth straight lateral edges that converge at *c.* 60°, and three short ridges running back from the rounded anterior crown edge (Fig. 9A, B). The central area of the crown is eroded, but the sides are well preserved and slightly higher than the central area. The scale neck is very short anteriorly and slightly deeper laterally; the base is strongly convex, and deepest below the level of the anterior crown. Closely spaced grooves encircling the base mark the insertion of Sharpey's fibre layers.

COMPARISON

Although larger than the type scales from the Garra Formation (Lochkovian) of central New South Wales, Australia, the scale matches their simple morphology (Burrow 2002: figs 16E-G, 30A-H). The well-preserved lateral crown edges indicate this region is composed of orthodentine rather than mesodentine or enameloid; both latter tissue types are strongly eroded in the Chukotka microremains. Scales of *Nostovicina lacrima* (Valiukevičius, 1994) (Valiukevičius 1994) from the Lochkovian of Taimyr and Timan-Pechora, northern Russia, and more recently identified from coeval deposits in central New South Wales (Burrow 2002) have a similar shape, but have a mesodentine crown, whereas scales of *Garralepis simplex* Burrow, 2002 are characterized by having orthodentine crowns with enameloid in upper central layers of the growth zones. The simple but characteristic morphology, associated with non-mesodentinous histology, have not been identified in scales of any other known taxa; however, as the identification is based on a single scale, it is only tentatively assigned to *Garralepis*.

ISCHNACANTHIFORMES? indet.
(Fig. 9C)

MATERIAL. — Specimen GIT 580-26: tooth with broken base.

LOCALITY AND STRATIGRAPHIC HORIZON. — Locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

DESCRIPTION

The tooth is *c.* 2.5 mm high, subtriangular in cross-section with at least one sharp vertical carina, and multiple canals visible in the broken base (Fig. 9C). Surficial tissue along the visible carina is well preserved compared with the rest of the tooth, indicating it is probably orthodentine while the rest of the tooth is probably mesodentine. The tooth appears to be flattened, presumably labio-lingually.

COMPARISON

The cross-sectional shape of the tooth resembles that of the main cusps on dentigerous jaw bones and tooth whorls of ischnacanthiform acanthodians, e.g., the poracanthodid *Zemlyacanthus menneri* (Valiukevicius, 1992) (Valiukevičius 1992: pl. 4.2; 8.1, 3) from the Lochkovian of Severnaya Zemlya. The relatively large size of the tooth is consistent

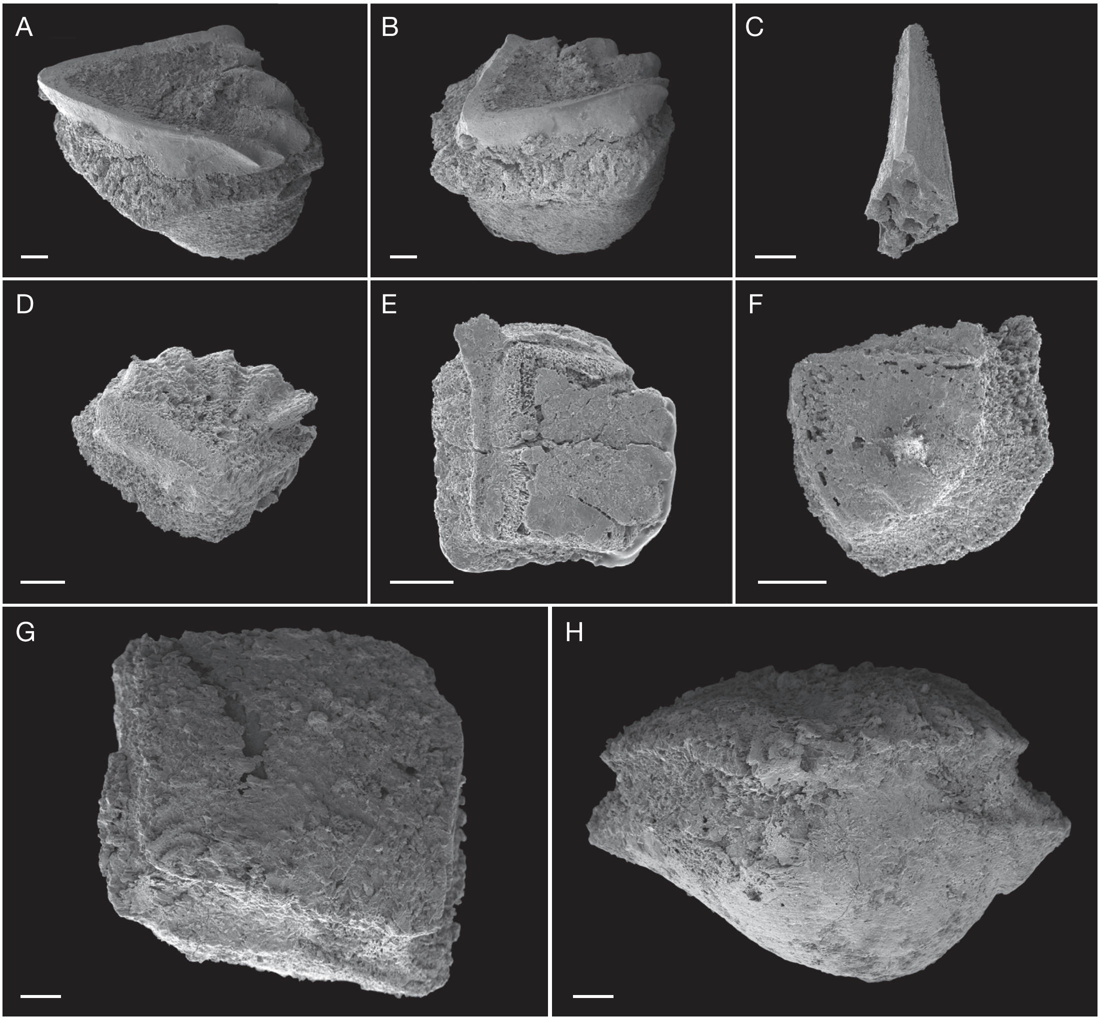

Fig. 9. — Acanthodian scales and tooth from the Lower Devonian of Chukotka, Arctic far-eastern Russia: **A**, **B**, *Garralepis simplex* Burrow, 2002 scale, specimen GIT 580-21 in laterocrown (**A**) and posterolateral (**B**) views; **C**, Ischnacanthiformes? indet., tooth GIT 580-26; **D**-**F**, *Nostovicina guangxiensis* (Wang, 1992) scales; **D**, specimen GIT 580-18; **E**, specimen GIT 580-14; **F**, specimen GIT 580-15; **G**-**H**, *Cheiracanthoides rarus* Valiukevičius, 1994 scale, specimen GIT 580-20 in crown (**G**) and anterior (**H**) views. All from locality (sample) 73, Tonnel'nyj Brook, Lower Member (1) of Enmakaj Formation, Lochkovian. Scale bars: A, B, G, H, 100 µm; C, 500 µm; D, E, 200 µm; F, 300 µm.

with the size range of these structures also, rather than the much smaller palatine teeth that are also found in ischnacanthiforms (e.g., Valiukevičius 1992: fig. 4C). Both tooth whorls and dentigerous jaw bone cusps of *Z. menneri* show a dense reticulated network of canals in the tooth bases (e.g., Valiukevičius 1992: fig. 8), and tissue differentiation between the tooth carinae (orthodentine) and the rest of the tooth (osteodentine), characters that are also seen in GIT 580-26. None of the acanthodian scale taxa in the Chukotka assemblage have been associated with dentigerous jaw bones or tooth whorls at other localities. The tooth is tentatively assigned to the Ischnacanthiformes, as it could possibly be from other acanthodians with tooth whorls having pointed main cusps (see Burrow & Turner 2010).

Incertae ordinis et incertae familiae
Genus *Nostovicina*
Valiukevičius & Burrow, 2005

Nostovicina guangxiensis (Wang, 1992)
(Fig. 9D-F)

Material. — Three specimens GIT 580-14, 580-15 and 580-18: scales.

Locality and stratigraphic horizon. — Locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

Description

Three scales conform to the three commonest morphotypes of *Nostovicina guangxiensis*, with all having equal width and length, a flat rhombic crown that is smaller than the base, and variably developed lateral crown edges (Fig. 9D-F). Scale GIT 580-18 (Fig. 9D) exemplifies the most common form of *N. guangxiensis*, with strong ridges extending back from the anterior edge, and short oblique ridges running down from the posterior corner of the crown; the scale is *c.* 1.3 mm long and wide. The crown on GIT 580-14 (Fig. 9E) is 0.7 mm long, heavily eroded and cracked, with scalloped anterior edges indicating the scale originally had four or five crown ridges. The lateral ledges join to form a posterior point extending slightly beyond the posterior corner of the base. Scale GIT 580-15 (Fig. 9F) is *c.* 1.4 mm long and wide, and is also very poorly preserved with worn remnants of one lateral ledge, a rounded anterior crown margin, and three ridges extending about a third the length of the crown.

Comparison

The lack of histological information hampers identification of the scales, with their shapes fitting within the broad range exhibited by those of *Nostolepis striata* Pander, 1856. Another taxon *Nostovicina laticristata* Valiukevičius, 1994 (Valiukevičius 1994) from various Lochkovian circum-Arctic localities in northern Canada and Russia has similar morphotypes, but its scales are very small with a deep rounded base. Type scales of *Nostovicina guangxiensis* are from the Early Devonian of Guangxi, China (Wang 1992); the taxon is one of the commonest acanthodians in microvertebrate assemblages from Lochkovian-early Pragian deposits throughout southeastern Australia (Burrow 2002). The older teleostome *Yealepis douglasi* Burrow & Young, 1999 from the Ludlow of Victoria, Australia (Burrow & Young 1999), has scales with identical morphotypes and comparable size to the Early Devonian ones, but their histology is unknown. Scales with the same shape and histology as *N. guangxiensis* are also found in Silurian-Devonian boundary beds of the Birch Creek Section BCII, Roberts Mountains, Nevada, USA and the Klonk section, Czech Republic (Burrow *et al.* 2010).

Incerti ordinis
Incertae familiae
Genus *Cheiracanthoides* Wells, 1944

Cheiracanthoides rarus Valiukevičius, 1994
(Fig. 9G, H)

Material. — Specimen GIT 580-20: scale.

Locality and stratigraphic horizon. — Locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian.

Description

The one scale GIT 580-20 is 1.0 mm wide, 1.0 mm long; the crown and base have a square outline (Fig. 9G, H). The crown surface is almost flat, curving down slightly along the anterior edges. Multiple short closely-spaced ridges probably ornamented these edges, although only those towards the centre of the scale are preserved with the rest of the crown being heavily eroded (Fig. 9G). The neck is concave and a constant depth of *c.* 0.15 mm all round. The base is convex, with a maximum depth of 0.4 mm. No pores are visible on the scale neck (Fig. 9H).

Comparison

The scale features are very poorly preserved, but the general shape and proportions match those of scales of *Cheiracanthoides rarus* from the Lochkovian of Taimyr, northern Russia.

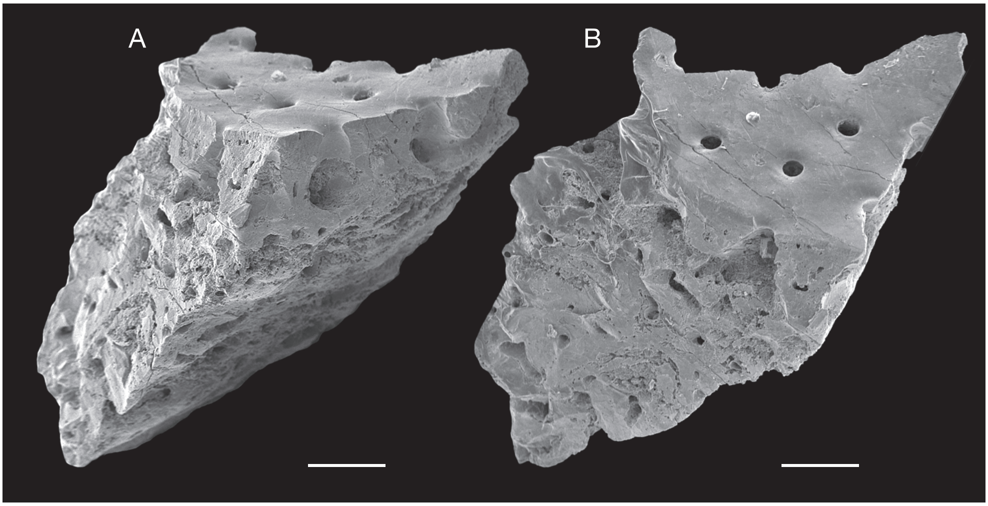

Fig. 10. — *Porolepis*? sp. from the Lower Devonian of Chukotka, Arctic far-eastern Russia, specimen GIT 580-27: **A**, lateral view; **B**, dorsolateral view. Locality (sample) 73, Tonnel'nyj Brook, Lower Member (1) of Enmakaj Formation, Lochkovian. Scale bars: 200 µm.

Class SARCOPTERYGII Romer, 1955
Clade RHIPIDISTIA Cope, 1887
Clade DIPNOMORPHA Ahlberg, 1991
†Order POROLEPIFORMES Jarvik, 1942
Family Porolepididae Berg, 1940
Genus *Porolepis* Woodward, 1891

Porolepis? sp.
(Fig. 10)

Material. — Specimen GIT 580-27: fragment of bone or scale.

Locality and stratigraphic horizon. — Locality (sample) 73, Tonnel'nyj Brook, south of De Long Strait, Chukotka; Lower Member (1) of Enmakaj Formation, Lochkovian. Cherkesova (1973: table) indicated an occurrence of *Porolepis* from the interval of the Member IV to the lower part of the Member VIII of the Enmakaj Formation. So, the fish was discovered not in the basal part of the formation, but in a somewhat higher level.

Description

The Enmakaj assemblage contains a single small fragment of a porolepiform sarcopterygian (GIT 580-27; Fig. 10). It has a smooth cosmine covered surface penetrated by pore-canals. In cross section the upper cosmine layer consists of the fused goblet-shaped odontodes, some of them showing segments of narrow pulp canals. Flask-shaped cavities separate the odontodes and end higher up with pores (Fig. 10A). Below cosmine is a rather compact layer of spongiosa (Fig. 10B). The fragment can be provisionally identified as belonging to a species of *Porolepis*.

Comments on stratigraphical distribution and taxonomy

The porolepidids are known from the Lower and Middle Devonian of many regions: Rhineland, Baltic area, Spitsbergen, Urals, ?Western USA, Canadian and Russian Arctic (including Novaya Zemlya), ?Vietnam (Ørvig 1957, 1969b; Mark-Kurik & Novitskaya 1977; Blieck & Janvier 1993; Vorobyeva 2004). In our case occurrences from the Lower Devonian are of particular interest. Earlier it was considered that porolepidids appeared in the Pragian (Siegenian) (Vorobyeva & Obruchev 1964). But re-assessment of age of several local stratigraphical units evidence that they were rather common already in the Lochkovian. Lochkovian stratigraphical units with *Porolepis* are: the Kureika Formation of the Siberian Platform (Cherkesova *et al.* 1994; Matukhin 1995), the Bely Kamen and Uryum Beds of the Ust-Tareya Regional Stage of Taimyr Peninsula (Cherkesova 1994), and the

Pshenitsyn River Formation of Kotelnyj Island, New Siberian Archipelago (Cherkesova 1975, 1988). Mark-Kurik (1974) mentioned the similarity of the Pshenitsyn River Formation fish assemblage to that of the Kureika Formation. *Porolepis* in the Enmakaj Formation of Chukotka came according to a later age dating also from the Lochkovian (Cherkesova, pers. comm. to EMK 1976) [see here the section "age and correlation"]. *Porolepis* is abundant in the Enmakaj Formation (Cherkesova 1973: 279). Two Siberian species have been formally defined: *Porolepis taimyrica* Vorobyeva, 1963 and *P. kureikensis* Vorobyeva, 1963. Ørvig (1969b) paid attention to contradictions in identification of porolepiform scales from different Arctic regions, including *Porolepis* species mentioned above. Porolepiforms were probably the top predators in the fish assemblage of the Enmakaj Formation. Other predators were represented by several acanthodians.

LOWER DEVONIAN FISH ASSEMBLAGES OF THE DE LONG STRAIT AREA

Enmakaj Formation

Of the two fish assemblages the richest and more variable one, even though it consists only of microremains, is that of the Lower Member (1) of the Enmakaj Formation. The assemblage from outcrop 73, the Tonnel'nyj Brook, includes exoskeletal fragments of heterostracans (tesserae and fragments of plates), thelodont scales, acanthodian scales and other remains, acanthothoracid placoderm platelets and one fragment of a sarcopterygian (Table 1). The present list of taxa of locality 73 is as follows:
– Heterostraci: Traquairaspididae? gen. et sp. indet., Poraspididae gen. et sp. indet., *Oniscolepis*? sp., *Lepidaspis*? sp., Heterostraci? indet.;
– Thelodonti: *Turinia pagei*?, *Turinia* sp. cf. *T. barentsia*, *Turinia* sp. cf. *T. composita*, *Turinia* sp. cf. *T. polita*, *Turinia* sp., *Nikolivia?* sp. cf. *N. gutta*, *Nikolivia*? sp.;
– Placodermi: Palaeacanthaspididae gen. et sp. indet.;
– Acanthodii: *Garralepis* sp., *Nostovicina guangxiensis*, *Cheiracanthoides rarus*, Ischnacanthiformes? tooth cusp.;
– Sarcopterygii: *Porolepis*? sp.

Pil'hikaj Formation

The Lower Member (4) of the Pil'hikaj Formation has yielded only heterostracans. Two remains with n° 73-4 (74-3) come probably from the basal part of the formation on the Tonnel'nyj Brook. A larger heterostracan plate remnant, preserved as an impression on rock (74-3), was found in the Poberezh'e (Coast) exposure (Table 1). All these fossils are determined as Traquairaspididae? gen. et sp. indet. Additionally, Novitskaya (1986, 2004) has determined a fragmentary dorsal disc as Pteraspidiformes indet. 1, from the "seashore behind Tonnel'nyj" (Novitskaya 1986: 119 and pl. XXIV: 1-2).

AGE AND CORRELATION

Lower Member (1) of Enmakaj Formation

This member has yielded the heterostracans *Oniscolepis*? sp. and *Lepidaspis*? sp. *Oniscolepis* is known from the Přidoli (Late Silurian) to the Lochkovian (Early Devonian) (Märss & Karatajūtė-Talimaa 2009). The type material of *Lepidaspis* comes from the North-West Territories of Canada in several localities (including the MOTH locality GSC 69014) that are dated as Lochkovian (Dineley & Loeffler 1976; Zorn *et al.* 2005). Turner *et al.* (1995: pl. 1: 1) also found *Lepidaspis* from site 4, Pwll-Y-Wrach near Talgarth, Breconshire, South Wales in the St Maughan's Group (equivalent *Psammosteus* Limestone Group), "within the *Phialaspis symondsi* zone" (Turner *et al.* 1995: 380; renamed *Traquairaspis* Biozone by Blieck & Janvier 1989: 152), thus earliest Lochkovian in age (Blieck & Janvier 1989: fig. 11). *Lepidaspis* also comes from other early Lochkovian localities in the World, e.g., Spitsbergen and northern France (Goujet & Blieck 1979; Blieck 1983). The other fragmentary remains of heterostracans in the Lower Member (1) of Enmakaj Formation are not biostratigraphically significant.

The thelodonts *Turinia pagei*?, *Turinia* sp. cf. *T. composita* and perhaps *Turinia* sp. cf. *T. barentsia,* and *Nikolivia*? sp. cf. *N. gutta*, provide an earliest Devonian age based on comparison with elsewhere in Europe and Arctic Russia (Talimaa 2000; Märss *et al.* 2007). *Nikolivia aligera* and *T. composita* are

Table 1. — List of specimens (macro- and microremains) from the outcrops 73 (Tonnel'nyj Brook) and 74 (Poberezh'e = the Coast), De Long Strait coastal section, Chukotka, Arctic far-eastern Russia; Lochkovian (probably Early Lochkovian, sample 73; and Middle to Upper? Lochkovian, samples ?73-4, 74-3). Collection numbers GIT 580-1 to 580-27 belong to the Institute of Geology at Tallinn University of Technology, Estonia; collection numbers PIN 3845/2 to 4 are of the Palaeontological Museum, Russian Academy of Sciences, Moscow, Russia.

Sample	Description	Identification	Collection no.	Figure
73	tessera	*Oniscolepis*? sp.	GIT 580-1	6E
	tessera	*Lepidaspis*? sp.	GIT 580-2	6D
	tessera	*Oniscolepis*? sp.	GIT 580-3	6F
	flank-scale (broken)	Poraspididae indet.	GIT 580-4	6G
	fragment	Traquairaspididae? indet.	GIT 580-5	6A, B
	fragment	Poraspididae indet.	GIT 580-6	–
	fragment	Poraspididae indet.	GIT 580-7	6H
	platelet	Heterostraci? indet.	GIT 580-8	6I
	scale	*Nikolivia*? sp.	GIT 580-9	7J, K
	scale (basal view)	*Nikolivia*? sp.	GIT 580-9	7I
	scale	*Turinia* sp. cf. *T. composita*	GIT 580-10	7C
	scale	*Turinia* sp. cf. *T. composita*	GIT 580-11	7D
	scale (broken)	*Turinia* sp.	GIT 580-12	7F
	scale	*Nikolivia*? sp. cf. *N. gutta*	GIT 580-13	7G, H
	scale	*Nostovicina guangxiensis*	GIT 580-14	9E
	scale	*Nostovicina guangxiensis*	GIT 580-15	9F
	scale (lost)	*Turinia pagei*?	GIT 580-16	7B
	scale	*Turinia* sp. cf. *T. polita*	GIT 580-17	7E
	scale	*Nostovicina guangxiensis*	GIT 580-18	9D
	scale (lost)	*Turinia pagei*?	GIT 580-19	7A
	scale	*Cheiracanthoides rarus*	GIT 580-20	9G, H
	scale	*Garralepis simplex*	GIT 580-21	9A, B
	skeletal element	Palaeacanthaspididae indet.	GIT 580-22	8A
	skeletal element	Palaeacanthaspididae indet.	GIT 580-23	8C
	fragment of plate	Palaeacanthaspididae indet.	GIT 580-24	8D
	fragment of plate	Palaeacanthaspididae indet.	GIT 580-25	8B
	tooth	Ischnacanthiformes? indet.	GIT 580-26	9C
	fragment	*Porolepis*? sp.	GIT 580-27	10A, B
73-4 (74-3)	fragment	Traquairaspididae? indet.	PIN-3845/2	6C
	dorsal spine	Traquairaspididae? indet.	PIN-3845/3	5D-F
74-3	large fragment, external mould	Traquairaspididae? indet.	PIN-3845/4	3, 4, 5A-C

found at different levels of the Pod'emnaya Formation outcropping along the Matusevich, Pod'emnaya and Spokojnaya rivers of the Severnaya Zemlya archipelago (late Lochkovian: Karatajūtė-Talimaa 2002; Blieck *et al.* 2002). The thelodont assemblage overall, even though only a few scales were recovered, allows good correlation with the Lochkovian series of the Old Red Sandstone Continent.

The placoderm remains are also significant for Lower Devonian age. Acanthothoracids are generally known from the Lower Devonian but they are particularly characteristic of the Lochkovian. They are known from the Lochkovian of Arctic Canada (Ørvig 1975; Goujet 1998), Kotelnyj Island, Arctic Russia (Mark-Kurik 1974), NW of the Siberian Platform (Norilsk area, Kureika and Koldy River outcrops), on four levels of the Lochkovian Ust'-Tareya Regional Stage of Taymyr Peninsula. *Kolymaspis* Bystrow, 1956, a specific acanthothoracid, was found in the Nelyudim Formation, Lochkovian of Eastern Yakutia (Denison 1978: 35; Matukhin 1995). Acanthothoracids occur in the Lochkovian of the Timan-Pechora province (Vozej and Lekejyaga drill cores), NE of European Russia (Mark-Kurik 1994). Tsyganko *et al.* (2000) mentioned also the occurrences of radotinids in the Lochkovian Ovinparma Regional Stage of the same province. The Lochkovian-Pragian of southeastern Australia has also yielded acanthothoracids (Basden *et al.* 2000). One of the earliest Lochkovian acanthothoracid, *Kimaspis* Mark-Kurik, 1973 comes from the Dzhalpak Formation, South Tien Shan, Central Asia (Mark-Kurik 1973). Classically, the representatives of these placoderms (*Palaeacanthaspis*, *Dobrowlania* Stensiö, 1944) were known from the Chortkiv Formation, Lower-Middle Lochkovian of Podolia, Ukraine (Stensiö 1944). Two acanthothoracid genera, *Radotina* and *Kosoraspis* Gross, 1959 came from the Radotin and Upper Koneˇprusy limestone, ranging from the lower to upper Lochkovian and reaching also the Pragian, in Czech Republic (Gross 1959).

Among acanthodians, the type material of *Garralepis* from the Garra Formation of central New South Wales, Australia, is Lochkovian in age (Burrow 2002). Type specimens of *Nostovicina guangxiensis* are from the Early Devonian of Guangxi, China; the taxon is one of the commonest acanthodians in microvertebrate assemblages from Lochkovian-early Pragian deposits throughout southeastern Australia (Burrow 2002). *Cheiracanthoides rarus* is from the Lochkovian of Taimyr, northern Russia (Valiukevičius 1994).

Thus, most of the vertebrate microremains from Lower Member (1) of the Enmakaj Formation give a Lochkovian, and perhaps early Lochkovian age.

Lower Member (4) of Pil'hikaj Formation

Obruchev (1973: 194) briefly mentioned an undeterminable pteraspid find from the Chukotka coast (behind Tonnel'nyj), collected by Y. G. Rogozov. Novitskaya (1986: 119 and pl. XXIV: 1, 2) described a pteraspid fragmentary dorsal disc from "Chukotka, seashore behind Tonnel'nyj" as Pteraspidiformes indet. 1 (housed in the collection of the Institute of Palaeontology of the Russian Academy of Sciences, Moscow, specimen PIN 3845/1; "Heterostraci Pteraspidae" in Cherkesova 1973). Novitskaya (1986: 125) mentioned that in its shape and depth of the pineal notch the plate resembles that in *Podolaspis*. Later, she (Novitskaya 2004: 170: Pteraspidiformes indet. 2; misprint for Pteraspidiformes indet. 1) compared this specimen with equivalent skeletal elements of the pteraspids *Podolaspis*, *Larnovaspis* Blieck, 1984 and "*Belgicaspis*" Zych, 1931 (now *Rhinopteraspis* Jaekel, 1919; see Blieck 1980, 1984) from the Ivane Horizon (formation), basal part of the Dniestr (Dnestr) Series of Podolia (Ukraine), and concluded that the age of the beds in the De Long Strait section [Lower Member (4) of Pil'hikaj Formation] could probably be Lochkovian in age.

The recent monograph of Voichyshyn (2011) on the Early Devonian of Podolia gives a review of all known agnathan (ostracoderm) and gnathostome remains in the latest Silurian – Early Devonian of this region. The pteraspids "?*Belgicaspis crouchi* Lankester, 1868", *Larnovaspis* spp. and *Podolaspis* spp. are distributed from the Middle Lochkovian (Chortkiv Formation) to the Lower Pragian (Khmeleva 1 Member of the Dniestr Formation), with the Lochkovian/Pragian (L/P) boundary being located at the base or within the Ustechko Member of the Dniestr Formation (Voichyshyn 2011: table 1), that is, in a somewhat lower stratigraphical location than in Dupret & Blieck (2009: fig. 4; see also Blieck 1984: fig. 74) who place the L/P boundary between the Old Red faunal zones I and II, above the Khmeleva 1 Member. So, after Novitskaya's (1986, 2004) comparison of the Chukotka pteraspid to Podolian species, the Lower Member (4) of the Pil'hikaj Formation might be either middle-late Lochkovian or early Pragian in age. The latter age would thus not be in disagreement with Cherkesova (1973) who proposed a Pragian-Emsian age for the Pil'hikaj Formation. However, the specimen on which Novitskaya's (1986, 2004) determination is based is a fragmentary dorsal disc with only part of its dermal bone preserved (Novitskaya 1986: pl. XXIV: 1, 2), thus without any generic diagnostic feature. Hence, this specimen does not give a precise dating for the lower Pil'hikaj Formation. So, let us consider the biostratigraphic informations given by the newly described material.

The heterostracan material described here as Traquairaspididae? gen. et sp. indet. is mostly comparable with traquairaspids from the Canadian Arctic, i.e. *Traquairaspis*? *retusa* (Dineley & Loeffler 1976: pl. 1: 1 and fig. 5), Traquairaspididae indet. Type 2 (Dineley & Loeffler 1976: pl. 4: 1 and fig. 16), Traquairaspididae indet. Type 3 (Dineley & Loeffler

1976: pl. 4: 3, fig. 17) and Traquairaspididae indet. Type 4 (Dineley & Loeffler 1976: pl. 4: 4 , fig. 18). All four taxa are from locality GSC 69017, 38 m above the base of the Delorme Formation, west of Natla river, North-West Territories of Canada; this locality is supposed to be Ludlow (Late Silurian) in age, but it has yielded a mixed fauna: part of its fish assemblage (*Pionaspis amplissima* Dineley & Loeffler, 1976, *Archegonaspis*? sp. indet. Type 2, *Poraspis polaris* Kiaer, 1930) comes from younger horizons and is equivalent to the MOTH locality GSC 69014, middle Lochkovian in age (see Dineley & Loeffler 1976: 7 for GSC 69017; Zorn *et al.* 2005 for the MOTH locality).

The traquairaspids from the lower Pil'hikaj Formation are also compared to *Weigeltaspis heintzi* (Tarlo 1964: pl. IV: 6, 7; 1965: pl. IV: 2; Blieck 1983: pl. VI: 5), which is from the *Vogti* horizon of the Red Bay Group, Ben Nevis Formation of Spitsbergen. This horizon is middle Lochkovian in age (Blieck 1983: fig. 5; 1984: figs 71, 74; Blieck *et al.* 2000: fig. 10).

So, the traquairaspid heterostracan material from Lower Member (4) of the Pil'hikaj Formation supports a Lochkovian, and probably Middle to Upper? Lochkovian age, but not a Pragian age.

TAPHONOMICAL REMARKS

The material from both the Lower Member (1) of Enmakaj Formation, and the Lower Member (4) of Pil'hikaj Formation has been collected in siliciclastic rocks, either siltsone or fine-grained sandstone. In locality 73 (Lower Member (1) of Enmakaj Formation), the thelodont and acanthodian scales are very poorly preserved. It seems that they have been etched severely, and they show an unusual preservation. Their surface is scoured, producing a microcrystalline texture (Figs 6I; 7A, C-F; 9D-H). In some the dentine is reduced to a shell with copious holes (Fig. 6E). On the thelodont scale GIT 580-19 the outer durodentine or enameloid layer has been stripped away and out layer of base, leaving exposed orthodentine tubules (Fig. 7A). The acanthodian material also does not have good histological preservation (many hyphae and recrystallization: Fig. 9).

We are uncertain as to the cause of these features. It might be diagenetic with mild metamorphism that led to pyritization. Alternatively, have the microremains been through something else's gut with consequent acidic attack? Surely, acid preparation did not cause the poor preservation of remains. Quite possibly leaching is responsible for the poor state of some of the microremains, although placoderm remains and the porolepid fragment are not so badly preserved.

In the younger localities (74 and 73-4 [74-3]) from the Lower Member (4) of Pil'hikaj Formation, only macroremains of incompletely preserved heterostracans have been collected. The superficial ornamentation of their dermal plates is rather well preserved even if, in some places, the outer surface of the tubercles is worn, with probably disappearance of the outermost layer, which is classically attributed to enameloid, but might just be a durodentine, i.e. the outer untubuled layer of normal dentine.

PALAEOBIOGEOGRAPHIC INTERPRETATION

The vertebrate remains that have been collected in the Early Devonian section along the De Long Strait, Chukotka, give various palaeobiogeographic signals, but most of the assemblage is typical for a detrital facies from the Old Red Sandstone Continent (ORSC). The traquairaspids from the upper level (Lower Member of the Pil'hikaj Formation) have strong affinities with the Lochkovian of other Arctic regions, that is both the Canadian Arctic (and in particular North-West Territories – NWT) and Spitsbergen. These regions are classically reconstructed at the "northern" edge of the Old Red Sandstone Continent (Scotese 2002: Early Devonian; Cocks & Torsvik 2002: figs 8, 9; Torsvik & Cocks 2004: fig. 5). One of the latest palaeogeographic reconstructions by Cocks & Torsvik (2011: figs 16, 17) includes a series of terranes in the equatorial regions, comprising both Arctic Alaska and Chukotka (the Arctic Alaska-Chukotka Terrane of Till *et al.* 2010; Arctic Alaska-Chukotka Microcontinent (AACM) of Cocks & Torsvik 2011) converging toward the "northern" margin of the ORSC (this continental drift would result in an oblique collision of the AACM with Laurussia – the ORSC – continuing until the end Devonian; see Cocks & Torsvik [2011: 30]). In such a configuration, the heterostracan faunas from Chukotka, NWT of Canada and Spitsbergen, would have been palaeobiogeographically connected through the shelf and narrow oceanic corridor that still separated the AACM and ORSC (Cocks & Torsvik 2011: fig. 17). This was also the case for the Early Devonian fish faunas of Severnaya Zemlya (an element of the Kara-Taimyr block) which had strong relations with Spitsbergen and the Canadian Arctic as well (see Blieck *et al.* 2002, section "palaeogeographical setting" for references and discussion). All these regions are representatives of what has been called the Arctic Province by Blieck & Janvier (1999: fig. 9.14) (Fig. 11).

The microremains from the lower level (Lower Member of Enmakaj Formation) of Chukotka also show strong affinities with the ORSC. Similarly, the thelodont assemblage has strong affinities with the Lochkovian of other Arctic regions, especially in Russia and Spitsbergen. The general composition with turiniid and nikoliviid-like scales, such as *Turinia composita* and possible *Nikolivia aligera* suggests closest affinity with that from the Lochkovian Pod'emnaya Formation from the Matusevich River at October Revolution Island, Severnaya Zemlya Archipelago (Karatajūtė-Talimaa 2002). Thelodont assemblages within the Lochkovian further afield such as Arctic and western North America in general show a similar composition (e.g., Märss *et al.* 2007).

Investigation of vertebrate distribution in older Silurian sections in Siberia and elsewhere has shown the prevalence of their remains in deposits of the more shallow facies of marine palaeobasins (Märss & Einasto 1978; Karatajūtė-Talimaa & Predtechenskij 1995; Žigaitė *et al.* 2011). Thelodonts and certain other vertebrates are found in nearshore environments in deltaic-lagoonal zone to shallow-water marine environments of epicontinental basins (e.g., Turner 1999) and this would also seem to have extended into the Devonian.

Of the identifiable acanthodian scales, the one tentatively assigned to *Garralepis*, is perhaps the only unusual element as this taxon is otherwise known only from eastern Australia in Lochkovian times. *Cheiracanthoides rarus* has only been recorded previously from the mid-Lochkovian type locality in Taimyr, northern Russia (Valiukevičius 2000: fig. 1). *Nostovicina guangxiensis*, however, has a wider distribution both stratigraphically and geographically, being common in the Lochkovian-early Pragian of southeastern Australia (Burrow 2002) and in Silurian-Devonian boundary beds of the Birch Creek Section BCII, Roberts Mountains, Nevada, USA and the Klonk section, Czech Republic (Burrow *et al.* 2010). The type scales from younger strata in China tend to have a higher base than the older material, and a trend to a higher base is detectable in successively younger southeastern Australian occurrences; the Chukotka scale bases are relatively shallow, conforming to the older material. Ischnacanthiforms with dentigerous jaw bones and tooth whorls bearing tooth cusps like the Chukotka specimen have a nearly worldwide distribution in the Lochkovian. These fish clearly had the ability to extend their range far wider than the other taxa, and can be treated as "pelagic".

CONCLUSIONS

Two Lochkovian assemblages of fossil fish comprising macro- and microfossils of heterostracans, turiniid and other thelodonts, acanthodians and acanthothoracid placoderms, typical of the Old Red Sandstone continental margins, is described for the first time from the basal members of the Enmakaj and Pil'hikaj formations in coastal exposures along the De Long Strait, central Chukotka, Arctic far-eastern Russia. In addition evidences of a sarcopterygian occurs in Member (1) of the Enmakaj Formation. The palaeobiogeographic affinities of these assemblages are most closely with other Arctic regions such as Severnaya Zemlya (October Revolution Island), Spitsbergen and the northern and north-eastern ORSC in general. More wide-ranging gnathostome taxa link the northeastern ORSC with East Gondwana.

Our knowledge of the macro- and microremains of certain taxa points to the necessity for a revision of both the traquairaspids and tessellated heterostracans as well as of Lochkovian thelodonts in the

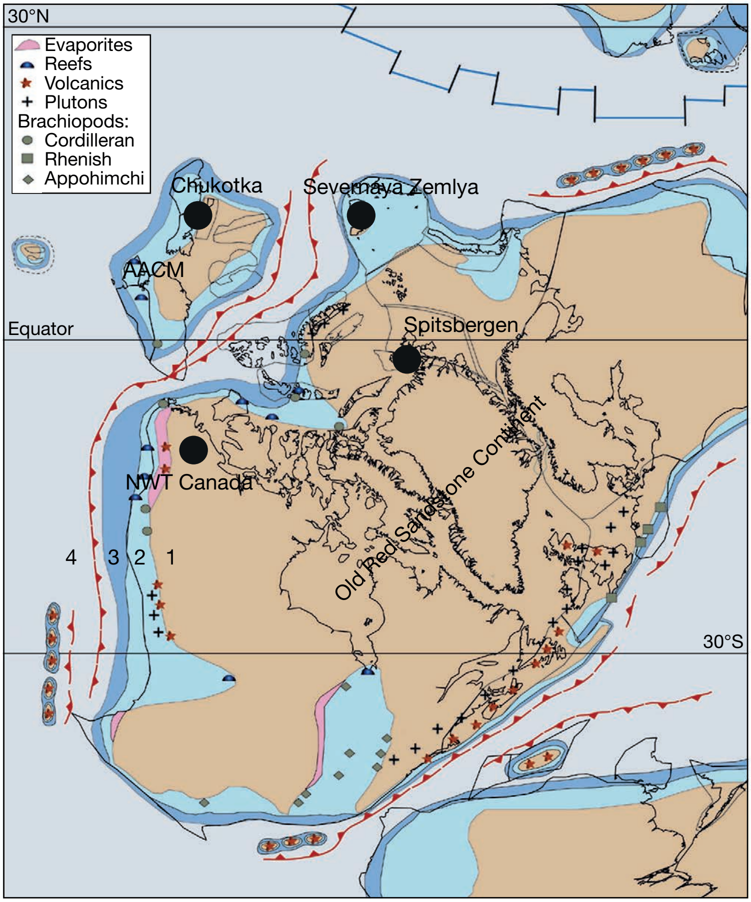

FIG. 11. — Palaeogeographical reconstruction for the Early Devonian by Cocks & Torsvik (2011: fig. 17, at –400 Ma) with Chukotka (Arctic far-eastern Russia), North-West Territories (NWT) of Canada, Spitsbergen and Severnaya Zemlya as elements of the Arctic Province of Blieck & Janvier (1999: fig. 9.14) in a trans-equatorial location. Captions for physiographic features (in various grey colours, as indicated on left side of the Old Red Sandstone Continent): **1**, land; **2**, shallow shelf; **3**, deep shelf; **4**, ocean. Abbreviation: **AACM**, Arctic Alaska-Chukotka Microcontinent.

Arctic north and western ORSC. Further research into early placoderm microremains in the Silurian to Lower Devonian is also needed; little is known.

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