Upper Silurian and Devonian heterostracan pteraspidomorphs (Vertebrata) from Severnaya Zemlya (Russia): a preliminary report with biogeographical and biostratigraphical implications

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Amphiaspids, corvaspids, cyathaspids, psammosteids, pteraspids, tesseraspids, traquairaspids, Silurian, Devonian, Kara-Tajmyr, Spitsbergen, Siberia, Old Red Sandstone Continent, bioevents.

ABSTRACT
Severnaya Zemlya (Kara-Tajmyr palaeocontinent) is a key-zone in understanding the palaeogeographical relationships of the Old Red Sandstone Continent and Siberia in Mid-Palaeozoic times. Its Upper Silurian-Devonian sedimentary sequence bears a rich fauna of heterostracans which allows biostratigraphical correlation to be made with Spitsbergen (on the Barentsian palaeocontinent), but also with the Canadian Arctic (on the Old Red Sandstone Continent) and Central Tajmyr-NW Siberia (Siberian palaeocontinent). This fauna is composed of various assemblages from the Ludlow (Upper Silurian) to the Frasnian (Upper Devonian), with the richest assemblages in the upper Lochkovian, and a gap in the Emsian (Lower Devonian).

RÉSUMÉ

Hétérostracés ptéraspidomorphes (Vertebrata) du Silurien supérieur et du Dévonien de Severnaya Zemlya (Russie) : données préliminaires et leurs implications biogéographiques et biostratigraphiques.

La Terre-du-Nord (Severnaya Zemlya, paléocontinent Kara-Taïmyr) est une zone charnière pour comprendre les relations paléogéographiques entre le Continent des Vieux Grès Rouges et la Sibérie au Paléozoïque moyen. Sa série sédimentaire d'âge silurien supérieur et dévonien renferme une riche faune d'hétérostracés autorisant des corrélations biostratigraphiques avec essentiellement le Spitsberg (paléocontinent Barentsia), mais aussi avec l'Arctique Canadien (sur le Continent des Vieux Grès Rouges) et le Taïmyr central-Sibérie du NW (paléocontinent Siberia). Cette faune est composée d'assemblages variés depuis le Ludlow (Silurien supérieur) jusqu'au Frasnien (Dévonien supérieur) ; les assemblages les plus riches proviennent du Lochkovien supérieur et on observe un hiatus à l'Emsien (Dévonien inférieur).

MOTS CLÉS
Amphiaspides, corvaspides, cyathaspides, psammostéides, ptéraspides, tesséraspides, traquairaspides, Silurien, Dévonien, Kara-Taïmyr, Spitsberg, Siberia, Continent des Vieux Grès Rouges, événements biologiques.

INTRODUCTION

The main objectives of the International Geological Correlation Program Project 406 "Circum-Arctic Lower-Middle Palaeozoic Vertebrate Palaeontology and Biostratigraphy" were: 1) to coordinate research into Lower and Middle Palaeozoic vertebrates of the Circum-Arctic area; 2) to study their taxonomy, stratigraphic distribution, and biological changes and events; 3) to determine their evolutionary relationships; 4) to improve their stratigraphical and geographical ranges; 5) to elaborate regional vertebrate zonal schemes; 6) to correlate vertebrate-bearing series of the Laurentian, Barentsian, Baltican and Siberian palaeocontinents; and 7) to contribute to palaeobiogeographical maps of the Circum-Arctic area for Palaeozoic times.

This paper is a contribution to points 1, 2, 4, 5, 6 and 7 of this project. It is based on results from new material of heterostracan pteraspidomorphs from the Lower and Middle Devonian of the Severnaya Zemlya Archipelago, in the Russian Arctic, brought by two of us (VNKT and EMK) and J. J. Valiukevičius from expeditions to the archipelago in 1978 and 1979. These results were obtained during several visits of one of the authors (ARMB) to the collections of the laboratory of the second (VNKT), between 1997 and 2002. This operation is in fact the most recent expression of a collaboration which began earlier, when all three authors were working on the taxonomy and biostratigraphy of thelodonts and pteraspidomorphs from the Circum-Arctic area and other regions of the World (see e.g., Obruchev & Mark-Kurik 1965; Karatajūtē-Talimaa 1978; Blieck 1984).

Our paper will comprise five different parts: 1) the geographical/palaeogeographical setting of the study; 2) its stratigraphical context; 3) some taxonomic notes on the fossil material; 4) a synthetic presentation of the biostratigraphical database, with correlations to other Circum-Arctic regions; and 5) a conclusion on biological events thus evidenced.

GEOGRAPHICAL LOCATION AND PALAEOGEOGRAPHICAL SETTING

Severnaya Zemlya is one of the major Arctic archipelagos. It is located North of the Tajmyr

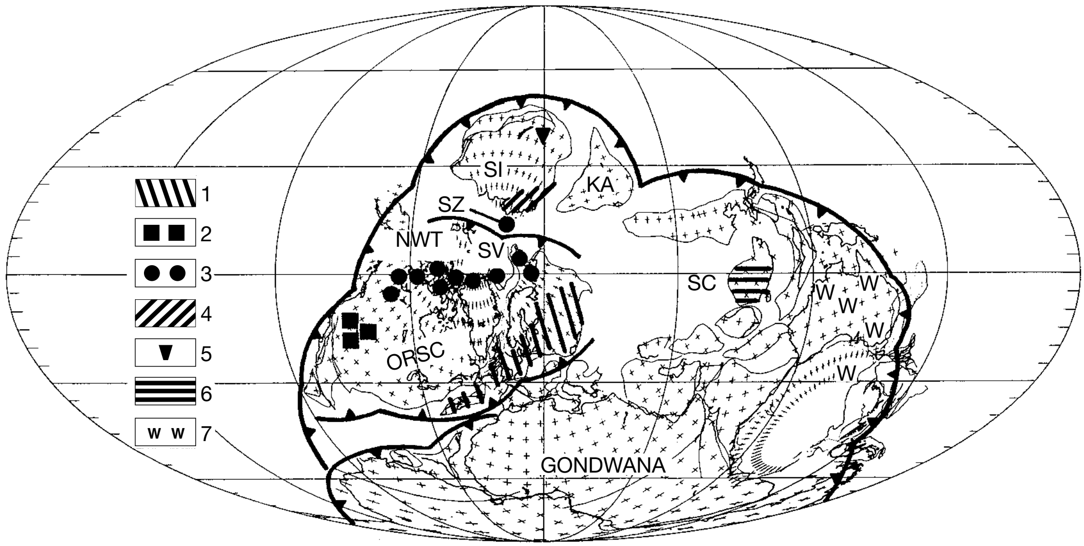

FIG. 1. — Early Devonian agnathan vertebrate provinces (Lochkovian). Palaeogeographical reconstruction after Scotese & McKerrow (1990: fig. 13) and Cocks & Scotese (1991: fig. 3) for the Lochkovian. Palaeobiogeographical provinces after Blieck & Janvier (1999: fig. 9.14) and Young (1990: fig. 3). **1**, North Atlantic Province (pteraspid-dominated faunas); **2**, Rocky Mountain Province (protaspid-*Allocryptaspis*-*Cardipeltis* fauna); **3**, Arctic Province (*Ctenaspis*-*Benneviaspis* and boreaspid-*Gigantaspis* faunas) (1 + 2 + 3 = Euramerica cephalaspid province of Young); **4**, Angaran Province (amphiaspid fauna) = Siberia amphiaspid province of Young; **5**, Tuvan Province (tannuaspid fauna) = Tuva tannuaspid province of Young; **6**, South Chinese Province (galeaspid-yunnanolepid faunas) = South China galeaspid-yunnanolepid province of Young; **7**, East Gondwana wuttagoonaspid-phyllolepid province of Young (this province is also defined by the pituriaspid agnathans in early Middle Devonian time: Young 1991). N.B.: Yunnanolepids, wuttagoonaspids and phyllolepids are placoderm taxa; all others are agnathan taxa. Abbreviations: **KA**, Kazakhstan; **NWT**, Northwest Territories of Canada; **ORSC**, Old Red Sandstone Continent; **SC**, South China; **SI**, Siberia; **SV**, Svalbard (Spitsbergen); **SZ**, Severnaya Zemlya.

Peninsula, between the Kara and the Laptev seas, and forms part of the northern Siberian shelf. However, in Mid-Palaeozoic times, Severnaya Zemlya was palaeogeographically distinct from Siberia: it was a part of a palaeocontinental block called "Kara-Tajmyr" including the northern part of Tajmyr. It was also distinct from the northeastern Russian block called "Chukotka" (see e.g., Churkin *et al.* 1981; Talent *et al.* 1987a, b; Blieck & Janvier 1991: fig. 18, 1993: fig. 5.1). The Kara-Tajmyr and Chukotka blocks are reconstructed as being connected to the Old Red Sandstone Continent in Devonian times because of close geological, palaeomagnetic, and palaeontological relationships between these three palaeocontinental elements (e.g., Ziegler 1988; Janvier & Blieck 1993: fig. 4.1; see also Kuršs & Pupils 1997: fig. 1, which shows a more fixist reconstruction where the various palaeocontinents are not represented in their relative locations). Severnaya Zemlya has indeed numerous Devonian fossil fishes in common with both Spitsbergen (SV, Fig. 1, as part of the Barentsia palaeocontinent; Ziegler 1988), and the Canadian Arctic areas (former districts of Mackenzie and Franklin in the Northwest Territories – now Mackenzie and Nunavut –, as parts of the Old Red Sandstone Continent; NWT, Fig. 1). This point is illustrated in the section on biostratigraphical correlations here below.

Severnaya Zemlya is a very interesting region as Devonian vertebrates are concerned. On Scotese & McKerrow's (1990: figs 13-16; also Scotese 1997: fig. "Early Devonian") reconstructions, it is located "north" of a subduction zone in between the Old Red Sandstone Continent and Siberia (Cocks & Scotese 1991: fig. 3) (it is this pattern which is illustrated on Fig. 1). Severnaya Zemlya has indeed numerous

FIG. 2. — Geological sketch map of the NW part of Severnaya Zemlya, after Männik *et al*. (2002); **1**, Cambrian and older strata; **2**, Ordovician; **3**, Silurian; **4**, Devonian and Quaternary (including ice cover); outcrops (A-E inside white rectangles): **A**, Matusevich River; **B**, Ushakov River; **C**, Spokojnaya River and Krasnaya Bay; **D**, Pod''emnaya River; **E**, Sovetskaya Bay. Abbreviations: **Bedov. R.**, Bedovaya River; **Krasn. Bay**, Krasnaya Bay.

taxa in common with the Old Red Sandstone Continent, but also some with Siberia (among them a few amphiaspid heterostracans: see section on biostratigraphical distribution; Blieck & Janvier 1999; Young 1990: fig. 3, 1993: figs 12.3, 12.7). So Severnaya Zemlya seems to have been a "contact zone" between both palaeocontinents, as far as their marine marginal shelves are concerned.

The problem is to know whether or not the subduction zone between the Old Red Sandstone Continent and Siberia has acted as a barrier for dispersal of marine faunas. Because of the taxa common to both blocks, it appears that these taxa have migrated from one to another block. This may have been facilitated by at least two geographical patterns: 1) the width of the oceanic area between both blocks was probably less than 750-1000 km, thus allowing dispersal of marine organisms, including fish (see e.g., Talent *et al.* 1987b: 92); and 2) the occurrence of island arcs parallel to the subduction zone (Fig. 1) may have helped this dispersal. The occurrence of numerous coral reefs linked to the island arcs and sea mounts of the extant Indo-Pacific tropical marine province does indeed provide "staging posts for the dispersal of shallow-marine biota" as e.g., molluscs (Talent 1985: fig. 1; Talent *et al.* 1987b: 92, fig. 1), but also teleostean fishes (Carcasson *in* Nolf 1988: 101). This process may have occurred in Mid-Palaeozoic times as well, between Siberia and the Old Red Sandstone Continent (Fig. 1). It has been called "sweepstake migration" by Simpson (1969: 70, "route de courses d'obstacles" in French; also Blieck & Janvier 1991: 378).

STRATIGRAPHICAL SETTING

All the material which has been studied for this project comes from sections located along rivers and coastal exposures of the October Revolution Island, in the NW part of Severnaya Zemlya (Fig. 2), that is the Matusevich River (A, Fig. 2), the Ushakov River (B, Fig. 2), the Spokojnaya River and Krasnaya Bay (C, Fig. 2), the Pod''emnaya River (D, Fig. 2), and the Sovetskaya Bay (E, Fig. 2).

Heterostracan pteraspidomorphs occur in the Silurian of the October Revolution Island (Karatajūtē-Talimaa & Blieck 1999). They consist mainly of fragmentary remains of cyathaspids which are currently under study by T. Märss. They come from both the Ust'-Spokojnaya and Krasnaya Bukhta (= Krasnaya Bay) formations. (Some other fragmentary remains of cyathaspids have also been collected in the Upper Silurian of Pioneer Island). Above this part of the sequence, heterostracans have also been collected from the lowermost Devonian up to the Frasnian, Vavilov Formation (Fig. 3). However, no heterostracan is known from the Emsian, Rusanov and Al'banov formations, where other vertebrates do occur.

Our work mainly deals with Lower and Middle Devonian taxa, from the lower Lochkovian, Severnaya Zemlya Formation up to the Eifelian, Vstrechnaya Formation (Fig. 3). These faunas include representatives of all the higher taxa of heterostracans, including the psammosteids. Psammosteids occur from the Eifelian, Vstrechnaya Formation up to the Frasnian, Vavilov Formation (Fig. 3). The correlation of the different formations to the standard Devonian sequence follows Männik *et al.*'s (2002) stratigraphical scale (see also Matukhin *et al.* 1997b; Lukševičs 1999: fig. 3, for the Givetian to lower Famennian part of the sequence). However, this scale differs from Mark-Kurik's (1991) conclusions concerning the Pragian/Emsian boundary. In Mark-Kurik's (1991) paper, the Pragian/Emsian boundary is located at the Rusanov/Al'banov boundary, based upon correlations of the placoderm assemblages (see also Karatajūtē-Talimaa & Blieck 1999). In Männik *et al.*'s (2002) paper, the Pragian/Emsian boundary is situated lower, in the Rusanov Formation, based upon the distribution of acanthodians, conodonts, ostracodes, and some other marine invertebrates (references in Männik *et al.* 2002; see also Abushik & Evdokimova 1999: fig. 9).

SYSTEM	SERIES	STAGE	FORMATION	
DEVONIAN	Upper	Famennian	Mal'yutka	
		Frasnian	Vavilov	✓
			Matusevich	✓
	Middle	Givetian	Gremyashchij	✓
			Vatutin	✓
		? Eifelian	Vstrechnaya	✓
	Lower	Emsian	Al'banov	
			Rusanov	
		Pragian	Spokojnaya	✓
		Lochkovian	Pod"emnaya	✓
			Severnaya Zemlya	✓
SILURIAN	Přidoli		Krasnaya Bukhta	✓
	Ludlow	Ludfordian/ Gorstian	Ust'-Spokojnaya	✓
	Wenlock	Homerian/ Sheinwoodian	Samojlovich	
	Llandovery	Telychian		
			Srednij	
		Aeronian	Golomyannyj	
		Rhuddanian	Vodopad	

FIG. 3. — Synthetic stratigraphical succession of the Silurian-Devonian of the October Revolution Island, Severnaya Zemlya, after Männik *et al.* (2002). V-shaped ticks on the right side designate the heterostracan-bearing formations.

The lower Upper Silurian (Ludlow), Ust'-Spokojnaya Formation consists mainly of marlstones with interbedded limestones yielding marine invertebrate assemblages. The upper Upper Silurian (Přidoli), Krasnaya Bukhta Formation is composed of siliciclastic rocks with a few limestone interbeds; it is interpreted as having been deposited in a "shallow-water restricted marine environment", characterized by an "extremely poor fauna" of invertebrates, but common micro- and macro-remains of vertebrates (Männik *et al.* 2002). There is a stratigraphical gap between the Silurian and the Devonian parts of the sequence. The Devonian strata are dominated by variegated terrigenous deposits, with only a few carbonate intervals in the Pragian (Spokojnaya Formation), the Emsian (Rusanov and Al'banov formations), the Givetian (Gremyashchij Formation), and the Frasnian (Vavilov Formation). The lower Lochkovian, Severnaya Zemlya Formation corresponds to a transgression, but still under "abnormal" marine conditions (Männik *et al.* 2002). The first carbonate layers appear sparsely in the upper part of the Severnaya Zemlya Formation, and more frequently in the upper Spokojnaya Formation which is interpreted as indicative of a new major transgression (Männik *et al.* 2002). The carbonates of the lower Rusanov Formation correspond to the maximum extent of the Early Devonian marine transgression. The Eifelian, Vstrechnaya Formation is mainly composed of brownish-red terrigenous sediments with impoverished invertebrate faunas and plants. The Givetian, upper Gremyashchij Formation corresponds to a regression, while the nearly 500 m-thick Givetian-Frasnian, Matusevich Formation, with its rhythmic interbedding of variegated and red detrital sediments, corresponds to gradually deepening conditions, before the maximum Late Devonian transgression in the Frasnian, Vavilov Formation (Männik *et al.* 2002).

TAXONOMIC NOTES

In the Devonian of Severnaya Zemlya, heterostracans are represented by higher taxa classically encountered in the Circum-Arctic areas, i.e. Corvaspidiformes, Traquairaspidiformes, Cyathaspidiformes and Pteraspidiformes (including psammosteids). To these taxa we can add Tesseraspidiformes and Amphiaspidiformes, the latter being endemic to southern Tajmyr and

NW Siberia (we note here that the genus *Boothiaspis* Broad, 1973 from the Canadian Arctic, originally attributed to amphiaspids, has been reinterpreted as a cyathaspid: Elliott & Dineley 1985, 1991). Most of the studied material is preserved as disarticulated specimens, with the exceptions of *Tesseraspis* Wills, 1936 and corvaspids which are represented by almost complete or partly articulated head carapaces and trunks.

Heterostracans have been mentioned in a few previous papers on the stratigraphy of the Silurian-Devonian of Severnaya Zemlya (Klubov *et al.* 1980 for Pioneer Island; Kurik *et al.* 1982; Karatajūtē-Talimaa 1983; Karatajūtē-Talimaa *et al.* 1986; Lukševičs 1999 for October Revolution Island; see also Blieck *et al.* 1987), a single species has been described and figured (*Tesseraspis mosaica* Karatajūtē-Talimaa, 1983), and another one has been briefly described ("new genus of Pteraspidiformes" *in* Karatajūtē-Talimaa & Matukhin 1997, corresponding to the Protopteraspididae gen. et sp. 2 in this study) (see the historical introductions of Matukhin *et al.* 1982; Mark-Kurik & Janvier 1995; Barwick *et al.* 1997; Mark-Kurik 1998; Afanassieva 1999 and Lukševičs 1999 for the other agnathans and for the gnathostomes). More recently, the corvaspids have been described and figured (Blieck & Karatajūtē-Talimaa 2001).

The classification and nomenclature that we use are the ones of Blieck *et al.* (1991) which have been formalized in Janvier (1996). Most earlier taxonomical determinations were preliminary and some of them have to be corrected as follows:

TRAQUAIRASPIDIFORMES

Former mentions of "*Weigeltaspis*" are listed as Traquairaspidiformes indet. in the biostratigraphical section here below (Fig. 4). "*Traquairaspis*" is renamed *Phialaspis* Wills, 1935 (*sensu* Tarrant 1991).

PTERASPIDIFORMES

"Doryaspididae" is renamed Protopteraspididae (*sensu* Blieck 1984). Former mentions of "*Protopteraspis*" are attributed to Protopteraspididae indet.; "*Podolaspis* (*Canadapteraspis*?)" to *Unarkaspis*?; "Pteraspididae", "*Podolaspis*?" and "*Pteraspis*" are simply attributed to Pteraspidiformes indet. because they are mainly represented by isolated plates or fragmentary remains of bones with "non-psammosteid" ornamentations, that is, superficial structures of dentine layers encountered in either Protopteraspididae or Pteraspididae (*sensu* Blieck 1984). No anchipteraspid has been recognized in the Silurian-Devonian of Severnaya Zemlya.

Former "Drepanaspida?" and "Psammosteida" (*sensu* Obruchev & Mark-Kurik 1965) are attributed to the family Psammosteidae, within the order Pteraspidiformes (*sensu* Blieck *in* Janvier 1996: fig. 4.9).

The new taxon here named Protopteraspididae gen. et sp. 2 ("new genus of Pteraspidiformes" of Karatajūtē-Talimaa & Matukhin 1997) from the Eifelian, Vstrechnaya Formation represents the probable stratigraphically youngest protopteraspidid. It is also one of the youngest "non-psammosteid" Pteraspidiformes. Other Middle Devonian "non-psammosteid" Pteraspidiformes are known from Spitsbergen (in association with psammosteids; references in Blieck & Heintz 1979). The youngest "non-psammosteid" Pteraspidiformes seem to come from the Givetian of western North America (Elliott *et al.* 2000a, b).

HETEROSTRACI

"Amphiaspidiformes" and "Heterostraci" were mentioned by Karatajūtē-Talimaa & Blieck (1999) in the uppermost Silurian, Krasnaya Bukhta Formation, based on fragmentary remains collected in locality 46, bed 6 and locality 51a, bed "v" of the Spokojnaya River (see Männik *et al.* 2002: fig. 9). These identifications are now considered to be very doubtful, and are not taken further into account. However, true heterostracans have been collected in the Upper Silurian, Ust'-Spokojnaya and Krasnaya Bukhta formations (T. Märss pers. comm. 1999).

BIOSTRATIGRAPHIC DISTRIBUTION AND CORRELATIONS

BIOSTRATIGRAPHIC DISTRIBUTION

Fig. 4 gives the present state of our knowledge of the stratigraphical distribution of heterostracans in the Upper Silurian and Devonian of October Revolution Island, Severnaya Zemlya Archipelago. The data for the heterostracans of the Ust'-Spokojnaya and Krasnaya Bukhta formations have been kindly provided by T. Märss. They are included with the data on the Lower to Upper Devonian heterostracans (that we have been working on) so as to provide a complete coverage of the distribution of the Heterostraci. The assemblages of the Upper Silurian, Ust'-Spokojnaya and Krasnaya Bukhta formations are dominated by cyathaspids. The assemblage of the lower Lochkovian, Severnaya Zemlya Formation is exclusively composed of tesseraspid and corvaspid species. The richest assemblages have been provided by the upper Lochkovian, Pod''emnaya Formation. The assemblages of the various localities of this formation consist of corvaspids, *Phialaspis*, *Lepidaspis*? Dineley & Loeffler, 1976, a few pteraspids (among which *Unarkaspis*? sp.), numerous cyathaspids (including *Ctenaspis* Kiaer, 1930, *Anglaspis* Jaekel, 1926, *Poraspis* Kiaer, 1930, *Irregulareaspis* Zych, 1931, *Homalaspidella* Strand, 1934), and amphiaspids (including *Putoranaspis*? Obruchev, 1964). These assemblages are cyathaspid-dominated. The assemblages of the Pragian, Spokojnaya Formation are less diversified and pteraspid-dominated, with a few traquairaspid remains, poraspids, and several pteraspids (including Protopteraspididae gen. et sp. 1 with a *Doryaspis*-like ornamentation of tuberculated dentine ridges [previously designated as *Doryaspis* sp. nov. by Karatajūtē-Talimaa *et al.* 1986], *Miltaspis*? Blieck, 1981, *Gigantaspis*? Heintz, 1962). No heterostracan has been collected in the Emsian, Rusanov and Al'banov formations. The Eifelian, Vstrechnaya Formation has yielded an assemblage completely different from the Early Devonian ones (Karatajūtē-Talimaa & Matukhin 1997). It is composed of Protopteraspididae gen. et sp. 2 as well as various psammosteids. The latter also occur in the Givetian to Frasnian, Vatutin, Gremyashchij and Matusevich formations (Kurik *et al.* 1982; Mark-Kurik 1991), as well as in the Frasnian, Vavilov Formation (unpublished material of VNKT).

BIOSTRATIGRAPHIC CORRELATIONS

Taxa such as *Corveolepis elgae* Blieck & Karatajūtē-Talimaa, 2001 (formerly *Corvaspis* sp. cf. *C. kingi* Woodward, 1934), *C.*? sp. cf. *C.*? *graticulata* (Dineley, 1955), *Phialaspis*, *Poraspis* sp. cf. *P. polaris* Kiaer, 1930, *Homalaspidella*, *Irregulareaspis*, *Anglaspis*, and *Ctenaspis* (Fig. 4) allow biostratigraphic correlations to be made with the Devonian sequence of both Spitsbergen and the Canadian Arctic region (Blieck 1984; Elliott 1984; Blieck *et al.* 1987). The pteraspidids *Unarkaspis*? Elliott, 1983, *Protopteraspis*? Leriche, 1924, *Miltaspis*? and *Gigantaspis*?, if confirmed at the generic level, would strengthen these correlations. However, the occurrence of amphiaspids suggests a correlation with the Lower Devonian of central Tajmyr and NW Siberia (Blieck & Janvier 1993). Some specimens from locality 23, bed 15 in the Pod''emnaya Formation along the Ushakov River (scales and fragments of head shields) are attributed to the amphiaspid *Putoranaspis*? (det. L. I. Novitskaya, Moscow). *Putoranaspis* occurs in the Kurejka Formation of the Kurejka basin, Noril'sk area, northwestern East Siberia, together with *Porolepis* Woodward, 1891, *Gunaspis* Bystrow, 1959 and *Argyriaspis* Novitskaya, 1971 (references in Blieck & Janvier 1993: fig. 5.4B). The latter three genera are also

FIG. 4. — Biostratigraphical distribution of heterostracans in the Upper Silurian and Devonian of the October Revolution Island, Severnaya Zemlya. Note that *Archegonaspis* sp. comes from the Ludlow of Pioneer Island, not October Revolution Island (T. Märss pers. comm. 1999); and that *Tolypelepis* sp. cf. *T. undulata* Pander, 1856 comes from material collected by E. Mark-Kurik along the Bedovaya River. Abbreviations: **Eifel.**, Eifelian; **Fam.**, Famennian.

SILURIAN		DEVONIAN											
Upper		Lower					Middle			Upper			
Ludlow	Přídolí	Lochkovian		Pragian	Emsian		Eifel.	Givetian		Frasnian		Fam.	
Ust'Spokojnaya	Krasnaya Bukhta	Severnaya Zemlya	Pod"emnaya	Spokojnaya	Rusanov	Al'banov	Vstrechnaya	Vatutin	Gremyashchij	Matusevich	Vavilov	Mal'yutka	
*													*Archegonaspis* sp.
*	*												Cyathaspididae indet.
	*												*Strosipherus*? sp.
	*												*Tolypelepis* sp. cf. *T. undulata*
		*											*Tesseraspis mosaica*
		*											*Tesseraspis* sp.
		*											*Corveolepis elgae*
		*	*										Corvaspididae indet.
		*	*										Corvaspididae? indet.
			*										Heterostraci indet.
			*										Amphiaspidiformes indet.
			*										Amphiaspidiformes? indet.
			*										*Putoranaspis*? sp.
			*										*Corveolepis*? sp. cf. *C.*? *graticulata*
			*										*Phialaspis* sp.
			*										*Phialaspis*? sp.
			*										*Ctenaspis* sp.
			*										*Ctenaspis* sp. 1
			*										*Anglaspis* sp.
			*										*Anglaspis* sp. 1
			*										*Poraspis* sp. cf. *P. polaris*
			*										*Poraspis*? sp.
			*										*Irregulareaspis* sp.
			*										*Irregulareaspis*? sp.
			*										Homalaspidella sp.
			*										*Lepidaspis*? sp.
			*										*Protopteraspis*? sp.
			*										*Unarkaspis*? sp.
			*	*									Traquairaspidiformes indet.
			*	*									Poraspididae indet.
			*	*									*Poraspis* sp.
			*	*									Pteraspidiformes indet.
			*	*									Pteraspididae indet.
				*									Protopteraspididae indet.
				*									Protopteraspididae gen. et sp. 1
				*									Protopteraspididae? indet.
				*									*Miltaspis*? sp.
				*									*Gigantaspis*? sp.
							*						Protopteraspididae gen. et sp. 2
							*						cf. *Schizosteus heterolepis*
							*						*Tartuosteus* sp.
							*						cf. *Pycnosteus* sp.
							*	*					Psammosteidae indet.
							*	*	*				Heterostraci? indet.
							*	*	*				*Psammolepis* sp.
							*	*		*	*		*Psammosteus* sp.
								*					*Tartuosteus*? sp.
									*				*Psammosteus*? sp.

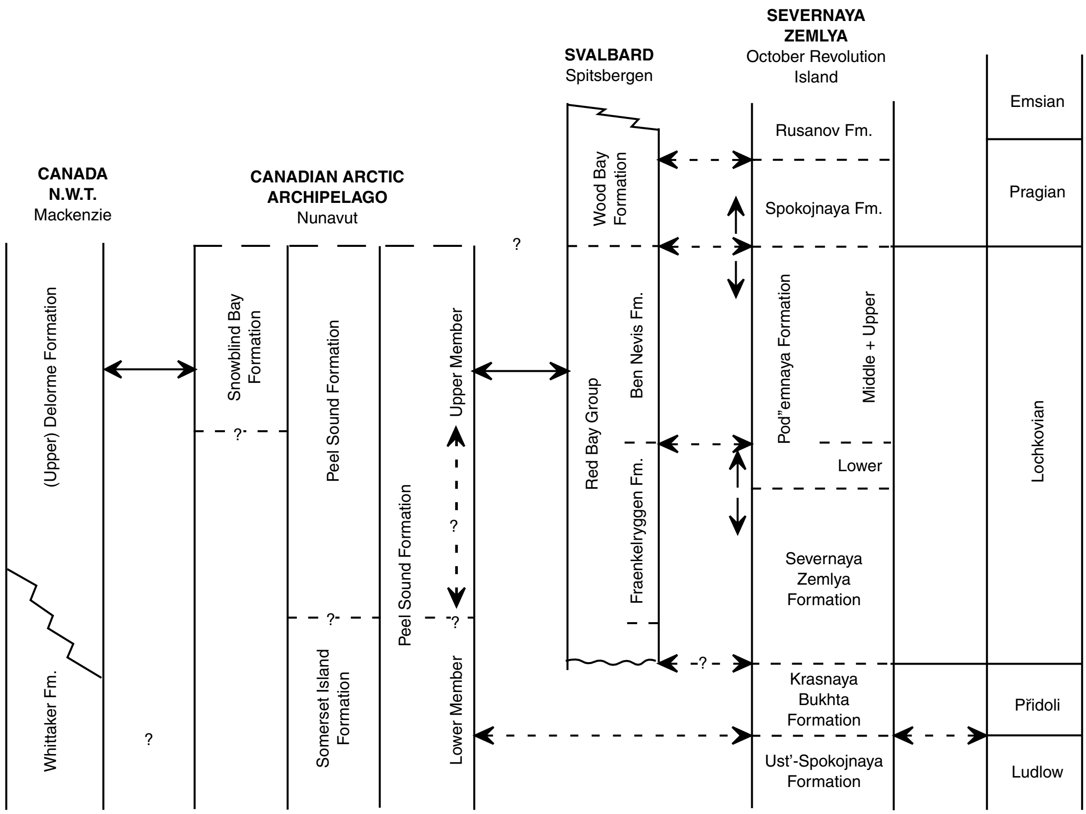

FIG. 5. — Biostratigraphical correlations for some of the Circum-Arctic, Upper Silurian-Lower Devonian heterostracan-bearing sequences, after Blieck *et al.* (1987: fig. 9, modified).

encountered in the Belyi Kamen' and Uryum "subhorizons" of the Tareya River section, in central Tajmyr (references in Blieck & Janvier 1993: fig. 5.4A); these subhorizons are now dated as Lochkovian and Pragian? respectively (Cherkesova *et al.* 1994). Nevertheless, correlations are easier with the series of the Devonian graben of NW Spitsbergen. The Pod''emnaya Formation is correlated to the Ben Nevis Formation of Spitsbergen, based on assemblages with *Corveolepis*? sp. cf. *C.*? *graticulata*, *Ctenaspis*, *Anglaspis*, *Poraspis* sp. cf. *P. polaris*, *Irregulareaspis*, *Homalaspidella*, *Lepidaspis*?, and *Miltaspis*? (Fig. 4). However, the lowermost part of the Pod''emnaya Formation may be equivalent to the uppermost Fraenkelryggen Formation of Spitsbergen (Fig. 5): this proposal is based on the occurrence of *Phialaspis* both in the lower Pod''emnaya Formation ("*Traquairaspis* cf. *symondsi*" in Karatajūtē-Talimaa 1983) and the Fraenkelryggen Formation ("*Traquairaspis* cf. *pococki*" in Blieck *et al.* 1987); but other fragmentary remains now attributed to either *Phialaspis* sp. or Traquairaspidiformes indet. ("*Traquairaspis*" auct.) also occur in the middle Pod''emnaya Formation and the Ben Nevis Formation. So the distribution of these traquairaspid taxa may not be conclusive evidence to correlate the lower boundary of the Pod''emnaya Formation.

The Spokojnaya Formation with its *Doryaspis*-like (Protopteraspididae gen. et sp. 1) and *Gigantaspis*? assemblage would thus be equivalent to part of the Wood Bay Formation of Spitsbergen (Blieck *et al.*

1987) (Fig. 5). However, *Miltaspis*? sp. and *Poraspis* sp. occur in the Spokojnaya Formation although *Miltaspis* and *Poraspis* do not occur in the Wood Bay Formation (however, they have been identified in the underlying Ben Nevis Formation). These discrepancies may be more apparent than real. We indeed consider here the heterostracan assemblage of each formation as a whole. After a detailed study of the distribution of species in each particular section, it may appear that the different taxa have partly different distributions, leading to more detailed correlations. In this case, the boundary between the Pod''emnaya and Spokojnaya formations may not correspond to the boundary between the Ben Nevis and Wood Bay formations (Fig. 5). In other words, the base of the Spokojnaya Formation may be equivalent to a level in the upper part of the Ben Nevis Formation.

On Severnaya Zemlya, the Pragian/Emsian boundary is now located in the lower Rusanov Formation on the basis of various invertebrates (references in Männik *et al.* 2002). In Spitsbergen this boundary is located in the upper Wood Bay Formation at about the base of the Stjørdalen faunal division (Blieck 1984: fig. 74; Blieck *et al.* 1987: fig. 8; Mark-Kurik 1991). This agrees with a Pragian age for the Spokojnaya Formation (Fig. 5).

The difference in taxic composition and thus in number of common taxa of the Upper Silurian-Lower Devonian sequences of Severnaya Zemlya and Spitsbergen on one side, and Tajmyr-Siberia on another side, is attributed by Matukhin *et al.* (1997a) to lithological differences. The sequence is mostly siliciclastic with numerous red beds in Severnaya Zemlya and Spitsbergen, while it is mostly made of "marine shelf" deposits in Tajmyr. Matukhin *et al.* (1997a) wonder whether these differences are due to Palaeogeographical (a barrier between both areas) or palaeoecological conditions. The plate tectonic model shortly presented in the section "Palaeogeographical setting" (Fig. 1) is an answer to this question: there was a palaeogeographical barrier.

The Vstrechnaya Formation of Severnaya Zemlya, with its unusual protopteraspidid-psammosteid assemblage, is dated Eifelian after its co-occurring gnathostomes (Mark-Kurik 1991; Karatajūtē-Talimaa & Matukhin 1997; Matukhin *et al.* 1997b; Valiukevičius in press). For the overlying heterostracan-bearing Vatutin to Vavilov formations (Fig. 3), we refer the reader to Lukševičs' (1999) and Männik *et al.*'s (2002) conclusions which lead to a correlation with the Givetian to Frasnian sequence of the East Baltic area (Lukševičs 1999: fig. 3). In this sequence, the Givetian/Frasnian boundary is located at (Lukševičs 1999) or just below the boundary between the Gauja and Amata Regional Stages (Mark-Kurik *et al.* 1999; although Mark-Kurik 2000 maintains an older point of view for the Givetian/Frasnian boundary that she provisionally locates higher at the Amata/Plavinas Regional Stages boundary) (see a review of this problem in Esin *et al.* 2000).

CONCLUSION: BIOEVENTS IN THE EVOLUTION OF HETEROSTRACAN ASSEMBLAGES OF THE UPPER SILURIAN-DEVONIAN OF SEVERNAYA ZEMLYA

These preliminary results on heterostracan distribution in the Upper Silurian-Devonian sequence of Severnaya Zemlya lead to a general scheme for the evolution of heterostracan assemblages in this region.

The Upper Silurian, Ust'-Spokojnaya and Krasnaya Bukhta formations are rather poor in taxa and their assemblages are cyathaspid-dominated. The lower Lochkovian, Severnaya Zemlya Formation assemblage is also poor and composed of tesseraspids and corvaspids. The upper Lochkovian, Pod''emnaya Formation assemblage is the most diversified and again cyathaspid-dominated. The differences in taxic composition between these formations seem to be linked to their lithological (lithofacial) differences: carbonate-dominated in the Ust'-Spokojnaya Formation, intercalated carbonate and red siliciclastic facies in the Krasnaya Bukhta Formation, siliciclastic in the Severnaya Zemlya Formation, siliciclastic but with finer-grained facies in the Pod''emnaya Formation. However, it is also probable that the Pod''emnaya Formation corresponds to a real adaptive radiation of heterostracans as opposed to a link to lithological differences (Fig. 4). The same pattern is observed in the upper Lochkovian, *Rhinopteraspis crouchi* Zone of Artois, northern France (Blieck *et al.* 1995), and in the upper Lochkovian, upper Ben Nevis Formation of Spitsbergen (Blieck *et al.* 1987). This is also true for the upper Lochkovian of the Canadian Arctic (Elliott 1984; Blieck & Janvier 1999). So it seems that this upper Lochkovian "blooming" is a world wide event in heterostracan history that may be correlated to a high stand of the world ocean level (Blieck *et al.* 1995). However, this hypothesis needs to be supported by a detailed sequence analysis of all the sections on October Revolution Island. This could help in determining the precise levels of either appearance or maximum abundance of the various taxa encountered and would also aid in precise correlation between the different outcrop sections.

A major change is observed at the transition from the Pod''emnaya Formation to the Spokojnaya Formation. The Pragian Spokojnaya Formation has a less diversified heterostracan assemblage which is pteraspid-dominated (Fig. 4). This is linked to the more detrital, red facies of an Old Red Sandstone type that dominate the Spokojnaya Formation. This event seems to correspond to the occurrence of heterostracans with developed bony superstructures (such as the rostral and cornual plates, and the dorsal spine of the head carapace of pteraspids) in relation to a more disturbed environment, where typically marine, benthic invertebrate communities cannot be established. This problem is general and world wide for the Old Red Sandstone-type sediments which are thus classically interpreted as non-marine, but may simply be proximal marine environments with impoverished invertebrate communities, but with rich vertebrate communities (see e.g., Goujet 1984; Blieck 1985).

The Emsian, Rusanov and Al'banov formations correspond on Severnaya Zemlya to a gap in the heterostracan record. Both formations correspond to the incoming of carbonate, partly dolomitized facies (already encountered in the upper Spokojnaya Formation), and we cannot yet explain that gap which may be due to either a real lack of fossils and/or a need for further field sampling.

The Eifelian, Vstrechnaya Formation, with its predominantly Old Red Sandstone-type sediments, has yielded a psammosteid-dominated assemblage which is typical for the Middle Devonian. However, this assemblage also contains an unusual new pteraspid which will probably give new interesting data on the latest steps of evolution of this group. The psammosteid assemblage continues up to the Frasnian where it disappears before the Frasnian/Famennian boundary (Fig. 4; also Lukševičs 1999). This pattern is not easier to explain than the Emsian gap, as in the best documented Upper Devonian psammosteid-bearing sequences, *Psammosteus* Agassiz, 1844 persists until the latest Frasnian (for instance on the East European Platform, in the Baltic and Timan regions, and the Central Devonian Field of Russia: Esin *et al.* 2000). Once again, the upper Frasnian gap in the heterostracan record of Severnaya Zemlya may be due to taphonomic and/or sampling conditions.

So, the Silurian-Devonian sequence of October Revolution Island gives a considerable amount of new information about the history of heterostracans. This should be compared to the data obtained from Pioneer Island (Klubov *et al.* 1980) to provide a more complete idea of the evolution of heterostracans on the Kara-Tajmyr palaeocontinental block, and to aid in more precise correlations with the other Circum-Arctic areas.

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