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Vertebrate microremains from the Lower Silurian of Siberia and Central Asia: palaeobiodiversity and palaeobiogeography

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ABSTRACT – The biostratigraphic and palaeogeographical distributions of early vertebrate microfossils from a number of Lower Silurian localities in northwestern Mongolia, Tuva and southern Siberia were reviewed. Vertebrate microremains showed high taxonomic diversity, comprising acanthodians, chondrichthyans, putative galeaspids, heterostracans, mongolepids, tesakoviaspids, thelodonts and possible eriptychiids. The majority of taxa have lower stratigraphic levels of occurrence compared to other Silurian palaeobiogeographical provinces, such as the European-Russian or Canadian Arctic. Vertebrate microremains are numerous within the samples, which may indicate warm-water low-latitude palaeobasins with rich shelf faunas. This disagrees with the recent interpretations of the territory as a northern high-latitude Siberian palaeocontinent. The palaeobiogeographical distribution of vertebrate taxa indicates an endemic palaeobiogeographical province of connected epeiric palaeoseas with external isolation during the early Silurian. In previous works separation between Tuvan and Siberian palaeobiogeographical provinces has been suggested. After careful revision of the vertebrate microfossil record of the region, we find that differences in a few vertebrate taxa do not provide not strong enough evidence to reliably distinguish these provinces. We therefore dispute the hypothesis of two biogeographical provinces in the early Silurian of the Siberian palaeocontinent, and propose a single unified Siberian–Tuvan palaeobiogeographical province. *J. Micropalaeontol.* **30**(2): 97–106, September 2011.

KEYWORDS: *vertebrates, Lower Silurian, Tuva, Mongolia, Siberia*

INTRODUCTION

The Silurian vertebrates of central Asia and Siberia have been explored over the last 50 years, with the first general report of early Silurian vertebrates from southern Siberia published by Obruchev (1958), followed by a more detailed report by Moskalenko (1968). A comprehensive study of the thelodonts of the entire region, middle to southern Siberia and Tuva Republic, was made by Karatajūtė-Talimaa in 1978. Following several seasons of extensive field work in the early 1980s, a comprehensive summary of the vertebrate record from southern Siberia was published by Karatajūtė-Talimaa & Predtechenskyj (1995). Subsequently, lower Silurian collections from northwestern Mongolia became available and were studied in a series of papers (Karatajūtė-Talimaa *et al.* 1990; Karatajūtė-Talimaa, 1995; Žigaitė, 2004; and Žigaitė, unpublished thesis, Université Lille – 1, 2008).

The present-day territory of central Asia and southern East Siberia is interpreted as a unified Siberian palaeocontinent – an independent landmass, which persisted not only in the Silurian, but during the whole Palaeozoic era (Cocks & Torsvik, 2007). In the Silurian period it comprised a large area of modern Russia (including Altai, Salair, Sayan, Siberia, Tomsk) and northwestern Mongolia, but also extended into the northwestern part of China. It was the only large terrane in the Northern Hemisphere for much of the Palaeozoic, starting from the Ordovician (Cocks & Torsvik, 2007). In the Late Ordovician, the Tuva–northern Mongolia terrane joined the main Siberian terrane area as a northern accretionary wedge (Cocks & Torsvik, 2007). The foreshore and lagoonal facies rich in vertebrate microremains, therefore, occur along a north–south transect of the Siberian palaeocontinent. The centre and the southeastern parts of Siberia were largely flooded by epeiric seas during the whole Silurian. In the early Silurian, this epicontinental sedimentary basin is suggested to have been a stable, persistent structure, favouring the presence of a rather isolated and species-rich palaeobiogeographical province, which can be inferred from the endemic vertebrate and invertebrate faunal composition (Tesakov *et al.*, 2003; Žigaitė & Blieck, 2006).

Vertebrate microremains (scales and tesserae of micromeric dermoskeleton) are abundant in the lower Silurian of northwestern Mongolia, central Tuva and southern Siberia, and show strong taxonomical differences from vertebrates of the other contemporaneous palaeobiogeographical provinces (e.g. Karatajūtė-Talimaa, 1995; Karatajūtė-Talimaa & Smith, 2004), such as the European-Russian palaeobiogeographical province (e.g. Karatajūtė-Talimaa, 1978; Karatajūtė-Talimaa & Brazauskas, 1994), which includes Eastern Europe and the European part of Russia (see Blieck, 2011; Žigaitė & Blieck, accepted), or the Canadian Arctic province (e.g. Märss *et al.*, 2002, 2006). Endemism has already been attributed to the majority of vertebrate taxa described from this region (Afanassieva & Janvier, 1985; Karatajūtė-Talimaa *et al.*, 1990; Karatajūtė-Talimaa, 1995; Blieck & Janvier, 1991, 1993; Žigaitė, 2004; Žigaitė & Blieck, 2006). The idea of pre-Silurian origination and speciation of vertebrates in supposedly warm equatorial epicontinental seas of the Siberian palaeocontinent has been proposed in several works (Blieck & Janvier, 1991, 1993; Žigaitė & Blieck, 2006). The recent study of Cocks & Torsvik (2007) suggests that the territory was situated in high northern palaeolatitudes, according to palaeomagnetic data and the presence of high-latitude faunal assemblages, e.g. the low-diversity (and, by inference, cold-water) *Tuvaella* fauna (see Cocks & Torsvik,

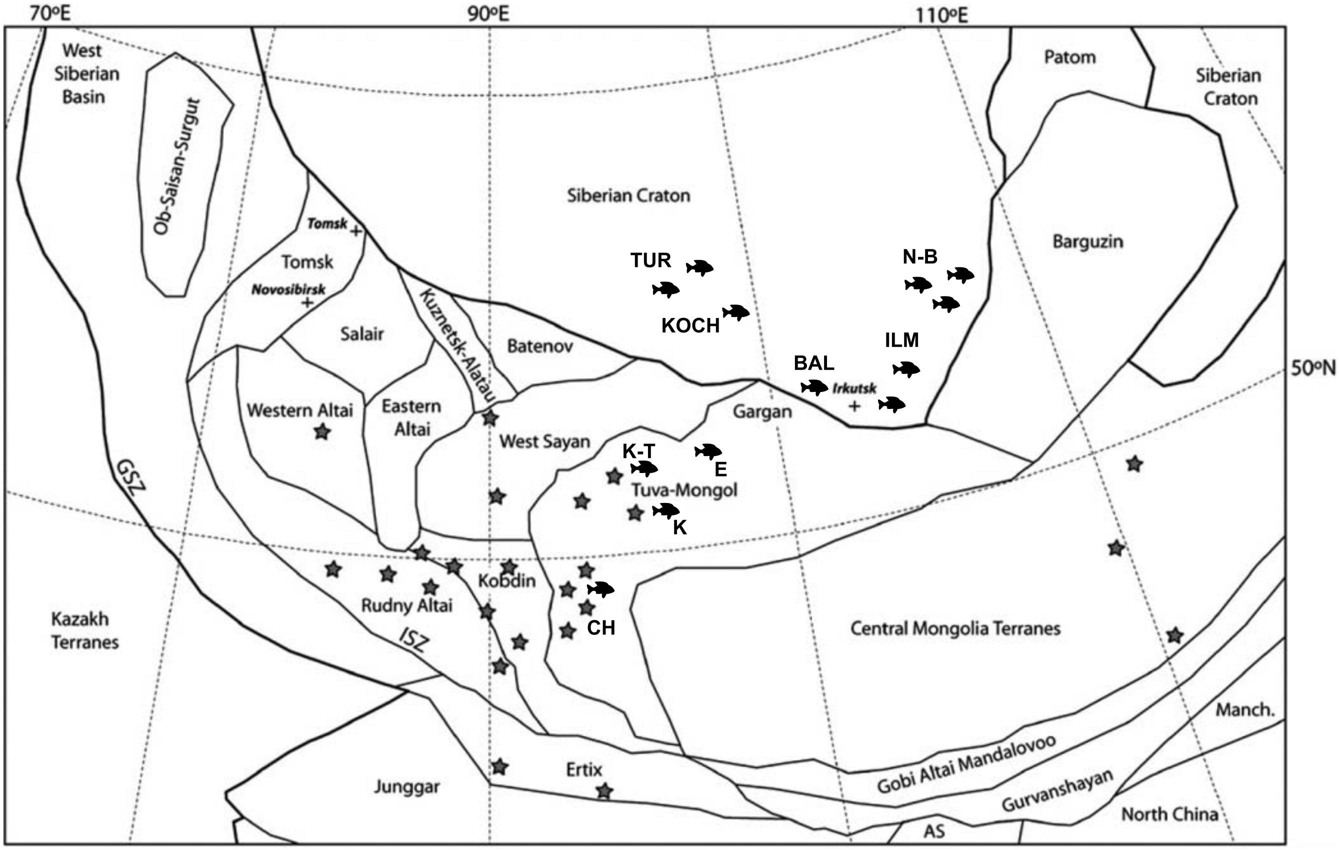

Fig. 1. The microvertebrate-bearing localities (indicated by black fish) and the *Tuvaella* brachiopod fauna records (shown as stars) in the Silurian of the Siberian palaeocontinent. Localities: CH, Chargat; E, Elegest; K, Kadvoj; K–T, Kyzyl-Tchiraa. Districts: BAL, Balturino; ILM, Ilim; KOCH, Kochumdekh; N-B, Nyuya–Beresovo; TUR, Turukhansk. Modified after Cocks & Torsvik (2007), brachiopod data after Rong & Zhan (1982) and Rozman (1986). Map of the southwestern part of the Siberian craton and adjacent terranes from Cocks & Torsvik (2007), including southern Siberia, Mongolia, eastern Kazakhstan, and northwestern China. AS, Ala Shan; Manch., Manchurides; GSZ, Gornostaev Shear Zone; ISZ, Irtysh Shear Zone.

2007). The invertebrate record of this region, however, contrasts with the rich and diverse early Silurian vertebrate record, revealed in previous works and this study.

In this article, we present a review of the most recent dataset of the lower Silurian vertebrate microfossil record from northwestern Mongolia, the Tuva Republic, and southern Siberia. We have reviewed the taxonomic composition of vertebrate microremains from this region, analysing their biostratigrapical and palaeogeographical record. We attempt to bring all the available information together and create an updated summary of the early Silurian vertebrate microfossil distribution in the region. We feel that this review is timely, particularly so as to refine and summarize the diversity and endemism of the lower Silurian vertebrates of the region, in the context of recent reconstructions of Silurian palaeogeography (Cocks & Torsvik, 2002, 2007). Our data summary brings new insight to the general palaeobiodiversity of the Siberian epeiric seas in the early Silurian. It should be noted that when talking about the 'vertebrate microfossils' and 'vertebrate microremains' in this work, we refer to the phosphatic scales and tesserae of the external micromeric bone armour (dermoskeleton) of the earliest fish, common in the lower Palaeozoic. We exclude conodonts, which may also be referred to as phosphatic vertebrate microfossils and are common in the lower Silurian sediments of central Asia and Siberia, but require additional and separate study.

GEOLOGICAL SETTING

Vertebrate microremains are abundant in the lower Silurian sediments of southern Siberia, Tuva and northwestern Mongolia. Vertebrate-yielding sites represent a wide range of facies including reef crest, restricted shallow shelf, brackish lagoon and coastal belt facies.

Northwestern Mongolia

The northwestern Mongolian samples come from the upper Llandoverian–Wenlockian sequences. The main locality is situated on the southeast slope of Mount Chargat, Lake Basin outcrop, 80 km north of lake Khara-Ubs-Nuur (Fig. 1, CH). The section exposes the Chargat Formation, which comprises a molasse-type sequence, characterized by brown and red-coloured conglomerates, clayey limestone breccias and concretionary sandstones with limestone intercalations rich in fauna (Minjin, 2001). These limestone layers represent marginal shallow-water sedimentary facies rich in fauna, including numerous vertebrate microfossils. The age of the formation is latest Llandovery–early Wenlock, which is based mainly on

Locality	NW Mongolia	SIBERIA										TUVA				
	Chargat locality	Thurukhansk district		Kochumdek district		Nyuya Beresovo district		Ilim district		Balturino district		Elegest locality		Kadvoj locality		Kyzyl-Tchiraa locality
Sample/ outcrop	16/3 1009	Yass-4 N-1				147-164		141	B-11	135	Barmo beds	K-70-134	224 225 226	660-1 660-4 694	662 663 664	253R 271R 702
Series	Ln/W	Ln	W	Ln	W	Ln	W	Ln	Ln	Ln	W	Ln	W	Ln	W	Ln
Acanthodians	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Anaspids (?)	●															
Chondrichthyes	●	●				●	●		●	●			●	●	●	
Eriptychiids	●															
(?) Galeaspids								●		●			●			
Heterostracans	●															
Mongolepids	●							●		●			●		●	
Tesakoviaspids								●		●						
Thelodonts	●	●		●	●	●	●	●	●	●	●	●	●	●	●	●
Conodonts				●	●	●	●	●								●
Corals	●	●	●	●	●		●	●	●	●		●	●	●	●	●
Tuvaella fauna	●							●		●		●	●	●	●	●

Fig. 2. The microvertebrate and some invertebrate fossil records in the Llandovery and Wenlock sections of northwestern Mongolia, Tuva Republic and southwestern Siberia. Locality and sample numbers after Karatajūtė-Talimaa *et al.* (1990), Karatajūtė-Talimaa & Ratanov (2002) and Karatajūtė-Talimaa & Smith (2003). Ln, Llandovery; W, Wenlock.

invertebrate biostratigraphy (see Karatajūtė-Talimaa *et al.*, 1990; Minjin, 2001).

Central Tuva

Lower Silurian samples of Tuva come from the Kyzyl-Tchiraa, Elegest and Kadvoi localities (Fig. 1: K-T, E, K), with sequences ranging from the upper Llandovery to Wenlock; dating is based on biostratigraphical data from invertebrate faunal assemblages (Vladimirskaya *et al.*, 1986). Lower and middle Llandovery is represented by the Alash Formation (Rhudanian–Aeronian), comprising fine-grained to coarse sandstones with limestone beds rich in fauna. The upper Llandovery contains two formations, the Kyzyl-Tchiraa Formation (lower Telychian), and the Angatchi Formation (upper Telychian); the latter has recently been interpreted as early Sheinwoodian in age (Karatajūtė-Talimaa & Ratanov, 2002). The formations are composed of fine-grained laminated sandstones with limestone intercalations. The lower Wenlock is represented by the Akchalym Formation (lower–middle Sheinwoodian), made up of siltstones with clayey inliers, and barren of vertebrate fauna. The upper Wenlock sediments correspond to the Dashtygoi Formation: upper Sheinwoodian–middle Ludlow (Karatajūtė-Talimaa & Ratanov, 2002; Karatajūtė-Talimaa & Smith, 2003). The formation is composed of condensed limestones with thin siltstone intercalations (Vladimirskaya *et al.*, 1986).

Southern Siberia

The Siberian early vertebrate localities represent the large East Siberian epicontinental sedimentary basin, which occupied a major part of the Siberian platform (East Siberia between the Yenisey and Lena rivers) and was exposed to continuous cyclical sedimentation during the Silurian (Tesakov *et al.*, 2003). Foreshore-lagoonal facies, composed of gypsiferous argillaceous dolostone with vertebrate microremains, are recorded along a north–south transect (Fig. 1). Unrestricted marine conditions associated with the deposition of carbonates with corals and stromatoporoids occurred only episodically, in the southeast (Tesakov *et al.*, 2003). The most southern part of the basin is composed mainly of variegated sandstone and siltstone (Tesakov *et al.*, 2003), which also contain large numbers of vertebrate microfossils (Žigaitė & Blieck, 2006).

Vertebrate-bearing samples are confined to the western and northeastern margins of the Tunguska Basin and to the western, southern and eastern parts of the Irkutsk Basin. The Silurian of East Siberia is divided into 'subregions' and 'districts' on the basis of persistent lithofacies (Tesakov *et al.*, 2003). Five subregions are recognized: North Tarym, North Preyenisey, Pretunguska, Nyuya–Beresovo and Irkutsk. Vertebrates are known from the Nyuya–Beresovo and Itrkutsk subregions, and a considerably smaller part comes from the North Preyenisey and Pretunguska subregions, Turukhansk and Kochumdek districts respectively (Figs 1, 2). Vertebrate microremains are known from the shallow-shelf facies, such as the brachiopod limestone in the Preyenisey subregion and the open shallow-shelf facies with diverse benthic fauna in the Pretunguska subregion. Lagoonal dolomitic marl with abundant fish and eurypterid fossils is known from the Nyuya–Beresovo subregion, and Nyuya–Beresovo lithostratigraphic district. The southernmost Irkutsk subregion, with the two lithostratigraphic districts of Ilim and Balturino, contains shallow-water, gypsum-bearing, dolomitic marl- and sandstone-dominated deposits (Tesakov *et al*., 2003). The sequences are particularly rich in microvertebrate remains, such as acanthodians (Karatajūtė-Talimaa & Smith, 2003) and thelodonts (Žigaitė, personal data), in particular. Summary reports on vertebrate fossil records from the late Ordovician and early Silurian of the Siberian platform were made by Karatajūtė-Talimaa & Predtechenskyj (1995).

Turukhansk district. Turukhansk stratigraphic district is located in the western Siberian platform, in the lower reaches of the Kureyka and Nizhnyaya Tunguska rivers (Fig. 1: TUR). The vertebrate microremains come from the Omnutakh Formation, upper Llandovery (uppermost middle Aeronian–Telychian), consisting of grey and greenish-grey marl that alternates with grey, platy and nodular limestone.

Kochumdek district. Kochumdek district is located along the northern Yenisey Ridge, close to the Kochumdek River, a tributary of the Podkamennaya Tunguska River (Fig. 1: KOCH). The oldest unit, Kochumdek Formation, lower Llandovery (Rhudanian–lower Aeronian), consists of grey nodular limestone with interbeds of grey marl increasing in abundance towards the top of the formation. The following Kulinna Formation, middle Llandovery (middle–upper Aeronian), consists of variegated mudstone and marl with interbeds of grey, nodular and wavy-bedded limestone. The overlying Razvilka Formation, upper Llandovery (Telychian), is made up of green marl with nodules and lenses of grey limestone. The upper part is composed mostly of limestone and dolostone, intercalated by marl with nodular limestone. The Wenlock series is represented in the lower part of the Usas Formation (Wenlock–uppermost Gorstian), and is composed of grey dolomitized limestone with biostromes (Tesakov *et al*., 2003).

Nyuya–Beresovo district. Nyuya–Beresovo stratigraphic district lies in the middle reaches of the Lena River and its Nyuya, Dzherba and Biryuk tributaries (Fig. 1: N-B). Vertebrate finds are restricted to the Llandovery series, represented by two formations, which correspond to the lower and upper Llandovery, respectively (Karatajūtė-Talima & Smith, 2003, 2004; Žigaitė, personal data). The older, Melichan Formation (Rhudanian–lower middle Aeronian), consists of grey dolostone and dolomitic marl with interbeds of grey, platy dolostone. The upper Llandovery is represented by the Utakan Formation (upper middle Aeronian–Telychian), which consists of variegated dolomitic marl with rare interbeds of platy dolostone that are gypsiferous at the top (Tesakov *et al*., 2003). Wenlock sequences belong to the Nyuya Formation.

Ilim district. The Ilim stratigraphic district, lying in the drainage basins of the middle Angara River and the Ilim River (Fig. 1: ILM), yielded vertebrates from the only Llandoverian unit, the Rassokha Formation (Rhudanian–Telychian), consisting of variegated siltstone with sandstone lenses (Tesakov *et al*., 2003). The Bratsk locality, which we decided to discuss separately in this work (Fig. 2), belongs to the Ilim lithostratigraphic district and is located north of the Sedanovo settlement, on the Bratsk–Ust–Ilimsk road. Collections come from the B-11 borehole, the upper Llandovery deposits of red argillite with sandstone beds (Karatajūtė-Talima & Smith, 2003).

Balturino district. The southernmost Balturino stratigraphic district, named after Balturino village, lies in the Uda and Biryusa river drainage basins (Tesakov *et al*., 2003) (Fig. 1: BAL). Its Llandoverian series is represented only by the Balturino Formation (Rhudanian–Telychian), composed of grey sandstone and green, red and rarely grey laminated siltstone. The Wenlock series is represented by the Barmo Beds, which include red and green sometimes calcareous mudstone and siltstone, with rare interbeds of grey sandstone.

MATERIAL AND METHODS

This work is based on the review of the published vertebrate taxonomic record, and the following analysis of biostratigraphic and palaeogeographical distribution of the taxa, which includes the construction of a vertebrate biozonation scheme for the region (see Fig. 3). We have taken into consideration the most recently published data, as well as non-peer-reviewed records from conference abstracts and field reports. We hope that this review will encourage the formal publication and/or taxonomic revision of these important faunas. In this respect our work has additional value, particularly regarding any possible future field work and further exploration of the region.

Localities and sample numbers used in Figure 2 correspond to those published by Karatajūtė-Talimaa *et al*. (1990), Karatajūtė-Talimaa & Ratanov (2002) and Karatajūtė-Talimaa & Smith (2003). The majority of vertebrate microfossils discussed in this work have been studied by the first two authors, Žigaitė and Karatajūtė-Talimaa. Consequently, many of the holotypes of these specimens are deposited in Vilnius University, Department of Geology and Mineralogy (Lithuania), as nominal collections of V. Karatajūtė-Talimaa. The collection series LGI (after the former Institute of Geology of Lithuania) has been kept, and the collection numbers are as follows: LGI M-1 for northeastern Mongolia; LGI-T for Tuva Republic and LGI-10 for the samples from central and southern Siberia.

VERTEBRATE FOSSIL RECORD

The sequences described above contain a number of endemic vertebrate microremains (Karatajūtė-Talimaa *et al*., 1990; Žigaitė, 2004). The taxonomic ranges of the lower Silurian vertebrates comprise the following taxa: acanthodians (Karatajūtė-Talimaa & Smith, 2003), anaspids (Karatajūtė-Talimaa *et al*., 1990), chondrichthyans (Karatajūtė-Talimaa *et al*., 1990; Karatajūtė-Talimaa & Ratanov, 2002), heterostracans (Karatajūtė-Talimaa *et al*., 1990), mongolepids (Karatajūtė-Talimaa *et al*., 1990; Karatajūtė-Talimaa & Novitskaya, 1992; Karatajūtė-Talimaa, 1995), putative galeaspids (Karatajūtė-Talimaa & Žigaitė, 2005), tesakoviaspids (Karatajūtė-Talimaa & Smith, 2004), thelodonts (Karatajūtė-Talimaa, 1978; Žigaitė, 2004, personal data), and possible eryptychiids (Karatajūtė-Talimaa *et al*., 1990).

The taxonomic content and distribution of six of these lower Silurian vertebrate groups (acanthodians, chondrichthyes, putative galeaspids, mongolepids, tesakoviaspids and thelodonts) are discussed below. The provisional record of heterostracans, possible astraspids and eriptychiids (Karatajūtė-Talimaa *et al*., 1990;

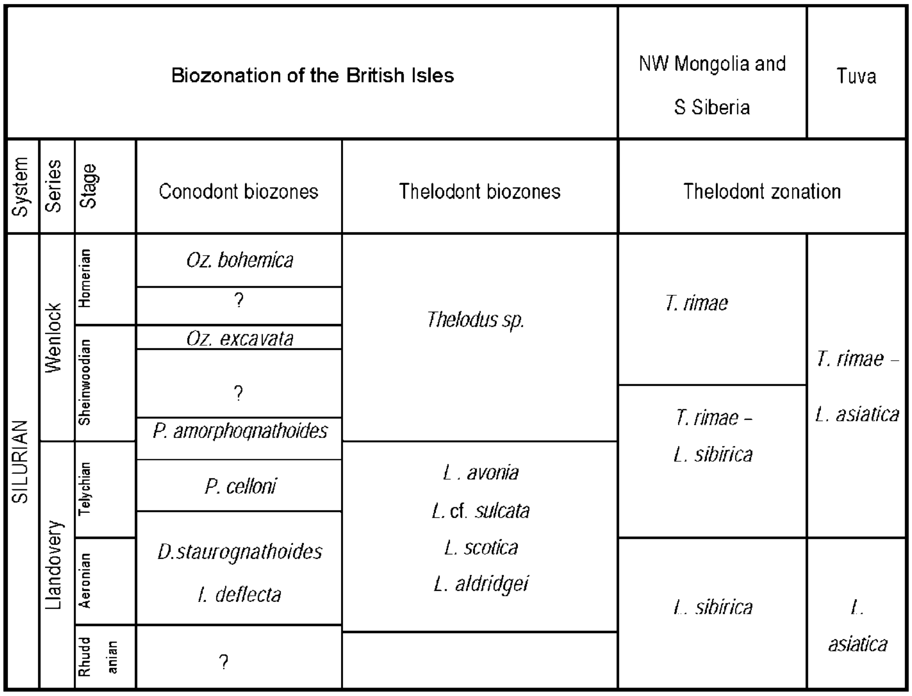

Fig. 3. Biostratigraphical distribution of the lower Silurian thelodonts from southern Siberia, Tuva and northwestern Mongolia, in comparison with the Lower Silurian vertebrate biozonation of the British Isles (Märss *et al*., 2007).

Karatajūtė-Talimaa & Predtechenskyj, 1995; Karatajūtė-Talimaa & Smith, 2003) is not explored further in this work, as these findings have not yet been properly described (work in progress). The possible appearance of unidentified osteostracans in the uppermost Wenlock-Ludlow sections (upper Dashtygoi Formation) of Tuva must be confirmed (Karatajūtė-Talimaa & Ratanov, 2002). However, fossil remains of osteostracan dermoskeleton are common in the upper Silurian deposits of the region, as well as in adjacent localities of the Lower Devonian (Afanassieva & Janvier, 1985; Sansom *et al*., 2008).

The vertebrate-yielding sections are also rich in invertebrate fossils, tabulate and rugose corals in particular. An endemic brachiopod assemblage known as the '*Tuvaella* fauna' is of great palaeobiogeographical importance. It is a relatively low-diversity, shallow-water benthic fauna, dominated by its eponymous brachiopod *Tuvaella plana*, and also includes the genera *Elegesta*, *Tuvaerhynchus* and *Lenatoechia* (see Vladimirskaya *et al*., 1986; Karatajūtė-Talimaa *et al*., 1990; Minjin, 2001). Siberia (including peri-Siberia and the territories of Tuva and northwestern Mongolia) is the only palaeocontinent where this distinctive *Tuvaella* fauna has been found (Cocks & Torsvik, 2007). Conodonts have been reported from the majority of Siberian localities (Tesakov *et al*., 2003), as well as from the Kyzyl-Tchiraa locality in central Tuva (Vladimirskaya *et al*., 1986). The fossil record of vertebrate taxonomic groups and some invertebrates is summarized in Figure 2.

Acanthodians

Acanthodians comprise two endemic genera, *Lenacanthus* Karatajūtė-Talimaa & Smith, 2003 and *Tchunacanthus* Karatajūtė-Talimaa & Smith, 2003, which are restricted to the Lower Silurian of southern Siberia, Tuva and northwestern Mongolia (Karatajūtė-Talimaa, 1997, Karatajūtė-Talimaa & Smith, 2003). *Lenacanthus* Karatajūtė-Talimaa & Smith, 2003 contains one single species, *L. priscus* Karatajūtė-Talimaa & Smith, 2003, and is common in the shallow shelf facies of the Siberian platform although it is absent in lagoon, beach and deltaic facies. Its horizontal distribution is limited to the localities of southern Siberia (Llandovery sections of Pritunguska and Nyuya–Beresovo districts). The genus *Tchunacanthus* is much more widespread and present in nearly all samples analysed (Karatajūtė-Talimaa & Ratanov, 2002; Karatajūtė-Talimaa & Smith, 2003), with the exception of the Llandovery sections of Kochumdekh district. It is recorded in a wide range of facies, including the reef crest facies. The main species of *Tchunacanthus* is *T. obruchevi* Karatajūtė-Talimaa & Smith, 2003, common both in Llandovery and Wenlock sequences of southern Siberia and northwestern Mongolia. Another possible species, *Tchunacanthus* sp. indet. Karatajūtė-Talimaa & Smith, 2003, is present in the lower Silurian localities of Tuva.

Chondrichthyans

At least two genera, *Elegestolepis* Karatajūtė-Talimaa, 1973 and *Polymerolepis* Karatajūtė-Talimaa, 1967 (in Obruchev & Karatajūtė-Talimaa, 1967), represent the Lower Silurian chondrichthyans of the region. *Elegestolepis conica* Karatajūtė-Talimaa, 1986 (in Novitskaya & Karatajūtė-Talimaa, 1986) has been described from the Llandovery sections of southern Siberia: the Balturino Formation (Balturino district), the Melichan and the Utakan formations (Nyuya–Beresovo district) and the Omnutakh Formation from the Thurukhansk district (see Karatajūtė-Talimaa & Predtechenskyj, 1995, fig. 8B–F).

The record of a possible new genus of Elasmobranchii was reported from the Nyuya–Beresovo district, Utakan Formation (see Karatajūtė-Talimaa & Predtechenskyj, 1995, fig. 8G–L). Lower Silurian chondrichthyes from Mongolian and Tuvan localities have not been properly identified yet and require further study (see Karatajūtė-Talimaa *et al.*, 1990; Karatajūtė-Talimaa & Ratanov, 2002). Possible new species of *Elegestolepis* and *Polymerolepis* are reported from the uppermost Llandovery–lower Wenlock Chargat Formation in northwestern Mongolia (Karatajūtė-Talimaa *et al.*, 1990), and another undetermined species of *Polymerolepis* from the Llandovery (Angatchi Formation) of central Tuva (Karatajūtė-Talimaa & Ratanov, 2002). Possible *Elegestolepis grossi*?, together with possibly two new species of genera *Elegestolepis* and *Polymerolepis*, are recognized from the Wenlock sections of central Tuva, Dashtygoi Fm. (Karatajūtė-Talimaa & Ratanov, 2002). In contrast to the uncertain lower Silurian record, scales of *Tuvalepis schultzei* Žigaitė & Karatajūtė-Talimaa, 2008 have been described from the upper Silurian of the same localities.

Putative galeaspids

Peculiar star-shaped tesserae are abundant in the upper Llandovery of southern Siberia, and might possibly represent a tesserated galeaspid (Karatajūtė-Talimaa & Žigaitė, 2005). Their microremains are common in the brackish lagoonal deposits, as well as deltaic sediments with 'bone-beds' of the Irkutsk Subregion, Ilim and Balturino districts. Some similar tesserae are also reported from the Wenlock of Central Tuva, Dashtygoi Formation (Karatajūtė-Talimaa & Ratanov, 2002). To date, galeaspids are known as early vertebrates with a dermoskeleton of macromeric shield, with occurrences in the Silurian and Devonian of China and Vietnam (Janvier, 1990; Zhu & Janvier, 1998; Wang *et al.*, 2005; Sansom, 2009). Therefore, this taxonomic attribution would have particular palaeogeographical significance, and yet should be regarded with caution.

Mongolepids

Mongolepids are endemic early vertebrates potentially related to chondrichthyans, and palaeogeographically unique to the territory. They were first discovered in the Chargat locality of northwestern Mongolia (Karatajūtė-Talimaa *et al.*, 1990). Mongolepids comprise four genera: *Mongolepis* Karatajūtė-Talimaa & Novitskaya, 1990, *Teslepis* Karatajūtė-Talimaa & Novitskaya, 1992, *Sodolepis* Karatajūtė-Talimaa & Novitskaya, 1997 and *Udalepis* Karatajūtė-Talimaa, 1995. All of them are attributed to the endemic order Mongolepidida Karatajūtė-Talimaa & Novitskaya, 1990, and to the endemic family Mongolepididae Karatajūtė-Talimaa & Novitskaya, 1990. The most common mongolepid species in the region is *Mongolepis rozmanae* Karatajūtė-Talimaa & Novitskaya, 1990. Mongolepid scales vary greatly in size, ranging from 0.4 mm to 3.5 mm in length, and have a particularly complex internal structure of polyodontodia type, with a compositional crown consisting of longitudinal 'odontocomplexes' (Karatajūtė-Talimaa, 1995, fig. 1). Mongolepids are known from the uppermost Llandovery–Wenlock series of northwestern Mongolia, from the Wenlock of central Tuva (Dashtygoi Formation), and from the Llandovery of southernmost Siberia, Ilim and Balturino districts (Karatajūtė-Talimaa *et al.*, 1990; Karatajūtė-Talimaa, 1995).

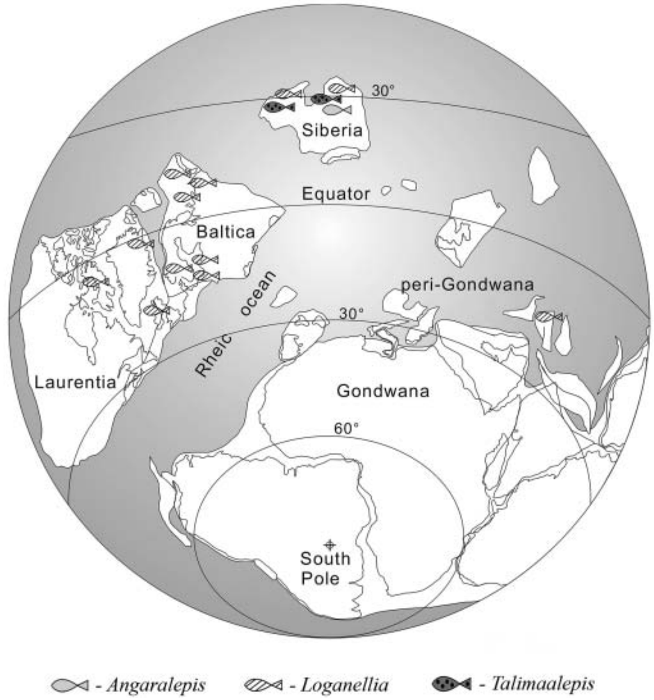

Fig. 4. Palaeogeographical distribution of thelodont genera *Angaralepis* (endemic), *Loganellia* (cosmopolitan) and *Talimaalepis* (endemic) during the early Silurian. Palaeogeography from Cocks & Torsvik (2002), modified after Hairapetian *et al.* (2008).

Tesakoviaspids

The tesakoviaspids are represented by the only described species *Tesakoviaspis concentrica* Karatajūtė-Talimaa & Smith, 2004, attributed to the endemic order Tesakoviaspidida, and endemic family Tesakoviaspididae. Their microremains consist of complex scales and tesserae of cyclomorial growth type and distinctive histology (see Karatajūtė-Talimaa & Smith, 2004). Tesakoviaspids are endemic and, as well as mongolepids, their findings are restricted to this region. Their microremains are known from the upper Llandovery of the Ilim and Balturino districts (Karatajūtė-Talimaa & Predtechenskyj, 1995), and several additional undescribed species have been suggested (Karatajūtė-Talimaa & Smith, 2004).

Thelodonts

Thelodonts are the most common vertebrate microremains of the region and comprise three genera: *Angaralepis*, *Loganellia* and *Talimaalepis*, and six species. *Angaralepis* and *Talimaalepis* are endemic genera, known only from localities in central Asia and southern Siberia, unlike the cosmopolitan *Loganellia*, known world-wide (Fig. 4). *Loganellia* is also the most common among the three genera and is endemic at the species level. It is represented by at least three species: *Loganellia asiatica* (Karatajūtė-Talimaa, 1978), *L. sibirica* (Karatajūtė-Talimaa, 1978), *L. tuvaensis* (Karatajūtė-Talimaa, 1978). *L. tuvaensis* is the only thelodont species restricted to the lower Silurian of central Tuva (Žigaitė & Blieck, 2006). Another species *L. sibirica*, which was not previously reported from the lower Silurian of Tuva (Karatajūtė-Talimaa, 1978), is now confirmed to be also present in the Wenlock sections of Kadvoj locality

(Žigaitė, personal data). Scales which could be attributed to *Loganellia scotica* (Traquair, 1898) have not been recognized in the lower Silurian of southern Siberia during the recent examination of collections (Žigaitė, personal data), although they were reported in the early descriptions of vertebrate microremains from the region (Karatajūtė-Talimaa, 1978). Further investigations may possibly clarify this species record. *Angaralepis* is a monospecific genus, represented by *Angaralepis moskalenkoae* (Karatajūtė-Talimaa, 1978; 1997), and the genus *Talimaalepis* contains two species (Žigaitė, personal data): *Talimaalepis kadvoiensis* (Karatajūtė-Talimaa, 1978) and *T. rimae* Žigaitė, 2004.

Angaralepis and *Loganellia* are common in shallow-water sediments, such as shallow shelf, marine delta and brackish lagoon facies, and have earlier stratigraphic occurrences than the younger *Talimaalepis*, which is recorded in both shallow and deeper shelf sediments. It is worth noting that the internal structure of *Angaralepis* and *Loganellia* scales is less complex than that of *Talimaalepis* (Žigaitė, 2004; Märss *et al*., 2007; Žigaitė, personal data). *Angaralepis*, with its single species *A. moskalenkoae*, is attributed to the order Sandiviiformes, while *Loganellia* and *Talimaalepis* supposedly both belong to the order of Loganelliiformes (Märss *et al*., 2007; Žigaitė, 2004).

To summarize, the three most abundant and taxon-rich vertebrate groups in the studied region are acanthodians, thelodonts and mongolepids. Therefore, special attention should be given to their stratigraphical distribution and role in palaeobiogeographical reconstructions. A possible new record of tesserated galeaspids (Karatajūtė-Talimaa & Žigaitė, 2005; work in progress), if confirmed, would serve as extremely important palaeobiogeographical evidence in discussions of the palaeolocations of the Siberia and North China terranes (see 'Palaeobiogeography' section below).

BIOSTRATIGRAPHY

Biostratigraphically, thelodonts appear to be the most significant vertebrate group due to their taxonomic variety and the abundance of their microfossils. Thereby, we have used their species stratigraphic distributions to create vertebrate biozones for northwestern Mongolia, Tuva and southern Siberia (Fig. 3), in parallel with the established vertebrate biozonation of the British Isles (see Märss & Miller, 2004; Märss *et al*., 2007). The stratigraphical level of appearance, as well as abundance of different thelodont taxa are both comparatively early in comparison to the corresponding data from the other early Silurian palaeobiogeographical provinces, such as the European–Russian province, the Acadian–Anglo-Welsh province (Fig. 3), and the Canadian Arctic province (Karatajūtė-Talimaa & Brazauskas, 1994; Märss & Miller, 2004; Märss *et al*., 2002, 2006). *Angaralepis* and *Loganellia* have a stratigraphically earlier appearance than *Talimaalepis*, which has a later first occurrence in all the localities studied. Three biozones of *L. sibirica*, *T. rimae–L. sibirica* and *T. rimae* are suggested for the territory of northwestern Mongolia and southern Siberia and only two biozones, *L. asiatica* and *T. rimae–L. asiatica*, for central Tuva (Fig. 3). This biostratigraphical distinction between the two regions may have considerable palaeogeographical implications (see the following 'Palaeobiogeography' section).

PALAEOBIOGEOGRAPHY

The horizontal (palaeogeographical) versus vertical (biostratigraphic) distribution of vertebrate taxa in the lower Silurian of the Siberian–Tuvan region implies a certain degree of connection between the different parts of the area. All the taxa discussed above – acanthodians, mongolepids and tesakoviaspids, in particular – show some degree of endemicity, which indicates a degree of palaeobiogeographical isolation and unity of the territory as a whole. The taxonomic composition of the late Silurian vertebrates known from this territory (including macrofossil vertebrates) appears to be distinct and also palaeogeographically restricted to the region (see Karatajūtė-Talimaa, 1978; Afanassieva & Janvier, 1985; Žigaitė, 2004; Žigaitė & Blieck, 2006; Žigaitė & Karatajūtė-Talimaa, 2008).

The limited occurrence of the thelodont *Loganellia tuvaensis*, which is known only from Wenlock to Pridoli deposits of central Tuva, indicates some degree of isolation of the Tuvan palaeobasin in relation to the other epicontinental palaeoseas of the Siberian palaeocontinent. In addition, the southernmost Siberian localities contain some characteristic vertebrates, such as the acanthodian *Lenacanthus*, which is limited to the Llandovery sections of Pritunguska and Niuya–Beresovo districts (Karatajūtė-Talimaa & Smith, 2003), and tesakoviaspids together with tesserae of possible galeaspids, both known only from the Ilim and Balturino districts (Karatajūtė-Talimaa & Žigaitė, 2005). These data support the interpretation of the Tuva terrane as a northern accretionary wedge, situated more or less separate from the main Siberian palaeocontinent (Fortey & Cocks, 2003).

However, the palaeobiogeographical distribution of the other early Silurian vertebrate taxa, such as thelodonts or chondrichthyans, suggests a joined Tuva–northern Mongolia–southern Siberia palaeobasin. For example, the presence of *Talimaalepis* in virtually all the localities studied is an indication of well-connected early Silurian epicontinental seas within the region. In addition, the palaeogeographical range of *Loganellia sibirica* has been revised in this work, and may also serve as more evidence for the existence of a united palaeobiogeographical province for the territory. This new record of *L. sibirica* in the lower Silurian of Tuva, together with its records in northwestern Mongolia and southern Siberia, supports the model of the region being a united Siberian terrane in the early Silurian.

In terms of palaeobiogeographical context other than vertebrates, it should be noted that cyrtophyllid corals, known elsewhere only from Siberia, the Ural Mountains, northeastern Russia and possibly Canada, are widely distributed in the Upper Ordovician of Mongolia (Tesakov *et al*., 2003). The distribution of the distinctive brachiopod *Tuvaella* and related low-diversity species (known as *Tuvaella* fauna) in the Silurian of the region, including also modern Altai-Sayan, many parts of northern and central (but not southernmost) Mongolia, and northwestern parts of China (Xinjiang, Heilongjiang and Inner Mongolia provinces), plays an important role confirming the palaeogeographical isolation and unity of the Siberian palaeocraton (Rong & Zhang, 1982; Rozman, 1986; Minjin, 2001; Cocks & Torsvik, 2007). Brachiopods are among the most palaeogeographically significant benthic invertebrates in the Palaeozoic; therefore, their distribution and endemism is a strong palaeobiogeographical argument for connected Siberian seas in the Silurian.

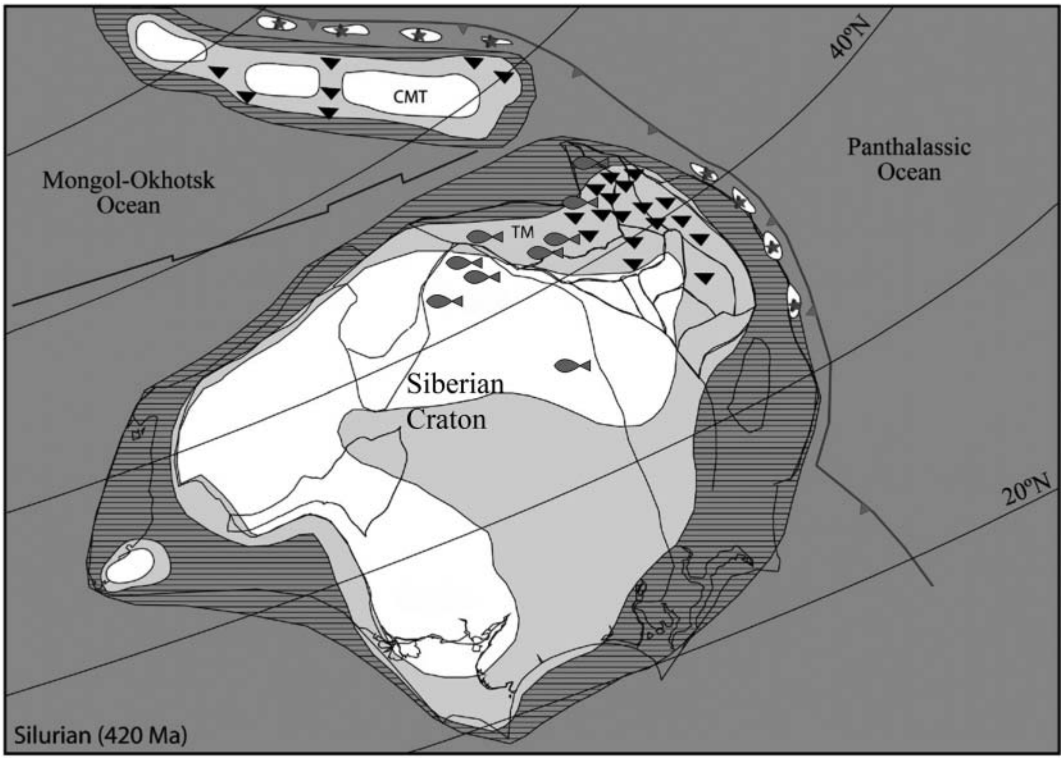

Fig. 5. Palaeogeographical map of the Siberian terrane and adjacent area during the Silurian at about 420 Ma. Inverted black triangles show the distribution of the *Tuvaella* fauna, and white fish indicate the localities where endemic Silurian early vertebrates have been recorded. TM, Tuva–northwestern Mongolia Terrane area; CMT, Central Mongolian Terrane assemblage. White, land; light grey, shallow shelf; horizontal shading, deep shelf; dark grey, ocean; stars, volcanoes; line with triangles, subduction zone; broken line, spreading ridge. Modified and supplemented after Cocks & Torsvik (2007).

It should be noted that later in the Silurian some vertebrate species discussed above seem to extend the limits of this palaeobiogeographical province, breaking the former isolation. An example would be the record of the thelodont *Loganellia* cf. *L. tuvaensis* in the Upper Silurian–Lower Devonian (Pridoli–Lochkovian) of North Greenland (Chester Bjerg Formation, Halls Grav and Monument localities, Hall Land; Turner & Peel, 1986; Blom, 1999). After detailed morphological and histological studies of the microremains (Žigaitė, personal data), *L.* cf. *L. tuvaensis* from North Greenland shows close morphological similarities to *L. tuvaensis* from central Tuva, described by Blom (1999) (see also Žigaitė & Blieck, 2006; Žigaitė, personal data). These two records of *L. tuvaensis* and *L.* cf. *L. tuvaensis* are particularly important concerning global Silurian palaeogeography, and may indicate that the Siberian palaeocontinent approached northeastern Laurentia at the end of the Silurian period, with its northern border from the west. Wider occurrence of *L. tuvaensis* would also infer further palaeobiogeographical connections with the Mixed Canadian Arctic–European Russian Province (Žigaitė & Blieck, accepted) during the late Silurian. The proximity of Siberia and Laurentia palaeocontinents has already been postulated in previous works, Laurentia facing and approaching the Siberian palaeocontinent during the Silurian (McKerrow *et al.*, 1991; Torsvik *et al.*, 1996; Cocks & Torsvik, 2002; Žigaitė & Blieck, 2006).

DISCUSSION

In the early Silurian, the Siberian terrane is interpreted to have been located entirely in the Northern Hemisphere, and continued to move northwards (Cocks & Torsvik, 2007). Widespread red gypsiferous marls and gypsum beds, representing much of the lower Silurian deposits in the area (Tesakov *et al.*, 2003), together with palaeomagnetic data (Cocks & Torsvik, 2007), witness Siberia's movement into more temperate palaeolatitudes, and also reflect the aridification of the climate. Extensive shallow-water siliciclastic sequences of the Tuva–Mongolia area may also indicate lower average seawater temperatures in the northern part of the terrane (Cocks & Torsvik, 2007). Consequently, Siberia has been suggested to be a northern terrane in the Silurian, with the characteristic high-latitude cold-water *Tuvaella* faunal assemblage (see Cocks & Torsvik, 2007).

Such cold-water palaeobasins do not, however, accord with the abundant and diverse Silurian vertebrates recorded in the region (see Fig. 2). The taxonomically rich vertebrate microfossil record in the localities studied contrasts with the low-diversity benthic invertebrate fauna. Notably, vertebrate fossils are also numerous in the late Silurian-age samples of the same localities of central Tuva (Karatajūtė-Talimaa & Ratanov, 2002; Žigaitė & Karatajūtė-Talimaa, 2008). A number of vertebrate species have relatively early Early Silurian stratigraphic occurrences (Fig. 3). This is despite the palaeoseas being reconstructed as at relatively high latitudes, at the northern margin of the Siberian palaeocontinent (Fig. 5). Therefore, high-latitude palaeobasins with abundant early Silurian vertebrates look very unusual with respect to other early Palaeozoic rich shelf faunal assemblages from a number of low-latitude palaeobiogeographical provinces (Žigaitė & Blieck, accepted). This contradiction may question the current interpretation of Siberia as a northern terrane during the Silurian (Cocks & Torsvik, 2007). Lower-latitude (and presumably warmer) palaeobasins could have existed on the Siberian palaeocontinent at the given time, if we consider its drift through the palaeoequator not only during the Ordovician (Cocks & Torsvik, 2002, 2007), but during the early Silurian as well. A possible deeper-water marine environment, which might have favoured biodiversity of the early Silurian fish but not that of benthic invertebrates such as brachiopods, would be another scenario explaining this discrepancy.

Following our review of the distribution of vertebrate microremains in the lower Silurian of northwestern Mongolia, Tuva and southern Siberia, we suggest an endemic and externally isolated early Silurian palaeobiogeographical province. This supports recent palaeogeographical interpretations of connected epeiric seas of the Siberian terrane during the Silurian, made by Cocks & Torsvik (2007). However, separate palaeogeographical provinces of Tuva and Siberia have been suggested for the early Silurian in previous works (Blieck & Janvier, 1991; Fortey & Cocks, 2003). Our study of the lower Silurian vertebrate record of the area, thelodonts and acanthodians in particular, infers the presence of intraconnected palaeoseas during the Llandovery and Wenlock (Figs 4, 5). For example, new findings of *Loganellia sibirica* scales, recently discovered in the lower Llandovery and upper Wenlock of central Tuva (Žigaitė, personal data), refute the previously reported palaeobiogeographical restriction of this species to the lower Silurian of Mongolia and southern Siberia (Žigaitė & Blieck, 2006) and indicate a united palaeobasin.

To conclude, the lower Silurian vertebrate microfossil record of the region supports the hypothesis of a unified Siberian terrane with connected epeiric palaeoseas. We also think that differences in a few taxa provide insufficient evidence in this case to separate the Tuvan and Siberian palaeobiogeographical provinces (Westermann, 2000; Cecca & Westermann, 2003; Servais & Sintubin, 2009; Žigaitė & Blieck, accepted). Taking this and other palaeofaunal distribution data (Cocks & Torsvik, 2007) into account, we refute the former distinction of two biogeographical provinces in the region during the early Silurian (Žigaitė & Blieck, 2006) and propose a single unified Siberian–Tuvan palaeobiogeographical province.

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