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Docteur de l'Université de Sciences et Technologies de Lille,
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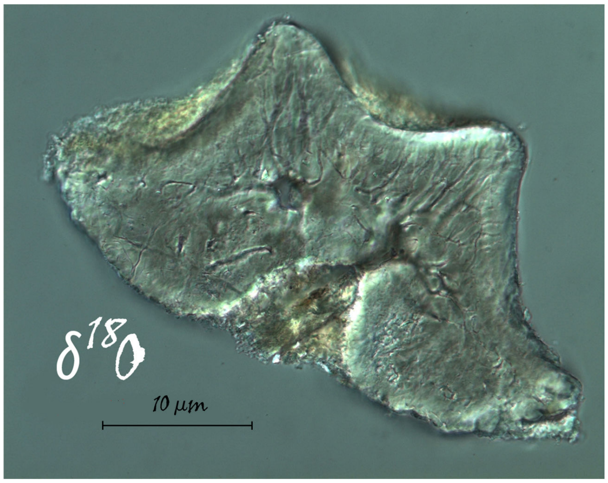
Discipline: Sciences de la Terre
Spécialité: Géosciences, Ecologie, Paléontologie, Océanographie

L'utilisation des vertébrés du Silurien pour la reconstitution de la paléogéographie et du paléoclimat



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Lille, France

PhD THESIS
for obtaining
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UMR 8157 of CNRS ‹Geosystems›
and
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presented by

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Discipline: Earth Sciences
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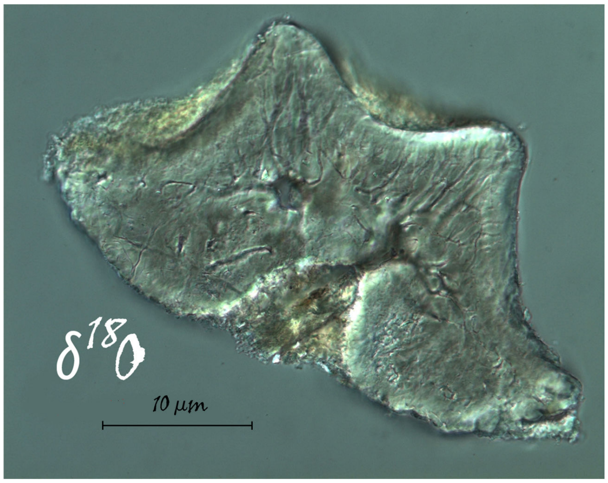
Early Silurian vertebrates as proxies for palaeogeographic and palaeoclimatic reconstructions



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Lille, France

Basic research is what I'm doing
when I don't know what I'm doing.
Werner von Braun (1912-1977)

To Those Who
have brought me up
as a person
and as a researcher

"Early Silurian vertebrates as proxies for palaeogeographical and palaeoclimatic reconstructions"
Ž. Žigaitė

ABSTRACT

The Silurian is a period of marine vertebrate outspread and diversification. Early vertebrate disarticulated exoskeleton microremains are common microfossils in the Silurian shallow water lagoon to open shelf sediments. Many early vertebrates are characterized by persistent taxa and can not be recognized as distinctive biostratigraphical markers, but several taxa with shorter time durations have been used globally to establish a Silurian biostratigraphic scale. Nevertheless they are particularly useful palaeogeographical indicators because of prevailing specific endemism. Moreover, phosphatic dentine scales and tesserae of vertebrates have a high potential in palaeoclimate reconstructions and chemostratigraphy.

Several new early vertebrate taxa (genera and species) from the Lower Silurian of northwestern Mongolia, Tuva and southern Siberia are described in this work; all the thelodont species are revised, redescribed and repictured, and their palaeobiogeographical distribution is analysed. All early vertebrate species studied can be considered as endemic, and indicate an existence of a single palaeobiogeographical province, which also confirms the territory as a unified Siberian palaeocontinent during the Silurian.

Comparative articulated squamation studies are made on seven *Loganellia scotica* specimens from the Lower Silurian of Scotland, a unique caudal squamation pattern is observed.

Early vertebrate microremains from the Lower Silurian of central Asia and southern Siberia, as well as from the Upper Silurian of the Baltic Basin of Lithuania are examined for the oxygen isotope composition. Conodont elements from the corresponding samples are analysed in comparison. The $\delta^{18}O$ values of vertebrate and conodont apatite are obtained from the PO_4^{3-} remnant under chemical treatment of Ag_3PO_4. Vertebrate and coeval conodont $\delta^{18}O_{apatite}$ values revealed show constant discrepancy between the two groups, conodont oxygen isotopic ratios resulting in more realistic palaeoseawater temperature estimations. Well preserved early vertebrate microremains are here considered to be less applicable in palaeoclimate reconstructions, but a promising tool for chemostratigraphy. The first biogenic apatite $\delta^{18}O$ curves are produced for the entire Pridoli section of the Baltic Basin (Lithuania).

The research led to preparation and publication of eight articles attached to the present thesis.

Key words: Silurian, microfossils, early vertebrates, palaeogeography, palaeoclimate, biogenic apatite, oxygen isotopes, chemostratigraphy.

“L’utilisation des vértebrés du Silurien pour la reconstitution de la paléogéographie et du paléoclimat”
Ž. Žigaitė

RÉSUMÉ

Le Silurien est une période d’expansion et de diversification des Vertébrés marins. Les microrestes isolés de l’exosquelette des Vertébrés inférieurs sont des microfossiles fréquents dans les sédiments originaires des environnements peu profonds des lagunes et des plates-formes ouvertes du Silurien. De nombreux Vertébrés inférieurs ont persisté sur de longues périodes de temps et, de ce fait, ne peuvent pas être utilisés en tant que marqueurs biostratigraphiques, mais ils constituent des indicateurs paléogéographiques utiles à cause de leur endémisme. Qui plus est, les écailles et tessères phosphatées de ces Vertébrés, comportant de la dentine, ont un potentiel important pour les reconstitutions paléoclimatiques et la chimiostratigraphie. Néanmoins, un certain nombre de taxons présentant des extensions stratigraphiques plus courtes ont été utilisés au niveau global pour établir une échelle biostratigraphique du Silurien.

Dans ce travail sont décrits plusieurs taxons nouveaux de Vertébrés (genres et espèces) du Silurien inférieur du nord-ouest de la Mongolie, de la région de Touva et du sud de la Sibérie; toutes les espèces de Thélodontes sont révisées, redécrites et refigurées, et leur distribution paléobiogéographique est analysée. Toutes les espèces étudiées peuvent être considérées comme endémiques à la région d’étude ; elles permettent de définir une seule province paléobiogéographique, ce qui confirme le fait que « Siberia » constituait un territoire unifié au Silurien.

Une étude comparée de squamations en connexion est menée à partir de sept spécimens de *Loganellia scotica* du Silurien inférieur d’Ecosse, sur lesquels un patron unique de la squamation de la région caudale a été observé.

Des microrestes du Silurien inférieur d’Asie centrale et du sud de la Sibérie ainsi que du Silurien supérieur du bassin balte en Lithuanie ont été étudiés pour leur composition en isotopes de l’oxygène. Des Conodontes provenant des mêmes échantillons ont été analysés pour comparaison. Les valeurs du $\delta^{18}O$ de l’apatite des Vertébrés et des Conodontes ont été obtenues à partir du PO_4^{3-} présent après un traitement chimique à l’Ag_3PO_4. Les valeurs obtenues pour ce $\delta^{18}O_{apatite}$ montrent des différences constantes entre les deux groupes (Vertébrés et Conodontes), les rapports isotopiques de l’oxygène des Conodontes donnant des résultats plus réalistes pour estimer les paléotempératures de l’eau de mer. Ainsi les microrestes bien conservés de Vertébrés inférieurs sont considérés ici comme moins utilisables dans le cadre de reconstitutions paléoclimatiques, mais ils constituent un outil prometteur pour la chimiostratigraphie. Des courbes de $\delta^{18}O_{apatite}$ d’origine biogénique sont fournies pour la première fois pour l’ensemble du Pridoli du bassin balte en Lithuanie.

L’ensemble de ce travail a conduit à la préparation et la publication de huit articles joints à la présente thèse.

Les mots clés: Silurien, microfossiles, Vertébrés inférieurs, paléogéographie, paléoclimat, apatite d’origine biogénique , isotopes de l’oxygène, chimiostratigraphie.

"Silūro ankstyvųjų stuburinių taikymas paleogeografijos ir paleoklimato rekonstrukcijose"
Ž. Žigaitė

SANTRAUKA

Silūro periodas – ankstyvųjų stuburinių rūšių formavimosi ir išplitimo jūrose laikotarpis. Jų fosilijos dažniausiai sutinkamos jūrinio šelfo ir priekrančių nuosėdinėse uolienose kaip dezintegruoto išorinio skeleto mikroliekanos. Facijinis ankstyvųjų stuburinių paplitimas varijuoja nuo seklių lagūninių iki gilaus atviro šelfo facijų. Silūro stuburiniai pasižymi rūšių ilgaamžiškumu, dėl ko jų gausios mikroliekanos deja negali būti taikomos kaip tikslūs biostratigrafiniai markeriai, nors globali stuburinių bizonų skalė išskirta trumpiau egzistavusių rūšių pagrindu. Tačiau ryškus ankstyvųjų stuburinių endemizmas suteikia jiems itin svarbų vaidmenį paleozojaus paleogeografinėse rekonstrukcijose. Dar daugiau, fosfatinės ankstyvųjų stuburinių mikroliekanos turi dideles potencialaus pritaikymo galimybes paleoklimato rekonstrukcijose bei chemostratigrafijoje.

Šiame darbe aprašytos naujos endeminės ankstyvųjų stuburinių gentys ir rūšys iš apatinio šiaurės-vakarų Mongolijos, Tuvos ir Sibiro platformos silūro; išsamiai peržiūrėta, perfotografuota ir naujai diagnozuota regiono telodontų fosilinė medžiaga, bei ištirtas jų paleobiogeografinis paplitimas. Visos ankstyvųjų stuburinių rūšys minėtame regione priskirtinos endeminėms, ir patvirtina atskiros silūro paleobiogeografinės provincijos egzistavimą, o taip pat analizuojamos teritorijos vientisumą ir nedalomo Sibiro paleokontinento egzistavimą silūro periode.

Lyginamosios išorinių skeletų anatomijos ir žvynų išsidėstymo modelių studijos atliktos lyginant keletą pilnai išlikusių telodonto *Loganellia scotica* fosilijų. Aprašytas naujas unikalus uodegos žvynų išsidėstymo modelis.

Deguonies izotopų sudėtis pirmą kartą analizuota anktyvųjų stuburinių mikroliekanose : centrinės Azijos ir pietų Sibiro apatinio silūro atodangų bei viršutinio Baltijos baseino silūro gręžinių medžiagoje. Palyginimui ištirti konodontų elementai tuose pačiuose pavyzdžiuose. Stuburinių bei konodontų apatito $\delta^{18}O$ vertės buvo nustatomos išskirtinai tik PO_4^{3-} likeanoje, nusodintoje apdorojant mikrofosilijas sidabro fosfatu (Ag_3PO_4). Gautos ankstyvųjų stuburinių ir to paties amžiaus konodontų $\delta^{18}O$ vertės pilnai nesutampa, konodontų apatito deguonies izotopų santykiai palankesni realistiškoms paleotemperatūrų aproksimacijoms. Naudojant konodontų paleotemperatūrų skaičiavimo metodą, stuburinių mikrofosilijos negalėtų būti tiesiogiai taikomos paleoklimato rekonstrukcijoms, tačiau rodo didelį pritaikomumą chemostratigrafijoje. Išskirta pirmoji biogeninio apatito $\delta^{18}O$ kreivė pržidolio serijai Baltijos baseine, Gėluva-99 gręžinio pjūvyje (Lietuva).

Šio daktarinio darbo rezultatai apibendrinti žemiau pateiktose aštuoniose mokslinėse publikacijose.

Raktiniai žodžiai: Silūras, mikropaleontologija, ankstyvieji stuburiniai, paleogeografija, paleoklimatas, biogeninis apatitas, deguonies izotopai, chemostratigrafija.

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Résumé substantiel

Les Vertébrés inférieurs du Silurien tels que les Acanthodiens, les Chondrichthyens, les Galéaspides tessérés, les Hétérostracés, les Mongolépides, les Ostéostracés, les Tésakoviaspides et les Thélodontes sont caractérisés par la présence d'un exosquelette souvent voire toujours composé de nombreuses écailles et tessères contiguës, disposées suivant des patrons morphofonctionnels complexes correspondant aux différentes régions du corps. Ces écailles et tessères sont constituées de tissus minéralisés variés (os, dentine) recouverts parfois d'une fine couche d'émailloïde. Les squelettes fossilisés des Vertébrés inférieurs sont souvent désarticulés et ne sont donc récoltés que sous la forme de microrestes phospatés abondants. Au Silurien, ces microrestes sont récoltés depuis des environnements de type lagunaire jusqu'à des environnements de plates-formes marines ouvertes. De nombreux Vertébrés inférieurs ont persisté sur de longues périodes de temps et, de ce fait, ne peuvent pas être utilisés en tant que marqueurs biostratigraphiques, mais ils constituent des indicateurs paléogéographiques utiles à cause de leur endémisme. Qui plus est, les écailles et tessères phosphatées de ces Vertébrés, comportant de la dentine, ont un potentiel important pour les reconstitutions paléoclimatiques et la chimiostratigraphie. Néanmoins, un certain nombre de taxons présentant des extensions stratigraphiques plus courtes ont été utilisés au niveau global pour établir une échelle biostratigraphique du Silurien.

Les Vertébrés inférieurs, et en particulier les Thélodontes, du Silurien inférieur d'Asie centrale (nord-ouest de la Mongolie et région de Touva) et du sud de la plate-forme sibérienne ont été étudiés en détail. Le matériel de Thélodontes a été attribué à deux familles, les Angaralepididae MÄRSS & KARATAJUTE-TALIMAA et les Loganelliidae (*sensu* KARATAJUTE-TALIMAA, 1978 emend. KARATAJUTE-TALIMAA, 1997) ; trois genres *Angaralepis* MÄRSS & KARATAJUTE-TALIMAA, 2002, *Loganellia* FREDHOLM, 1990, et *Talimaalepis* ŽIGAITE, 2004; et six espèces : *A. moskalenkoae* (KARATAJUTE-TALIMAA, 1978), *L. asiatica* (KARATAJUTE-TALIMAA, 1978), *L. sibirica* (KARATAJUTE-TALIMAA, 1978), *L. tuvaensis* (KARATAJUTE-TALIMAA, 1978), *T. rimae* ŽIGAITE, 2004, et *T. kadvoiensis* (KARATAJUTE-TALIMAA, 1978) ŽIGAITE 2004 comb. nov. Toutes les descriptions précédentes de Thélodontes de cette région ont été revues et corrigées et le matériel a été refiguré. Du matériel complémentaire a été décrit et illustré. En dehors des Thélodontes, a été décrit un nouveau genre / nouvelle espèce particulière de Chondrichthyen de la transition Silurien-Dévonien de la Touva : *Tuvalepis schultzei* ŽIGAITE & KARATAJUTE-TALIMAA, 2008. La répartition paléobiogéographique de tous les taxons a été analysée en détail, en y incluant les informations issues des travaux précédents. Toutes les espèces étudiées peuvent être considérées comme endémiques à la région d'étude; elles permettent de définir une province paléobiogéographique séparée. Leur répartition conduit à prendre en compte l'existence au Silurien d'un paléocontinent « Siberia » unifié couvrant l'ensemble de la région étudiée ici.

Une étude comparée de squamations en connexion a été menée à partir de sept spécimens de *Loganellia scotica* du Silurien inférieur de Lesmahagow, dans le sud de l'Ecosse. Le rapport moyen permettant d'estimer la longueur totale du corps de *L. scotica* à partir de la largeur de son pédoncule caudal a été établi sur la base des mesures faites sur 11 spécimens complets ; il a été utilisé pour évaluer de façon approximative les longueurs corporelles d'individus incomplets. La longueur totale du corps du spécimen le plus grand qui ait conservé les parties précaudale et caudale de l'exosquelette a été évaluée à au moins 450 mm, ce qui dépasse largement la longueur maximale estimée jusqu'à présent pour l'espèce *L. scotica*. Tous les patrons de la squamation ont été décrits et figurés. Le patron de type rostral a été retrouvé sur *L. scotica* contrairement à ce que laissaient penser les descriptions les plus récentes de l'espèce. Un schéma de distribution unique de la région caudale (pinnale) a été observé sur un spécimen: il présente au moins 20 longs rayons de la nageoire, bifurquant seulement à partir du lobe hypocerque au sein de la palette natatoire caudale. De façon générale, lorsqu'on analyse l'assemblage des microrestes de Vertébrés inférieurs, on devrait toujours prendre en considération les patrons de l'écaillure (squamation) parce qu'un seul échantillon de roche peut très bien renfermer les écailles et tessères de plusieurs espèces différentes mais aussi des éléments d'âges ontogénétiques différents, d'animaux de tailles adultes différentes, et de différentes régions du corps pour chacune des espèces concernées.

La stratigraphie séquentielle et le contexte tectonique du Silurien du bassin balte ont été revisés dans le cadre d'une étude collective. La tendance générale qui a été dégagée à partir du schéma de stratigraphie séquentielle indique une régression en relation avec le dépassement de la production sédimentaire et la progradation de la plate-forme carbonatée à la périphérie du bassin balte au Silurien. L'absence de toute déformation tectonique après le Silurien a permis la conservation des sédiments en position subhorizontale avec un gradient thermique très faible.

Des microrestes du Silurien inférieur d'Asie centrale et du sud de la Sibérie ainsi que du Silurien supérieur (Pridoli) du bassin balte en Lithuanie ont été étudiés pour leur composition en isotopes de l'oxygène. La série du Pridoli du bassin balte a été privilégiée pour trois raisons : 1) l'état de conservation relativement bon des microfossiles, 2) l'absence de connaissance des courbes du $\delta^{18}O_{apatite}$ et du $\delta^{18}O_{calcite}$ pour ce Pridoli des régions baltes, et 3) la co-occurrence des Conodontes dans les échantillons à Vertébrés, en quantité suffisante pour permettre une analyse isotopique.

Des travaux antérieurs ont suggéré que l'apatite des Conodontes a un fort potentiel de rétention de l'information chimique primaire de l'eau de mer : elle est secrétée en quasi-équilibre avec l'eau de mer environnante par comparaison avec les autres apatites biogéniques et elle conserve mieux le rapport isotopique de l'oxygène. L'ultrastructure microcristalline dense de la dentine et de l'émailloïde des Vertébrés inférieurs a des propriétés physicochimiques comparables à celles des tissus coronaux des Conodontes. L'objectif principal de la présente étude était d'examiner l'apatite fossile des Vertébrés en tant qu'enregistreur et « proxy » paléoenvironnemental par comparaison avec les Conodontes. C'est la 1ère fois que des microrestes de Vertébrés étaient testés en matière de $\delta^{18}O$ dans ce contexte.

Les valeurs du $\delta^{18}O$ des Vertébrés et des Conodontes ont été obtenues à partir du PO_4^{3-} présent (supposé dépendre de la composition et de la paléotempérature de l'eau de mer environnante) après un traitement chimique à l'Ag_3PO_4. Les valeurs du $\delta^{18}O_{apatite}$ des Conodontes pour le Silurien supérieur du bassin balte varient de 17,7 à 19,2‰ V-SMOW, avec des valeurs moyennes autour de 18,3‰ tandis que les valeurs contemporaines du $\delta^{18}O_{apatite}$ des Vertébrés sont décalées de 2,5‰ V-SMOW, entre 15,2 et 17,4‰ V-SMOW, avec des valeurs moyennes autour de 16,3‰ V-SMOW.

Les paléotempératures de l'eau de mer ont été calculées: 1) en partant de l'hypothèse que la composition isotopique en oxygène de cette eau au Silurien était de –1‰ V-SMOW, comme celle qui est supposée pour la période chaude (« greenhouse ») du Dévonien, en considérant que les eaux océaniques de basses latitudes du bassin balte au Silurien supérieur étaient chaudes, et 2) en utilisant l'équation suivante :

$$T[°C] = 113,3 – 4,38 (\delta^{18}O_{apatite} - \delta^{18}O_{eau\ de\ mer})$$

KOLODNY et al., 1983.

Les paléotempératures de l'eau de mer pour le Pridoli, déduites de l'apatite des Conodontes, varient de 24,8 à 31,5 °C ; celles qui sont déduites de l'apatite des Vertébrés inférieurs sont approximativement supérieures de 10 °C : elles varient de 32,6 à 38,1°C. Les valeurs du $\delta^{18}O_{apatite}$ des Vertébrés et des Conodontes montrent un écart constant de 2,5‰ V-SMOW, ce qui conduit à un ΔT moyen d'environ 10°C (entre 9,4°C et 11,6°C) ; cet écart ne peut pas être expliqué de façon satisfaisante. Le fait que les valeurs du $\delta^{18}O_{apatite}$ des Conodontes fournissent des paléotempératures plus réalistes suggère que les éléments isolés des Conodontes enregistrent plus fidèlement les paléotempératures du Paléozoïque que ceux des Vertébrés. Cependant, le fait que l'écart observé de 2,5‰ V-SMOW entre Conodontes et Vertébrés est constant tout au long de la série étudiée et le fait que la tendance générale des deux courbes obtenues est similaire suggèrent que les deux groupes d'organismes enregistrent les mêmes changements environnementaux du Silurien supérieur. (Une autre hypothèse serait que l'ultrastructure fine des Conodontes et des Vertébrés est suffisamment différente pour enregistrer de façons distinctes les variations de l'environnement)

La 1ère courbe des variations du $\delta^{18}O_{apatite}$ des Conodontes a ainsi été obtenue pour le Pridoli du bassin balte à partir des données du sondage Gėluva-99. Un décalage (« shift ») significatif vers des valeurs basses du $\delta^{18}O_{apatite}$ est observé entre les profondeurs 696 m et 687 m, avec un rapport isotopique décroissant de 1,1‰, de 18,1 à 19,2‰ V-SMOW, correspondant aux valeurs minimales de ce $\delta^{18}O_{apatite}$ des Conodontes analysés dans le présent travail. La valeur négative maximale du $\delta^{18}O_{apatite}$ a été enregistrée 0,2 m en dessous de la limite inférieure de la Formation Lapės, dans la partie sommitale de la Formation Vievis, à – 687 m (Fig. 1). Cette « excursion » négative des courbes de l'apatite à la fois des Vertébrés et des Conodontes est en excellent accord avec la chute connue du niveau marin pour le Pridoli moyen; ceci peut s'interpréter en terme de changement de faciès sédimentaire depuis des faciès marginaux (dolomies à gypse) vers des faciès de plate-forme peu profonde (calcaires détritiques organogéniques) correspondant à la transition entre la Formation Vievis et la Formation Lapės. Une chute significative d'environ 5 °C de température de l'eau de mer peut ainsi être estimée au passage entre Formation Vievis et Formation Lapės, soit entre – 696 m (29,5°C) et – 687 m (24,8°C), interprété en terme de refroidissement climatique.

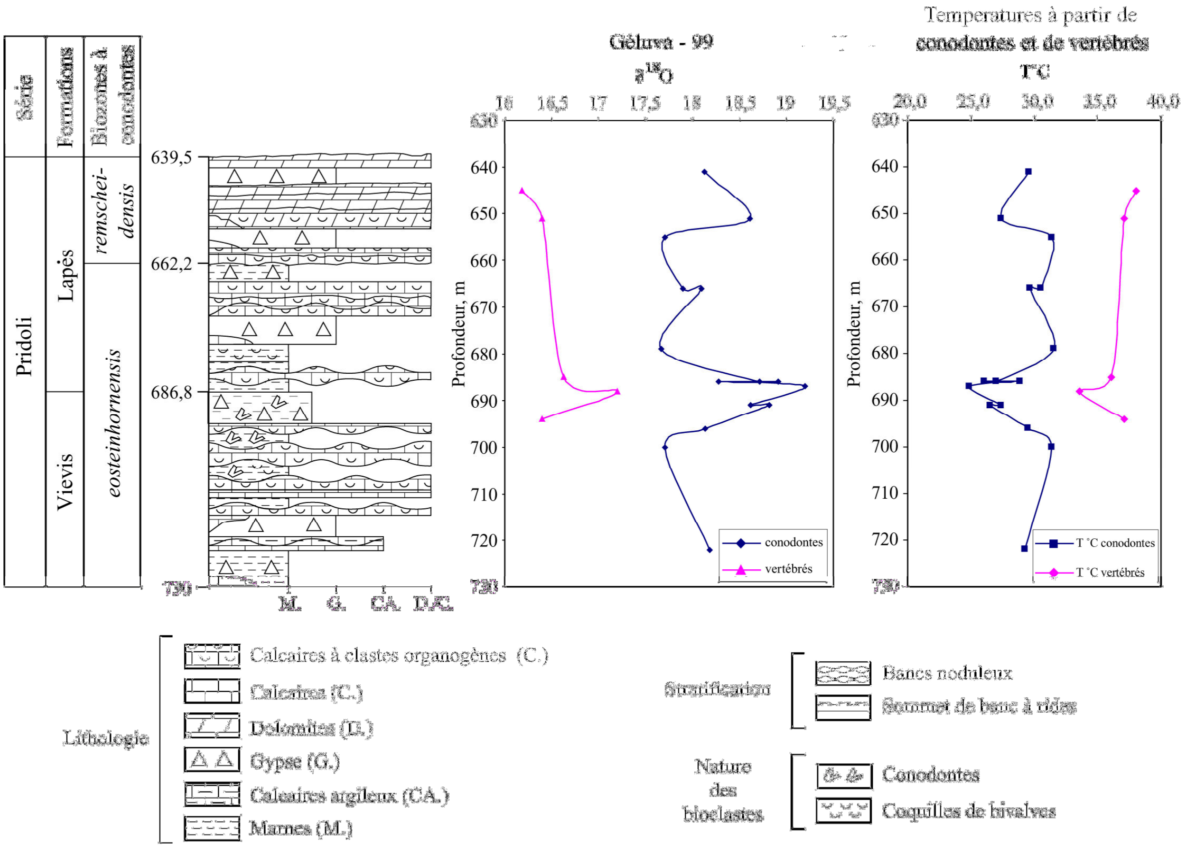

Fig. 1- Comparaison des valeurs mesurées du $\delta^{18}O_{apatite}$ et des paléotempératures (T °C) estimées à partir des Vertébrés inférieurs et des Conodontes du Silurien supérieur (Pridoli) de la coupe du sondage Gèluva-99, dans la zone faciétale centrale du bassin balte en Lithuanie.

Le $\delta^{18}O_{apatite}$ des Vertébrés a également été mesuré dans un certain nombre d'échantillons du Silurien inférieur d'Asie centrale (nord-ouest de la Mongolie, Touva) et du sud de la Sibérie. Différents groupes de Vertébrés ont été testés séparèment (Acanthodiens, Chondrichthyens, Galéaspides, Hétérostracés, Thélodontes). Malheureusement ce matériel n'a pas donné de résultats satisfaisants : les valeurs du $\delta^{18}O_{apatite}$ obtenues apparaissent trop faibles pour aboutir à des évaluations réalistes des paléotempératures de l'eau de mer. Ces valeurs du $\delta^{18}O_{apatite}$ varient de 11,0 à 16,4‰ V-SMOW en fonction des différentes localités, avec une valeur moyenne de 14,2‰ V-SMOW. Dans la plupart des échantillons étudiés, les écailles de Vertébrés ne présentent pas de bons critères de conservation en terme de couleur et de texture, ce qui implique qu'elles ont subi des altérations diagénétiques thermiques. Les valeurs du $\delta^{18}O_{apatite}$ des Vertébrés du Silurien inférieur d'Asie centrale ne pourraient être considérées comme raisonnables que si on suppose que ces Vertébrés étaient des habitants d'eaux saumâtres ($\delta^{18}O_{eau} = +5$), ce qui n'est pas l'hypothèse retenue pour les groupes d'organismes étudiés.

En résumé, les courbes concomittantes des valeurs du $\delta^{18}O$ des apatites de Vertébrés et de Conodontes peuvent être utilisées non seulement pour des reconstitutions paléoclimatiques, mais aussi pour des corrélations inter-régionales et globales (chimiostratigraphie et stratigraphie séquentielle). Les paléotempératures calculées à partir des valeurs du $\delta^{18}O_{apatite}$ des Conodontes indiquent que : 1) l'hypothèse d'une valeur du $\delta^{18}O_{eau}$ de l'eau de mer au Pridoli de –1‰ V-SMOW est relativement réaliste, et 2) un événement de refroidissement significatif est intervenu au milieu du Pridoli ; cet événement coïncide avec un changement de faciès observé à une limite de formations dans le bassin balte. Néanmoins, au terme de cette étude-ci, les microrestes bien conservés de Vertébrés sont considérés comme d'usage moins fiable pour les reconstitutions paléoclimatiques bien qu'ils constituent un outil prometteur de chimiostratigraphie.

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Contents

Introduction

Generally warm Silurian climate and favourable palaeogeography with major cratonic areas concentrated close to the Equator, allowed extensive worldwide deposition of carbonates in tropical shelf-seas, which were starting to be amply inhabitated by the earliest marine vertebrates. Early vertebrates comprise the fossil Palaeozoic vertebrates, which lived from about 470 Ma to 250 Ma ago (JANVIER, 1996). Silurian early vertebrates include jawless anaspids, heterostracans, galeaspids, osteostracans and thelodonts, as well as jawed acanthodians, chondrichthyans and placoderms. Their phosphatic exoskeleton was composed of separated contiguous scales and tesserae, or amalgamated bone plates, and served as a protection and body armature. In Silurian early vertebrates are most commonly preserved in shallow to deep shelf sediments as disarticulated macro or microfossils.

The Silurian is supposed to be a period of predominantly warm climate, with exceptions of few colder intervals, most of which are recorded chemostratigraphically as isotopic record anomalies (MUNNECKE et al., 2003; LEHNERT et al., 2007; VERNIERS et al., 2008). The only facial evidence would be the Wenlock tillite records, confirming the Early Silurian glaciation (CAPUTO, 1998; DIAZ-MARTINEZ et al., 2001). Absence of any ice-cover traces later in the Silurian tends to favour greenhouse climate conditions. However, several prominent isotope anomalies together with coeval biostratigraphical events and sea-level changes, are reported throughout the Silurian, and several glaciations may be suggested (LEHNERT et al., 2007; VERNIERS et al., 2008; ERIKSSON & CALNER, 2008). Still, the climate of the latest Silurian remains undetermined, and no sufficient global eustatic signature has been defined for the Pridoli series, because of the lack of data (VERNIERS et al., 2008).

Therefore, the Pridoli section of the Baltic Basin has been chosen for the fundamental palaeoclimate reconstructions via $\delta^{18}O$ isotope analysis of biogenic apatites. A number of chemostratigraphical analyses on carbon ^{13} C and oxygen ^{18}O isotopes have been made within the Llandovery to Ludlow successions of the Baltic Basin, including biogenic apatite studies, e.g., Gotland in Sweden (WENZEL et al., 2000; MUNNECKE et al., 2003), and some localities in Estonia and Lithuania (MARTMA et al., 2005). However, Pridoli series is not preserved on Gotland, and in the uppermost Silurian of Lithuania it has not yet been sufficiently chemostratigraphically elaborated. The main advantage of the Baltic Basin is an almost complete Silurian succession, which is rich in vertebrate and conodont microfossils, and has undergone negligible tectonic deformation after the Silurian, with sediments preserved mostly subhorizontally stratified (VERNIERS et al. 2008). Subsequently these strata have permeated through a very low heating, preventing fossil material from redundant thermal alteration, which is a crucial condition to obtain primary isotope composition and reliable palaeoseawater temperature estimations. The continuous carbonate succession of the Baltic Basin should also be a perfect sedimentary environment for chemostratigraphy, because of shallow shelf limestone facies, which are supposed to give more exact isotope records than clayish deep sea sequences.

The oxygen isotope values are first revealed from the early vertebrate biogenic apatite in this work, and produce the first $\delta^{18}O$ curve for the Pridoli of the Baltic Basin. The $\delta^{18}O$ analysis has been chosen for palaeoclimatic reconstructions, because the PO_4^{3-} remnant of biogenic apatites respond sensitively during their formation to the aqueous environment: phosphatic tissues obtain $^{18}O/^{16}O$ ratio very close to that of the ambient sweater, and then retain their record perfectly after, during the fossilization (KOLODNY et al., 1983; PUCÉAT et al., 2004). Previous studies have shown the conodont apatite as a reliable proxy for high-resolution palaeotemperature curve reconstruction (JOACHIMSKI & BUGGISH, 2002; JOACHIMSKI et al., 2003, 2004). Accordingly, early vertebrate apatite tissues might have the properties required for an ideal geochemical recorder as well, and have been selected for isotope treatment for several reasons as follows: 1) they consist of carbonate-fluor apatite, while fossil biogenic apatites are considered the best material for oxygen isotope ratio measurements and palaeoseawater tremperature estimations; 2) early vertebrate dentine and enameloid are compact tissues, close in ultrastructure to the crown tissues of conodont elements, which are supposed to retain primary oxygen isotope ($\delta^{18}O$) signature very well, and serve as ideal proxies for palaeoenvironmental studies; 3) abundand early vertebrate microremains in the Silurian successions of the Siberian platform, northwestern Mongolia, Tuva, and the Baltic Basin, were available for geochemical studies; 4) the external characteristics of the early vertebrate microremains, particularly from the Upper Silurian of the Baltic Basin, have undergone negligible diagenetic thermal alteration, which should result in reliable palaeoenvironmental reconstructions; 5) because of the dense vertebrate tissues, it is much easier to get a minimal mass of apatite for successful $\delta^{18}O$ point measurement compared to contemporaneous Silurian conodonts, whose fossil elements are very light and tiny, hampering the isotope studies by difficulties to collect an amount of apatite required.

Silurian early vertebrates are particularly abundant and diverse not only in the Upper Silurian deposits of the Baltic Basin, but also in the Lower Silurian successions of central Asia and the Siberian platform. The latter region yields a big variety of early vertebrates, posing some contradiction with recent palaeogeographical reconstructions, which place Siberia palaeocontinent north of Laurussia at comparatively hight latitudes, which correspond to rather cold water palaeobasins. To reveal the situation, the taxonomy of a considerable number of Silurian early vertebrate microremains from northwestern Mongolia, central Tuva and southern Siberia have been studied in this work. The tempting opportunity to reveal Silurian palaeoenvironmental data from this unique region also led to the additional oxygen isotope analysis on these microfossils.

The present study comprises wide range of topics form taxonomy, histology, palaeobiogeography of early vertebrates, up to the chemostratigraphy of the Silurian sedimentary successions and reconstructions of palaeoclimate.

The introductory chapters presented below comprise description and results of the research subjects as follows: (chapter 1) thelodont squamation patterns' studies after the example of articulated specimens of *Loganellia scotica*; (chapter 2) systematic palaeontology and histology of the Lower Silurian thelodont and chondrichthyan taxa from central Asia (northwestern Mongolia and central Tuva) and southeastern Siberia (the Siberian platform); (chapter 3) palaeogeographic distribution and endemism of the Silurian early vertebrates of the Siberian palaeocontinent; (chapter 4) sequence stratigraphical review of the Silurian succession of the Baltic Basin (Lithuania); and finally (chapter 5) – the $\delta^{18}O$ isotope analysis on early vertebrate and conodont apatite with the chemostratigraphical isotope curve interpretation. The enclosed articles are arranged in the corresponding order.

1. Palaeontology of disarticulated early vertebrate exoskeleton microremains: significance of articulated squamation studies

Article I - **ŽIGAITĖ, Ž.**, GOUJET, D., *submitted*. New observations on the squamation patterns of articulated exoskeletons of *Loganellia scotica* (Vertebrata: Thelodonti) from the Lower Silurian of Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*.

Phosphatic exoskeleton composed of numerous contiguous scales or tesserae, which are arranged in complex morpho-functional squamation patterns corresponding to different regions of the body, is characteristic for several groups of early Palaeozoic vertebrates, such as acanthodians, chondrichthyans, tesserated galeaspids, hetereostracans, mongolepids, osteostracans, tesakoviaspids, and thelodonts. The scales or tesserae may be composed of various bone and dentine tissues, sometimes covered with thin layer of enameloid.

These external cover of scales embedded in soft dermal tissues of the animal, served as protection and body armature for the first vertebrates, which did lack intrinsic bone skeleton. Particular sculpture of these exoskeletal elements, as well as their internal structure, allows determining vertebrate species from a few detached scales. It is necessary to study not only separate scales or tesserae, but also to get a picture of the squamation in general, because species determined from discrete elements are understood as an assemblage of morphological types. For determination of discrete exoskeletal elements, their morphology, histology of defined tissue types of crown and basal plate, way of their growth, system of internal vascular, and changes occurring during the morphogenetic development of dermal skeletal elements as well as squamation changes during animals ontogenetic development, should be taken in consideration (KARATAJŪTĖ-TALIMAA, 1998). The most recent studies of thelodonts and chondrichthyan scale ultrastructure, have documented specific fine crown surface patterns, which can be considered in species determination as well (MÄRSS et al., 2007). The major problem in taxonomy of disarticulated early vertebrate material consists of scale and tesserae differences and variation within the species, making their taxon identification complicated in many cases, and subjects early vertebrate palaeo-species to be considerably artificial.

The histology of dermal scales and tesserae of early vertebrates, composed of basal root bone tissue with pulp canal, dentine and enamel cover, is homologous to the teeth of succeeding jawed vertebrates. As predecessors of the teeth of evolutionary later vertebrates, they migrated inwards the internal body together with the jaw arc bones, to form dentate vertebrate jaws undertaking further evolution of Gnathostomata.

In case of thelodonts (Thelodonti), which are the main objects of the study below, the exoskeleton is composed of approximately couple tens of thusands of dentine scales (TURNER, 1991), averaging 300 to 500 µm in diameter each, if concerning Silurian species. Whereas the whole body length of articulated thelodonts known so far ranges from a few centimeters up to 60 cm (MÄRSS et al., 2007). Each thelodont scale is composed of a non-expanding through its growth but centripetally thickening dentinous crown, and an expanding base of acellular bone tissue, presumed to be aspidine. The aspidine base is penetrated by narrow canals occupied by partly mineralized Sharpey's fibers, which attach and embed the scale into the soft dermal tissues while thelodont is alive. Thelodonts possess the ability to grow new scales throughout their life, replacing old shedding scales by an increasing number of new scales to compensate for growth in total body surface area (TURNER, 1991, 1992; MÄRSS & RITCHIE, 1998). The average scale size in juvenile individuals is also smaller than that in adult specimens (MÄRSS, 1982, 2007). Scale size also differs in between the particular areas the body of an individual fish, paralleling squamation patterns which correspond to the different morpho-functional parts of thelodont body. Noticeable fact is that thelodont scale size varies not only between and within the species: the size of scales has been increasing with time, throughout the evolution of the group. The scales of the Middle-Late Ordovician and the Early Silurian thelodonts are in general significantly smaller than those belonging to the Early and Middle Devonian species. In contrast, the scale mass and solidity are observed to degrease in time, becoming thinner, and lighter towards the Devonian, as for example is the case in species of *Amaltheolepis* and *Apalolepis*. This is due to the evolutionary response in order to lighten the overall exoskeleton weight and hydrodynamic efficiency, recognized in the other early vertebrate groups, e.g., osteostrancans (MÄRSS, 2007).

The five main squamation patterns of thelodont exoskeleton and corresponding morphological scale types can be distinguished (MÄRSS, 1986; MÄRSS & RITCHIE, 1998; MÄRSS et al., 2006, 2007). The head scales of all thelodonts, corresponding to rostral type of squamation, are contiguous, and therefore do not overlap each other. The trunk squamation, comprising cephalo-pectoral, post-pectoral, and precaudal squamation patterns, is made up of regular rows of scales, which can be either contiguous or imbricated. *Loganellia scotica*, whose articulated squamations have been studied in detail and are presented further in this work, has imbricated arrangement of trunk scales in its exoskeleton. The scales could be referred correspondingly to the morphological types as follows: rostral (in earlier works referred to as oral), cephalo-pectoral, postpectoral, precaudal, and pinnal. This classification of different squamation areas was first elaborated on *Phlebolepis elegans* articulated specimens by MÄRSS (1986).The postpectoral squamation may be considered of particular significance, both by means of extent, as it covers the bulk of the thelodont body, and by means of the thelodont taxonomy, because the holotype scales of disarticulated material of thelodonts are usually chosen from the postpectoral squamation area.

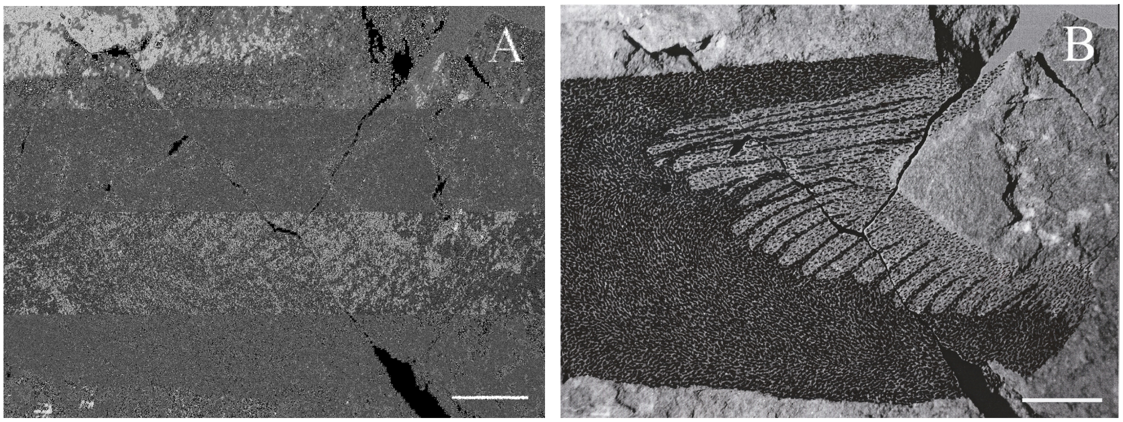
Revealing the intraspecific variability of thelodont microremains, studies of the scale diversity within the articulated specimens are necessary. That also serves as a strong background in arguing the "artificial" palaeontological species to be sufficiently close to a natural palaeospecies. Thus studies of complete early vertebrate fossil with articulated squamations preserved are essential for systematic studies of disintegrated material.

Silurian thelodonts are mostly preserved in shallow-water lagoonal to deep-water marine sedimentary environments, rarely in sediments which are interpreted as brackish (TURNER, 1999; MÄRSS, et al. 2007). Complete thelodonts with articulated squamations tend to fossilize best in the deposits of low energy and rapid sedimentation environments, and remain completely preserved in the regions of minor subsequent tectonic activity.

Seven complete *Loganellia scotica* (TRAQUAIR, 1898) specimens from the Lower Silurian of Scotland have been studied for their articlulated squamations, concentrating on the squamation patterns within the different parts of the thelodont body, and are presented further below in this work. For the present study, attempts have been made not to overlap with previous works on an intraspecific scale variation studies of *L. scotica*, most recently made in appreciable detail by MÄRSS and RITCHIE (1998), together with analysis of articulated squamations and revised diagnosis of *L. scotica*. The first specialized publication on thelodont squamation has been made by TURNER (1994). According to the previous studies, *L. scotica* is widely distributed in the Llandovery of Eurasia (ALDRIDGE & TURNER, 1975; KARATAJŪTĖ-TALIMAA, 1978; MÄRSS, 1989; TURNER, 1973; TURNER et al., 1994), and also known in late Llandovery and Wenlock of North America (TURNER & NOWLAN, 1995; MÄRSS et al., 1997, 2006), and is used for correlation between these areas and Britain.

All the *L. scotica* specimens considered in further study, come from the *Jamoytius* Horizon at the Birk Knowes, the Lesmahagow Lower Silurian inliers, which is the earliest Scottish occurrence of complete articulated thelodonts. It is also the site of the first report of *L. scotica* which was originally named *Thelodus scoticus* by TRAQUAIR and described by him in 1898. The lower fish beds of the Scottish Silurian inliers containing *L. scotica* are composed of mudstones and laminated siltstones interbedded in a sequence of marine turbidites (greywackes) with a poor shelly fauna (RITCHIE, 1968; MÄRSS et al., 2007). The environment of these Scottich fish-bearing beds has been interpreted as a quite, anaerobic, offshore-marine, unlikely slightly brackish, basin or bay (BLIECK & JANVIE, 1991; ROLFE, 1992). The material studied has been purchased from a private collector on the initiative of Daniel Goujet, and is presently stored in the National Museum of Natural History in Paris, Palaeontological collections of vertebrates (series numbers GBP n° 360, 361, 366, 367, 374, 376, and 381). Three of the speciments represent complete thelodont fossils, and four are partially preserved postpectoral, precaudal and caudal parts of the exoskeleton.

The all five main types of thelodont squamation, that is rostral, cephalo-pectoral, postpectoral, precaudal, and pinnal, have been observed within the articulated squamations of the specimens. The specific squamations of orbital, branchial, and bucco-pharyngeal areas, characteristic of *L. scotica*, have not been observed due to the poor or non-preservation of these particular areas within the specimens studied. The Rostral squamation is suggested to be present within the exoskeleton of *L. scotica*, contrary to the most recent descriptions of the articulated squamations of this species (MÄRSS & RITCHIE, 1998). Preceding studies indicate that *L. scotica* possesses more squamation varieties than the five main ones of MÄRSS & RITCHIE (1998), though it has been argued it does not possess any typical rostral scales (MÄRSS & RITCHIE 1998, p. 152), and supportive comparison with *Phlebolepis elegans* has been made (MÄRSS, 1986). In our opinion, *Ph. elegans*, representing the family Phlebolepididae BERG, 1940, which is quite a different group of thelodont by means of scale structure and general morphology, can not be a proper reference. Referring to the intraspecific scale varieties (morphological sets) within the different species of loganiid thelodonts (MÄRSS et al., 2007; ŽIGAITĖ, *in press*), and our study of the articulated squamations of *L. scotica*, we suggest the rostral squamation to be present in *L. scotica*. Moreover, rostral scales of *L. scotica* have been clearly figured by MÄRSS et al. (2007, fig. 42A: a; fig. 42B: a).



Text-fig. 1. Pinnal squamation of the caudal fin of *Loganellia* scotica, specimen GBP n° 367: (A) natural view of the caudal part of the specimen, (B) drawing in enhanced contrast., National Museum of Natural History (MNHN), Paris.

Tail morphology and pinnal squamation patterns of the caudal fin have been studied in particular detail, and the constitution of the caudal fin rays has been analyzed. STETSON (1931) was the first to describe hypocercal tail fins in thelodonts, and the thin film of scales, covering continuously the flexible intra-posterior part of the caudal fin, as well as presumable fin rays. He described a tail of a large specimen of *L. scotica* with caudal fin-web and up to 18 possible internal cartilaginous fin rays (STETSON, 1931).

Hererin, at least 20 long fin rays, forking from the hypocercal lobe solely within the pinnal squamation web of the caudal fin, have been observed on the specimen GBP n° 367 (Text-fig. 1, A). VAN DER BRUGGHEN (1994, fig. 8E) has already mentioned and drew these caudal rays in the first description of the specimen, implying them to reflect traces of the former cartilaginous caudal rays. Apparently, these caudal rays represent lines of denser squamation within the articulated film of pinnal (caudal fin) squamation pattern (Text-fig. 1, B). Appending to the previous interpretations of the caudal fin rays of *L. scotica* as internal cartilaginous outgrowths, it should be concluded that, by means of squamation pattern, caudal fin rays consist of accentuated scale cover lines within the contiguous film of pinnal (caudal fin) squamation.

Additionally, the mean ratio coefficient, permitting estimation of the total body length of *L. scotica* animal from the width of its caudal peduncle, has been derived on the basis of measurements of 11 complete specimens of *L. scotica*, and has been used to approximate the body lengths of the incomplete fossils studied. The total body length of the largest specimen preserved as precaudal and caudal parts of the exoskeleton (GBP n° 366), and studied in this work, has been estimated to reach at least 450 mm in length, which exceeds the so far considered maximum length of the species (TURNER, 1992; MÄRSS et al., 2007). The former maximum body length of *L.scotica* had been estimated to go up to 400 mm, but this also has been inferred from detached caudal fins (TURNER, 1992).

In conclusion, while working with vertebrate microremains, a rock sample, rich in early vertebrate microoremains, may include not only scales and tesserae of several early vertebrate taxa, but also morphogenetically young and old scales, as well as scales from small and large animals, and scales from the different regions of the body from one or more individuals of the same species. However, all thelodont scales will possess the same fundamental structure, and have gone through the same morphogenetical development (KARATAJŪTĖ-TALIMAA, 1998). The palaeoenvironmental factors as habitat and climate have been considered to influence the shape of early vertebrate exoskeletal elements as well, including thelodont scales (FREDHOLM, 1992; MÄRSS 1999b; TURNER & YOUNG, 1992). All this should be considered when evaluating the assemblage of early vertebrate microremains. Consequently, the knowledge of articulated fossil squamations is essential for palaeontological and systematic studies of disintegrated material.

2. Early Silurian vertebrates from central Asia and the Siberian platform – taxonomy and endemism

Article II - ŽIGAITĖ, Ž., 2004. A new thelodont from Lower Silurian of Tuva and north-west Mongolia. *Acta Universitatis Latviensis*, 679: 158-165.

Article III - ŽIGAITE, Ž., KARATAJUTE-TALIMAA, V., **2008**. New genus of chondrichthyans from the Silurian – Devonian boundary deposits of Tuva. *In:* M. Ginter (ed.), *Acta Geologica Polonica*, 58 (2): 127-131.

Article IV - ŽIGAITĖ, Ž., *submitted*. Endemic thelodonts (agnathan vertebrates) from the Lower Silurian of central Asia and the Siberian platform. *Geodiversitas.*

Early vertebrates, particularly thelodonts, from the Lower Silurian of central Asia (noerthwestern Mongolia and Tuva) and the Siberian platform have been studied in detail. Thelodont microremains have been attributed to two families, Angaralepididae MÄRSS & KARATAJŪTĖ-TALIMAA, and Loganelliidae *sensu* (KARATAJŪTĖ-TALIMAA, 1978) *emend* KARATAJŪTĖ-TALIMAA, 1997; three genera *Angaralepis* MÄRSS & KARATAJŪTĖ-TALIMAA, 2002, *Loganellia* FREDHOLM, 1990, and *Talimaalepis* ŽIGAITĖ, 2004; and six species as follows: *A. moskalenkoae* (KARATAJŪTĖ-TALIMAA, 1978), *L. asiatica* (KARATAJŪTĖ-TALIMAA, 1978), *L. sibirica* (KARATAJŪTĖ-TALIMAA, 1978), *L. tuvaensis* (KARATAJŪTĖ-TALIMAA, 1978), *T. rimae* ŽIGAITĖ, 2004, and *T. kadvoiensis* (KARATAJŪTĖ-TALIMAA, 1978) ŽIGAITĖ 2004 comb. nov., respectively.

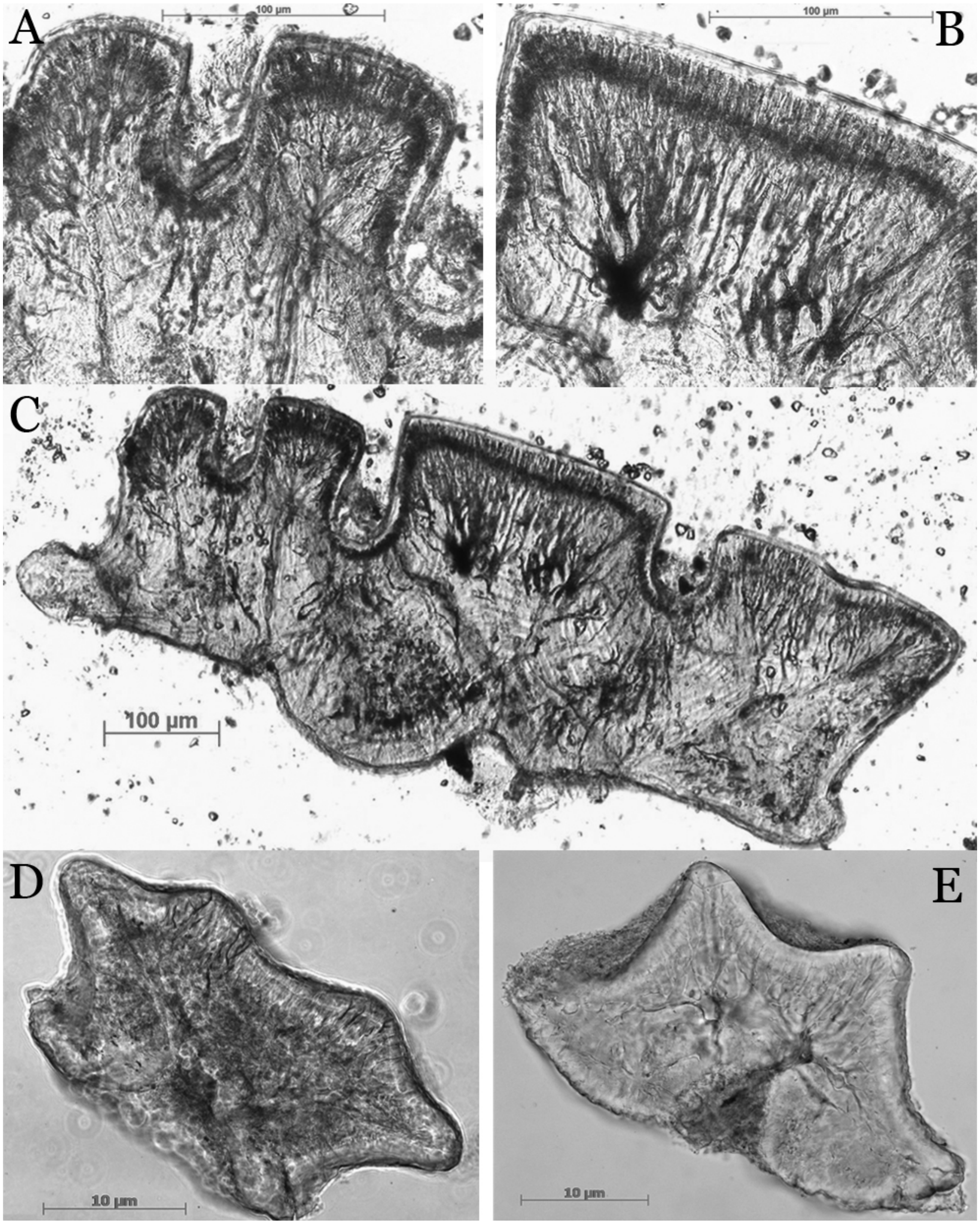
The present day territory of northwestern Mongolia, Tuva, and the Siberian platform, are infered to have been united as a single Siberian palaeocraton, an independent geological terrane which existed during all the Palaeozoic (COCKS & TORSVIK, 2007). Its comparative isolation at relatively high latitudes has been proved, referring to the fact that the area was colonised throughout the Palaeozoic by marine benthic faunas and in the later Palaeozoic by both marine and land floras and faunas which are not found elsewhere on Earth, and these biota were often sufficiently distinctive to form the basis of faunal palaeoprovinces at various times (Cocks & Torsvik, 2007). The separate palaeobiogeographical province has already been suggested for the region during the first vertebrate studies (Karatajūtė – Talimaa, 1978; Blieck and Janvier, 1993). The early vertebrate distribution and species content of the region confirms this theory. Abundant and numerous thelodont species have all been considered as endemic (Žigaite & Blieck, 2006; Žigaite, *in press*). The other vertebrate taxa, such as endemic Mongolepids (Karatajūtė-Talimaa et al., 1990), new form of enywhere else unknown tesserated galeaspids (Karatajūtė-Talimaa & Žigaite, 2005), as well as recently published new chondrichthyan genus and species (Žigaite & Karatajūtė-Talimaa, 2008), all support the theory of a separate palaeobiogeographical province.

The localities of the region studied for early vertebrates include northwestern Mongolia, central Tuva, as well as the Siberian platform area, which comprises central and southern parts of East Siberia, between Yenisey and Lena rivers. Early vertebrate material from these regions have been collected during frequent geological expeditions in the seventies and eighties, made by Lithuanian and Russian scientists during the Soviet time. The Mongolian samples come from the northwestern part of the country, near the Tchargat Mountain north of the lake Ubs-Nuur, and have been provided by L. Rosman and I. Sodov. The vertebrate material of Tuva comes from several localities in the central part of the country, and has been collected by T. Moskalenko, L. Aksenova, N. Kulkov, and L. Ratanov (Novosibirsk, Russia) in the years 1968-1987 (Karatajūtė-Talimaa & Ratanov, 2002). The subsequent expeditions in the East Siberia have been held in the years 1982 and 1984, when vertebrate collections have been made by V. Karatajūtė-Talimaa, Y. Predtechenskyj, Y. I. Tesakov, T. Moskalenko, and J. Valiukevičius. The Silurian of East Siberia is divided into “subregions” and “districts” on the basis of persistent lithofacies (Tesakov et al., 2003). Early Silurian vertebrates are recorded in the five following subregions of Siberia: North Tarym, North Preyenisey, Pretunguska, Nyuya-Beresovo, and Irkutsk. Thelodonts from the four latter have been studied in detail. The first description of vertebrate microremains in some part of the collections has been made in Russian by prof. V. Karatajūtė-Talimaa (1978).

Presently these collection samples, including already published material, and the following described below, are stored in Vilnius University, Department of Geology and Mineralogy (Lithuania), as private collections of prof. V. Karatajūtė-Talimaa.

New full revised and complemented descriptions of all the thelodont material available from these collections, including additional material with new taxa, revealed for this study from numerous uprocessed samples, are presented further below. Compared to the first descriptions of the vertebrates from this region, the new analytical methods allowed advanced data, and some species descriptions are corrected, or followed by assignation to several new taxa (ŽIGAITĖ, 2004; ŽIGAITĖ & KARATAJŪTĖ-TALIMAA, 2008; ŽIGAITĖ, *in press*). General distribution of early Silurian vertebrates is improved concerning the most recent works on thelodont palaeontology and palaeobiogeography (KARATAJŪTĖ-TALIMAA & MÄRSS, 2004; MÄRSS et al., 2007). New terminology for thelodont squamation patterns, and corresponding assignation of the scales is used further below: the former classification of head, transitional, and body scale categories, have been adopted to the most recent division of thelodont scales (MÄRSS, 1986b) as follows: rostral (=head); cephalo – pectoral (=transitional, and 'transitional' body scales, a part of body scales contiguous the head scales and terminating near the pectoral fins); postpectoral and precaudal (=most of the body scales); and the pinnal (=special) scales, the latter including the frequently-reported special thelodont scales of the edges of the fins. SEM pictures of the complete morphological set of the species have been made. Thin sections, prepared and published as drawings by V. KARATAJŪTĖ-TALIMAA in 1978, has been re-examined and pictured. New thin sections and histological pictures have been prepared (Text-fig. 2).

Among the thelodont taxa studied, the genus *Talimaalepis* deserves special consideration. The species content of *Talimaalepis,* so far known for consisting of a single species, has been revised further in this work, evolving into two species. Histology of *Talimaalepis* scales show an intermediate position between the *Loganellia* (Fam. Loganellidae) and *Helenolepis* (Fam. Phlebolepidae) ones, remaining higher taxonomic affiliation of *Talimaalepis* under further consideration. Phylogenetic relationships of *Talimaalepis* remain difficult to clearify beacause of its palaeobiogeographical isolation, as well as the abundance and endemism of contemporaneous palaeobiogeographically

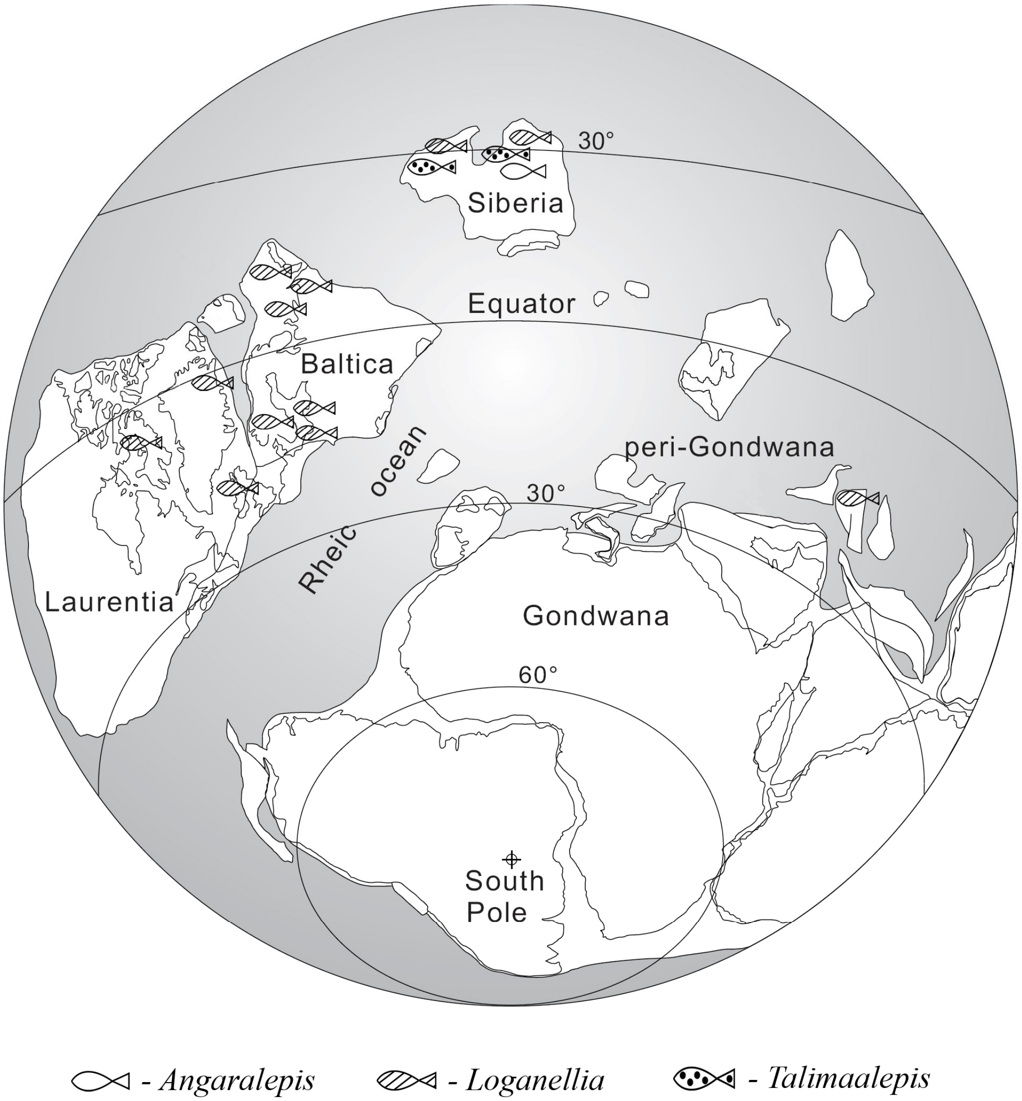


Text-fig. 2. The histological cross-sections of the scales of *Helenolepis obruchevi* Karatajūtė-Talimaa 1978, n°102 (A,B,C), *Talimaalepis rimae* Žigaitė 2004, n°28 (D), and *Talimaalepis kadvoiensis* (Karatajūtė-Talimaa 1978) Žigaitė 2004 comb. nov. n°29 (E).

related thelodont species. The attribution of *Talimaalepis* by MÄRSS et al. (2007) to the family Loganelliidae (KARATAJŪTĖ-TALIMAA, 1978, *emend.* KARATAJŪTĖ-TALIMAA, 1997), appears to be disputive on the basis of the histology of the scales, as loganiids do not possess any thick dentine tubules, which is the characteristic feature of the genus *Talimaalepis*. However, the presence of one single pulp canal, which is typical for the genus *Loganellia*, as well as sparse anastomoses of usually straight dentine canals, makes *Talimaalepis* close to loganiid thelodonts. The presence of monolithic crown is the first diagnostic feature of the family Loganelliidae, and it is not the case for *Talimaalepis*, where the ridges of the crown end in free posterior spines, and lateral segments are distinct. Moreover, well-defined thick dentine canals, opening into more than one pulp canal, characteristic to *Talimaalepis* as well, are the diagnostic features of the genus *Helenolepis*, and do not at all present in any scale of loganiid thelodonts. Nevertheless, *Helenolepis* possesses several, usually more than three pulp canal, according to a number of crown segments (KARATAJŪTĖ-TALIMAA, 1978, p. 236, fig. 14), which is never the case in *Talimaalepis*, possessing one single pulp canal present despite of the crown's sculpture. Each pulp canal in helenolepid scales is following its net of thick, and near the surface of the crown thin dentine tubules (Text-fig. 2). Though considering the histology of helenolepids, the internal structure of *Helenolepis* scales is very close, but much more complex than that of *Talimaalepis*. On the basis of these pronounced histological differences, *Talimaalepis* is distinct from both *Loganellia*, and *Helenolepis*. Furthermore, according to our study, the proposed assignation of *Talimaalepis* to the family Phlebolepididae BERG 1940 (ŽIGAITĖ, 2004, p. 159), together with helenolepids on the basis of possession of similar histology and sensory line pores, encountering adequate morphological differences as well, is now refuted by the present study. Previously described sensory line pores within the scales of *Talimaalepis* (ŽIGAITĖ, 2004, p. 162, Pl. 2, fig. H), have been revealed not to be present, contrary to the other genera of Fam. Phlebolepididae. Nevertheless, it is necessary to admit that some helenolepids share strong morphological similarities to the scales of both of the *Talimaalepis* species. Some of the rostral scales and pinnal scales of the edges of fins in both of the *Talimaalepis* species are very similar to those of *Helenolepis*, especially to those of *Helenolepis obruchevi* KARATAJŪTĖ-TALIMAA, 1978, sharing an extremely high vertical anchoring posterior process of the base in older scales. Though it is easy to distinguish between them by examining the internal structure of the scales, but morphologically all are quite similar. The main difference in the external structure of these scales would be the pattern of the anterior notches of the crowns – *Talimaalepis* has oblique, less deep and slightly wider notches than those belonging to *Helenolepis*, which are straight, very narrow and deep-cutting, and also more numerous in most of the cases (MÄRSS et al., 2007, fig. 81, F, G, J). Referring to the histological and morphological features listed above (the internal scale composition of thick tubule dentine, segmented crown morphology, etc.), *Talimaalepis* remains to keep an uncertain intermediate position between the genera *Loganellia* (Fam. Loganellidae) and *Helenolepis* (Fam. Phlebolepididae) (ŽIGAITĖ, *in press*).

The new phylogenetic suggestion is proposed further in this work, and is based on the strong morphological affinities between the scales of *Talimaalepis* species, and some shieliids, particularly *Shielia taiti* (STETSON, 1931) (see in MÄRSS & RITCHIE (1998, figs. 27A, 30A,B, 31), and also to some *Paralogania* species, such as *P. consimilis* MÄRSS & KARATAJŪTĖ-TALIMAA, 2002 (see MÄRSS et al., 2007, fig. 59, G-H), and *P. kaarmisensis* MÄRSS 2003 (see MÄRSS et al., 2007, fig. 59, J), should be taken in consideration. The presence of similar wedge-shape base with a horizontal thalamus-shaped anterior part, and a long narrow anchoring posterior process both in talimaalepid and in shieliid scales, deserves a special attention. The uplifted median and lateral segments, the median having a shape of a rhombic trough, are common features of these two groups as well. Nevertheless, on morphological basis *Talimaalepis* being slightly closer to loganelliid than to phlebolepidid thelodonts, is kept in this work within the family Loganelliidae, and the order Loganelliiformes (see MÄRSS et al., 2007, p. 60), but further examinations on talimaalepid, helenolepid, and shieliid histology are required.

Both *Angaralepis* and *Talimaalepis* genera are strongly endemic to the province, with the exception of the cosmopolitan genus *Loganellia* (Text-fig. 3), though it is endemic at the species level. If concerning *Loganellia* species content inherent for the region, *L. tuvaensis* appears to be the only species, whose distribution in the Lower Silurian is restricted to localities of central Tuva. This could infer some degree of



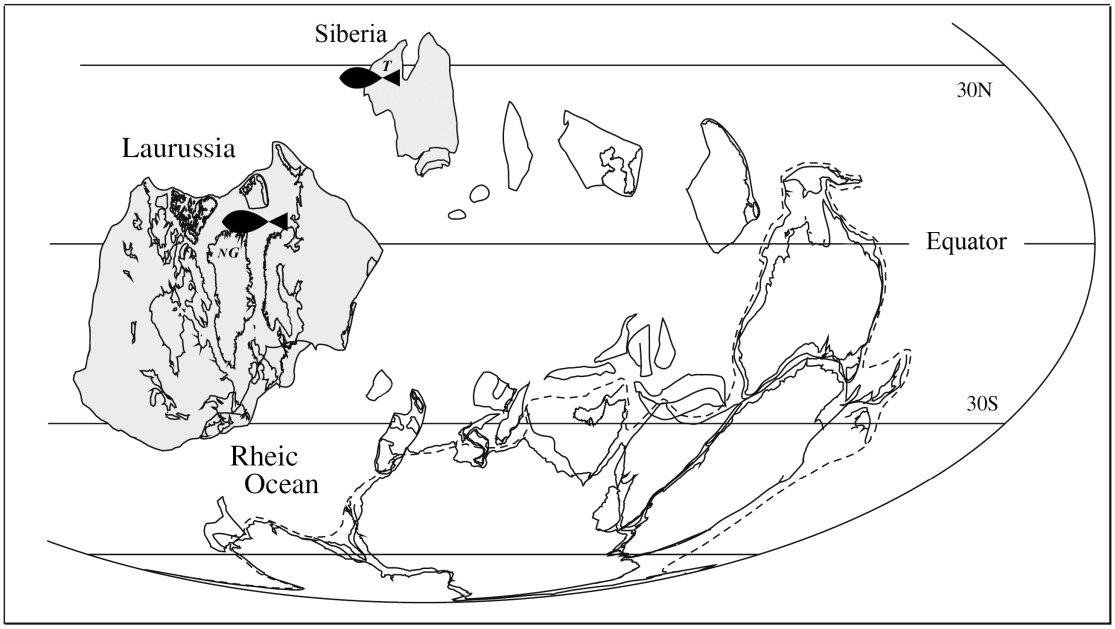
Text-fig. 3. Presently known distribution of thelodont genera *Angaralepis* (endemic), *Loganellia* (cosmopolitan), and *Talimaalepis* (endemic). Palaeogeography from COCKS & TORSVIK, 2002; modified after HAIRAPETIAN et al., 2008.

isolation of Tuvan palaeobasin in relation to the other epicontinental palaeoseas of the Siberian terrane. The record of *L.* cf. *L. tuvaensis* in the Upper Silurian – Lower Devonian (Pridoli–Lochkovian) series of North Greenland (BLOM, 1999b) appears to be very close and maybe conspecific to *L. tuvaensis* from Siberian terrane (Text-fig. 4), and may indicate Siberian palaeocontinent approaching the northeastern Laurentia (western

Laurussia) with its northern border from the west at the end of the Silurian period (ŽIGAITĖ & BLIECK, 2006).

Additional records of *L. sibirica*, which is typical Lower Silurian thelodont in Siberian platform, has been revealed in the Lower Silurian of Tuva. Together with previous distribution in northwestern Mongolia and Siberian platform (ŽIGAITĖ & BLIECK, 2006), this new record indicates the region as a single highly endemic palaeobiogeographical province, and supports the theory of integral Siberian terrane during the Early Silurian (COCKS & TORSVIK, 2007).

Presence of *Loganellia scotica* (TRAQUAIR, 1898) scales in the Lower Silurian of the Siberian platform (KARATAJŪTĖ-TALIMAA, 1978) reported in the first description of the material, has not been considered to be evident, and is not reported in this work. Further studies of the thelodont material from the region might clarify this problem.



Text-fig. 4. Records of *Loganellia tuvaensis* (KARATAJŪTĖ-TALIMAA 1978) in northern Siberian palaeocontinent (T-Tuva), and *L. cf. L. tuavensis* (Blom, 1999) in norther Laurentia (NG-North Greenland); both indicated by black fish marks. Palaeogeography (420 Ma) from COCKS & TORSVIK, 2002; modified after LEHNERT et al., 2007.

Apart from thelodonts, new peculiar chondrichthyan microremains from the uppermost Silurian of Tuva are studied further in this work. Sections through the Silurian-Devonian boundary beds, located in central Tuva (Tchaadan region, Bazhyn-Alaak locality), yield various vertebrate microremains, including the new genus and species of Chondrichthyes described below. A single sample from Tchaadan region of Tuva, Bazhyn-Alaak locality, Khondergei Formation, contained scales of this new chondrichthyan, *Tuvalepis schultzei* ŽIGAITĖ & KARATAJŪTĖ-TALIMAA, 2008, together with another chondrichthyan *Elegestolepis grossi* KARATAJŪTĖ-TALIMAA 1973, and numerous scales of thelodont *Helenolepis navicularis* KARATAJŪTĖ-TALIMAA 1978 (ŽIGAITĖ & KARATAJŪTĖ-TALIMAA, 2008). After the very first studies of these vertebrate microremains, they have been ascribed to elegestolepids (KARATAJŪTĖ-TALIMAA & RATANOV 2002: ?*Elegestolepis* gen. nov.). Though the new genus and species described in this work share some similarities with elegestolepids, fundamental differences are present in growth pattern, histology, and morphology as well. Scales of *T. schultzei* display significant morphological variety, and are characterized by a very fine, comparatively wide and flat crown with longitudinal ribs, with small and short neck. Flat and fine general morphology of the scales is the main morphological feature of the new chondrichthyan, separating the species from elegestolepids.

The internal crown structure of *T. schultzei* scales is characterized by thick dentine canals, similar to that of *E. grossi* scales, but the canals are much shorter, their network is branchy, in contrast to more regular pattern of *E. grossi*. *T. schultzei* scales possess two pulp canal openings: the wider one is on the base, the narrower opening on the side of the neck, and both are very close to each other because of the flatness of *T. schultzei* scales. Contrary, in *E. grossi* those two canals extend at a right angle to each other, open at a right angle and significant distance from each other: on the side of the high neck, and in the central part of the base (ŽIGAITĖ & KARATAJŪTĖ-TALIMAA, 2008).

The scale growth pattern is very different from elegestolepids too – the scales grow by appositional addition of layers towards the distal side of the crown, which is opposite to *E. grossi*, where an initial monodontodium just grows inwards and deep into the soft tissues on account of the base, and any kind of concentric appositional growth lines is not present (KARATAJŪTĖ-TALIMAA, 1973; ØRVIG, 1977; KARATAJŪTĖ-TALIMAA, 1998).

The morphological and histological differences and especially distinct growth patterns, are the main reasons for describing these scales not as a new species of genus *Elegestolepis*, but as a new genus and species of chondrichthyans. The flattened and light scales of *T. schultzei* may infer to the flattened body as well, and probably benthic palaeoecological niches, as it is in the case of most of the benthic thelodont species, possessing dorso - ventraly flattened body, and flattened general shape of the scales respectively (MÄRSS et al., 2007).

To conclude, it may be stated that the region of northwestern Mongolia, Tuva, and the Siberian platform, is supposed to represent epeiric seas of the same Siberian palaeocontinent during the Silurian (COCKS & TORSVIK, 2007). The palaeoregion may also be considered as a separate and highly endemic palaeobiogeographical province, particularly referring the early vertebrate distribution and taxonomical content, which is presented in detail further in this study (ŽIGAITĖ, *in press*).

3. Palaeobiogeographical province of central Asia and southern Siberia – early vertebrate speciation and radiation source in the Early Silurian

Article V - ŽIGAITĖ, Ž., BLIECK, A., **2006**. Palaeobiogeographical significance of Early Silurian thelodonts from central Asia and southern Siberia. *GFF*, 128: 203-206.

Early vertebrates (acanthodians, chondrichthyans, galeaspids, heterostracans, mongolepids, tesakoviaspids, and thelodonts) known from the Lower Silurian of northwestern Mongolia, central Tuva and the Siberian platform, show specific and distinct taxonomical content, if compared to the other contamporaneous Silurian vertebrates from different regions (KARATAJŪTĖ-TALIMAA, 1978; AFANASIEVA & JANVIER, 1985; KARATAJŪTĖ-TALIMAA et al., 1990; KARATAJŪTĖ-TALIMAA & SMITH,

2003, 2004; ŽIGAITĖ, 2004; ŽIGAITĖ & KARATAJŪTĖ-TALIMAA, 2005, 2008; ŽIGAITĖ, *in press*).

Silurian vertebrates from the nowadays area of central Asia and southern East Siberia presented in this work and discussed in the previous chapter, reveal an existence of rather isolated vertebrate palaeobiogeographic province within the territory, and infer to highly endemic palaeobasins during the Early Silurian (ŽIGAITĖ & BLIECK, 2006). All this present day territory existed as unified Siberian palaeocraton - an independent geological terrane, which persisted not only in the Silurian, but during the whole Palaeozoic era (COCKS & TORSVIK, 2007). In the Silurian period it has comprised not only large area of modern Russia (including Altai, Salair, Sayan, Siberia, Tomsk) and northwestern part of Mongolia, but also extended into the northwestern part of China, and it has been the only large terrane in the northern hemisphere for much of the Palaeozoic, since the Ordovician (COCKS & TORSVIK, 2007). The comparative isolation at relatively high latitudes of Siberia also meant that the area was colonised throughout the Palaeozoic by marine benthic faunas, and in the later Palaeozoic by both marine and land floras and faunas which are not found elsewhere on Earth (e.g. *Tuvaella* brachiopod in the Silurian), and these biota were often sufficiently distinctive to form the basis of faunal palaeoprovinces at various times. In terms of palaeobiogeographic relationships other than vertebrate, 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. 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 and northwestern parts of China (Inner Mongolia), plays an important role confirming the high-latitude isolation of the Siberian palaeocraton (RONG & ZHANG, 1982; ROZMAN, 1986; MINJIN, 2001; COCKS & TORSVIK, 2007). The occurrence of endemic early vertebrate taxa attributable to the Silurian Siberian terrane goes in well accordance with this suggestion and preceding data (ŽIGAITE, *in press*).

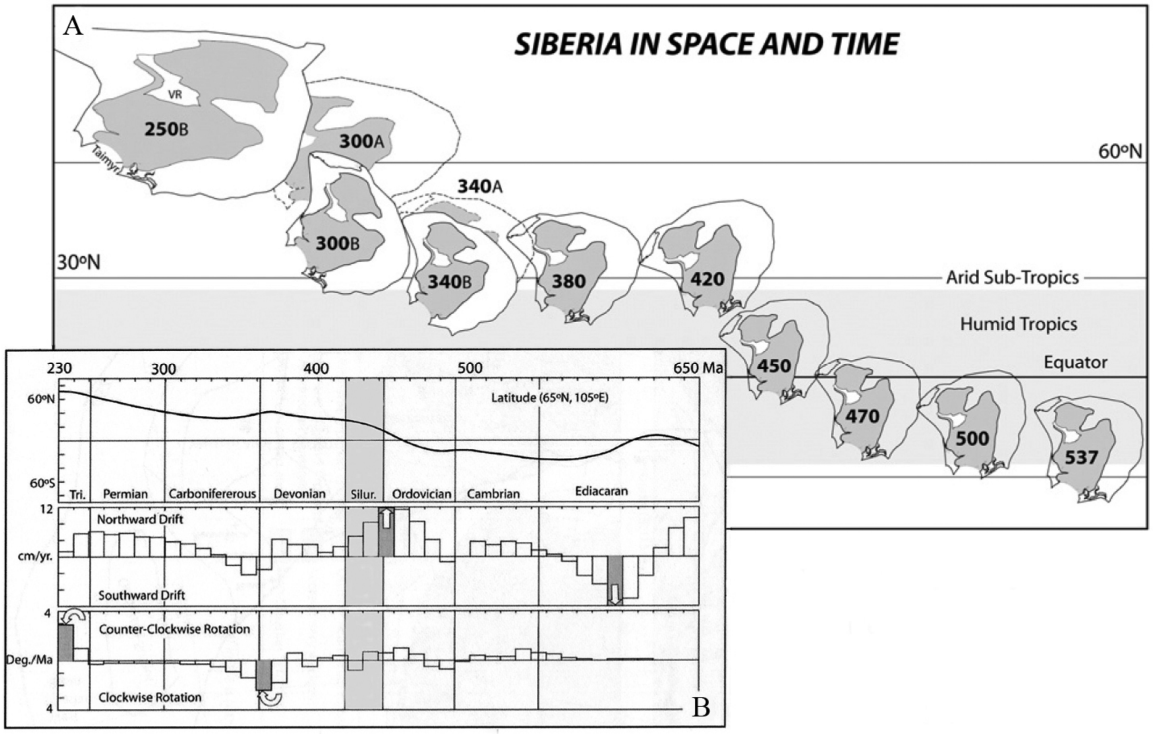
All the thelodont species revealed in this study, as well as the other early vertebrates reported from the region and listed above, are strongly endemic, and show palaeobiogeographical unity of the territory. The distribution of the thelodont species shows close connection between the Early Silurian basins of northwestern Mongolia, Tuva, and the Siberian platform. If separated Tuvan and Siberian palaeogeographical provinces appear to be possible during the early and middle Llandovery (BLIECK & JANVIER, 1991; FORTEY & COCKS, 2003), the distribution of thelodonts and acanthodians (KARATAJŪTĖ-TALIMAA & SMITH, 2003), mongolepids (KARATAJŪTĖ-TALIMAA et al., 1990), and probably galeaspids (KARATAJŪTĖ-TALIMAA & ŽIGAITĖ, 2005, 2006), are evidence for a common Silurian palaeobiogeographical province of central Asia and Siberia, and therefore unified Siberian terrane corresponding to all the area studied (COCKS AND TORSVIK, 2007). For instance, the horizontal distribution of *Talimaalepis* is a good supporting evidence for assuming the existence of a continuous palaeobasin, or at least presence of well connected epicontinental seas within these regions during the Early Silurian (ŽIGAITĖ & BLIECK, 2006). The palaeobiogeographical range of *L. sibirica* has been revised in this work, and serves as one more evidence for the united palaeobiogeographical province for the whole territory studied. Regardless its abundance and specificity for the Lower Silurian of the Siberian platform, a few scales have been recorded in the Wenlock of northwestern Mongolia, and more additional material has been revealed from the lower Llandovery and upper Wenlock of central Tuva. Thus the palaeobiogeographical restriction of the species to the Lower Silurian of Mongolia and the Siberian platform (ŽIGAITĖ & BLIECK, 2006) is now refuted: it is more widely characteristic to the Siberian – central Asian region (ŽIGAITĖ, *in press*).

The worldwide distribution of the thelodont genera *Angaralepis, Loganellia,* and *Talimaalepis* during the Silurian is shown above (Text-fig. 3). The *Angaralepis* and *Talimaalepis* are strongly endemic, referred so far only from the Lower Silurian localities discussed in this work, although *Loganellia* is cosmopolitan. Though the endemism of *Loganellia* is still sustained at the species level: all the three species, *L. asiatica, L. sibirica*, and *L. tuvaensis* are restricted to the Lower Silurian of central Asia and the Siberian platform.

Exception for the suggested totally-endemic early vertebrate content in the area would be the reports of *Loganellia* sp. cf. *L. tuvaensis* from the Upper Silurian–Lower Devonian (Pridoli–Lochkovian) of North Greenland, the Halls Grav locality and Monument, Hall Land, Chester Bjerg Formation (TURNER & PEEL, 1986; BLOM, 1999; see the section above). This record of *L.* sp. cf. *L. tuvaensis* on the northeastern Laurentia, is particularly important as concerned with Silurian palaeobiogeography. This gives an evidence for a possible proximity of the Siberian and Laurentian palaebiogeographical provinces during the Late Silurian (ŽIGAITĖ & BLIECK, 2006). The adjacency of Siberia and Laurentia palaeocontinents has already been postulated in previous works, Laurentia facing and approaching Siberian palaeocontinent during the Silurian (MCKERROW et al., 1991; TORSVIK et al., 1996; COCKS & TORSVIK, 2002). Reclusive occurrence of *L. tuvaensis* in the Silurian beds of Tuva solely, goes in some accordance to the preceding hypothesis that Tuva terrane being situated more or less separately from the main Siberian palaeocraton (BLIECK & JANVIER, 1991; FORTEY & COCKS, 2003). Nevertheless, the uniformity and endemism of the majority of the Early Silurian thelodont species studied, is in a noteworthy agreement with the hypothesis of the well-connected Silurian seas and joined Siberian palaeocontinent.

Apart from endemic thelodonts, other Silurian endemic early vertebrate taxa are inherent to the territory of Siberian palaeocontinent as well. The most notable would be the following: *Tesakoviaspis concentrica* KARATAJŪTĖ-TALIMAA & SMITH 2004 (corresponding even to the endemic order Tesakoviaspidida, KARATAJŪTĖ-TALIMAA & SMITH, 2004); osteostracans *Tannuaspis*, *Tuvaspis*, and *Ilemoraspis* (AFANASIEVA & JANVIER, 1985); a peculiar genus *Ilimia*, which is considered as special case of tessearted galeaspids (KARATAJŪTĖ-TALIMAA & ŽIGAITĖ, 2005); two endemic genera of acanthodians, *Lenacanthus* KARATAJŪTĖ-TALIMAA & SMITH, 2003 and *Tchunacanthus* KARATAJŪTĖ-TALIMAA & SMITH, 2003, restricted to the Lower Silurian of the region (KARATAJŪTĖ-TALIMAA & SMITH, 2003); Mongolepidida, an early vertebrate group discovered in northwestern Mongolia and represented by *Mongolepis rozmanae* KARATAJŪTĖ-TALIMAA & NOVITSKAYA, 1990, since known from nowhere else in the world (KARATAJŪTĖ-TALIMAA et al., 1990); and finally particluar Chondrichthyes, such as *Elegestolepis, Polymerolepis*?, and *Tuvalepis* (ŽIGAITĖ & KARATAJŪTĖ-TALIMAA, 2008). The latter comprise a single species *Tuvalepis schultzei* ŽIGAITĖ & KARATAJŪTĖ-TALIMAA, 2008, revealed from the Silurian – Devonian boundary deposits of Tuva and described in detail in this work below: it shows a particular morphological and histological specificity, distinguishing it from affined contamporaneous elegestolepids (Karatajūtė-talimaa & Žigaitė, 2008).

To summarize, the distribution of all the early vertebrate taxa studied as well as those reported in the literature to be inherent for the Silurian of Siberian palaeocontinent, lead to define a separate and strongly endemic palaeobiogeographical province. This has already been assumed in previous studies (Karatajūtė – Talimaa 1978; Blieck & Janvier 1993). The distribution patterns of Silurian early vertebrates refer to the unified Siberian terrane corresponding to all the area studied (Žigaitė & Blieck, 2006; Cocks & Torsvik, 2007).



Text-fig. 5.(A) Drift and rotation history of Siberia palaeocontinen from 537 Ma to 250 Ma, based on palaeomagnetic data interpolation. The core Siberian craton is shown in black, and peri-Siberian accretionary wedges and contiguous fold belts in white; (B) Latitudinal drift for a location at 65°N and 105°E in northern Siberia. Modified after Cocks & Torsvik, 2007.

The abundance of endemic thelodonts and richness of other early vertebrate species in the Lower Silurian of northwestern Mongolia, Tuva, and the Siberian platform refers to warm and productive palaeobasins and indicates them as a possible place for genesis and radiation of at least some early vertebrates (BLIECK & JANVIER, 1993).

The area studied, containing numerous endemic Silurian vertebrate species, are supposed to be the northern margin of the Siberian palaeocontinent during the Silurian (COCKS & TORSVIK, 2002, 2007). Accordingly, foreshore and lagoonal facies rich in early vertebrates, occur along a north-south transect of the Siberian palaeocraton (COCKS & TORSVIK, 2007). It is considered that Tuva and northwestern Mongolia have been a terrane collage separate from Siberia in the Precambrian and Early Palaeozoic. Afterwards in the Late Ordovician, Tuva-northern Mongolia terrane has acceded to the main Siberian terrane area as northern accretionarry wedges (COCKS & TORSVIK, 2007).

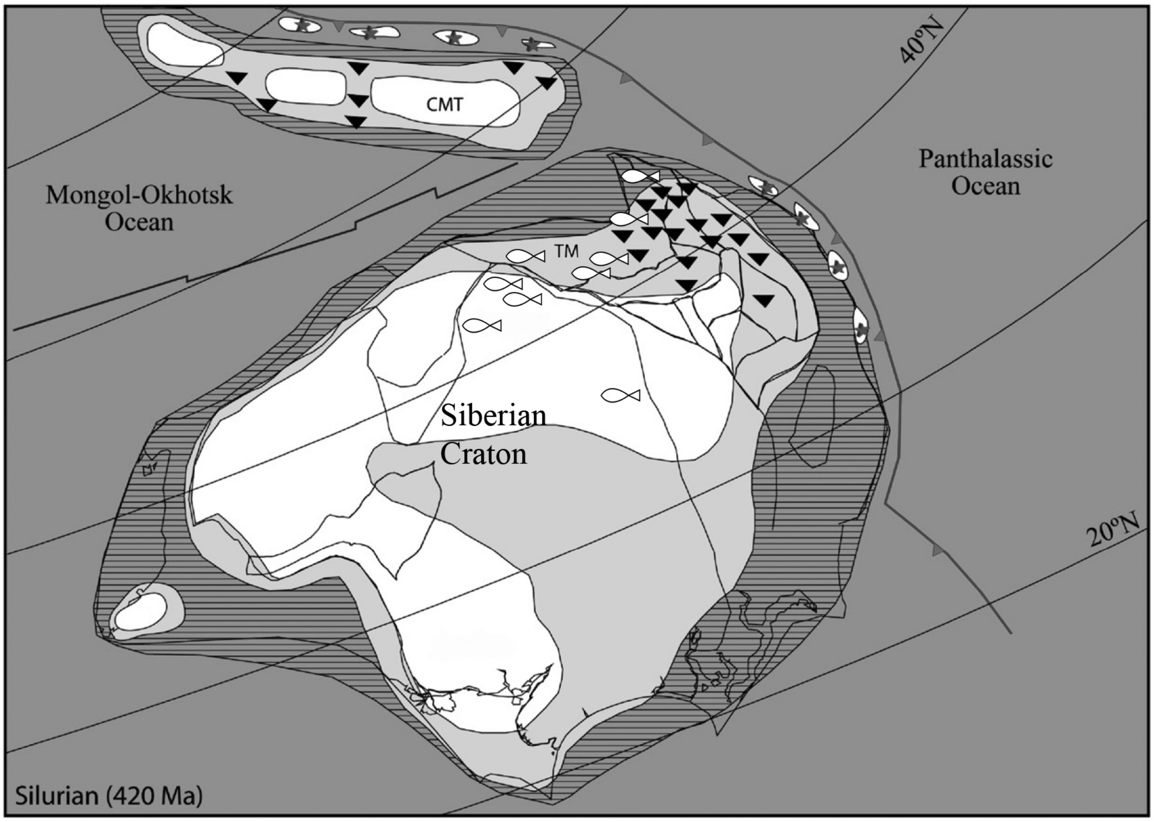
During the whole Silurian, the centre and the southeastern part of the Siberian palaeocraton have been largely flooded by epeiric seas (COCKS & TORSVIK, 2007). This epicontinental palaeobasin is suggested to be a stable, persistent structure in the Early Silurian, favouring the presence of rather isolated and rich in species palaeobiogeographical province, which can be inferred from the endemic vertebrate and invertebrate faunal composition (Text-fig. 6).

These supposed warm and productive palaeobasins may have existed on the Siberian palaeocontinent during its drift through the palaeoequator (COCKS & TORSVIK, 2002), and may have occupied the northern margin of the Panthalassic Ocean (COCKS & TORSVIK, 2007). Referring to the most recent studies, the northward movement of the Siberia palaeocontinent is estimated to pass it just by the equator in the Early Silurian (Text-fig. 5), and subsequently for the most of the Late Silurian, Siberia terrane was the only large palaeocontinent to be situated entirely within the northern hemisphere (COCKS & TORSVIK, 2007).

The comprehensive sedimentological studies infer a large epicontinental sedimentary basin, which have occupied the major part of the Siberian platform in the Silurian (East Siberia between the Yenisey and Lena Rivers), and was featured with continuous cyclic sedimentation (TESAKOV et al., 2003). Widespread red gypsiferous marls and gypsum beds, found over much of the Siberian palaeocraton area in Silurian rocks, together with palaeomagnetic data, indicate movement of the terrane into more temperate palaeolatitudes, and also reflect the shift to more arid climates (TESAKOV et al., 2003; COCKS & TORSVIK, 2007). The extensive shallow-water siliciclastics deposited in the Tuva-Mongolia area presumably partly reflect the lower average temperatures in the northern part of the Siberian terrane collage (COCKS & TORSVIK, 2007). Consequently, the Siberian palaeocontinent has been suggested as a northern terrane, representing high-latitude cold-water faunal assemblages, which has been subsequently attributed to the rich *Tuvaella* fauna with certain reluctance (COCKS & TORSVIK, 2007). However this does not go in accordance with rich and diverse vertebrate fauna, recorded from the Early Silurian of this region (ŽIGAITĖ, *in press*), and barely correct regarding the common organism preferences in ecological niches as well. The latter would suggest any rich shelf faunal assemblages tending to occur in warm-water basins in the Early Palaeozoic. In accordance to this suggestion, vertebrate microremains are numerous, and appear in a wide range of facies of the Lower Silurian of the Siberian platform, referred to as bar belt, restricted shallow shelf, brasckish lagoon and coastal belt facies (KARATAJŪTĖ-TALIMAA & PREDTECHENSKYJ, 1995), and as in shallow water facies of Tuva. For instance, thelodonts *Angaralepis* and *Loganellia* are common in shallow water sediments such as shallow shelf, marine delta and brackish lagoon facies, whereas *Talimaalepis* is recorded both in shallow and deeper shelf sediments. The north-west Mongolian early vertebrate material comes from the molasse – type Wenlockian facies, rich in the same unique *Tuvaella* fauna (MINJIN, 2001), which accompaniment provides strong implication of the edemism of the province, as mentioned above (COCKS & TORSVIK, 2007).

The low stratigraphical level of the occurence of most of the early vertebrate taxa studied, as well as abundance and endemism of different groups of vertebrates, all indicate early appearence and intensive forward “bloom” of Silurian vertebrates, compared to the corresponding data from the other palaeobiogeographical provinces, such as the Baltic Basin or Canadian Arctic in the Silurian (KARATAJŪTĖ-TALIMAA & BRAZAUSKAS, 1994; MÄRSS et al., 2002, 2006). This may infer the region not only as a separate palaeobiogeographical province, but also as a place of origin and radiation of at least some early vertebrates. This idea of pre-Silurian early vertebrate origination and speciation in equatorial epicontinental seas of the Siberian terrane has already been rised in previous works (BLIECK & JANVIER, 1993).

To conclude, the abundance of endemic early vertebrates in the Silurian of central Asia and the Siberian platform, together with the richness of other endemic faunal groups reported in the literature, refer to warm and productive palaeobasins spread as epeiric seas over the Siberian palaeocontinent, and indicates it as a possible place of origin and radiation of early vertebrates (BLIECK & JANVIER, 1993; COCKS & TORSVIK, 2002).



Text-fig. 6. 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; triangled line, subduction zone; broken line, spreading ridge. Modified and complemented after COCKS AND TORSVIK, 2007.

4. Sequence stratigraphy and tectonic setting of the Silurian Baltic Basin

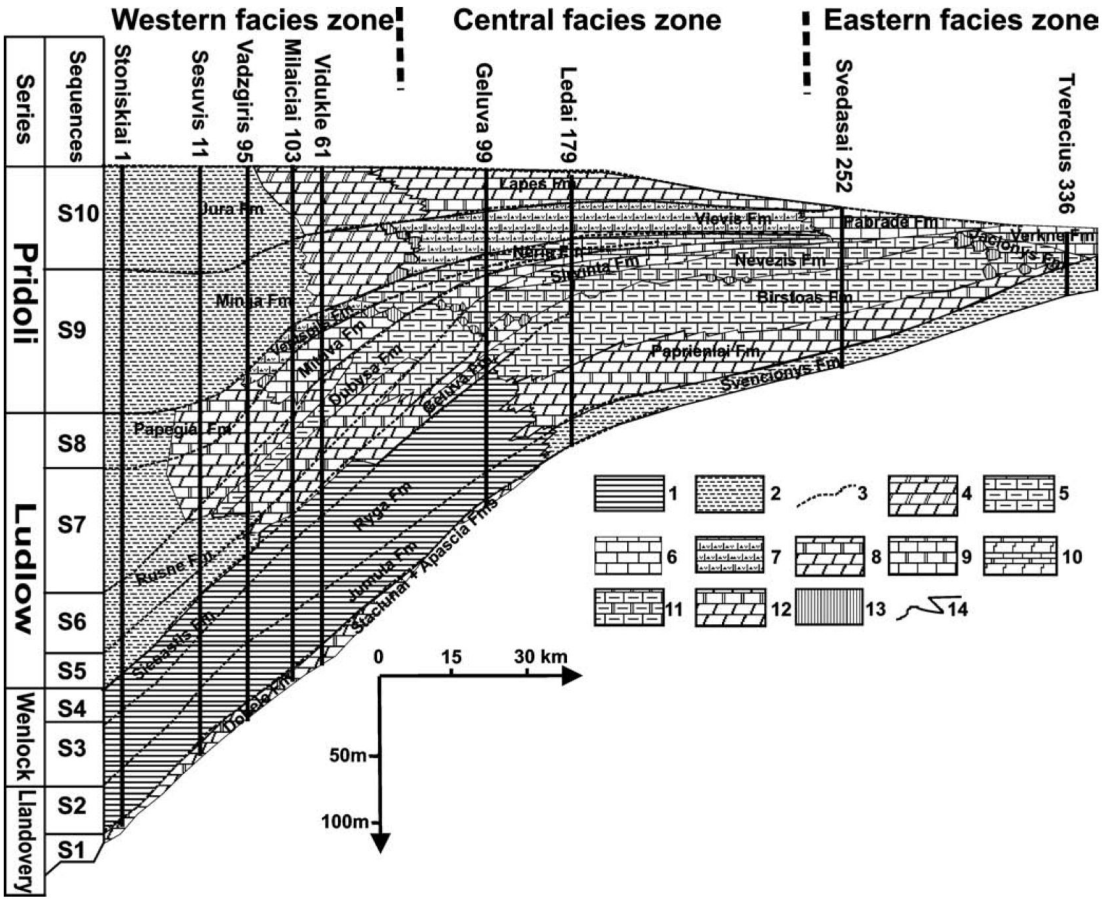
Article VI - VERNIERS, J., MALETZ, J., KRIZ, J., **ŽIGAITE, Ž.**, PARIS, F., SCHÖNLAUB, H-P., WRONA R., **2007**. An overview of the Silurian System of Central Europe. *Acta Palaeontologica Sinica*, 46 (Suppl.): 507-510.

Article VII - J. VERNIERS, J. MALETZ, J. KRIZ, **Ž. ŽIGAITE**, F. PARIS, H-P. SCHÖNLAUB, R. WRONA., **2008**. "SILURIAN". *In:* T. McCann (ed.) "The Geology of Central Europe". *Special Publication of the Geological Society, London*, 249-302.

The Baltic Basin was a part of the Baltica palaeocontinent, which existed in the Silurian. Warm greenhouse Silurian climate (HALLAM & WIGNALL, 1997; BRENCHLEY et al., 2001; VERNIERS et al., 2008), and relatively alkaline sea-water pH of about 8 (WILDE et al., 1991) allowed extensive worldwide deposition of calcium carbonate in the Silurian tropical shelf-seas. Carbonate shelf sediments were broadly deposited on the large Baltica palaeocontinent during the Silurian period as well, though major part of the Silurian succession of the Baltic Basin presently traces in the subsurface (Lithuania, Poland), outcrop areas exposing only northwards (Estonia and Gotland, Sweden).

The Baltic Basin originated on the southwestern margin of the East-European craton during the Early Palaeozoic, as a part of a marginal sedimentary basin system (LAZAUSKIENĖ et al., 2003). Established on the southwest Baltica as a continental margin basin in the beginning of the Palaeozoic, in response to the breaking apart of the Rodinia megapalaeocontinent, the Baltic Basin has reacted as a rather passive margin during the Silurian. Nevertheless, some tectonic stresses has been induced from one side by the mid Silurian start of Laurentia-Baltica collision, the Scandian orogeny, and the closure of the Tornquist Sea with soft docking of Far Eastern Avalonia and Baltica starting in the Late Ordovician (VERNIERS et al., 2008), early or mid Ashgill times, which is proven by transport of sediments and reworked microfossils over the Tornquist suture (VECOLI & SAMUELSSON, 2001a, b). Hence the Baltic Basin is interpreted as a flexural foreland basin (POPRAWA et al., 1999) to which an additional tectonic load at the southwestern margin is required for the model to explain fully the shape of the Baltic Basin (LAZAUSKIENĖ et al., 2002). Implying from the geodynamic modeling, the Baltic foreland basin originated as a result of the complex interaction of orogenesis and dynamic loading (LAZAUSKIENĖ et al., 2002), suggested from the geodynamics constraints and lithofacies analysis (LAZAUSKIENĖ et al., 2003).

The Silurian of the Baltic Basin is remarkably undeformed and well preserved on the southwestern part of the Baltic shield. Any subsequent tectonic deformation of the Silurian succession after the Pridoli or Lochkovian has not occurred, and hence the sediments underwent very low heating and are mostly subhorizontally stratified.

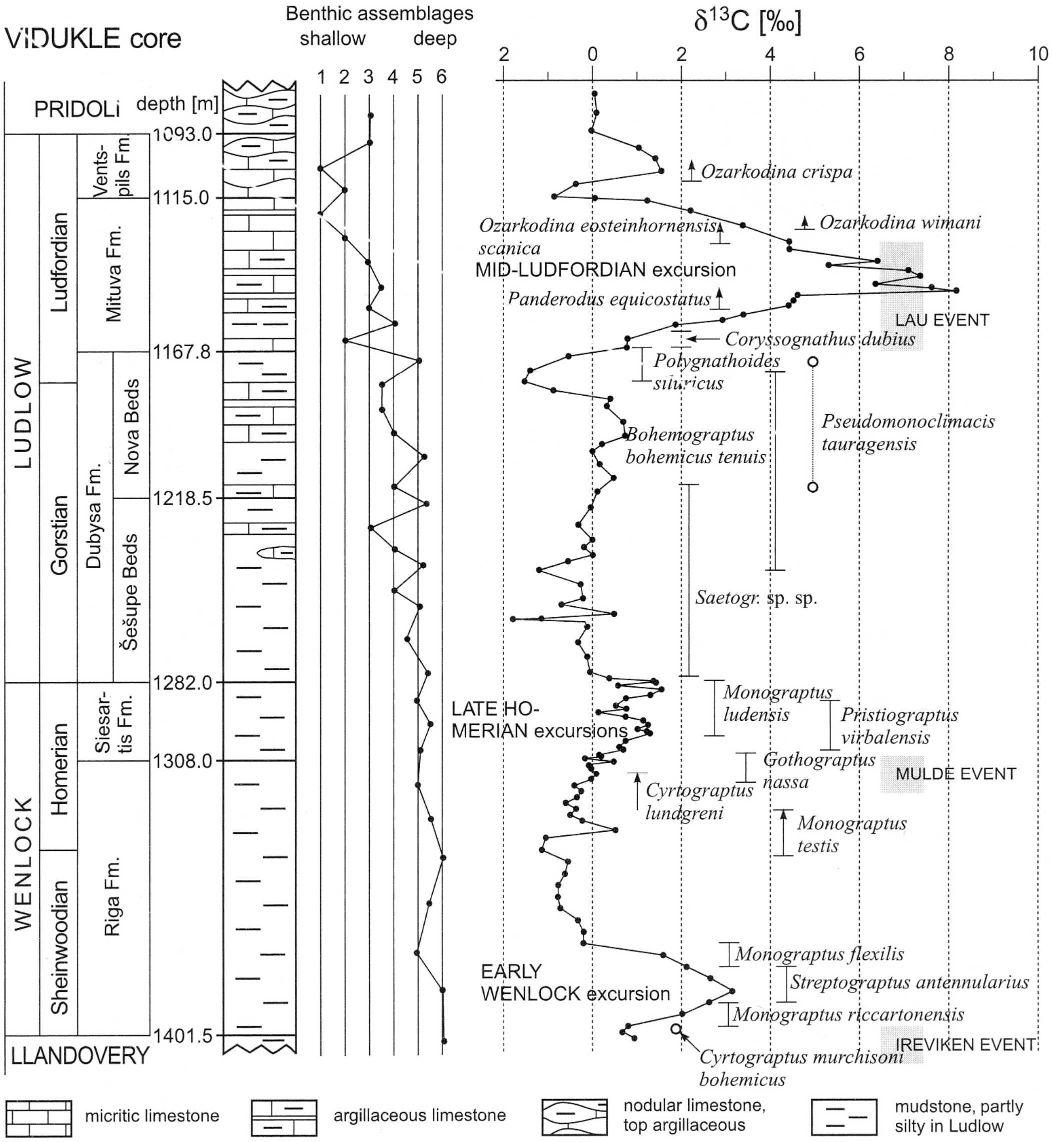


Text-fig. 7. Lithofacies cross-section throughout the central and eastern parts of the Silurian Baltic Basin, distribution of depositional sequences and main tectono-sedimentary stages of basin development. Key: 1, shales; 2, carbonaceous claystones; 3, boundaries of sequences; 4, carbonaceous marlstones; 5, clayey limestones; 6, limestones; 7, organoclastic limestones; 8, clayey limestones and marlstones; 9, dolomites; 10, dolomites and gypsum; 11, clayey dolomites; 12, dolomites interbedded with marlstones; 13, reefs; 14, boundaries of formations. From VERNIERS et al., 2008.

The Baltic Basin is considered to contain the thickest Silurian beds and stratigraphically the most complete geological section in Baltica from the lowest Llandovery to the top of the Pridoli. There are no hiatuses recognized in the central part of the basin, but only small stratigraphical breaks on the southeastern slope of the Baltic Basin, in the lower and upper parts of the section (PAŠKEVIČIUS, 1997). It can be characterized as a mixed clastic and carbonate succession, with siliciclastic sedimentation dominating in the westernmost part of the basin, and mixed carbonates and clastics in the central and marginal zone. Graptolite shales dominate the sedimentary succession in the western and central parts of the Baltic Basin, grading into marlstones in the transitional zone, and to the carbonate platform in the shallow eastern margin of the Lithuanian part of the Baltic Basin (Text-fig. 7). Investigation of various faunal groups shows the continuous sedimentation in the axial part of the Baltic Basin, with only short sedimentation breaks occur as pyritized rock surfaces and sudden changes in rock composition (PAŠKEVIČIUS, 1997).

Early vertebrate microremains are most common in carbonaceous – clayey facies lacking graptolites, which also represents the regression of the basin and occurs in the Upper Ludlow and Pridoli. During Ludlow and Pridoli time the Silurian basin was becomming significantly narrower and the sediment accumulation rate is supposed to be increasing (VERNIERS et al., 2008).

Several bio-events can be traced in the Silurian in the Baltic Basin, such as the severe extinction event of conodonts and acritarchs at the base of the Wenlock (Ireviken Event, JEPPSON, 1987), or major crisis amongst the graptolites, corresponding to the Mulde Event in the Baltic Basin, and the most prominent early – middle Ludfordian event (Lau Event) with profound changes in δ^{13}C content (MARTMA et al., 2005) as well as in faunal composition of vertebrates, graptolites, ostracoderms, acritarchs, corals and conodonts (VERNIERS et al., 2008) (Text-fig. 8). Finnaly, a middle Pridoli event with extinction amongst corals, conodonts, graptolites and a diversity rise in the chitinozoans (KALJO et al., 1991), can be clearly distinguished in the Upper Silurian succession of the Baltic Basin as formation boundary, and simultaneously documented as chemostratigraphical shift by δ^{18}O analysis on biogeneic apatites (ŽIGAITĖ et al., 2008), discussed further below in this work. The models proposed by JEPPSON (1990, 1998) relate all these bio-events (especially those of conodonts), recorded in the Silurian succession of the Baltic Bassin, to changes in climate oceanic circulation and terrestrial input, resulting in the humid episodes with high bio productivity and mainly estuarine circulation on the shelf, alternating with more arid episodes with low bio productivity and mainly anti-estuarine circulation on the shelf (CALNER et al., 2004).

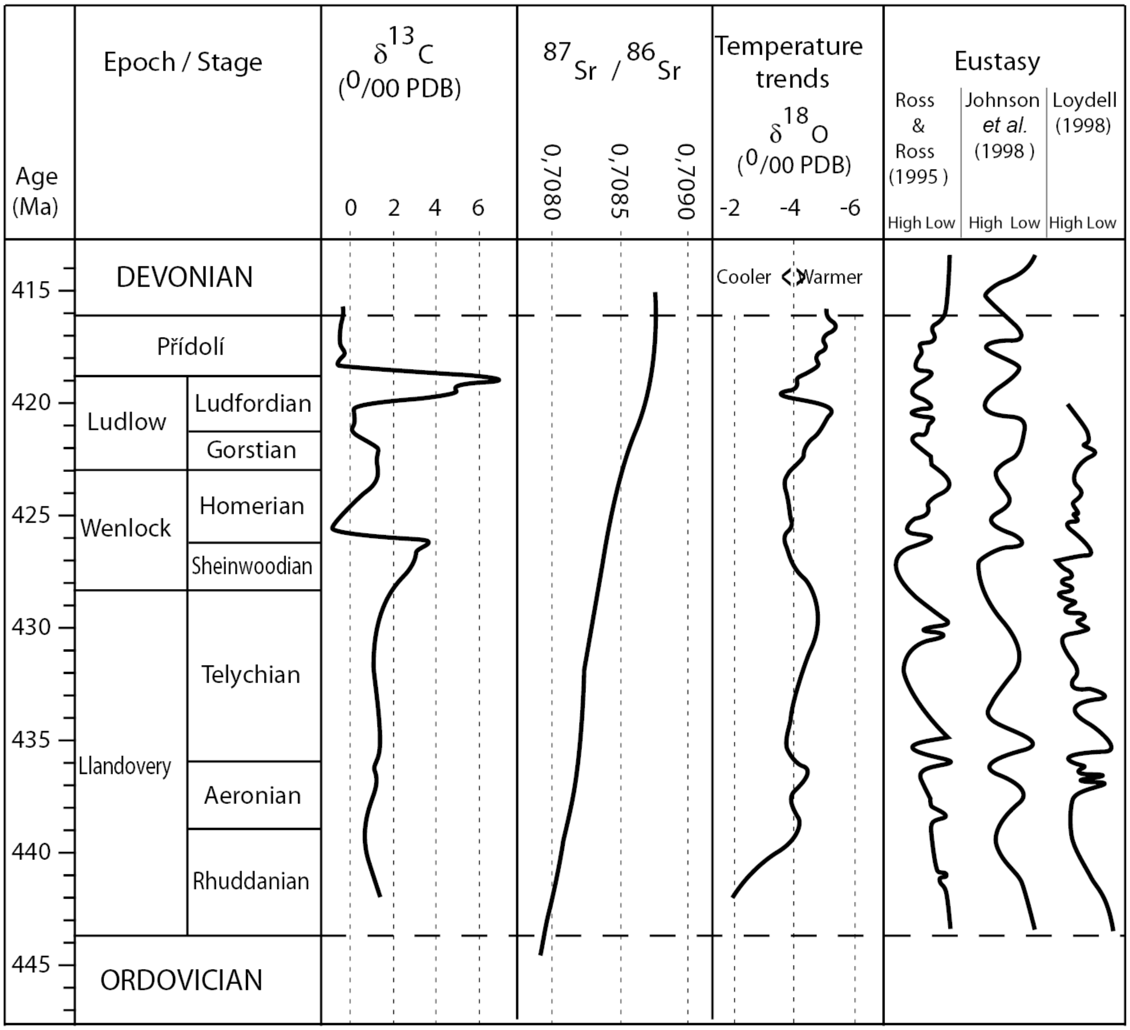


Text-fig. 8. The Viduklė core section: stratigraphy, lithology, sea level changes interpreted as benthic assemblage (BA) succession, and the $\delta^{13}C$ trend dated by graptolites as well as conodonts. From MARTMA et al., 2005.

Several reconstructions of the global eustatic sea-level curve for the Silurian can be reported from the literature (MCKERROW, 1979; Lenz, 1982; JOHNSON et al. 1991, 1998; ROSS & ROSS, 1996; LOYDELL, 1998) (Text-fig. 9). The four high stands are excluded in the Llandovery series, which may be explained by the melting of the ice sheets remaining from the Late Ordovician (VERNIERS et al., 2008). The low sea-level are recored at the base and the top of the Wenlock series, with a sea-level high in between. The Ludlow generraly represents a sea-level high, with a major sea-level drop in the middle Ludfordian, corresponding to the Lau Event, well traced in the Baltic Basin.

Concerning the Pridoli, no clear global eustatic signature is emerging caused by the insufficient data (VERNIERS et al., 2008). Taking into account this data incompletion, as well as the arguable sequence stratigraphy determination for the Upper Silurian of the Baltic Basin (LAZAUSKIENĖ et al., 2003) discussed above, further chemostratigraphic data such as isotope curves, could be essential contribution for the global eustatic reconstructions of the Pridoli. The isotope stratigraphy, such as $\delta^{18}O$ curves of the biogenic apatite, revealed in this research and presented in the following chapter below, together with facies analysis and biostratigraphy, appear to be important tools in constructing sequence stratigraphy frameworks of sedimentary basins.

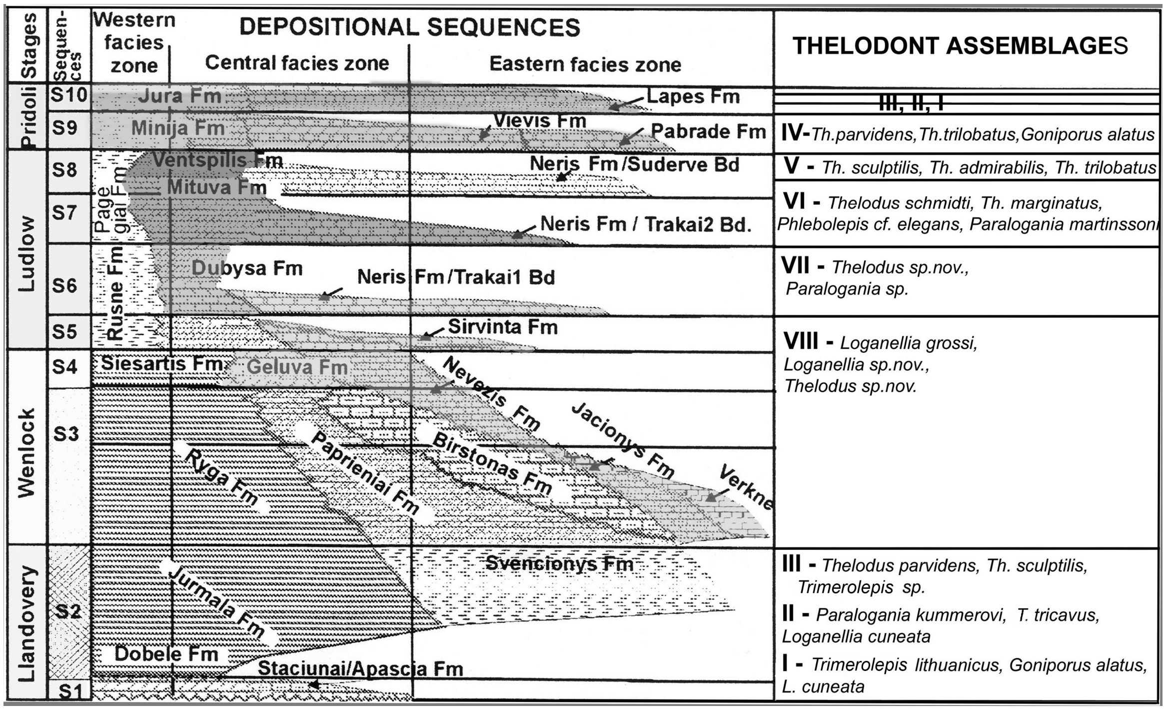
Regarding the sea-level changes in the Baltic Basin, after the Hirnantian glaciation in the southern hemisphere at the end of the Ordovician, the entire area of East Baltic was only covered by a very shallow basin. The transgression took place from the early to late Llandovery. The metabentonites inliers preserved indicate deep water marine sedimentary environment. In the late Llandovery a shallower facies started to overlap deep water transgressive succession. The presence of a shoreline and deltas in the east and southeast of the Baltic Basin correspond to the sea-level high stand, as they are devoid of terrigenous material, this indicates possible southward extension of the basin. In the early Wenlock the basin were becomming shallower and a gradual replacement of the clayey facies by the carbonaceous ones occurred.



Text-fig. 9. Silurian sea-level curves in comparison to strontium, carbon, and oxygen isotope curves. After MELCHIN et al., 2004; from VERNIERS et al., 2008.

The clear regression started at the second half of the early Wenlock in the Baltic Basin, and continued up to the lower Ludlow. The area occupied by the basin decreased and regressive deposits were formed under rapid sedimentation conditions. Later on, in the second half of Ludlow, the regression reached its maximum and the marginal zone of the basin show continental – lagoonal type facies, with inferred lower (or sometimes higher) water salinity and the oxic conditions of an arid climate. At the end of Ludlow a short-term marine transgression occurred.

The last significant Silurian regression in the Baltic Basin took place in the middle of the Pridoli. Although the large thickness of Pridoli strata in southwestern Lithuania indicates a rapid sedimentation within a basin, that remained rather small.
Composition of the early vertebrate – thelodont assemblages in the Baltic Basin appears to be mostly facial but formational dependant, which gives a good evidence of water dept, basin evolution, and stratigraphic sequences as well. Still the formational dependence and facial distribution of Wenlock and Lower Ludlow thelodont assemblages remains under consideration. The vertical and horizontal distribution of the eight thelodont assemblages in the Silurian (Wenlock, Ludlow and Pridoli) of Lithuania described so far (KARATAJUTĖ-TALIMAA & BRAZAUSKAS, 1994), have been plotted to illustrate the sedimentary sequences biostratigraphically (Text-fig. 10).



Text-fig. 10. Generalized chart of the depositional sequences and the corresponding distribution of the early vertebrate (thelodont) assemblages of the Silurian Baltic Basin of Lithuania (for the key lithology see Text-fig. 6). Modified after LAZAUSKIENĖ et al., 2003.

The distribution of the earliest thelodont assemblage, represented by *Loganellia grossi* vertebrate biozone (KARATAJUTĖ-TALIMAA, 2000), and rangin from Jočionys Fm., Verknė Fm., Nevėžis Fm., and Vėluva Fm. of the Wenlock series to Širvinta Fm. and Trakai beds in lower Ludlow, is not in agreement with the sequence stratigraphy model, proposed by LAZAUSKIENĖ et al. (2003). Concerning the distribution of thelodont taxa, attribution of Trakai beds to the sequence S6 (Text-fig. 10) is implausible. The Pridoli series of the is particularly rich in early vertebrate microremains, which allowed to analyse their oxygen isotope composition, presented below in this work. Tholodont specific composition change rapidly in the uppermost Silurian of the Lithuanian Baltic Basin, making two separate thelodont assemblages in the lower Pridoli, and two different assembleges in the upper Pridoli (KARATAJUTĖ-TALIMAA & BRAZAUSKAS, 1994), after the middle Pridoli event, discussed further below in this work.

Sequence stratigraphic framework, based on conodont biostratigraphy, well-log and core data of reference wells of the main Silurian lithofacies zone representing the Baltic Basin of Lithuania, have been made attempting to reconstruct the depositional evolution of the Silurian succession (LAZAUSKIENĖ et al., 2003). The sequence stratigraphic analysis defined 10 depositional sequences in the estern half of the Silurian Baltic Basin (Text-fig. 10). Low terrigenous influx has been suggested for the Llandovery sequences, while the Wenlock and Lower Ludlow sequences depict the accelerating depositional environment. Sequences of the Late Ludlow and Pridoli comprise the final stages of basin infilling (LAZAUSKIENĖ et al., 2003).

Five main periods of the Baltic Basin development can be distinguished: middle Llandovery – early Wenlock, late Wenlock – early Ludlow, late Ludlow, and Pridoli (PAŠKEVIČIUS, 1997). They all are related to eustatic sea level changes, tectonic development and local facies distribution, and are reflected in the arrangement of the sedimentary sequences.

In conclusion, the general sedimentary trend throughout the Silurian based on the sequences stratigraphy framework, indicates a regression of the palaeobasin that is related to outpace of the carbonate sediementation and progradation of the carbonate platform on the periphery of the Silurian Baltic Basin. The sedimentation pattern of the Silurian Baltic Basin was closely related to the evolution of the orogenic systems in the west that controlled subsidence and sedimentation rates in the foreland (LAZAUSKIENĖ et al., 2003). Absence of any tectonic deformation after the Silurian has preserved the sediments mostly subhorizontally stratified, and has permeated through very low heating.

Pridolian succession of Lithuania is the thickest in Baltica and almost complete, dominated by shelf carbonate sediments, and can be characterized by prevailing early vertebrate fauna. The chemostratigraphical data incompletion on the Pridoli successions worldwide (VERNIERS et al., 2008) has induced the $\delta^{18}O$ analysis of early vertebrate and conodont fossil apatite from the Pridoli sections of the Baltic Basin of Lithuania, which was a part of this work and is presented in the following chapter below.

5. Early vertebrate and conodont fossil apatite as a proxy in palaeoclimate reconstruction and chemical stratigraphy

Article VIII - Žigaitė, Ž., Joachimski, M.M., Lehnert, O., *ready for submission*. The ($\delta^{18}O$) composition of conodont apatite indicates climatic cooling during the Middle Pridoli seal level fall in the Baltic Basin.

The biogenic apatites are supposed to have the properties required for an ideal geochemical recorder: they respond sensitively during their formation to the aqueous environment, and then preserve perfectly their record after death of the organism (KOLODNY et al., 1983). Recent studies on early Palaeozoic conodonts (WENZEL et al., 2000; JOACHIMSKI & BUGGISH, 2002; JOACHIMSKI et al., 2003, 2004; LEHNERT et al., 2007) show the conodont apatite as a reliable proxy for high-resolution palaeotemperature curve reconstruction. The oxygen isotope composition of phosphate remnant (PO_4^{3-}) in fossil apatite of marine ectotherm organisms (fish, conodonts, lingulids) depend on ambient palaeoseawater temperature and composition (KOLODNY et al., 1983; PUCÉAT et al., 2004). It has been shown in number of works on phosphate geochemistry, that the isotopic exchange between aqueous inorganic solutions and PO_4^{3-} ions is so slow as to be negligible even over geological time scales, except of at a high temperatures (TUDGE, 1960; WINTER et al., 1940; BRODSKII & SULIMA, 1953). And it has been demonstrated repeatedly (TUDGE, 1960; DAHMS & BOYER, 1973) that in enzyme-catalysed reactions the exchange of ^{18}O between water and and PO_4^{3-} is extremely rapid, thus mechanisms suggested for the biological formation of apatites would result in a oxygen isotope composition of biogenic apatites nearly identical to the ambient palaeowater (LEONARD & SCULLIN, 1969).

The conodont apatite has been distiguished among other apatites for being secreted in the most near-isotopic equilibrium with paleoseawater (KOLODNY et al., 1983), and also better preserve an unaltered $^{18}O/^{16}O$ ratio compared to commonly analysed brachiopod apatite or brachiopod calcite (encountering even diagenetically stable brachiopod low magnesium calcite) (WENZEL & JOACHIMSKI, 1996; JOACHIMSKI & BUGGISH, 2002; JOACHIMSKI et al., 2004). The oxygen isotopic composition of conodont apatite is supposed to be minimal affected by increasing burial temperatures and no prominent difference in the oxygen isotopic ratios between conodont taxa have been observed occurring preferentially in shallow water or pelagic deposits (WENZEL at al., 2000; JOACHIMSKI et al., 2003). Conodont apatite susceptibility to the pH variations of the ambient sea water is also close to a negligible margin, contrary to the brachiopod calcite, which is highly affected by sea-water pH change (JOACHIMSKI et al., 2004). The brachiopod and conodont apatite $\delta^{18}O$ values from the Silurian successions (Llandovery-Ludlow) of the Baltic Basin have been compared, brachiopod apatite gaving significantly lower $\delta^{18}O$ values than coeval conodont apatite, resulting in a wide variation of brachiopod data (13.0 to 17.5‰ V-SMOW), while homogenous conodont $\delta^{18}O$ data had variation close to the analytical precision (± 0.2‰) (WENZEL et al., 2000). Moreover, the $^{18}O/^{16}O$ of conodont biogenic apatite is very similar to the $\delta^{18}O_{apatite}$ values of modern and Mezozoic tropical biogenic apatites, and gives comparatively realistic palaeotemperatures by assuming a modern 'ice-free' oxygen isotope composition of the contamporaneous palaeoseawater (WENZEL et al., 2000).

Quoting the fact that the $\delta^{18}O$ values of conodont apatite translate into more realistic palaeotemperatures, conodont apatite record of Palaeozoic temperatures has been considered as more reliable compared to that of coeval brachiopod calcite or apatite (JOACHIMSKI et al., 2003, 2004). The very important point in palaeoeclimate estimations is also the supposed exceptionally marine habitats of conodont animals (SANSOM et al, 1992; DONOGHUE et al., 2000). Further in this study oxygen isotopic composition of conodont biogenic apatite is considered as the best proxy known so far for unraveling the oxygen isotope ratio of ancient oceans, and hence to reconstruct oceanic palaeotemperature and water salinity.

Although the supposed good resistance of conodont fossils to diagenetic alteration and their ubiquity in Palaeozoic marine sedimentary sequences make conodonts particularly attractive for geochemical palaeoseawater studies, issues of post-depositional chemical overprinting of primary compositions should be taken in consideration. The primary biogenic apatite composition may still be strongly modified by diagenetic proceses and altered samples can provide erroneous temperature estimates. It is thus critical for palaeoenvironmental interpretations to distinguish between pristine and alterated phosphatic remains (TROTTER et al., 2007). The physical properties, crystalline structure, and inherent permeability of the component conodont tissues determine their chemical integrity and succeptibility to diagenesis, which is crucial in characterizing palaeoseawater composition and palaeoenvironmental changes (PUCÉAT et al., 2004; TROTTER et al., 2007). The subsequent comprehensive investigations by transmission electron microscopy (TEM) and parallel Raman spectroscopy cristallinity studies (both discussed in detail further in this work) suggest that cancellate albid crown of conodonts is the most resistant apatite tissue to diagenetic modification (PUCÉAT et al., 2004; TROTTER & EGGINS, 2006; TROTTER et al., 2007). Summarizing, the conodont crown albid tissue apatite can be considered in many aspects as the most suitable material for oxygen isotope investigations and palaeoseawater reconstructions, if preserved under favorable diagenetic circumstances (HOLMDEN et al., 1992; TROTTER & EGGINS, 2006; TROTTER et al., 2007).

However, attempts to use conodont apatite for oxygen isotopic analysis are frequently hampered the very small size of the conodont elements in the Early Palaeozoic, icluding the Silurian. Laser-based microsampling or high-temperature reduction techniques (TC-EA) have made it possible to measure the oxygen isotopic composition of conodont microsamples, not exceeding ≤ 1 mg (JOACHIMSKI & BUGGISH, 2002). Despite the advanced geochemistry technologies, it is still quite difficult to get 1 mg of conodont fossils in Silurian, sometimes more than 100-200 conodont elements are required. While contemporaneous early vertebrate fossils, which are presented by larger, more massive and robust exoskeletal microremains (dentine scales), can reach 1 mg sample with only a few scales.

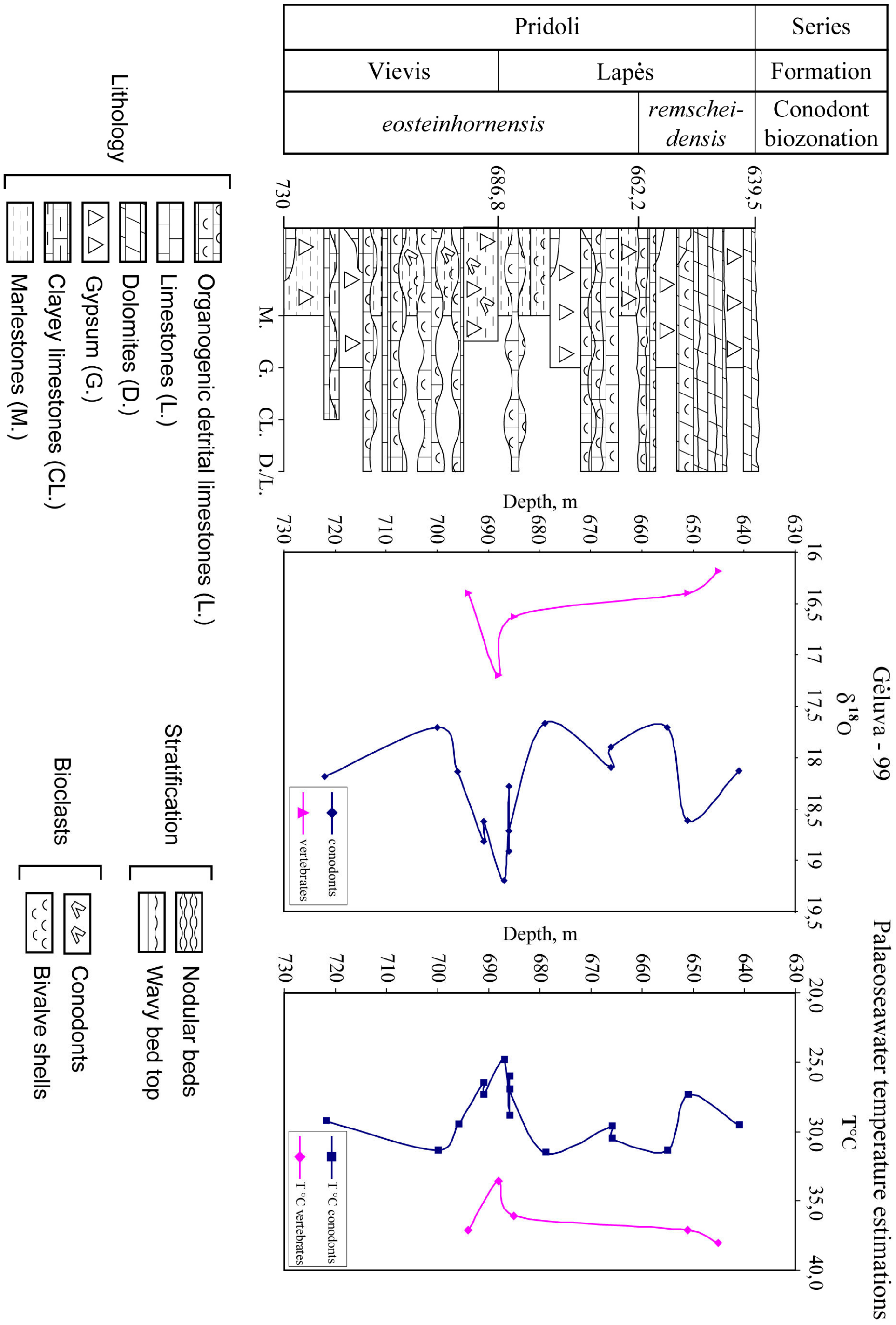
The Palaeozoic early vertebrate fossil apatite high density phosphatic tissues as dentine and enameloid are comparable in the physico-chemical properties to conodont crown tissues, although they have not yet been properly tested for $\delta^{18}O_{apatite}$ composition and palaeotemperature calculations. The early vertebrate exoskeleton microremains (dermal scales) possess homologous teeth histology, with compact surface layer of diagenetically-resistant enameloid covering the dentine scales (MÄRSS et al., 2007). The dense microcrystalline ultrastructure of conodont apatite is close in its consistence to vertebrate tooth enamel (JOACHIMSKI et al., 2004), and it has been shown that tooth enamel is also relatively resistant to any diagenetic modification of the primary isotopic composition (QUADE et al., 1992; SHARP et al., 2000). Moreover, initially it was the oxygen isotope composition of fossil fish biogenic apatites which have been used to reconstruct past seawater temperature variations (KOLODNY & LUZ, 1991).

The main idea and aim of this study was to test vertebrate fossil apatite as the $\delta^{18}O$ recorder and palaeoenvironmental proxy in comparison to coeval conodont apatite (ŽIGAITĖ et al., 2008). The chemostratigraphical usability of early vertebrate and conodont apatite was tested while producing the first $\delta^{18}O$ biogenic apatite curve for the Pridoli series of the Baltic Basin, on example of Gėluva-99 borehole.

The Pridolian sequence of the Upper Silurian of the Baltic Basin has been chosen for the early vertebrate and conodont $\delta^{18}O$ analyses for several reasons: 1) The phosphatic fossil material (both conodonts and early vertebrates) are supposed to be minimum diagenetically alterated, if to compare with the other Late Silurian sedimentary basins worldwide, due to the tectonic stability and unalteration of the Silurian strata of the Baltic Basin (see the discussion in previous chapter above). Any tectonic deformation has not occurred after the Silurian in the Baltic Basin, and hence the sediments underwent very low heating and are mostly subhorizontally stratified (VERNIERS et al., 2008). Subsequently, the phosphatic microfossils tend to retain their primary composition: conodont elements show colour alteration index (CAI) being less than ≤ 1.5, and early vertebrate microremains with minimal colour alteration respectively; 2) Conodont elements and early vertebrate microremains are very abundant fossils in the late Silurian sediments of the Baltic Basin of Lithiuania, even if considering relatively small core samples, so it was easy to collect the required quantity of phosphatic remains in the choosen stratigraphical points; 3) Neither the $\delta^{18}O_{apatite}$ nor $\delta^{18}O_{calcite}$ isotope curves have yet been made for the Pridoli series of the Baltic Basin.

The revealed conodont $\delta^{18}O_{apatite}$ values of the Upper Silurian (Pridoli) of southern Baltic Basin (Lithuania) ranged within from 17.7 to 19.2‰ V-SMOW with average values around 18.3‰., and the early vertebrate $\delta^{18}O_{apatite}$ values offset in 2.5 ‰ V-SMOW from the corresponding Pridolian conodont samples of the Baltic Basin, ranging from 15.2 to 17.4‰ V-SMOW respectively, with average values around 16.3‰ V-SMOW (Text-fig. 11).

The Late Silurian (Pridoli) palaeoseawater temperatures derived from the conodont apatite ranged from 24.8 – 31.5 °C, and those derived from the early vertebrate $\delta^{18}O_{apatite}$ are approximatelly in 10 °C higher, and range from 32.6 – 38.1 °C correspondingly (Text-fig. 11). Early vertebrate samples from several reference boreholes have been analysed, and give similar palaeotemperature estimations (Text-fig. 12). The temperatures revealed from conodont $\delta^{18}O_{apatite}$ record are rather realistic: a bit higher than those derived from conodonts of the Middle Devonian (Eifelian to early Givetian), but lower that those of the Late Devonian (Frasnian), the latter being close to or above the lethal termal limit for at least marine invertebrates (JAOCHIMSKI et al., 2004). The temperatures derived from the early vertebrate $\delta^{18}O_{apatite}$, are higher, and thus translate into unrealistic warm palaeotemperatures, if using the equation proposed by KOLODNY et al. (1983). This discreapancy in the $\delta^{18}O_{apatite}$ values of early vertebrates and conodonts in the coeval Pridolian samples of the Baltic Basin can not currently be explained satisfactorily. The resulted conodont apatite $\delta^{18}O$ values translating into more realistic palaeotemperatures confirm that conodont elements record Palaeozoic temperatures more faithfully than coeval early vretebrate exoskeleton microremains.



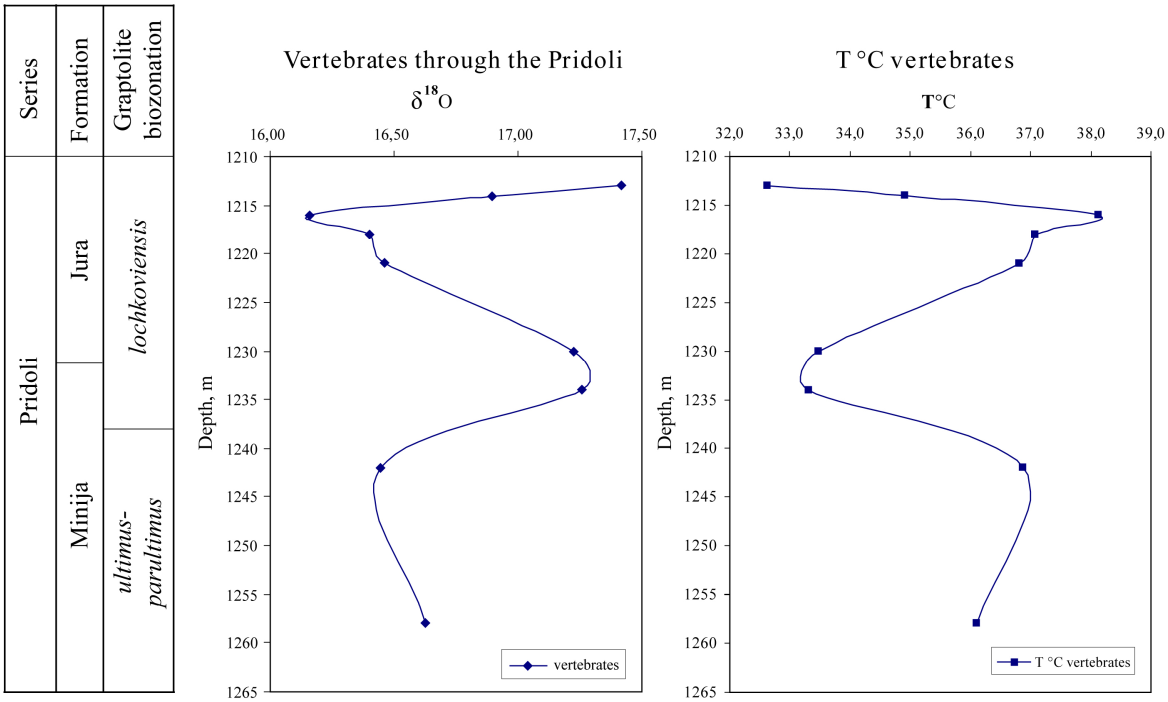
Text-fig. 11. Comparison of $\delta^{18}O_{apatite}$ values measured, and palaeotemperatues (T °C) estimated respectively on early vertebrates and conodonts from the Upper Silurian

Pridolian section of the Gėluva-99 borehole, the Silurian central facies zone of Lithuania (Baltic Basin, Lithuania).

The palaeoseawater temperatures have been calculated using the following equation, as well as assumption that the oxygen isotopic composition of seawater during the Silurian, considering the warm oceanic water at the low latitudes of the Baltic Basin in Late Silurian, (JOACHIMSKI et al., 2003, 2004; LEHNERT et al., 2007):

$$T[°C] = 113.3 - 4.38\,(\delta^{18}O_{apatite} - \delta^{18}O_{sea\text{-}water})$$

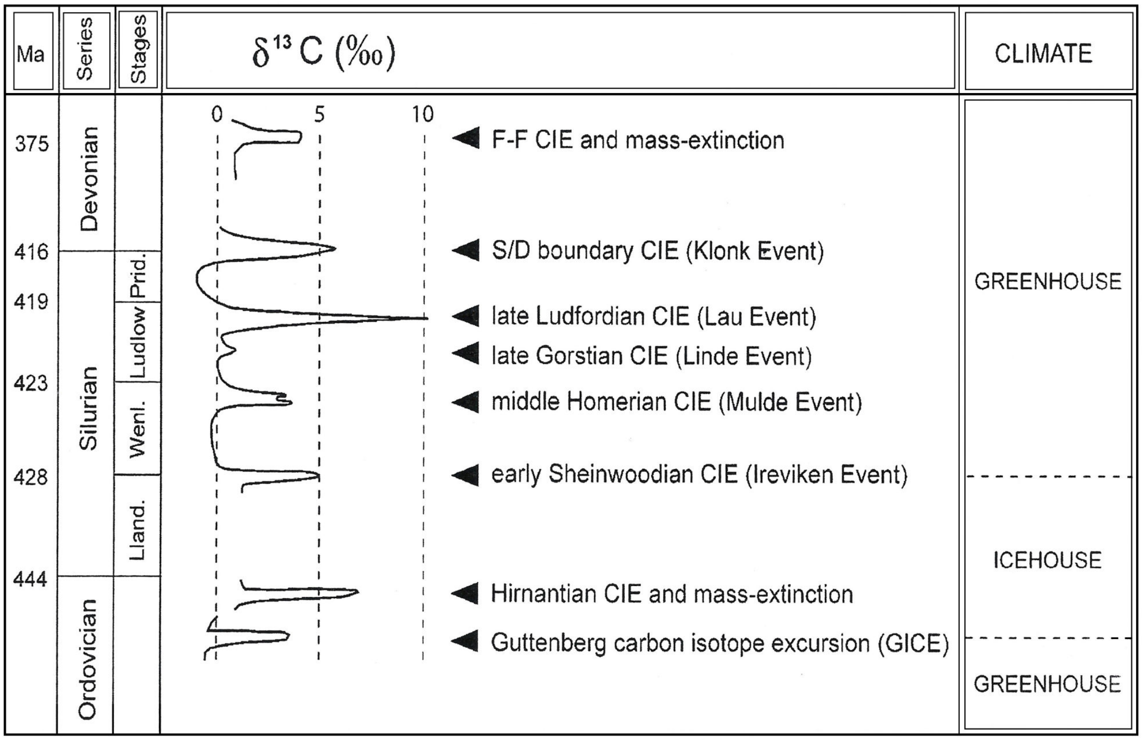
KOLODNY et al., 1983.



Text-fig. 12. The $\delta^{18}O_{apatite}$ values measured, and palaeotemperatues (T °C) estimated respectively on early vertebrates from the Upper Silurian Pridolian sections in the following boreholes of the Silurian western facies zone of Lithuania: Gėluva-119 (3 points), Liepkalnis-137 (1 point), Stoniškiai-7 (1 point), and Nida-44 (4 points). The formation boundary and depth referrences correspond to Nida-44 borehole (Baltic Basin, Lithuania).

A major limitation while estimating the palaeoseawater temperatures is the unknown primary $\delta^{18}O_{water}$ composition of the palaeo-oceans, which depended on general palaeoclimate, water temperature and salinity, is the main limitation in the palaeoseawater temperature estimations. An ideal case would be if one could independently obtain a value for $\delta^{18}O_{paleowater}$ in each case.

The palaeoclimate influence greatly the $\delta^{18}O_{water}$ of the palaeo-oceans, as well as the salinity. Global cooling and glaciations at the Earth poles deplete ocean water from light ^{16}O, which is easier to evaporate as meteoric water, and get stored in the extensive ice-caps. Breaking this accordance, the equatorial ocean water goes in the same equilibrium during high warming periods, and is depleted from light ^{16}O as well, since an increase in evaporation eliminates light ^{16}O easier as meteoric wapour (HOEFS, 1997). Moreover, water salinity reflect an important control on the oxygen isotopic composition of sea-surface waters, as the same increase in evaporation will enrich such waters in ^{18}O. Oposite, fresh water dilution will result in an enrichment in ^{16}O (GROOTES, 1993). Consequently, the value of $\delta^{18}O_{paleowater}$ is not easy to estimate.



Text-fig. 13. The major positive carbon isotope excursions of the middle Palaeozoic and their relationship to biotic events. Modified and extended from MUNNECKE et al., 2003; after ERIKSSON & CALNER, 2008.

Silurian is reported as a greenhouse climate period (HALLAM & WIGNALL, 1997; BRENCHLEY et al. 2001; VERNIERS et al., 2008), and a global Silurian temperature of 20°C has been reconstructed, which is significantly warmer than the modern global average of 15°C (BUDYKO et al., 1987). Thoug the Silurian climate was still somewhat cooler than the Devonian one (WILDE et al., 1991). Carbon, oxygen en strontium isotope curves have been produced in recent years in order to reconstruct the Silurian climate (MELCHIN et al. 2004; VERNIERS et al, 2008). The $\delta^{18}O$ curves published by SAMTLEBEN et al. (1996), WENZEL & JOACHIMSKI (1996), BICKERT et al. (1997b), AZMY et al. (1998), HEATH et al. (1998) show similar trends of reduction in values indicating possibly an overall global warming in the Silurian. Subsequently the Pridoli is reported as a warm period, with global greenhouse conditions (MUNNECKE et al., 2003; ERRIKSON & CALNER, 2008), thus the estimation of $\delta^{18}O_{sea\text{-}water} = -1$ ‰ V-SMOW for Pridoli seas appear to be reasonable (see Text-fig. 13).

Concerning chemostratigraphical $\delta^{18}O_{apatite}$ data application, the carbon isotope curves show the same general trend as the oxygen isotope curves: smaller scale positive excursions coincide with eustatic low stands.

The first $\delta^{18}O$ curve on biogenic conodont apatite for the Pridoli (Upper Silurian) of the Baltic Basin has been produced in this work. A significant shift to lower $\delta^{18}O_{apatite}$ values in the middle Pridoli of the Gėluva-99 borehole section is observed, with oxygen isotope ratios decreasing in 1.1‰, from 18.1 to 19.2‰ V-SMOW respectively. This negative excursion of both vertebrate and conodont apatite curves goes in a noteworthy accordance with middle Pridoli sea-level drop, which may be interpreted on a well-defined facies change from marginal (dolomites with gypsum), to the shallow shelf ones (organogenic detrital limestones), corresponding the Vievis Fm. – Lapės Fm. boundary (Text-fig. 11). This also well reflect a significant change in vertebrate faunal associations, from *Goniporus alatus* and *Thelodus trilobatus* in Vievis Fm., to *Loganellia cuneata*, *Paralogania kummerovi*, *Thelodus sculptilis*, *Trimerolepis (=Katoporodus) tricavus*, and

Trimerolepis (=Katoporodus) lituanicus in Lapės Fm. (KARATAJŪTĖ-TALIMAA & BRAZAUSKAS, 1994), (see Text-fig. 10 above).

The middle Pridoli event, discussed herein, featured a worldwide extinction amongst corals, conodonts, graptolites and a diversity rise in the chitinozoans (KALJO et al. 1991). It can be clearly distinguished in the Upper Silurian succession of the Baltic Basin, according to lithostratigraphic and biostratigraphic data (KALJO et al. 1991; VERNIERS etal., 2008), and finnaly the chemostratigraphical biogenic apatite $\delta^{18}O$ data presented in this work (ŽIGAITĖ et al, 2008).

Concerning the $\delta^{18}O_{apatite}$ curve application to sequence stratigraphy, the variations in the oxygen isotopic signals correlate negatively with changes in sea level (WENZEL & JOACHIMSKI, 1996, fig. 8). Heavy oxygen (^{18}O) signals coinside with sea-level lowstands, whereas light (^{16}O) signals are recorded during sea-level highstands. Sea-level highstands subsequently indicate the formation of warm saline waters on subtropical epicontinental shelves, including oxygen-deficiency in the basins. The low $\delta^{18}O$ values infer the ^{18}O depletion in surface waters owning to the storage of ^{18}O-enriched saline waters in the basins (WENZEL & JOACHIMSKI, 1996). It has been proven in previous works, that the most prominent faunal extinction events in the Llandovery and Wenlock correlate well with the $\delta^{18}O$ and $\delta^{13}C$ positive excursions are linked with sea level low stands, which sometimes following related glacial episodes (CAPUTO, 1998; MELCHIN et al., 2004, VERNIERS et al., 2008).

A global eustatic sea-level low in the middle Pridoli has been suggested for by JOHNSON et al. (1998) (see Text-fig. 9 above). Global sea-level drop could indicate climatic cooling, if regional tectonic activity control is not considered (LAZAUSKIENĖ et al., 2003; see also the discussion above). As a consequence, we tend to interpret the observed shift in $\delta^{18}O_{apatite}$ as a change in temperature. According to the $\delta^{18}O$ results of conodont apatite revealed in this work, a significant palaeoseawater temperatures drop in almost 5 °C can be estimated for the Vievis Fm. – Lapės Fm. boundary, observed between the samples of 696 m (29.5 °C), and 687 m depth (24.8 °C), and therefore corresponding climate cooling is suggested.

Early vertebrate $\delta^{18}O_{apatite}$ has been also measured in a number of the Lower Silurian samples from the central Asia (northwestern Mongolia, Tuva and southern

Siberia). Several early vertberate groups have been tested separately, such as acanthodians, chondrichthyans, galeaspids, heterostracans, and thelodonts. Unfortunatelly, this material has not given any satisfying results: the revealed $\delta^{18}O_{apatite}$ values appear to be too low for realistic seawater palaeotemperature calculations. The $\delta^{18}O_{apatite}$ values ranged from 11.0 to 16.4 ‰ V-SMOW depending on the locality, with 14.2 ‰ V-SMOW in average, which is significantly lower compared to the unaltered early vertebrate apatite from the Baltic Basin, which give $\delta^{18}O_{apatite}$ values of 16.3‰ V-SMOW in average (see discussion above). Evidently, the vertebrate microfossils from the Lower Silurian of central Asia do not retain their primary oxygen isotope composition, and taking that into account, any phosphatic fossil apatite from this region has not been considered further.

The reason for this $\delta^{18}O$ deviation could be possible diagenetic thermal alteration of vertebrate microremains. This can be implied both from the fossils themselves (color and texture alteration), and from the tectonic setting of the region: the rocks in the centre of the Siberian platform have been slightly tectonically alterated during the Phanerozoic, including the extensive Lower Silurian successions outcropping along the Lena River, which have dips of less than two degrees (COCKS & TORSVIK, 2007, see the capter 3 above). In most of the cetral Asian and Siberian samples, the vertebrate scales do not show good preservation by means of color and texture, according to TWAY et al. (1986). Most of the scales have been blanched, resulting in light brown or light grey to completely white color, and porous texture, while the best preserved early vertebrate scales should retain a translucent dark brown color supposed to be a reflection of very minor thermal alteration of phosphatic vertebrate microremains (TWAY et a., 1986). The early vertebrate $\delta^{18}O$ values from the Lower Silurian of central Asia might be considered reasonable for the palaeotemperature calculations only if assuming the vertebrates as brackish ($\delta^{18}O_{water} = +5$) water dwellers, which is not supposed to be the case for most of the taxa tested (acanthodians, heterostracans, thelodonts).

In conclusion, early vertebrate oxygen isotope values are lower, and follow the conodont data offsetting regularly in approximately 2.5 ‰ V-SMOW (which makes ΔT of 10°C (ΔT range: 9,4°C - 11,6°C). This can be compared to the Late Devonian fish teeth $\delta^{18}O_{apatite}$ values from the Rheinische Schiefergebirge (Germany), shifting negatively from the conodont oxygen isotope ratios (see JOACHIMSKI & BUGGISH, 2002, fig.1). The fact that the observed offset of 2.5 ‰ V-SMOW between conodont and vertebrate $\delta^{18}O_{apatite}$ values is constant, and the general curve trends are similar, suggest that both groups of organisms record the same environmental changes (Text-figs. 11, 12).

With this consideration, the $\delta^{18}O$ value curves of contamporaneous vertebrate and conodont apatites can be used not only for palaeoclimate reconstructions, but also for interregional and global correlations, by means of chemostratigraphy and sequence stratigraphy. The calculated palaeotemperatures from conodont $\delta^{18}O_{apatite}$ values indicate that first, the assumption of a Pridolian seawater $\delta^{18}O_{water}$ value of –1 ‰ V-SMOW results in relatively realistic equatorial surfacewater temperatures, and second, a significant cooling event occured during the middle Pridoli, coinsiding with the facies change and Formation boundary in the Baltic Basin.

Conclusions and research perspectives

The Early vertebrates studied in the Silurian successions of northwestern Mongolia, Tuva and the Siberian platform, all are considered as endemic at species level, and most of the genera known as well. Separate palaeobiogeographical province can be distinguished on the basis of the early vertebrate content and distribution. Two new genera, three new early vertebrate species have been described, and all the thelodont species have been revised (ŽIGAITĖ & KARATAJŪTĖ-TALIMAA, 2008; ŽIGAITĖ *in press*). The higher taxonomical position of genus *Talimaalepis* ŽIGAITĖ 2004 remains unclear and further studies of helenolepid, loganiid and shieliid thelodonts are required.

The occurence of *Loganellia tuvaensis* (KARATAJŪTĖ-TALIMAA 1978) restricted to the Silurian deposits of Tuva, and refered record of *L.* cf. *L. tuvaensis* (KARATAJŪTĖ-TALIMAA 1978) from the Silurian – Devonian boundary section of the North East Greenland (BLOM, 1999), give palaeogeographical implication of the Siberia paaleocontinent approaching Laurussia in the Late Silurian.

The peculiar findings of newly recognized group of tesserated galeaspids in the Lower Silurian of Irkutsk Basin in the southernmost Siberian platform, confirm the palaeobiogeographical specifity of the region. This record is a stunning palaeogeographical reference on the relationships between the Siberia palaeocontinent and the North / South China terranes (BLIECK & JANVIER, 1999): strong affinities of this new form to *Hanyangaspis chaohuensis* (WANG et al., 1980), known from the Lower Silurian of southeastern China, refer to certain connectivity between corresponding palaeobasins (KARATAJŪTĖ-TALIMAA & ŽIGAITĖ, 2005, 2006). The publication of this extraordinary galeaspid discovery is now under realization.

The diversity and abundance of vertebrate taxa refer to warm and productive palaeobasins respectively, which most likely have existed as well connected epeiric seas on the integral Siberian palaeocontinent in the Silurian. They might be a proper place for origin and radiation of at least some early vertebrates in the Early Silurian (ŽIGAITĖ & BLIECK, 2006). Nevertheless, recent palaeogeographical studies place Siberia at high northern latitudes, inferring the inherent endemic *Tuvaella* Fauna as a cold-water one

(COCKS & TORSVIK, 2007). Yet, the results of present study tend to contradict this assumption.

Early vertebrate biogenic apatite has been tested as a proxie for the Silurian palaeoclimate reconstructions. Silurian palaeoseawater temperatures have been estimated from the $\delta^{18}O_{apatite}$ values of early vertebrate scales from the Lower Silurian of the southern Siberia and central Asia, and from the Upper Silurian of the Baltic Basin. The Asian and Siberian early vertebrate apatite appeared to be too diagenetically altered for obtaining realistic palaeoseawater temperatures, while the vertebrate microremains from the Pridoli of the Baltic Basin show good preservation and presumably retain primary oxygen isotope composition. However, conodont apatite $\delta^{18}O$ values from the from the corresponding samples reflect Silurian palaeoseawater temperatures more reliable than those revealed from the early vertebrate apatite, if estimated using the method proposed by KOLODNY et al. (1983), and assuming the $\delta^{18}O_{sea\text{-}water}$ of –1 ‰ V-SMOW. Subsequently, conodonts are once more confirmed as the best proxies for palaeoclimate reconstructions.

The discrepancy of 2.5 ‰ V-SMOW observed between contamporaneous vertebrate and conodont $\delta^{18}O_{apatite}$ values is constant, and the isotope curves show the same trends, which infer that both groups of organisms record the same palaeoenvironmental changes. In order to reveal the cause of this discrepancy, and to elaborate early vertebrate tissue internal ultrastructure, synchrotron studies of the Silurian vertebrate microremains are planned on the Synchrotron ‹‹Soleil›› IPANEMA platform, Paris, France.

The main formation boundary in the Pridoli section of the Baltic Basin has been traced precisely by the $^{18}O/^{16}O$ ratios changes in both the biogenic apatites, thus it can be concluded that not only conodonts, but early vertebrate microfossils as well are powerful tools in chemostratigraphy.

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List of enclosed publications / Liste des publications incluses

I **Žigaitė, Ž.,** Goujet, D., *submitted*. New observations on the squamation patterns of articulated exoskeletons of *Loganellia scotica* (Vertebrata: Thelodonti) from the Lower Silurian of Scotland. *Transactions of the Royal Society of Edinburgh: Earth Sciences*.

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Article I

New observations on the squamation patterns of articulated exoskeletons of *Loganellia scotica* (Vertebrata: Thelodonti) from the Lower Silurian of Scotland

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ABSTRACT

Articulated squamations of *Loganellia scotica* (TRAQUAIR 1898) from the Lower Silurian Lesmahagow inliers of southern Scotland have been studied. They include seven articulated specimens, three of them representing complete thelodont fossils, and four partially preserved postpectoral, precaudal and caudal parts of the exoskeleton. All the five main types of thelodont squamation, that is rostral, cephalo-pectoral, postpectoral, precaudal, and pinnal, have been observed within the articulated squamations of the specimens. The specific squamations of orbital, branchial, and bucco-pharyngeal areas, characteristic of *L. scotica*, have not been observed due to the poor or non-preservation of these particular areas within the specimens studied. Tail morphology and squamation patterns of the caudal fin have been studied in particular details, the constitution of the caudal fin rays squamation has been analyzed. The rostral squamation is argued to be characteristic to *L. scotica*.

Key words: dentine, rostral scales, articulated squamation, thelodonts, early vertebrates.

Introduction

Loganellia scotica (TRAQUAIR 1898) from the *Jamoytius* Horizon at the Birk Knowes is the earliest Scottish occurrence of complete articulated thelodonts. It is also the site of the first report of *Loganellia scotica* which was originally named *Thelodus scoticus* by TRAQUAIR and described by him in 1898. The species has been regarded as a marine one, with a wide geographical range within the Euramerican province (BLIECK et al., 1988; MÄRSS et al., 2006; 2007).

Seven new specimens of articulated squamations of *L.scotica* have been studied, and are decribed in this work. The specimens possess quite well preserved continuous pieces of articulated squamation or are preserved mostly as natural moulds, with some areas of the exoskeleton still with the complete squamation present. The specimens come from the Lower Silurian, upper Llandovery beds of Birk Knowes, Lesmahagow locality of southern Scotland, purchased from the private collector on the initiative of the second author (D.G.). The material is stored in the National Museum of Natural History in Paris, Palaeontological collections of vertebrates (series numbers GBP n° 360, 361, 366, 367, 374, 376, and 381). The four of the specimens (numbers GBP n° 360, 361, 366, and 367) have already been attributed to the species by VAN DER BRUGGHEN (1994), though any articulated squamation has not been studied.

The articulated exoskeletons of thelodonts are not abundant, and most of the thelodont species have been described from disarticulated microremains (scales). Generally, the thelodont exoskeleton is a contiguous squamation of great complexity, composed approximately of 20 000 to 30 000 microscopic scales (TURNER, 1991), ranging from 0.1 mm to 1 mm in length (MÄRSS et al., 2007), each scale with a non-expanding, but centripetally thickening dentinous crown and an expanding base of acellular tissue, presumed to be aspidine (MÄRSS et al., 2007). The structure of a particular thelodont scale depends both on its stage of morphogenetic development (age), and on its functions and place within exoskeleton (represented squamation type). The scales could be referred to several different morphological types, and several squamation types respectively (MÄRSS, 1986b; MÄRSS & RITCHIE, 1998; MÄRSS et al., 2006; 2007). The five main squamation patterns are: rostral (in earlier works referred to as oral), cephalo-pectoral, postpectoral, precaudal, and pinnal. New observations of all of them have been made on the *L. scotica* specimens studied, and are described and presented herein. To understand the intraspecific variability of thelodont microremains, studies of the scale diversity within the articulated specimens are necessary. They also serve a strong background in arguing the "artificial" palaeontological species to be sufficiently close to a natural palaeospecies. Thus detailed study of articulated fossils in this aspect is crucial for thelodont taxonomy.

This work is an attempt to study squamation patterns of *L. scotica*, on the new articulated specimens, in order to dertermine variability and types of the squamations within the species. We have not intended to repeat an intraspecific scale variation (morphological set) studies on the articulated squamations of *L. scotica*, which have already been presented in a number of previous works, most recently in appreciable detail by MÄRSS and RITCHIE (1998). Trying to avoid any recurrence, we have concentrated on the study of squamation patterns within the different parts of the body of *L. scotica.*

Historical account

Loganellia scotica originally was named *Thelodus scoticus* and first described by TRAQUAIR in 1898 and later years (TRAQUAIR 1898, 1899, 1905), then by STETSON (1931).

These descriptions and reconstructions have been used until recent time, and the initial concept of 'conventional' thelodont body constitution is still strongly based on the Scottish thelodont articulated findings. GROSS (1967) has eatblished the new genus *Logania*, and has split the previously described '*Thelodus scoticus*' into five species, among which *Logania scotica*. He was the first to divide scales of the thelodonts into different morphological types, as head, transitional and trunk scales (GROSS, 1967). He has figured the denticulated platelets of *Logania*, which later have been noticed by RITCHIE (1968) as well. Further reconstructions of *Loganellia scotica* have been made by TURNER (1970, 1991, 1992), including the correction of the genus name from former *Logania* to present *Loganellia*. The distribution patterns of denticles and denticle-bearing platelets inside the exoskeleton of *L. scotica* have been described by VAN DER BRUGGHEN and JANVIER (1993). VERGOOSSEN (1992) has described scale sets, several scales fused together, from the branchial areas of *L. scotica* from the *Jamoytius* Horizon, and it is apparent that there are remaining problems in the interpretation of thelodont scale variations and patterns.

First specialized publication on thelodont squamation has been made by TURNER (1994). The most recent detailed study of articulated squamations and revised diagnosis of *L. scotica* have been made by MÄRSS and RITCHIE (1998), which allowed more detailed subdivision of the scales into five squamation types, viz. orbital, cephalo-pectoral (including the rostral area of the body, as *L. scotica* was supposed not to possess any typical rostral squamation: MÄRSS & RITCHIE, 1998; further arguments on this topic is considered in discussion below), postpectoral, precaudal and pinnal squamations (MÄRSS & RITCHIE, 1998; KARATAJŪTĖ-TALIMAA & MÄRSS, 2004; MÄRSS et al., 2006; 2007). This classification of different squamation areas was first elaborated on *Phlebolepis elegans* articulated specimens by MÄRSS (1986a). It has also been revealed in her work, that not only morphology, but also histology of the scales varies between different squamation patterns. For example, the rostral (previously oral) and most of anterior cephalo-pectoral scales do not possess any pulp canal, while it is present in the scales of other squamation areas (MÄRSS, 1986a). Later some more squamation patterns of thelodonts have been described by TURNER (2000). Finally, combining data of thelodont scale morphology, histology, and squamation patterns, a refined scheme of scale asocciations has been presented as a tool to deal with disarticulated microremains (MÄRSS, 1986a,b).

Squamation patterns of the bucco-pharyngeal and branchial areas of *L.scotica* have been studied in detail by MÄRSS and RITCHIE (1998). Several postpectoral squamation patterns have been presented in the same work, illustrating both the dorsal and ventral sides (by making latex casts) of the postpectoral squamation. Presence of separate rostral squamation in *L. scotica* has been declined, and the cephalo-pectoral squamation has been regarded as the main from bucal to pectoral areas of the body (MÄRSS & RITCHIE, 1998). The intraspecific scale variety of *L. scotica* has also been studied in the latter paper.

According to the previous studies, *Loganellia scotica* is widely distributed in the Llandovery of Eurasia (ALDRIDGE & TURNER, 1975; KARATAJŪTĖ-TALIMAA, 1978; MÄRSS, 1989; TURNER, 1973; TURNER et al., 1994), and also known in late Llandovery and Wenlock of North America (TURNER & NOWLAN, 1995; MÄRSS et al., 1997, 2006), and is used for correlation between these areas and Britain.

Geological setting

The articulated squamation material presented in this study comes from the Silurian locality of Lesmahagow, 30 km south of Glasgow, in Lanarkshire, southern Scotland (Fig. 1). Lesmahagow locality is world-renowned, as many important collections of Silurian vertebrates have been made there since the mid to late 1800's. The campus named "Camp Siluria" has been set up near Lesmahagow in 1890's by the Geological Society of Glasgow to signify its geological importance. It is now very difficult to obtain permission to collect from these rocks as a result of inappropriate collecting. Birk Knowes SSI - Site of Special Scientific Interest having special protection under Scots law - is also known as the *Jamoytius* Horizon named by RITCHIE (1960, 1968) after the rare soft-bodied fish found from this locality. This site has been made off-limits to all collecting for the time being.

The Lesmahagow Inlier is a block of Silurian sediments surrounded by sediments of Carboniferous age. The inlier consists of shales and sandstones with occasional pebble conglomerates of a lagoon or lake. The articulated squamations and imprints have been collected in the *Jamoytius* Horizon outcrops at Birk Knowes, which are three small exposures on Logan Water, in the Lesmahagow Inlier. The vertebrates from these three fish-bearing horizons are amongst the oldest in Britain. Vertebrate fauna here described so far is restricted to two species, *Loganellia scotica* and *Jamoytius kerwoodi*, with a possible third, *Thelodus planus*, recorded by TRAQUAIR (1898), but regarded by RITCHIE (1968) as dubious.

The *Jamoytius* Horizon lies within the Patrick Burn Formation at the base of the Priesthill Group. The Patrick Burn Formation consists of at least 400 m of greywackes and shales which may be divided into two types: dark, finely laminated siltstones and non-laminated olive mudstones. Vertebrates, together with crustacean fossils, occur in the laminated siltstones. Recent evidence indicates a late Llandoverian age of the Horizon (COCKS et al., 1992, fig. 2.8; WELLMAN & RICHARDSON, 1993, p. 158).

The *Jamoytius* Horizon is 10 m thick, consisting of alternating grey-black finely laminated carbonaceous siltstones and non-laminated olive to greyish green mudstones. Macroscopic remains are almost entirely confined to the organic-rich laminated siltstones. The sequence within the Priesthill Group represents a transition from marine to fluvial and deltaic conditions (RITCHIE, 1985), though the *Jamoytius* Horizon corresponds to truly marine sediments. Both the greywackes and shales of the Patrick Burn Formation have slump structures reflecting unstable bottom conditions. Ripple marks indicate current directions towards the north-north-east for the formation as a whole. Equivalents of the Lesmahagow rocks in the Baltic area range through a variety of facies with vertebrates in clearly marine conditions as well (BLIECK et al., 1988).

The fossils occur throughout the *Jamoytius* Horizon but are noticeably more abundant and better preserved in the middle 7 m. Calcareous concretions occur throughout; those found within the mudstone nearly always enclose fossils. The concretions also contain thelodont remains, either as articulated individuals, patches of exoskeleton or, more commonly, as coprolitic layers of denticles (RITCHIE, 1968). The *Jamoytius* Horizon is the only unit in the Patrick Burn Formation in which articulated thelodonts occur. According to the most recent stratigraphy of the Silurian inliers at Lesmahagow (WALTON & OLIVER, 1991; ROLFE, 1992; WELLMAN & RICHARDSON, 1993) the *Jamoytius* Horizon of the Birkenhead Burn outcrop fish beds are treated as belonging to the upper Llandovery (Fig. 2). This study provides a new additional record of *L. scotica* in the *Jamoytius* horizon at the Birk Knowes locality of the Lesmahagow Inlier.

Material and methods

The material studied comprises articulated squamations with complete or mostly partially preserved exoskeletons of thelodont *Loganellia scotica*. The specimens are deposited in the National Museum of Natural History in Paris, Palaeontological collections of vertebrates, series GBP, and collection numbers: GBP n° 360, 361, 366, 367, 374, 376, and 381.

Articulated pieces of exoskeleton were photographed using a Nikon Coolpix 4500 digital camera; details of the squamations and close-ups were studied and imagined by high resolution optical microscope Zeiss Axioplan2 Imaging with digital image processing, and under binocular with a Canon PowerShot G5 digital camera. Contrast enhancing technique has been used for macroimaging: specimens have been whitened by MgO dust. SEM imaging within the premises of MNHN has not been possible because of the oversize of the samples.

In descriptions of the articulated thelodont squamations, size has been ascribed referring to the classification presented by MÄRSS et al., (2006), which is as follows: very small, up to 5 cm in lengh; small, up to 10 cm; medium, up to 20 cm, and large, up to 40 cm or more. The size of scales is subdivided as follows: very small, 0.1-0.5 mm; small, 0.5-1.0 mm; medium, 1-2 mm; and large, 2-3.7 mm. The approximation of the total body length of the incomplete articulated exoskeletons has been made deriving a relationship from the known fully preserved exoskeletons of *L. scotica*. The width of caudal peduncle has been used as a reference and indication of an approximate total body length of the thelodont. The width of caudal peduncle is the most evident, presumably most adequate measurement in relation to the total body length of the animals, and the best preserved feature in all the articulated fossils studied and considered for the calculation. The body lengths and widths of caudal peduncles of 8 more articulated specimens of *L. scotica* have been taken from the work of MÄRSS & RITCHIE (1998, Table 2, p. 150), collection numbers: NMS.G.1967.65.18B, BMNH.P.10137, GSE1137, AM.F.89434A, AM.F.89433B, NMS.G.1905.3.5, AM.F.89432, and NMS.G.1905.3.4. From our new material, the measurements of three complete thelodont exoskeletons have been considered in the same manner (specimens GBP n° 361, GBP n° 374 and GBP n° 376). Summarizing all the data available, a mean ratio coefficient for the total body length approximation on the width of the caudal peduncle, has been obtained. The equations used are as follows:

$$L_{app} = P \times C \qquad (1)$$

Where: L_{app} – approximate total body length; P – known width of the caudal peduncle; C – mean ratio coefficient.

$$R = L/P \qquad (2)$$

Where: R – ratio of the total body length to the width of caudal peduncle; L – actual body length; P - width of the caudal peduncle.

$$C = \bar{R} = \frac{1}{n} \sum_{i=1}^{n} Ri = 9.826 \qquad (3)$$

Where: R - ratio of the total body length to the width of caudal peduncle; n – number of specimens (11 complete fossils of *L. scotica* known so far have been measured); C - mean ratio coefficient, which has been derived and used in this work as C = 9.826, to approximate total body lengths of incomplete specimens.

The terminology of squamations corresponds to the five main categories of body regions of *L. scotica*, according to those first distinguished in the exoskeleton of *Phlebolepis elegans* PANDER 1856 (MÄRSS, 1986a), which represent distinct scale morphologies as well as specific functions. They are as follows: rostral, cephalo-pectoral, postpectoral and precaudal, and pinnal body areas, scales, and squamations respectively (Fig. 3).

In the synonymy of species, only publications containing illustrations have been considered.

Systematic palaeontology

Subclass Thelodonti KIAER, 1932
Order Loganelliiformes TURNER, 1991
Family Loganelliidae KARATAJŪTĖ-TALIMAA, 1997
Genus *Loganellia* FREDHOLM, 1990
Type species *Loganellia scotica* (TRAQUAIR, 1898)

Complemented synonymy list after MÄRSS et al., 2006; where only publications containing illustrations are considered:

1898 *Thelodus scoticus* TRAQUAIR, p. 72.
1899 *Thelodus scoticus*; TRAQUAIR, p. 829 *partim*, pl. 1, figs 1-2, 5-10; *non* pl. 1, figs 3-4.
1899 *Thelodus planus*; TRAQUAIR, p. 831, pl. 2, figs 1-3.
1905 *Thelodus scoticus*; TRAQUAIR, p. 880, pl. 1, figs 1-4.
1931 *Thelodus scoticus*; STETSON, p. 141, fig. 1A-B.
1958 *Thelodus scoticus*; STENSIÖ, p. 417, fig. 218.
1964 *Thelodus scoticus*; STENSIÖ, p. 371, fig. 124A.
1967 *Logania scotica* (TRAQUAIR); GROSS, p. 32, pl. 5, figs 12-25, text-fig. 13C-F.
1967 *Logania taiti* (STETSON); GROSS, p. 33, pl. 5, figs 26-42, text-fig. 13N-Q.
1975 *Logania scotica* (TRAQUAIR); ALDRIDGE & TURNER, p. 419-420, pl. 1, figs 1-3, 7-9.
1975 *Katoporus*? sp. GROSS 1967; ALDRIDGE & TURNER, p. 419-420, pl. 1, figs 4-6.
1991 *Loganellia scotica* (TRAQUAIR); TURNER, fig. 1f.
1992 *Loganellia scotica* (TRAQUAIR); TURNER, p. 26, text-fig. 2.

1992 *Loganellia scotica* (TRAQUAIR); VERGOOSEN, p. 51, figs 2-3, 5-24.

1993 *Loganellia scotica* (TRAQUAIR); VAN DER BRUGGHEN, p. 88, figs 1-3.

1993 *Loganellia scotica* (TRAQUAIR); TURNER & VAN DER BRUGGHEN, p. 132, fig. 2.

1994 *Loganellia scotica* (TRAQUAIR); VAN DER BRUGGHEN, figs. 2-3, 5-8.

1998 *Loganellia scotica* (TRAQUAIR); MÄRSS & RITCHIE, p. 147, figs 7-21, 33E.

1998a *Loganellia scotica* (TRAQUAIR); MÄRSS et al., pp. 56, 60, figs 2-3.

1998b *Loganellia scotica* (TRAQUAIR); MÄRSS et al., p. 37, fig. 1.

1999 *Loganellia scotica* (TRAQUAIR); BLOM, p. 98, fig. 2.

2006 *Loganellia scotica* (TRAQUAIR); MÄRSS et al., p. 17-20, pl. 1, figs 1-5, 7-17; text-fig. 7A-Z.

2007 *Loganellia scotica* (TRAQUAIR); MÄRSS et al., p. 49-52, fig. 42A,B.

Lectotype. TRAQUAIR, 1899, pl. 1, fig. 1, specimen GSE 5996 from the British Geological Survey Museum, Keyworth, deposited in the National Museum of Scotland, Edinburgh.

Type locality and horizon. Patrick Burn Formation, Priesthill Group, upper Llandovery; Logan Water, Lesmahagow Inlier, southern Scotland.

Material studied. See section 'Material and methods' above.

Locality and horizon of the material studied. *Jamoytius* Horizon, Patric Burn Formation, Priesthill Group, upper Llandovery; Birk Knowes, Lesmahagow Inlier, southern Scotland.

Occurrence. Lower Silurian, upper Llandovery, lower fish beds (articulated), Patrick Burn, Kip Burn & Blaeberry formations, Lesmahagow, Scotland; upper Llandovery, Wych Formation, *Pentamerus* beds, Purple Shale Formation, Welsh Borderland; upper Llandovery, Kilbride Formation, Ireland (in part); upper Llandovery, Lafayette Bugt Formation, Hall Land, northern Greenland; upper Llandovery, Wulff Land Formation, Thors Fjord Member, *Monograptus spiralis* Biozone, Greenland; upper Llandovery, Rumba Formation, Raikkula Stage, Estonia; upper Llandovery, lower Visby Formation, Gotland, Sweden; lower Llandovery, Clemville and Weir formations, Quebec, eastern Canada; upper Llandovery, Limestone Point Formation, New Brunswick, eastern Canada; upper Llandovery, Anse Cascon and Anse a la Pierre Loiselle formations, Quebec, eastern Canada; Cape Phillips Formation, Devon Island, Canadian Arctic; upper Llandovery, Baillie-Hamilton Island, Canadian Arctic, Avalanche Lake, Mackenzie Mountains, northern Canada (MÄRSS et al., 2007).

Diagnosis (modified after MÄRSS et al., 2007). Medium to large thelodonts. Postpectoral and precaudal scales are elongate, wedge-shaped, elliptical and sometimes carinate; raised median rhombic area of the crown common; base tending to be arched anteriorly in older scales, and an anterior process common; deep, open pulp cavity in young scales, reduced to a slit-like groove leading to a single pulp canal opening, located at the distal end in older scales; specialized branchial scales.

Description. Size of the specimens of articulated squamations studied varies from 107 mm to 450 mm in length. According to TURNER (1991, p.89; 1992, text-fig. 3B) the body of *L. scotica* is usually 275 mm in length, but may reach 300 -

400 mm based on disarticulated tail (MÄRSS & RITCHIE, 1998). The material studied in this work, comprises one small thelodont specimen (GBP n° 374), three medium sized ones (GBP n° 360, 361, and 376), and three very large exoskeletons (GBP n° 366, 367, and 381), though only postpectoral, precaudal and caudal parts of the large ones are being preserved. The maximum body length based on the width of caudal peduncle of the specimen, enables us to estimate the total length of *L. scotica* body up to 450 mm (Fig. 5, B). The summary of length and width of the specimens studied, as well as the approximated total body lengths on the basis of the length ratio of caudal peduncle, are given in Table 1. Four of the seven articulated squamations studied are incomplete exoskeletons of large animals; the smaller three are complete fossils, even if the best parts are preserved as natural moulds, lacking the bulk of their squamation (Fig. 4: A, B, C). Tails in all of the specimens possess a clearly hypocercal asymmetrical caudal fin with a very wide hypocercal lobe, best contrasted on the tail of GBP n° 361 (Fig. 4, B). This wide hypocercal lobe has already been noticed in its first description by VAN DER BRUGGHEN (1994). Exception would be the biggest of the specimens studied, GBP n° 366, which has caudal fin lobes of similar size (Fig. 5 B), providing accordance to S. Turner's ideas that large specimens of *L. scotica* might have more symmetrical tails, reflecting a change of their life habit with age (TURNER, 1991; MÄRSS & RITCHIE, 1998; MÄRSS et al., 2007).

The rostral, cephalo-pectoral, postpectoral, precaudal, and pinnal squamations (Fig. 3) have been observed and studied on the specimens. The pinnal squamation pattern is particularly well preserved on several articulated caudal fins (Fig. 5: A_1, A_3). Pinnal squamation of pectoral fins or pectoral flaps (MÄRSS et al., 2007), of dorsal and annal fins are less clearly preserved within the specimens studied. Neither scale cover of bucco-pharyngeal area, with its specific denticles, well described by MÄRSS & RITCHIE in 1998, and named lateral squamation, nor orbital squamation have been observed within the material studied (see MÄRSS & RITCHIE, 1998; fig. 9, fig. 10).

Rostral squamation, or an anterior cephalo-pectoral squamation, according to MÄRSS & RITCHIE (1998), has been observed within the specimens GBP n° 361 and 374. A clear rostral squamation pattern is present on the anterior bucco-lateral sides of the head of the complete articulated specimen GBP n° 376 (Fig. 4, C_1). The rostral scales are round to oval in shape, very small, 0.2 – 0.4 mm in diameter; the crown is of a symmetrical oak-leaf-like shape, with a smooth and slightly bunchy surface, and crenulations on the margins (Fig. 4, C_2). These features are sufficiently distinct when compared with the crown sculpture of the cephalo-pectoral scales, which tend to be elongated, with clearly discernible pointy and shorter anterior part, and wider obtuse posterior part of the crown (Fig. 6, A). Natural moulds of rostral squamation have been observed on the specimens GBP n° 361 and 374.

Cephalo-pectoral squamation is particularly well preserved within the exoskeleton of the specimen GBP n° 361 (Fig. 4, B), and it has also been observed as natural moulds within the specimens GBP n° 374 (Fig. 4, A) and 376 (Fig. 4, C_1). Some cephalo-pectoral scales are present on the anterior part, and within the concentrated squamation of the pectoral flap (pectoral fin), preserved within the specimen GBP n° 360 (Fig. 6, A).

Postpectoral squamation is the main squamation pattern of thelodonts (see the discussion below), and it comprises the best part of the articulated squamations studied. The postpectoral squamation patterns are very well preserved within the specimens GBP n° 360 (Fig. 6: B, C, D), 361, 366, 367, and 381 (Fig. 7a: A, B). Natural moulds of postpectoral squamation have also been observed within the specimens GBP n° 374, and 376, with an exception of few patches of postpectoral scale cover on the latter one.

Precaudal squamation is characterized by very thin and elongated scales, and covers the zone of the tail up to the caudal fin. Referring to the specimens observed, it is necessary to admit that the change of squamation pattern going from postpectoral to precaudal is very gradual. In some cases, especially considering older and larger specimens, the scale cover of the precaudal zone (Fig. 7b, E), may be treated as postpectoral squamation of younger individuals of *L. scotica* (Fig. 6, B). The squamation of the tail in larger specimens becomes completely typical precaudal and narrow-scaled just on the forefront of caudal fin (Fig. 7b: F, H). Although the characteristic narrow and pointy shape of precaudal scales, compare to the wider and rhombic postpectoral ones, is being kept through all the articulated squamations observed.

Pinnal squamation is the most peculiar pattern of all the squamations present. Pinnal scales of the caudal fin are very tiny (0.2-0.3 mm in diameter) and narrow (less than 0.01 mm in width). Being much smaller and more elongate compared to precaudal ones, they cover continuously the flexible ray area of the caudal fin. The caudal fin squamation is exceptionally well preserved on the specimen GBP n° 367, possessing well preserved fully articulated continuous pinnal squamation of caudal fin, with caudal rays well expressed as accentuated lines of denser scale cover (Fig. 5: A_1, A_3). The scale cover is accentuated (significantly denser) in the area of the rays forming arch-shaped ramifications, wider near the base of the caudal lobes, and narrowing towards the posterior end of caudal fin (Fig. 5, A_2). At least 20 caudal rays can be observed on the hypocercal lobe of the tail of the specimen GBP n° 367. The tail itself is strongly asymmetrical, referring to a rather young age of the thelodont animal. The maximum width of the hypocercal lobe reaches 2.5 cm, while the epichordal lobe is less than 1.0 cm in width, and the ventral side of the hypocercal lobe still retains rather postpectoral-like squamation. These well expressed caudal rays have also been observed within the specimens GBP n° 366 and 381, though the squamation of these caudal fins is much less well preserved. Distinct pinnal squamation patterns have been observed on the leading edges of caudal fins (specimens GBP n° 366 and 381), present as a concentration of the particular pinnal scales, typical for the leading edges of the fins, ontop of the precaudal squamation (Fig. 7a, C; Fig. 7b, G).

Pinnal squamation of the dorsal fin has been observed with the specimens GBP n° 360 and 361. The squamation pattern of the anal fin is rather well preserved in the specimen GBP n° 381 (Fig. 7a, D). The shape of the dorsal fin of a young *L. scotica* is well preserved as a natural mould in the specimen GBP n° 374 (Fig. 4, A). The anal fin has been observed only as a natural mould on the specimen GBP n° 361 (Fig. 4, B), and as an incomplete articulated squamation on the specimen GBP n° 381 (Fig. 7a).

Discussion

Referring to the previous studies, *L. scotica* possesses more squamation varieties than the five main ones of MÄRSS & RITCHIE (1998), though it has been argued it does not possess any typical rostral scales (MÄRSS & RITCHIE, 1998, p. 152), and reference comparison with the *Phlebolepis elegans* has been made (MÄRSS, 1986a). In our opinion, *Ph. elegans* being a representative of the family Phlebolepididae BERG 1940, which is quite a different group of thelodonts by means of scale structure and general morphology. Referring to the intraspecific scale varieties (morphological sets) within the different species of loganiid thelodonts (MÄRSS et al., 2007, ŽIGAITĖ, *in press*), and our study of the articulated squamations described above, we suggest the rostral squamation to be present in *L. scotica*. The examples could be the rostral squamations of the specimens GBP n° 361 and 374. The squamation patterns on the most anterior parts of the blunt head, and on the sides of the branchial (or lateral, according to MÄRSS & RITCHIE, 1998) area within these speciments (Fig. 4: C_1, C_2, C_3) we consider as rostral squamation. Moreover, rostral scales of *L. scotica* have been clearly figured by MÄRSS et al., 2007, fig. 42A: a; fig. 42B:a).

STETSON (1931) was the first to describe hypocercal tail fins in thelodonts, and the thin film of scales, covering continuously the flexible intra-posterior part of the caudal fin, as well as presumable fin rays. He described a tail of a large specimen of *L. scotica* with caudal fin-web and up to 18 possible internal cartilaginous fin rays (STETSON, 1931). We have observed at least 20 long fin rays, forking from the hypocercal lobe solely within the pinnal squamation web of the caudal fin, on the specimen GBP n° 367 (Fig. 5: A_1, A_3). VAN DER BRUGGHEN (1994, fig. 8E) has already mentioned and drew these caudal rays in the first description of the specimen, implying them to reflect traces of the former cartilaginous caudal rays. Considering our recent observation of the fossil, the caudal rays represent the denser squamation lines within the articulated film of pinnal (caudal fin) squamation pattern (Fig. 5, A_2).

Conclusions

Seven articulated squamations of *L. scotica* have been studied, revealing new data on different patterns of thelodont squamation. The mean ratio coefficient, permitting estimation of the total body length of *L. scotica* animal from the width of its caudal peduncle, has been derived on the basis of measurements of 11 complete specimens of *L. scotica*. It has been used to approximate the body lengths of the incomplete fossils studied. The total body length of the largest specimen preserved as precaudal and caudal parts of the exoskeleton (GBP n° 366), and studied in this work, has been estimated to reach at least 450 mm in length, which exceeds the so far considered maximum length of the species (TURNER 1992, MÄRSS et al., 2007). The former maximum body length of *L.scotica* had been estimated to go up to 400 mm, but this also has been inferred from detached caudal fins (TURNER 1992).

Rostral squamation has been suggested to be present within the exoskeleton of *L. scotica*, contrary to the most recent descriptions of the articulated squamations of this species (MÄRSS

AND RITCHIE, 1998). The postpectoral, precaudal and caudal fin squamation patterns of *L. scotica* have been observed and presented in this work. It is important information regarding further studies of the taxonomy of disarticulated thelodonts. The postpectoral squamation is of particular significance, both by means of extent, as it covers the bulk of the thelodont body, and by means of the thelodont taxonomy, because the holotype scales of disarticulated material of thelodonts are usually chosen from the postpectoral squamation area.

The pinnal squamation of caudal fins of *L. scotica* have been studied and described in detail, reflecting its complex structure of caudal fin rays. Appending to the previous interpretations of the caudal fin rays of *L. scotica* as internal cartilaginous outgrowth (STETSON, 1931), we conclude that by means of squamation pattern, caudal fin rays consist of accentuated scale cover lines within the contiguous film of pinnal (caudal fin) squamation.

Acknowledgements

We are grateful to Dr. Didier GEFFARD-KURIYAMA (National Museum of Natural History, USM 0203, Department of the earth History, Laboratory of Palaeontology, Paris, France) for the supervision of the high resolution optical imaging of the specimens; Dr. Vincent DUPRET (University of Lille – 1, CNRS-UMR 8157 «Géosystèmes», Villeneuve d'Ascq, France) for the appreciable contribution during the work with the collections in the National Museum of Natural History in Paris, and Dr. Alain BLIECK (University of Lille – 1, CNRS - UMR 8157 «Géosystèmes», Villeneuve d'Ascq, France) for valuable comments.

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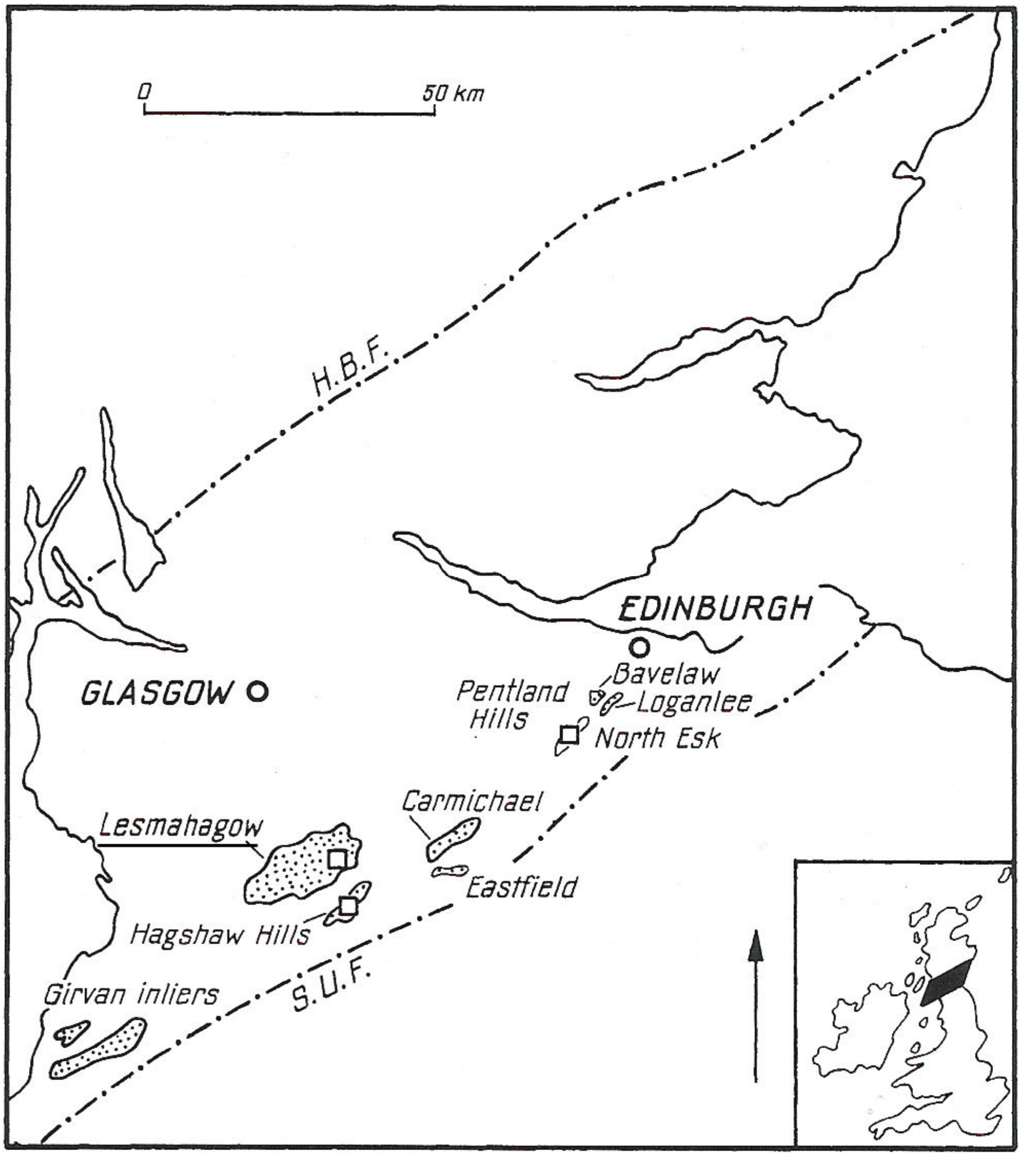

Fig. 1. Main vertebrate localities (white squares) in the Silurian inliers (dotted areas) of southern Scotland (sketch map after WELLMAN & RICHARDSON, 1993). H.B.F. – Highland boundary fault; S.U.F. – Southern Uplands fault.

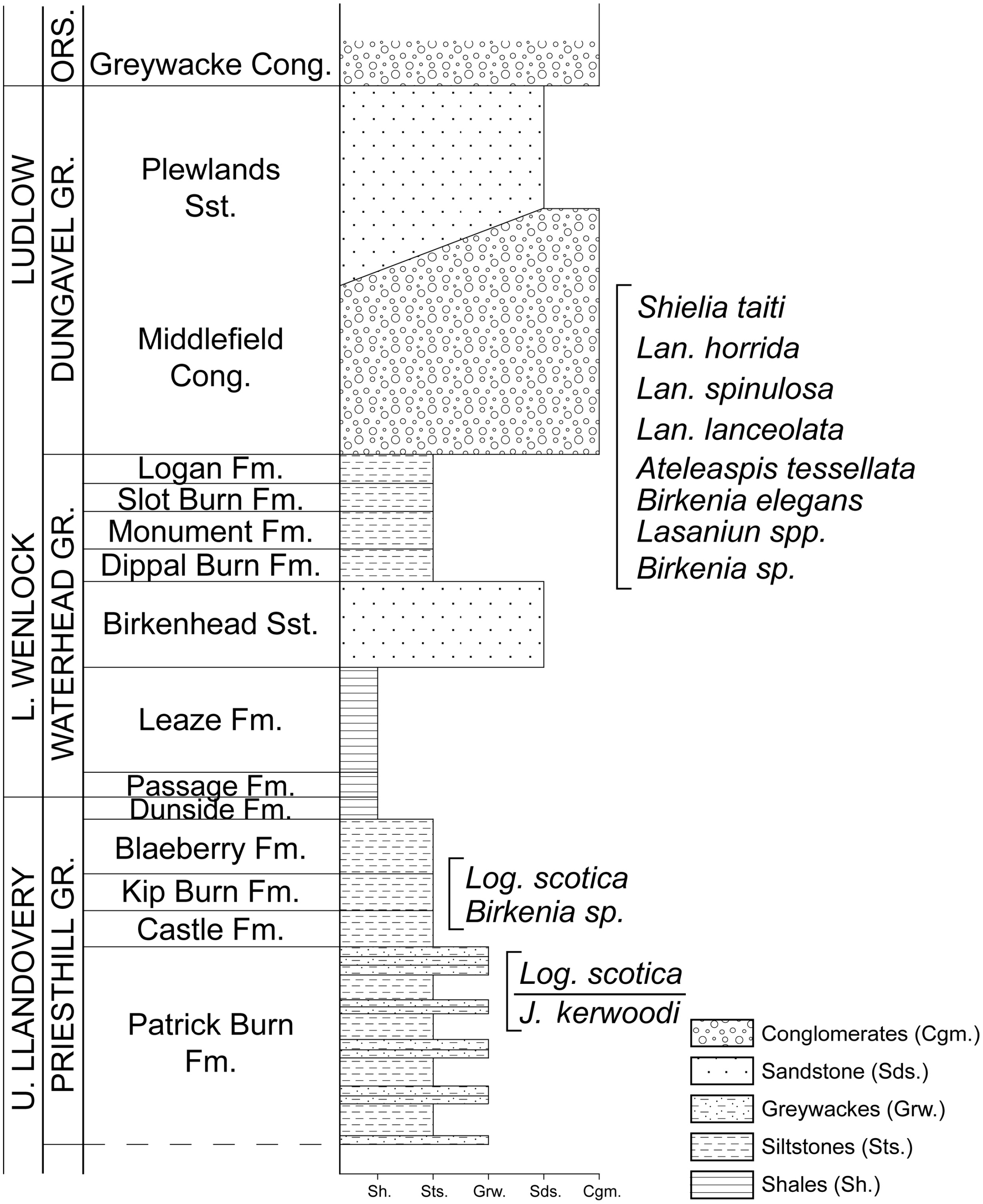

Fig. 2. Vertebrate bearing horizons in the sections of the Silurian inlier of the Lesmahagow locality (modified after MÄRSS & RITCHIE, 1998).

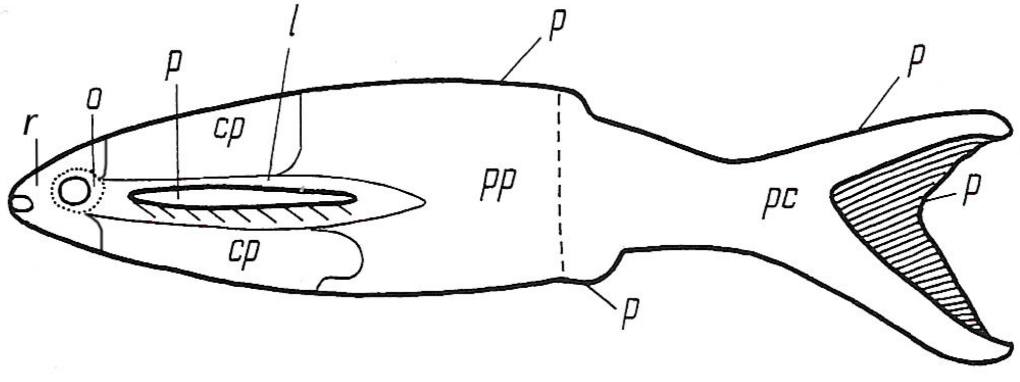

Fig. 3. Squamation patterns in the *Loganellia scotica* (TRAQUAIR 1898) exoskeleton. Abbreviations: cp – cephalo-pectoral squamation; l – lateral squamation; o – orbital squamation; p – pinnal squamation; pc – precaudal squamation; pp – postpectoral squamation; r –rostral squamation (modified after MÄRSS & RITCHIE, 1998).

Table 1. Body length and width of *L. scotica* articulated squamations studied in this paper:

Specimen	Length of the specimen, part of the body (mm)	Length of the caudal fin (mm)	Width of the caudal peduncle (mm)	Width of the caudal fin (mm)	Body length (mm); **approximated lengths in brackets**
GBP n° 360	192	41	20	59	*(197)*
GBP n° 361	190	35	27	29	190
GBP n° 366	175	85	45	67	*(442)*
GBP n° 367	141	84	33	40	*(324)*
GBP n° 374	107	30	8	20	107
GBP n° 376	201	35	11	32	201
GBP n° 381	195	116	40	54	*(393)*

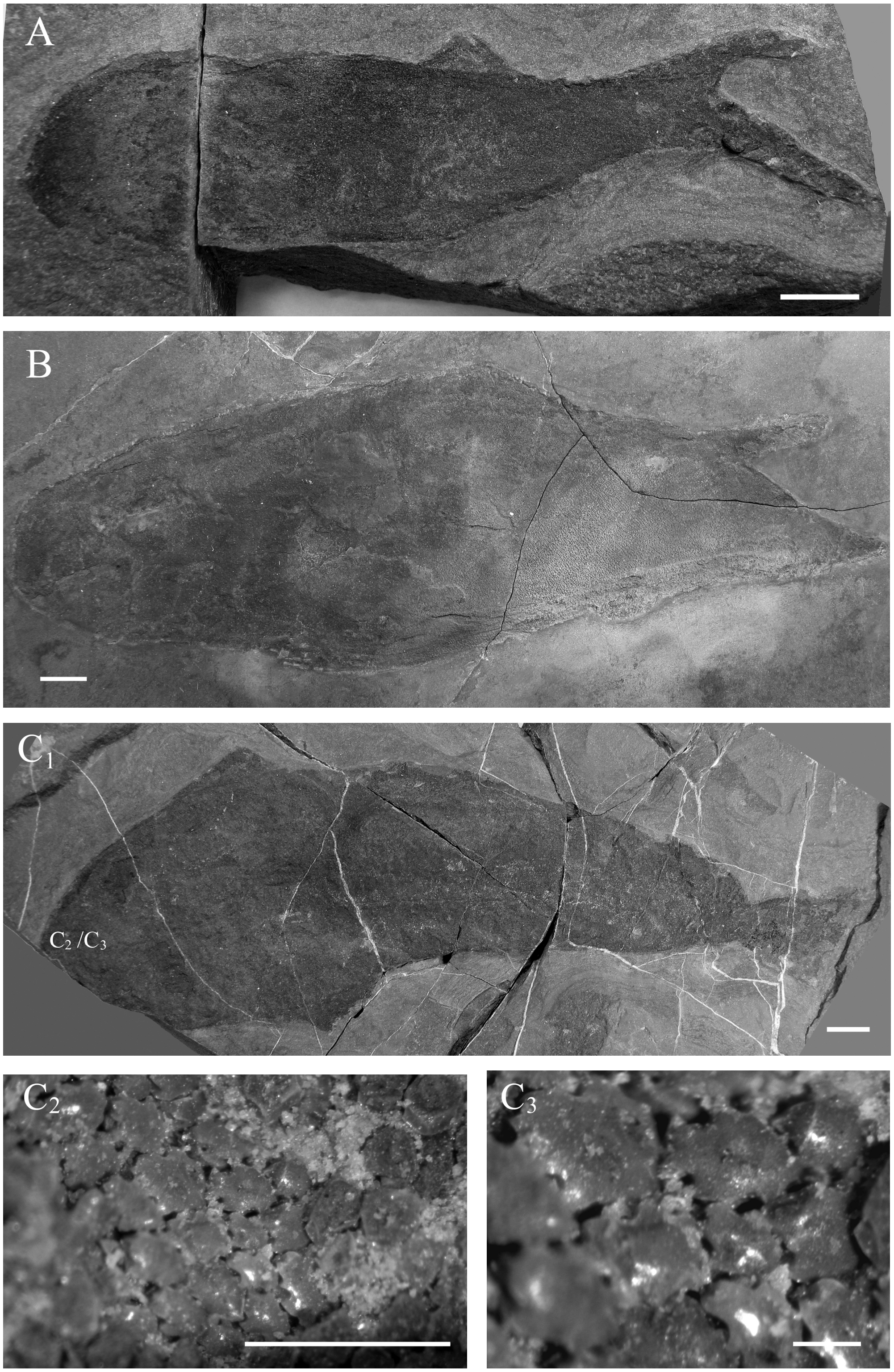

Fig. 4 Articulated specimens of *Loganellia scotica* TRAQUAIR 1898: GBP n° 374 (A), GBP n° 361 (B), GBP n° 376 (C_1); rostral squamation pattern (coronal view) in GBP n° 376 (C_2, C_3). Scale bars: 1 cm (A-C_1), 1 mm (C_2), 0.2 mm (C_3).

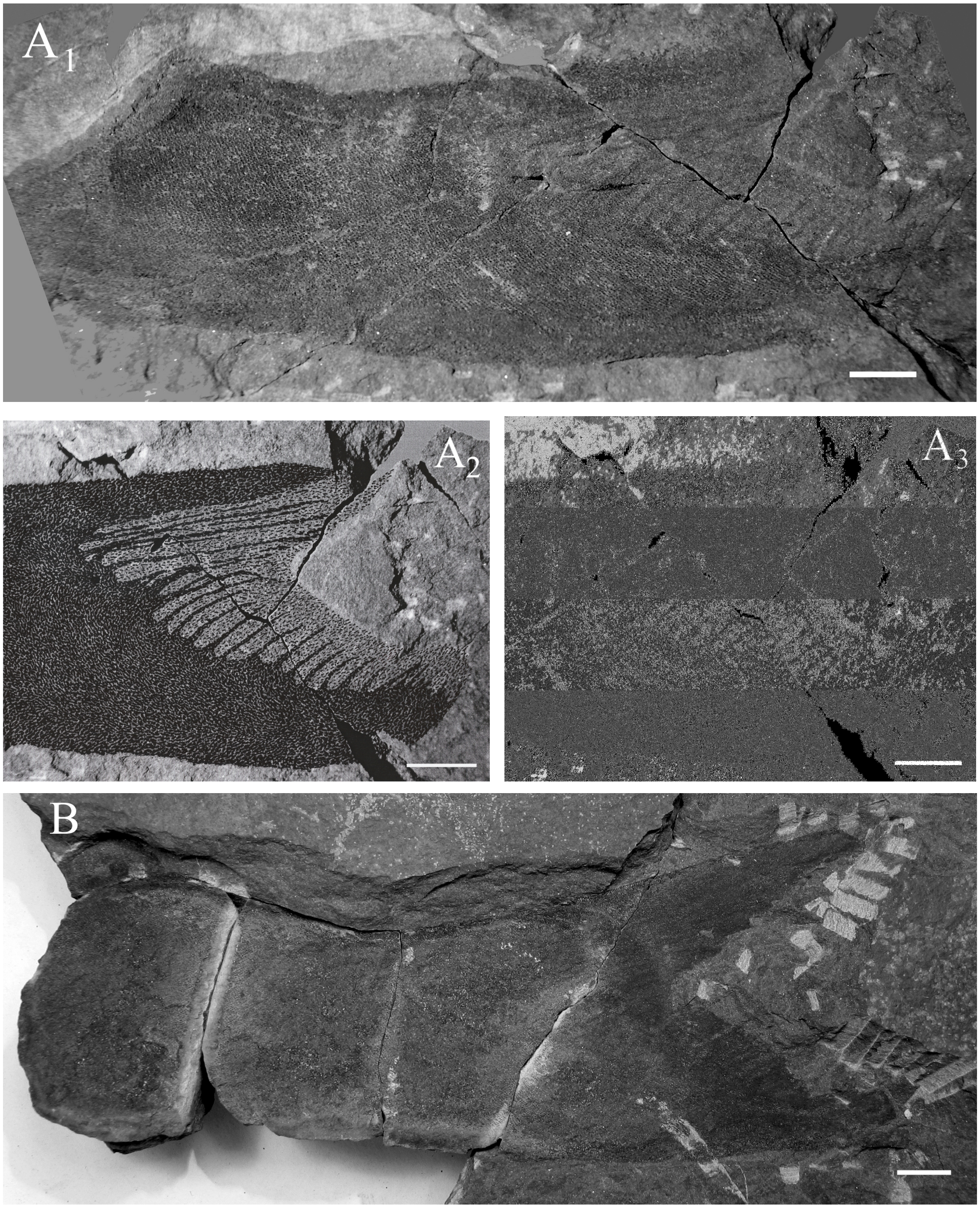

Fig. 5 Caudal and precaudal articulated squamations (tails) of *Loganellia scotica* TRAQUAIR 1898: GBP n° 367 (A$_1$, A$_2$, A$_3$), GBP n° 366 (B). Scale bar: 1 cm (for all).

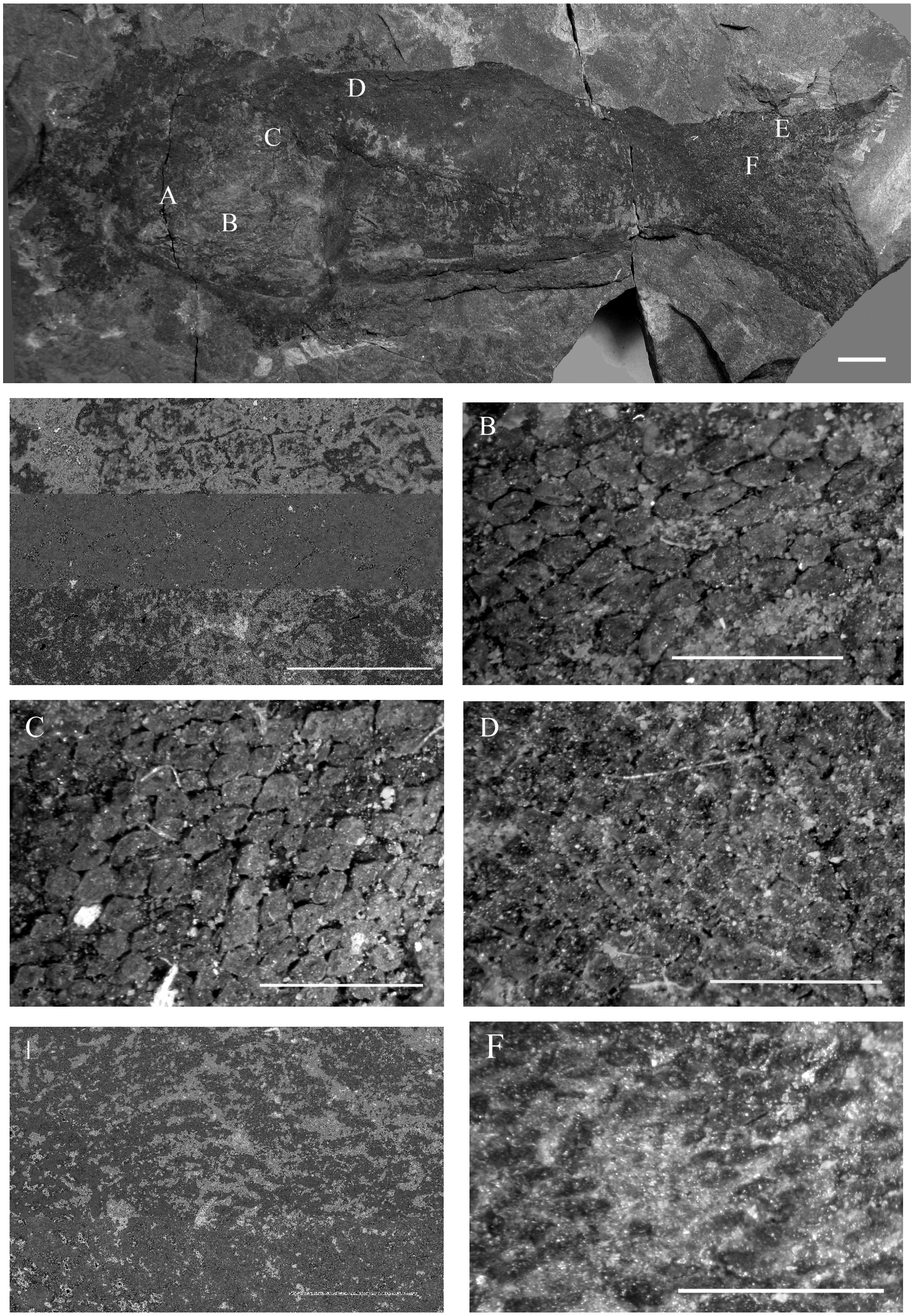

Fig. 6 Squamation patterns (basal view) of *Loganellia scotica* TRAQUAIR 1898, specimen GBP n° 360: with details of the: cephalo-pectoral squamation, (A), postpectoral squamation, (B, C, D), pinnal squamation of caudal fin, (E). Scale bars: 1 cm (articlulated exoskeleton), 1 mm (A-E).

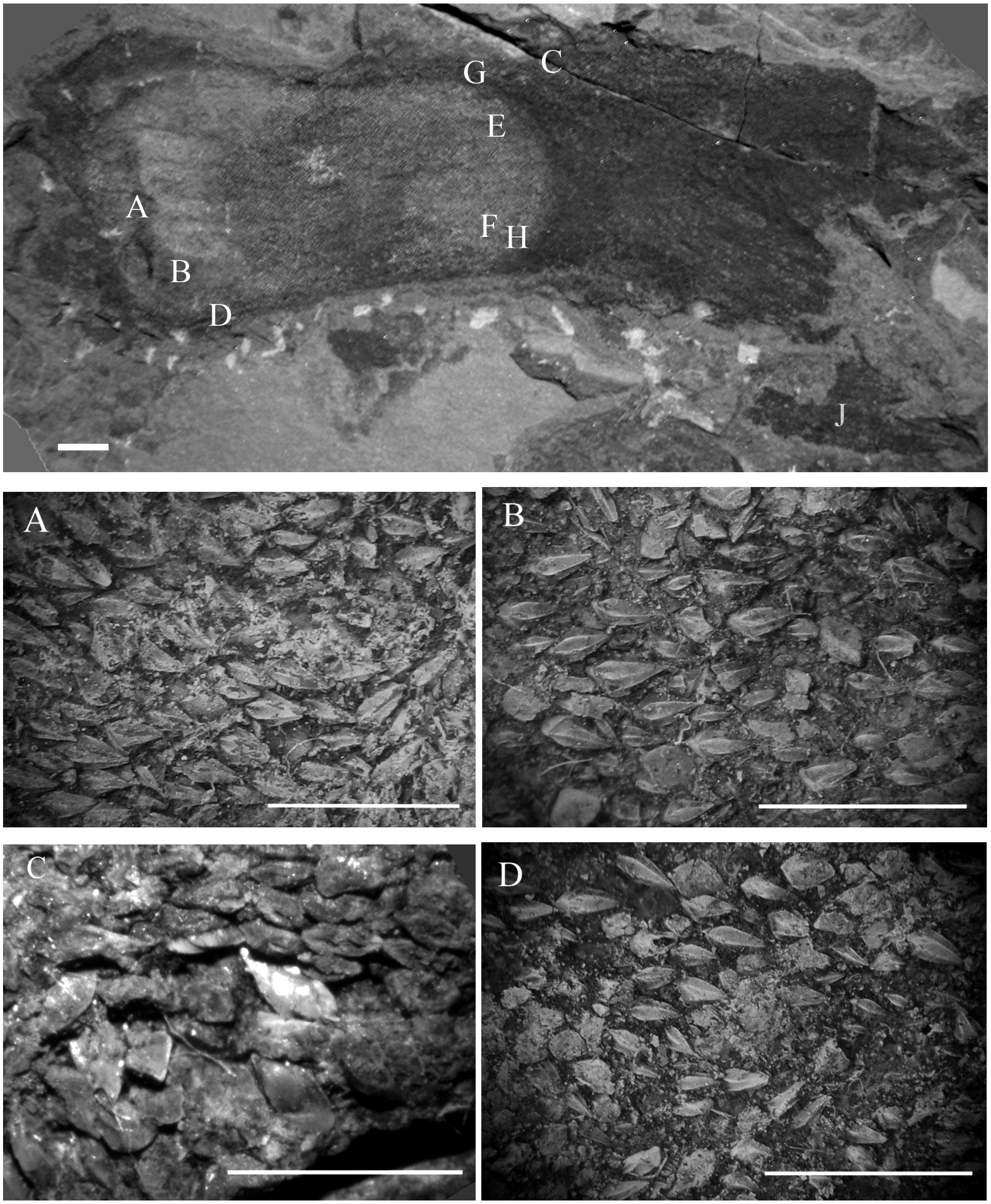

Fig. 7a Squamation patterns (coronal view) of *Loganellia scotica* TRAQUAIR 1898, specimen GBP n° 381, with details of the: postpectoral squamation (A, B), squamation of the leading edge of caudal fin (C), squamation of anal fin (D). Scale bars: 1 cm (articulated exoskeleton), 1 mm (A-D).

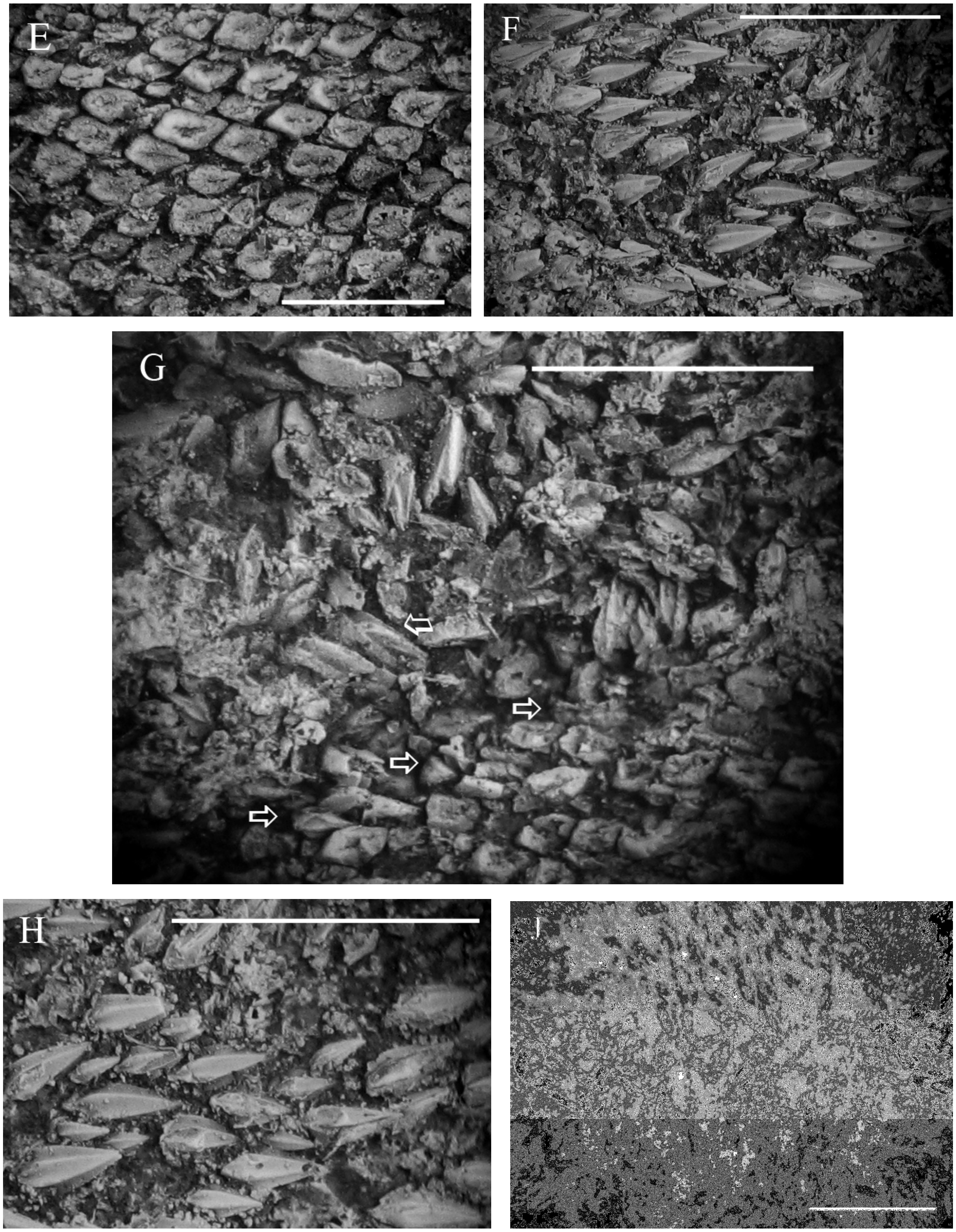

Fig. 7b Squamation patterns of *Loganellia scotica* TRAQUAIR 1898, specimen GBP n° 381, with details of the: precaudal squamation (E, basal view ; F, H, coronal view), squamation of the leading edge of caudal fin (G, coronal and basal view), pinnal squamation of caudal fin (J, basal view). Scale bar: 1 mm (G-J).

Article II

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A new thelodont from Lower Silurian of Tuva and north-west Mongolia

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The new thelodont genus and species *Talimaalepis rimae* is described from the upper Llandovery – Wenlock, Silurian of Central Asia (Tuva and north - west Mongolia) based on isolated exoskeletal microremains. Five major morphological types of dentine scales, namely rostral, cephalo-pectoral, postpectoral, precaudal and pinnal, are distinguished. Scales with pores of the sensory-line system are also established. According to morphology of scales and the internal structure of dentine tissue, the new thelodont taxon is considered to take an intermediate position between the genera *Loganellia* Turner, 1991 and *Helenolepis* Karatajūte-Talimaa, 1978.

Key words: Central Asia, Lower Silurian, Thelodonti.

Introduction

The Central Asia region yields endemic Lower Silurian vertebrate fauna (Karatajūte – Talimaa 1978; Blieck and Janvier 1993). Lower Silurian vertebrate material from outcrops of north-west Mongolia and Tuva have been studied for the present paper. Six samples with thelodont remains come from north-west Mongolia from the Chargat formation (Minjin, 2001), Lake Basin locality (Upper Llandovery – Wenlock; I. Sodov, P. Kosbayar and K. S. Rozman collections) (in Karatajūte-Talimaa *et al*. 1990). Ten scale samples from Tuva, the Kyzyl-Tchiraa, Elegest and Kadvoj sequences represent thelodonts from Upper Llandovery to Wenlock beds (V. Karatajūte-Talimaa collections).

A new thelodont *Talimaalepis rimae* gen. et sp. nov. was established and is described below. The form is suggested to take an intermediate position between the thelodont genera *Loganellia* and *Helenolepis*.

This work is a contribution to IGCP Project 491 "Middle Palaeozoic vertebrate biogeodiversity and climate".

Systematic palaeontology

Class AGNATHA Cope, 1889
Subclass THELODONTI Kiaer, 1932
Order PHLEBOLEPIDIFORMES (?) Berg, 1938
Family PHLEBOLEPIDAE (?) Berg, 1940

Talimaalepis gen. nov.

Etymology. In honour of Habil. Dr. Valentina Karatajūtė-Talimaa; *lepis* (Greek), scale.

Type species. *Talimaalepis rimae* gen. et sp. nov.

Diagnosis. As for type species.

Remarks. The description of the new taxon is based on the isolated microremains of exoskeleton, the dentine scales. It has intermediate position between the two thelodont genera – *Loganellia* (Fam. Loganellidae) and *Helenolepis* (Fam. Phlebolepidae). *Talimaalepis* possesses one single pulp canal, which is typical to genus *Loganellia*. Though well-defined thick dentine canals opened into pulp canal are very specific to genus *Helenolepis*.

Talimaalepis rimae sp. nov.
Figs 1-3

1978 *Logania ? kadvoiensis*, Karatajūtė -Talimaa; p. 82-86; tab. XII, XIII, fig. 3-6; tab. XIX, fig.14; tab. XXII, fig. 1-6; fig. 15, fig. 5-9.
1991 *Loganellia ? kadvoiensis*, Turner; p. 111.
1991 *Helenolepis* sp., supposed, Turner; p. 111.
2002 *Loganellia* sp. nov., Žigaite; p. 229-230; fig. A, B.
2003 *Helenolepis* sp. nov., Žigaite; p. 57-58.
2004 *Helenolepis* ? sp. nov., Žigaite; p. 37-38.

Etymology. *Rima, ae*, f. (Latin) meaning a gap, a slot. Name emphasizes the type species of genus *Talimaalepis* gen. nov. placed between thelodont genera *Loganellia* and *Helenolepis*.

Holotype. LGI M-1/224, cephalo-pectoral scale, Fig. 1 herein.

Type locality and stratigraphy. South-east slope of mount Chargat, 80 km north from lake Khara-Ubs-Nuur, Lake Basin outcrop No 21, north-west Mongolia; Chargat Formation, Salhit Regional Stage, upper Llandovery – Wenlock, Silurian.

Material. About 800 scales stored in the Institute of Geology and Geography, Lithuania; collection numbers LGI M-1 and LGI T.

Diagnosis. Elongated scales of medium size, up to 1.4 mm long, 0.6 – 0.8 mm on the average. The elongate and flattened crown of most common cephalo-pectoral scales divided into main central and paired shorter lateral parts. Crown surface with longitudinal sculpture composed of central groove and lateral pairs of ribs. Wedge-shape base usually

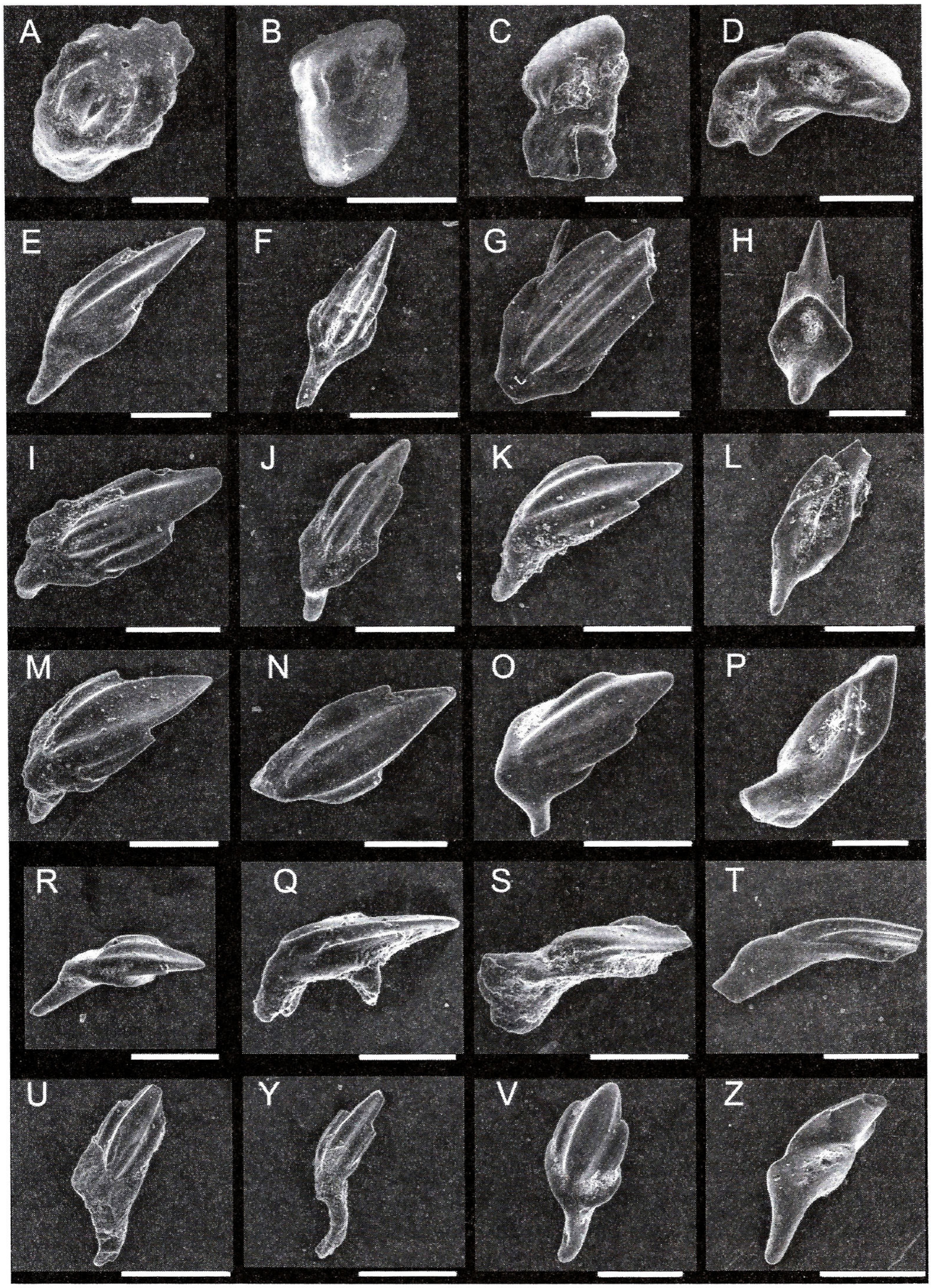

Fig. 1. *Talimaalepis rimae* gen. et sp. nov. scale morphological varieties. Lake Basin outcrop No 21, north west Mongolia; Chargat Formation, Salhit Regional Stage, Upper Llandovery – Wenlock, Lower Silurian. **A**, LGI M-1/201, oral scale; **B**, LGI M-1/254, oral scale; **C**, LGI M-1/203, oral scale; **D**, LGI M-1/204, oral scale; **E**, LGI M-1/224, holotype, cephalo-pectoral scale; **F**, LGI M-1/258, cephalo-pectoral scale; **G**, LGI M-1/234, cephalo-pectoral scale; **H**, LGI M-1/231, cephalo-pectoral scale; **I**, LGI M-1/233, cephalo-pectoral scale; **J**, LGI M-1/232, cephalo-pectoral scale;

with large anterior spur-like process. Pulp opening allocated just behind the vertical projection of the base. Only one well-defined pulp canal present. Straight separate dentine canals, rather thin in the periphery, anostomose and become thicker close to the pulp canal. Pore scales of sensory line-system present.

Description.

Morphology. Five major morphological types of the scales have been distinguished – the rostral, cephalo-pectoral, postpectoral, precaudal and pinnal (according to Märss 1986a, b; Märss and Ritchie 1998). Rostral scales (Fig. 1 A-D; Fig. 2 A-C) are slightly rhombic to oval, with a massive basal plate which is usually larger than the crown. The crown has isometrically serrated edges. The surface of the crown is smooth and lacks any kind of sculpture. Cephalo-pectoral scales (Fig. 1 E-L; Fig. 2 D-L) are large, elongate and relatively flat, with distinct crown sculpture. The crown surface contains a sharp longitudinal central depression or groove, surrounded by symmetrical ribs on both sides, and one or two pairs of lateral ribs. The crown goes over the smooth base. The neck is not well expressed. The posterior edge of the crown is notched and stretches over the base. The base is large, wedge shaped, often with a specific strong anterior spur-like process. Postpectoral scales (Fig. 1 M-P) are characterized by a wide and shallow central crown depression and one pair of lateral ribs. The crown is usually wider and longer than the base. The difference between cephalo-pectoral and postpectoral scales is transitional. Precaudal scales (Fig. 1 Z; Fig. 2 M) are comparatively tiny, up to 0.5 mm long. The crown sculpture, the central groove and ridges are not very clear. Pinnal (fin) scales (Fig. 1 R-V; Fig. 2 N, O) are narrow and elongate as are crown sculpture elements. The base is strongly wedge-shaped, its vertical projection lies almost at a right angle with the crown. The crown is rather needle shaped, so called "*cuneata*" type (Märss 1986a, b). These scales might have been allocated on the fins of this thelodont. The shape of the scales reflects the higher flexibility of fins. The scales possessing pores of the sensory-line system are also established (Fig. 2 H).

Histology. The internal structure of *Talimaalepis rimae* gen. et sp. nov. is rather similar to that of genus *Helenolepis*. The horizontal longitudinal thin sections of the scales show thin dentine canals which are directed from the periphery towards the pulp canal, gradually thickening and anastomosing. In the central part of the scale, several thick dentine canals enter into a wide single pulp canal which takes approximately 2/3 of the crown length (Fig. 3).

Comparison. The morphology of rostral and cephalo-pectoral scales of *Talimaalepis rimae* gen. et sp. nov. is rather similar to that of *Helenolepis obruchevi* Karatajūte-Talimaa, 1978. A common feature is the extremely high vertical projection of the base of adult scales. The internal scale structure and the possession of thick dentine canals display a close relation to genus *Helenolepis* too. Though possession of a single pulp

K, LGI M-1/237, cephalo-pectoral scale; **L**, LGI M-1/227, cephalo-pectoral scale; **M**, LGI M-1/207, post-pectoral scale ; **N**, LGI M-1/208, post-pectoral scale; **O**, LGI M-1/223, post-pectoral scale; **P**, LGI M-1/235, post-pectoral scale; **R**, LGI M-1/220, pinnal scale; **Q**, LGI M-1/238, pinnal scale; **S**, LGI M-1/213, pinnal scale; **T**, LGI M-1/214, pinnal scale; **U**, LGI M-1/226, pinnal scale; **Y**, LGI M-1/200, pinnal scale; **V**, LGI M-1/206, pinnal scale; **Z**, LGI M-1/239, precaudal scale. Scale bars: A, D, E, H, N, P, 200 μm; B, C, G, I, K, M, O, R-T, V, 300 μm; F, J, L, U, Y, Z, 400 μm.

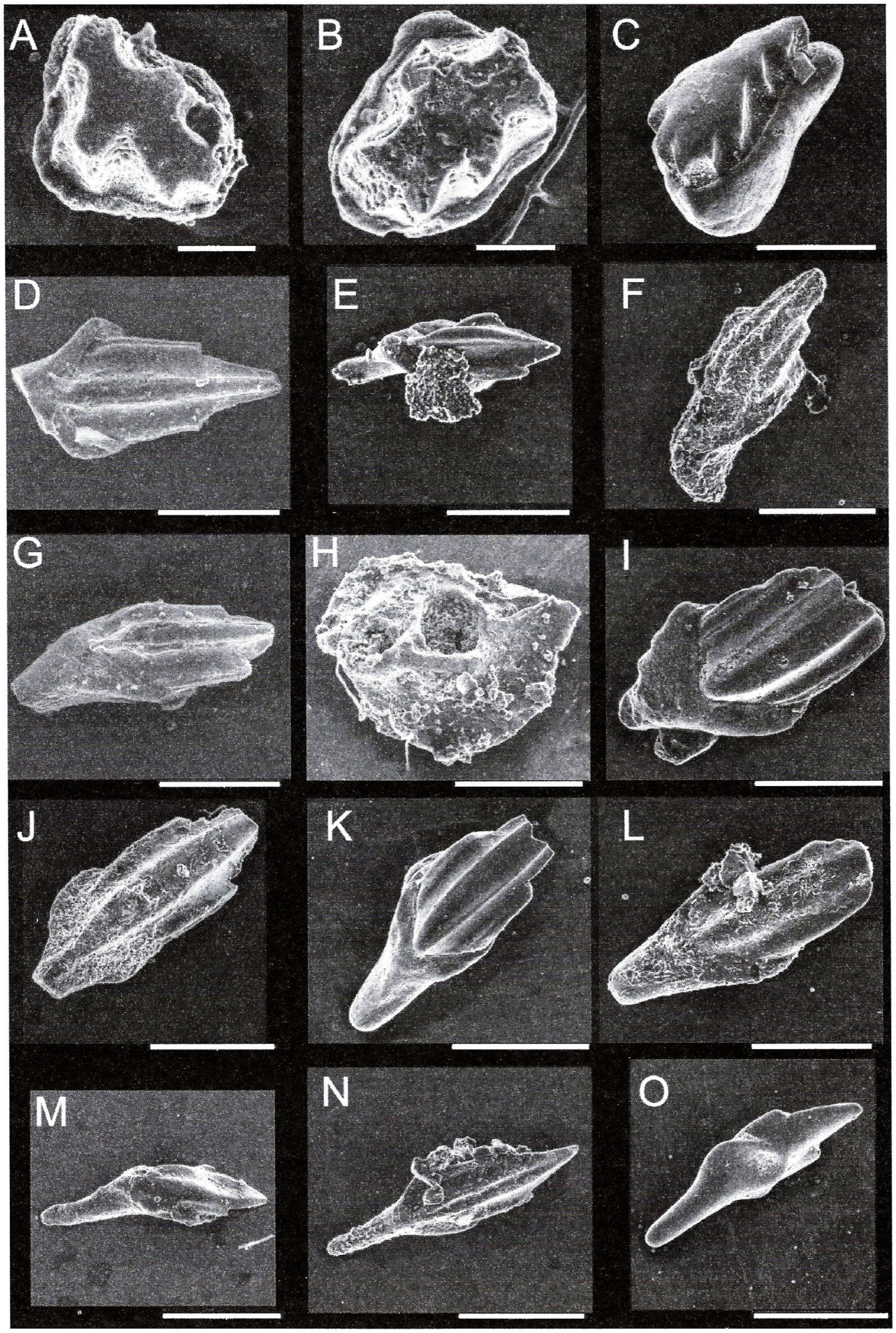

Fig. 2. *Talimaalepis rimae* gen. et sp. nov. scale morphological varieties. Kyzyl-Tchiraa outcrop, Central Tuva; Tchergak series, Kyzyl-Tchiraa Regional Stage, Upper Llandovery, Lower Silurian. **A**, LGI M-1/240, oral scale; **B**, LGI M-1/241, oral scale; **C**, LGI M-1/242, oral scale; **D**, LGI M-1/248, cephalo-pectoral scale; **E**, LGI M-1/257, cephalo-pectoral scale; **F**, LGI M-1/250, cephalo-pectoral scale; **G**, LGI M-1/246; **H**, LGI M-1/222, pore sensory canal – system scale; **I**, LGI M-

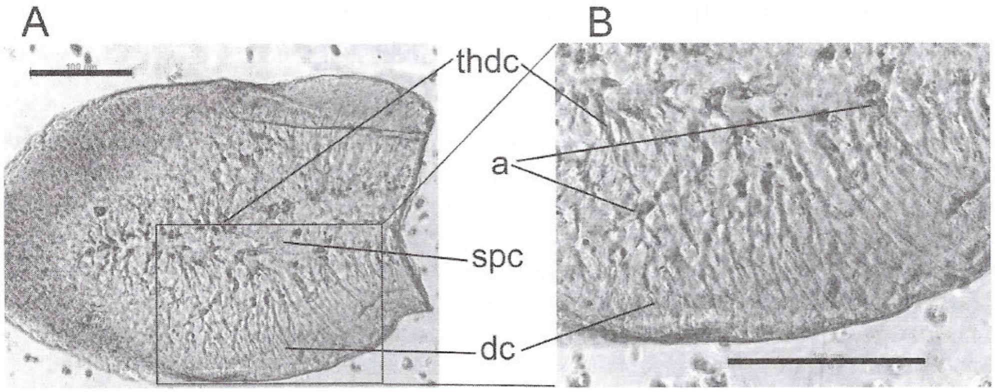

Fig. 3. Talimaalepis rimae gen. et sp. nov., cephalo-pectoral scale, horizontal longitudinal thin section (B is part of A). Lake Basin outcrop No 21, north west Mongolia; Chargat Formation, Salhit Regional Stage, Upper Llandovery – Wenlock, Lower Silurian. Thin section No 80, Institute of Geology and Geography, Lithuania. Abbreviations: **a** – anastomoses; **dc** – thin dentine canals; **spc** – single pulp canal; **thdc** – thick dentine canals. Scale bars: 100 µm.

canal makes a substantial difference, as in *Helenolepis* scales, there are three or more pulp canals, subject to a number of crown segments (Karatajūte-Talimaa 1978, p. 236, Fig. 14). Sparse anastomoses of usually straight dentine canals make the histology of the scales closer to that of genus *Loganellia*. Scales with sensory pore canal system elements are described in Family Phlebolepididae, Loganelliidae, Shieliidae, Boothialepididae, Turiniidae, and in Furcacaudifrmes (Gross 1968, Märss 1979, Miller and Märss 1999, Märss 1999, Märss and Miller 2004, Turner 1991, Wilson and Caldwell 1998). On the basis of a different central part of the crown, and shorter lateral areas, as well as the presence of a single pulp canal, the taxon can be ascribed neither to genus *Loganellia*, nor to *Helenolepis*.

Distribution. Apart of the type locality, remains of *Talimaalepis rimae* gen. et sp. nov. are found in several localities of the Central Tuva: outcrop Kyzyl-Tchiraa (Kyzyl-Tchiraa Formation, Kyzyl-Tchiraa Regional Stage, upper Llandovery), outcrop Elegest (Dashtygoi Formation, Dashtygoi Regional Stage, upper Wenlock), Kadvoj sequence (Tchergak Formation, Angatchi and Dashtygoi regional stages, upper Llandovery and upper Wenlock).

1/247, cephalo-pectoral scale; **J**, LGI M-1/243, cephalo-pectoral scale; **K**, LGI M-1/245, cephalo-pectoral scale; **L**, LGI M-1/229, cephalo-pectoral scale; **M**, LGI M-1/219, precaudal scale; **N**, LGI M-1/249, pinnal scale; **O**, LGI M-1/221, pinnal scale. Scale bars: A, B, 100 µm; C, D, F, G, J, L, 200 µm; E, H, I, N, 300 µm; O, 400 µm; K, M, 500 µm.

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Jauna telodontu ģints un suga no Tuvas un ziemeļrietumu Mongolijas apakšējā silūra

ŽIVILĖ ŽIGAITĖ

Jauna telodontu ģints un suga *Talimaalepis rimae* ir aprakstīta pēc izolētām ārējā skeleta mikroskopiskām atliekām no centrālās Āzijas (Tuvas un ziemeļrietumu Mongolijas) silūra Landoveras augšdaļas – Venlokas. Ir izdalīti pieci dentīna zvīņu morfoloģiskie tipi: rostrālās, cefalopektorālās, postpektorālās, prekaudālās un pinnālās. Tāpat atrastas zvīņas ar sānu līnijas kanālu sistēmas porām. Ņemot vērā zvīņu uzbūvi un dentīna audu iekšējo struktūru, jaunais telodontu taksons ieņem stāvokli starp ģintīm *Loganellia* Turner, 1991 un *Helenolepis* Karatajūte-Talimaa, 1978.

Article III

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New genus of Chondrichthyans from the Silurian – Devonian boundary deposits of Tuva (Russia)

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ABSTRACT:

ŽIGAITĖ, Ž. & KARATAJŪTĖ-TALIMAA, V. 2008. New genus of Chondrichthyans from the Silurian – Devonian boundary deposits of Tuva (Russia). *Acta Geologica Polonica*, **58** (2), 127-131. Warszawa.

A new genus of Chondrichthyes from the uppermost Silurian–lowermost Devonian deposits of central Tuva (Russia) is described on the basis of the microremains (scales). A sample from the Khondergei Formation of the Bazhyn-Alaak locality in the Tchadan region contained scales of a new chondrichthyan, *Tuvalepis schultzei* gen. et sp. nov., together with another chondrichthyan, *Elegestolepis grossi* KARATAJŪTĖ-TALIMAA, 1973, as well as numerous scales of the thelodont *Helenolepis navicularis* KARATAJŪTĖ-TALIMAA, 1978. The scales of *T. schultzei* display significant morphological variation and are characterized by a very fine, comparatively wide and flat crown with longitudinal ribs and a small and short neck. The growth pattern of *T. schultzei* scales is very different from that of elegestolepids described so far – the scales grew by appositional addition of layers towards the distal side of the crown, in contrast to the scales of *Elegestolepis grossi* which lack any kind of concentric growth lines.

Key words: Chondrichthyans, Elegestolepids, Silurian, Devonian, Tuva.

INTRODUCTION

Sections through the Silurian-Devonian boundary beds in the Bazhyn-Alaak locality in the Tchadan region of central Tuva have yielded various vertebrate microremains, including the new genus and species of Chondrichthyes described herein. One of the samples collected in the area (number 119R), from the Khondergei Formation (Tauganteli Regional Stage, Upper Silurian – Khondergei Regional Stage, Lower Devonian), contained scales of the new chondrichthyan taxon (KARATAJŪTĖ-TALIMAA & RATANOV 2002), together with another chondrichthyan *Elegestolepis grossi* KARATAJŪTĖ-TALIMAA, 1973, as well as numerous scales of the thelodont *Helenolepis navicularis* KARATAJŪTĖ-TALIMAA, 1978.

The samples were collected by L.S. RATANOV (Novosibirsk, SNIIGGiMS, Russia) in 1987, and the fossil material was loaned to one of us [V. K.-T.] by L. M. AKSENOVA (SNIIGGiMS, Novosibirsk, Russia) in 1988. Currently it is stored in the Institute of Geology and Geography, Vilnius, Lithuania, under the collection numbers LGI T-130 – LGI T-180.

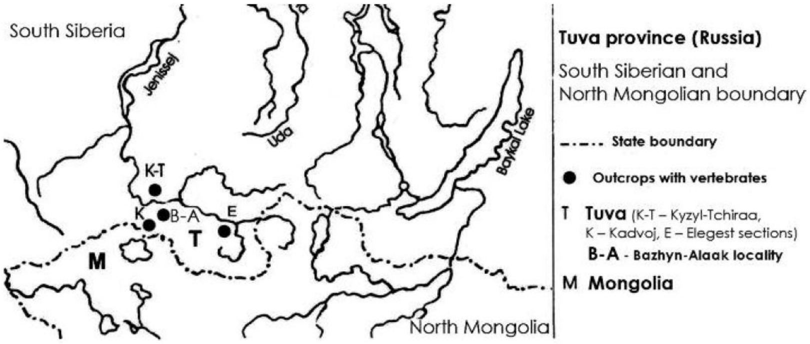

Fig. 1. Vertebrate-bearing localities of central Tuva (Russia)

GEOLOGICAL SETTING

The material studied comes from the Bazhyn-Alaak Silurian–Devonian locality near the river Tchadan in central Tuva (Russia). The outcrop is located near other well-known vertebrate-bearing Silurian and Lower Devonian localities, such as Kyzil-Tchiraa, Kadvoj, and Elegest (Text-fig. 1). Sample 119R, containing the new chondrichthyan genus and species described herein, was collected from terrigenous deposits of the lowermost Khondergei Formation, referred roughly to the Silurian–Devonian (Pridoli–Lochkovian) boundary interval, within the boundary beds between the Tauganteli (S_2) and Khondergei (D_1) Regional Stages (Karatajūtė-Talimaa & Ratanov 2002).

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Order Incertae Sedis
Family Incertae Sedis
Genus *Tuvalepis* gen. nov.

Tuvalepis gen. nov.

TYPE SPECIES: *Tuvalepis schulzei* sp. nov.

ETYMOLOGY: After the region of Tuva.

DIAGNOSIS: The scales distinguished by fine, flat crown, very low and flat base, and reduced neck. Distal part of crown characterized by concentric growth lines. Longitudinal ribs present on proximal surface of crown.

Tuvalepis schultzei sp. nov.
(Text-figs 2-3)

ETYMOLOGY: In honour of Prof. Hans-Peter Schultze (Kansas, USA).

HOLOTYPE: (Text-fig. 2C). Collection number T-122 (Lithuanian Institute of Geology and Geography, V. Karatajūtė-Talimaa collection).

TYPE LOCALITY: River Tchadan, Bazhyn-Alaak locality, Tuva (Russia).

TYPE HORIZON: Terrigenous deposits of the Tauganteli (S_2) and Khondergei (D_1) Regional Stages, lowermost Khondergei Formation, sample Nr. 119R.

STRATIGRAPHIC RANGE: The Silurian – Devonian (Pridoli–Lochkovian) boundary interval, within the boundary beds of the Tauganteli and Khondergei Regional Stages, lowermost Khondergei Formation.

MATERIAL: About 50 well preserved scales.

DIAGNOSIS: Same as for the genus.

DESCRIPTION: The scales show a significant morphological variety, and are characterized by a comparatively wide and flat, very fine crown, which is connected to the comparatively small, thin, flat base by a small and short neck. The pulp cavity is poorly expressed, as the scales are extremely flat.

MORPHOLOGY: The morphological set of the *T. schultzei* scales contains several distinct morphological types (Text-fig. 2). The first type is characterized by symmetrical scales with a very simple smooth crown

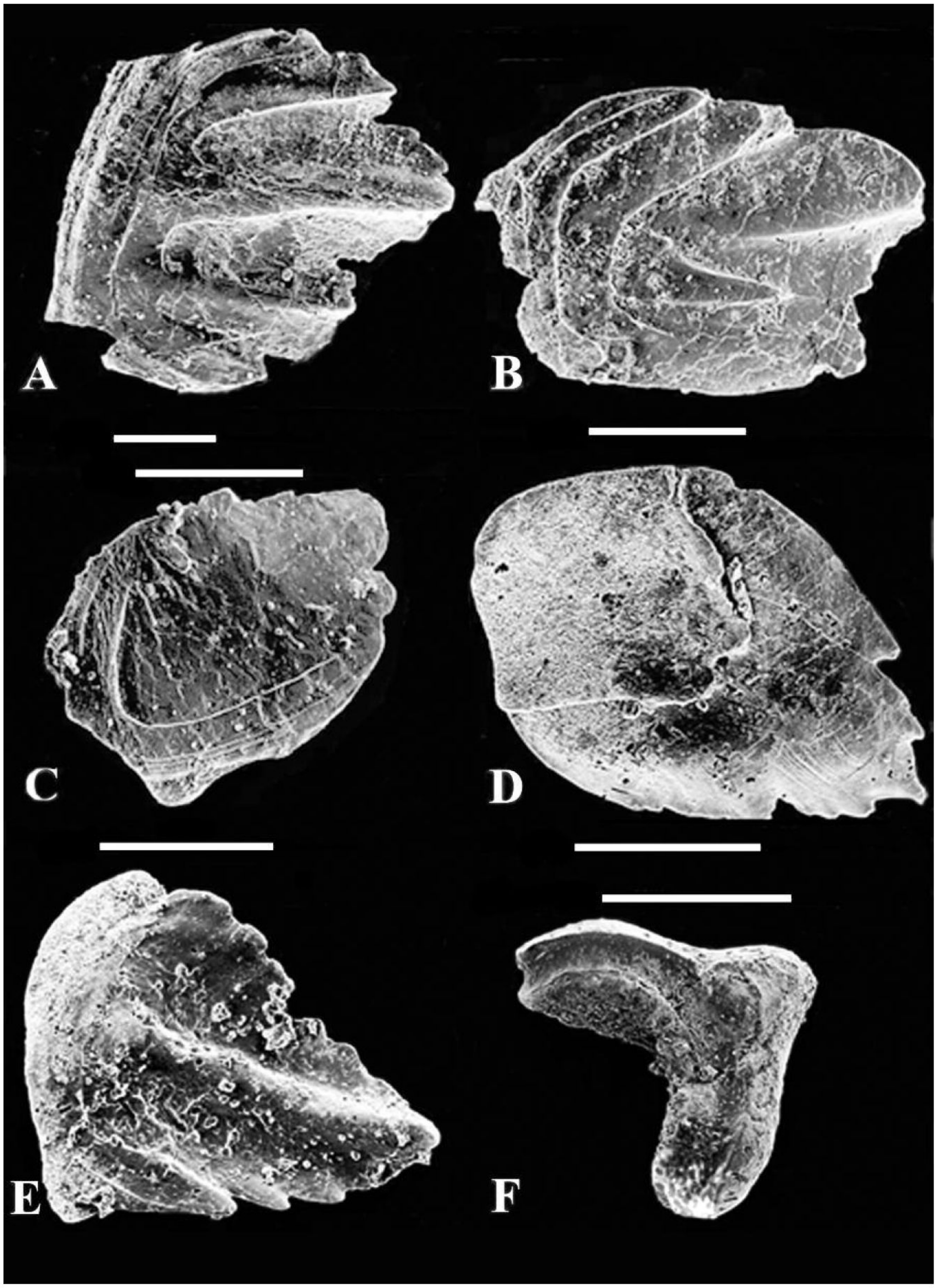

Fig. 2. Morphological set of the scales of *Tuvalepis schultzei* gen. et sp. nov. A – ribbed type body scale, T-120, × 106; B – ribbed type body scale, T-121, × 169; C – holotype, smooth crown type body scale, T-122, × 201; D – smooth crown type body scale, ventral view, T-123, × 195; E – asymmetrical body scale, T-124, × 172; F – keel-shaped scale, T-125, × 93,7. Scale bars equal 200 µm., except Fig. F - 500 µm

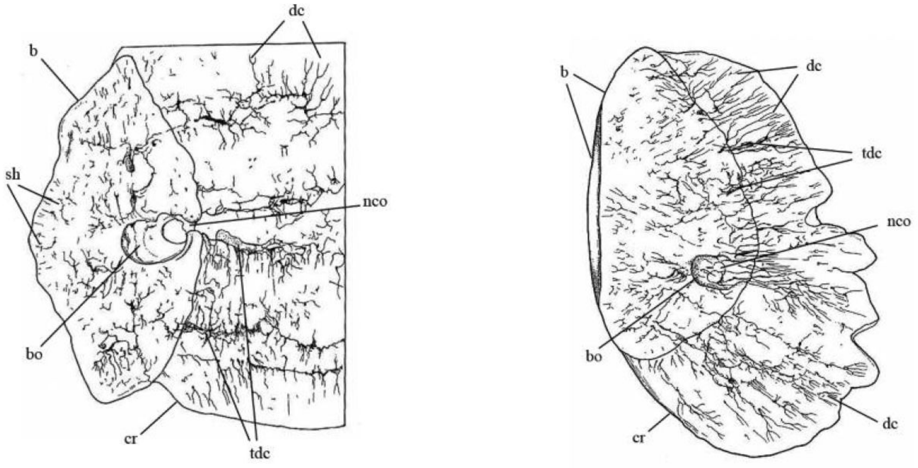

Fig. 3. Histology of the scales of *Tuvalepis schultzei* gen. et sp. nov. (anise oil microscopy). A – Proximal part of an asymmetrical body scale (ventral view). B – Complete ventral view of an asymmetrical body scale. Abbreviations: b – base; bo – base opening; cr – crown; dc – dentine canals; nco – neck canal opening; sh – Sharpey's fibres; tdc – thick dentine canals

with one or several concentric growth lines, and a sharp distal part (Text-fig. 2C, 2D). Longitudinal ribs are present on the distal part of the crown surface in some cases. Another scale type shows a crown with complex sculpture. In the proximal part of the scales several growth lines can be distinguished. The main part of the crown is ornamented by several longitudinal ribs – a long central rib, and two or three pairs of shorter lateral ribs (Text-fig. 2A, 2B). The distal part of the scales is strongly sharpened. The crown is still symmetrical in overall shape. The third scale type is represented by several scales with a similar complex sculpture of the crown to that of the previous type, but the scales are strongly asymmetric (Text-fig. 2E).

The *T. schultzei* microremains additionally include contain keel-shaped scales of uncertain affinity (Text-fig. 2F), with a very thick longitudinal central rib, and fine narrow lateral ribs.

HISTOLOGY: The relatively good preservation and general construction of the scales give the possibility of analyzing the internal structure without thin-sectioning. The histology of the scales can be studied in anise oil. The internal structure of the crown is characterized by a few rather short and thick dentine canals in the anterior part of the scale, and by a branching network of numerous thin dentine canals in the remainder of the scale. Mesodentine lacunae are not developed. The scales possess two pulp canal openings: the wider one is on the base, and the narrower opening is on the side of the neck (Text-fig. 3A, 3B). Both neck and base canals are very short, and open close to each other.

COMPARISON: These vertebrate microremains were first ascribed to elegestolepids (KARATAJŪTĖ-TALIMAA & RATANOV 2002; ?*Elegestolepis* gen. nov.). However, although *Tuvalepis schultzei* shows some similarity to elegestolepids, there are also fundamental differences in growth pattern, histology, and morphology. The scales of *Elegestolepis grossi* have a high crown with a thick base and a well developed high neck. In contrast, the base of the *Tuvalepis schultzei* scales is very flat and low, the neck is reduced, and the space between the crown and the base is very narrow. The sculptured crown type scales of *T. schultzei* have fewer longitudinal ribs on the crown (up to two or three pairs), in contrast to those of *E. grossi*, which usually have more than three pairs of longitudinal ribs.

The internal structure of the crown of *T. schultzei* scales is characterized by thick dentine canals, similar to those of *E. grossi* scales, but the canals are much shorter. The network of thin dentine canals of *T. schultzei* scales is branched and well developed in contrast to the more regular pattern of the thin dentine canals in *E. grossi* scales, which spread only close the surface of the crown. *T. schultzei* scales possess two pulp canal openings: the wider one is on the base, while the narrower opens on the side of the neck; both are very close to each other because of the flatness of the scales. In contrast, in *E. grossi* scales these two canals extend at a right angle to each other, open at a sharp right angle, and open at a significant distance from each other, one on the side of the high neck, and the other in the central part of the base.

The growth pattern of *T. schultzei* scales is very different from that of elegestolepid scales – the scales grow by appositional addition of layers towards the distal side of the crown, in contrast to *E. grossi* scales, where an initial monodontodium just grows inwards and deep into the soft tissues, due to enlargement of the base solely, and any appositional growth is absent (KARATAJŪTĖ-TALIMAA 1973; ØRVIG 1977; KARATAJŪTĖ-TALIMAA 1998).

DISCUSSION: The differing morphologies of the scales of *Elegestolepis* and *Tuvalepis* may have some palaeoecological and palaeobiological implications. The high and sculptured scales of *E. grossi*, with a well expressed neck, could correspond to a more or less rounded body shape and a nektonic mode of life, as in the case of other early vertebrates – for example, the high, massive, and elevated scales of the actively swimming acanthodians (JANVIER 1996). In contrast, the flattened fine scales of *T. schultzei* most probably correspond to a flattened body, and probably to a benthic palaeoecological niche, as in the case of most of the benthic thelodont species possessing a dorsoventraly flattened body and a flattened general shape of the scales (MÄRSS & & 2007).

The most problematic of all the types of *T. schultzei* scales are the keel-shaped ones. The asymmetric scales of *T. schultzei* should be attributed to special functions and corresponding parts of the exoskeleton, while the symmetrical ones should represent the main scale cover of the body (KARATAJŪTĖ-TALIMAA 1973, 1998). However, the keel-shaped scales are very different from the rest of of the *T. schultzei* scale types, and therefore both their function and position on the body are open to question. If the assumption of *T. schultzei*'s benthic life style and flattened shape of the body is correct, such scales with a strong and high keel may not have had any use on the back of the body. Nevertheless the keel-shaped scales are histologically comparable to the rest of the *T. schultzei* scales, as they possess a comparable short neck and base canals, opening close to each other. Another reason for the assignment of these special scales to *T. schultzei* is that the rest of the vertebrate micromaterial in the sample belongs to two thelodont species of the genus *Helenolepis*, the above-mentioned *Elegestolepis grossi*, and osteostracans (KARATAJŪTĖ-TALIMAA & RATANOV 2002). None of the species mentioned above could have possessed keel-shaped scales with this kind of histology.

CONCLUSIONS

Scales of *Tuvalepis schultzei* gen. et sp. nov. have a flat and fine general morphology, which is the main feature of the exoskeleton microremains that separates this new species from elegestolepids. The growth pattern of *T. schultzei* is also very different from that of elegestolepids – the scales grow by appositional addition of layers towards the distal side of the crown. The morphological and histological differences and especially the distinct growth patterns are the main reasons for describing these scales not as a new species of the genus *Elegestolepis*, but as a new genus and species of chondrichthyan.

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Article IV

Endemic thelodonts (agnathan vertebrates) from the Lower Silurian of central Asia and the Siberian platform

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ABSTRACT

The thelodont microremains from the Lower Silurian of northwestern Mongolia, Tuva, and Siberian platform have been studied, attributing the material to two families, three genera and six species. All the taxa can be considered as endemic, with exception of cosmopolitic genus *Loganellia*, which is the most abundant and numerous in species as well. Genera *Angaralepis* and *Talimaalepis* are inferred as strongly endemic. The species content of genus *Talimaalepis,* so far known for consisting of a single species, has been revised, evolving into two species described herein consequently. Histology of *Talimaalepis* scales show an intermediate position between the *Loganellia* (Fam. Loganellidae) and *Helenolepis* (Fam. Phlebolepidae), remaining phylogenetic affiliation of *Talimaalepis* under further consideration. *L. tuvaensis* is the only species, which distribution in the Lower Silurian is restricted to localities of central Tuva. This could infer some degree of isolation of Tuvan palaeobasin in relation to the other epicontinental palaeoseas of the Siberian terrane. Additional reference of *Loganellia sibirica* in the Lower Silurian of Tuva, together with its findings in northwestern Mongolia and Siberian platform, supports the region as the united Siberian terrane in the Early Silurian. The record of *L.* cf. *L tuvaensis* records in the uppermost Silurian of North East Greenland indicates certain connections between the palaeobasins of Siberia and Laurussia. Considerable abundance of thelodont taxa in the Lower Silurian of central Asia and the Siberian platform, together with the richness of other Early Silurian vertebrate species of the area, reported in the literature, infer warm and productive palaeobasins spread as epeiric seas over the Siberian palaeocontinent, and indicates it as possible place of origin and radiation of at least some early vertebrates (BLIECK & JANVIER, 1993, COCKS & TORSVIK, 2002). The distribution of endemic thelodonts in the region studied serves as a strong palaeobiogeographical evidence for the Silurian palaeogeography, confirming the territory of Siberian platform, Tuva and northwestern Mongolia as united Siberian terrane in the Early Silurian (COCKS & TORSVIK, 2007).

KEY WORDS: Angaralepis, Loganellia, Talimaalepis, early vertebrates, palaebiogeography, Mongolia, Tuva, Siberia.

INTRODUCTION

Early Silurian vertebrate microremains from the central Asia – northwestern Mongolia and Tuva, as well as from central and southern parts of the East Siberia between Yenisey and Lena rivers (Siberian platform), has been studied. All this present day territory existed as united Siberian palaeocraton, the independent geological terrane which existed during the Palaeozoic (COCKS & TORSVIK, 2007). In the Silurian period it has comprised not only large area of the modern Russia (including Altai, Salair, Sayan, Siberia, Tomsk) and northwestern part of Mongolia, but also extended into the northwestern part of China, and it has been the only large terrane in the northern hemisphere for much of the Palaeozoic, since Ordovician (COCKS & TORSVIK, 2007). Its comparative isolation at relatively high latitudes of Siberia also mean that the area was colonised throughout the Palaeozoic by marine benthic faunas and in the later Palaeozoic by both marine and land floras and faunas which are not found elsewhere on Earth, and these biota were often sufficiently distinctive to form the basis of faunal palaeoprovinces at various times.

Accordingly, the early vertebrate material studied, have yielded a number of thelodont species, all considered as endemic (ŽIGAITE & BLIECK, 2006). This allows us to suggest separate palaeobiogeographical province for the region, which has been already assumed in the preceeding studies (KARATAJŪTĖ – TALIMAA 1978; BLIECK AND JANVIER 1993). The Mongolian material has been collected in the north-west of the country, near the Tchargat Mountain north of the lake Ubs-Nuur, and have been provided by L. ROSMAN, and more recently by I. SODOV. The vertebrate material of Tuva comes from several localities in the central part of the country, and has been collected by T. MOSKALENKO, L.AKSENOVA, N. KULKOV, and L. RATANOV (Novosibirsk, Russia) in the years of 1968-1987 (KARATAJŪTĖ-TALIMAA & RATANOV 2002).

The first description of vertebrate microremains in some part of the collections has been made in 1978 in Russian, by prof. V. Karatajūtė-Talimaa (KARATAJŪTĖ-TALIMAA, 1978). Additional material from has been revealed, SEM pictures of the complete morphological set of the species has been made. Thin sections, prepared and published as drawings by V. Karatajūtė-Talimaa in 1978, has been re-examined and pictured. New thin sections and histological pictures has been prepared (Plates 7 and 8).

Present study contains revised, complementary, and new full descriptions of all the thelodont material available from the collections, including the emended species and the new ones. If compared to the first descriptions made by Karatajūtė-Talimaa in 1978, in Russian, the species descriptions presented further in this work are complemented regarding the additional material revealed, improved concerning the most recent works on thelodont palaeontology and palaeobiogepgraphy (KARATAJŪTĖ-TALIMAA & MÄRSS, 2004; MÄRSS et al., 2007), and new terminology for thelodont squamation patterns, and corresponding assignation of the scales is used: former classification of head, transitional, and body scale categories, have been adopted to the most recent division of thelodont scales (MÄRSS, 1986b) as follows: rostral (=head); cephalo – pectoral (=transitional, and 'transitional' body scales, a part of body scales contiguous the head scales and terminating near the pectoral fins); postpectoral and precaudal (=most of the body scales); and the pinnal (=special) scales, the latter including the frequently-reported thelodont scales of the edges of the fins. The new high quality SEM pictures and new morphological sets of the scales of the species are being presented.

The material, including already published samples, and the following described below, is presently stored in Vilnius University, Department of Geology and Mineralogy (Lithuania), as private collections of prof. V. KARATAJŪTĖ-TALIMAA, though the original series number LGI (after the Institute of Geology and Geography of Lithuania) has been kept.

GEOLOGICAL SETTING

Mongolian early vertebrate microremains come from the Lower Silurian section of the northwestern Mongolia, south-east slope of mount Tchargat, 80 km north from lake Khara-Ubs-Nuur (Fig. 1). The section is represented by Tchargat Formation, which comprises molasse-type sequence, characterized by brown and red-coloured conglomerates, clayey limestone breccias, and concretionary sandstones with limestone intercalations containing rich faunas (MINJIN et al., 2001). These limestone inliers represent marginal shallow water sedimentary facies rich in fauna, including numerous vertebrate microremains (KARATAJŪTĖ-TALIMAA et al., 1990). Vertebrate microremain material comes from the Lake Basin outcrop in Tchargat locality, the Khutsyn-Bulag member of Tchargat Formation, Lower Wenlock in age (MINJIN et al., 2001), dating is based mainly on conodont data (KARATAJŪTĖ-TALIMAA et al., 1990).

Apart from thelodonts presented in this work, complementary vertebrate fauna comprise abundant acanthodian, chondrichthyan, heterostracan and mongolepid microremains (KRATAJŪTĖ-TALIMAA et al., 1990).

Vertebrate samples of Tuva have been collected from the Kyzyl-Tchiraa, Elegest, and Kadvoi sequences represent thelodonts from Upper Llandovery to Wenlock beds. Dating of the Lower Silurian sequences has mainly been based on conodont data (VLADIMIRSKAYA et al., 1986). Lower and middle Llandovery is represented by Alash Formation (Rhudanian – Aeronian), comprising fine grained to coarse sandstones with limestone intercalations rich in fauna. The upper Llandovery is represented by two formations, the Kyzyl-Tchiraa Formation (lower Telychian), and the Angatchi Formation (upper Telychian), the latter has recently been argued to be lower Sheinwoodian in age (KARATAJŪTĖ-TALIMAA & RATANOV, 2002). The formations are composed of fine grained laminated sandstones with limestone intercalations. The lower Wenlock corresponds to the Akchalym Formation (lower – middle Sheinwoodian), made up of siltstones with clayey inliers, baren in vertebrate fauna. The upper Wenlock sediments correspond to the Dashtygoi Formation (upper Sheinwoodian – middle Ludlow), composed of condenced limestones with thin siltstone intercalations (VLADIMIRSKAYA et al., 1986; KARATAJŪTĖ-TALIMAA & RATANOV, 2002).

Most of the Siberian vertebrate microremains presented in this work come from the Lower Silurian rocks which have been exposed to some alteration, especially in the centre of the Siberian platform, where little tectonical alterateration occured during the Phanerozoic (COCKS & TORSVIK, 2007). For ex., the very extensive Silurian successions outcropping along the Lena River mostly have dips of less than two degrees. Silurian exposures studied 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; Early Silurian vertebrates have been recorded in all of them and the thelodonts from the four latter are discussed in this study.

The early vertebrate microremains belong to the shallow-shelf facies, such as brachiopod limestone in the Preyenisey subregion, open shallow shelf facies with diverse benthic fauna in Pretunguska subregion, lagoonal dolomitic marl with abundant fish and eurypterid fossils in Nyuya-Beresovo subregion, and shallow-water, gypsum-bearing, dolomitic marl and sandstone from the two lithostratigraphic districts of Irkutsk subregion (TESAKOV et al., 2003).

Early Silurian thelodont microremains are most abundant in the Nyuya-Beresovo and Itrkutsk subregions, smaller part of the material have been revealed from the North Preyeniseya and Pretunguska subregions, Turukhansk and Kochumdec districts respectively (Fig. 1). Turukhansk stratigraphic district is located in the western Siberian platform, in the lower reaches of the Kureyka and Nizhnyaya Tunguska Rivers (Fig. 1). The thelodont microremains come from the Omnutakh Formation, upper Llandovery (uppermost middle Aeronian – Telychian), consisting gray and greenish–gray marl that alternates with gray, platy and nodular limestone. The invertebrate fauna is dominated by *Favosites gothlandicus*, *Mesofavosites dualis*, *Cystiphyllum densum*, *Anabaria rara*, *Septatrypa magna*, *Morinorhynchus proprius*, *Beyrichia quadricornuta*, *Monograptus distans*, and *Streptograptus nodifer* (TESAKOV et al., 2003). Kochumdek district is located along the northern Yenisey Ridge, close to the Kochumdek River, a tributary of the Podkamennaya Tunguska River. Thelodont microremains have been revealed from all the four Silurian formations of the district as follows. The Kochumdek Formation, lower Llandovery (Rhudanian – lower Aeronian), consisits of grey nodular limestone with interbeds of grey marl, which increase in abundance towards the top of the formation. The invertebrate fauna includes *Alispira gracilis*, *Brevilamnulella undatiformis*, *Isorthis neocrassa*, and *Calamopora alveolaris*. The middle Llandovery is represented by the Kulinna Formation (middle – upper Aeronian), which cinsists of variegated mudstone and marl with interbeds of grey, nodular and wavy-bedded limestone. The invertebrate fauna is dominated by *Mesofavosites dualis*, *Favosites gothlandicus*, *Pentamerus oblongus*, *Eocoelia hemisphaerica*, and *Isorthis neocrassa*. The overlying Razvilka Formation (upper Llandovery, Telychian), is made up of green marl with nodules and lenses of grey limestone. The upper part is mostly composed of limestone and dolostone, intercalated by marl with nodular limestone. The main invertebrate fossils are *Labechia venusta*, *Mesofavosites dualis*, *Cratolacrinites borealis*, *Beyrichia patagium*, *Eocoelia hemisphaerica*, and *Pentamerus oblongus*. The Wenlock series is represented as a lower part of Usas Formation (Wenlock – uppermost Gorstian), and is composed of grey dolomitized limestone with biostromes. The invertebrate fauna includes *Labechia condensa*, *Mesosapporipora porosa*, and *Favosites gothlandicus* (TESAKOV et al., 2003).

The majority of the thelodont material has been revealed from the southern and south-eastern part of Siberian platform, corresponding to the Nyuya-Beresovo and Itrkutsk subregions (Fig. 1). The area is subdivided into the three lithostratigraphic districts: Nyuya-Beresovo, Ilim and Balturino districts respectively (TESAKOV et al., 2003).

Nyuya-Beresovo stratigraphic district lies in the middle reaches of the Lena River and its Nyuya, Dzherba, and Biryuk River tributaries (Fig. 1). The thelodont findings are restricted to the Llandovery series, reperesented by two formations as follows. The Melichan Formation, lower Llandovery (Rhudanian – lower middle Aeronian) consists of grey dolostone and dolomitic marl with interbeds of grey, platy dolostone. The most common taxa are *Lenatoechia elegans*, studied further in this work. *Icriodella discreta* and *Distomodus kentuckyensis*, and vertebrate *Loganellia sibirica*. The upper Llandovery is composed of the Utakan Formation (upper middle Aeronian – Telychian), consisting variegated dolomitic marl with rare interbeds of platy dolostone that are gypsiferous at the top. The known taxa include echinoid *Lenatoechia elegans*, conodont *Panderodus unicostatus*, and two common vertebrate species, *Elegestolepis conica*, and *Loganellia sibirica*, the latter is presented in this work below.

The Silurian sequences of the southernmost Irkutsk subregions are particularly rich in early vertebrate fauna. The Ilim stratigraphic district, lying in the drainage basins of the middle Angara River and the Ilim River, yielded vertebrates from the only Llandoverian formation, the Rassokha Formation (Rhudanian – Telychian), consisting of variegated siltstone with sandstone lenses (TESAKOV et al., 2003). The common invertebrate fauna of the Rassokha Formation is composed of *Mesofavosites dualis, Lenatoechia ramose*, *Eotomaria gatlense*, and *Pseudoproetus bellus*. The abundant vertebrates are represented by two thelodont species, *Loganellia sibirica* and *L. asiatica*, both studied below in this work. The southernmost Balturino stratigraphic district, named for Balturino village, lies in the Uda and Biryusa River drainage basins (TESAKOV et al., 2003). Its Llandoverian series is represented by the only Balturino Formation (Rhudanian – Telychian), composed of grey sandstone and green, red, and rarely grey laminated siltstone. The common invertebrate taxon is *Eotomaria gatlense*, though the main faunal composition is represented by vertebrate taxa: *Tesakoviaspis concentrica*, *Elegestolepis conica*, and *Loganellia scotica*, the latter studied in this work below. The Wenlock series is represented by Barmo Beds, which include red and green sometimes calcareous mudstone and siltstone, with rare interbeds of grey sandstone. The most common faunal taxon of Barmo Beds is thelodont *Loganellia asiatica*, further discussed in this work below.

In conclusion, virtually the entire Silurian of the southeastern part of the East Siberian Basin (Nyuya-Beresovo and Ilim districts) is composed of gypsiferous argillaceous dolostone. Unrestricted marine conditions associated with the deposition of carbonates with corals and stromatoporoids occurred only episodically (in the Wenlock in the Nyuya-Beresovo district). In the southern basin (Balturino district) the vertebrate-yielding Silurian is composed mainly of variegated sandstone and siltstone (TESAKOV et al., 2003).

MATERIAL AND METHODS

The material studied here includes disarticulated microremains of phosphatic early vertebrate exoskeleton, obtained by dissolving carbonate rocks of outcrop and core samples, provided from the expeditions to Mongolia, central Tuva, and East Siberia, and complemented by already prepared phosphatic microremains from V. Karatajūtė-Talimaa collection, together with material given by Russian colleagues. Majority of the vertebrate microremains studied have been revealed from the outcrop samples, with exception of a few borehole samples from the Siberian platform.

The collections have been made during the Soviet geological expeditions in the northwestern Mongolia by L. ROSMAN (sample P 16/3) and I. SODOV (samples 1009/1-4), the latter material has been received as the whole rock samples, and has been processed and first studied by the first author (ŽIGAITĖ, 2004). The collections in the central Tuva have been made in the years 1968 and 1971 by V. KARATAJŪTĖ-TALIMAA, E. V. VLADIMIRSKAYA, L.AKSENOVA, N.KULKOV, and L. RATANOV. The subsequent expeditions in the East Siberia have been held in the years 1982 and 1984, vertebrate collections have been made by V. KARATAJŪTĖ-TALIMAA, Y. PREDTECHENSKYJ, Y. I. TESAKOV, T. MOSKALENKO, and J. VALIUKEVIČIUS. The material is deposited in Vilnius University, Departament of Geology and Mineralogy (Lithuania) as private collections of prof. V. Karatajūtė-Talimaa, former stored in the Institute of Geology of Lithuania, and is referenced here after as LGI, followed by the collection series numbers LGI M-1 (corresponding to the northeastern Mongolia) LGI-T (corresponding to the Tuva), and LGI-10 (corresponding to the Siberian platform).

Altogether, vertebrate samples of the Lower Silurian of central Asia and the Siberian platform, ranging in age from Early Llandovery to Late Wenlock, have been obtained for study of vertebrate micro remains. All the Mongolian outcrop samples have been completely processed by the first author: organic rich limestones have been dissolved using 5% acetic acid solution; the acetic acid residues containing phosphatic early vertebrate microremains have been sorted out and studied. The material from the localities of central Tuva, as well as the Siberian outcrop and core samples, have been received dissolved, as acetic acid residues separated for phosphatic micromaterial (V. Karatajūtė-Talimaa collections). Vertebrate microremains have been picked up and sorted manually from all the residues and collection samples.

For the present study, more than 1000 isolated scales have been photographed under a SEM FEI Quanta 200, with X-ray microanalysis and digital imaging, in the Team of Palaeozoic Palaeontology and Palaeogeography of CNRS research unit UMR 8157 "Géosystèmes", at the University of Lille 1 (France). For histological study, about 150 scales have been thin sectioned manually, using the matrix of Canadian balsam, and histology of the tissues has been studied in detail in about 100 of the thin sections, then photographed under high resolution light optical microscopes Zeiss Axioplan and Zeiss Axioscop in the same CNRS research unit.

In addition, the internal structure of approximately 100 scales of thin and light constitution has been studied under the optical microscope without thin sectioning, submerged in Anise oil.

In description of thelodont scales, the size was subdivided as follows: very small, 0.1-0.5 mm; small, 0.5-1.0 mm; medium, 1-2 mm; and large, 2-3.7 mm (afer MÄRSS et al., 2006). The morphological sets of scales of each different species have been arranged under the clusters of morphological varieties, organized according to the sculpture of the scales. These varieties in scale sculpture imply to the different skeletal functions of the scales, and different parts of the body respectively. Referring to the corresponding squamation patterns of the thelodont exoskeleton, the following five main morphological types of scales have been distinguished: rostral, cephalo-pectoral, postpectoral, precaudal, and pinnal scales. In fact, the palaeospecies which are reconstructed with this method may correspond to artificial species. However, according to our knowledge of a few articulated species described, where the intra-specific variability of exoskeleton elements (dermal scales) is known (MÄRSS & RITCHIE, 1998; MÄRSS et al., 2006), we may assure that these palaeospecies do correspond to nearly biological species.

SYSTEMATICS

Phylum CHORDATA BATESON, 1885
Subphylum VERTEBRATA LINNAEUS, 1758
Class THELODONTI KIAER, 1932
Order SANDIVIIFORMES KARATAJŪTĖ-TALIMAA & MÄRSS, 2004
Family ANGARALEPIDIDAE MÄRSS & KARATAJŪTĖ-TALIMAA, 2002
Type genus *Angaralepis* KARATAJUTE-TALIMAA, 1997
Type species *Angaralepis moskalenkoae* (KARATAJUTE-TALIMAA, 1978)

Angaralepis moskalenkoae (KARATAJUTE-TALIMAA, 1978)

Plate 1, A-U; Plate 7, A.

1967 *Logania* cf. *cruciformis* GROSS, p. 36-37, pl. 4, fig. 1-9, 12 A-J.
1978 *Logania* cf. *cruciformis* GROSS 1967; *in* KARATAJUTE-TALIMAA, p.86, pl. XX, 1, 13, 14; fig. 18, 4-6.
1978 *Logania moskalenkoae* KARATAJŪTĖ-TALIMAA, p.86, Pl. XX, 15-19; Fig. 18, 7-9.
1991 *"Logania" moskalenkoae* TURNER, p. 108.
1995 *Loganellia*? *moskalenkoae* KARATAJŪTĖ-TALIMAA & PREDTECHENSKYJ, p. 43, Fig. 4-5.
1997 *Angaralepis moskalenkoae* KARATAJŪTĖ-TALIMAA, p. 9, 10; Fig. 5, 6.
2007 *"Logania?"* cf. *cruciformis* (KARATAJŪTĖ-TALIMAA, 1978) MÄRSS et al., p. 61.

Holotype. LGI 10-148, body scale, Tab. XX, Fig. 17, KARATAJŪTĖ-TALIMAA 1978.

Type locality and horizon. Nizhniaya Tchunku river outcrop, Kochumdek district, Pritunguska subregion, western Siberia, Russia; Lower Silurian, Upper Llandovery, Razvilka Formation, outcrop Nr. 2 (MOSKALENKO, 1968).

Material. Several thousands of well-preserved scales; collection series number LGI 10; of which LGI 10-301 to LGI 10-320 are presented photographed under the SEM; and LGI 10-174, as thin section.

Geographical and stratigraphical range.

Lower Silurian, Upper Llandovery, Agidyan Regional Stage, Razvilka Formation; Kochumdek district, Pretunguska subregion, western Siberian platform, Russia.

Lower Silurian, Middle and Upper Llandovery, Khaastyrian and Agidyan Regional Stages, Utakan Formation; Niuya – Beresovo district, Niuya –

Beresovo subregion, southern Siberian platform, Russia.

Lower Silurian, Lower and Upper Llandovery, Moyerocanian and Agidyan Regional Stages, Rassokha Formation; Ilim district, Irkutsk subregion, southern Siberian platform, Russia.

Diagnosis (after KARATAJŪTĖ-TALIMAA, 1997; modified). Scales are small (0.2 – 0.4 mm long), wide and high in comparison to their length. The crown is strongly serrated, with sharp central crest and at least two, most often three pairs of uniformly sharp lateral ribs, all converging towards a sharp pointy arrow-like posterior end. Sharp notches of the ribs characterize the anterior rim of the crown, while the posterior part has 1 or 3 pointy end-notches. Neck is high, usually with vertical ridgelets on its posterolateral walls. The base is smaller than the crown except in the older rostral scales, low, rhomboid, and the pulp depression is wide and shallow. Any scale possessing a high and thick base, with overgrown pulp opening has not been observed. Internal structure of the scales represents regular thin tubule dentine; a pulp canal is absent. Dentine tubules are narrow, do not branch and extend regularly, especially in the posterior part of the crown.

Remarks. First collection of the scales from a locality on the Lower Tchunku river (Kochumdek district, Pritunguska subregion, western Siberia, Russia) was made by T. A. MOSKALENKO in 1968, and this was the basis on which *Logania moskalenkoae* KARATAJŪTĖ-TALIMAA 1978 was described. But that series contained only a few head and body scales (KARATAJŪTĖ-TALIMAA, 1978, Table XX, Fig. 13-19). Later numerous material has been found in the Middle Llandovery rocks (Niuya – Beresovo district, Niuya – Beresovo subregion, souther Siberia, Russia), yielding well-preserved transitional and body scales, and has been determined as *Loganellia? moskalenkoae* by KARATAJŪTĖ-TALIMAA & PREDTECHENSKYJ (1995). This allowed to complement the morphological series, as well as histological study, and ascribe the species to a new genus, *Angaralepis* KARATAJŪTĖ-TALIMAA (1997); a new family, Angaralepididae MÄRSS & KARATAJŪTĖ-TALIMAA (2004); and a new order, Sandiviiformes Karatajūtė-Talimaa & Märss (2004); Märss *et al.* (2007).

Further material has been revealed from the Upper Llandovery of the Ilim district, Ilim subregion, and Niuya – Beresovo district, Niuya – Beresovo subregion (souther Siberia, Russia), as well as from the Lower Llandovery (Ilim district, Ilim subregion, souther Siberia, Russia).

Additionally, we refer to *A. moskalenkoae* a set of cross-shaped scales, originally attributed to *L.* sp. *cf. L. cruciformis* by KARATAJŪTĖ-TALIMAA (1978, p. 96, pl. XX: 1, 13, 14; fig. 18: 4-6). The interpretation of these scales as the head scale morphological type of some particular loganiid species, suggesting *L. cuneata*, has already been proposed with their first description (KARATAJŪTĖ-TALIMAA, 1978). Possible reference of these scales to *L. moskalenkoae* has been also noted in the same work (KARATAJŪTĖ-TALIMAA, 1978, p. 98). The most recent suggestion of *"Logania?"* cf. *cruciformis* (KARATAJŪTĖ-TALIMAA 1978) as the head scales of some *Loganellia* species, has been made by MÄRSS et al. (2007, p. 61). According to the analysis of new complementary material of *A. moskalenkoae*, as well as refering the histology of micro remains, the *L.* sp. *cf. L. cruciformis* scales should be interpreted as the rostral (head) scales of *A. moskalenkoae.*

Scales of leading edges of fins have not been distinguished morphologically during the first description by KARATAJŪTĖ-TALIMAA in 1978, though the histological thin section on one of this type of scales has been made and published (KARTAJŪTĖ-TALIMMA, 1978; Fig. 18, 7).

The scales of *A. moskalenkoae* are often sampled with *Loganellia sibirica*; they are abundant in the Lower Silurian of the Siberian platform.

Description.

Morphology. Rostral scales are low, round, slightly oval or cross-shaped. The crown is low, with sharply and unevenly notched edges, forming specifical cross-shaped wings of the crown (Plate 1, A-D). The number of the notches usually varies from 4 to 6, leaving corresponding number of more or less sharpened cross-shaped crown ridges. The surface of the crown is smooth, flat or slightly bunchy. The neck is reduced. The base is very low, thin, and sometimes nearly not visible in the earliest stages of scale development. In the last case rostral scales possess a very fine general morphology. In older scales the base may become wider than the crown, which is the only case of wider base considering the whole morphological set of the species. The low cross-shaped scales of *L.* sp. *cf. L. cruciformis* (KARATAJŪTĖ-TALIMAA 1978, p. 96, pl. XX: 1, 13, 14; fig. 18: 4-6), are attributed to the rostral scales of *A. moskalenkoae* herein.

Cephalo-pectoral scales correspond to the previously determined transitional scales of KARATAJŪTĖ-TALIMAA (1978). They are oval, sharply wedged and still slightly cross-shaped as the rostral scales (Plate 1, E-H). This type of *A. moskalenkoae* scales is the less numerous in quantity as compared to the other morphological types.

Postpectoral and precaudal scales are rhombic and slightly laterally expanded, with a typical serrated sculpture of the crown. The crown is high, wider than the base, with a sharp central crest and most often three pairs (Plate 1, I-K) or at least two pairs (Plate 1, L-P) of uniformly sharp lateral ribs of similar height all converging towards a sharp pointy posterior end. The crown can be divided into its high anterior part, covered with longitudinal ribs, and smaller and narrower, arrow or anchor shaped posterior part, which is usually separated from the anterior part by lateral cavities. The anterior rim of the crown is sharply notched, and the posterior part is arrow-like, with one (Plate 1, O) or three (Plate 1, K) pointy end-notches. Sometimes the crown can be double-notched in its posterior part so that the most lateral pair of ribs forms a lower plane with an anchor-shaped end, and the central rib forms a arrow-shaped pointy end above it (Plate 1, M). The inner surface of the crown is smooth, only traces of lateral cavities can be distinguished. The posterior end of the crown is uplifted, at an about 25° - 30° angle in comparison to the base plane. The neck is high, often possessing vertical ridgelets on its posterolateral walls. The neck can also be divided into anterior and posterior parts, separated by very sharp ridges, descending from the last pair of the lateral ridges of the crown. The base is considerably less wide than the crown; it is low and has a shape of a wide rhomb, with usually wide and shallow pulp depression. The pulp opening is never overgrown, even in mature scales. Any scale with a high thick base has not been observed.

Pinnal scales are pointy and hook–shaped, very high, with distinct very sharp lateral ribs, continuously extending from the neck throughout the crown, and converging to a pointy posterior end of the crown (Plate 1, R-U). Central and lateral ridges are rather uniform in width, shape and sharpness, except that the central ridge is the longest one. The anterior and posterior parts can not be distinguished on the crown contrary to the postpectoral and precaudal scales, but the pointy posterior end of the crown is considerably uplifted in comparison to its anterior rim, at about 40° angle in comparison to the base plane. The inner surface of the crown is not smooth, with the same sharp ridges as the outer surface. The neck is completely serrated, with vertical ridges along all of its walls, indistinctly continuous with the crown. The base is extremely low, slightly rhomboid; the pulp depression is very wide.

Histology.

The internal structure of the *A. moskalenkoae* scales represents a regular thin tubule dentine: the dentine tubules are narrow, comparatively long, do not branch and extend rather straight, especially in the posterior part of the crown. Just some tubules near the base are slightly wider and branching (Plate 7, A). The pulp canal is not developed. Dentine tubules open directly onto the pulp depression, or onto the surface of the base, sometimes even on the lower surface of the crown. Few Sharpey's fibers have been observed in the base (Plate 7, A). As the base is very low and comparatively small, most of the scale is composed of the dentine tissue.

Comparison.

Angaralepis moskalenkoae posseses a very distinct morphology, compared to the other thelodont species, recorded in the region studied. The specific sharp wedge-shaped midline trough and high number of lateral ribs are not encountered in the other species of the genera *Loganellia* and *Talimaalepis* described so far. *Angaralepis* has a very distinct and high neck, contrary to the always low or strongly reduced neck of loganiid and talimaalepid scales. Though the internal structure of the *Angaralepis* scales shares some similarities with loganiid scales, for example the absence of pulp depression and thicker dentine tubules, the thin tubule dentine has a regular tubule branching pattern, contrary to the irregular one of loganiids.

Order LOGANELLIIFORMES TURNER, 1991
Family LOGANELLIIDAE (KARATAJŪTĖ-TALIMAA, 1978) *emend* KARATAJŪTĖ-TALIMAA, 1997
Type genus *Loganellia* FREDHOLM, 1990
Type species *Loganellia scotica* (TRAQUAIR, 1898)

Nomenclaturian note: Recently MÄRSS et al. (2007, P. 49) has attributed the family name Loganelliidae to MÄRSS et al. 2002 (see also HAIRAPETIAN et al., 2008). However KARATAJŪTĖ-TALIMAA has first introduced family Loganiidae (KARATAJŪTĖ-TALIMAA, 1978, p. 66), and then later she has created the subfamily name Loganelliinae (KARATAJŪTĖ-TALIMAA,1997, p. 14), following the emendation of the genus name (*Logania* = *Loganellia*, FREDHOLM, 1990, p. 69). By creating the subfamily name, KARATAJŪTĖ-TALIMAA has in the same time coordinated family name Loganellidae (INTERNATIONAL COMMISSION ON ZOOLOGICAL NOMENCLATURE, 1999, ARTICLE 36.1). So the accurate family name quotation is "LOGANELLIIDAE (KARATAJŪTĖ-TALIMAA, 1978) *emend* KARATAJŪTĖ-TALIMAA, 1997" (see also MÄRSS et al., 2006, p. 16).

The genus name *Loganellia*, in replacement of both "*Logania*" Gross 1967, and "*Loganella*" Turner and Peel, 1986, has traditionally been attributed to Turner (1991), see e.g., KARATAJŪTĖ-TALIMAA AND MÄRSS (2004, p. 18), MÄRSS ET AL. (2006, p. 17). However, the name *Loganellia* has been first published by FREDHOLM (1990, p. 69), who cited the article of TURNER, which was in press at that time. So, the accurate name must be "*Loganellia* FREDHOLM 1990" (see MÄRSS et al., 2007, p. 49; HAIRAPETIAN et al., 2008).

Loganellia asiatica (KARATAJUTE-TALIMAA, 1978)

Plate 2, A-U; Plate 7, C,D.

1978 *Logania asiatica* KARATAJŪTĖ-TALIMAA, P. 73-76, Pl. XXI, 1-18; Fig. 6, 7A-B.

1995 *Loganellia* cf. *asiatica* KARATAJŪTĖ-TALIMAA & PREDTECHENSKYJ, p. 45-49, Figs. 4,5.

1997 *Loganellia asiatica* KARATAJŪTĖ-TALIMAA, p. 2; p. 11, Fig. 7B.

2004 *Talimaalepis rimae* ŽIGAITĖ, p. 160, *partim* Pl. 1, fig, B, *non* Pl. 1, figs. A, C-Z ; P. 162, *partim* Pl. 2, figs. A, B, *non* Pl. 2., figs. C-O.

Holotype. LGI T-381, body scale, KARATAJŪTĖ-TALIMAA 1978, Pl. XXI, Fig. 8.

Type locality and horizon. Kyzyl-Tchiraa locality, central Tuva, Russia; Lower Silurian, Upper Llandovery, Kyzyl-Tchiraa Formation, Kyzyl-Tchiraa outcrop, sample Nr. 702 (KARATAJŪTĖ-TALIMAA, 1978).

Material. More than 800 scales of different preservation; collection series number LGI T; of which LGI T-550 to LGI T-571 are presented photographed by SEM; and LGI T-592 as thin section.

Geological and geographical range.

Lower Silurian, Wenlock, Salhit Regional Stage, Tchargat Formation; Lake Basin outcrop Nr. 20, Tchargat locality, lake Khara-Ubs-Nuur, north-west Mongolia (sample: P 16/3).

Lower Silurian, Wenlock, Salhit Regional Stage, Tchargat Formation; Lake Basin outcrop Nr. 21, Tchargat locality, lake Khara-Ubs-Nuur, north-west Mongolia, (samples: 1009/1, 1009/2, 1009/3, and 1009/4).

Lower Silurian, Upper Llandovery, Kyzyl-Tchiraa Formation, and Angatchi Regional Stages, Kyzyl-Tchiraa Formation, and Angatchi formations; Kyzyl-Tchiraa locality, central Tuva, Russia.

Lower Silurian, Upper Wenlock, Dashtygoi Regional Stage, Dashtygoi Formation; Elegest and Kadvoi localities, central Tuva, Russia.

Lower Silurian, Lower Llandovery, Moyerocanian Regional Stage, Melichan Formation; Niuya – Beresovo district, Niuya – Beresovo subregion, southern Siberian platform, Russia.

Lower Silurian, Lower, Middle, and Upper Llandovery, Moyerocanian, Khaastyrian, and Agidyan Regional Stages, Rassokha Formation; Ilim district, Irkutsk subregion, southern Siberian platform, Russia.

Lower Silurian, Lower, Middle, and Upper Llandovery, Moyerocanian, Khaastyrian, and Agidyan Regional Stages, Balturino Formation; Balturino district, Irkutsk subregion, southern Siberian platform, Russia.

Diagnosis (complemented after MÄRSS et al., 2007). Scales are small, broad, short and thick, rounded-rhomboidal in shape, and quite uniform in size (length 0.3 - 0.6 mm and width 0.24 – 0.37 mm.). The crown is characterized by distinct rhomboid middle segment, sharply sagged towards a median line. Lateral segments of the crown are wide, lower than the median one, and joined posteriorly in the same level. There is only one pair of lateral segments, rarely two pairs (Plate 2, R). The groove between the crown and the base is low. The base is high, with distinct anterior vertical thickening. The pulp depression is situated in the posterior part of the scale, behind the vertical thickening of the base, overgrown in older scales.

The histology represents the irregular thin tubule dentine, with absence of pulp canal, and slightly wider dentine tubules instead. The thin dentine tubules branch close above the base.

Remarks. Some scales initially ascribed to *L. asiatica* by KARATAJŪTĖ-TALIMAA (1978, p. 297, Pl. XXI, figs. 17a, b) as body scales, now are assigned to *Talimaalepis rimae* ŽIGAITĖ 2004, as postpectoral scales. This is particularly due to the morphological affinities in the crown sculpture, considering sharp rhombic uplifted trough in the center of the scale.

L. cf. *asiatica* described by KARATAJŪTĖ-TALIMAA & PREDTECHENSKYJ (1995, p. 45-49, Figs. 4,5) is now attributed to *L. asiatica*, which after these records appears to be the most common and most abundant Lower Silurian thelodont species in the region studied.

Description.

Morphology. Rostral scales present two main types: a first type consists round or oval scales, not high and flat in shape, with rather low base (Plate 2, A,B), and a second type, represented by round scales with a bit pointy proximal part of the crown, and a very high base (Plate 2, C,D). The surface of the crown in both of the types is flat and smooth, sometimes slightly bended. The crown is always notch-edged; the notches vary in length, from short to quite deep. In general the base is wider than the crown. The pulp cavity of the low rostral scales is rhomboid or wedge-shaped, and occupies the central part of the base rather prominently. In the rostral scales with very high base, the pulp cavity is usually overgrown.

Cephalo-pectoral scales are elongated, oak-leaf-like, with a sharp and pointy posterior end of the crown. The crown morphology varies greatly, from broad rhomboid, with a significantly wider posterior part (Plate 2, E), to very tiny, long, and narrow (Plate 2, F,G). Ribs are wide and rounded, joining to form a wide, rounded, and not very prominent central crest, which usually does not stretch along the whole length of the crown. It may start from the middle of the scale or terminate before the posterior part of the crown. The central crest termination in the middle of the scale length is particularly characteristic to the narrow and very elongated type of cephalo-pectoral scales, where the next pair of lateral ribs usually fuses to continue the crest. The base of cephalo-pectoral scales is usually not very high, wider than the crown, and thicker in its anterior part. The pulp depression is elongated, in older scales it can be partially overgrown, and presented as a set of small openings.

Postpectoral and precaudal scales have prominent rounded-rhomboid overall shape, they are broad, short, and thick. The crown is usually well-embedded in rather massive and high base, and can be characterized by distinct rhomboid middle segment, sharply sagged towards a median line. The rhomboid median segment can be divided into two parts lengthways: a short and rounded anterior part, and a much longer and pointy posterior part (Plate 2, H-S). On the sides of the median segment of the crown, there is usually one pair (rarely two) of lateral segments, which stretch over the median part in length, and fuse at the posterior end of the crown. The edge of posterior end is often slightly uneven. The lateral segments are not entirely flat, but lie at an angle to the median segment. If a second pair of lateral segments is present, usually it is very short and indistinct, hiding beneath the always well expressed first pair of lateral segments. The anterior part of the crown is always relatively lowered in comparison to the base, contrary to its always rising posterior part (Plate 2, H-S). The posterior part of the crown never overhangs a lot over the base – usually in one third or less of its length. The inner side of the crown is smooth. The base is wider than the crown, and rather high, with distinct anterior vertical thickening. The pulp depression is oval and elongated, situated in the posterior part of the scale, behind the vertical thickening, and is often overgrown in older scales. It may also be overgrown, or partialy overgrown and presented as a linear set of small openings, situated behind the anterior vertical thickening of the base.

Pinnal scales are characterized by a less lowered and steep-edged anterior part of the crown, and extremely high base, with particularly amplified anterior part. The crown still has significantly uplifted and pointy posterior end, but the characteristic median segment is much less distinguished than that of postpectoral and precaudal scales. Two pairs of lateral segments are always present, and they lie at a steeper angle to the median segment, thus can be described as lateral ridges rater than flattened segments. The base is still slightly wider than the crown, and extremely high, usually 2–3 times of the crown height. The anterior part of the base is especially vertically elongated.

Histology. The scales are composed of two main dentine and bone-like tissues: the bulk of the scale constitutes of irregular thin tubule dentine, with tubules branching close above the base (Plate 7, C,D). The inner part of the base, lacking any dentine tubules, is being composed of acellular bone-like tissue called aspidine (MÄRSS ET AL., 2007, P. 8, 41). The net of thin dentine tubules is the densest in the posterior part of the scale, along its median line. The pulp canal is not developed, dentine tubules open directly on the surface of the posterior part of the base around the pulp depression, and slightly widen at their terminal ends. Nevertheless branching irregularly, dentine tubules tend to keep vertical line within the anterior part of the scale, and become inclined in the uplifting posterior part. The thinnest dentine tubules can be found near the surface of the crown. Within the high vertical thickening of the base dentine tubules are sparse, instead Sharpey‘s fibers are numerous, usually extending sidelong to the base surface, and eventually bowing at the highest end of the base.

Comparison. *L. asiatica* in its scale morphology is related to *L. sibirica*, and particularly to *L. scotica*, the type species of the genus, with which it shares similar feature of a distinct rhomboid median segment. But histologically *L. asiatica* is closer to *L. sibirica* and *L. tuvaensis*, which all can be asigned to the same irregular thin dentine tubule histological type, with the absence of a pulp canal. Concerning the presence of this kind of uplifted median segment of the crown, *L. asiatica* is also slightly morphologically similar to *Talimaalepis kadvoiensis* (KARATAJŪTĖ-TALIMAA 1978) ŽIGAITĖ 2004 COMB. NOV. as well, though histological differences are fundamental: genus Talimaalepis scales are composed of the thick tubule dentine (Plate 7, G,H; Plate 8, D,E), while all the loganiids are characterized by thin tubule dentine (Plate 7, B-F).

Loganellia sibirica (KARATAJŪTĖ-TALIMAA, 1978)

Plate 3, A-Z; Plate 7, B.

1968 *“Phlebolepis”* sp., MOSKALENKO, fig. 2: 12a,b, 13, 14.

1978 *Logania sibirica* KARATAJŪTĖ-TALIMAA, p. 70-73, Pl. XX, 2-12; Fig. 18, 10-13.

1991 *Loganellia sibirica* TURNER, p. 87.

1995 *Loganellia ex. gr. scotica* KARATAJŪTĖ-TALIMAA & PREDTECHENSKYJ, p. 45-49, Figs. 4,5.

1997 *Loganellia sibirica* KARATAJŪTĖ-TALIMAA, p. 2; p. 11, Fig. 7a.

1997 *Loganellia ex. gr. scotica* KARATAJŪTĖ-TALIMAA, p. 12, Fig. 8a,b,f.

Holotype. LGI 10-147, body scale, KARATAJŪTĖ-TALIMAA 1978, Pl. XX, Fig. 12,.

Type locality and horizon. Nizhniaya Tchunku river outcrop, Kochumdek district, Pritunguska subregion, western Siberia, Russia; Lower Silurian, Middle Llandovery, Kulinna Formation, outcrop Nr. 3 (MOSKALENKO, 1968).

Material. More than 600 scales, some of rough preservation, sculpture elements being obscure; collection series number LGI 10; of which LGI 10-260 to LGI 10-284 are presented photographed by SEM, and LGI-488 as thin section.

Geological and geographical range.

Lower Silurian, Lower Llandovery, Moyerocanian Regional Stage, Kochumdek Formation; Lower Tchunku River, Kochumdek district, Pretunguska subregion, western Siberian platform, Russia.

Lower Silurian, Middle Llandovery, Khaastyrian Regional Stage, Kulinna Formation; Lower Tchunku River, Kochumdek district, Pretunguska subregion, western Siberian platform, Russia.

Lower Silurian, Lower Llandovery, Moyerocanian Regional Stage, Melichan Formation; Niuya – Beresovo district, Niuya – Beresovo subregion, southern Siberian platform, Russia.

Lower Silurian, Middle, and Upper Llandovery, Khaastyrian and Agidyan Regional Stages, Utakan Formation; Niuya – Beresovo district, Niuya – Beresovo subregion, southern Siberian platform, Russia.

Lower Silurian, Lower, Middle, and Upper Llandovery, Moyerocanian, Khaastyrian, and Agidyan Regional Stages, Rassokha Formation; Ilim district, Irkutsk subregion, southern Siberian platform, Russia.

Lower Silurian, Lower Llandovery, Moyerocanian Regional Stage, lower Balturino Formation; Balturino district, Balturino subregion, southern Siberian platform, Russia.

Lower Siliurian, Middle Llandovery, Alash Regional Stage, Alash Formation; outcrop Kadvoi, central Tuva, Russia (sample Kadvoi 694).

Lower Siliurian, Upper Wenlock, Dashtygoi Regional Stage, Dashtygoi Formation; outcrop Kadvoi, central Tuva, Russia (Kadvoi 662-663).

Lower Siliurian, Upper Wenlock, Dashtygoi Regional Stage, Dashtygoi Formation; outcrop Kadvoi, central Tuva, Russia (sample Kadvoi 664).

Lower Silurian, Wenlock, Salhit Regional Stage, Tchargat Formation; Lake Basin outcrop Nr. 20, Tchargat locality, lake Khara-Ubs-Nuur, north-west Mongolia (sample P 16/3).

Diagnosis (complemented after MÄRSS et al., 2007). Scales are small and elongated (0.2 – 0.6 mm long; 0.1 -0.2 mm wide). The crown is narrow, comparatively high, with deep median trough and pointy posterior end, with two pairs of lateral ribs, the first pair of which usually as well expressed as the crests of central trough. The lateral ribs, especially the first pair and sometimes even the second, is longer than the median pair of ribs. The base ia vertical, thickened in the anterior part, and conus-shaped. An anterior spur-like process of the base is not developed. Scales are composed of irregular thin tubule dentine, with absence of pulp canal.

Remarks . Three scales of *L. sibirica* were sketched by T. A. MOSKALENKO (1968) as scales similar to the ones of genus *Phlebolepis* (MOSKALENKO, 1968, Fig. 2: 12a,b, 13, 14). They were later described as *Logania sibirica* by KARATAJŪTĖ-TALIMAA (1978), and then determined as *Loganellia sibirica* (KARATAJŪTĖ-TALIMAA, 1978) by TURNER (1991). *Loganellia* ex. gr. *scotica* (KARATAJŪTĖ-TALIMAA & PREDTECHENSKYJ, p. 45-49, fig. 4,5) scales first described in the Lower Silurian of the Siberian platform, is now attributed to *L. sibirica* as well. Very few scales have been recorded in the Wenlock of northwestern Mongolia. Additional material has been revealed from Lower Llandovery and Upper Wenlock samples of central Tuva as well, thus the palaeobiogeographical restriction of the species to the Lower Silurian of Mongolia and Siberian platform (ŽIGAITĖ & BLIECK, 2006) is now refuted.

Description.

Morphology. Rostral scales are represented by small round or oval scales, with a comparatively high base and a low notch-edged crown. The crown has flat and smooth surface, steep edges, but not very deep notches (Plate 3, A-C). The base is slightly wider than the crown, its height depends on an ontogenetic development stage of a scale (Plate 3, D). The pulp cavity is in the center of the base, it is rather wide and shallow.

Cephalo-pectoral scales are elongated and rather narrow. The crown is high with high central crest and lateral ribs, which are sharp, rounded, and well expressed. The sculpture of the crown varies from oak-leaf-like in shape, with two or three pairs of descending lateral ribs (Plate 3, E), to slightly cylindrical with several pairs of descending lateral ribs (Plate 3, F-H). The central crest sometimes begins from the median pair of ribs, joining into a central rising in the posterior part of the scale (Plate 3, F-H). All the ribs are more or less inclined, topping towards the posterior end of the crown, giving a shape of pointy rising triangle (Plate 3, F,G). The distal junctions of rib pairs often form a central crest on the top of the crown in the posterior part of the scale. The base is usually lower than the crown, though the height of the base depends on the individual age of each scale. In comparison to the base, the crown does not overhang in length significantly.

Postpectoral and precaudal scales range from very narrow and elongated to oval and finally gently rhomboid ones (Plate 3, I-U). The crown is less high and at least half of it overhangs the base in length, contrary to cephalo-pectoral scales. The anterior part of the crown of postpectoral scales is usually wider (Plate 3, I-R), in comparison with throughout narrow and tiny precaudal scales (Plate 3, S-U). A shallow median trough between the central ribs extends along the crown top surface, narrowing and finally closing up at the posterior end of the crown. Lateral troughs, as well as lateral ribs, are situated below the median ones. The inner side of the crown is smooth. A groove separating the crown from the base is rather shallow. The base height varies greatly, and depends on separate position in the exoskeleton, as well as on the ontogenetic development stage of the scale. The pulp depression is comparatively long and narrow, well expressed in most of the scales, and tends to retain even in old ones.

Pinnal scales are narrow, strongly pointed, with a well expressed base, often keeping 'root' in the same axis as the pointy posterior end of the crown. The crown is rounded, pointy, and often bobbin-shaped. The ribs of the crown are sharp, similar as in cephalo-pectoral scales. Usually there is only one central rib on the top surface of the crown, and two pairs of lateral ribs on the sides below it (Plate 3, W-Z). In cases where the crown and the base retain the same longitudinal axis, the crown is always wider than the base, capping it in the anterior part, and the ribs are set around towards the ventral side of the crown, fusing on the pointy posterior end, and the base is adequately bobbin-shaped (Plate 3, W-Z). The crown of these scales is often slightly convex.

Histology. The sales are composed of irregular thin tubule dentine. Dentine tubules are thin numerous, branching, and tightly packed. The pulp canal is not developed. Significantly thicker dentine tubules or enlarged lacunae are also absent, even in postpectoral and precaudal scales. Some indistinct terminate lacunae can be present near the depression of the base (Plate 7, B). But usually thin dentine tubules slightly widen and open straight onto the ventral side of the scale, particularly arround the depression of the base. The base, especially if well developed, often possess Sharpey‘s fibers (Plate 7, B).

Comparison.

L. sibirica and *L. asiatica* scales are two closely related species in both their morphological and histological features. Both of the species represent the same histological type of irregular thin tubule dentine, with absence of pulp canal. Their postpectoral and precaudal scales are rather similar in general external constitution. The average size of the scales is the same as for the type species *L. scotica*. Scales of *L. sibirica* are notably more elongated in comparison with majority of other loganiid thelodont scales, except of strongly elongated scales of *L. exilis* MÄRSS et al. (2002), and *L. prolata* MÄRSS et al. (2002).

Loganellia tuvaensis (KARATAJŪTĖ-TALIMAA, 1978)

Plate 4, A-Z; Plate 7, E, F.

Complemented synonymy list after BLOM, 1999:

1978 *Logania tuvaensis* KARATAJŪTĖ-TALIMAA, P. 76-79, Pl. XVIII, 1-6; Pl. XIX, 1-13; fig. 18, 1-3; fig. 19, 7.
1986 *Loganellia* cf. *L. tuvaensis* TURNER & PEEL, p. 82-84, fig. 3, D, E.
1997 *Loganellia tuvaensis* KARATAJŪTĖ-TALIMAA, p. 2; p. 11, fig. 7d; p. 12, fig. 8g.
1999 *Loganellia* cf. *L. tuvaensis* BLOM, p. 15-17, *partim*, fig. 5, A-K, N, O; *non* fig. 5, L, M.

Holotype. LGI T-395, body scale, KARATAJŪTĖ-TALIMAA 1978, Pl. XVIII, Fig. 1.

Type locality and horizon. Elegest locality, central Tuva, Russia; Upper Silurian, Pridoli, Pitchi-Shui Formation, Elegest outcrop, sample Nr. 236 (KARATAJŪTĖ-TALIMAA, 1978).

Material. More than 600 well-preserved scales; collection series number LGI T; of which LGI T-609 to LGI T-632 are photographed by SEM; and LGI T-183 as thin section.

Geological and geographical range.

Lower Silurian, Upper Wenlock, Dashtygoi Regional Stage, Dashtygoi Formation; Elegest and Kadvoi localities, central Tuva, Russia. It is also known from the Upper Silurian (Ludlow and Přídolí) of central Tuva.

Diagnosis (complemented after MÄRSS ET AL., 2007). Medium sized scales (0.4 - 1.0 mm. long, and 0.2 – 0.5 mm. wide), regularly rhombic, sagittate in shape, with characteristic flat and saggy surface of the very low crown. The crown edges are even and smooth, except the anterior rim, which is commonly marked by one or few shallow notches. The lateral segments are narrow and indistinct, rimming flat rhombic median part of the crown. Rarely more than one pair of lateral segments. The base is slightly convex and comparatively regular in its height, anterior part sometimes being slightly higher. The pulp depression situated in the middle of the base, overgrown in older scales. Histologically the scales are constituted of irregular thin tubule dentine, tubules branching and concentrated posteriorly; some odd wider tubules are present. Sharpey's fibers are well expressed.

Remarks. The species is restricted to the localities of central Tuva, ranging from the Lower to the Upper Silurian, though not present in any sample from northwestern Mongolia or from the Siberian platform. This record of *L. tuvaensis* is particularly important as concerned with Silurian palaeobiogeography. *Loganellia* cf. *L. tuvaensis* has been reported from the Upper Silurian–Lower Devonian (Přídolí–Lochkovian) of North Greenland - the Halls Grav locality and Monument, Hall Land, Chester Bjerg Formation (TURNER & PEEL, 1986; BLOM, 1999). Reffering to morphology and histology of the microremains studied, *L.* cf. *L. tuvaensis* from North Greenland appears to be the same species as *L. tuvaensis* from central Tuva (excluding a few scales, described by BLOM (1999), see synonymy above). This gives an evidence for a possible close relationship between the Siberian and Laurentian palaebiogeographical provinces during the Silurian (ŽIGAITĖ & BLIECK, 2006).

Description.

Morphology. Rostral scales precisely round, or oval, and even rhombic in overall shape (Plate 4, A-D), which is unusual for rostral scales in other loganiid species. Sometimes two or three rostral scales grow-up together and have a joint base, or even joined crown, if scales fuse together in early enough stage of their development. This may occure due to their special function, probably for surrounding eyes or nasal openings. The crown is usually low, with equaly notched edges. The notches are not very deep. The base is rather shallow in young scales, with wide pulp depression in the middle of its ventral side, and becomes higher in older scales.

Cephalo-pectoral scales are elongated, oval, sometimes slightly rhombic, and oak-leaf-like in shape, with a slightly pointed posterior end of the crown (Plate 4, E-G). The base is usually low. The pulp depression is extensive, oval in shape.

Postpectoral and precaudal scales are prominently rhombic and sagittate in shape; they may be regular rhombic or strongly elongated (Plate 4, H-U). The crown has a characteristic flat surface and a very plane low crown. The edges of the crown are smooth and even, except in the anterior part of the crown, which is usually marked by one discriminate wedge-shaped notch or few shallow notches. The sole distinct wedge-shaped notch on the side of the anterior rim of the crown is very common (Plate 4, R, U). The lateral segments are presented by one nearly indistinct and very narrow pair (rarely two pairs) rimming median part of the flat rhombic crown. Some scales are extremely elongated and narrow (Plate 4, N, O). The base is medium to high in older scales, comparatively regular in its thickness, slightly convex, and usually bunchy in the anterior part. The pulp depression is much less prominent than in rostral and cephalo-pectoral scales, often overgrown in older scales.

Pinnal scales are irregularly rhombic, with wider anterior and elongated pointy posterior part of the crown. The base is usually high, most likely corresponding to a deep implanting in soft tissues, according to the special functions of the scales. The base is wider and obtrudes the crown in the anterior part of the scale (Plate 4, W-Z).

Histology. The scales are composed of irregular thin tubule dentine; a central pulp canal is not developed, and dentine tubules open directly to the base, on the surface of pulp depression or former place of overgrown pulp depression. Thin dentine tubules are numerous, most densely branching in the central and posterior parts of the scale (Plate 7, E, F). Beginning in the neck area (which is highly reduced) and going to the base, dentine tubules straighten and stretch perpendicular to the crown surface; few of them may get slightly wider and form small lacunae (Plate 7, F). Sharpey's fibers are prominent within the base, especially in older scales, and stretch perpendicular to the base surface.

Comparison. According to the presence of lateral ribs on sides of the crown, rounded rostral scales with typical sculpture, oak-leaf shaped cephalo-pectoral scales, and low neck of the body scales, *Loganellia tuvaensis* can be assigned to the genus *Loganellia*. But it is also highly distinct from the other species of the genus, because of the number of strongly elongated scales, especially low crown with very flat surface and even rims, and reduced neck. *L. tuvaensis* is the only who has a pronounced rhombic shape of the crown with barely one indistinct pair of lateral ribs, while other species of *Loganellia* possess much narrower crowns, with a characteristic wedge-shaped trough along the midline, and often two or three pairs of lateral ribs. Nevertheless, the main histological features, such as absence of pulp canal, or irregularly branching, numerous thin dentine tubules, attach it firmly to the genus *Loganellia*, as histology is decisive in the systematic at the genus level (KARATAJŪTĖ-TALIMAA, 1998).

Talimaalepis ŽIGAITĖ 2004

Diagnosis (modified after ŽIGAITĖ, 2004). Scales are middle size, flattened and elongated, rectangular to oval in shape. The crown possesses several pairs of sharp longitudinal ridges, of which a median pair is much longer, and divides the crown into a long central part, and paired shorter lateral wings. The neck is not well expressed. The wedge-shape base has a horizontal thalamus-shaped anterior part, sometimes with a spur-like outgrowth, and a long narrow anchoring posterior process, descending at an angle. The pulp opening is located just behind the vertical projection of the base. The internal structure of the scales is composed of thick tubule dentine. The dentine tubules extend regularly, thin near the surface of the crown, getting thicker and anastomosed pulpwards. The pores of sensory line canals are not present.

Remarks. The attribution of *Talimaalepis* by MÄRSS et al. (2007) to the family Loganelliidae (KARATAJŪTĖ-TALIMAA, 1978) emend. KARATAJŪTĖ-TALIMAA, 1997, appears to be disputive on the basis of the histology of the scales, as loganiids do not possess any thick dentine tubules, which are the characteristic feature of the genus *Talimaalepis*. However, the presence of one single pulp canal, which is typical for the genus *Loganellia*, as well as sparse anastomoses of usually straight dentine canals, makes *Talimaalepis* close to loganiid thelodonts. The possession of monolithic crown is the first diagnostic feature of the family Loganelliidae, and it is not the case for *Talimaalepis*, where the ridges of the crown end in free posterior spines, and lateral segments are distinct (Plate 5, I-W; Plate 6, I-U). Moreover, well-defined thick dentine canals, opening into more than one pulp canal, characteristic to *Talimaalepis* as well, are the diagnostic features of the genus *Helenolepis*, and not at all present in any scales of loganiid thelodonts. Nevertheless, *Helenolepis* possesses several, usually more than three pulp canal, according to a number of crown segments (KARATAJŪTĖ-TALIMAA 1978, p. 236, fig. 14). This is never the case in *Talimaalepis*, which has one single pulp canal present despite of the crown's sculpture. Each pulp canal in helenolepid scales is following its net of thick, and near the surface of the crown thin dentine tubules (Plate 8, A-C). Though considering the histology of helenolepids, the internal structure of *Helenolepis* scales is very close, but much more complex than that of *Talimaalepis*. On the basis of these pronounced histological differences, *Talimaalepis* is distinct from both *Loganellia*, and *Helenolepis*. Furthermore, according to our study, the proposed assignation of *Talimaalepis* to the family Phlebolepididae BERG 1940 (ŽIGAITĖ, 2004, p. 159), together with helenolepids on the basis of possession of similar histology and sensory line pores, encountering adequate morphological differences as well, is now refuted. Previously described sensory line pores within the scales of *Talimaalepis* (ŽIGAITĖ, 2004, p. 162, Pl. 2, fig. H), have been revealed not to be present, contrary to the other genera of Fam. Phlebolepididae. Nevertheless, it is necessary to admit that some helenolepids share strong morphological similarities to the scales of both of the *Talimaalepis* species. Some of the rostral scales and pinnal scales of the edges of fins in both of the *Talimaalepis* species are very similar to those of *Helenolepis*, especially to those of *Helenolepis obruchevi* KARATAJŪTĖ-TALIMAA, 1978, sharing an extremely high vertical anchoring posterior process of the base in older scales. Though it is easy to distinguish between them by examining the internal structure of the scales, but morphologically all are quite similar. The main difference in the external structure of these scales would be the pattern of the anterior notches of the crowns – *Talimaalepis* has oblique, less deep and slightly wider notches (Plate 5, G; Plate 6, D, Z) than those belonging to *Helenolepis*, which are straight, very narrow and deep-cutting, and also more numerous in most of the cases (MÄRSS et al., 2007, fig. 81, F, G, J).

Refering to the histological and morphological features listed above (the internal scale composition of thick tubule dentine, segmented crown morphology, etc.), *Talimaalepis* fills an intermediate position between the genera *Loganellia* (Fam. Loganellidae) and *Helenolepis* (Fam. Phlebolepididae).

Moreover, the strong morphological affinities between the scales of *Talimaalepis* species, and some shieliids, particularly *Shielia taiti* (STETSON, 1931) (see in MÄRSS & RITCHIE (1998, figs. 27A, 30A,B, 31), and also to some *Paralogania* species, such as *P. consimilis* MÄRSS & KARATAJŪTĖ-TALIMAA, 2002 (see MÄRSS et al., 2007, Fig. 59, G-H), and *P. kaarmisensis* MÄRSS 2003, (see MÄRSS et al., 2007, fig. 59, J), should be taken in consideration. The presence of similar wedge-shape base with a horizontal thalamus-shaped anterior part, and a long narrow anchoring posterior process both in talimaalepid and in shieliid scales, deserves a special attention. The uplifted median and lateral segments, the median having a shape of a rhombic trough, are common features of these two groups as well. Further examination on talimaalepid, helenolepid, and shieliid histology is required.

Nevertheless, on the morphological basis, *Talimaalepis* is slightly closer to loganeliid than to phlebolepidid thelodonts, and in this work we keep the affiliation of the genus to the family Loganelliidae, and the order Loganelliiformes subsequently (see MÄRSS et al., 2007, p. 60).

Type species *Talimaalepis rimae* ŽIGAITĖ 2004

Species: *Talimaalepis kadvoiensis* (KARATAJŪTĖ-TALIMAA, 1978) ŽIGAITĖ 2004 comb. nov.

Talimaalepis rimae ŽIGAITĖ 2004

Plate 5, A-Z; Plate 8, D.

1978 ?*Logania kadvoiensis*, KARATAJŪTĖ -TALIMAA; p. 82-86; p. 295, Pl. XIX, fig.14; p. 298, Pl. XXII, fig. 1-6; p. 230, *partim* Fig. 15: 5-6; *non* Fig. 15: 7-9.

1978 *Loganellia asiatica,* KARATAJŪTĖ –TALIMAA ; p. 73-76 ; Pl. XXI, fig. 17a,b.

1991 ?*Loganellia kadvoiensis*, TURNER; p. 111.

1991 *Helenolepis* sp. "supposed", TURNER; p. 111.

2004 *Talimaalepis rimae* gen. et sp. nov., ŽIGAITE; pp. 158-165; p. 160, *partim* Pl. I, figs. E-J, L, Q; *non* Pl. I, figs. A-D, K, M-R, S-Z; p. 162, *partim* Pl. II, figs. D, E, G, N, O; *non* Pl. II, figs. A-C, F, H-M.

2007 *Talimaalepis kadvoiensis* (KARATAJŪTĖ-TALIMAA, 1978) ŽIGAITĖ comb. nov.; MÄRSS et al., pp. 60-61, *partim*, fig. 57, D-G; *non* fig. 57, A-C, H-M.

Holotype. LGI M-1/224, cephalo-pectoral scale, NW Mongolia, sample 1009/3, ŽIGAITĖ 2004, p. 160, Pl. 1, fig. E. (Plate 5, R herein).

Paratype. LGI T-599, postpectoral scale, Tuva, Kadvoi 662 (Plate 5, M herein).

Type locality and horizon. South-east slope of mount Chargat, 80 km north from lake Khara-Ubs-Nuur, north-west Mongolia; Lake Basin outcrop Nr. 20, sample P-16/3; Chargat Formation, Salhit Regional Stage, upper Llandovery – Wenlock, Lower Silurian.

Paratype locality and horizon. Kadvoi locality, central Tuva, Russia; Kadvoi locality, sample Nr. 662; Angatchi Formation, Angatchi Regional Stage, uppermost Llandovery, Lower Silurian.

Material. Over 400 scales of good preservation; collection series numbers LGI M-1 and LGI T; of which LGI M-1 214, 221-224, 231-233, 248, as well as LGI T 901-904, 912, 914-918, and T 920-926 are photographed by SEM; and LGI M-1 28 as thin section.

Geological and geographical range. Lower Silurian, Wenlock, Salhit Regional Stage, Tchargat Formation; Lake Basin outcrop Nr. 20, Tchargat locality, lake Khara-Ubs-Nuur, north-west Mongolia (sample P 16/3).

Lower Silurian, Wenlock, Salhit Regional Stage, Tchargat Formation; Lake Basin outcrop Nr. 21, Tchargat locality, lake Khara-Ubs-Nuur, north-west Mongolia (samples 1009/1 and 1009/3).

Lower Siliurian, Upper Wenlock, Angatchi Regional Stage, Angatchi Formation; outcrop Kadvoi, central Tuva, Russia (Kadvoi 660-1).

Lower Siliurian, Upper Wenlock, Dashtygoi Regional Stage, Dashtygoi Formation; outcrop Kadvoi, central Tuva, Russia (Kadvoi 662-663).

Lower Siliurian, Upper Wenlock, Dashtygoi Regional Stage, Dashtygoi Formation; outcrop Elegest, central Tuva, Russia (Elegest 226).

Lower Silurian, Upper Llandovery, Agidyan Regional Stage, Omnutakh Formation; Turukhansk district, North Prienissey subregion, western Siberian platform, Russia.

Lower Silurian, Wenlock, Khakomian Regional Stage, Usas Formation; Kochumdek district, Pritunguska subregion, western Siberian platform, Russia.

Lower Silurian, Wenlock, Khakomian regional stage; Balturino Formation; Balturino district, Irkutsk subregion, southern Siberian platform, Russia (sample Balturino 135-63).

Diagnosis (modified after KARATAJŪTĖ-TALIMAA, 1978, and ŽIGAITĖ 2004). Scales are of medium size (0.3 – 1.4 mm. long, and 0.1 – 0.5 mm. wide), flattened, elongated and rectangular to oval in shape, with discriminate parallel longitudinal ridges (usually at least six, or more), and narrow indistinct median trough. In the case of bobbin shaped rostral and cephalopectoral scales, the longitudinal ridges are oblique, converging toward the pointy end of the crown. The median pair of longitudinal ribs is usually significantly longer than the lateral pairs of longitudinal ribs, dividing the crown into longer central part, and shorter lateral parts. The troughs separating the central and the lateral parts of the crown are sharper and deeper than the central trough. The neck is not well expressed. The base is wedge-shaped, with a thalamus-like horizontal crown-rimming part, distinct spur-like outgrowth on its anterior part, and long narrow anchoring process, descending downwards at an obtuse angle, sometimes almost at a right angle. The pulp opening is wide, located just behind the vertical projection of the base. The histology of the scales is represented by thick tubule dentine. One single pulp canal is present, dentine tubules extend regularly, being thin near the surface of the crown, getting thicker and anastomosed pulpwards. The pores of sensory line canals are not present in any of the scales.

Description.

Morphology

Rostral scales are round and bunchy; their crown is high, with 8, 10 or 12 sharp ridges, converging towards the uplifted central point, creating a shape of notched stack (Plate 5, A-D). The ridges are similar in size and sharpness, and spread uniformly around the crown, as well as do the troughs between them. The base is very low, repeating the shape and slightly obtruding the crown, with a very wide pulp depression.

Cephalo-pectoral scales are bobbin-shaped, elongated and roundish, with at least 6 to 12 or more oblique and sharp crown ridges, converging towards the high pointy posterior end of the crown. The converging ridges may form a sharp crest in the median–posterior part of the crown, extending towards the pointy posterior end (Plate 5, E-H). The base is small, slightly wider and obtruding the crown, but not yet really forming thalamus-like shape, as the crown is very high. In younger scales, the posterior long narrow anchoring process of the base may not be completely developed, but in the older ones it is rather well expressed, descending downwards at an obtuse, or sometimes at an almost right angle. A distinct spur-like outgrowth on the anterior part of the base is also visible (Plate 5, A-G).

Postpectoral scales are comparatively large, flattened, elongated, and rectangular to oval in shape. Longitudinal ridges are discriminately parallel, sharp, bunchy, having a rounded crest shape. The median trough is narrow, straight and indistinct. There are at least six (three pairs) or more of lateral ridges; the troughs separating the central and the lateral parts of the crown are sharper and deeper than the central trough (Plate 5, I-R). Though the median pair of longitudinal ribs is usually significantly longer than the lateral pairs of longitudinal ribs, dividing the crown into a longer central, and shorter lateral parts on the sides of the crown. The crown is implanted in a smooth, thalamus-like base (Plate 5, K, M, N, T). The neck is not well expressed. The posterior edge of the crown is fine, sculptured, and overhangs the base. The base is wedge-shaped, composed of thalamus-like horizontal crown-rimming part, possessing a distinct spur-like outgrowth on its anterior part, and long narrow anchoring process, descending downwards at an obtuse, or sometimes at an almost right angle (Plate 5, I, K, R, P). The pulp opening is wide, located just behind the vertical projection of the base.

Precaudal scales are narrower and less flat in comparison to the postpectoral ones. The crown sculpture is still similar to that of postpectoral ones, possessing sharp and parallel longitudinal ridges, narrow uniform troughs. Though the number of lateral ridges is smaller, usually only four (or two pairs) ridges are present (Plate 5, S-W). Even with a single pair of lateral longitudinal ribs, the crown is still divided into a longer median part, and shorter paired lateral wings, at it is in postpectoral scales. The median section is often elevated in comparison to the lateral ridges. The posterior narrow process of the base is still long, but much more horizontal, sometimes stretching within the same plain, and forming no angle with an anterior thalamus-like part of the base (Plate 5, T, W).

Pinnal scales are quite robust, elongated, slightly bobbin-shaped and not flattened. Sharp longitudinal ridges are still present, forming parallel narrow troughs. The base is comparatively uniform, the flat anterior part is reduced, and the posterior process is comparatively massive, descending at an almost right angle in respect to the crowns plain (Plate 5, X-Z).

Histology. The scales are composed of thick tubule dentine. Horizontal longitudinal thin sections of the scales show thin dentine canals near the crown surface extending rather regularly, and then getting gradually thicker and anastomosing towards the single pulp canal. In the central part of the scale, usually several thick dentine canals enter wide single pulp canal which takes approximately 2/3 of the crown length (Plate 8, D). Pores of sensory line canals have not been observed in any scales.

Comparison. Scales are more rectangular, and wider in comparison to those of *T. kadvoiensis*. The longitudinal ribs are parallel, forming sharp, narrow and parallel troughs instead of a distinct wide rhombic central trough as that of *T. kadvoiensis*. The number of longitudinal ridges is much higher than that of *T. kadvoiensis*, especially in the case of postpectoral scales. The longitudinal ridges themselves are bunchy, having a rounded crest shape, contrary to simply sharp brims as it is in *T .kadvoiensis* scales. The base possess more or less well expressed outgrowth on its anterior part, which is not the case for the base of *T. kadvoiensis.*

Talimaalepis kadvoiensis (KARATAJUTE-TALIMAA 1978) ŽIGAITE 2004 comb. nov.

Plate 6, A-Z; Plate 7, G, H; Plate 8, E.

1978 ?*Logania kadvoiensis*, KARATAJŪTĖ -TALIMAA; p. 82-86; p. 288, *partim* Pl. XII, figs. 1a, 3, 6, 7, 8, 9 a,b; *non* Pl. XII, figs. 1b, 2, 5; p. 289, *partim* Pl. XIII, fig. 4 a,b; non Pl. XIII, figs. 3a,b,c, 5, 6; p. 230, *partim* Fig. 15: 7-9; *non* Fig. 15: 5-6.

1991 ?*Loganellia kadvoiensis*, TURNER; p. 11

1991 *Helenolepis* sp. “supposed”, TURNER; p. 111.

2004 *Talimaalepis rimae* gen. et sp. nov., ŽIGAITE; pp. 158-165; p. 160, *partim*, Pl. I, figs. A, C, D, K, M-R, S-Z; *non* Pl. I, figs. B, E-J, L, Q; p. 162, *partim,* Pl. II, figs. C, I, J-M; *non*, Pl. II, figs. A, B, D-H, N, O.

2007 *Talimaalepis kadvoiensis* (KARATAJŪTĖ-TALIMAA, 1978) ŽIGAITĖ comb. nov. ; MÄRSS et al., pp. 60-61, *partim*, fig. 57: A-C, H-M; *non* fig. 57, D-G.

Holotype. LGI T-059, described as a body scale by KARATAJŪTĖ-TALIMA (1978), P. 288, PL. XII, FIG. 9 A, B; re-attributed here to a postpectoral scale (MÄRSS, 1986b).

Paratype. LGI M-1/206, postpectoral scale, NW Mongolia, sample Nr. 1009/4 (Plate 6, J herein).

Type locality and horizon. Kadvoi locality, central Tuva, Russia; Kadvoi outcrop, sample Nr. 664; Dashtygoi Formation, Dashtygoi Regional Stage, Lower Ludlow, Upper Silurian.

Paratype locality and horizon. South-east slope of mount Chargat, 80 km north from lake Khara-Ubs-Nuur, north-west Mongolia; Lake Basin outcrop Nr. 21, sample S-1009/4; Chargat Formation, Salhit Regional Stage, Upper Llandovery – Wenlock, Lower Silurian.

Material. Over 200 scales of good preservation; collection series numbers LGI M-1 and LGI T; of which. LGI M-1 200, 2007, 226, 242, and 280-289, as well as LGI T 944-952 are photographed by SEM; and LGI M-1 27 and M-1 29 as thin sections.

Geological and geographical range. Lower Silurian, Wenlock, Salhit Regional Stage, Tchargat Formation; Lake Basin outcrop Nr. 21, Tchargat locality, lake Khara-Ubs-Nuur, north-west Mongolia (samples 1009/2 and 1009/4).

Lower Silurian, Upper Llandovery, Kyzyl-Tchiraa Regional Stage, Kyzyl-Tchiraa Formation; outcrop Kyzyl-Tchiraa, central Tuva, Russia (samples 702, 271R, 253R).

Lower Siliurian, Upper Wenlock, Angatchi Regional Stage, Angatchi Formation; outcrop Kadvoi, central Tuva, Russia (sample Kadvoi 660-4).

Lower Siliurian, Upper Wenlock, Dashtygoi Regional Stage, Dashtygoi Formation; outcrop Elegest, central Tuva, Russia (sample Elegest 226).

Lower Siliurian, Upper Wenlock, Dashtygoi Regional Stage, Dashtygoi Formation; outcrop Kadvoi, central Tuva, Russia (sample Kadvoi 664).

Lower Silurian, Middle Llandovery, Khaastyrian Regional Stage, Talikit Formation; Ilim district, Irkutsk subregion, western Siberian platform, Russia (sample 141-26).

Lower Silurian, Upper Llandovery, Agidyan Regional Stage, Balturino Formation; Balturino district, Irkutsk subregion, southern Siberian platform, Russia (samples Balturino 135-47/46).

It is also known from the Silurian – Devonian boundary (Přídolí–Lochkovian), Uppermost Tauganteli, and lowermost Khondergei Regional Stages, uppermost Khondergei Formation; river Tchadan outcrop, Bazhyn-Alaak locality, central Tuva, Russia (sample 119).

Diagnosis (modified after KARATAJŪTĖ-TALIMAA, 1978, and ŽIGAITĖ 2004). Scales are of medium size (0.3 – 1.2 mm. long, and 0.2 – 0.3 mm. wide), flattened and elongated, oval or rhombic in shape, with discriminate central elongated rhomb-shaped trough. The longitudinal ridges are sharp, median pair is much higher than the lateral ones. The median pair of longitudinal ribs is significantly longer than the lateral pair of ribs, dividing the crown into longer central, and shorter down stepped lateral parts on the sides of the crown. The rostral and cephalopectoral scales are rhombic, with a densely sidelong notched and flat on the surface crown. Usually there is only one pair of underlying lateral longitudinal ribs, sometimes two pairs. The neck is not well expressed. The base is wedge-shaped, with a thalamus-like horizontal crown-rimming part, and long narrow anchoring process, descending downwards at an obtuse angle. The pulp opening is narrow, located just behind the vertical projection of the base. The histology of the scales is represented by thick tubule dentine. Single pulp canal is present, dentine tubules extend regularly, being thin near the surface of the crown, getting thicker and anastomose pulp wards. Pores of sensory line canals are not present in any scales.

Remarks. Referring to our studies of numerous vertebrate microremain samples of the region, we claim that the first descriptions of the taxon *Logania*? *kadvoiensis* by KARATAJŪTĖ-TALIMAA (1978) include some scales which belong to the genus *Helenolepis* (KARATAJŪTĖ-TALIMAA, 1978; p. 288, Pl. XII, fig. 1b, 2, 5, and p. 289, Pl. XIII, fig. 3a,b,c, 5, 6).

Description.

Morphology.

Rostral scales are rhombic to oval in crown shape, with massive base, which is usually larger than the crown (Plate 6, A-D). The crown edges are densely notched; the notches are slightly oblique, short, dense and wide. The surface of the crown is smooth and lacks any kind of sculpture. The base is high and of the same width as the crown, sometimes slightly obtruding the crown at its anterior rim.

Cephalo-pectoral scales are oval and elongated, with an oak-leaf like, notched, and comparatively high crown. The notches of the crown are oblique, short, dense, and comparatively narrow. The base is wedge-shaped, comparatively large, with distinct horizontal anterior part, and long narrow anchoring posterior process, descending downwards at an obtuse angle (Plate 6, E-H). Though the anterior horizontal part of the base is not yet thalamus-like due to a comparatively high crown.

Postpectoral scales are flattened and elongated, oval and slightly rhombic, with discriminate central elongated, rather shallow and wide rhomb-shaped trough. The longitudinal ridges are sharp, median pair being more distinct and uplifted compare to the lateral ones. The median pair of longitudinal ribs is significantly longer than the lateral pair of ribs, dividing the crown into longer central, and shorter down stepped lateral parts on both sides of the crown (Plate 6, I-P). The crown is usually wider and longer than the base. The base is wedge-shaped, composed of two distinct parts - a thalamus-like horizontal one, rimming anterior edges of the crown, and a long narrow anchoring posterior process, descending downwards at an obtuse angle (Plate 6, J, M, O). The pulp opening is small and narrow, located just behind the vertical projection of the base.

Precaudal scales are flattened, elongated and comparatively narrow. The crown usually possesses no more than two pairs of longitudinal ridges, the median pair being longer and uplifted in comparison to the lateral ones, which form down stepping wings on the both sides of the crown (Plate 6, R-U). The base is narrow wedge-shaped, composed of two distinct parts - a thalamus-like horizontal one, rimming anterior part of the crown, and a very long narrow anchoring posterior process, descending downwards at an very obtuse angle, or sometimes stretching nearly in the same crow plain (Plate 6, S, T).

Pinnal scales are elongated and slightly rhombic in shape, with notched anterior rim of the crown, though any longitudinal ridges extending longitudinally throughout the crown are not visible. Instead, some short ridgelets, following the notched crests of the anterior rim of the crown, are present. The crown itself is slightly uplifted posterior wards, with a pointy end (Plate 6, W-Z). The base is very high, wedge-shaped, with a smooth flat horizontal part, obtruding anterior edges of the crown, and a long massive anchoring posterior process, descending downwards at an obtuse angle, or at nearly right angle.

Histology. The scales are composed of thick tubule dentine. Thin dentine canals near the crown surface extend rather regularly, then getting gradually thicker and anastomosing towards the single pulp canal (Plate 7, G, H; Plate 8, E). In the central part of the scale, usually several thick dentine canals enter wide single pulp canal which takes approximately 2/3 of the crown length. The pores of sensory line canals are not eatblished in any of the scales.

Comparison. Scales are more rhomboid and oval than those of *T.rimae*. The longitudinal ribs are few, sharp, forming a distinct wide rhombic median trough in between the central pair of ridges. The median part of the crown is longer and uplifted in comparison to the shorter and down stepped lateral wings, contrary to uniform flattened pattern of *T. rimae* scales. The outgrowth on the anterior part of the base is not as well expressed as in the case of *T. rimae*.

PALAEOBIOGEOGRAPHY AND PALAEOCLIMATE

Early vertebrate microremains are numerous in the Lower Silurian of northwestern Mongolia, central Tuva and the Siberian platform, and show specific differences from the other contemporaneous agnathans. The vertebrate microremains appear in wide range of facies of the Lower Silurian of the Siberian platform, including bar belt, restricted shallow shelf, brasckish lagoon and coastal belt facies (KARATAJŪTĖ-TALIMAA & PREDTECHENSKYJ, 1995) as well as in shallow water facies of Tuva. The Silurian of Siberian platform (East Siberia between the Yenisey and Lena Rivers) featured an epicontinental sedimentary basin with continuing cyclic sedimentation (TESAKOV et al., 2003). The East Siberian epicontinental basin was a stable, persistent structure in the Early Silurian. Foreshore-lagoonal facies with fish are recorded along a north-south transect.

To specify the palaeogeographical implications of the thelodonts studied, it should be mentioned that the genera *Angaralepis* and *Loganellia* are common in shallow water sediments such as shallow shelf, marine delta and brackish lagoon facies, whereas genus *Talimaalepis* is recorded both in shallow and deeper shelf sediments. The north-west Mongolian material comes from the molasse – type Wenlockian facies, rich in unique *Tuvaella* fauna (MINJIN, 2001), which accompaniment provides strong implication of the edemism of the province (COCKS & TORSVIK, 2007). Apart from the thelodonts studied below (genera *Angaralepis*, *Loganellia*, *Talimaalepis*), the early vertebrate material of the have revieled a number of endemic early vertebrate taxa, such as new genus *Tesakoviaspis* (Tesakoviaspida), new genus *Ilimia*, which is considered as special case of tesserated galeaspids (KARATAJŪTĖ-TALIMAA & ŽIGAITĖ, 2005) , particluar Chondrichthyes, such as *Elegestolepis, Polymerolepis*?, *Tuvalepis* (ŽIGAITĖ & KARATAJŪTĖ-TALIMAA, 2008), Mongolepidida (KARATAJŪTĖ-TALIMAA et al., 1990), and endemic acanthodians *Lenacanthus* and *Tchunacanthus* (KARATAJŪTĖ-TALIMAA & SMITH, 2003).

All the thelodonts investigated, as well as the other early vertebrates reported from the region, such as chondrichthyans, acanthodians (KARATAJŪTĖ-TALIMAA & SMITH, 2003; ŽIGAITĖ & KARATAJŪTĖ-TALIMAA, 2008), are strongly endemic, and show palaeobiogeographical unity of the territory. Two endemic genera of acanthodians have been reported from the Lower Silurian of the region (KARATAJŪTĖ-TALIMAA 1997, KARATAJŪTĖ-TALIMAA & SMITH 2003). *Lenacanthus* KARATAJŪTĖ-TALIMAA & SMITH, 2003 is common to restricted shallow shelf facies of Siberian platform though it is absent in lagoon, beach and submarine - deltaic facies, whereas genus *Tchunacanthus* KARATAJŪTĖ-TALIMAA & SMITH, 2003 is widespread in each of the facies mentioned above (including the bar belt facies) of the Siberian platform, Tuva (KARATAJŪTĖ-TALIMAA & RATANOV, 2002), and northwestern Mongolia (KARATAJŪTĖ-TALIMAA et al., 1990). The distribution of all the vertebrate taxa of the region refers to the strong endemism and the separate palaeobiogeographical province. Thus the thelodont species described below may be considered as endemic to this palaeobiogeographical Silurian province as well.

The worldwide distribution of the thelodont genera *Angaralepis, Loganellia,* and *Talimaalepis* during the Silurian, are shown in Fig. 2. The genera *Angaralepis* and *Talimaalepis* are strongly endemic, referred so far only from the Lower Silurian localities discussed in this work, although *Loganellia* is cosmopolitan. The endemism of the region in the Early Silurian is sustained at the species level of *Loganellia*: all the three species, *L. asiatica, L. sibirica*, and *L. tuvaensis* are restricted to the Lower Silurian of central Asia and the Siberian platform, except the reports of *Loganellia* sp. cf. *L. tuvaensis* from the Upper Silurian–Lower Devonian (Pridoli–Lochkovian) of North Greenland (the Halls Grav locality and Monument, Hall Land, Chester Bjerg Formation: TURNER & PEEL, 1986; BLOM, 1999). This record of *Loganellia* sp. cf. *L. tuvaensis* is particularly important as concerned with Silurian palaeobiogeography. Refferring to morphology and histology of the microremains studied, *L.* cf. *L. tuvaensis* from North Greenland appears to be the same species as *L. tuvaensis* from central Tuva (excluding a few scales, described by BLOM (1999), see synonymy above). Referring to the material studied for this work, *L. tuvaensis* (Karatajute-Talimaa, 1978) is restricted to the Silurian deposits of central Tuva (Wenlock to Přídolí series). This fact confirms the preceding hypothesis that Tuva terrain has been situated more or less separate from the main Siberian palaeocraton (FORTEY AND COCKS, 2003). Nevertheless, the uniformity and endemism of the Early Silurian thelodont species studied, goes in a noteworthy accordance with the hypothesis of the joined Tuva-northern Mongolia terranes as northern accretionarry wedges of the Siberian Palaeocraton since the Late Ordovician. It is considered that Tuva and northwestern Mongolia have been a terrane collage separate from Siberia in the Precambrian and Early Plalaeozoic, and later accreted to the main Siberian Palaeocraton during the Late Ordovician (Cocks & Torsvik, 2007).

L. cf. *L. tuvaensis* has been recorded in the Upper Silurian of North Greenland (TURNER & PEEL, 1986; BLOM, 1999), which was on northeastern Laurentia, facing and approaching Siberian palaeocontinent in the Silurian time (COCKS & TORSVIK, 2002). This gives an evidence for a possible proximity of the Siberian and Laurentian palaebiogeographical provinces during the Silurian (ŽIGAITĖ & BLIECK, 2006). The adjacency of Siberia and Laurentia palaeocontinents has already been postulated in previous works, because of the large sedimentary sequence in Scotland (former part of Laurentia) deduced to be derived from Siberian during the late Ordovician and early Silurian (MCKERROW et al., 1991; TORSVIK et al., 1996); though the idea has been argued recently (COCKS & TORSVIK, 2007). In terms of other palaeobiogeographic relationships, 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. The distribution of distinctive brachiopod *Tuvaella* and related low-diversity species (known as *Tuvaella* Fauna) in the Silurian of the region, plays an important role confirming the high-latitude isolation of the Siberian Palaeocraton (ROZMAN, 1986; MINJIN, 2001; COCKS & TORSVIK, 2007).

The palaeobiogeographical areal of *L. sibirica* can be revised according to our studies. Regardless its abundance and specificity for the Lower Silurian of the Siberian platform, a few scales have been recorded in the Wenlock of northwestern Mongolia, and more additional material has been revealed from the lower Llandovery and upper Wenlock of central Tuva. Thus the palaeobiogeographical restriction of the species to the Lower Silurian of Mongolia and Siberian platform (ŽIGAITĖ & BLIECK, 2006) is now refuted: it is more widely characteristic of s Siberian – central Asian region.

The distribution of thelodonts shows interrelationship between the Early Silurian basins of northwestern Mongolia, Tuva, and the Siberian platform. If separated Tuvan and Siberian palaeogeographical provinces appear to be possible during the early and middle Llandovery (BLIECK & JANVIER, 1991; FORTEY & COCKS, 2003), the distribution of thelodonts and acanthodians (KARATAJŪTĖ-TALIMAA & SMITH, 2003), mongolepids (KARATAJŪTĖ-TALIMAA et al., 1990), and probably galeaspids (KARATAJŪTĖ-TALIMAA & ŽIGAITĖ, 2005, 2006), are evidence for a common biogeographical province of central Asia and Siberia in the late Llandovery and early Wenlock (Fig. 3), and unified Siberian terrane corresponding to all the area studied (COCKS AND TORSVIK, 2007). E. g., the horizontal distribution of *Talimaalepis* is a good supporting evidence for assuming the existence continuous palaeobasin, or at least presence of well connected epicontinental seas within these regions during Early Silurian (ŽIGAITĖ & BLIECK, 2006). These palaeobasins are supposed to have occupied the northern margin of the Panthalassic Ocean (COCKS & TORSVIK, 2007).

The abundance of endemic thelodonts and richness of other early vertebrate species in the Lower Silurian of central Asia and the Siberian platform refers to warm and productive palaeobasins and indicates them as a proper place for genesis and radiation of early vertebrates (BLIECK & JANVIER, 1993). These basins may have existed on the Siberian palaeocontinent during its drift through the palaeoequator (COCKS & TORSVIK, 2002). The northward movement of the Siberia palaeocontinent is estimated to pass it just by the equator in the Early Silurian (COCKS & TORSVIK, 2007). Subsequent widespread red gypsiferous marls and gypsum beds, found over much of the Siberian palaeocraton area in Silurian rocks, together with palaeomagnetic data, indicate movement of the terrane into more temperate palaeolatitudes, and also reflecting the shift to more arid climates (TESAKOV et al., 2003; COCKS & TORSVIK, 2007).

Finally, the endemism and restricted palaeobiogeographical distribution of the early vertebrate taxa, can serve for the indication of palaeotemperatures in the particular palaeobasins as well. Phosphatic fossils of early vertebrate exoskeleton, if only being well-preserved and not strongly altered by diagenetic processes, may be used for oxygen isotope analysis. The oxygen isotope ratios of the early vertebrate apatite then may be translated into realistic palaeotemperatures, using the method of phosphate remnant oxygen isotope ratio calculations for conodont apatite (JOACHIMSKI & BUGGISCH, 2002; JOACHIMSKI et al., 2003, 2004). The Lower Silurian early vertebrate microremains (thelodonts, acanthodians, chondrichthyans, hetrerostracans, and mongolepids) from the region studied (northwestern Mongolia and south Siberia (Ilim and Balturino districts), and from the entire Silurian sections (Llandovery to Pridoli) of central Tuva) have been processed to establish the $\delta^{18}O_{apatite}$ values. The oxygen isotope ratios appeared to be too low for appropriate palaeotemperature reconstructions (JOACHIMSKI et al., 2004), therefore the possibilities of strong freshwater influx as well as diagenetic alterations have been suggested, as most of the Palaeozoic rocks in the centre of the Siberian platform have been little tectonically altered during the Phanerozoic (Cocks & Torsvik, 2007; ŽIGAITĖ et al., 2008).

DISCUSSION

The abundance of thelodont microremains, represented by numerous and endemic species, as well as abundance of other early vertebrate taxa, such as acanthodians (KARATAJŪTĖ-TALIMAA & SMITH, 2003), mongolepids (KARATAJŪTĖ-TALIMAA et al., 1990), and probably galeaspids (KARATAJŪTĖ-TALIMAA & ŽIGAITĖ, 2005, 2006), in the Lower Silurian of central Asia and the Siberian platform refers to warm and productive palaeobasin (see "Palaeobiogeography and Palaeoclimate" section above). Moreover, the stratigraphical level of appearance, as well as abundance of different thelodont taxa are both comparatively early if considering the corresponding data from the other palaeobiogeographical provinces, such as Baltic Basin or Canadian Arctic in Early Silurian (KARATAJŪTĖ-TALIMAA & BRAZAUSKAS, 1994; MÄRSS et al., 2002, 2006). This may infer the region not only as a separate palaeobiogeographical province, but also as a place of origin and radiation of early vertebrates. This idea of pre-Silurian early vertebrate origination and speciation in equatorial epicontinental seas of the Siberian terrane has already been rised in previous works (BLIECK & JANVIER, 1993; ŽIGAITĖ & BLIECK, 2006).

The abundant and rich in endemic thelodont species, the areas studied (Tuva, northwestern Mongolia, and south Siberia), are supposed to be the northern margin of this northern palaeocontinent (COCKS & TORSVIK, 2002). In addition, the most recent studies suggest Siberian palaeocontinent as a northern terrane, representing high-latitude cold-water fauna assembleges, which has been subsequently attributed to the rich *Tuvaella* fauna with certain reluctance (Cocks & Torsvik, 2007). In our opinion, this inference is barely correct regarding the common organism preferences in ecological niches, which would suggest any rich shelf faunal assemblages tending to occure in warm-water basins in the Early Palaeozoic.

L. tuvaensis is a newsworthy thelodont species to discuss, as reffering to morphology and histology of the microremains of *L. tuvaensis* studied, *L.* cf. *L. tuvaensis* from the Upper Silurian–Lower Devonian (Pridoli–Lochkovian) North Greenland (Blom 1999) appears to be very close and conspecific to *L. tuvaensis* from Siberian terrane. These records of *L. tuvaensis* and *L.* cf. *L. tuvaensis* are particularly important as concerned with Silurian palaeobiogeography (see “Palaeobiogeography and Palaeoclimate” section above).

The particular attention should be divided to the taxonomy of the genus *Talimaalepis* ŽIGAITĖ 2004, which, regarding the internal structure of its exoskeleton, shows an intermediate position between the genera *Loganellia* (Fam. Loganellidae) and *Helenolepis* (Fam. Phlebolepidae). Two species of *Talimaalepis* are considered in this work on the basis of morphological differences, though the taxonomical position of the genus depends more on the histological characteristics, and on this point it occupies a quite well-defined intermediate position between other thelodont genera - *Loganellia* and *Helenolepis*. The presence of thick dentine tubules in the dentine of *Talimaalepis* indicates a more complex, and presumably advanced internal structure of the exoskeleton in respect of that of loganiid thelodonts, which is represented by thin dentine tubules only. In the case of disarticulated microremains of the exoskeleton of thelodonts, it is always difficult to decide not only about the intraspecific variantion of the scales, but about the higher taxonomical affiliation of the species as well. Nevertheless, on the morphological basis, *Talimaalepis* is slightly closer to loganeliid, than to phlebolepidid thelodonts and we keep the affiliation of the genus to the family Loganelliidae, and to the order Loganelliiformes (see MÄRSS et al., 2007, p. 60). Moreover, the strong morphological affinities between the scales of *Talimaalepis* species, and some shieliids, particularly *Shielia taiti* (STETSON, 1931), see in MÄRSS & RITCHIE (1998, Figs. 27A, 30A,B, 31), and also to some *Paralogania* species, such as *P. consimilis* MÄRSS AND KARATAJŪTĖ-TALIMAA, 2002 (see MÄRSS et al., 2007, p. 67, Fig. 59, G-H), and *P. kaarmisensis* MÄRSS 2003, (see MÄRSS et al., 2007, p. 68, Fig. 59, J), should be taken in consideration. The common general constitution, encountering the presence of similar wedge-shape base with a horizontal thalamus-shaped anterior part, and a long narrow anchoring posterior process, both in talimaalepid and in shieliid scales, deserves special attention. The uplifted median and lateral segments, the previous of a rhombic trough shape, are common features of these two groups as well.

Phylogenietic relationships of *Talimaalepis* are yet difficult to clearify, beacause of its palaeobiogeographical isolation, as wel as the abundance and endemism of contamporaneous palaeobiogeographically related thelodont species. To dissolve higher taxonomical affiliations, further examination on talimaalepid, helenolepid, and shieliid histology is required.

Presence of *Loganellia scotica* (TRAQUAIR, 1898) scales in the Lower Silurian of Siberian platform (KARATAJŪTĖ-TALIMAA, 1978) reported in the first description of the material, has not been considered to be evident, and is not conceded in this work. Further studies of the thelodont material from the region might clearify the perplexity.

CONCLUSIONS

The thelodonts from the Lower Silurian of northwestern Mongolia, Tuva, and Siberian platform can be attributed to three genera, *Angaralepis*, *Loganellia* and *Talimaalepis*, and six species accordingly, which all are considered as endemic of the region. *Loganellia* is most abundant and numerous in species: *L. asiatica* (KARATAJŪTĖ-TALIMAA, 1978) *L. sibirica* (KARATAJŪTĖ-TALIMAA, 1978), and *L. tuvaensis*

(KARATAJŪTĖ-TALIMAA, 1978). The species content of genus *Talimaalepis,* so far known for containing a single species, has been revised, evolving into two species described herein consequently. *Angaralepis* is represented by a single species *A. moskalenkoae*, distinct in morphology, and attributed to the order Sandiviiformes, contrary to *Loganellia* and *Talimaalepis*, which belong to the order Loganelliiformes.

Among the thelodonts studied, *L. tuvaensis* is the only species, which distribution in the Lower Silurian is restricted to localities of central Tuva. This could infer some degree of isolation of Tuvan palaeobasin in relation to the other epicontinental palaeoseas of the Siberian terrane. Then *L.* cf. *L. tuvaensis***,** from the Upper Silurian – Lower Devonian section of North Greenland (BLOM, 1999), may indicate Siberian palaeocontinent approaching the northeastern Laurentia with its northern border from the west, at the end of the Silurian period.

Additional reference of *Loganellia sibirica* in the Lower Silurian of Tuva, together with its findings in northwestern Mongolia and Siberian platform, supports the region as the united Siberian terrane in the Early Silurian.

Both *Angaralepis* and *Talimaalepis* genera are strongly endemic to the province, with the exception of cosmopolitan *Loganellia* (Fig. 2), though it is endemic at the species level.

The distribution of endemic thelodont taxa in the region explored is a strong palaeobiogeographical evidence for the Silurian palaeogeography, confirming the territory of Siberian platform, Tuva and northwestern Mongolia as a united Siberian terrane in the Early Silurian (COCKS & TORSVIK, 2007).

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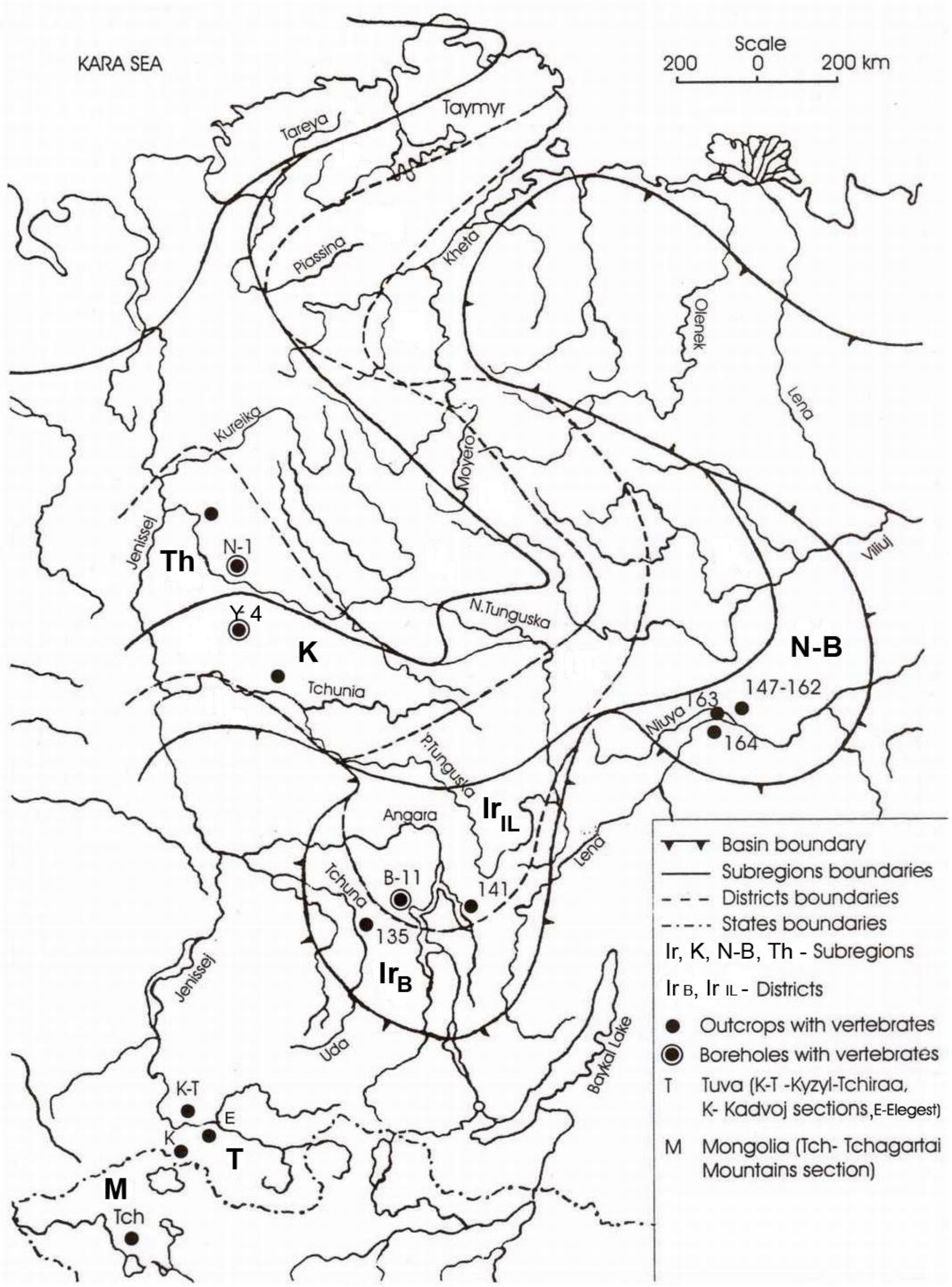

Fig. 1. Geographical position of the Lower Silurian localities studied in central Asia and the Siberian platform. M, northwestern Mongolia; T, Tuva; Ir, Irkutsk subregion, Ir-B, Balturino district; Ir-IL, Ilim district; K; Kochumdeck district; N-B, Nyuya-Beresovo district; Th, Thurukhansk district. Modified from ŽIGAITĖ & BLIECK, 2006.

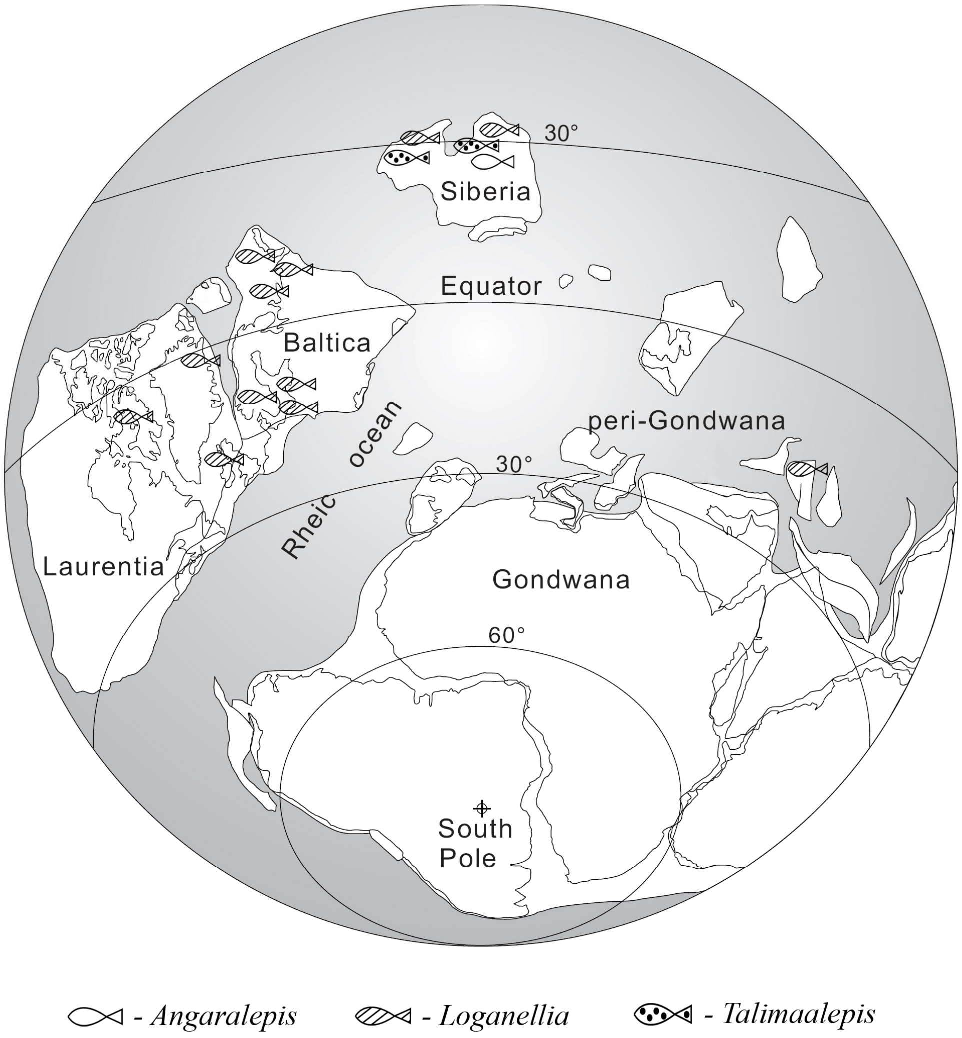

Fig. 2. Presently known distribution of thelodont genera *Angaralepis* (endemic), *Loganellia* (cosmopolitan), and *Talimaalepis* (endemic). Palaeogeography from COCKS & TORSVIK, 2002; modified after HAIRAPETIAN et al., 2008.

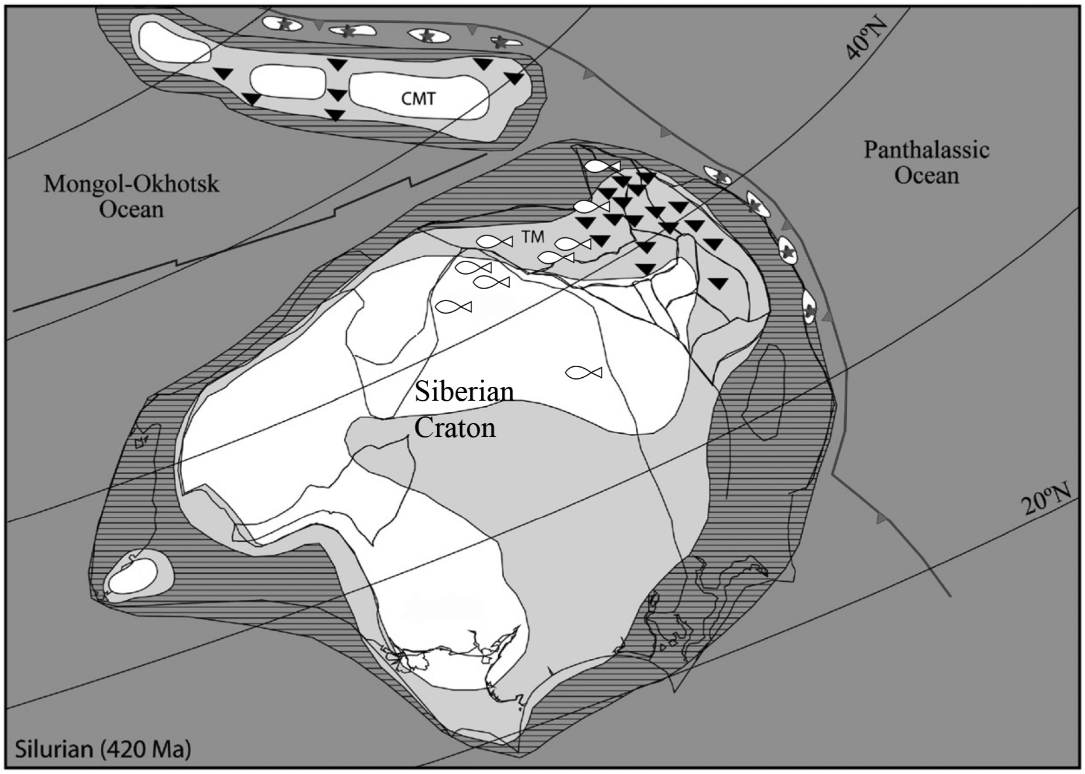

Fig. 3. Palaeogeographical map of the Siberian Terrane and adjacent area during the Silurian at about 420 Ma. Inverted black triangles show the distribution of the *Tuvaella* fauna, and white fish indicate the localities where endemic Silurian early vertebrates have been recorded. TM, Tuva – northwestern Mongolia Terrane area; CMT, Central Mongolian Terrane assemblage. White, land; light grey, shallow shelf; horizontal shading, deep shelf; dark grey, ocean; stars, volcanoes; triangled line, subduction zone; broken line, spreading ridge. Modified and complemented after COCKS AND TORSVIK, 2007.

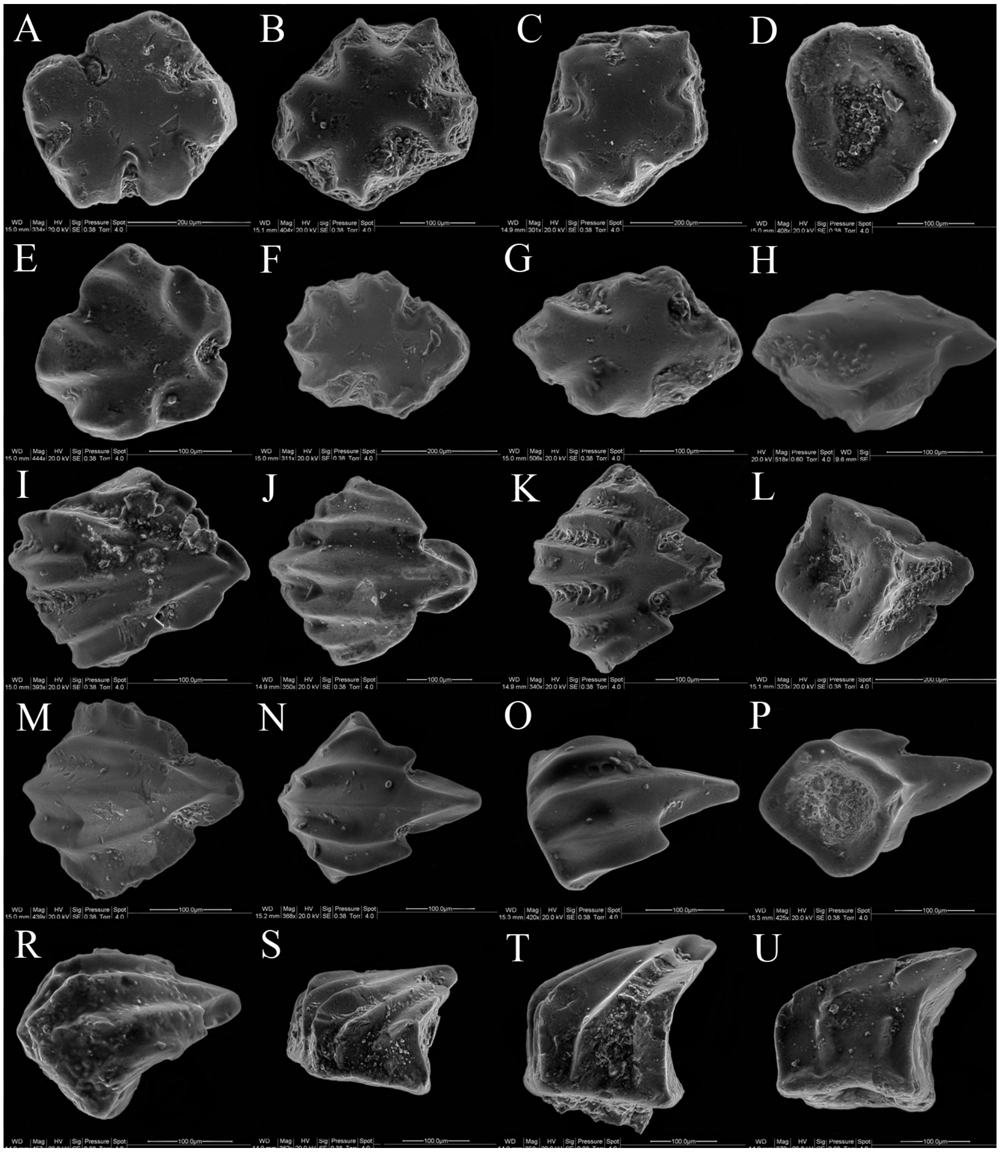

Plate 1. *Angaralepis moskalenkoae* (Karatajūtė-Talimaa, 1978). Rostral scales: 10-301 (**A**); 10-303 (**B**); 10-302; (**C**), 10-304, basal view (**D**); cephalo-pectoral scales: 10-305 (**E**); 10-306 (**F**); 10-307 (**G**); 10-308 (**H**); postpectoral and precaudal scales: 10-309 (**I**); 10-310 (**J**); 10-311 (**K**); 10-312, basal view (**L**); 10-313 (**M**); 10-314 (**N**); 10-315 (**O**); 10-316, basal view (**P**); pinnal scales: 10-317(**R**); 10-318 (**S**); 10-319 (**T**); and 10-320 (**U**).

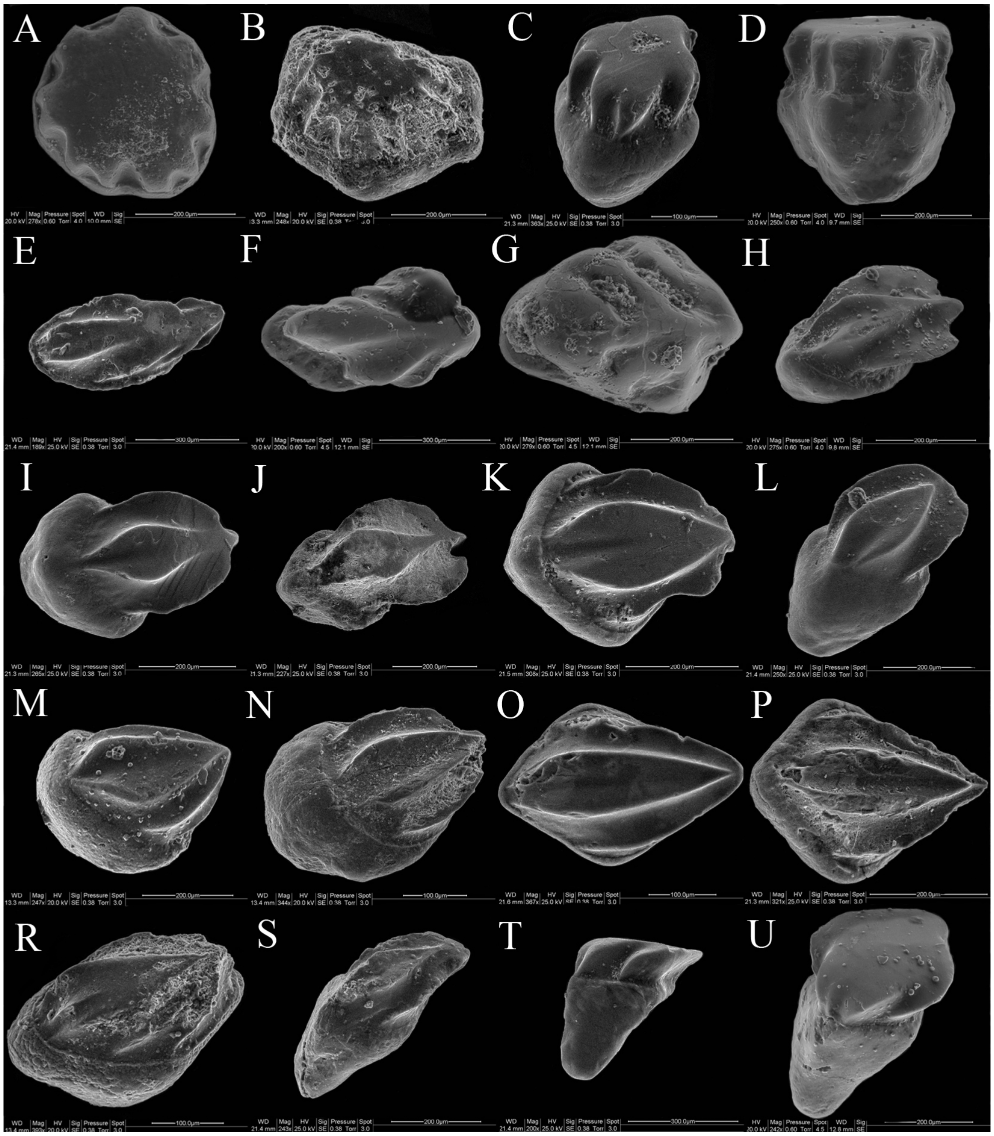

Plate 2. *Loganellia asiatica* (Karatajūtė-Talimaa, 1978). Rostral scales, *type A*: T-550 (**A**); T-551 (**B**); rostral scales, *type B*: T-554 (**C**); T-555 (**D**); cephalo-pectoral scales: T-556 (**E**); T-557 (**F**); T-558 (**G**); postpectoral and precaudal scales: T-559 (**H**); T-560 (**I**); T-561 (**J**); T-562 (**K**); T-563 (**L**); T-564 (**M**); T-565 (**N**); T-566 (**O**); T-567 (**P**); T-568 (**R**); T-569 (**S**); pinnal scales: T-570 (**T**); T-571 (**U**).

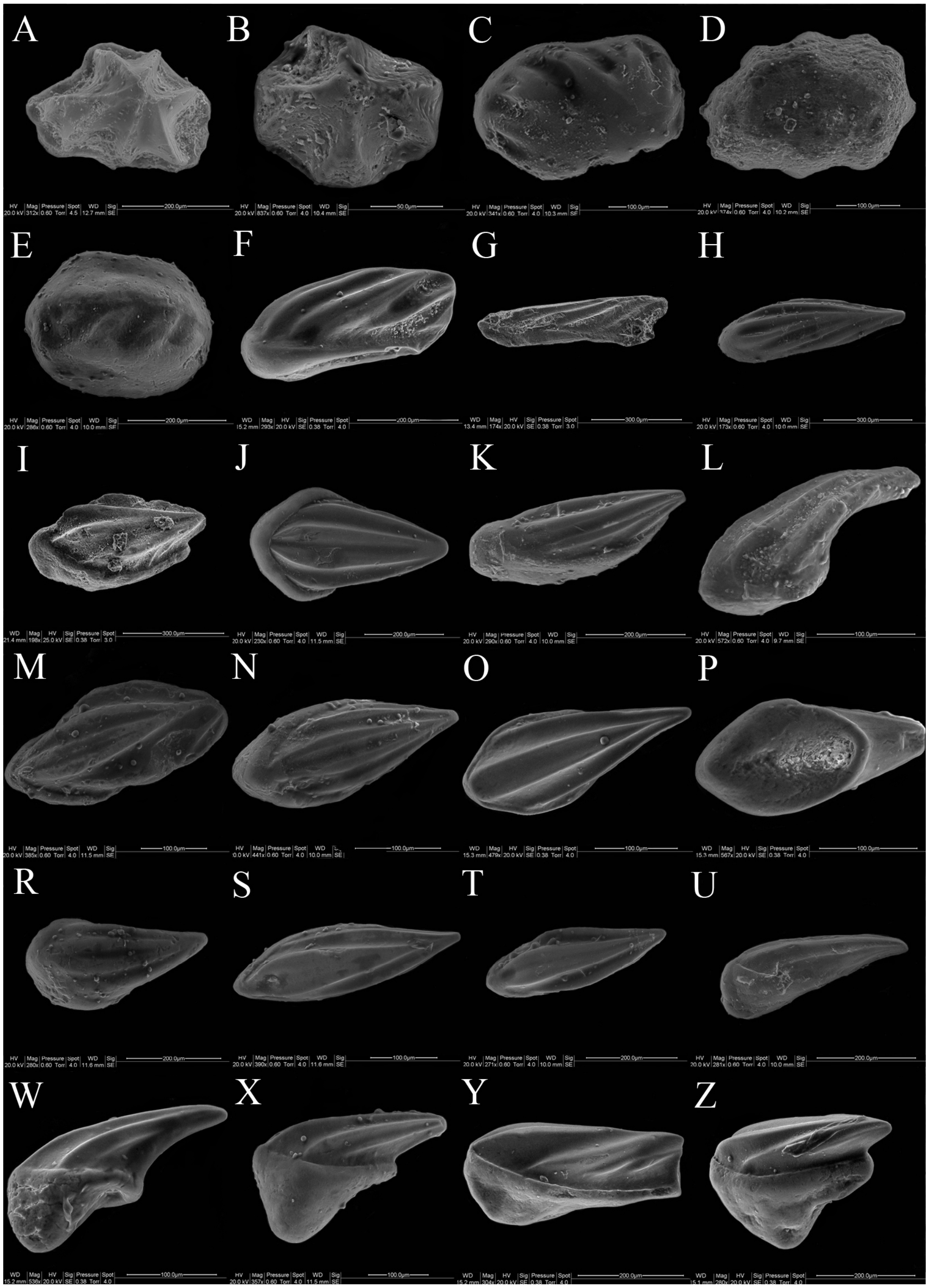

Plate 3. *Loganellia sibirica* (Karatajūtė-Talimaa, 1978). Rostral scales: 10-260 (**A**); 10-261 (**B**); 10-262 (**C**); 10-263, basal view (**D**); cephalo-pectoral scales: 10-264 (**E**); 10-265 (**F**); 10-266 (**G**); 10-267 (**H**); postpectoral and precaudal scales: 10-268 (**I**); 10-269 (**J**); 10-270 (**K**); 10-271 (**L**); 10-272 (**M**); 10-273 (**N**); 10-274 (**O**); 10-275, basal view (**P**); 10-276 (**R**); 10-277 (**S**); 10-278 (**T**); 10-279 (**U**); pinnal scales: 10-280 (**W**); 10-283 (**X**); 10-284 (**Y**); 10-282 (**Z**).

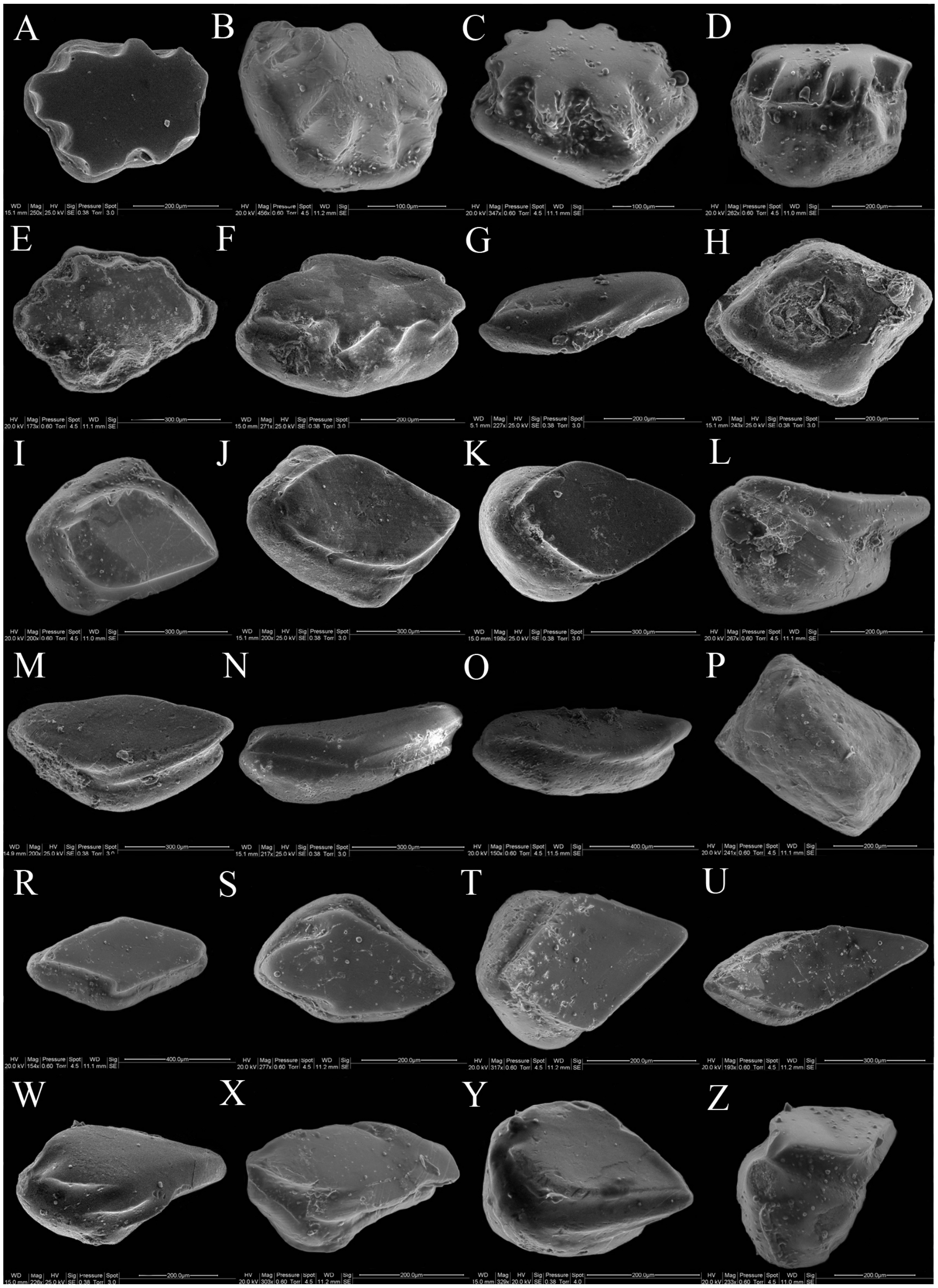

Plate 4. *Loganellia tuvaensis* (Karatajūtė-Talimaa, 1978). Rostral scales: T-609 (**A**); T-610 (**B**); T-611 (**C**); T-612 (**D**); cephalo-pectoral scales: T- 613 (**E**); T-614 (**F**); T-615 (**G**); postpectoral and precaudal scales: T-616, basal view (**H**); T-617 (**I**); T-618 (**J**); T-619 (**K**); T-620 (**L**); T-621 (**M**); T-622 (**N**); T-623 (**O**); T-624, basal view (**P**); T-625 (**R**); T-626 (**S**); T-627 (**T**); T-628 (**U**); pinnal scales: T-629 (**W**); T-630 (**X**); T-631 (**Y**); T-632 (**Z**).

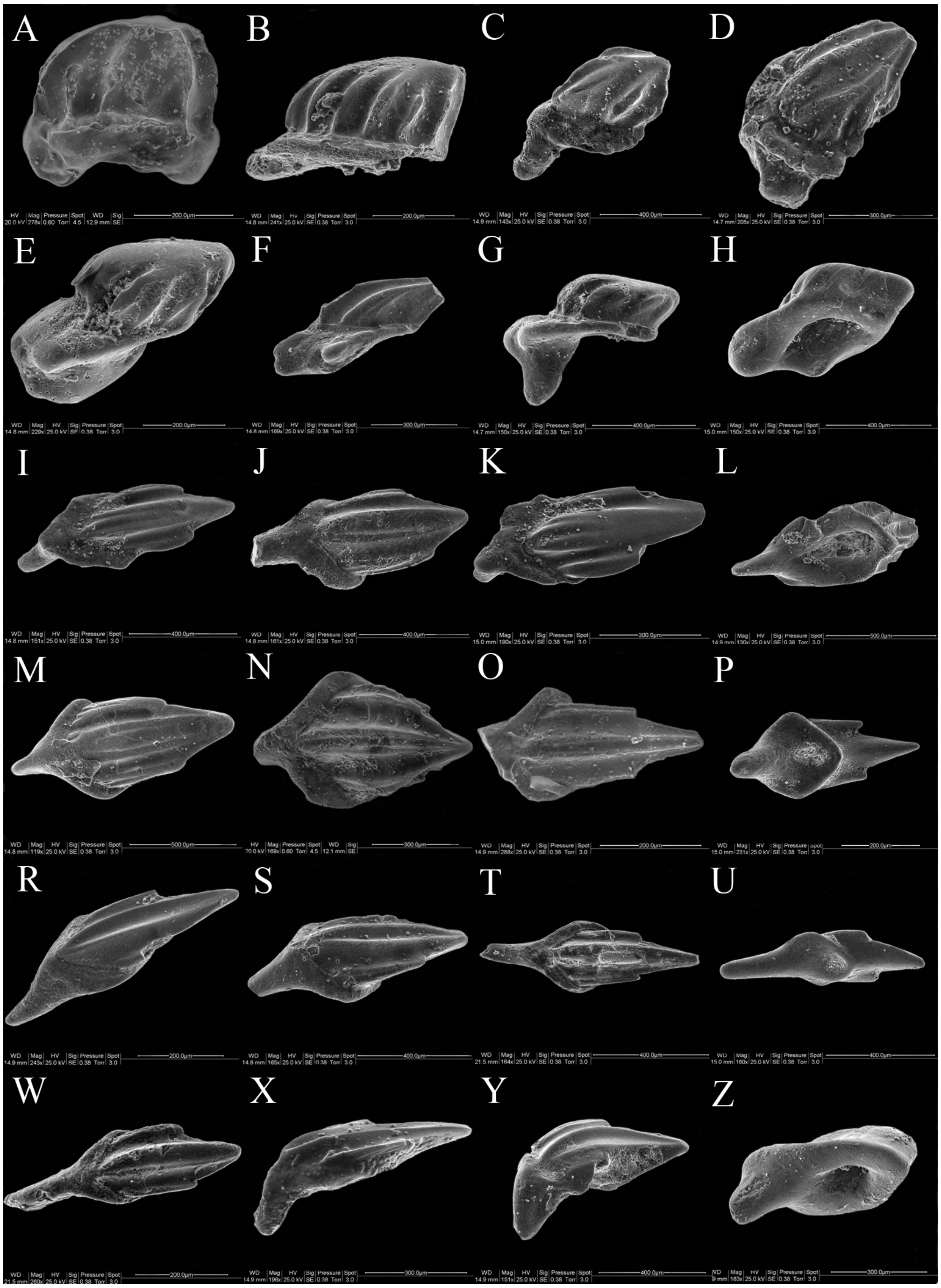

Plate 5. *Talimaalepis rimae* Žigaitė 2004. Rostral scales: T-901 (**A**); T-902 (**B**); T-903 (**C**); T-904 (**D**); cephalo-pectoral scales: T-914 (**E**); T-912 (**F**); T-915 (**G**); T-916 (**H**); postpectoral scales: M-1 232 (**I**); T-920 (**J**); T-921 (**K**); T-917 (**L**); M-1 233, paratype (**M**); T-922 (**N**); M-1 248 (**O**); M-1 231 (**P**); M-1 224, holotype (**R**); precaudal scales: T-294 (**S**); M-1 214 (**T**); M-1 221 (**U**); T-923 (**W**); pinnal scales: T-925 (**X**); T-926 (**Y**); T-918 (**Z**).

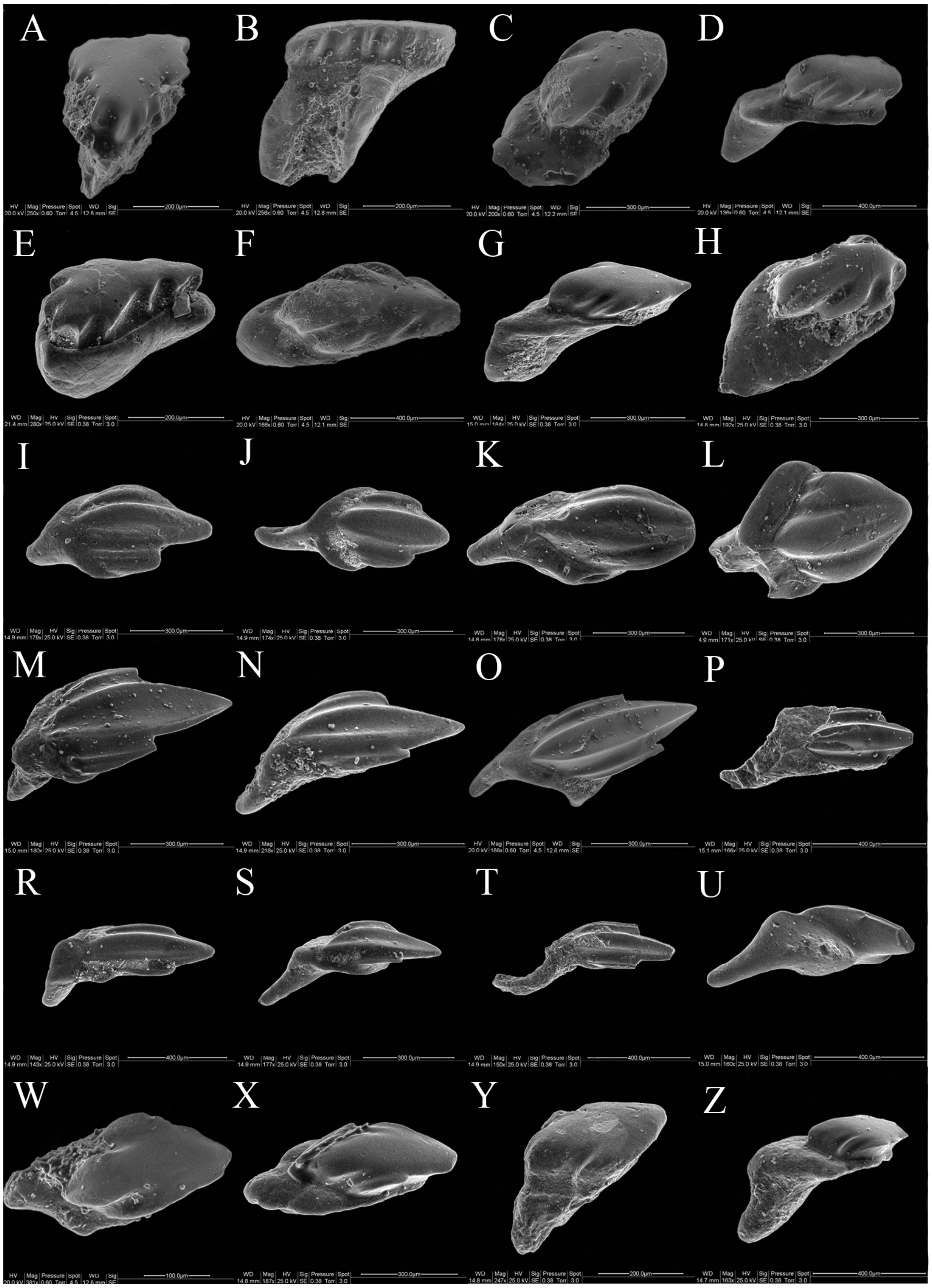

Plate 6. *Talimaalepis kadvoiensis* (Karatajūtė-Talimaa, 1978) Žigaitė 2004 comb. nov. Rostral scales: M-1 280 (**A**); M-1 281 (**B**); M-1 288 (**C**); M-1 289 (**D**); cephalo-pectoral scales: M-1 242 (**E**); T-944 (**F**); T-945 (**G**); T-946 (**H**); postpectoral scales: M-1 282 (I); M-1 206, paratype (J); M-1 283 (K); T-947 (**L**); M-1 207 (**M**); T-948 (**N**); T-950 (**O**); M-1 226 (**P**); precaudal scales: T-949 (**R**); T-951 (**S**); M-1 200 (**T**); T-952 (**U**); pinnal scales: M-1 285 (**W**); M-1 284 (**X**); M-1 287 (**Y**); M-1 286 (**Z**).

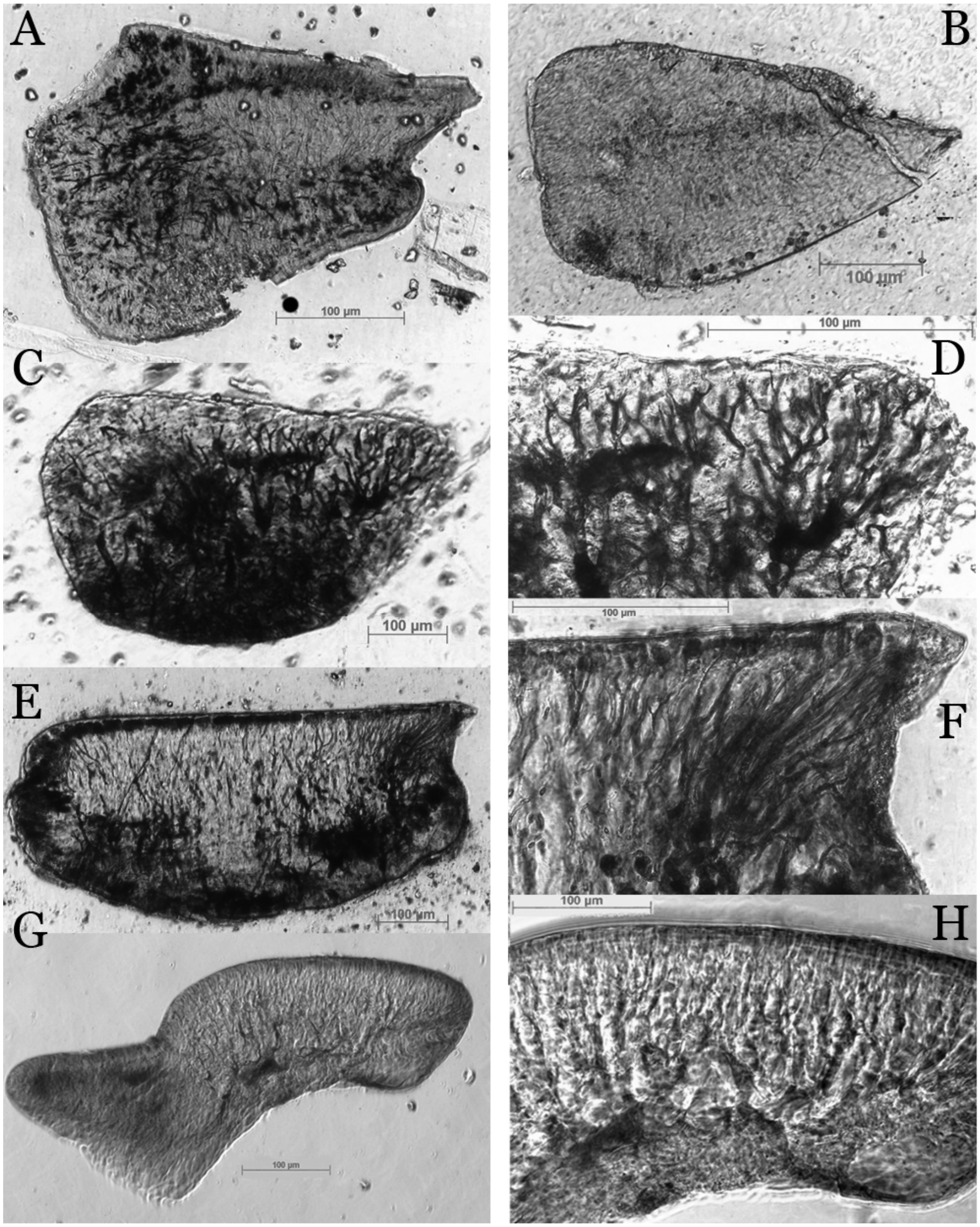

Plate 7. The cross-sections of the scales of *Angaralepis moskalenkoae*, n°174 (**A**), *Loganellia sibirica* n°488 (**B**), *Loganellia asiatica*, n°592 (**C**,**D**), *Loganellia tuvaensis*, n°183 (**E**,**F**), and *Talimaalepis kadvoiensis* n°27 (**G**,**H**).

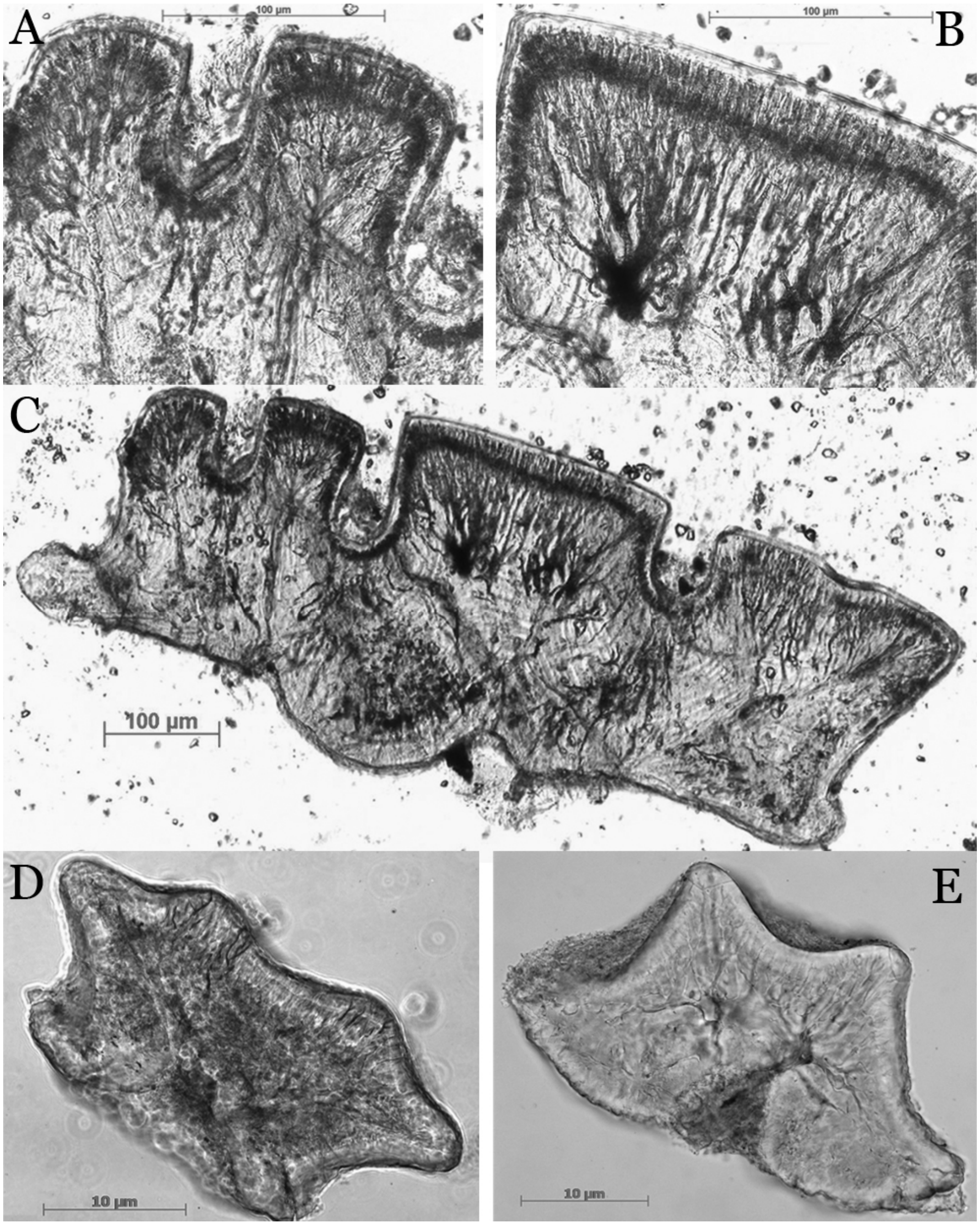

Plate 8. The cross-sections of the scales of *Helenolepis obruchevi* Karatajūtė-Talimaa 1978, n°102 (**A**,**B**,**C**), *Talimaalepis rimae*, n°28 (**D**), and *Talimaalepis kadvoiensis*, n°29 (**E**).

Article V

GFF volume 128 (2006), pp. 203–206.

Note

Palaeobiogeographical significance of Early Silurian thelodonts from central Asia and southern Siberia

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Abstract: Early Silurian vertebrates, especially agnathans, from central Asia (Tuva and northwestern Mongolia) and southern Siberia are abundant and diverse. The numerous microremains indicate that the strata of this region were deposited in warm, productive, shallow marine basins. The thelodont microremains concerned with in this paper are assigned to three genera, viz., *Loganellia* Turner, 1991, *Angaralepis* Karatajtė-Talimaa, 1997, and *Talimaalepis* Žigaitė, 2004, of which the latter two are endemic to the region. In central Tuva, *L. tuvaensis* Karatajtė-Talimaa, 1978 is restricted to the Lower Silurian. This species is, however, considered to occur also in the Upper Silurian–Lower Devonian of north Greenland. Taking into account the taxonomic record of early thelodonts, central Asia and southern Siberia may be considered as a centre of origin and radiation of Silurian thelodonts. It may have corresponded to a palaeobiogeographical province.

Keywords: Lower Silurian, vertebrates, thelodonts, palaeobiogeography, Mongolia, Tuva, Siberia.

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Introduction

Vertebrate and vertebrate-like taxa have their first records in the Cambrian–Ordovician (Blieck & Turner 2003). Thelodonts are first recorded in the Ordovician, and are the most widely distributed vertebrates in the Silurian. They are of significance for long-distance biostratigraphical correlations. Some Silurian thelodont taxa, however, are more or less endemic and allow palaeobiogeographical provinces to be defined (Blieck & Janvier 1991). The material discussed here allows the Siberian (Angaran) and Tuvan provinces of Blieck & Janvier (1991) to be more precisely defined. This definition is based upon recent taxonomic studies (Žigaitė 2004) and work that are still in progress by the senior author.

Localities and geological setting

The vertebrate material comes from Lower Silurian outcrops and boreholes of central Asia and four subregions of middle and southern Siberia (Fig. 1). The localities sampled in central Asia include Tchargat (Tchargat Formation) in northwestern Mongolia, north of the lake Ubs-Nuur. The Tchargat Formation is dated uppermost Llandovery to lower Wenlock (Fig. 2; Minjin 2001). Moreover, the Elegest, Kyzyl-Tchiraa and Kadvoj outcrops were sampled in central Tuva. In this region the Alash, Kyzyl-Tchiraa, and Angatchi formations are of Llandovery age, whereas the Akchalym and Dashtygoi formations are of Wenlock age (Fig. 2; Karatajtė-Talimaa & Ratanov 2002).

The Siberian material consists of numerous samples from five districts and four subregions of southern and middle Siberia, i.e., the Turukhansk district in the North Prienissey Subregion (Omnutakh Formation, uppermost Llandovery), the Kochumdek district in the Pretunguska Subregion (the Kochumdek, Kulinna and Razvilka formations – Llandovery, and Usas Formation –Wenlock), the Niuya-Beresovo district in the Niuya-Beresovo Subregion (the Melichan and Utakan formations, lower and upper Llandovery respectively), the Ilim district (the Rassokha Formation, Llandovery), and the Balturino district (the Balturino and Barmo formations, Llandovery and Wenlock, respectively) in the Irkutsk Subregion (Figs. 1, 2; Karatajtė-Talimaa & Smith 2003; Tesakov et al. 2003).

Material and methods

Numerous samples with vertebrate microremains have been analysed from the southern Siberia, Irkutsk and the Niuya-Beresovo Subregions; 46 samples from the Rassokha Formation, 45 from the Balturino Formation, 28 from the Melichan Formation, 53 from the Utakan Formation, and 2 samples from the Niuya Formation. The material from the middle Siberian outcrop and borehole consists of 1–4 samples per formation. The material from central Tuva (10 samples) was particularly rich in vertebrate microremains, as well as 6 samples (undissolved rock) of the Tchargat Formation, northwestern Mongolia.

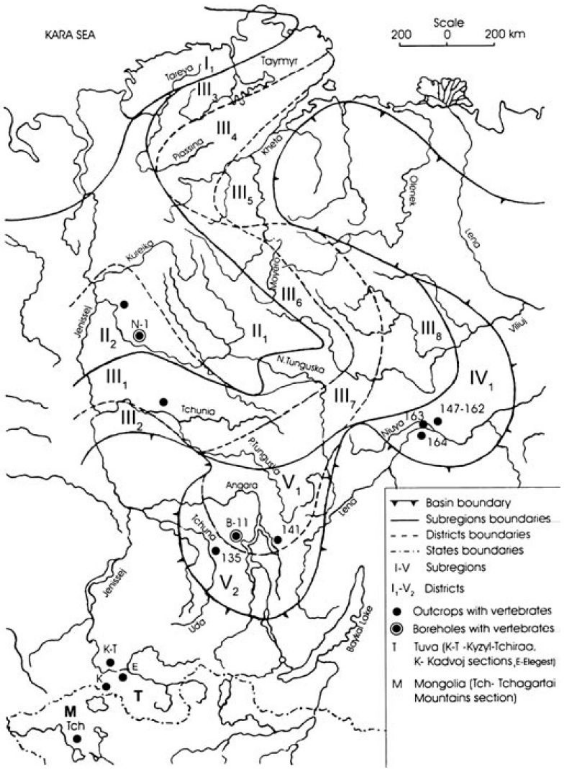

Fig. 1. Stratigraphical zonation of the Siberian Platform Silurian palaeobasin and geographical position of the localities studied. Tch – Tchargat locality in northwestern Mongolia; K – Kadvoj, K-T – Kyzyl-Tchiraa; E – Elegest localities in central Tuva. I – Taymyr Subregion; II – North Prienissey Subregion (II_2 – Turukhansk district); III – Pretunguska Subregion (III_1 – Kochumdek district); IV – Niuya-Beresovo Subregion (IV_1 – Niuya-Beresovo district); V – Irkutsk Subregion (V_1 – Ilim district; V_2 – Balturino district). Modified from Karatajtė-Talimaa & Smith (2003, fig. 1; see also Tesakov et al. 2003, fig.1).

All samples were processed with acetic acid and the phosphatic microvertebrate remains were hand-picked from the residues. Morphological analyses were carried out using a Scanning Electron Microscope (FEI Quanta 200) with X-ray microanalysis and digital imaging equipment. The histology of the scales was studied in thin sections (Canada balsam), immersed in anise oil, using high resolution photonic microscopes (Zeiss Axioplan and Zeiss Axioskop) and digital imaging equipment. A morphological set of exoskeletal elements for each thelodont species was established and subdivided into five different morphotypes; oral, cephalo-pectoral, post-pectoral, precaudal, and pinneal scales sensu Märss (1986).

Taxonomic record

The samples studied were rich in vertebrate microremains. They correspond to various lithofacies reflecting lagoon, beach and submarine – deltaic to shallow shelf environments (see references in Karatajtė-Talimaa & Smith 2003). Different higher early vertebrate taxa such as thelodonts, heterostracans, acanthodians, and mongolepids, are abundant and most of the species are endemic (Karatajtė-Talimaa et al. 1990). Two Early Silurian endemic genera of thelodonts, *Angaralepis* and *Talimaalepis*, as well as two endemic genera of acanthodians, *Lenacanthus* and *Tchunacanthus*, have so far been described from the region (Karatajtė-Talimaa 1997; Karatajtė-Talimaa & Smith 2003; Žigaitė 2004). The samples from northwestern Mongolia and central Tuva were rich also in benthic fossils, including the well-known, endemic brachiopod *Tuvaella* (see Minjin 2001).

The thelodont exoskeletal elements have been attributed to three genera, *Loganellia* Turner, 1991, *Angaralepis* Karatajtė-Talimaa, 1997, and *Talimaalepis* Žigaitė, 2004, of which the latter two are endemic. *Angaralepis moskalenkoae* Karatajtė-Talimaa, 1997 is recorded in the Lower Silurian of the Siberian Platform only. *Loganellia* is the most common genus and is represented by four species; *L. asiatica* Karatajtė-Talimaa, 1978, *L. sibirica* Karatajtė-Talimaa, 1978, *L. tuvaensis* Karatajtė-Talimaa, 1978, and *Loganellia* sp. indet. The latter was previously known as *Loganellia* ex gr. *scotica* (Fig. 2; Karatajtė-Talimaa & Predtechenskyj 1995). *Angaralepis* and *Loganellia* are common in strata formed in shallow-water environments, such as shallow shelves, marine deltas, and brackish lagoons, whereas *Talimaalepis* is present in strata formed in both shallow and deeper shelf environments. *Talimaalepis rimae* Žigaitė, 2004, described from the Llandovery of Tuva, and first identified as *Loganellia*? *kadvoiensis* by Karatajtė-Talimaa (1978), is widespread in the Upper Llandovery of northwestern Mongolia, Tuva, and southern Siberia. *Loganellia sibirica* is common in the Llandovery of southern Siberia and has been recorded also in northwestern Mongolia. Hence, the geographical distribution of *T. rimae* and *L. sibirica* shows a closer affinity between NW Mongolia and Siberia than between NW Mongolia and Tuva (Fig. 2).

Loganellia tuvaensis is an important thelodont species as it is restricted to a few Silurian outcrops in central Tuva. It has been recorded in the Upper Silurian Pitchi–Shui Formation at the Elegest and Kadvoj localities (Karatajtė-Talimaa & Ratanov 2002), and in the Lower Silurian Dashtygoi Formation (Fig. 2) at Elegest. This record of *L. tuvaensis* is particularly important in terms of Silurian palaeobiogeography. *Loganellia* cf. *L. tuvaensis* is reported from the Upper Silurian–Lower Devonian (Přídolí–Lochkovian) of north Greenland (the Halls Grav locality and Monument, Hall Land, Chester Bjerg Formation; Blom 1999). Based on the morphology and histology of the studied material, *L.* cf. *L. tuvaensis* appears to be identical to, and conspecific with, *L. tuvaensis* from central Tuva. This suggests a close relationship between the Siberian and Laurentian palaeocontinents during the Silurian (Fig. 3).

Discussion

The abundance of endemic vertebrate species in the Lower Silurian of central Asia and southern Siberia suggests that the strata of this region were formed in warm and productive palaeobasins. These basins may have existed on the Siberian palaeocontinent during its drift across the equator (Cocks & Torsvik 2002). These

Fig 2. Distribution of thelodonts in the Lower Silurian of the Siberian Platform, Tuva and northwestern Mongolia (modified from Karatajtė-Talimaa & Smith 2003).

Series	Stage	Regional Stage	Siberian Platform										Tuva		North – West Mongolia	
			North Prienissey Subregion		Pritunguska Subregion		Niuya - Beresovo Subregion		Irkutsk Subregion							
			Turukhansk district		Kochumdek district		Niuya – Beresovo district		Ilim district		Balturino district					
Wenlock	Sheinwoodian Homerian	Khakomian	Uragdan		Usas	*Tl .rimae*	Niuya		Deshyma		Barmo	*L* .sp. indet. *Tl. rimae*	Dashtygoi	*L .asiatica* *L. tuvaensis* *Tl. rimae*	Tchargat	*L. asiatica* *L. sibirica* *Tl. rimae*
													Akchalym			
Llandovery	Telychian	Agidyan	Omnutakh	*Talimaalepis rimae*	Razvilka	*Angaralepis moskalenkoae* *Loganellia sibirica* *L*. sp. indet.	Utakan	*A.moskalenkoae* *L. sibirica*	Rassokha	*A.moskalenkoae* *L. sibirica* *L*. sp. indet.	Balturino	*L*. sp. indet. *Tl. rimae*	Angatchi	*L. asiatica* *Tl. rimae*		
													Kyzyl-Tchiraa	*L. asiatica* *Tl. rimae*		
	Aeronian	Khaastyrian	Talikit		Kulinna	*L. sibirica* *L*. sp. indet.				*L. sibirica* *L*. sp. indet.		*L*. sp. indet.	Alash	*L. asiatica*		
	Rhuddanian	Moyerocanian	Chamba		Kochumdek	*L. sibirica*	Melichan	*L. sibirica*		*A.moskalenkoae* *L. sibirica* *L*. sp. indet.		*L. sibirica*				

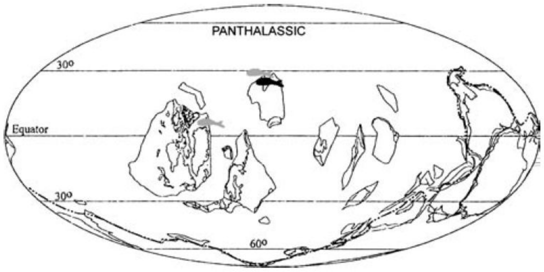

Fig. 3. Presently known record of *Loganellia tuvaensis* Karatajtė-Talimaa, 1978, and *L*. cf. *L. tuvaensis* (Blom 1999). Early Silurian localities in black, Late Silurian ones in grey. Palaeogeographical reconstruction for the latest Ordovician–earliest Silurian (440 Ma) by Cocks & Torsvik (2002).

vertebrate records further suggest that this region was a center of origin and radiation of the earliest vertebrates (Blieck & Janvier 1993). The distribution of thelodonts shows interrelationships between the Early Silurian basins of NW Mongolia, Tuva and southern Siberia. Two separate palaeobiogeographical provinces (Tuva and Siberia) appear to have existed during the Early and Middle Llandovery (Blieck & Janvier 1991). However, the distribution of thelodonts and other vertebrates such as acanthodians (Karatajtė-Talimaa & Smith 2003), mongolepids, and probably galeaspids (Karatajtė-Talimaa & Žigaitė 2005) suggest a common biogeographical province of central Asia and Siberia in the Late Llandovery and early Wenlock (Fig. 2). This is probably related to the opening of an epicontinental sea-way, connecting the Early Silurian basins in NW Mongolia, Tuva, and southern Siberia at that time.

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Article VI

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欧洲中部志留系概述

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提要 对欧洲中部的志留系进行全面回顾，涉及北海、立陶宛、罗马尼亚和法国西南部。志留纪时限较短，约为28Ma，但在地球生命历史上具有重要地位。它记录了奥陶纪末灭绝事件之后兰多维列世生物多样性的恢复，即显生宙第二个重要的复苏期。在赫南特期多样性危机之后，温洛克、罗德洛和普里道利世的部分生物群的多样性达到峰值。罗德洛见证了原始陆生维管植物的成功登陆。志留纪气温突然急剧上升，产生温室效应，导致大气和海洋表层水的氧含量较低。而兰多维列世出现过几次冰室效应，在海平面下100m处，有机质大量富集，多于任何其他时期，产生缺氧环境，导致志留纪黑色沉积物的形成。全球碳循环变化异常，与海平面变化关系十分密切，从而对海洋动物群的生物多样性产生深远影响。

关键词 地层学，盆地演化，志留纪，欧洲中部

AN OVERVIEW OF THE SILURIAN SYSTEM OF CENTRAL EUROPE

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1 INTRODUCTION

During the Silurian Central Europe was more widely spread out over the globe than at present with at least two oceans that have disappeared since. Several large palaeocontinents such as Baltica in the NE and the northern part of Gondwana in the S co-existed with smaller palaeoplates such as Avalonia in the W, Far Eastern Avalonia in the N and NW and Peri-Gondwana terranes such as Perunica in the centre. They were separated by two oceans the Tornquist Sea and the Rheic Ocean. The palaeocontinents were joined together by subduction of oceanic crust, closing of the oceans and the subsequent Caledonian and Variscan orogenies. The

Alpine orogeny brought additional pieces of Peri-Gondwana into the study area. They are included in the basement of the Alps in several tectonic windows (e.g. Carnic Alps) and called Proto-Alps.

2 PALAEOGEOGRAPHIC RECONSTRUCTION

Some palaeocontinents such as Baltica were situated in the subtropical latitudes where, locally, small reefs could develop on the shallow platforms. Other palaeocontinents such as northern or Peri-Gondwana were situated at high latitude and characterized by the occurrence of glacial or glacio-marine diamictites in the Hirnantian, immediately preceding the Silurian. Avalonia and Far Eastern Avalonia were situated at temperate or low latitude. The latter had collided with Baltica in the Ashgill whereas the former collided with Laurentia and Far Eastern Avalonia during the Silurian.

Outcrop areas are rather scarce in Central Europe, but some subcrop areas were intensely drilled, adding information to the database. The Silurian on Baltica is present in outcrops in the two parts of the Holy Cross Mountains, in Bornholm and in numerous boreholes of northern Poland NE of the Trans European Suture Zone and in Lithuania. The Silurian from Far Eastern Avalonia was only reached in boreholes in the Koszalin-Chojnice Zone of western Pomerania. The Silurian from the part of Avalonia in the study area is outcropping in Belgium (Brabant Massif, Condroz Inlier) and Germany (Ebbe anticline) and present in boreholes in the Brabant Massif, the North Sea and East Anglia. Peri-Gondwanan terranes, caught in the Variscan structures Franconia, Mid-German Crystalline Rise, Saxothuringian Zone and Moldanubian Zone, are found in numerous small outcrop areas in central Germany with complete successions in the Thuringian Forest, and in the Czech Republic where they are observed in the large, well-known outcrop area of the Prague Basin. Other Peri-Gondwanan terranes are included in Alpine tectonic units such as the Apulia/Italia Terrane. Many smaller outcrop areas occur in Austria north and south of the important Alpine fault: the Periadriatic Line, in northern Italy and Croatia. A well-studied outcrop area is the Carnic Alps succession. Another Alpine terrane, the Hellenic/Bosnian-Noric Terrane contains small outcrop areas in Croatia and Serbia. Moesia is another Peri-Gondwana terrane where the Silurian is observed in several boreholes. Outcrops of the Silurian from Northern Gondwana have been found in the Montagne Noire and the Maures Massif.

3 DEPOSITIONAL FRAMEWORK

The facies often consists of anoxic sediments such as black or calcareous shales and limestones, and varies according to three factors. (1) The relation to local water depth, modulated by eustasy, ranging from lagoonal, shallow, middle or deep shelf environment over the continental slope to deep marine with turbidites or radiolarites. (2) The facies is also controlled by palaeolatitude: carbonates with occasional small reefs were only formed in shallow and middle shelf environment on low latitude, i.e., on Baltica and, in the upper Silurian, on Avalonia. (3) Different tectonic settings, such as passive or active margins, result in important differences in thickness. Baltica, except along its SW margin, Peri-Gondwana and northern Gondwana did not suffer crustal mobilisation during the Silurian. Hence, sedimentation mostly happened on a passive margin, situated distally from the emergent land masses, south of the study area, with low terrigenous influx and reduced subsidence, resulting in sequences of only a few tens to hundreds meter thickness. The facies mostly is water depth controlled. But around faulted areas with half-graben structures and occasionally active intra-plate volcanism, such as the Prague Basin and the Greywacke Zone of Austria, much variation in thickness on the otherwise stable passive margin of Peri-Gondwana is observed.

In the numerous outcrop areas of Peri-Gondwana, five main facies are developed. (1) The most common is the calm, relatively deep shelf, Thuringian Facies, characterized by thin sequences of dysaerobic or anoxic dark shales and cherts in the lower Silurian, and typically thick aerobic limestones with interbedded thin quartzite beds in the upper Silurian, called *Ockerkalke* in Germany. It is found in a.o. Saxothuringia, parts the Prague Basin and the Carnic Alps where it is called the Bischofalm Facies. (2) The Bavarian Facies, quite similar to the Thuringian Facies, consists of grey-green shales with interbedded graptolithic shales and *alum shales*; but without limestones in the upper Silurian. It is sometimes interpreted as deposited on a very deep shelf with radiolarites. It occurs in narrow bands in the Saxothuringian Zone. (3) The Shelly Fauna Facies contains thick calcareous shales with limestone nodules and lenses rich in shelly fauna (cephalopod limestones) and is supposedly deposited on moderately to shallow shelf. It occurs in Saxothuringia, the Prague Basin, the Montagne Noire and the Carnic Alps where it is subdivided in a shallower Wolayer Facies and a less shallow Plöcken Facies. An intermediate facies between the Shelly Fauna Facies and the Thuringian Facies is called the Findenig Facies. (4) The "Prague Basin Facies" is formed in very shallow water on the gentle slopes of the Wenlock-Ludlow volcanic archipelago in the Prague Basin, with thick basic volcanics and macrofauna-rich bioclastic carbonates. The facies also developed in Austria. (5) A fifth facies is developed in Austria proximal to local land areas with a high input of siliciclastic material, sometimes turbiditic. Due to Variscan or Alpine deformation and metamorphic overprint with greenschist or amphibolite metamorphic facies in several areas, it is not always possible to deduce the original composition of the rocks.

Extensive subsidence allowed often kilometre thick Silurian sequences to be deposited on the two active margins within the study area: the Heligoland-Pomerania Deformation Zone between Baltica and Far Eastern Avalonia and the Anglo-Brabant Silurian Basin and Deformation Zone between Far Eastern Avalonia and Avalonia.

4 PROGRESS IN SILURIAN RESEARCH

At the 1996 meeting in Rochester (USA) the International Subcommission on the Silurian System, overviews were presented of the Silurian stratigraphy, sedimentology and estimates of water depth for all palaeocontinents. In the last ten years, advances on the Silurian in the study area were mainly achieved by a multidisciplinary approach. Studies continued to concentrate on refinement of the litho- and biostratigraphy but also on petrology and geochemistry of magmatic and metamorphic rocks, provenance studies of the sediments as on Saxothuringia (Linnemann, 2003).

The Brabant Massif (Verniers *et al.*, 2001), the Condroz Inlier (Vanmeirhaeghe, 2006), West Pomerania and NW Poland (Podhalańska and Modliński, 2006). Other studies also included basin analysis and history of formation to deformation of the sedimentary basins, palaeomagnetic studies and geophysical studies of the deep crust to determine the exact boundaries of the terranes such as the SW limit of Baltica and the boundaries between Far Eastern Avalonia and Avalonia (EUROPROBE and PACE projects, Verniers *et al.*, 2002; Winchester *et al.*, 2002, 2006; Pharaoh *et al.*, 2006). A German multi-disciplinary study on the Variscides, produced new models for the Silurian protoliths within the different Variscan structural units (Franke *et al.*, 2000), also on Saxothuringia (Linnemann, 2003) and on a smaller scale for the Rügen Caledonides (Katzung, 2001). The history of plate movements in the Silurian was further elucidated with evidence for the Peri-Gondwana affinity of Moesia (Vaida and Verniers, 2006), the presence and movement of separate terrane Far Eastern Avalonia (Verniers *et al.*, 2002) and the palaeogeographical position of the two parts of the Holy Cross Mountains during the Silurian, attached to Baltica but possibly not fixed.

While in recent years much progress was made in Silurian isotope research in combination with detailed biostratigraphical studies, e.g., Gotland (Calner *et al.*, 2006; Kaljo and Martma, 2006) these techniques might also be used in the future in the better developed Silurian sequences of the study area. In the near future more details are also expected about the Peri-Gondwana palaeoplate configuration and history (IGCP Project 491 by Linnemann and co-workers).

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Article VII

6 Silurian

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In an overview of the Silurian of Central Europe, it is important to realize that during this period the study area was spread more widely over the globe than nowadays because at least two oceans were present in the area which have since disappeared. Several palaeocontinents such as Baltica or Gondwana, smaller palaeoplates such as Avalonia and Far Eastern Avalonia, and Peri-Gondwana terranes such as Perunica, were separated by the Tornquist Sea and the Rheic Ocean. These palaeocontinents were brought together in the present-day configuration by closing of the oceans and the subsequent orogenic collisions, respectively termed the Caledonian and Variscan orogenies. Plate movements before and during the Alpine orogeny also brought pieces of northern Gondwana into the study area. These Proto-Alps are now included in the basement of the Alps and are observable in several tectonic windows (e.g. Carnic Alps).

The Ordovician–Silurian boundary

The Global Stratotype Section and Point (GSSP) of the base of the Silurian System, equivalent to the base of the Llandovery Series and the Rhuddanian Stage, is situated outside the study area in Dob's Linn, near Moffat in the Southern Uplands of Scotland (Bassett 1985; Cocks 1985; Holland 1985; Williams & Ingham 1989). The base was put at the lowest occurrence level of the graptolite *Parakidograptus acuminatus* s.l. After a systematic revision of the fauna another species was selected as index fossil. The lowest occurrence level of *Akidograptus ascensus* was then chosen to indicate the base of the Silurian (Melchin 2004). The Silurian System consists of four series, from bottom to top: Llandovery, Wenlock, Ludlow and Přídolí. The lower three are further subdivided into seven stages (Fig. 6.1).

Palaeoclimate

During the Silurian the climate was recovering globally from the Hirnantian glaciation (latest Ordovician), during which an icecap was centred on a large part of Gondwana. At the transition from the Ordovician to the Silurian, the Hirnantian icehouse climate changed rapidly to a greenhouse climate (Hallam & Wignall 1997; Brenchley *et al.* 2001). Hence, reconstructions all show a temperature increase through the Silurian (Frakes *et al.* 1992; Azmy *et al.* 1998). On the other hand, many parameters presumably connected with biotic productivity were declining during the Silurian such as low atmospheric oxygen, low organic carbon in the oceans (see below) and depletion of δC^{13} (Wilde *et al.* 1991; see below).

Budyko *et al.* (1987) reconstructed a global inventory of the masses of major lithofacies for the Silurian and proposed a global average temperature of 20°C, which is warmer than the modern global average of 15°C. The temperature was somewhat lower than during the even warmer Ordovician and Devonian, explained by a combination of increased land area in the northern hemisphere and evaporative cooling in the shallow tropical embayments (Wilde *et al.* 1991). The Silurian atmospheric carbon dioxide has been calculated as *c.* 900 ppm (three times modern values) which represents a clear decline from the 1200 ppm values in the Upper Ordovician (Budyko *et al.* 1987). According to the model of these authors, atmospheric oxygen declined from 65% of the present atmospheric level (PAL) at the base of the Silurian to *c.* 35% PAL in the late Silurian, following a general trend from the Early Ordovician to the Mid-Devonian. It resulted in anoxic water below about 100 m and in most bottom waters of the middle and deeper shelf during highstands. The atmospheric oxygen started to rise again in the Devonian due to the rapid spreading of plants over the continents. Berner (1989) also obtained a decline of atmospheric oxygen during the Silurian, but listed higher values (from 75% to 60% PAL).

According to Wilde *et al.* (1991) the low atmospheric oxygen levels, together with a warmer climate than today, imply that the oceanic surface mixed water contained less oxygen during the Silurian than today. This resulted in a thick pycnocline throughout the Silurian. For a tropical position they calculated a pycnocline with oxygen levels near zero between depths of 100 m and 3000 m, with some oxygen above and below. Due to this low oxygen level in the Silurian oceans, far less organic matter was required to trigger anoxic conditions in the seas than in other periods.

The area of continental shelf-seas decreased during the Silurian from about 40% to 30% (Budyko *et al.* 1987). This decrease reduced the area of surface water in contact with the atmosphere and also the volume of seawater saturated with oxygen in the upper part of the water column. This factor also contributed to an increase of the anoxic zone in deeper waters during the Silurian. The result is that worldwide Silurian sediments were often deposited in anoxic conditions and are dark in colour due to a certain amount of organic matter. On the other hand, the combination of high carbon dioxide levels and higher temperature allowed deposition of calcium carbonate in tropical shelf-seas, where a relatively alkaline pH of *c.* 8 prevailed (Wilde *et al.* 1991).

Sea-level changes

Silurian shelf sequences were well exposed on large areas of North America (Laurentia), Norway, Gotland, Estonia (Baltica), England and Wales (Avalonia), Siberia, South China and Australia (Gondwana). In the stratigraphical succession on stable platforms, shifts are repeatedly observed from shallow coral–stromatoporoid communities, through brachiopod-dominated communities to deeper high-diversity graptolite assemblages and back to the shallow communities. This variation has allowed

CHRONOSTRATIGRAPHY Global Standard Stratigraphy				LOCATION OF BASAL BOUNDARY STRATOTYPE (GSSP)
System	Series		Stages	
SILURIAN	UPPER	Přídolí		Požáry Section Barrandian
		Ludlow	Ludfordian	Sunnyhill Quarry Ludlow District
			Gorstian	Pitch Coppice Ludlow District
	LOWER	Wenlock	Homerian	Whitwell Coppice Wenlock District
			Sheinwoodian	Hughley Brook Wenlock District
		Llandovery	Telychian	Cefn Cerig Section Llandovery District
			Aeronian	Trefawr section,Cwm-coed-Aeron Farm Llandovery District
			Rhuddanian	Dob's Linn Southern Uplands of Scotland

Fig. 6.1. The standard Silurian chronostratigraphy (after Holland 1989).

several authors to reconstruct eustatic sea-level curves for the Silurian (McKerrow 1979; Lenz 1982; Johnson *et al.* 1991, 1998; Ross & Ross 1996; Loydell 1998; Johnson 2006) (Fig. 6.2). The eustatic curves of the latter three studies often show the same trend, though around several levels the trends are opposite (Fig. 6.2). Further studies are needed to explain the discrepancies, which are possibly due to less refined dating of the levels. Loydell (1998) had the advantage to study the graptolitic facies of the deeper shelf and he could easily link all the bathymetric excursions to the graptolite biozonations (Kaljo *et al.* 2003; Melchin *et al.* 2004). According to Loydell (1998) four highstands occurred in the Llandovery following the important sea-level low in the lower and middle part of the Hirnantian (uppermost Ordovician) with a postulated drop of 40 m (Long 1993), 100 m (Brenchley 1989) or much more (Moreau *et al.* 2004). These are the Rhuddanian/Aeronian transition (between the *Coronograptus cyphus* and the *Coronograptus gregarius* zones), the mid-Aeronian (lowest *Stimulograptus sedgwickii* Zone), the lowest Telychian (*Spirograptus turriculatus* Zone) and the upper Telychian (*Monoclimacis crenulata* Zone and higher Telychian biozones). Community replacements in the Llandovery are symmetrical from bottom to top, suggesting gradual sea-level changes. Several authors explain the Llandovery eustatic changes as being related to the melting of remaining ice sheets, proven by the presence of several diamictite horizons in the early Aeronian, in the early and in the late Telychian in South America (Brenchley & Newall 1984; Grahn & Caputo 1992; Caputo 1998; Kaljo *et al.* 2003).

At its base (*Cyrtograptus centrifugus* and *Cyrtograptus murchisoni* zones) and at its top (*Pristiograptus/Colonograptus ludensis* Zone), the Wenlock is characterized by a low sea level according to the curve of Loydell (1998). A high sea level can be observed within the upper part of the Sheinwoodian (from the *Monograptus riccartonensis* to the *Cyrtograptus ellesae* zones). The Ludlow, according to the same curve, shows a high sea level in the mid-Gorstian (*Lobograptus scanicus* Zone), a low sea level in

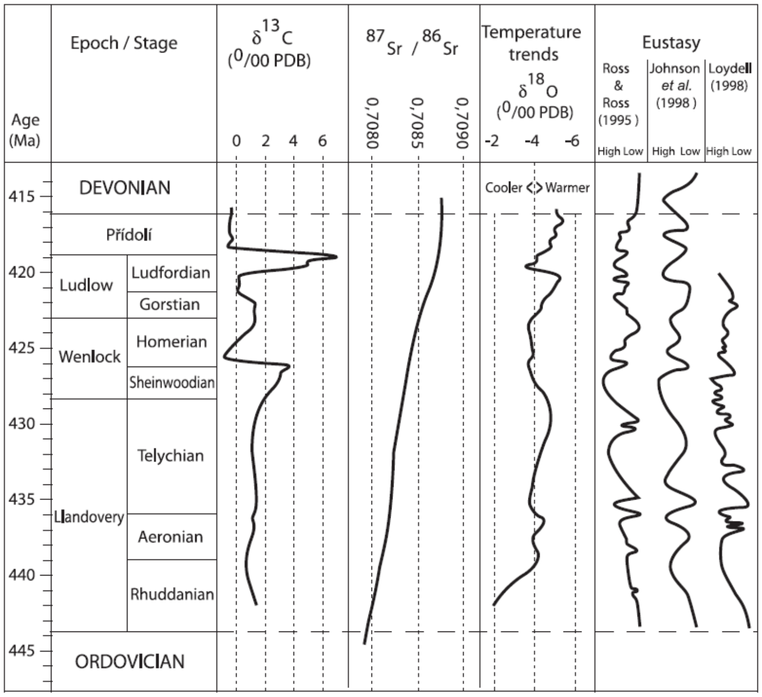

Fig. 6.2. Silurian sea-level curves and strontium, carbon and oxygen isotope curves (after Melchin *et al.* 2004).

the basal Ludfordian (*Saetograptus leintwardinensis* Zone) and a high sea level at the top of the Ludfordian. For the Přídolí there is no clear eustatic signature (Fig. 6.2).

Global and regional events

As Calner & Eriksson (2006) put it: 'the view of the Silurian as a time of stable greenhouse conditions has been successively challenged during the last decade. The increased use of carbon and oxygen stable isotopes in stratigraphy has resulted in one of the most important advances in Silurian research for decades'. According to them, the geochemical data repeatedly showed that the Silurian was characterized by recurrent anomalies in the global carbon cycle (GCC). The size of these anomalies is comparable or larger than those associated with Phanerozoic mass extinctions. Studies integrating these data with graptolite, conodont and chitinozoan biostratigraphy indicated that the Silurian GCC anomalies are coupled with moderate to substantial diversity changes and/or extinctions among the contemporary marine faunas. The GCC anomalies are also closely related to sea-level changes that in many cases appear to be global. Much work still needs to be done before the total rate of extinction and origination associated with the GCC anomalies can be estimated.

Silurian isotope curves have been produced for carbon, oxygen and strontium (Melchin *et al.* 2004). The $\delta^{18}O$ curves published by Samtleben *et al.* (1996), Wenzel & Joachimski (1996), Bickert *et al*. (1997), Azmy *et al*. (1998) and Heath *et al*. (1998) show similar trends with a reduction in values of all three isotopes, possibly indicative of an overall global warming. Detailed $\delta^{13}C$ curves for the Llandovery were published by Melchin & Holmden (2006). Smaller-scale events visible in the $\delta^{13}C$ and δ ^{18}O curves in the Llandovery and early Wenlock in Estonia were thought to coincide with glacial events as described by Caputo (1998) in South America (Kaljo *et al*. 2003). However the youngest glaciation in South America was shown to be poorly dated and was proven not to be early Wenlock but Llandovery in age (Caputo 2003). Several events in the late Wenlock and Ludlow correspond in two of the three curves of Figure 6.2 with eustatic sea-level drops. Apparent asynchroneities between the three curves may be the result of correlative inaccuracies rather than real offsets in the timing of the events (Melchin *et al.* 2004). The carbon isotope curves show the same general trend as the oxygen isotope curves. Smaller-scale positive excursions coincide with eustatic lowstands (Melchin *et al.* 2004). Strontium isotope curves by Ruppel *et al*. (1998) and Azmy *et al*. (1999) indicate that the $^{87}Sr/^{86}Sr$ ratio increased steadily upwards through the Silurian, and this trend has been attributed to higher input of radiogenic Sr by rivers induced by climatic warming (Melchin *et al.* 2004).

The Silurian Period does not witness major extinction events, such as the latest Ordovician extinction event linked to the Hirnantian glaciation, nor is there any evidence of other important events such as major sea-level drops, meteorite impacts, extensive plateau basalt effusions, or falls in primary production. However there are still some 15 medium-order bioevents recorded during the Silurian (Fig. 6.3), of which two are particularly important: the severe extinction event of conodonts at the base of the Wenlock (Ireviken Event; Jeppsson 1987), where a turnover in the acritarch flora is observed with more originations than extinctions (Gelsthorpe 2004), and a major crisis amongst the graptolites, called the Great Crisis or the *lundgreni* Event (Jaeger 1991; Koren' 1987; Porębska *et al.* 2004). Three further events are observed: an early Ludfordian event has been recognized affecting the graptolites, ostracoderms, acritarchs and conodonts; a mid-Ludfordian event, the Lau event (Jeppsson 1987) with profound changes in the vertebrates, graptolites, corals and conodonts; and a mid-Přídolí event with extinction amongst corals, conodonts, graptolites and a diversity rise in the chitinozoans (Kaljo *et al*. 1991) (Fig. 6.3). Štorch (1995) discussed eight larger and smaller extinction events in graptolite evolution for the Silurian (Fig. 6.3), based mainly on research in Bohemia, but incorporating information from other regions. He gave an accurate estimation of the graptolite diversity changes in central Europe during the Silurian. The changes in diversity were compared with worldwide sea-level changes, showing that the adaptive radiations of Silurian graptolites occurred during sea-level rises when anoxic environments with black shale deposits were brought onto the shelves.

According to Melchin *et al*. (2004) some of the extinction events in the Llandovery and Wenlock correlate well with the $\delta^{18}O$ and $\delta^{13}C$ positive excursions linked with sea-level lowstands, some of which may be related to glacial episodes described by Caputo (1998, 2003) in South America (see above). The models proposed by Jeppsson (1990, 1998), modified and restricted to low latitudes by Bickert *et al.* (1997), attempted to relate all bioevents, especially those affecting conodonts, to changes in climate, oceanic circulation and terrestrial input. In these models humid episodes with high bioproductivity and mainly estuarine circulation on the shelf, alternated with more arid episodes with low bioproductivity and mainly anti-estuarine circulation on the shelf (see Calner *et al*. 2004; Johnson, 2006). However, the model ought to take into account more lithological, geochemical and palaeontological parameters in order to be more useful for the delimitation of the climatic–oceanic episodes (Kaljo *et al.* 2003)

Central European Silurian stratigraphy

The term Silurian was introduced by Murchison in 1837, named after the Celtic people living in Wales whom the Romans called the *Silures.* The history of subdivision of the Silurian System has been summarized in Holland (1989). Recent advances in the chronostratigraphy and biostratigraphy of the Silurian are summarized in Melchin *et al.* (2004). The Silurian is mainly dated using biozonations based on three fossil groups: graptolites used to define the bases of the series, stages and substages, conodonts used in shallow-marine carbonate facies, and the chitinozoans used in both shallow-marine and basinal facies. Three other fossil groups are also used for biozonation: the sporomorph groups, acritarchs and spores, and the vertebrates (Fig. 6.3).

As mentioned above, the Silurian System is divided into four series. The Llandovery Series is divided into three stages, from bottom to top: Rhuddanian, Aeronian and Telychian. The GSSPs of the bases of the latter two stages are situated in southern Wales near the town of Llandovery. The base of the Aeronian is located in the Trefawr forestry road section, 500 m north of Cwm-coed-Aeron Farm, just below the lowest occurrence level of the graptolite *Monograptus austerus sequens* representing the *Demirastrites triangularis* Zone (Cocks 1989). The GSSP of the base of the Telychian is situated in a small abandoned quarry on the west side of the Cefn Cerig road, approximating as closely as possible to the base of the *Spirograptus turriculatus* Zone (Cocks 1989). Diagnostic graptolites are not abundant in the GSSP area and the stratotype for the base of the Telychian is taken at a point just above the highest record of the brachiopod *Eocoelia intermedia* and below the earliest record of the succeeding species *Eocoelia curtisi* (Bassett 1985; Cocks 1985, 1989). The base of the Telychian is now usually shown at the base of the

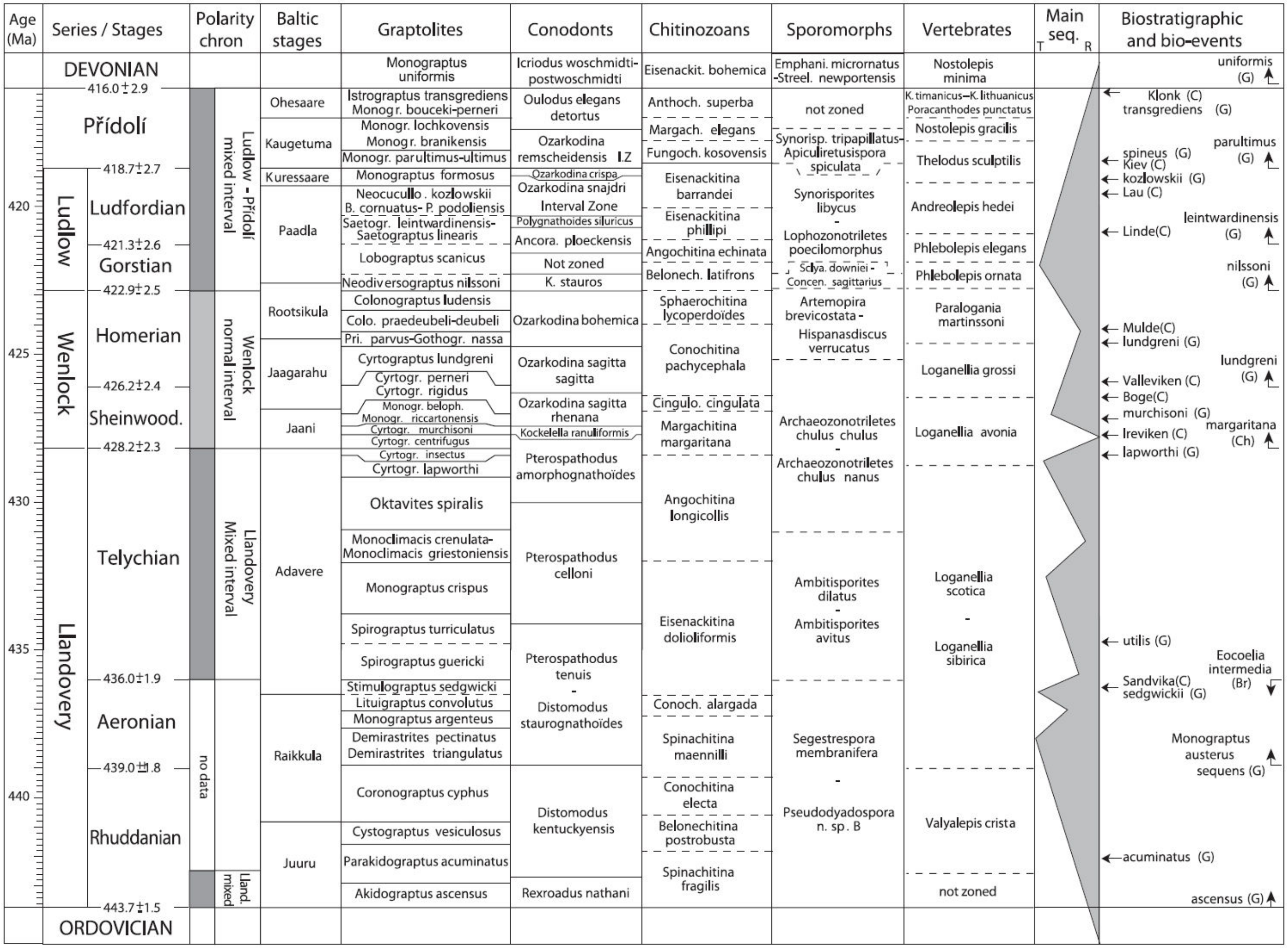

Fig. 6.3. Silurian biozonations and chronostratigraphy (graptolites, conodonts, chitinozoans, acritarchs, spores, vertebrates) (after Melchin *et al.* 2004). Right column: horizontal arrows indicate events with their names; (G): events in graptolites; (c) events in conodonts. Arrows pointing towards top: lowest occurrence datums of graptolite (G) and chitinozoan (Ch) species; arrows pointing down: highest occurrence datum of brachiopod species (Br).

Spirograptus guerichi Zone (see Koren' *et al*. 1995, 1996). This is based on the study by Loydell *et al*. (1993), who described *Spirograptus guerichi* as a new species, restricted to the lower part of the former *Spirograptus turriculatus* Zone and effectively subdividing the *Spirograptus turriculatus* Zone into a lower *Spirograptus guerichi* Zone and an upper *Spirograptus turriculatus* Zone. Following refined correlation studies, it remains unclear what the precise correlation is of the GSSP with the graptolite biozonation, but it appears to be within the upper part of the *Stimulograptus sedgwickii* Zone (Melchin *et al*. 2004).

The base of the Wenlock Series is defined in Shropshire (Welsh Borderland, UK) in Ape Dale, NW of the prominent ridge of Wenlock Edge. The section is a small outcrop along Hughley Brook, near Leasows Farm, close to the village of Hughley. The chosen level at the base of unit G in Bassett *et al*. (1975, p. 13 and fig. 5) contains no graptolites but was presumed to correlate with the base of the *Cyrtograptus centrifugus* Zone (Bassett 1985; Holland 1985; see history in Holland 1989 and details in Bassett 1989). Later studies in the GSSP on conodonts and chitinozoans indicated that the GSSP level might correspond with the base of the *Cyrtograptus insectus* Zone (Jeppsson 1997; Mullins 2000) or the base of the *Cyrtograptus murchisoni* Zone (Loydell *et al.* 2003; Mullins & Aldridge 2004). A working group of the International Subcommission of the Silurian Stratigraphy (ISSS) is currently addressing this problem. The Wenlock Series is divided into two stages: Sheinwoodian below and Homerian above. The base of the Homerian is situated in a stream section in Whitwell Coppice, north of Homer and Much Wenlock (Shropshire) at the first occurrence level of the graptolite *Cyrtograptus lundgreni* (Bassett 1985, 1989; Holland 1985).

The base of the Ludlow Series is also defined in Shropshire (Welsh Borderland, UK) close to the town of Ludlow, in a quarry at Pitch Coppice. White (1981) found few poorly preserved and not firmly determined graptolites in the GSSP and more graptolites 375 m and 30 km away. Lawson & White (1989) indicate that these records provide a strong indication that the lowest beds of the Ludlow series in the type area should be assigned to the *Neodiversograptus nilssoni* Zone. The base of the latter biozone is taken as the base of the Ludlow Series. The Ludlow Series is divided into two stages: the Gorstian below and the Ludfordian above. The base of the Ludfordian is situated in the Sunnyhill Quarry close to Ludlow at a horizon considered to correlate with the first occurrence of the graptolite *Saetograptus leintwardinensis* (Holland *et al*. 1980; Bassett 1985; Holland 1985; Lawson & White 1989).

The base of the Přídolí Series is defined in the Prague basin at the GSSP in the Požáry Quarries near Praha-Řeporyje (see below), where it coincides with the base of the *Monograptus parultimus* Zone within bed no. 96 of the Požáry Formation (Bassett 1985; Holland 1985; Kříž *et al*. 1986; Kříž 1989) (see below Fig. 6.19 below). The Přídolí Series is not subdivided into stages.

The base of the Devonian, the first GSSP of a system to be decided upon (in 1968), is also defined in the Prague basin (Chlupáč *et al*. 1972) at the first appearance level of the graptolite index species *Monograptus uniformis* in the Klonk section near Suchomasty (see Belka & Narkiewicz 2008).

Several absolute timescales have been proposed for the Silurian although few radiometric age determinations are available. Melchin *et al.* (2004) have evaluated all available data from radiometric age dating, the presumed evolutionary rates of graptolites and conodonts, and the observed stratigraphical thicknesses. After statistical analyses of the data they proposed the following radiometric ages for the bases of the series: Llandovery, 443.7 Ma; Wenlock, 428.2 Ma; Ludlow, 422.9 Ma; and Přídolí, 418.7 Ma. These are also the ages used in the international timescale of Gradstein *et al*. (2004).

Tectonic setting

The Silurian sediments in Central Europe were deposited on several palaeocontinents: (1) on the large Baltica palaeocontinent; (2) on the edge of the very large Gondwana palaeocontinent, a part often referred to as northern Gondwana; (3) on one of the many smaller palaeoplates that rifted off the Gondwana palaeocontinent during Palaeozoic times, such as Avalonia and Far Eastern Avalonia; and (4) the many other peri-Gondwana terranes. A distinction is made between plates and terranes. Plates were moving in previous times and could include a continent, i.e. an area of continental crust. When the plates lost their identity by subsequent plate tectonic movements they are referred to as palaeoplates. Terranes are usually smaller and are at present bordered by fault contacts. They represent the collided or docked parts of previously moving (micro)plates.

Silurian palaeocontinents

The following palaeocontinents or terranes are recognized to have existed in the Silurian within the present-day study area. In most cases they have become amalgamated and have moved considerably in relation to their Silurian position. Several of them were later emplaced in different tectonic regimes of the Variscan and Alpine orogenies and represent various structural levels in foldbelts and nappe-stacks (Fig. 6.4):

Baltica. Although the area is large, it represents only a smaller part of the huge palaeocontinent Baltica. In the north and east of the study area much Silurian is present in the subsurface, but outcrops are only present in SE Bornholm and in both the Łysogory and the northern margin of Małopolska parts (Kielce region) of the Holy Cross Mountains. There is agreement that the two terranes Łysogory and Małopolska were attached to Baltica in the Silurian.

Avalonia. Silurian strata from this palaeomicrocontinent are present in outcrops and the subsurface of the Anglo-Brabant Deformation Belt, in the Condroz Inlier (a thrust wedge in the Variscan front), in the northern Rhenish Massif (= Rheinisches Schiefergebirge) and in the Northern Phyllite Zone; they belong to the eastern part of Avalonia. Parts of Avalonia, now attached to North America from Newfoundland to Long Island, are called western Avalonia, while other parts of Avalonia now found in southern Ireland, southern Britain, and NW Europe, are called eastern Avalonia. Cocks *et al*. (1997) demonstrated with faunal similarities that in the Ordovician and Silurian, both parts formed only one palaeocontinent, Avalonia, which was split into two by the Mesozoic opening of the Atlantic Ocean.

Far Eastern Avalonia. This is a completely subsurface terrane, introduced by Verniers *et al*. (2002), where no Silurian sediments were proven until now (Silurian sediments from boreholes in the Koszalin-Chojnice Zone in NW Poland were estimated to belong to Far Eastern Avalonia, but are now thought to have been deposited on the edge of Baltica). The terrane has a boundary in the north and NE with Baltica along the Thor Suture, a remnant of the Tornquist Sea, and along the Heligoland-Pomeranian Deformation Belt, the orogenic belt resulting from the collision

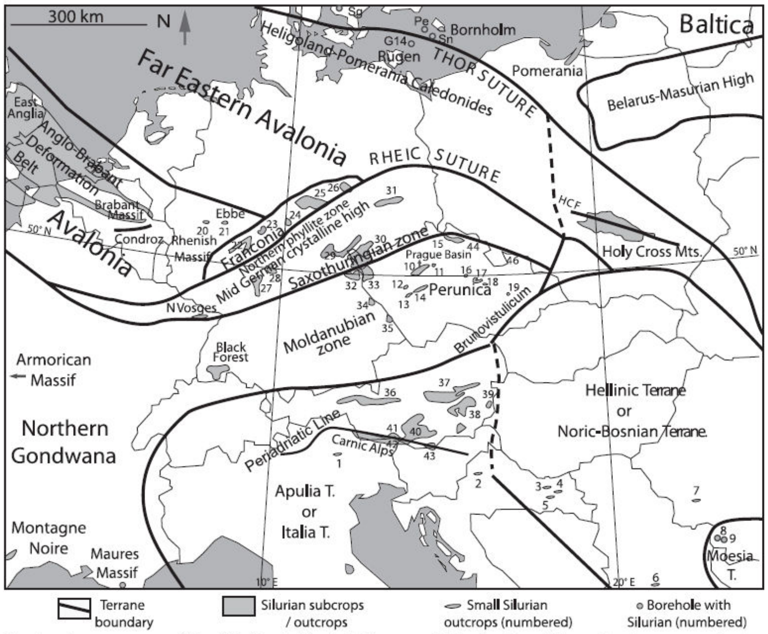

Fig. 6.4. Outcrop areas and subsurface presence of the Silurian in Central Europe, with indication of the palaeoterranes and sutures from the Silurian period and the names of post-Silurian tectonic units and faults. HCF, Holy Cross Mountains Fault; P.L., Periadriatic Line. Locations: 1, Agordo; 2, Medvednica Mountains; 3, Psunj Mountains; 4, Papuk Mountains; 5, Krndija Mountains; 6, Kacanik-Veles/Raska; 7, Suprabetic Nappes; 8, Girla Mare borehole; 9, Oprisor borehole; 10, Prague Basin; 11, NE Prague; 12, Rožmital; 13, Mirovice; 14, "Islet" zone; 15, Lužice Region and Ještěd mountains; 16, Vápenný Podol; 17, Hlinsko; 18, Polička; 19, Stínava; 20, Remscheid inlier; 21, Ebbe inlier; 22, Dill & Lahn Synclines; 23, Kellerwald; 24, Werra; 25, Upper and Lower Harz Mountains; 26, Flechtingen Horst; 27, Odenwald; 28, Spessart; 29, Thüringer Wald; 30, Erzgebirge; 31, Lausitz; 32, Oberfranken; 33, Vogtland; 34, Ober-Pfalz; 35, Bavarian Forest; 36, western Grauwacke Zone; 37, eastern Grauwacke Zone; 38, Graz; 39, South Burgenland; 40, Gurktal Nappes; 41, Nötsch; 42, Carnic Alps; 43, Karawanken Mountains; 44, Kaczawa Mountains; 45, Bardo Mountains; Sg., Slagerse-1 borehole; G14 borehole; Pe: Pernille-1 borehole; Sn: Stina-1 borehole.

of Baltica and Far Eastern Avalonia. In the NW it has a boundary with Laurentia along the Iapetus Suture, the remnant of the Iapetus Ocean, and along the Scottish-Scandinavian Caledonian Orogenic Belt. In the SE it has a boundary with peri-Gondwana terranes along the Rheic Suture, and in the SW with Avalonia along a fault zone north of the Anglo-Brabant Deformation Belt. The Ordovician fauna and microflora in the Rügen boreholes have an Avalonian affinity (Servais & Katzung 1993; Servais 1994; Katzung, 2001) and therefore it was previously included in Avalonia. Due to the presence of a subduction-related calc-alkaline magmatic arc running from East Anglia to the southern Brabant Massif, an oceanic crust had to be postulated NE of the Anglo-Brabant Deformation Belt and hence to the NE of it the presence of another Peri-Gondwana Terrane: Far Eastern Avalonia. This microcontinent is supposed to have moved away from Gondwana close to Avalonia (Verniers *et al.* 2002).

Peri-Gondwana and northern Gondwana

Northern Gondwana was part of the large Gondwana palaeocontinent. The peri-Gondwana terranes are a number of units of various size located along the southern margin of the Rheic Ocean and north of northern Gondwana. Some of these separated in a northward drift possibly as early as the Early Ordovician, but others separated during the Devonian (Paris & Robardet 1990). These units are present in many outcrop or subcrop areas in the southern part of Central Europe. They are sometimes referred to as Northern Gondwana Terranes. They are now incorporated in tectonic units of a later deformation age as the Variscan Moldanubian or Saxothuringian zones, or as the Alpine Hellenic or Apulia Terranes.

Peri-Gondwana terranes

An extensive overview of the complex terrane history of the terranes 4 to 7 in the Variscides is given by Franke (2000), McKerrow *et al*. (2000) and Tait *et al.* (2000).

Franconia. This hypothetical suspect terrane (Franke 2000), is present in two structures: (a) the upper plate of the Mid-German Crystalline High and (b) the Giessen-Werra-Harz Nappes, cropping out in the Dill Syncline near Marburg/Giessen, in Kellerwald, in the Upper Harz and in the Lower Harz. The root of this nappe is located between the Northern Phyllite Zone and the Mid-German Crystalline High; this plate might be linked or positioned very close to the following plate.

Saxothuringia (Saxo-Thuringia in Franke 2000). This is present in the Saxothuringian zone of Kossmat (1927). A well-studied outcrop area with Silurian rocks occurs in the Thuringia Forest (= Thüringer Wald), Oberfranken and Vogtland (Germany) (Heuse *et al*. 2006) and the northern part of the Vosges.

Perunica. This terrane contains the classic Prague Basin in the southeastern Barrandian Region of the Bohemian Massif. It is situated in the middle of the highly metamorphosed and deformed Moldanubian zone of the Variscan Belt. However, it escaped most of this deformation and displays one of the most complete Silurian outcrop areas in the world. Comparable to other areas of peri-Gondwana or northern Gondwana, it drifted from high southern to low northern latitudes during the Palaeozoic. Havlíček *et al.* (1994) argued the existence of this independent palaeoplate on the basis of brachiopod and trilobite assemblages. This was challenged by others (Servais & Lehnert 2006) who claimed that Perunica was only a part of northern Gondwana.

Moldanubia. This is a terrane where the Silurian crops out in the Bavarian Forest, the Oberpfalz Forest and in the southern Black Forest.

Brunovistulicum. This is a terrane which was strongly deformed during the Variscan Orogeny and consequently is of disputed origin, but because of its Neoproterozoic basement is considered as a part of peri-Gondwana.

Eastern Alps. Silurian sediments are present in **four tectonic units in the eastern Alps** (Austria and northern Italy). Three are situated north of an important Alpine structural divide, the Periadriatic Line, and one south of it: the Carnic Alps with the well-known Silurian outcrop area. They are situated in the present-day northern part of the Italia Terrane, also called the Apulia Terrane (Stampfli *et al.* 1998; Cocks & Torsvik 2002). The Silurian deposits with graptolites in the Medvednica Mountain, north of Zagreb, Croatia (Sremac & Mihajlović-Pavlović 1983) could also belong to this terrane.

Noric-Bosnian Terrane. (Raumer & Neubauer 1993). Also called the Hellenic Terrane (Stampfli *et al.* 1998; Cocks and Torsvik 2002), the Noric-Bosnian Terrane yields Silurian rocks in SE Serbia, in the Suva Planina Mountain, west of Kosovska–Mitrovica (Kříž & Veselinovič 1975) and in the South Carpathians (Iordan & Stanoiu 1993). The possible presence of Silurian rocks is mentioned in the Psunj, Papuk and Krndija mountains of northern Croatia (Jerenic *et al.* 1994) and also in SE Serbia, in Raška and East of Kosovska–Mitrovica (Kostić-Podgorska 1956).

Northern Gondwana terranes

Montagne Noire. This region contains Silurian sediments in tectonic thrust wedges and klippes on the southern edge of the Massif Central. They belong to the large northern Gondwana terrane, together with areas outside the study area in SW Europe such as the South Armorican Domain, Aquitaine and the Pyrenees.

Maures Massif. The Maures Massif (southern France) in the SW of the study area (Fig. 6.4) has one metamorphic Silurian formation containing rare fossiliferous lenses. The massif is not thought to belong to a separate palaeoplate. However, the fauna discovered is too limited and the facies too metamorphosed to link the Maures Massif either to the previous area or to the basement of the western Alps.

Peri-Gondwana or northern Gondwana terranes

Moesia Terrane. This terrane, located south of the Carpathians, with Silurian in the subsurface, was also a part of northern Gondwana or a derived peri-Gondwana palaeoplate. It is linked by several authors to the Bruno-Moravo-Silesia Terrane, north of the Carpathians. In the study area, Silurian rocks were demonstrated in two boreholes, Oprisor and Girla Mare (Iordan *et al.* 1985; Iordan 1984, 1999*a*, *b*; Yanev 2000; Vaida *et al.* 2005; Vaida & Verniers 2006).

Palaeomagnetism

The few palaeomagnetic studies over the last 15 years in Silurian strata of the study area have proposed a generally consistent position for Laurentia, Baltica and Avalonia. Laurentia, with its numerous warm-water carbonates and evaporites, was positioned around the equator and in the two subtropical belts through most of the Cambrian until the Devonian (MacNiocaill & Smethurst 1994; Torsvik *et al.* 1996). Baltica was situated in the southern subtropical belt, with Gotland at about 20°S in the Wenlock (Claesson 1979; Trench & Torsvik 1991). The Iapetus Ocean lay between Laurentia on one side and Baltica, Far Eastern Avalonia and Avalonia on the other side. The ocean closed in the early Wenlock in Ireland and in the early to mid-Wenlock in northern England (Hutton & Murphy 1987; Arthurton *et al.* 1988; Soper & Woodcock 1990; Kneller 1991; Kneller *et al.* 1993). In the early Wenlock, the latitude of the Welsh part of Avalonia (just west of Fig. 6.4) was estimated at about 13°S (Trench & Torsvik 1991).

The main divergences in published models relate to the very large palaeocontinent of Gondwana and especially northern Gondwana and the peri-Gondwana terranes. Two contrasting apparent polar wander paths for the Palaeozoic have been proposed for Gondwana: path X (Bachtadse & Briden 1991) and path Y (Schmidt & Embleton 1990) (see Van der Voo 1993; Tait *et al.* 1997). One model (Scotese & Barret 1990), also supported by lithofacies data, shows the South Pole in the latest Ordovician in West Africa moving to southern Brazil in the earliest Devonian. This implies that during the Silurian there was a northward shift of the areas of northern Gondwana and the peri-Gondwana palaeoplates from higher to lower latitudes, from cool to temperate waters.

Terranes 4 to 9 and 11 have been grouped by early palaeomagnetic studies as ‘Armorica’ (Van der Voo 1979, 1982) or later in the ‘Armorican Terrane Assemblage’ (Tait *et al.* 1997). Recent authors such as Fortey & Cocks (2003), restrict Armorica to the Armorican Massif, Montagne Noire and the Iberian Peninsula. Others (e.g. Robardet 2001, 2003; Linnemann *et al.* 2004) have considered this grouping as oversimplified and as neglecting the geological evidence from Iberia and France and reject the term altogether. These authors argue that several of these areas, mostly the western areas from Portugal up to Saxothuringia, remained attached to mainland northern Gondwana until at least the Devonian while other parts, such as Perunica, might have separated much earlier.

Data for the supposed position of Perunica (Bohemian Massif) have been summarized by Krs *et al.* (1986, 1987). Early Mid-Cambrian greywackes from the Příbram–Jince Basin, a few tens of kilometres west of the Prague Basin, show a palaeolatitude of about 39°S, and Late Cambrian andesites from this basin have a palaeolatitude of about 29°S. Early Ordovician chert and tuffaceous rock in the Prague Basin record a palaeolatitude of 28°S, and Lower Devonian micritic limestones in this basin show a latitude of 5–9°S. The independent development of Perunica is suggested because of its probable rotation, as shown by changes in palaeomagnetic directions from about 65° in the Mid Cambrian through 90° in the Late Cambrian, to 127–132° in the Early Ordovician (Krs *et al.* 1986). These data support the older data of Burrett (1983), who interpreted the apparent polar wander path and suggested that the Bohemian Massif moved independent from 'Armorica' during the Early Palaeozoic. Palaeomagnetic data from the Grauwacke Zone in the Upper Australo-Alpine Nappe Complex gave a palaeolatitude of 45–50°S for the late Silurian. The Proto-Alps in the Silurian, according to this study, were not part of northern Gondwana but a separate (peri-Gondwana) terrane (Schätz *et al*. 2002).

Palaeogeographic setting

The complex palaeoplate configuration of the study area reflects the involvement of very different tectonic settings during the Silurian. On larger stable palaeocontinents such as the interior parts of Baltica and northern Gondwana, the subsidence rates were rather low, with little or no tectonic deformation. At the edges of the large palaeocontinents passive margins developed with higher subsidence rates. On the active margins of the palaeocontinents high subsidence occurred with turbiditic sedimentation and tectonic deformation as in the Scandinavian Caledonides, the Heligoland-Pomerania Caledonides and the Anglo-Brabant Deformation Belt.

In SW **Baltica**, the stable platform on the East European Craton behaved mainly as a passive margin. Subsidence analysis of the Silurian strata indicates high subsidence in the Baltic Sea area, increasing in space towards its border with the Tornquist Sea (Oslo Graben, northern Poland and Lithuania) and increasing in time towards the upper Silurian (Poprawa *et al*. 1999; Lazauskienė *et al*. 2002). This can be explained by a combination of tectonic stresses induced by the mid-Silurian onset of the Laurentia–Baltica collision and later nappe formation and stacking in the Scandinavian Caledonides (i.e. the Scandian Orogeny) on one side, and the closure of the Tornquist Sea and soft docking and collision of Far Eastern Avalonia with Baltica, on the other. This closure commenced in the Ashgill and continued throughout the Silurian with the formation of the Heligoland-Pomerania-Deformation Belt (Winchester & the PACE TMR Network Team 2002; Winchester *et al*. 2002), formerly called the North German–Polish Caledonides, or the Pomeranian Caledonides (Dadlez 2000). It is sometimes differentiated from west to east into the Schleswig Caledonides, the Rügen Caledonides and the Pomeranian Caledonides (Katzung 2001). The Baltic Basin is thus interpreted as a flexural foreland basin formed during the oblique collision of Baltica and Far Eastern Avalonia (Poprawa *et al*. 1999) to which an additional tectonic load at the SW margin is required for the model to explain fully the shape of the Baltic Basin (Lazauskienė *et al*. 2002). There was no tectonic deformation after the Silurian or Lochkovian and hence the sediments are mostly subhorizontally stratified, and they underwent only very low heating by sediment load and burial metamorphism.

The docking of Far Eastern Avalonia and Baltica in the late Ordovician to Silurian is connected with the development of a foreland basin at the southern rim of Baltica. The sedimentation shows a distinct shift in the area of maximum deposition northwards over time. In the mid-Llandovery (*Spirograptus guerichi* Zone) more than 200 m of clastic, deep-water sediments were deposited in the southern Baltic Sea (G-14 borehole, Adlergrund, north of Rügen Island; Maletz 1997), after which the depocentre shifted northwards to the island of Bornholm and southern Sweden (Skåne/Scania), forming the *Colonus* Shale Basin in the Wenlock and Ludlow (Lindström 1960). The depocentre was migrating away from the approaching Caledonian Deformation Front (Vejbaek *et al*. 1994; McCann 1996; Katzung 2001). The final stage in the development of this basin can be recognized in the shallow-marine to terrestrial sediments of the Öved-Ramsasa Group in the Ludlow–Přídolí of Skåne/Scania in southern Sweden (Beier *et al*. 2000).

Avalonia and Far Eastern Avalonia detached from Gondwana in the Early to early Mid-Ordovician (for an overview see Prigmore *et al*. 1997). Prior to rifting, it was located in an area extending from what is now the northern coast of South America to somewhere between the northern coast of South America and Senegal in west Africa, where the terranes of Florida and Carolina were situated. This is based not only on the similarities of Proterozoic zircon ages but also on faunal evidence. The fauna from the British part of Avalonia is more similar to that of South America than to the fauna of north and west Africa (Villas *et al*. 2006).

The Rheic Ocean formed when northern Gondwana and Avalonia separated. Avalonia and Far Eastern Avalonia moved during the Mid- and Late Ordovician with a high drift rate towards Baltica, while the ocean in between, the Tornquist Sea, was being subducted. Far Eastern Avalonia collided with Baltica by early or mid-Ashgill times. This can be proven by the presence on the southern edge of Baltica of early or mid-Ashgill age sediments which contain reworked Lower Ordovician microfossils with a typical high latitude signature, the same as in Lower Ordovician sediments from high latitude parts of Gondwana. This can only be explained by accepting that by early or mid-Ashgill times both continents were in contact, with no ocean in between and that high latitude Lower Ordovician sediments were eroded and transported over the Tornquist Suture onto low latitude Baltica (Vecoli & Samuelsson 2001*a*, *b*). Following the onset of collision, the eastern part of Avalonia is postulated to have rotated 55° anticlockwise from the late Caradoc/Ashgill until the Mid-Devonian (Piper 1997). This resulted in short-lived subduction magmatism from Caradoc to Llandovery times and a slow long-lived deformation from the late Llandovery to early Eifelian in the Anglo-Brabant Deformation Belt (Debacker 2001; Verniers *et al*. 2002).

In the study area, Avalonia exhibits two different depositional settings in the Silurian: (1) a deep shelf with a mainly graptolitic shale facies in a sucession several hundred metres thick is present in the prolongation of the Midlands microcraton south of East Anglia, into the southern Brabant Massif and in the Condroz Inlier; and (2) a deeper environment in a postulated foreland basin setting, with at least 3 (possibly 7) km thick pile of Silurian turbidites deposited in the central and northern part of the Brabant Massif (Van Grootel *et al*. 1997; Verniers *et al*. 2002). Beneath the southern bight of the North Sea and under East Anglia, a Silurian succession several kilometres thick is suggested from geophysical modelling; it lies in the prolongation of the central and northern parts of the Brabant Massif (Lee *et al*. 1993). Deformation, under greenschist metamorphic conditions, transformed these regions into a slate belt, the Anglo-Brabant Deformation Belt. This belt occurs on the eastern end of Avalonia and close to the southern edge of Far Eastern Avalonia (Verniers *et al*. 2002).

To the south, are some areas that have been interpreted as belonging to Avalonia. In the intensely deformed Variscides of Central Europe several Silurian sedimentary or volcanic successions are present, sometimes highly metamorphosed and deformed by the Variscan Orogeny. However, this has not precluded a reconstruction of their Silurian palaeogeography. According to the hypothesis proposed by Franke (2000), a volcanic island arc formed at the southern margin of Avalonia during the late Silurian and early Devonian, as a result of the subduction to the north of the Rheic Ocean beneath Avalonia. Remnants of this arc are found in the lower plate of the Mid-

German Crystalline High and in the Northern Phyllite Zone present in the southern Taunus. These areas, if they belong to Avalonia, would represent a third depositional setting in Silurian times.

Peri-Gondwana and northern Gondwana

Although present over a wide area, and possibly on different palaeoplates, the Silurian sediments of peri-Gondwana and northern Gondwana are all rather similar to each other. Local variations include extensional basins with synsedimentary faults and half-graben structures with varying degrees of subsidence, or a volcanic archipelago with various water depths. If deformation occurred, it can mainly be attributed to later Variscan or Alpine tectonism.

In general, according to Kříž *et al.* (2003), there are two types of sedimentary successions on Silurian northern and peri-Gondwana: proximal and distal. The proximal type of succession with largely coarse-grained siliciclastic terrigenous sediments is found to the south and so is located outside of our study area, and close to the emergent land mass in north Africa. The second type of succession is distal with a low terrigenous influx and rather thin successions, sometimes not thicker than 50 m for the entire Silurian. This suggests low subsidence rates on a distal, more outer-shelf environment on a extensive passive margin. They consist typically of either black shales or calcareous shales and limestones (Berry & Boucot 1967). Within this second distal type of succession, five main facies developed: a deep shelf ‘Thuringian facies’, a possibly deeper shelf ‘Bavarian facies’, a ‘Shelly fauna facies’ on a moderately to shallow shelf, a very shallow ‘Prague Basin facies’ around the emerging volcanic archipelagos, and an unnamed facies proximal to local land areas with a high siliciclastic input sometimes of turbiditic nature.

The ‘Thuringian facies’ is the most common facies and consists of thin sequences of dark shales and cherts in the lower part of the Silurian. The absence of current indicators points to a calm, relatively deep environment, under dysaerobic or anoxic conditions. In the upper part of the Silurian typically thick aerobic limestone beds occur (Ockerkalke in Germany) with interbedded thin quartzite beds, possibly of turbiditic origin. These were deposited in Saxothuringia, in the Prague Basin on Perunica and in the Carnic Alp, where locally it is called the Bischofalm facies.

The Bavarian facies is quite similar to the Thuringian facies but consists of grey-green shales with interbedded graptolitic shales and alum shales; in addition, no limestones developed in the upper part of the Silurian. It is sometimes interpreted as a deeper shelf facies, too deep for limestone development. Alternatively, it has been interpreted as a shallower shelf facies (Kurze & Tröger 1990). It occurs in narrow bands on Saxothuringia.

The Shelly fauna facies mostly consists of thick calcareous shales and limestone nodules and lenses with shelly fauna, often dominated by bivalves (*Cardiola*), and sometimes by other shelly fossils as in the cephalopod limestones. It is supposed to have been deposited on an intermediate shelf, below wave base but within the reach of surface currents ventilating the seafloor. It occurs in Saxothuringia, the Prague Basin on Perunica, the Carnic Alps where it is subdivided in a shallower Wolayer Facies and a deeper Plöcken Facies, and also in the Montagne Noire. In the Carnic Alps there is a facies intermediate between this and the Thuringian facies called the Findenig facies.

The Prague Basin facies consists of thick basic volcanics and bioclastic carbonates, rich in brachiopods, bivalves, cephalopods, crinoids, corals and trilobites (Kříž 1991, 1998*b*). They were deposited in very shallow water on the gentle slopes of the Wenlock–Ludlow volcanic archipelago in the Prague Basin. The environment around the emerging volcanoes offered a unique environment favourable for the establishment of distal benthic communities (Kříž *et al*. 2003). The facies also developed in the volcanic centre of Graz in the Rannach Nappe and possibly in the Gurktal Nappe.

A fifth facies developed proximal to land areas and records a high input of siliciclastic material, sometimes turbiditic. It is situated in some outcrop areas of Austria north of the Periadriatic Line, such as the Glemmtal unit in the western Grauwacke Zone.

In addition to sedimentological similarities, close faunal relationships exist between all of the northern and peri-Gondwana areas in and outside the study area such as Morocco, Spain, the Pyrenees, Montagne Noire, the South Armorican domain, Sardinia and the Carnic Alps (Kříž & Serpagli 1993; Robardet *et al*. 1994; Kříž 1996, 1999*b*; Kříž *et al*. 2003; Robardet 2003). These relationships suggest that all of these areas were located in Silurian times on the margin of northern Gondwana. The latter regions, however, differ slightly in their Silurian sedimentological and faunal characteristics from those of the Algerian Sahara, southern Morocco, central Iberia and, more surprisingly, from those of the northern and central Armorican Domain. This suggests that the Montagne Noire and related areas were located northwards of the northern and central Armorican Domain during the Silurian (Robardet *et al*. 1994; Paris 2000). According to Robardet (2003) faunal and lithofacies evidence indicate that these microplates were attached to mainland northern Gondwana at least until the Devonian.

Franconia and Saxothuringia

The palaeoplates of Franconia and Saxothuringia were situated close to each other, and south of the Rheic Ocean, which was decreasing in width during the Silurian. The sediments in the Giessen-Werra-Harz Nappes are supposed to have originated between Franconia and Saxothuringia. They contain a tectonic melange of Silurian shales and limestones. Diamictites, recognized in the uppermost Ordovician strata, are used as an argument to locate Franconia as a peri-Gondwana terrane in high latitudes and hence close to northern Gondwana.

On Saxothuringia, Silurian shelf and slope sediments were deposited that now crop out in the Thuringia Forest (= Thüringer Wald). From the same location the uppermost Ordovician diamictites in the *Lederschiefer* unit have been used to attribute Saxothuringia to a peri-Gondwana terrane or to northern Gondwana. Not only does the fluxoturbiditic glaciomarine nature of the diamictites point to a high latitude, also the fossils in the clasts in the diamictites are not originally from the Thuringia Forest but are very similar to the northern Gondwana areas such as on the Armorican Massif, the Iberian Peninsula and north Africa. One of the latter areas is supposed to be the source area of the diamictites (Schallreuter & Hinz-Schallreuter 1998).

Between Saxothuringia and Perunica a short-lived Saxothuringian ocean is postulated that later subducted to the south below Bohemia (see Franke 2000). Evidence from zircons from Saxothuringia would indicate that this microcontinent remained attached to mainland northern Gondwana until Variscan times (Linnemann *et al*. 2004).

Another series of outcrops is probably related to a peri-Gondwana terrane, but without clear evidence. They comprise low-, medium- or high-grade metamorphic rocks of which radiometric ages and, in some cases, convincing fossil evidence indicate Silurian protoliths. They include part of the northern

Vosges (France), where the Steige Slate represents the less metamorphic Palaeozoic unit (Piqué *et al*. 1994). In this slate, Doubinger (1963) and Doubinger & von Eller (1963) discovered remains of microfossils they referred to as Silurian chitinozoans. The identifications of these possible microfossils were, however, subsequently questioned, due to their poor preservation (F. Paris in Kříž *et al*. 2003). As demonstrated in a similar context in the Black Forest in Germany (Montenari *et al. 2*000), scanning electron microscope investigations are required to ensure that these remains are chitinozoans before giving any firm age assignment to the Steige Slate.

Perunica

The Perunica Terrane (Havlíček *et al*. 1994), simlar to other peri-Gondwana terranes, drifted from a high southern latitude in the Cambrian to a low northern latitude in the latest Palaeozoic. It now lies within the Moldanubian Zone, a Variscan structural unit. The northerly position of the Perunica terrane in the late Silurian is reflected by the presence of carbonate platforms, characterized by very rich brachiopod-dominated communities and other benthic elements (e.g. corals, crinoids, trilobites and molluscs). The bivalve-dominated communities described from northern Gondwana in SW Europe by Kříž (1999*b*) are closely related to each other but are different from the communities in the Prague Basin on Perunica. These bivalve-dominated communities in Perunica show a generally higher diversity than those of northern Gondwana in SW Europe.

Early Silurian sedimentation on the Perunica Terrane was still influenced by the Late Ordovician glaciation. Seawater temperature was probably relatively low in the post-glacial period. In the early Silurian the sea was anoxic or strongly dysaerobic and black graptolitic shales were deposited in all of the basins of the Bohemian Massif. During the Telychian, the sea temperature slowly increased and intense water circulation commenced (Holland & Bassett 2002). In the Prague Basin, this is related to the deposition of calcareous shales. In the Wenlock, and especially during the Homerian, the limestone lithofacies in the Prague Basin is indicative of a further increase in temperature, reaching a maximum in the Přídolí (Kříž 1991). The development of this partly climatically influenced facies could correspond to a Silurian position for the Perunica Terrane of between 30° to 10°S palaeolatitude.

Moldanubia

Four areas, all in Germany, with medium- to high-grade metamorphism were shown to contain organic-walled microfossils such as acritarchs and chitinozoans, indicating in part a Silurian age. The Badenweiler-Lenzkirch Zone and the South Schwarzwald Granite and Gneiss Complex in the Black Forest belong to the Moldanubian Zone and provided an age for the protolith that was partly Silurian (Hann *et al.* 1995; Sawatski *et al.* 1997; Montenari *et al.* 2000; Vaida *et al.* 2000, 2004). The earlier two publications did not provide convincing photographs but the later two publications proved the presence of the organic-walled microfossils. In the Spessart and also in the northern Bavarian Forest, possible Silurian spores have been reported (Reitz 1987, 1992).

The Montagne Noire and northern Gondwana in SW Europe

Local Silurian palaeomagnetic data are absent or not convincing enough to provide any precise palaeogeographic location for the Montagne Noire during Silurian times. Sedimentological and faunal criteria are therefore used for the approximate palaeogeographic position of the area. The development of carbonates, especially in the Wenlock and Přídolí of the Montagne Noire, contrasts with their scarcity during the Ordovician on northern Gondwana. This indicates a northern drift of the area towards latitudes moderate enough to allow the deposition of these carbonates.

Lenses of crinoidal limestones and Silurian graptolite-bearing black shales have been reported (Gueirard *et al.* 1970) in a structurally complex and epizonal metamorphic context from the SW part of the Maures Massif, SE France (Crevola & Pupin 1994).

Peri-Gondwana in Brunovistulicum

The Silurian succession in the Moravo-Silesian region in the Drahany Highland, Stínava (see below and Fig. 6.4) most probably belongs to the Brunovistulicum microplate, which is considered to be a part of peri-Gondwana (Fig. 6.4). Remains of this microplate now form the southeastern Bohemian Massif (Suk 1979; Dudek 1980). For this reason, the Bohemian Massif is assumed to be a composite unit formed by elements from northern Gondwana, Perunica and other peri-Gondwana terranes. The presence of Baltica in Brunovistulicum was also suggested by Cambrian trilobites with a supposedly Baltican affinity (Havlíček *et al*. 1994), but the Neoproterozoic basement points to a Gondwana affinity. Perunica extends northwards to the Mid-European Rheic Suture that originated during the closure of the Rheic Ocean and now represents the boundary between the Saxothuringian and Rhenohercynian zones in the Variscan Orogen (Burrett & Griffiths 1977). The tectonic contact between Perunica and Brunovistulicum is associated with overthrusts and nappes with a pronounced eastern vergence, originally recognized by Suess (1912). Pre-Devonian sediments of unknown original extent and thickness were deposited in the basin between Perunica and Brunovistulicum, but were mostly destroyed during the collision of these blocks (Havlíček *et al*. 1994). South of Perunica, a Moldanubian Ocean has been postulated and on the ill-defined Moldanubia palaeoplate poorly dated and strongly metamorphic Silurian rocks have been recognized (Kříž *et al.* 2003).

Further south, the Proto-Alps Terrane, possibly belonging to the present-day Apulia Terrane, displays a northern Gondwana appearance. During the Silurian the Proto-Alps continued to shift from higher to lower latitudes. Based on the evidence presented below, it is estimated that the Austrian inliers were at a palaeolatitude of approximately 30–40ºS. During the Silurian, close faunal relations existed with northern Europe (H. P. Schönlaub in Kříž *et al*. 2003).

Peri-Gondwana in the Proto-Alps

Within the Proto-Alps Terrane, the Silurian of the Carnic Alps, one of the numerous Austrian Silurian inliers, has been studied in much detail. Silurian faunas, generally typified as cosmopolitan, give little information of the palaeolatitudinal position of the individual areas (Schönlaub 1992). However, conodonts suggest a close affinity with coeval faunas from central, southern and southwestern Europe but differ from the more equatorial position of Avalonia and southern Baltica in terms of their more diverse assemblages (Bergström 1990; Aldridge & Schönlaub 1989). Silurian trilobites from the Carnic Alps are closely related to those from Bohemia, as well as other central European regions and Morocco (Alberti 1969, 1970; Santel 2001). Acritarch distributions suggest an intermediate position for the Austrian inliers between the high latitude *N. carminae* and the tropical *Domasia-Deunffia* biofacies (Priewalder 1987). Chitinozoans show a close relationship with Bohemia especially in the upper Ludlow to lower Lochkovian (Paris & Kříž 1984; Kříž *et al*. 1986; Dufka 1992; Kříž 1992). Chitinozoans in the Ashgill show a clear high latitude (peri-Gondwana) affinity (Priewalder 1997). Beginning in the late Llandovery, nautiloids became the predominant organisms in the carbonate facies of the Austrian Alps. The orthoceratids, abundant in the Wenlock and Ludlow, decreased during the Přídolí (Ristedt 1968, 1969; Schönlaub & Histon 1999) and are again abundant in the latest Přídolí (Histon 2002). Their diverse faunas appear to be closely related to those of Bohemia as well as to those of the Montagne Noire and Sardinia (Kříž & Serpagli 1993; Kříž 1996, 1998*b*, 1999*a*). The distribution of other molluscs, in particular bivalves, generally resembles that of the nautiloids. According to Kříž (1979), the Silurian cardiolid bivalves from the Carnic Alps and the western Grauwacke Zone inhabited a warm equatorial belt or were dispersed by surface currents.

In general, the corals were prominent constituents of a probable shallow-marine environment in the tropical belt. During the early Silurian, only weak indications of provincialism are seen among tabulate and rugose corals at the generic level. However, long-lived and far-floating (teleplanic) larvae might also have been transported by ocean currents over long distances (Kaljo & Klaamann 1973; Pickett 1975; McLean 1985; Pedder & Oliver 1990).

Rugose and tabulate corals occur in the upper Llandovery of central Carinthia and in the Ludlow near Graz, but are very rare in the shallow-marine and locally coated-grain-bearing limestones in the upper Llandovery of the western Grauwacke Zone (Schönlaub 1994*b* and references therein).

Ninety-seven K-bentonite levels have been recorded from the Upper Ordovician (Ashgill) to Lower Devonian (Lochkovian) successions of the Carnic Alps (sections Cellon, Oberbuchach, Nölblinggraben and Zollnersee Hütte). They occur in shallow- to deep-marine fossiliferous sediments which suggest a constant movement from a moderately cold climate of approximately 50° S in the Upper Ordovician, to the tropical belt in the Devonian. The distribution of the volcanic ash levels is consistent with current palaeogeographical reconstructions for the position of the Carnic Alps during the late Ordovician to early Devonian interval (Histon *et al*. 2007).

Sedimentary rock precursors in different basement areas of the Alps, such as quartz phyllites and amphibolite-grade metamorphic rocks in Austria, may also be Silurian in age (H. P. Schönlaub in Kríž 2003). In the Palaeozoic basement of the French Alps, greenschist occurs in the Belledonne Massif. A Silurian age was suggested without, however, firm fossil evidence (Ménot *et al*. 1994; F. Paris in Kříž *et al*. 2003). Recently at Agordo, NE Italy, middle Llandovery graptolites were discovered in the South Alpine greenschist metamorphic basement (Dieni *et al*. 2005).

Peri-Gondwana in SE Europe

In Croatia, Sremac & Mihajlović-Pavlović (1983) described Silurian sediments and graptolites in a deep-water marine facies. In eastern Serbia, Ludlow, Přídolí and Lochkovian bivalves have been described from the Suva Planina Mountains (Kříž & Veselinovič 1975). Another richly fossiliferous Silurian outcrop area occurs in the Godeanu Mountains (Romania) in the Danubian nappes of the Southern Carpathians. All three areas probably belong to the Noric-Bosnian Terrane.

Moesia, partly represented in the SE corner of the study area, is known only from the subsurface. In the Walachian Plain (Romania), several boreholes passed through Silurian strata dated with fossils, belonging to the characteristic fauna of northern Gondwana or peri-Gondwana. They are located on the western Moesia palaeoplate with a postulated northern Gondwana affinity (Iordan 1999*a*, *b*; Yanev 2000; Vaida *et al*. 2004; Vaida *et al*. 2005; Vaida & Verniers 2006).

Outside the study area, in Bulgaria, the Noric-Bosnian Terrane (Hellenic Terrane) has a typical Gondwana fauna in the Ordovician (Gutierrez-Marco *et al*. 2003).

Laurussia

To be exhaustive on the Silurian it should be mentioned that by the end of the Silurian a new plate tectonic configuration emerged following the joining of Baltica Avalonia and Laurentia to form the huge Laurussia palaeocontinent. The mostly Devonian–Lower Carboniferous sedimentation in the Rhenohercynian Basin locally commenced in the latest Silurian on the consolidated early Caledonian basement of the southern passive margin of this palaeocontinent. This is the case in northern France in the subsurface of the Liévin (Racheboeuf 1986), in the southern part of the Ardennes (Belgium and northern France; Godefroid 1995; Godefroid & Cravatte 1999), south of the Stavelot Massif (Petites Tailles Fm; Geukens 1965, 1999; Verniers *et al*. 2001), in the Rhenish Massif (= Rheinisches Schiefergebirge) of Sauerland (Köbbinghausen Schichten; Deutsche Stratigraphische Kommission 2002) and in the Hunsrück-Taunus area (Graue Phyllite Formation; Deutsche Stratigraphische Kommission 2002).

Silurian basins of Central Europe

In Central Europe the Silurian is only rarely present in outcrops. Even in the subsurface it is not present over large areas (Fig. 6.4). Well-studied successions with their lithofacies, biofacies and special features are discussed below for each palaeocontinent clockwise and starting in the north.

Baltica

The Silurian is remarkably undeformed and well-preserved on both sides of the southern half of the Baltic Sea, on the SW part of Baltica. This palaeocontinent is formed by the Baltic Shield, a Precambrian crystalline craton, called the East European Craton (EEC). Areas of this craton covered with Palaeozoic strata are often referred to as the East European Platform (EEP). Well-studied areas with Silurian outcrops include Gotland and Skåne/Scania in southern Sweden, the Oslo Graben, most of Estonia (all areas outside the study area) and Bornholm (Denmark). An overview of the stratigraphy and palaeogeography of Baltica, including the parts outside the study area, is given by Baarli *et al*. (2003). In the subsurface of Latvia (outside the study area), Lithuania, the Kaliningrad enclave, northern Poland and northern Germany (Adlergrund, Vorpommern) many boreholes have facilitated an accurate reconstruction of the Silurian basin on a passive margin and on what used to be called the (East) Baltic Syneclise or recently more simply the Baltic Basin. Silurian deposits in the Polish sector of the EEP are limited to the SW by the Trans-

European Suture Zone. In the SE, and on the margin of the Baltica palaeocontinent one can observe the Silurian outcrops of the Holy Cross Mountains (Poland), with well-studied and fossiliferous sections.

The Baltic Basin

A shelf-sea covered the southern Baltic Sea area. The seafloor sloped to the SW, towards the WNW–ESE edge of the Baltica continent forming a series of depth-related belts, each with a different facies. Jaanusson (1976) and Nielssen (1995) recognized three different facies belts, broadly orientated parallel to the Silurian coastline, and called confacies belts. Closest to the inferred palaeocoastline is the shallowest Lithuanian Confacies Belt, at an intermediate depth is the Central Baltoscandian Confacies Belt and in the deepest part of the shelf the (Oslo-) Scandian Confacies Belt (Fig. 6.5).

The shelf had a NE–SW directed axial part, the Latvian saddle or the Livonian tongue which formed the deepest part of the sea and was the area of maximum subsidence (Fig. 6.6). Gentle deformation, after the Silurian, altered the original depositional pattern, when parts were uplifted as the Baltic Shield, the smaller Łeba High, the important Belarus–Masurian High (in the literature its Polish part is referred to as the Belarus–Suwałki Uplift, or Anteclise; Paskevicius 1997) and the Sławatycze Horst. On these uplifted areas the Silurian was partly or completely eroded. Coeval subsidence in the Baltic Basin, the Podlasie Basin and the Bug Basin, resulted in the preservation of the Silurian strata. As a result the Silurian can now be observed in a series of tectonic structures from NW to SE: (1) the SE-dipping slope of the Baltic Shield; (2) (the axial part of) the Baltic Basin; and (3) the NW-dipping slope of the Belarus–Masurian High, the Podlasie Basin and the Bug Basin (Fig. 6.7).

The axial part of the Baltic Basin contains the thickest Silurian succession and stratigraphically the most complete geological section in Baltica, from the lowest Llandovery to the top of the Přídolí. There are only locally small stratigraphical breaks on the east and SE margins of the basin in the lower and upper parts of the section. Investigations of various faunal groups show that sedimentation was nearly continuous in the axial and deepest part of the basin. Short breaks in sedimentation occur and are indicated by pyritized rock surfaces and sudden changes in rock composition. The maximum thickness of the Silurian in the study area lies in Lithuania, in the Baltic Basin, and amounts to 836 m (Nida-1 borehole) (Fig. 6.7).

The Silurian in the Baltic Basin commences with a lower Llandovery limestone complex which is up to 40 m thick. Black mudstones, dark grey clays and marl deposits overlie this complex. The Přídolí strata comprise greenish grey carbonaceous clays, marls and limestones.

The thickness of the Silurian on the NW-dipping slope of the Belarus–Masurian High varies from 251 m in the central part of Lithuania (Prienai-3 borehole) (Fig. 6.6) to 140 m in the Vilnius area. From the Llandovery to the Ludlow there was an intermediate zone between the clay facies with a graptolite fauna in the Baltic Basin and a carbonaceous facies with a benthic fauna on the NW-dipping slope of the Belarus–Masurian High. This intermediate zone is important because it can be used for correlation in the Baltic area of stratigraphical units between the deep clay and the shallow carbonate facies, and also with other

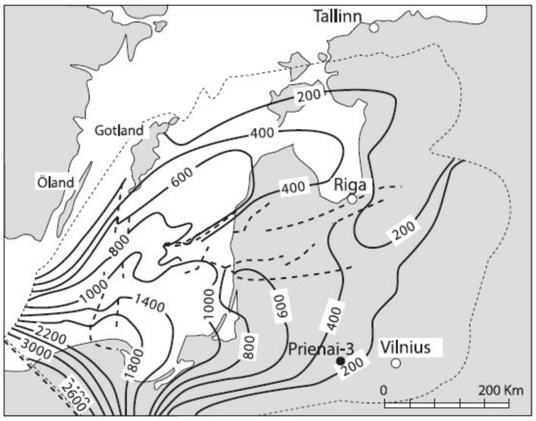

Fig. 6.6. Uncompacted thickness of the Silurian sediments in the Baltic Basin (after Lazauskienė *et al*. 2002).

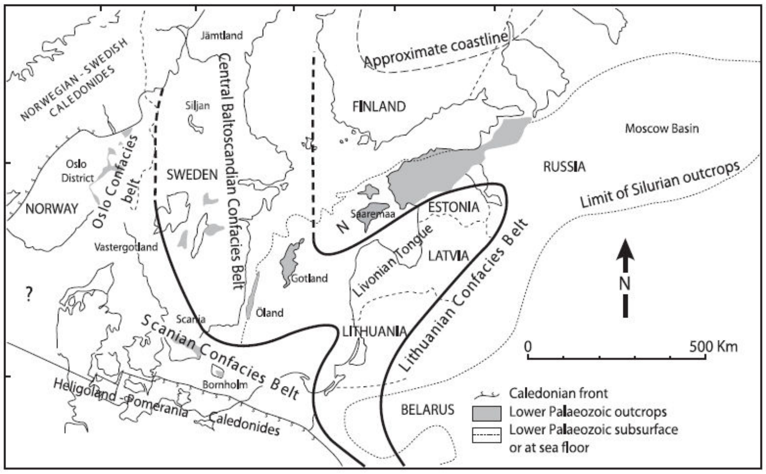

Fig. 6.5. Silurian outcrop and subcrop map of Baltic area with confacies belts (after Jaanuson 1976; Nielsen 1995).

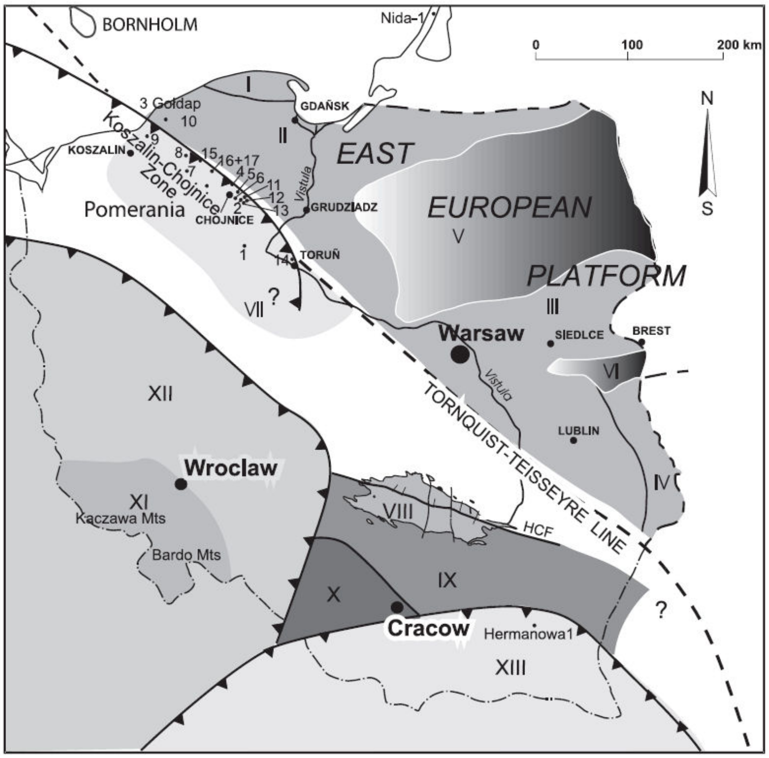

Fig. 6.7. Simplified structural map of Poland. Names of structures, I, Łeba Elevation; II, Baltic Basin; III, Podlasie Depression; IV, Bug Depression; V, Masurian-Suwałki Uplift; VI, Sławatycze Horst; VII, Pomerania, Koszalin-Chojnice Zone; VIII, Holy Cross Mountains; IX, Małopolska Massif; X, Upper Silesia Massif; XI, Sudetes; XII, Variscides; XIII, Carpathians. Boreholes described in text: 1, Bydgoszcz IG1; 2, Chojnice-3; 3, Darłowo-2; 4, Gołdap IG1; 5, Lutom-1; 6, Nicponie 1; 7, Okukino-1; 8, Polanów-1; 9, Skibno-1; 10, Słupsk IG1; 11, Stobno-1; 12, Stobno-2; 13, Stobno-3; 14, Toruń IG1; 15, Trzebelino; 16, Wierzchocina-1; 17, Wierzchocina-4.

areas throughout Europe. A carbonate clayey facies without graptolites in the Upper Ludlow and Přídolí represents a regression in the basin. The thickness of these Upper Ludlow and Přídolí strata ranges from 71 m in Jezioro Okrągłe (Poland) to 522 m in the Kunkojai-12 borehole (Lithuania). During Ludlow and Přídolí times the Silurian basin became significantly narrower, but the accumulation rate increased.

Baltica in Lithuania

Litho- and biostratigraphy

The lower Silurian (Llandovery and Wenlock) contains four rather thin formations. At the bottom the Apascia – Staciunai Formation contains nodular limestone deposits and is well exposed in the western part of Lithuania. It is dated as early Llandovery. The upper Llandovery and Wenlock are represented by the Barta Group, with three formations, from bottom to top, the Rasyte Formation (containing the *Coronograptus cyphus – Stimulograptus sedgwickii* and *Cyrtograptus lapworthi – Rastrites linnaei* zones), the Ragaine Formation (containing the *Monograptus riccartonensis – Cyrtograptus centrifugus*, *Cyrtograptus radians – Monograptus flexilis* and *Testograptus testis* zones) and the Siesartis Formation (containing the *Colonograptus ludensis – Gothograptus nassa* Zone). The formations are comprise black and dark grey mudstone with graptolite faunas in the western part of Lithuania, and marls with intercalated nodular limestones in the eastern part.

The upper Silurian contains four thick formations: two in the Ludlow, the Rusne Formation (*Neodiversograptus nilssoni*, *Lobograptus scanicus–Lobograptus progenitor* and *Pseudomonoclimacis tauragensis* graptolite zones) and the Pagegiai Formation (*Slovinograptus balticus* and *Monograptus formosus–Monograptus valleculosus* Zones); and two in the Přídolí, the Minija Formation (*Monograptus ultimus–Monograptus parultimus* and lower part of the *Neolobograptus lochkovensis* graptolite zone) and the Jura Formation (also *Neolobograptus lochkovensis* graptolite zone). The entire upper Silurian is represented by extensive calcareous clay deposits with nodular limestone units in the western part of Lithuania and by shallow marine basin and marginal facies with limestones, marls or dolomite, and detritic nodular limestones tracing a reef belt in the eastern part.

Lithofacies and palaeogeography

Four successive periods of basin development can be distinguished: mid Llandovery–early Wenlock (sequences S1 to S3), late Wenlock–early Ludlow (sequences S4 to S6), late Ludlow (sequences S7 and S8) and Přídolí (sequences S9 and S10) (Paskevicius 1997) (Fig. 6.8). These periods can be related to eustatic sea-level changes, tectonic development and local facies distribution.

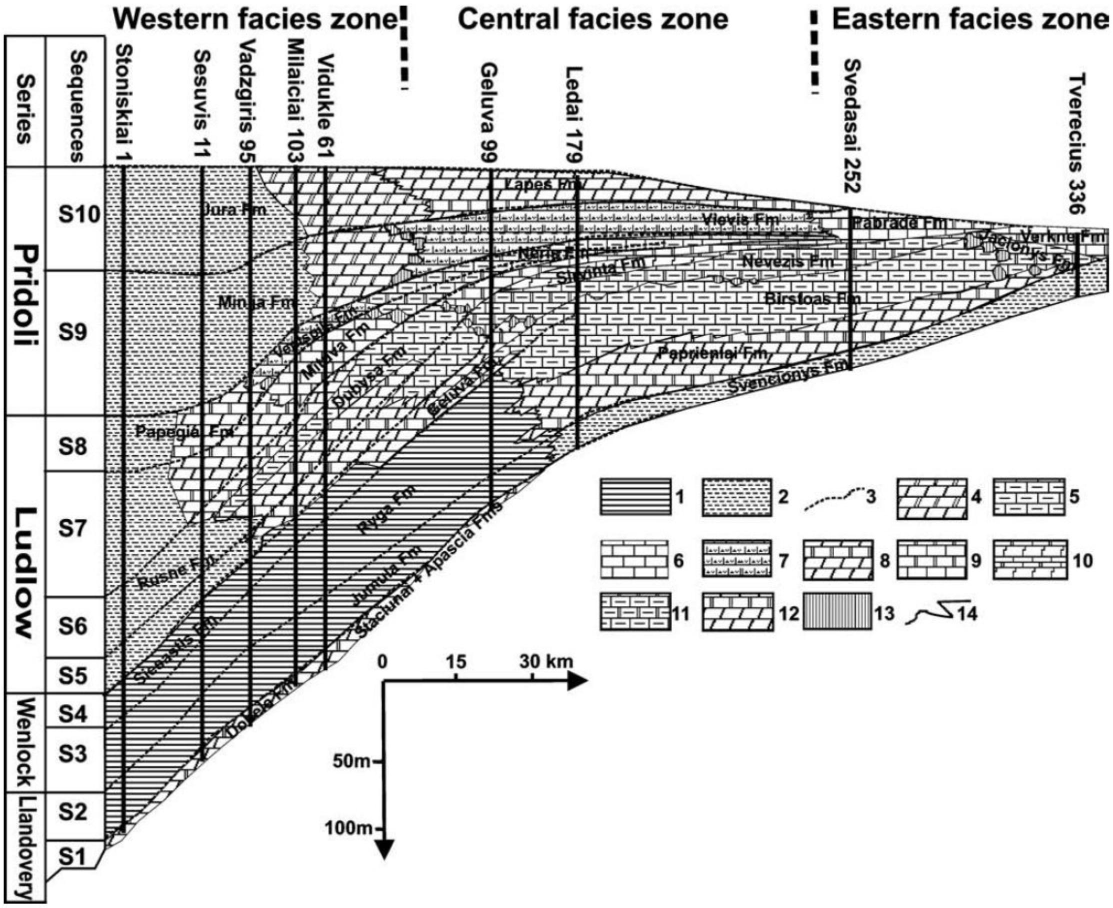

Fig. 6.8. Lithofacies cross-section throughout the central and eastern parts of the Silurian Baltic Basin, distribution of depositional sequences and main tectonosedimentary stages of foreland basin development. Key: 1, shales; 2, carbonaceous claystones; 3, boundaries of sequences; 4, carbonaceous marlstones; 5, clayey limestones; 6, limestones; 7, organoclastic limestones; 8, clayey limestones and marlstones; 9, dolomites; 10, dolomites and gypsum; 11, clayey dolomites; 12, dolomites interbedded with marlstones; 13, reefs; 14, boundaries of formations (modified after Lazauskienė *et al.* 2003).

At the end of the Ordovician the entire East Baltic area was covered by a very shallow marine and marginal basin. In SW Lithuania a stratigraphical hiatus is present. This was related to a large marine regression, presumably caused by the major eustatic sea-level fall due to the Hirnantian glaciation in the southern hemisphere.

In the early Llandovery a marine transgression took place in Lithuania from the west and NW over the low relief formed at the end of the Ordovician. Organic-material-rich clayey sedimentation was predominant across the area. In the late Llandovery and early Wenlock the sea further transgressed eastwards causing a corresponding distribution of facies and facies changes from lagoonal, through shallow-marine to shelf facies. Intensive volcanic activity occurred at that time in the zone of active Caledonian deformation in the west and south. Air-borne ashes were introduced into the Baltic Basin and bentonite layers formed, which were preserved in the deep-marine area. In the late Llandovery a shallower marine facies prevailed in the basin, explained as being the result of basin infill at the end of a highstand. In the east and SE of the Baltic Basin the presence of a shoreline and deltas has been proven. However, in the south the facies is devoid of terrigenous material with no indication of marginal environments, indicating a possible southward extension of the basin. The Wenlock–Ludlow transgression and increasing sedimentation rates are interpreted as the consequence of the regional tectonic activity at the SW margin of Baltica. In the early Wenlock the basin became shallower and a gradual replacement of the clayey facies by an organic-rich facies with dark graptolitic shales occurred. Due to the sea-level changes different facies overlap, and can repeat each other, forming sequences (see Fig. 6.8); the shallow carbonate shelf moved westwards. In SW Lithuania dolomitization of the carbonate deposits was common (Lazauskiene *et al.* 2003).

A regression commenced in the late early Wenlock in the Baltic Basin and continued through the remaining part of the Wenlock and into the early Ludlow. The area occupied by the basin decreased in size and regressive deposits were formed under conditions of rapid sedimentation. Metabentonite interlayers are less frequent due to either reduced volcanic activity in the Caledonian deformation zone, or the subsequent erosion and removal of the volcanic material. At the end of the Wenlock in central Lithuania a short transgression is noted. During the early Ludlow, on the NW-dipping slope of the Belarus–Masurian Uplift, dolomitic lagoonal deposits were formed containing nests of gypsum. During the late Ludlow the size of the Baltic Basin was generally decreasing, despite the occurrence of a short-term transgression. In the latest Ludlow the basin became shallower, ending with a transition from a marine basin to a lagoon with lower, or sometimes higher, water salinity. The late Ludlow maximum sea-level low is thought to represent the Lau Event (see Fig. 6.2) first observed in the Silurian of Gotland, north of the study area (Martma *et al.* 2005).

After the most prominent transgression at the beginning of the Přídolí, a marine regression occurred at the end of the Přídolí. The large thickness of Přídolí strata in SW Lithuania indicates rapid sedimentation within a basin that remained rather small. In the peripheral parts of the basin, Přídolí strata are less thick, and represented by shallow-marine and marginal red-coloured beach and lagoonal facies, usually rich in vertebrate fossils. The extensive terrigenous deposits indicate that the shoreline, at the end of the Silurian, extended in a SW–NE arc across central Lithuania. Three short-term marine transgressions took place during the late Přídolí, though a general regressive trend in the basin and a retreat of the shoreline to the west have been confirmed (Paskevicius 1997; Lazauskiene *et al.* 2003).

Baltica in Poland

In Poland the Silurian bio- and chronostratigraphy is mainly based on graptolites and can easily be correlated with the international standard stratigraphical framework (Fig. 6.9) (for summary see Tomczykowa & Tomczyk 1981; Tomczyk 1970; 1991; Urbanek & Teller 1997; Jaworowski 2000; Modliński & Szymański 2001; Podhalańska 2003; Szymański & Modliński 2003). Undisturbed Silurian strata have been encountered subsurface in hundreds of deep boreholes throughout the Palaeozoic sedimentary cover above the Polish portion of the Baltica. These deposits yield rich and varied fossil assemblages that have attracted the interest of many geologists and palaeontologists since the mid-1950s. The history of research and the results have been summarized by Teller (1997). The Palaeozoic sedimentary cover of the East European Platform was later affected by slight uplift or subsidence, resulting in the formation of two uplifted areas, the Masurian-Suwałki Uplift, part of the Belarus–Masurian High and the Sławatycze Horst, where the Palaeozoic strata were eroded, and three intervening structural depressions, with Palaeozoic strata still present and conventionally called, from NW to SE, the Baltic, Podlasie and Bug basins (Fig. 6.7).

The Koszalin-Chojnice Zone

The Silurian of Western Pomerania is known from 15 deep boreholes (Bydgoszcz IG1, Chojnice-3, Klosnowo IG1, Lutom-1, Nicponie 1, Okukina-1, Polanów-1, Skibno-1, Stobno-1, Stobno-2, Stobno-3, Toruń IG1, Trzebielino and Wierzchocina-1 and -4: Fig. 6.7) located in a narrow NW–SE zone in northwestern Poland, the so-called Koszalin-Chojnice Structural Zone (e.g. Dadlez 1978, 2000; Teller 1969, 1974, 1997; Teller & Korejwo 1968*a*, *b*, *c*; Tomczyk 1968, 1980; Katzung 2001; Podhalańska & Modliński 2006). This structure comprises strongly folded Lower Palaeozoic rocks and is situated to the SW of the Teisseyre-Tornquist Line (i.e. the western margin of East European Platform). The deformation at a high structural level, probably accompanied by thrusting, is indicated by the steeply dipping beds, predominantly more than 45° and some overturned bedding, changing over short distances within the boreholes, as well as the high frequency of slickenside and intense fracturing (Dadlez 1978). It is regarded as a continuation of the Danish–North German Caledonides (Pożaryski 1990), part of the Heligoland-Pomerania-Deformation Belt (Winchester & the PACE TMR Network 2002). The Silurian sequence in Western Pomerania is considered by Jaworowski (2000) as a Caledonian accretionary prism that supplied clastic material for the proximal Baltic Basin in Eastern Pomerania. The Silurian succession is composed of black and grey graptolitic shaly siltstones and mudstones, several hundred metres thick. In terms of age, the succession includes Llandovery, Wenlock and Ludlow units unconformably overlain by Devonian and younger deposits (Modliński 1968, Teller & Korejwo 1968*a*, *b*, *c*; Czermiński 1967; Dadlez 1967; Hajłasz 1967).

The Silurian in this area appears to be lithologically similar to the Ordovician, but differs in terms of the numerous siltstone intercalations which are found in the Llandovery and the upper Ludlow to Přídolí, and which are considered to be turbiditic in origin (Teller 1969, 1974; Tomczyk 1987). The Ludlow succession occasionally contains dolomites, whereas the Přídolí beds consist of dark grey siltstones with very thin intercalations of limestones, partly organo-detritic, and containing abundant faunas of bivalves, brachiopods, ostracods, sporadically trilobites, tentaculites and crinoid stems. Graptolites enable the Llandovery, Wenlock and Ludlow to be recognized, whereas ostracods are used for the Přídolí (Żbikowska 1974; Teller 1974). Intercalated limestones and dolomites also indicate shallow-water depositional conditions at this time, but sediment influx from the south at the beginning and the end of the Silurian is marked (Katzung 2001). Samuelsson *et al*. (2002) noted that the chitinozoans of the Upper Ordovician and Silurian in the boreholes are similar to those of Avalonia and are generally closer to Baltica than to northern Gondwana. Newer studies suggest that the area was situated on the edge of Baltica, close to the suture (Poprawa 2006).

Other Polish parts of the Baltic Basin

The Polish sector of the (Peri-)Baltic Basin extends from Koszalin in the west to Jezioro Okrągłe at the Lithuanian border in the east, and includes smaller structures, the Łeba Elevation (High) and Gdańsk Bay. The Silurian typically consists of monotonous, almost exclusively siliciclastic deposits represented by claystones and mudstones with thin sandstone interbeds and carbonate intercalations (for a summary see Jaworowski 2000; Szymański and Modliński 2003). The succession is *c.* 300 m thick (Gołdap IG1 borehole) in the eastern part of the region increasing to *c.* 3300 m (Słupsk IG1 borehole) in the western part (Teller 1969; Tomczyk 1968, 1970). The Llandovery deposits contain black claystones with graptolites and thin dolomitic limestones with a benthic fauna (brachiopods) or subordinate nodular limestone, and they unconformably overlie the Upper Ordovician. The Wenlock rocks are monotonous, locally calcareous claystones with abundant and well preserved graptolites, probably deposited during the Silurian transgression and substantial expansion of the basin (Teller 1997). The Ludlow rocks are similar but with a different graptolitic fauna (Urbanek 1966, 1970, 1997; Kozłowska-Dawidziuk 1995). The Přídolí rocks comprise claystones with frequent carbonate intercalations with an abundant benthic fauna deposited in a regressive setting. In the upper part of the succession these deposits are truncated by pre-Permian erosion.

The Silurian sedimentation of this region is comparable to the

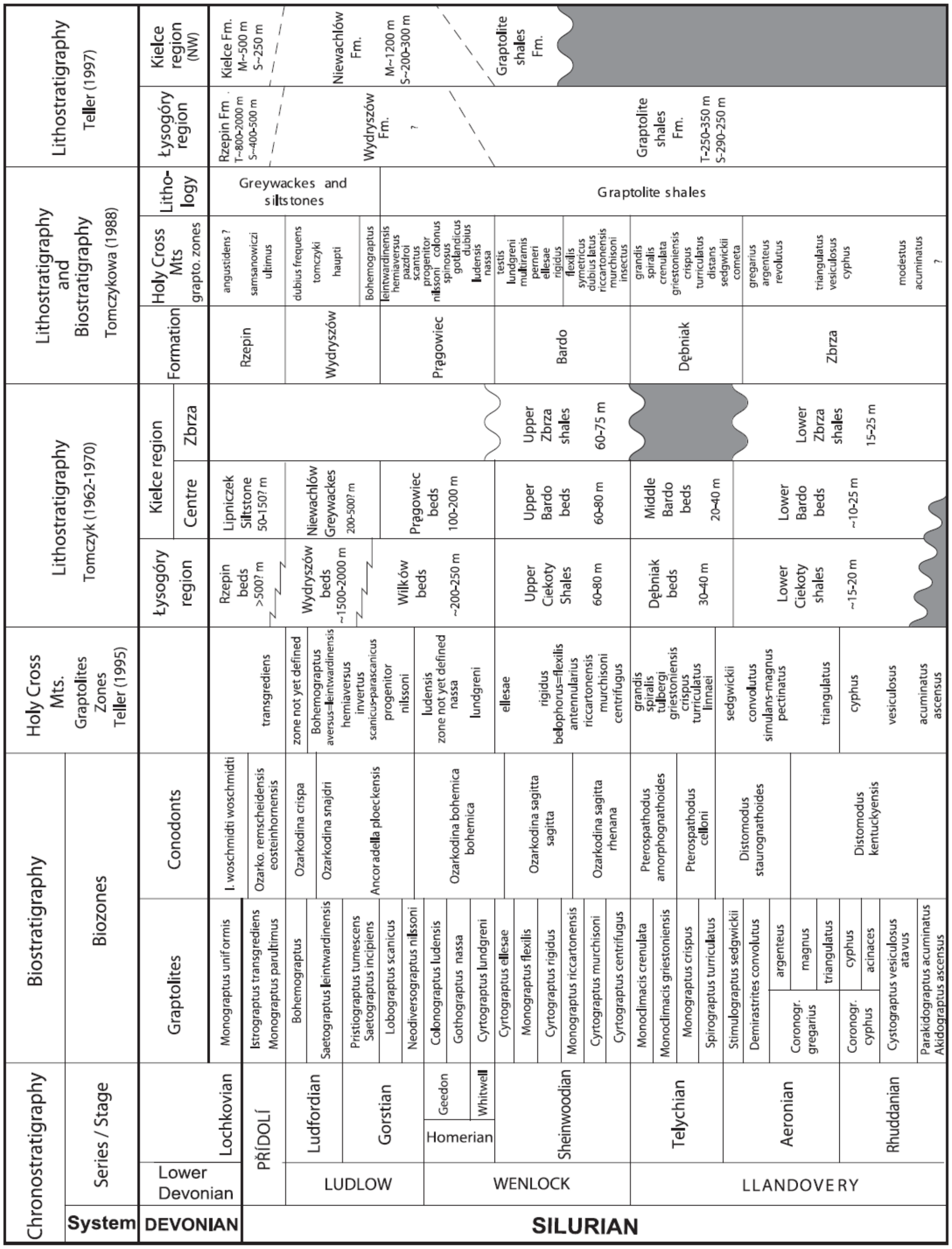

Fig. 6.9. Silurian litho- and biostratigraphy of the Holy Cross Mountains (after Modliński & Szymański 2001).

Silurian facies belts elsewhere in the Baltic Basin, suggesting that the calcareous claystones with carbonate intercalations were deposited in the relatively shallow conditions of an epicontinental sea (Einasto *et al.* 1986). In the western part of the Baltic Basin in northern Poland (Pomerania) the Silurian graptolitic clays and muds are located in the foreland of the Pomeranian Caledonides and are considered by Jaworowski (2000) to have been deposited in a hemipelagic environment with anoxic bottom waters. Their deposition under low-energy conditions during the Wenlock and Ludlow was repeatedly disturbed by silty debris flows and turbidity currents of clastic material derived from the Caledonian Orogen. The basin extended along the SW edge of the East European Craton coincident with the collision zone of Baltica and Far Eastern Avalonia (Jaworowski 2000).

Podlasie Basin

The Silurian deposits in this basic are mainly mudstones and shales with graptolites, ranging from 300 m to 1300 m in thickness, and unconformably overlying the Ordovician succession. They are unconformably overlain by Carboniferous, Permian or Jurassic strata. These deposits yield abundant and diverse graptolites and trilobites, used as the basis for biostratigraphy (Urbanek 1963, 1966, 1970, 1971; Tomczykowa 1988; Teller 1971). They are sparsely bioturbated and were deposited in relatively shallow-marine conditions in an epicontinental, outer-shelf environment.

Bug Basin

In this basin the Silurian-age deposits range from Wenlock through to the Devonian. The sediments are similar to those of the Podlasie Basin, namely graptolitic clayey and muddy calcareous shales with limestone nodules and intercalations, which increase in relative proportion upwards. The carbonate layers contain an abundant and diverse benthic fauna, including trilobites, bivalves, crinoids, brachiopods and tentaculites (Teller 1964; Korejwo & Teller 1964; Tomczykowa & Tomczyk 1979; Tomczykowa 1975). These undisturbed Silurian and Lower Devonian deposits extend southwards into the Ukrainian portion of the East European Platform. The basin shows signs of relatively shallow conditions on an epicontinental, outer-shelf environment, with a gradual shallowing and disappearing sea during the latest Silurian (Přídolí) (Teller 1997).

Holy Cross Mountains

There is an ongoing discussion as to the palaeoplate affinity of the Holy Cross Mountains during the Cambrian (either Baltica or Gondwana), but there is also consensus that during the Silurian it was attached to Baltica (see Belka *et al.* 2002; Cocks 2002; Cocks and Torsvik 2005; Elicki *et al.* 2008; Krawczyk *et al.* 2008). The Silurian of the Holy Cross Mountains has been studied since the mid-nineteenth century by several generations of prominent geologists and palaeontologists (Modliński & Szymański 2001). The Palaeozoic core of the Holy Cross Mountains is divided into two tectonostratigraphic, structurally different geological regions: the northern Łysogóry region and the southern Kielce region, separated by the Holy Cross Fault (Fig. 6.10).

The Silurian deposits of the Holy Cross Mountains are important for the understanding the amalgamation history of the Polish portion of the Trans-European Suture Zone (Belka *et al.* 2002). Fossil assemblages and sedimentary facies allow the succession to be subdivided into several local, poorly defined and thus informal biostratigraphical and lithostratigraphical units (Fig. 6.11 & 6.12) (for summaries see Tomczykowa & Tomczyk 1981; Modliński & Szymański 2001).

Łysogóry region

The Silurian of the Łysogóry region occurs in several outcrops and tens of boreholes (for details of location and review see Modliński & Szymański 2001). The Silurian succession consists of clastic marine sediments, without sedimentary breaks. These comprise black and grey shales with abundant graptolites (Ciekoty Beds) representing the Llandovery to Lower Ludlow deposits, and are approximately 100 to 140 m thick. They are overlain by grey and greenish clayey siltstones with carbonate interbeds and lenses (Wilków Beds), assigned to the upper

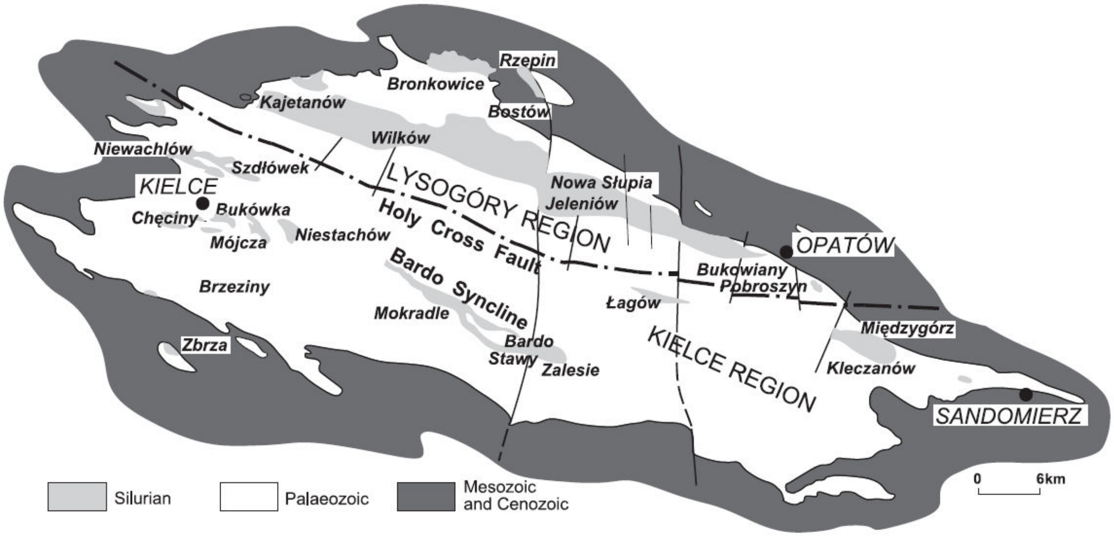

Fig. 6.10. Distribution of the Silurian deposits in the Holy Cross Mountains (modified after Modlinski & Szymanski 2001).

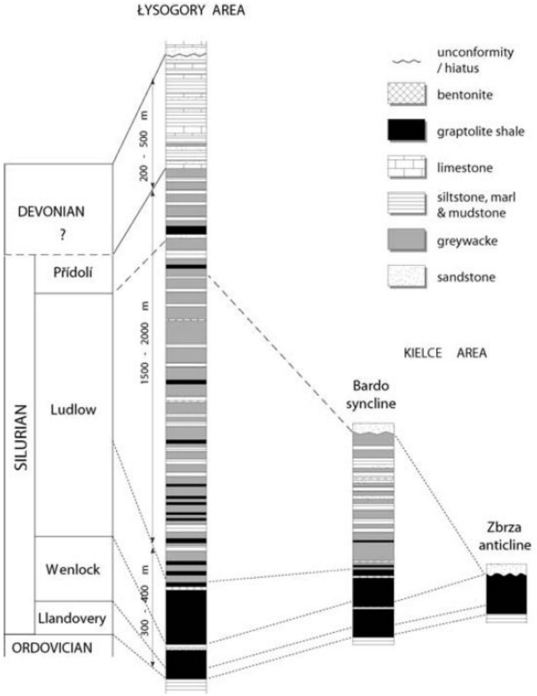

Fig. 6.11. Simplified lithostratigraphical profiles of the Silurian in the Góry Świetokrzyskie (Holy Cross Mountains) (modified after Tomczyk 1970; Modlinski & Szymański 2001).

Wenlock (Homerian) to lowermost Ludlow (Gorstian), and which are up to 250 m in thickness. These sediments are overlain by the Wydryszów Beds and Rzepin Beds with a poorly defined boundary in between. The latter are very thick, up to 2000–2500 m, and consist of grey-greenish shaly siltstones, mudstones and fine-grained sandy shales, sandstones and greywackes with numerous volcaniclastic interbeds and organoclastic limestones yielding bivalves, brachiopods, ostracods, trilobites, crinoids and sporadically graptolites (Tomczykowa & Tomczyk 1981). The fine-laminated mudstones and siltstones of the Rzepin Beds (at the Ludlow–Přídolí boundary) also contain abundant *Cooksonia*-like land plant fragments (Bodzioch *et al.* 2003). The succession is assigned to the Upper Ludlow to Přídolí and passes upward into the coarser-grained Devonian sediments (Tomczykowa & Tomczyk 1981; Tomczykowa 1988). The continuous sedimentary succession from the Silurian through the Devonian is similar to that on the foreland of the East European Platform, indicating a possible palaeogeographical connection (Stupnicka *et al.* 1991; Stupnicka 1992).

The graptolitic shales of the Llandovery to lower Ludlow were deposited in a deep marine basin (Porębska 2002), whereas the huge complex of clastic deposits (mainly greywackes) forming the Wydryszów and Rzepin beds were rapidly deposited (turbiditic character) in a shallow-water setting, which, at the Silurian–Devonian transition, gradually evolved to a shallow marine, nearshore and lagoonal, periodically brackish environment (Malec 2001; Kozłowski 2002, 2003; Bodzioch *et al.* 2003).

Kielce region

The Kielce region forms the northern margin of the Małopolska Massif to which it structurally belongs (Pożaryski & Tomczyk 1968). The Silurian of the region crops out in the central Kielce-Łagów Synclinal Zone, the Zbrza Anticline, the Bardo Syncline, the Łagów Syncline and the Międzygórz Syncline, as well as in more than a dozen boreholes (for detail of location and review see Tomczyk 1970; Modliński & Szymański 2001).

The Silurian succession of the central Kielce region consists of monotonous dark-coloured graptolitic shales with lydite interbeds. They are distinguished as the Bardo Beds and assigned to the Llandovery and lower Wenlock (Sheinwoodian). Their total thickness varies from 80 m to 150 m (Tomczykowa & Tomczyk 1981; Modliński & Szymański 2001). The Bardo Beds are overlain by the Prągowiec Beds of late Wenlock and early Ludlow (Gorstian) age. They comprise up to 200 m of calcareous grey and black shales and siltstones with graptolites and syngenetic calcareous concretions (Tomczykowa & Tomczyk 1981; Modliński & Szymański 2001). The overlying Niewachlów Beds represent a rapid change in sedimentation and are composed of sandstones and coarse-grained greywackes up to 500 m thick, which are assigned to the upper Ludlow (Malec 1991; Modliński & Szymański 2001). The Niewachlów Beds are overlain by the Lipniczek Beds, assigned to the uppermost Ludlow–Přídolí, and composed of siltstones and fine-grained sandstones, with marine fauna at the top (Tomczykowa & Tomczyk 1981; Modliński & Szymański 2001). These greywackes contain sedimentary structures indicating turbiditic transport. They were mainly derived from local volcanic sources (Przybyłowicz & Stupnicka 1991; Malec 1993). Lithologically, the entire succession resembles the Silurian of the Łysogóry region, albeit thinner and with numerous distinct sedimentary breaks, supposedly caused by pre-Variscan, synorogenic movements.

A somewhat different Silurian succession is present in the southwestern part of the Kielce Region, in the Zbrza Anticline (Fig. 6.10). Only Llandovery and Wenlock sediments up to 100 m thick are recognized (Lower and Upper Zbrza Shales). These sediments comprise black and grey bituminous clayey, siliceous and calcareous shales with rare limestone concretions (Deczkowski & Tomczyk 1969; Modliński & Szymański 2001).The erosionally truncated top of the Silurian succession in the Kielce region is unconformably overlain by Lower Devonian (Emsian) deposits; the break has been interpreted as a result of latest Silurian–pre-Emsian tectonic movements (Malec 1993; Przybyłowicz & Stupnicka 1989; Modliński & Szymański 2001).

Radom region

Silurian rocks are also encountered in three deep boreholes in the Radom region, adjacent and to the north of the Łysogóry region (for review see Modliński & Szymański 2001). The most representative section for this region is known from the entirely cored Ciepielów IG1 borehole. There, the Silurian is a monotonous sequence of grey laminated claystones and siltstones with graptolites (Tomczyk 1974) and chitinozoans (Wrona 1980) and with intercalated sandy and muddy siltstones, which may be calcareous. All of these deposits contain rare calcareous concretions and volcanogenic clasts. The biostratigraphy is based on a fairly diverse graptolite fauna, especially in the uppermost Ludlow and Přídolí (Tomczyk 1974; Tomczyk *et al.* 1977; Tomczyk & Tomczykowa 1983). The Silurian strata were not fully penetrated by the boreholes, but their thickness varies from *c.* 400 m to 650 m and they probably extend from the Upper Ludlow (Ludfordian), through the Přídolí, passing upwards with sedimentary continuity into Lower Devonian (Lochkovian) marine deposits (Żelichowski 1972; Tomczyk 1974; Tomczyk & Tomczykowa 1983; Teller 1997). The Silurian succession in the Radom region has so far not been subdivided into regional formal lithostratigraphic units (Modliński & Szymański 2001). The upper Ludlow beds in this region may be correlated with an informal regional stratigraphic unit, the lower Rzepin Beds of the Łysogóry region and with the uppermost part of the upper Siedlce Beds of the East European Platform (Tomczyk 1974). The Přídolí deposits may be considered as equivalents of another informal regional stratigraphic unit, the Upper Rzepin Beds of the Łysogory region, and can be correlated with the Podlasie Beds of the East European Platform (Tomczyk 1974).

Southern part of the Małopolska and Upper Silesia massifs

The Silurian of the southern part of the Małopolska Massif is known only from deep boreholes located to the south of the Holy Cross Mountains in the Nida region (Miechów Trough) and extending to the south to the Upper Silesia Massif (for details of location and review see Buła 2000; Modliński & Szymański 2001). There the Silurian strata comprise graptolitic shales with thin-bedded cherts (lydites in the Alpine region terminology), organoclastic limestones and dolomitic limestones, and fine-grained sandstone intercalations, unconformably overlying the Ordovician rocks. At the top of the section the mainly black or grey clayey shales are dominated by an unfossiliferous clastic unit comprising mainly siltstones, sandstones and conglomerates and comparable with the greywackes in the adjacent Kielce region (Jurkiewicz 1975). The total thickness can amount to several hundreds of metres. The sediments are erosionally truncated and unconformably overlain by Devonian or Triassic rocks (Jaworowski *et al.* 1967; Bednarczyk *et al.* 1968; Jurkiewicz 1975).

The Silurian succession of the Małopolska Massif has been compiled from discontinuous core profiles and comprises Llandovery, Wenlock and Ludlow deposits, which can be correlated with the coeval sequence exposed in the southern region of the Holy Cross Mountains (the Zbrza Anticline), and represents the same facies and graptolite succession (Bednarczyk *et al.* 1968). The Silurian succession of the Upper Silesia Massif has been subdivided into well defined lithostratigraphic units (Buła 2000): the Zawiercie (Ordovician–Lower Silurian), Mrzygłód (Wenlock–Ludlow) and Łapczyca formations (Přídolí).

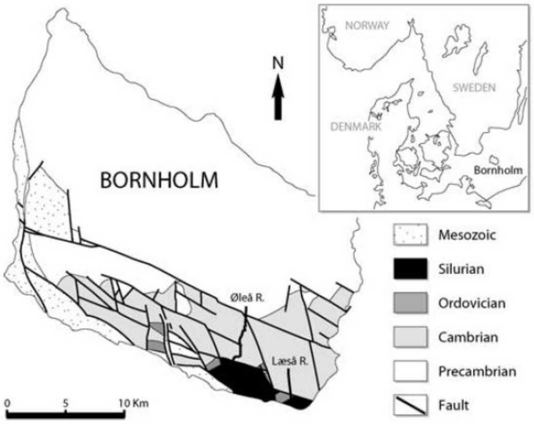

Fig. 6.12. Outcrop map of the Silurian in Bornholm (after Pedersen & Klitten 1990).

Early Silurian, Llandovery and Wenlock sequences of the Małopolska and Upper Silesia massifs were deposited on a deep marine shelf that gradually evolved to a shallow marine environment. The coarse-grained, sandy and conglomerate deposits of Ludlow age from the Upper Silesia Massif characterize the general regressive pattern of the basin and this can be interpreted in terms of Caledonian tectonic events (summarized in Buła 2000; Modliński & Szymański 2001).

Baltica in Bornholm and surrounding area

Bornholm and the surrounding area formed an integral part on the southwesternmost edge of Baltica in the Silurian. It lies in the (Oslo-) Scanian Confacies Belt of Jaanusson (1976) and Nielssen (1995), the deepest facies belt of the Baltic Basin. Subsidence analysis of the Upper Ediacaran (ex-Vendian) and Lower Palaeozoic of the basin indicates that in the Silurian there was a marked increase in subsidence and sediment thickness, especially along its southwestern margin (Fig. 6.6), adjacent to the location of the Heligoland-Pomerania Caledonides (North German–Polish Caledonides).

The island of Bornholm is situated on a SW-dipping fault block with gently south dipping Silurian strata covering the thin Ordovician and Cambrian deposits. The Silurian crops out in a few block-faulted areas in the southeastern part of the island (Fig. 6.12). The outcrop area is a strip 12 km long and 3 km wide parallel to the coast. It extends from the southern tip of the island to the lower reaches of the Øleå River and also along the lower reaches of the Læså River. Exposures occur only along the rivers and along the coast where it is found in blocks on the beach or below sea level (up to 300–400 m off the coast and at depths of up to 6 m) (Bjerreskov 1975; Bjerreskov & Jørgensen 1983; Bjerreskov & Stouge 1985; Böhnke & Katzung 2001). Two formations have been defined and these contain predominantly grey to black marine shales with a total thickness of 160 m (Bjerreskov 1975) or nearly 200 m (Böhnke & Katzung 2001). There are also more than 20 bentonite beds (Bjerreskov 1975).

The Llandovery Rastrites Shales Formation consists of grey to dark grey silty shales with some pyrite and organic matter; in the middle part, calcareous interbeds up to 6 cm thick also occur. The contacts with the underlying Ashgill Tommarp Mudstone Formation and with the dark shales of the *Glyptograptus persculptus* Zone, a high γ-ray interval, are observed only in boreholes. The Rhuddanian has a weak fining-upward trend from silt-streaked shales and silty shales into grey mud shales. The shales are interpreted as density flows which occurred in an area of increasing depth (middle to outer shelf) and under anoxic to weakly oxic conditions (Pedersen 1989). The *Akidograptus ascensus, Parakidograptus acuminatus* and *Cystograptus vesiculosus* zones (Rhuddanian) are recognized in the Billegrav-1 and Bavnegård boreholes near the Øleå River (Bjerreskov 1975; Koren’ & Bjerreskov 1997). The *Cystograptus vesiculosus, Monograptus revolutus, Coronograptus gregarius*, *Lituigraptus convolutus*, *Spirograptus turriculatus, Monograptus crispus, Monoclimacis griestoniensis, Oktavites spiralis* and *Cyrtograptus lapworthi* zones from the upper Rhuddanian to upper Telychian are also recognized (Bjerreskov 1975). The thickness is estimated at 85 m (Bjerreskov 1975) or at 125 m (Böhnke & Katzung 2001).

The Wenlock *Cyrtograptus* Shales Formation contains grey and greenish grey shales with limestone concretions and some clay beds. The formation crops out in the lower reaches of the Læså River (Bjerreskov 1975; Pedersen & Klitten 1990). The only lower Wenlock graptolite biozone recognized is the *Cyrtograptus centrifugus* Zone, with a thickness of more than 30 m. No other graptolite biozone has been identified on Bornholm with the exception of the 25 m thick *Cyrtograptus lundgreni* Zone (Homerian, Upper Wenlock) discovered in blocks on the beach east of the Øleå River. Whether hiatuses or a simple condensed section are present remains unsolved. The highest biozone recognized contains dark grey silty-sandy mudstones with intercalations of light grey tuffs and limestones. Six lithotypes are recognized including laminated siltstones, mudstones, microscale flaser to lenticular bedded silt-mudstones, limestones, graded sandstones and tuffs. These suggest an environment of deposition of between *c.* 300 and 1000 m depth (Bjerreskov & Jørgensen 1983) and is interpreted as deep-marine with anoxic conditions. The sediments are predominantly mud deposits or hemipelagites with intercalated silt and fine sand produced as a result of bottom currents and intermittent turbidite flows from the northern carbonate shelf platform (Böhnke & Katzung 2001), and air-fall water-deposited tuffs (Bjerreskov & Jørgensen 1983). In the tuffaceous sediments a ^{207}Pb/^{206}Pb analysis on single zircons gave a mean age of 430 ± 1.9 Ma. The subduction-related calc-alkaline magmatic arc volcanism giving rise to the tuffs is interpreted to be the result of subduction preceding the closure of the Tornquist Sea (Obst *et al*. 2002). The sediments of the Bornholm succession underwent early diagenesis often with pyrite formation in graptolites prior to compaction (Bjerreskov 1991) and later deep burial diagenesis exceeding 90°C due to the accumulation of *c.* 4 km of upper Silurian sediments (Vejbaek 1985; Pedersen 1989).

The Silurian succession in offshore boreholes in the area surrounding Bornholm exhibits a similar facies but is often thicker. Additional Silurian intervals, not found in Bornholm, are present in the boreholes and the succession is therefore considered to be more complete. Seismic stratigraphy indicates that the offshore Silurian succession has a thickness of more than 4 km (Vejbaek 1985). The Pernille-1 borehole (Fig. 6.4) contains at least 47 m of Silurian deposits dated with graptolites as the *Cyrtograptus ellesae* Zone (Upper Sheinwoodian), whereas the Stina-1 borehole has 399 m of Silurian (Katzung 2001). The Slagerse-1 borehole on Sjælland, with 150 m of grey shales and siltstones, belongs to the *Monograptus crispus* Zone (Poulsen 1974).

Baltica in Germany

The Ordovician and Silurian strata of the G-14 borehole (Adlergrund, north of Rügen island, offshore Germany), situated south of Bornholm, are closely comparable to the Skåne/Scania and Bornholm successions and belong to the Scanian Confacies belt (see above) deposited on Baltica. Beier *et al*. (2000) described the Silurian succession and suggested that it was deposited in a peripheral foreland basin during the collision of Far Eastern Avalonia and Baltica. The Silurian is underlain by a typical Baltica shelf succession of Ordovician age, followed by turbiditic Llandovery silt- and sandstones, interpreted as the northward prograding basin fill of this foreland basin.

The base of the Silurian is characterized by a change from the sandy-silty Jerrestad Formation of Ashgill age (Beier *et al.* 2001) to the mudstones of the lower part of the *Rastrites* Shale Formation (Katzung *et al.* 2004). The mudstones grade upward into graded silt- and sandstones with intercalated coarse sandstones with clay clasts and microconglomerates, containing coral and brachiopod fragments. McCann (1996) differentiated four facies types in the *Rastrites* Shale Formation. Layers of laminated mudstones (1), up to 4.5 mm thick, represent the hemipelagic background sedimentation. Graded mudstones (2) with rare *Planolites* sp. are regarded as low energy turbidites. Graded silt- and sandstones (3) in layers up to 24 cm thick, showing sharp bases and rippled surfaces, internally with cross-bedding, lamination or well developed Bouma sequences, rarely bioturbated, indicate low energy turbidites, at least in part produced by storm events. Microconglomerates (4) are represented by up to 20 cm thick layers, mostly graded, containing predominantly mudstone intraclasts and some bioclasts. Trace fossils are common indicating oxic conditions during deposition. Silurian graptolites are found *c.* 72 m above the lithologically defined base of the Silurian. A 240 m thick interval in the drillcore can be referred to the '*Monograptus' gemmatus* Subzone of the *Spirograptus guerichi* Zone (Maletz 1997). The *Rastrites* Shale Formation of Skåne/Scania and Bornholm are much more strongly condensed than the succession in the G-14 drillcore and an increase in sedimentation rate occurred during deposition of the Wenlock–Ludlow *Colonus* Shales. The Silurian succession of the G-14 drillcore was interpreted to represent the deep-water phase of a peripheral foreland basin, filled during the late Mid-Ordovician until the mid- to late Llandovery (Beier *et al.* 2000). At that marked time the foreland basin was dominated by subsidence and received an increasing amount of sediment. Due to the continuing obduction of the accretionary wedge onto the SW margin of Baltica, the depocentre of the basin migrated in a SW–NE direction (Beier *et al.* 1997; Maletz *et al*. 1997). The main depocentre is located in Skåne/Scania in the Late Wenlock–Early Ludlow, as is seen from the up to 600 m thick *Colonus* Shales, overlain by the Öved-Ramsåsa Group, a shallow marine carbonate-rich succession, representing the final filling of the basin, and overlain by terrestrial deposits.

Northern Gondwana and peri-Gondwana terranes

The Franconia Terrane in the Harz Mountains (Oberharz, Niederharz)

The Silurian rocks of the Harz Mountains are generally considered to be preserved as olistostromes in a Lower Carboniferous matrix. Identifiable successions are lacking and the Silurian of the Harz Mountains has to be pieced together from numerous, biostratigraphically datable, small outcrops (Alberti 1995; Burmann 2006). The thickness of the Silurian has been estimated by various authors to be between 50 and 200 m, but could be considerably higher. The lithology is dominated by dark grey to black, often finely laminated shales in the Llandovery to early Ludlow. Silicified shales or cherts are locally known from around the town of Benneckenstein in the central Harz region. Sandstones and greywackes are locally present. Limestones first appear in the upper Wenlock in the eastern part of the Harzgeröder Zone (in the eastern Harz) (see Fig. 6.13). In the Ludlow the lithologies are less monotonous. Limestones occur and sandstone and tuffs are common.

Graptolites are the most common faunal elements, known from numerous localities. They are exclusively present in the early Silurian. In the Upper Wenlock diverse shelly faunas with brachiopods, gastropods, nautiloids, crinoids and bivalves appear, but are most common from the *Neodiversograptus nilssoni* Zone onwards. Jaeger (1991) proved the presence of all Silurian stages based on graptolites and considered that there are no large

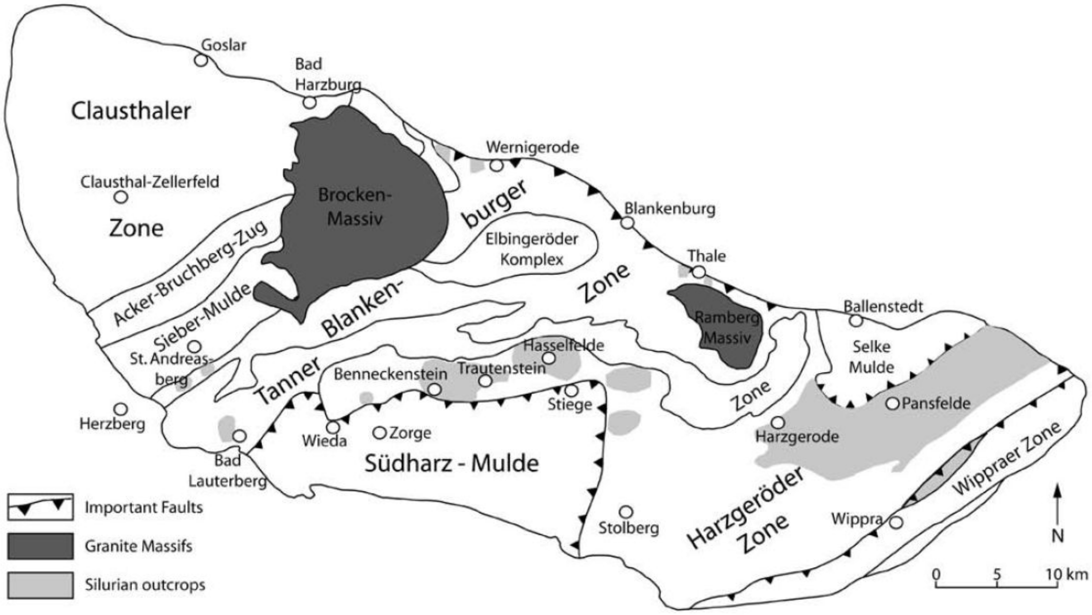

Fig. 6.13. Map of the Harz Mountains in Germany, with large tectonic units (zones, muldes (synclines), etc.) (after Burmann 2006).

biostratigraphical gaps, even though not all of the graptolite biozones have been recognized.

The faunas of the Silurian of the Harz Mountains are closely comparable to those of Saxothuringia. The *Scyphocrinus* horizon has been used, especially for correlation purposes, in the Upper Silurian of Germany. Interestingly, the lithofacies differs considerably from that of Saxothuringia. Basically the entire Silurian succession of the Harz Mountains consists of monotonous, so-called 'Graptolite Shales' (Reuter 1960; Jaeger 1991). It lacks, however, the typical cherts and alum shales of the Unterer Graptolithenschiefer (Lower Graptolite Shale) Formation of Saxothuringia. Lithostratigraphic differentiation, however, is almost impossible due to the strong tectonic overprint and the lack of exposure. Limestones are rare in this succession and are restricted to the upper Silurian, but some of the old records may have been misidentified and belong instead to the Lower Devonian. The limestones in the upper part of the Harz Silurian are less compact than the Ockerkalk in Saxothuringia. The Silurian–Devonian boundary is represented by fossil evidence without any lithological change in the western part of the Harzgeröder Zone (Maronde 1966, 1968). Jaeger (1991) considered the Silurian of the Harz Mountains to be closely comparable to the Unterer Steinhornschichten of the Kellerwald region.

The Franconia Terrane in the Dill Syncline, Marburg and Giessen

Little is known about the Silurian succession of this region since exposure is poor (Anderle 2006*a*, *b*). Despite this, Upper Silurian rocks have been identified as the oldest preserved in the area. The succession of the Lindener Mark region near Giessen covers only a minor part of the Silurian. The Ostrakodenkalk Formation (Ostracod Limestone Formation) consists of *c*. 5–10 m of thick, mostly massive limestones, grading upwards into bedded limestones with cherts. The limestones contain a poorly preserved fauna of ostracods, brachiopods, trilobites and graptolites. The age of the unit appears to be late Wenlock to Ludlow or Přídolí (Jaeger 1962). It is overlain by the Orthocerenkalk Formation (Orthoceras Limestone Formation) which comprises thin (*c*. 5 m) silty shales with carbonate concretions, rich in nautiloids, brachiopods, bivalves and graptolites, indicating a Přídolí to Lochkovian age. Schallreuter (2001*a*, *b*) suggested that there was a close relationship between the diverse ostracod fauna of the Lindener Mark area and faunas from Bohemia, Baltica and even North America.

The Taunus region of the SE Rhenish Massif (= Rheinisches Schiefergebirge) contains Silurian brachiopod faunas with *Dayia shirleyi*, indicating a Přídolí age in the Kellerskopf Formation (= Graue Phyllite), overlain by fossiliferous shales of Lochkovian, early Devonian age. However, older Silurian strata are unknown (Anderle 2006*a*).

The Franconia Terrane in the Kellerwald

Graptolites in the Kellerwald region (Kupfahl 1953, 1954) indicate the presence of Wenlock to Přídolí strata in a number of poorly exposed successions. The Silurian is exposed in small slivers, rarely more than 10 m thick, exposing only minor parts of the time interval. Jaeger (1962) revised the stratigraphy and suggested that the complete Silurian succession comprised graptolite shales with rare limestone intercalations. Anderle (2006*b*) differentiated the Altenteich unit of Llandovery to Wenlock age and the Lower and Upper Steinhorn units. The limestones in the Lower Steinhorn Unit contain graptolites (*Istrograptus transgrediens*), conodonts and crinoids (*Scyphocrinus* horizon) of Přídolí age, while the Upper Steinhorn Unit yielded graptolites of the *Monograptus hercynicus* Zone of early Devonian age (Jaeger 1962; Anderle 2006*b*).

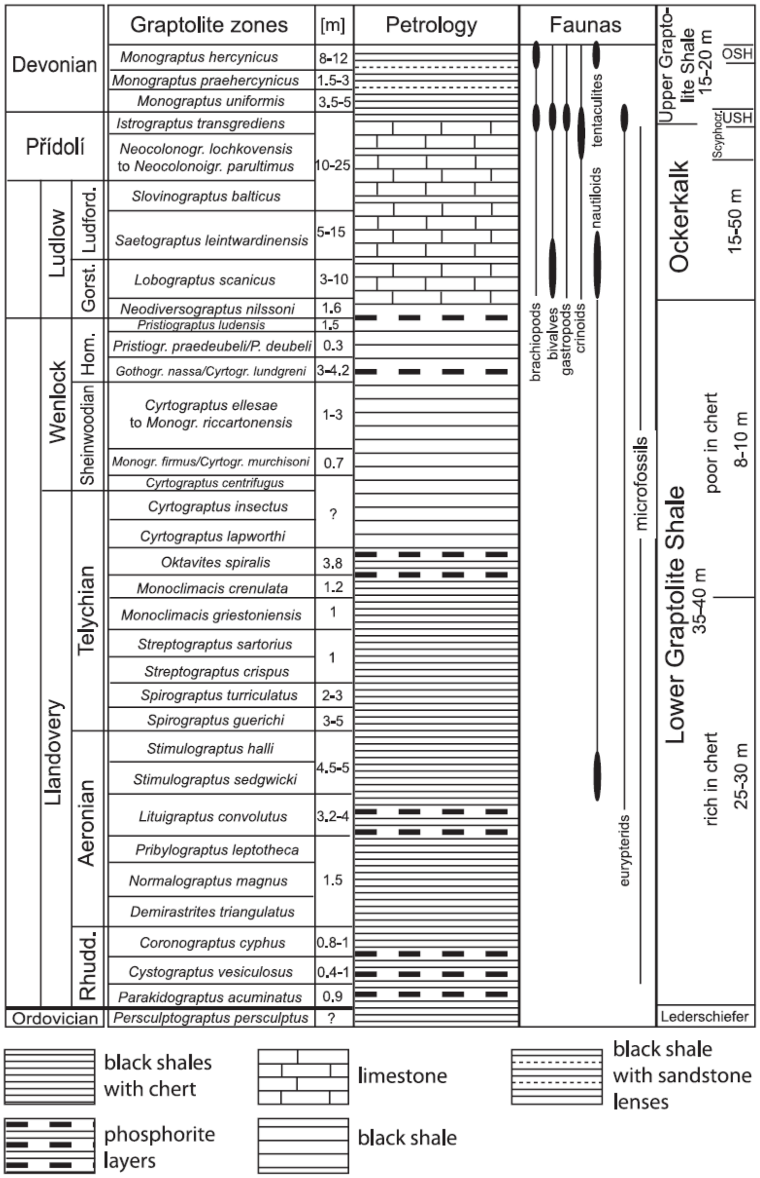

Fig. 6.14. Silurian to basal Devonian succession in Thuringia. OSH, Oberer Schalenbank Horizont (upper shelly horizon); USH, Unterer Schalenbank Horizont (lower shelly horizon). Some graptolite biozones are combined due to limited space (modified after Maletz & Katzung 2003).

The Saxothuringian Terrane in Thüringen, Oberfranken and Vogtland

This region includes one of the best studied Silurian areas in Germany, as noted in the detailed review on the Silurian of Germany published by the German Stratigraphical Commission (Deutsche Stratigraphische Kommission 2002, 2006). The succession in the Thuringia Forest (= Thüringer Wald) is the only complete succession with a well-established graptolite biozonation, but it has been condensed to less than 100 m (Maletz & Katzung 2003).

Silurian strata are widely distributed in Thuringia, Vogtland, Saxonia, Erzgebirge and the Lausitz regions (Fig. 6.4). In general, the successions are fairly similar, but poor preservation and limited exposures often make a detailed comparison difficult. The succession in the Erzgebirge differs considerably from that of the Thuringian succession due to the presence of tuffs which comprise up to 40% of the succession thickness (Geissler & Schauer 2006). Slightly different successions are also found in the Görlitzer and Frankenberger Schiefergebirge. The Silurian of the Görlitzer Schiefergebirge (Lausitz region), in general, matches the Saxothuringian succession. However, the Ockerkalk equivalent appears to be less massive (maximum thickness *c.* 10 m) and is dated at early to mid-Ludlow (Brause 2006). In the Frankenberger Zwischengebirge the Silurian succession is more condensed than in Saxothuringia, but the outcrop situation is extremely poor. The Ockerkalk Formation is represented by a few metres of greenish-grey shales (Jaeger 1977; Kurze 2006).

The Silurian in Thüringen, Oberfranken and Vogtland is represented by the Gräfenwarth Group, which extends up into the Lower Devonian (Emsian). It is dated using a rich graptolite fauna that has been studied for more than 150 years (Geinitz 1842; Maletz 2001). The group includes the Unterer Graptolithenschiefer Formation (Lower Graptolite Shale Formation), the Ockerkalk Formation and the Oberer Graptolithenschiefer Formation (= Upper Graptolite Shale Formation) (Fig. 6.14). The tripartite differentiation of the Silurian to Lower Devonian succession was originally documented by Gümbel (1879), based on initial mapping in Thuringia. The Silurian is widely distributed, but is poorly exposed in the region and strongly deformed by later Variscan activity. The Silurian part of the Gräfenwarth Group is less than 100 m thick (Maletz & Katzung 2003). An extensive overview of the geology of Saxothuringia was recently produced by Linnemann *et al.* (2003*a*, *b*) and Linnemann (2003*a*, *b*, *c*), outlining the stratigraphical successions of the region, the tectonic evolution and interpreting the plate tectonic history of the terrane and its relationship to the peri-Gondwana terrane assemblage.

The base of the Silurian coincides with a lithological change close to the base of the Unterer Graptolithenschiefer Formation. The Upper Ordovician glaciomarine Lederschiefer Formation (Katzung 1999) grades conformably into graptolitic shales with chert beds (= Kieselschiefer, also called lydites) (Schauer 1971). The base of the Silurian is lithologically considered to coincide with the base of the first chert horizon and biostratigraphically coincides with the first occurrence of the graptolite *Akidograptus ascensus* (Jaeger 1988).

The Unterer Graptolithenschiefer Formation is estimated to be *c.* 35–40 m thick, but complete sections through the unit do not exist. Alum shales (dark, organic-rich shales, containing iron pyrite, forming alum when weathering) with a large number of chert horizons characterize its lower part. The formation shows a typical alternation of chert beds, up to 10 cm thick, and thin alum shales beds. This alternation grades upwards into alum shales of the upper unit of the Unterer Graptolithenschiefer Formation. Phosphate concretions, often containing well-preserved fossils, are common and usually concentrated at certain levels.

The base of the Ockerkalk Formation coincides with the first distinct limestone bed. The Ockerkalk Formation consists of platy to thick-bedded limestones and intercalated thin shale layers. The formation is variable in thickness, partly due to tectonic deformation, and reaches 15 to 50 m. The amount of limestone in this formation varies between 60 and 80%. Diverse shelly faunas have been found in the limestones, whereas the intervening shale layers may contain poorly preserved graptolite faunas.

The Oberer Graptolithenschiefer Formation consists of black shales with rare beds and lenses of fine sandstones and siltstones. It is lithologically distinct from the underlying Unterer Graptolithenschiefer Formation. Only the lowermost 1 m belongs to the Silurian *Istrograptus transgrediens* Zone, whereas the major part of the formation is now considered to belong to the Devonian *Monograptus uniformis* to *Monograptus hercynicus* zones.

The Unterer and Oberer Graptolithenschiefer formations of the Gräfenwarth Group have been interpreted as deep-water sediments deposited under low energy conditions by most authors. Coarser-grained clastics and sedimentary structures are rare and restricted to a few levels, especially in the upper part of the succession, carrying specific names such as lower shelly horizon (USH), upper shelly horizon (OSH) and *Scyphocrinus* horizon. Hundt (1965) documented current activity in the Unterer Graptolithenschiefer Formation, based on the presence of current ripples and current-orientated graptolite accumulations. The sedimentation rate was extremely low so that individual graptolite biozones may be only a few centimetres thick. They are often difficult to detect in an outcrop due to the strong tectonic deformation, which may locally squeeze out some of the biozones (Jaeger 1991). The Ockerkalk Formation corresponds to a time of sea-level fall and more oxic conditions than the under- and overlying formations. A diverse benthic fauna appears, including trilobites, nautiloids, gastropods, brachiopods, bivalves and crinoids. The Oberer Graptolithenschiefer Formation corresponds to a return to anoxic conditions, as can be seen by the return to the deposition of black, organic-rich shales. However, an increase in sediment input led to a distinct thickness increase and the formation of decimetre-thick siltstone and sandstone beds.

Saxothuringian Zone in the Spessart Crystalline Complex

The metamorphic series of the Spessart Crystalline Complex is a large NE–SW orientated antiform in which two tectonic complexes can be differentiated (Kroner *et al.* 2008; McCann *et al.* 2008). The tectonically lower complex in the central Spessart is formed by the Mömbris, Hörstein-Huckelheim and Geiselbach formations. The upper complex is represented by the Alzenau Formation to the north and the Elterhof Formation to the south. Granitoid intrusions in the Mömbris Formation represent a Silurian age (418 Ma; Dombrowski *et al.* 1995). In addition, the Spessart Crystalline Complex yielded pteridophyte spores in garnet-bearing schists at *c.* 500 m above the base of the Geiselbach Formation in the lower complex. This is a quartzite unit formerly correlated with the early Ordovician Frauenbach and Phycoden groups of Thuringia. The unit is now referred to the Wenlock–Ludlow (Reitz 1987). Detailed information about the lithology and palaeontology of the unit was given by Hirschmann & Okrusch (2001).

Saxothuringian Zone in the Black Forest (= Schwarzwald)

Silurian rocks are found in the Badenweiler-Lenzkirch Zone, up to 5 km wide, in the southern Black Forest (Fig. 6.4). Greywackes of Late Devonian to Early Carboniferous age are well-known, but more recently acritarchs and chitinozoans suggest Early Ordovician to Silurian ages for some strata. The rocks are interpreted as a tectonic melange which includes units of Silurian age. The more highly metamorphosed rocks have yielded only rare and poorly preserved microfossils, of which the biostratigraphical value can be questioned. Similarly, the metamorphic Wetzldorf-Group and the Anglmühle Unit of the Bavarian Forest (= Bayerischer Wald) and Upper Pfalz Forest (=Oberpfälzer Wald) (Fig. 6.4) are referred to the Silurian on the basis of a rare fossil record. Stettner (2006) suggested a comparison of the phyllites of the Wetzldorf Group with the Lower Graptolite Shale Formation of Saxothuringia, partly based on the record of radiolarians and graptolites by Stürmer (1962).

The Moldanubian Zone with the Prague Basin on the Perunica Terrane (Czech Republic)

Most of the Silurian rocks of the Bohemian Massif were deposited on the Perunica Terrane which is regarded by some authors as a microplate that detached from Gondwana during Ordovician times (Havlíček *et al*. 1994) (Figs. 6.4 & 6.15). The existence of Perunica in the Silurian is supported by palaeomagnetic data (Krs *et al*. 1986) and by the distribution of Ordovician and Silurian fossils. It includes the Prague Basin (Fig. 6.15), the most fossiliferous Silurian outcrop area of Central Europe and a complete Silurian succession only slightly disturbed by later deformation (Fig. 6.16). The region was incorporated during the Variscan Orogen as a separate terrane between the Gondwana and Baltica palaeocontinents (Fig. 6.4).

Another Silurian outcrop area in the Bohemian Massif locally called the 'Islet Zone' (Fig. 6.17), is situated on the central Bohemian granite pluton and includes successions altered by contact and regional metamorphism. Other metamorphosed and biostratigraphically dated Silurian deposits are developed in the Rožmitál area, the Mirovice metamorphic area, the Železné Hory Mountains (Vápenný Podol), in the Hlinsko Lower Palaeozoic Region and in the Lužice Region (Fig. 6.17). Silurian rocks were also recorded from a borehole in the Bohemian Cretaceous Basin near Jablonné, Podještědí (Fig. 6.17) (Kříž *et al.* 2003). The Silurian sequence in the Moravo-Silesian area in the Drahany Highland, Stínava (Fig. 6.17) is similar to that of the Prague Basin (Kettner & Remeš 1935). It is considered to be part of the Brunovistulicum terrane (Havlíček 1980).

Facies and volcanism

Three of the distal Silurian facies in northern Gondwana occur in Bohemia, namely: the shelly fauna facies, the Prague Basin facies and the Thuringian facies (Kříž *et al.* 2003). They are sometimes called the 'Variscan' facies (Kříž *et al.* 2003), but are not to be confused with the tectonic events bearing the same name over large parts of Europe. The **shelly fauna facies** is characteristic for the upper Wenlock and the Ludlow of deeper parts of the Prague Basin. The shallow-marine **Prague Basin facies** (Kříž *et al.* 2003) differs from the Thuringian facies in its greater thickness (250–580 m).

In the Prague Basin, the earliest Silurian sediments were pelitic, black graptolitic shales. During the Telychian (Llandovery) and especially in the early Sheinwoodian (Wenlock), the presence of carbonates increased progressively. In the mid-Llandovery (Aeronian) and from the mid-Wenlock to the mid-Ludlow, sedimentation in the Prague Basin was influenced by the activity of a volcanic archipelago with the resultant deposition of volcaniclastics and related magma intrusions, tuffs and lava flows (Fig. 6.18). Several volcanic centres developed along synsedimentary growth faults and at their junctions (Fig. 6.18). Around the volcanic centres shallow-marine highs with slopes developed, favourable for the growth of the rich benthic faunas, mentioned above. During periods of minimal sediment supply isolated carbonate platforms developed. In the region of the Svatý Jan Volcanic Centre (Fig. 6.18), reworked limestone pebbles and fragments of algae, bryozoans, corals and stromatoporoids document intertidal or shallow subtidal environments during the late Wenlock (Kříž 1991, 1998b). This would suggest the existence of an emergent volcanic island at least at that time (see below). Temporary emergence of other volcanic centres is also indicated by the presence of volcaniclastic rocks and subaerial lava flows (Kříž 1992).

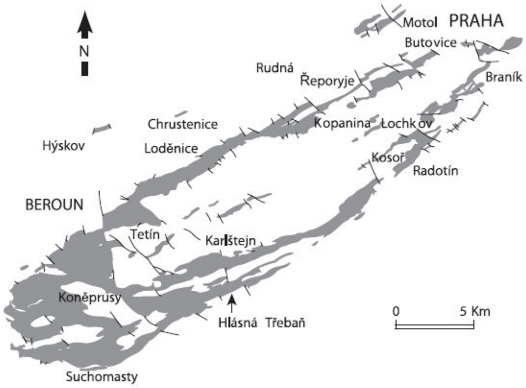

Fig. 6.15. Distribution of the Silurian rocks in the Prague Basin (after Kříž 1992).

In the late Wenlock (Homerian) and the Ludlow eustatic movements were a primary cause of basin shallowing (Kříž 1991, 1998*b*). In the deeper parts of the basin but still in a shelf environment, eustasy had less influence and the facies and pelitic or tuffaceous-pelitic sedimentation of the shelly fauna facies was dominant. During periods of volcanic activity the tuffaceous admixture of volcaniclastics increased.

The activity of the Svatý Jan Volcanic Centre (Fig. 6.18) terminated during the latest Wenlock and early Ludlow (Gorstian) with repeated basaltic lava flows into the shallow-marine environment (Fiala 1982). A thick lava sheet (up to 60 m thick) covers earlier volcaniclastic deposits. The latest Přídolí brachiopod and crinoid limestones of the carbonate platform locally overlay the lava sheet. This indicates that during the late Homerian, Gorstian, Ludfordian, and most of the Přídolí, the top of the volcano was above sea level. A land flora with a highly diverse assemblage of trilete miospores and cryptospores of the *Artemypyra brevicosta–Hyspanaediscus verrucatus* Assemblage Zone was discovered in close proximity to the Svatý Jan Volcanic Centre in upper Wenlock tuffaceous shales and limestones (Dufka 1995*a*,*b*). These fossils support the hypothesis that the volcano formed, at least at that time, a subaerial volcanic island.

The Přídolí in the Prague Basin is characterized by laminated limestones and calcareous shales. The international boundary stratotype of the base of the Přídolí Series is defined in this basin (Fig. 6.19) (Kříž *et al*. 1986). The late Přídolí regression led to the deposition of shallow-marine bioclastic limestones with abundant cephalopods, bivalves, brachiopods and crinoids (similar to the Carnic Alps, eastern Serbia, and the Montagne Noire). In other parts of the world, this lowstand culminated in a transition from marine to non-marine facies (Kříž *et al.* 2003).

The most important feature for correlation with other Gondwana regions is the cephalopod limestone lithofacies which is found in the shelly fauna facies of the Prague Basin form at least 11 horizons (Kříž 1998*a*), notably across the Homerian–Gorstian boundary, in the late Gorstian, the early and late Ludfordian, and in the earliest and latest Přídolí. This lithofacies was deposited below storm wave base, but within the reach of surface currents ventilating the sea bottom (Ferretti & Kříž 1995). It is characterized by the presence of recurring communities dominated by bivalves (*Cardiola* Community Group; Kříž 1999*a*), and by abundant cephalopods and other molluscs whose larvae could be

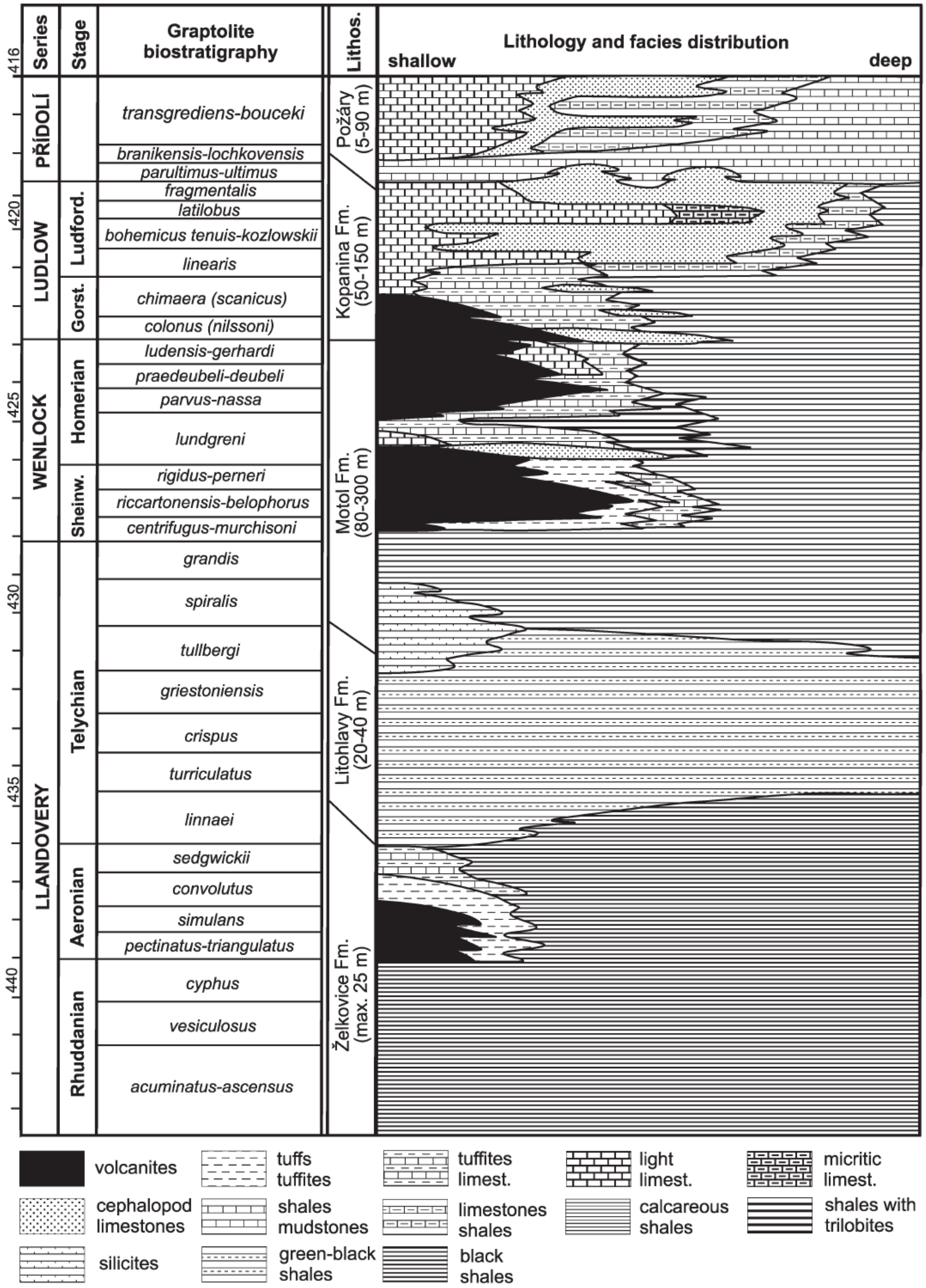

Fig. 6.16. Silurian biostratigraphy, lithostratigraphy and facies development of the Prague Basin (after Kříž 1992, 1999*b*).

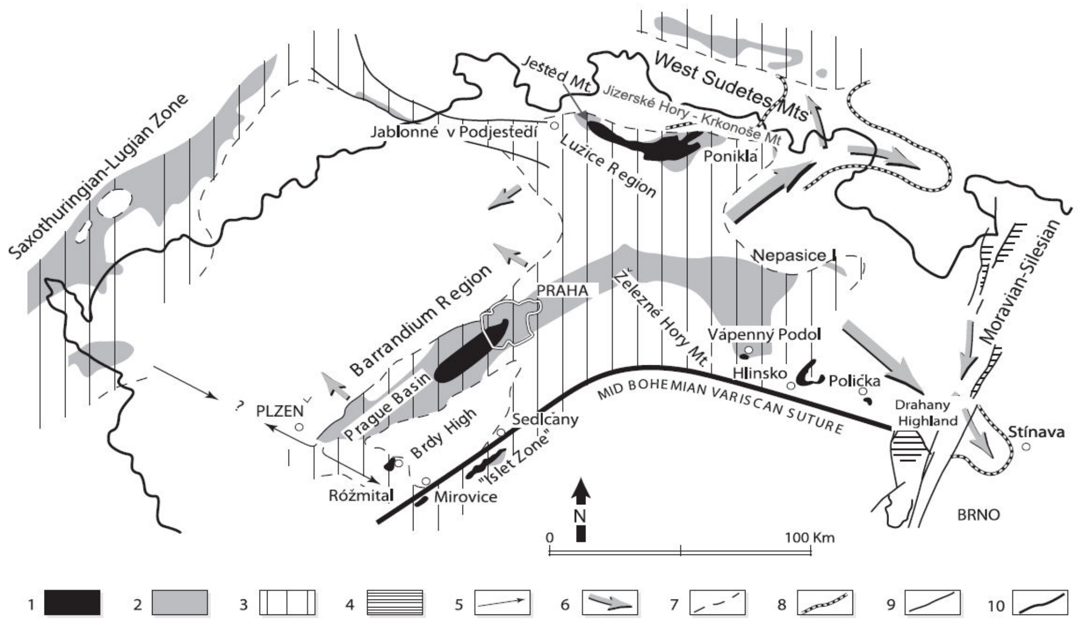

Fig. 6.17. Silurian in the Bohemian Massif. Key: 1, Silurian outcrops and subcrop; 2, Ordovician outcrops and subcrop; 3, presumed original extent of Ordovician; 4, crystalline rocks of possible Ordovician and Silurian age; 5, zone of possible communication between the middle Bohemian Region and the Saxothuringian–Lugian Zone; 6, Silurian transgression directions outside the Ordovician basins; 7, presumed Ordovician shoreline; 8, presumed Silurian shoreline where it differs from the Ordovician seashore; 9, younger faults responsible for the reduction of the original areal extent of Palaeozoic basin; 10, younger faults bordering limnic Permo-Carboniferous of the Boskovice Furrow (after Havlíček 1980).

transported by surface currents to other northern Gondwana areas (Kříž 1998*a*).

The Silurian near Stínava in the Drahany Highland (Fig. 6.17) is similar to that of the deeper parts of the Prague Basin. The lower part of the sequence is represented by black graptolitic shales (upper Telychian) and the upper part by a shelly fauna facies, represented by calcareous shales with limestone nodules (lower Gorstian) containing cephalopods, bivalves (*Cardiola, Patrocardia* and *Dualina*) and crinoids. The thickness is *c.* 100 m (Bouček 1935).

Outside the Prague Basin and the Moravo-Silesian region, the Silurian of the Bohemian Massif contains the **Thuringian facies** typically developed in the Thuringia Forest (see above) (Kříž *et al.* 2003). In central Bohemia in the 'Islet Zone' and the Železné Hory Mountains, the Silurian (Llandovery–Ludlow) contains black graptolitic shales and, in the upper part, black crinoidal limestones with cephalopods. In the 'Islet Zone' Silurian rocks have undergone contact metamorphism into chiastolite–cordieritite graphitic slates and hornfels, with graptolites still recognizable and hence allowing a general dating as the Silurian (Chlupáč 1989). Thin carbonate beds with remains of *Scyphocrinites* are developed at the Přídolí–Lochkovian boundary.

The Silurian in the Jizerské Hory–Krkonoše Mountains (west Sudetes) is developed as dark graphitic phyllites and laminated cherts (Chlupáč 1993). A limestone at the top of the Silurian near Křižany, in the Ještěd Mountains (Fig. 6.17), exhibits a lithology similar to that of the Ockerkalk Group known elsewhere in the Saxothuringian Zone. Black graptolitic shales with cherts constitute the thin Silurian succession of the Sedlčany-Krásná Hora metamorphic 'Islet Zone', the Rožmitál area and the Mirovice metamorphic area (Havlíček 1977; Štorch *et al.* 1984) and of the Hlinsko Region (Horný 1956). The entire Silurian in the Rožmitál area is only 40–50 m thick (Havlíček 1977).

The Thuringian facies is believed to be a deep-marine deposit. However, in the Silurian of the Bohemian Massif there are indications of possible subaerial emergence during Silurian times. In the Rožmitál area, Lower Devonian conglomerates contain boulders of Cambrian sandstones and of non-metamorphosed or slightly metamorphosed Proterozoic sedimentary rocks. The presence of volcaniclastic rocks supports the idea that exposed areas of Cambrian rocks in the Brdy High (also called Brdy Elevation) (Fig. 6.17) were not covered by the Ordovician and Silurian seas (Havlíček 1980). Additionally, in the Nepasice borehole (Fig. 6.17) near the town of Hradec Králové, Lower Devonian sediments have been documented directly overlying a Proterozoic basement (Havlíček *et al.* 1994).

Lithostratigraphy in the Prague Basin

The Želkovice, Litohlavy, and Motol formations span the early Silurian (Kříž 1975) (Fig. 6.16). The base of the Želkovice Formation correlates with the Ordovician–Silurian boundary and is identified by the dark shales of the *Akidograptus ascensus – Parakidograptus acuminatus* zones. The Litohlavy

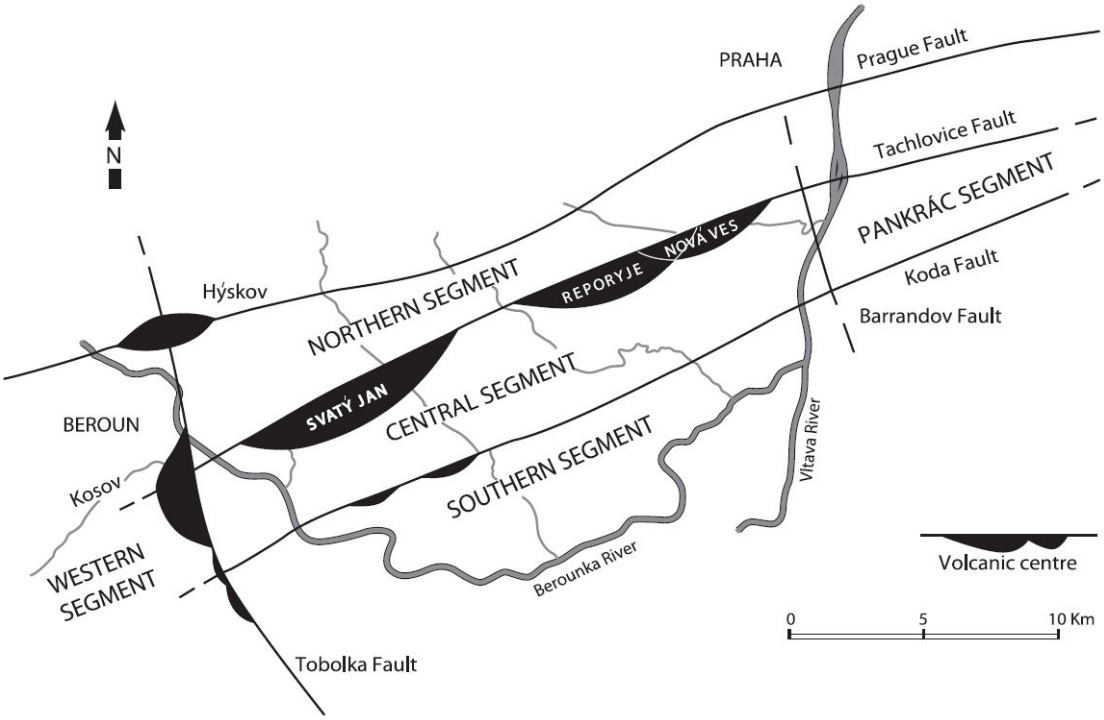

Fig. 6.18. Map with Silurian synsedimentary tectonics, volcanic centres and segments (sub-basins) in preserved parts of the Prague Basin (after Kříž 1991).

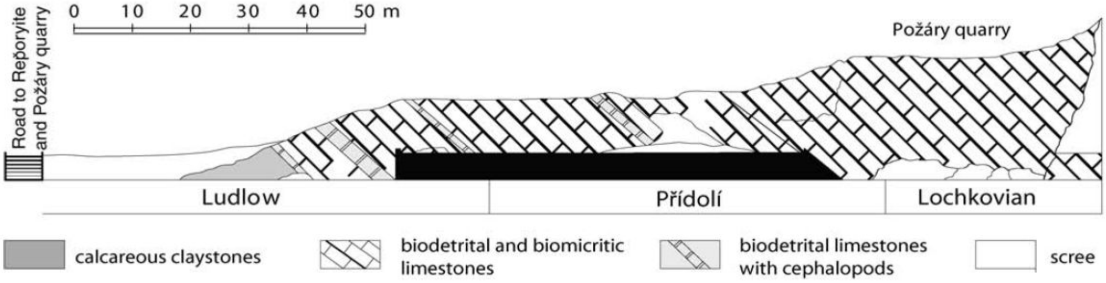

Fig. 6.19. Schematic representation of the GSSP international boundary stratotype in the Požáry quarry near Praha-Řeporyje (after Kříž *et al.* 1986).

Formation, developed as an alternation of black graptolite shales and greenish bioturbated calcareous claystones, overlies these dark shales. A thick band of green calcareous shales to clayey limestones defines the base of the Litohlavy Formation. Above this formation the Motol Formation is developed as calcareous dark shales.

The late Silurian (Ludlow and Přídolí) is represented by the Kopanina and the Požáry formations (Fig. 6.16). Considerable facies diversity has led to the definition of the lower boundary of the Kopanina Formation at the base of the *Colonograptus colonus* (= *Neodiversograptus nilssoni*) Zone. The lower boundary of the Požáry Formation at its stratotype in the Požáry Quarries near Praha-Řeporyje (Fig. 6.18) is defined just above the top of the massive cephalopod limestone (Kříž *et al.* 1986).

The thickness of the Silurian rocks in the Prague Basin (Fig. 6.16) is more than 580 m in those regions of igneous activity where thick volcaniclastic successions occur (Kosov and Svatý Jan volcanic centres). In the deep-water areas of the western and southern parts of the Prague Basin, the prevailing shelly fauna facies sediments have a maximum thickness of 450 m. The thickness is much less in the eastern part of the southern and northern segments of the basin.

Biostratigraphy of Perunica

The Silurian fossils of Bohemia have been studied for more than 230 years since the first reports by Zeno (1770). Joachim Barrande (1799–1883) travelled throughout the whole area of central Bohemia during 1840–46 (Barrande 1846) and surprised the scientific world in 1852 with the first volume of his monumental work 'Silurian System in Central Bohemia' with accurate drawings and detailed observations. Between 1872 and 1881 he published a further 20 volumes describing more than 2000 Silurian species of fossil crustaceans, cephalopods, brachiopods and bivalves.

In all of the Bohemian regions, the Silurian is dated mostly by graptolites (Štorch 1994). At Poniklá in the west Sudetes (Fig. 6.17) Horný (1964) described well preserved graptolites from phosphatic concretions embedded in graphitic phyllite, which indicated a Wenlock age. The upper part of the Ockerkalk Group limestone contains columnals and stems of the crinoid *Scyphocrinites*, the only fossil which could be identified. *Scyphocrinites* typically occurs in the uppermost Silurian and in the lowermost Devonian. Graptolites in shales of the Rožmitál area of the Bohemian 'Islet Zone' indicate the presence of the Telychian–Sheinwoodian boundary, the Homerian and the early Gorstian. In the Mirovice metamorphic 'islet', graptolites allowed the rocks to be dated to the Homerian. Two horizons in the Sedlčany-Krásná Hora metamorphic 'islet' are dated by graptolites as mid-Llandovery and as close to the Llandovery–Wenlock boundary. In the Železné Hory Mountains, the Silurian phyllitic black shales are dated using the presence of late Telychian, Sheinwoodian, Homerian and earliest Gorstian graptolites. The occurrence of *Scyphocrinites* in upper black limestones indicates a Přídolí age. In the Lower Palaeozoic Hlinsko Region several graptolite biozones from the Aeronian and Telychian have been recognized.

In the Prague Basin, the entire Silurian succession is palaeontologically well-dated (see Kříž 1991, 1992, 1998*b*) (Fig. 6.16). Štorch (1994) recognized 27 graptolite biozones in the Llandovery and Wenlock. Štorch (1995*a*) recognized eight graptolite biozones in the Ludlow, and Jaeger (in Kříž *et al*. 1986) six graptolite biozones in the Přídolí. Walliser (1964) identified 11 successive conodont biozones in the Wenlock to Přídolí carbonate facies. Schönlaub (in Kříž *et al*. 1993) studied the Wenlock–Ludlow boundary conodonts. A detailed (bed by bed) conodont biostratigraphy was established for the Ludlow–Přídolí boundary interval (Schönlaub in Kříž *et al*. 1986). Chitinozoan biostratigraphy for the Ludlow–Přídolí boundary interval was documented in detail by Paris (in Kříž *et al*. 1986). Dufka (1992, 1995*a*) and Dufka *et al*. (1995) recognized the Lower Silurian chitinozoan biozones from the global chitinozoan biozonation of the Silurian (Verniers *et al*. 1995). The Silurian near Stínava is correlated with the *Oktavites spiralis* and *Stomatograptus grandis* zones (late Telychian) and the *Cyrtograptus lundgreni* and *Colonograptus ludensis* zones (Homerian). Co-occurrences of graptolites and bivalves (*Cardiola, Patrocardia* and *Dualina*) allowed correlation of the uppermost part of the succession with the *Colonograptus colonus* Zone of the lower Ludlow (Bouček 1935). Bouček & Přibyl (1955) and Hansch (1993) developed a biostratigraphy based on ostracods, and Kříž (1999*c*) established a biostratigraphy of the upper Wenlock, Ludlow and Přídolí based on bivalve-dominated communities occurring in the shales and cephalopod limestone levels. He correlated these communities in the shelly fauna facies between Perunica and other areas of Gondwana such as eastern Serbia and Moesia or the East European Platform (Kříž *et al*. 2003). Each cephalopod limestone level in the Prague Basin has been well dated by graptolites and conodonts (Kříž 1998*a*).

Italia or Apulia Terrane (Austria)

In the Austrian part of the Alps well-studied, sometimes richly fossiliferous, Silurian outcrops occur in different nappes or tectonic windows. The most continuous sections are present in the Carnic and Karawanken Alps (northern margin of the Southern Alps), which show a facies very similar to northern Gondwana and are thought, by some authors, to belong to the same terrane. Further to the north, the Grauwacke Zone trends east–west from Styria via Salzburg to the Tyrol. In the Rannach Nappe, near Graz (Styria) and in the Gurktal Nappe, a facies similar to the Prague Basin facies is present.

Since the discovery of Silurian fossils in the Austrian Alps by Hauer (1847), knowledge of the Silurian has increased considerably. The Cellon section in the Carnic Alps became not only the stratotype section for the Silurian in the eastern and southern Alps (Fig. 6.20), but also the standard for the globally applicable conodont biozonation (Walliser 1964). An extensive summary of the Silurian of Austria is given in Schönlaub (1993, 1994*b*) and Kříž *et al*. (2003); the summary below is based on these works, as well as Schönlaub & Histon (1999) and Schönlaub *et al*. (2004).

The Silurian deposits of Austria vary from shallow-marine carbonates to graptolitic shales, with regionally similar thicknesses (normally not more than 60 m) and differences in facies patterns, rates of subsidence, source areas, fossil distributions, degrees of volcanic activity and the spatial and temporal relationships of climate-sensitive rocks such as coral and algal-bearing limestones, ooliths, coal beds and evaporites (Schönlaub 1993). The strata can be locally very fossiliferous with different distinct faunal assemblages containing varying amounts of nautiloids, trilobites, bivalves, brachiopods, graptolites, conodonts, foraminiferans, acritarchs, chitinozoans and ostracods. Complete but condensed successions occur in the carbonate-dominated facies and a continuous succession is present in the graptolite-bearing sequences, especially in the Carnic and Karawanken Alps. In other areas, due to poor preservation, the lack of fossils and metamorphic overprinting, stratigraphic continuity has yet to be demonstrated. The strata have mostly been dated by graptolites and conodonts, but other groups such as trilobites, bivalves, chitinozoans and acritarchs have also been used. Brachiopods, bivalves, and nautiloids are used for palaeoecological and palaeogeographical reconstructions.

The Periadriatic Line is a structurally important Alpine fault zone (Fig. 6.20). The Carnic and Karawanken Alps are located to the south of it whereas the Grauwacke Zone, the Rannach Nappe in the Graz area and the Gurktal Nappe are to the north. Although there are some similarities between these two areas, separated by the fault zone, there are also important differences. For example, siliciclastic rocks of Ordovician to Devonian age, as well as intense basic volcanism indicating crustal extension, dominate the area north of the fault, while thick carbonate deposits of Devonian age including reef limestones mainly occur in the Carnic Alps to the south of the Periadriatic Line. Interestingly, in the stratigraphic record corals make their first appearance north of the Periadriatic Line in the late Llandovery, i.e. some 20 Ma earlier than in the south where they first show up in strata of Ludlow age. The increased input of siliciclastic material of Ordovician to Silurian age suggests proximity to a continental source for the northern area, while the region to the

Fig. 6.20. Main regions of anchizonal to lower greenshist metamorphosed Palaeozoic strata in Austria. The Periadriatic Line separates the Carnic Alps and the Karawanken Mountains (Southern Alps) from other Alpine Palaeozoic remnants belonging to the Eastern Alps. The Wildseeloder and the Glemmtal units are too small to be located on the map: they are situated in the Kitzbühel Alps (after Hubmann *et al.* 2003).

south may represent an open marine setting far from any continental influence.

Carnic and Karawanken Alps

In the Carnic Alps, the Silurian transgression begins in the earliest Llandovery. At present, there is no record in the Carnic Alps of the *Akidograptus ascensus* Zone, the basal biozone of the Silurian, but the overlying *Parakidograptus acuminatus* Zone is present and situated very close to the Ordovician–Silurian boundary. Due to the unconformable contact separating the Ordovician and Silurian strata in both the Carnic and Karawanken Alps, a sedimentary rock unit is inferred to be missing. This gap may cover several Llandovery and Wenlock conodont biozones. In some locations where basal Lochkovian strata disconformably rest upon Upper Ordovician limestones, the Silurian may even be absent (Schönlaub 1971).

Four major depth- and energy-related (litho)facies have been distinguished for the Silurian of the Carnic and Karawanken Alps reflecting areas with different rates of subsidence. The first two are equivalent to the shelly fauna facies of northern Gondwana and the fourth to the Thuringian facies. The third facies is intermediate. The Wolayer facies was deposited in the shallowest, current-influenced environment. The Plöcken facies represents a moderately deep-marine, but still shelf environment and is exposed in the classic Cellon section. The Findenig facies is intermediate between the deeper shelf and the basinal environment and the graptolitic Bischofalm facies was deposited in a euxinic stagnant water basinal setting. Sediments from the Llandovery to the lower Ludlow indicate a steady trend of basin subsidence and an accompanying increase in water depth. This rise in sea level apparently decreased in the Upper Ludlow and possibly ceased during the Přídolí leading to uniform limestone deposition. Simultaneously, the black graptolitic shales in the Bischofalm facies were replaced by the green and grey shales of the Middle Bischofalm Shale. The appearance of the Bischofalm facies signals the reestablishment of a deep-water graptolitic environment at the top of the Silurian which subsequently persisted until the end of the Lochkovian (Fig. 6.21).

In the shallow environment of the **Wolayer facies** fossiliferous limestones with abundant orthocone nautiloids, numerous trilobites and bivalves, small brachiopods, gastropods, crinoids and rare corals were deposited (Gaertner 1931; Haas 1968; Ristedt 1968; Kříž 1979, 1999*b*; Schönlaub 1980; Histon 1999, 2002; Ferretti *et al*. 1999; Santel 2001). The Wolayer facies is named after the Upper Ordovician cystoid-bearing Wolayer Limestone. Due to the slow rate of subsidence and a hiatus at the base this facies is only 10 to 15 m thick. The type sections, including the Rauchkofel Boden section (Figs. 6.20 & 6.22), are located in the Lake Wolayer region of the central Carnic Alps (Gaertner 1931; Schönlaub 1971, 1980; Schönlaub & Histon 1999; Ferretti *et al*. 1999). This unit is overlain by the grey highly fossiliferous Orthoceras Limestone of latest Llandovery, Wenlock and Ludlow age (Ferretti 2005). Where this facies occurs the uppermost Ordovician to the lower Silurian strata are missing, in a sedimentary gap ascribed to the Hirnantian eustatic sea-level fall and its aftermath. In the overlying strata, conodonts of the *Ozarkodina sagitta* Zone (basal Homerian) are fairly abundant. The appearance of the conodont index species *Kockelella variabilis* suggests the base of the Ludlow as is the case in Bohemia (H.P. Schönlaub in Kříž *et al.* 1993). The overlying Cardiola Formation corresponds to the *Polygnathoides siluricus* conodont Zone of the same formation in the Cellon section. It is succeeded by pinkish and greyish limestones corresponding to the Alticola and Megaerella limestones of the Cellon section. However, diagnostic conodonts have not yet been found in these latter units at Rauchkofel Boden except from the uppermost limestone level. This highest conodont fauna contains common specimens of the *Ozarkodina remscheidensis eosteinhornensis*

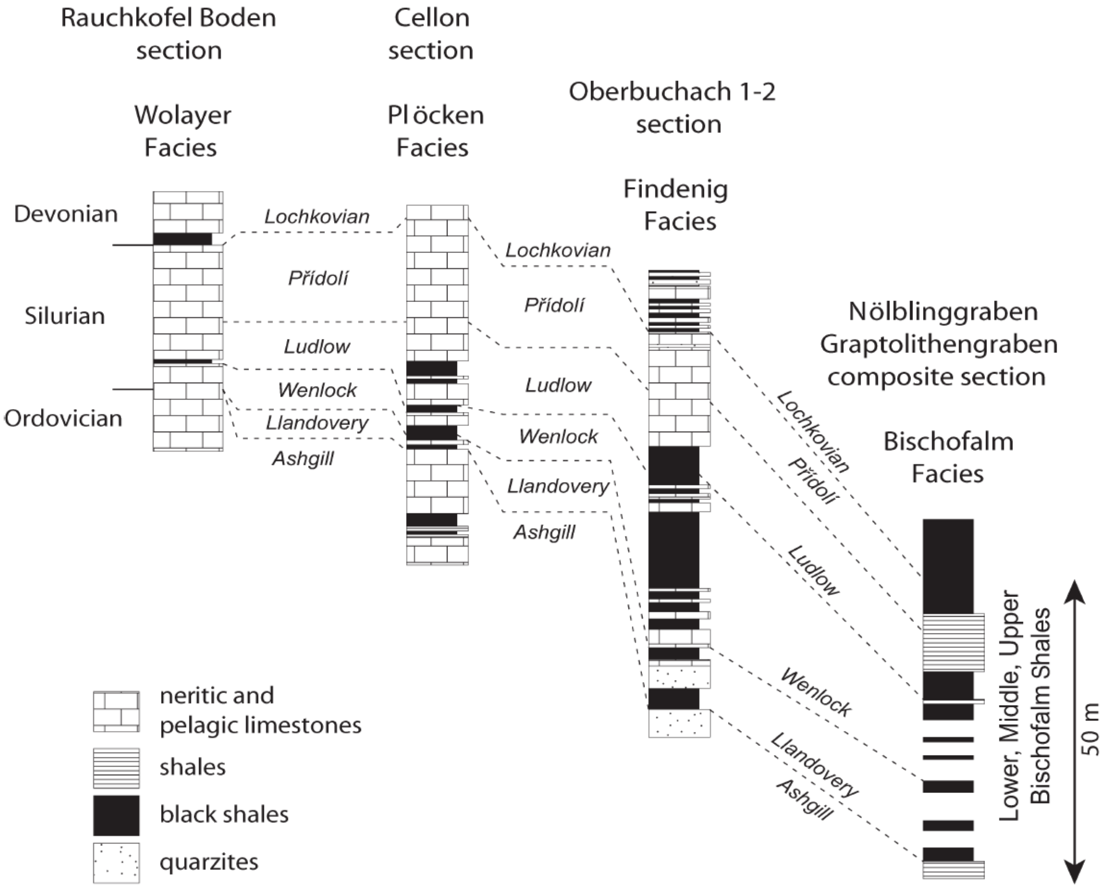

Fig. 6.21. Lithology and lithostratigraphical column of the Silurian of the four different lithofacies of the Carnic Alps. The black shales include C_{org}-rich graptolite-bearing shales and cherts and C_{org}-rich carbonates of the Wolayer facies; other shales are C_{org}-poor. In the Nölblinggraben-Graptolithengraben composite section Lower Silurian sediments are not continuously exposed (after Wenzel 1997).

Zone, indicating that the uppermost Přídolí is in bed number 331 (Schönlaub 1980; Schönlaub & Kreutzer 1994; Kříž 1999*b*) and the Silurian–Devonian boundary is situated just above this level and below the beds containing *Scyphocrinites*. Preliminary palaeoecological and palaeogeographical analyses from the Rauchkofel Boden section indicate a shallow-marine depositional environment with significant current activity. Orthocone cephalopod conchs are orientated from SW to NE in the Kok Limestone and change to a NNE to SSW direction in the overlying Lochkovian suggesting significant changes in the oceanic circulation systems around the Silurian–Devonian boundary (O. K. Bogolepova in Schönlaub & Kreutzer 1994).

The **Plöcken facies** contains, from bottom to top (Fig. 6.23), the Plöcken Formation (calcareous sandstone, Hirnantian, 4.8 m); the Kok Formation (pelagic ferruginous nautiloid limestones, with shale interbeds at the base, upper Llandovery to Wenlock, 13 m); the Cardiola Formation (alternating black limestones, marls and shales, Ludlow, 3.5 m); the Alticola Limestone (grey and reddish), nautiloid-bearing limestones, Ludlow to Přídolí, 20 m); and the Megaerella Limestone (grey, fossiliferous limestones, Přídolí, 8 m). It forms part of a continuous Ordovician to Devonian succession where several small hiatuses were recognized reflecting sea-level changes within an overall shallow-marine to moderately deep marine environment (Schönlaub & Histon 1999). The type section is the classic 60 m thick Cellon section, well-known for its globally applicable Silurian conodont biozonation established by Walliser (1964), and refined and partly revised in other areas. According to Schönlaub (1985, 1988) and Schönlaub & Sheehan (2003) the Ordovician–Silurian boundary can be drawn between the Plöcken and Kok Formations. From the basal Kok Formation at least six graptolite and two conodont biozones are missing in the lower Silurian. Deposition began in the late Llandovery, within the *Pterospathodus celloni* Zone. Based on graptolites and conodonts, the Llandovery–Wenlock boundary should be placed between samples 11 and 12 of Walliser (1964) (Fig. 6.23) and the thickness of the Llandovery does not exceed *c.* 3 m (Schönlaub 1997). The boundary between the Wenlock and Ludlow is drawn between

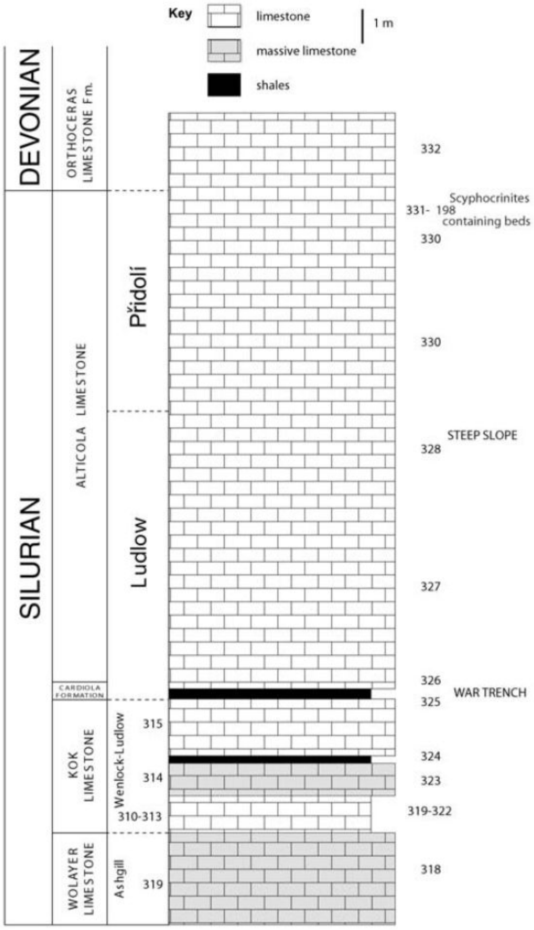

Fig. 6.22. Stratigraphic column of the Rauchkofel Boden section in the Wolayer facies. Numbers to the right of the column indicate sample numbers (after Ferretti *et al.* 1999).

samples 15B1 and 15B2 of Walliser (1964) through correlation with the stratotype in England. The thickness of the Wenlock in the Cellon section is not more than *c.* 5 m. Graptolites of the *Cyrtograptus rigidus* Zone in the shaly interbed between samples 12B and 12C clearly indicate a late Sheinwoodian age. Schönlaub (1994*b*) inferred that the lowest Homerian is missing.

The Ludlow–Přídolí boundary was placed, based on conodonts at 8 m above the base of the Alticola Limestone, a few centimetres above sample 32, by Walliser (1964) (see H.P. Schönlaub in Kříž *et al.* 1986) through comparison with the Bohemian sections and subsequently, confirmed by the occurrence, at that level of the basal Přídolí index graptolite *Monograptus parultimus* and of the basal Přídolí bivalve *Cardiolinka bohemica* community (Kříž 1999*b*). The thickness of the Ludlow is 16.45 m. The Silurian–Devonian boundary at Cellon is placed at the bedding plane between samples 47A and 47B of Walliser (1964). The Přídolí attains a thickness of *c.* 20 m at the Cellon section. The distribution of acritarchs, chitinozoans, brachiopods, bivalves, and taxonomically unrevised nautiloids and trilobites is summarized in Schönlaub & Kreutzer (1994).

A depositional gap around the base of the Silurian was caused by the latest Ordovician glacially induced sea-level fall, as in the Wolayer facies. Thereafter renewed sedimentation began in a moderately shallow-marine environment extending up into the earliest Wenlock. Bioturbated wackestones with algae and lumachelles indicate a very shallow-marine to intertidal environment at the base of sample 11 of Walliser (1964) (Fig. 6.23). Later in the Wenlock a progressive deepening occurred interrupted, however, at a sequence boundary by a hiatus at the Wenlock–Ludlow boundary. During the deposition of the Cardiola Formation, a pelagic offshore environment is indicated by the presence of radiolarian-bearing, black, marly interbeds and pelagic limestones with a diverse *Cardiola docens* community and *Cardiola pectinata* subcommunity (Kříž 1999*b*). The overlying Alticola Limestone reflects stable conditions in a pelagic setting that ended with a short regressive pulse with laminated grainstones and lumachelles recorded at a possible sequence boundary (Walliser 1964). A further deepening trend at the base of the Megaerella Limestone can be assumed (for details see Kreutzer in Schönlaub & Kreutzer 1994; Schönlaub & Histon 1999; Histon *et al*. 1999).

The **Findenig facies** (Figs. 6.20–6.24) is intermediate between the deeper shelf and the starved basinal environment and comprises interbedded, black, graptolitic shales, marls and blackish limestone beds. It is best developed in the Oberbuchach section where fossils, other than graptolites and conodonts, are very rare. The 10 m thick Hirnantian siliciclastic Plöcken Formation contains the graptolite ?*Normalograptus normalis* *c.* 1 m below its top; it is locally covered at its base by quartzose sandstones and higher up by a mixed argillaceous–calcareous lithology referred to as the Nölbling Formation (*c.* 50 m) of Llandovery to early Ludlow age. The lower siliciclastic part of the formation is overlain by an unnamed unit of interbedded laminated pyritic sandstones, bedded black cherts and black shales with a graptolite fauna of the *Coronograptus gregarius* and the *Demirastrites triangulatus* zones (early Aeronian). It is not yet clear whether the lower Llandovery is missing or simply unfossiliferous at this section. Higher up in the succession, a second horizon of graphitic sandstones with a late Llandovery age occurs. This is inferred from the presence of diagnostic conodonts of the *Pterosphatodus celloni* Zone in limestones overlying this siliciclastic interval. The limestones are overlain by an alternating sequence of dark argillaceous limestones, black graptolite shales and cherts. Index conodonts occur only from the uppermost Llandovery to the Wenlock while graptolites occur over a larger range from the uppermost Llandovery to the Ludlow. In the overlying shales, graptolites occur at several levels indicating the *Monograptus riccartonensis* Zone (Sheinwoodian) up to the *Neodiversograptus nilssoni* Zone (lower Gorstian). At the Oberbuchach section the Wenlock–Ludlow boundary is placed some 40 m above the base of the graptolite-bearing sequence starting near the base of the Silurian. Strata containing the remaining part of the Ludlow and Přídolí are up to 20 m thick. This interval consists of lithologically distinct grey, and almost unfossiliferous pyritiferous limestones with a characteristic weathered surface (Schönlaub 1980).

The stagnant-water graptolitic **Bischofalm facies** is represented by 60–80 m of black siliceous shales, black cherty beds, and clayey alum shales containing abundant graptolites. The purely graptolitic facies is best exposed in the so-called 'Graptolithengraben' north of the Obere Bischofalm in the central Carnic Alps. Graptolites and a few conodonts on bedding planes

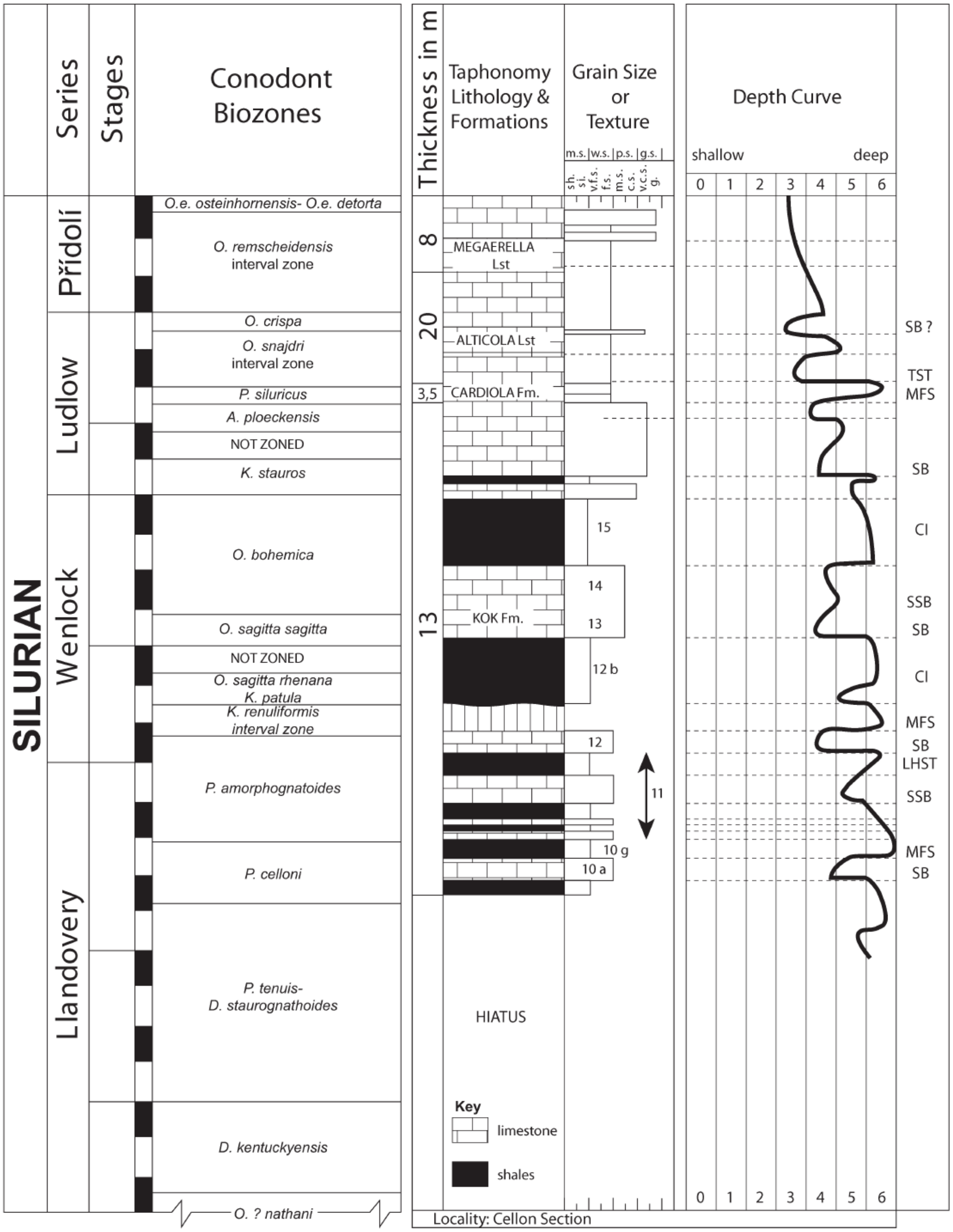

Fig. 6.23. Conodont stratigraphy, lithology, grain size, significant taphonomic features, depth curve and elements of the sequence stratigraphy of the Silurian of the Cellon section (modified from Schönlaub 1997). Abbreviations in grain size/texture column: m.s., mudstone; w.s., wackestone; p.s., packstone; g.s., grainstone; sh., shale; s.i., silt; v.f.s., very fine sand; f.s., fine sand; m.s., medium sand; c.s., coarse sand; v.c.s., very coarse sand; g., gravel; numbers represent Walliser samples. Abbreviations in depth curve column: CI, contourite interval; LHST, late highstand systems tract; MFS, maximum flooding surface; SB, sequence boundary; SSB, subsequence boundary; TST, transgressive systems tract (modified from Schönlaub 1997).

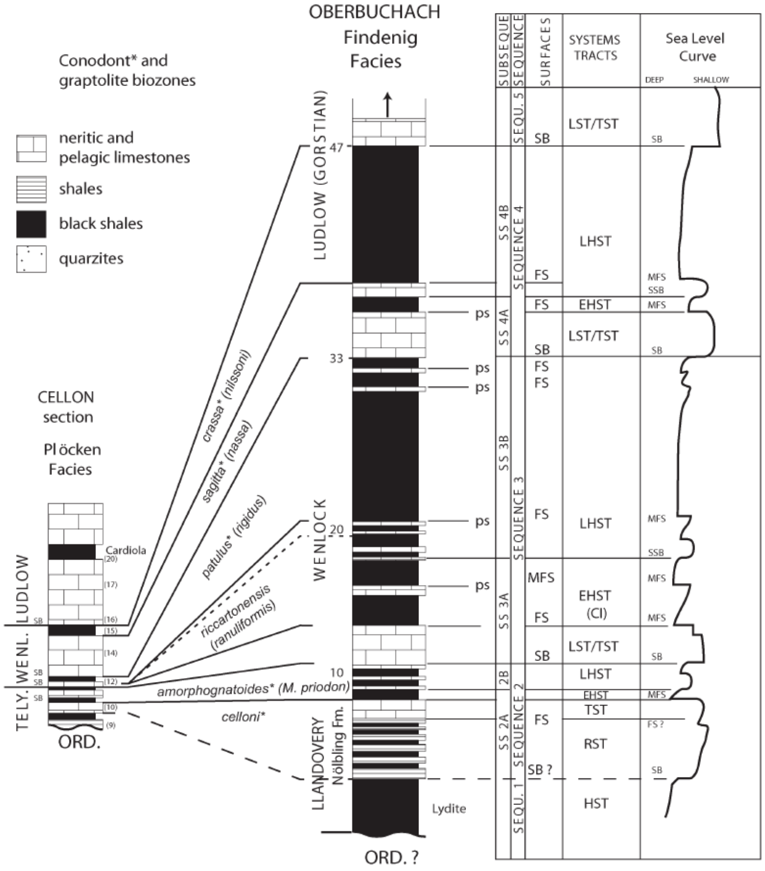

Fig. 6.24. Correlation and sequence stratigraphical interpretation of the Llandovery to Lower Ludlow of the Carnic Alps (after Brett & Schönlaub, 1998). Abbreviations: CI, contourite interval; EHST, early highstand systems tract; FS, flooding surface; HST, highstand systems tract; LHST, late highstand systems tract; LST/TST, lowstand systems tract and transgressive systems tract; MFS, maximum flooding surface; SB, sequence boundary; SSB, subsequence boundary; SS2A, subsequence 2A; TST, transgressive systems tract (after Brett & Schönlaub 1998).

are the only fossils found and have been known in the Alps since their discovery by Stache (1872). The graptolites are common in many layers both in the alum shales and in the siliceous shales. Some intervals, however, are almost barren of graptolites. The best exposed, and tectonically least disturbed, section is the main section (Hauptprofil), which has been studied in great detail since 1965 (e.g. Jaeger 1975; Flügel *et al.* 1977; Jaeger & Schönlaub 1977, 1980, 1994; Schönlaub 1985). Jaeger (1975) subdivided the Bischofalm facies into three units, the Lower, Middle and Upper Bischofalm Shales. They are included in a monotonous sequence of interbedded radiolarian-bearing cherts and alum shales. The cherts dominate the Llandovery and Wenlock while the shales prevail in the upper part of the succession. The green and grey shales of the Middle Bischofalm Shales yield only a few graptolites in very thin layers (H. Jaeger in Flügel *et al.* 1977). An almost 20 m thick undisturbed sequence is present in the main section and covers the interval from the *Pristiograptus ludensis* Zone of the uppermost Wenlock to the Lower Devonian *Monograptus hercynicus* Zone. The thickness of the composite section of graptolite-bearing Silurian to Lochkovian rocks ranges from 50 to 100 m. The very complete graptolite biozonal succession and the condensed nature of the succession are probably due to a very low, but nevertheless continuous, rate of deposition. The environmental conditions were anoxic or strongly dysaerobic except during the short interval corresponding to the deposition of the Middle Bischofalm Shale (Jaeger 1975; Flügel *et al.* 1977). The Silurian–Devonian boundary is within a homogenous black-shale facies of the Upper Bischofalm Shale, with no physical break at the boundary (H. Jaeger in Flügel *et al.* 1977). However, a distinct change in facies from green and grey shales to black shales preceded by one graptolite biozone marks the faunal change at the boundary. Additionally the Middle Bischofalm Shale occupies the same stratigraphic position as the non-graptolitic Ockerkalk of Thuringia.

The abundant presence of K-bentonite horizons in the Llandovery–middle Ludlow successions of the Carnic Alps is similar to that recorded in the British Isles, Sweden, Canada and North America, and documents widespread volcanism related to the closing of the Iapetus Ocean. Silurian K-bentonites of Přídolí age may be comparable with those described from Podolia

(Ukraine) for which a source area in the Rheic Ocean has been indicated (Bergström *et al.* 1998; Huff *et* al. 1998, 2004).

The Grauwacke Zone

The locations of the outcrop areas described below are given for their respective Austrian provinces (Länder), for example Styria or Salzburg Land. The Grauwacke Zone which contains a thick Lower Palaeozoic succession extends over a great distance in a series of different nappes; in the east (Steiermark) it comprises the eastern Grauwacke Zone and in the west (Salzburg Land and Tyro) the western Grauwacke Zone. The Silurian of the Grauwacke Zone in the Tyrol and Salzburg Land is fairly well known, but less so in Steiermark. The bio- and chronostratigraphy is based on conodonts and graptolites (Schönlaub & Kreutzer 1994).

In the eastern Grauwacke Zone, the 50 m thick Silurian succession shows two successive facies: (1) a crinoid- and nautiloid-bearing limestone with local intercalations of Llandovery basic volcanics, overlain by (2) black graptolite shales. These two facies pass laterally and vertically into interbedded limestones and shales, overlain by upper Ludlow and Přídolí limestones (Schönlaub 1979; Schönlaub & Heinisch 1993).

In the western Grauwacke Zone close together and more specifically in the Kitzbühel Alps two other lithofacies occur (Heinisch 1988). Both facies are incorporated in the two nappes: the Wildseeloder Unit in the north and the Glemmtal Unit in the south. Lithologically the Silurian comprises black shales, locally with graptolites, cherts, siliceous pelagic limestones to condensed cephalopod limestones, and dolomitic rocks (a variation of the shelly fauna facies).

In the Wildseeloder Unit the thick Upper Ordovician Blasseneck Quartz porphyry is overlain by several metres of Silurian deposits. Two important sections are representative for the two facies: the classic graptolite-bearing Lachtal-Grundalm section and the Spießnägel section. The first of these is located near the village of Fieberbrunn, east of Kitzbühel. There are no biostratigraphic data to locate precisely the Ordovician–Silurian boundary (Schönlaub & Kreutzer 1994). The less than 5 m thick middle and upper Llandovery 'Lydit-Kieselkalk-Komplex' comprises a mixed pelagic shale-limestone succession. The basal chert interval comprises black, massive cherts (lydites in the Alpine terminology) with radiolarian-bearing dolostones and reddish, cherty limestones that grade vertically into crinoidal limestones. The fauna consists of ostracods, foraminifers, brachiopods, radiolarians, conodonts and echinoderms. Additionally, bivalves, solitary corals, trilobites and orthocone nautiloids occur in the lower 1.40 m of the crinoidal limestone. The basal 2.10 m of the crinoidal limestone succession is assigned to the *Pterospathodus celloni* Zone (Telychian) and the upper part to the *Pterospathodus amorphognathoides* Zone (Llandovery–Wenlock transition). It is overlain by a 5 m thick Dolomit-Kieselschiefer-Komplex (Bedded Dolostone-Chert Formation) (Mostler 1966) a lithology resembling the Nölbling Formation of the Finderig facies in the Carnic Alps. The only identifiable graptolites occur in a horizon near the top of the Dolomit-Kieselschiefer-Komplex (Jaeger 1978); *Bohemograptus bohemicus* are characteristic of the *Neodiversograptus nilssoni* Zone (lower Gorstian).

The Spießnägel section, south of the village of Kirchberg and west of Kitzbühel, is one of the few sections with an exposed transition from presumably Upper Ordovician greywackes into the basal Silurian. According to Al-Hasani & Mostler (1969), the Silurian begins with 0.70 m of bioturbated mudstones with varying amounts of siliciclastic and tuffaceous material grading into 0.15 m of wackestones. Both units contain diagnostic conodonts of the *Pterospathodus celloni* Zone (late Llandovery). It is succeeded by 1.10 m of limestones with interbedded shales and thin limestone lenses, containing packstones with thin hash layers of bivalves, brachiopods, ostracods and echinoderms. The limestones are in turn overlain by greyish laminated dolostones assigned to the *Pterospathodus amorphognathoides* Zone and the lower Wenlock *Kockelella patula* Zone.

In the western part of the western Grauwacke Zone (Tyrol), the Dolomit-Kieselschiefer-Komplex is covered in turn by upper Silurian platform carbonates with dolomitic rocks and magnesite. According to Mostler (1966), the base of these carbonates can be assigned to the *Polygnathoides crassa* Zone near the Wenlock–Ludlow boundary or to the base of the overlying *Ancoradella ploeckensis* Zone near the Gorstian–Ludfordian boundary. No record of the Přídolí is yet available, although it may be present in the recrystallized dolostones.

The Glemmtal Unit comprises, in contrast to the Wildseeloder Unit, a mainly siliciclastic succession of more than 1000 m known as the Wildschönau Group with two formations. Locally, the Klingler Kar Formation comprises up to 50 m of intercalated condensed pelagic limestones, marls, interbedded cherts, siliceous shales and basalts. The lower part of Klingler Kar Formation is dated as upper Silurian by conodonts. The facies laterally grades into the turbiditic facies of the Löhnersbach Formation which is not yet dated.

Graz area

The best outcrops for the Palaeozoic of the Graz area are in the Rannach Nappe, the uppermost nappe of the Graz Thrust Complex. The Silurian is dominated by alkaline mafic lavas and volcaniclastics, suggesting an initial rift stage. The latter are overlain by Upper Silurian and Devonian carbonates. The Silurian of the Graz area is best displayed in the Eggenfeld section.

According to Fritz & Neubauer (1988) and Neubauer (1989), sedimentation in the Silurian Kehr Formation was controlled mainly by volcanism. During the early Ludlow, the eastern depositional area was characterized by a proximal shallow-marine setting with lavas and coarse lapilli tuffs, whereas the western area was characterized by a distal facies with intercalations of lapilli-rich beds, agglomerates, shales, and pelagic limestones. The Kehr Agglomerate consists of 1 to 3% quartzite, dolostones, chert and reworked limestones clasts. During late Silurian times, the volcanic centres were covered by fossiliferous carbonates that include a *c.* 4 m thick bedded dolostone with lenses of crinoid-, brachiopod-, trilobite- and nautiloid-bearing dolomitic limestones interbedded with tuffs and tuffitic shales. Based on conodonts, a late Ludlow (Ludfordian) to Přídolí age has been determined for the upper part of this succession (Ebner 1994).

Fossils in the Eggenfeld section allow dating of the Silurian volcanic activity in the eastern Alps. Even with poor outcrop conditions a well-constrained lithostratigraphy has been established (Ebner 1994). The succession commences with massive green basalts that interfinger with pinkish to greenish tuffs with graptolites, which are overlain by dark dolostones (unit D/1) containing crinoids, brachiopods, nautiloids and tabulate corals (*Favosites* sp.) and are succeeded by tuffs and tuffaceous shales. Further up-section a second unit (unit D/2) of dark dolostones contains lens-like accumulations of crinoids, brachiopods, trilobites, nautiloids and rare corals (e.g. *Syringaxon* sp.). The uppermost Silurian (unit D/3) consists of tuffs and tuffaceous shales again with intercalations of dark dolostones containing the same fossil groups as the underlying unit. The biostratigraphy is based on the fairly abundant conodonts and brachiopods present in all of the calcareous levels. Diagnostic conodonts in the lower dolostone (unit D/1) immediately above the basalts indicate a Ludfordian age for the end of basaltic volcanism. This age is confirmed by the graptolite *Bohemograptus bohemicus tenuis* in the basal volcaniclastic layer which interfingers with the green basalt (Hiden 1996). The index species of the *O. snajdri* Zone in association with *Ozarkodina remscheidensis eosteinhornensis* in the second carbonate level (D/2) also indicates a Ludfordian age.

Similar environmental conditions are suggested for the upper Silurian rocks of the other nappes in the Graz area, where the pelagic, nodular limestone development persisted from the late Silurian through the Devonian. Indeed both carbonate production and volcanic activity subsequently increased in Devonian times.

Burgenland

During the last 20 years new fossil assemblages have been discovered from weakly metamorphosed interbedded limestones, dolomites and shales in the south of Burgenland, eastern Austria (Fig. 6.20). Based on index conodonts, an Upper Silurian portion can be clearly identified underlying a Lower Devonian rugose- and tabulate-coral-bearing carbonate succession suggesting a similar development to that of the Graz area (Schönlaub 1984, 1994*a*). Of particular interest is the first record of serpulid tubes in the late Silurian carbonate beds near Kirchfidisch and the recognition of Silurian–Devonian boundary beds with conodont index species by Suttner & Luckender (2004) and Suttner *et al.* (2004).

The Gurktal Nappe

The Gurktal Nappe, situated in central Carinthia and southern Styria, is composed of several hundred metres of volcanic and siliciclastic rocks with intercalated limestones. The Lower Palaeozoic of the Gurktal Nappe system is characterized by volcanic rocks occurring at different times, and which are of varying intensity and of different geochemical character, reflecting different palaeotectonic settings (Loeschke & Heinisch 1993). The Silurian part of the succession comprises coral-bearing bioclastic limestone lenses at the Llandovery–Wenlock transition and locally 5–10 m thick limestones and dolostones of late Silurian age. Facies development suggests a subdivision into a carbonate-rich and a carbonate-poor facies. However, bad exposures and poor fossil control do not allow the reconstruction of a composite Silurian section (Buchroithner 1979; Ebner *et al.* 1990; Schönlaub & Heinisch 1993).

Montagne Noire, France

The Palaeozoic sediments of the Montagne Noire are widely exposed and richly fossiliferous (Feist in Robardet *et al.* 1994). Silurian strata, however, are less well represented since they occur only in restricted areas in the south of the Albigeois area, the region around the city of Albi, and in the Cabrières Klippes (Fig. 6.25). Elsewhere, for example, in the 'nappes' area, Silurian deposits are absent and lower Lochkovian nearshore strata rest unconformably on the Lower Ordovician (e.g. Mont Peyroux). Thus, in the area of the nappes, pre-Devonian erosion removed a large part of the Lower Palaeozoic succession (Feist & Echtler in Feist *et al.* 1994). No recent studies have been carried out on the black carbonates and shales cropping out south of the Albigeois age, which have yielded orthocone cephalopods and bivalves (Chaubet 1937), as well as conodonts (Centène 1977) of Silurian age.

The most complete Silurian sequence of the Montagne Noire is exposed in its SE part (Chaubet 1937), in the Falgairas and Laurens plateaus belonging to the Cabrières Klippes (Feist & Echtler in Echtler *et al.* 1994). This Silurian succession, including Llandovery to Přídolí strata, is interpreted as part of a huge olistolith preserved in a Visean matrix (Engel *et al.* 1982). The setting of this gravitationally transported Silurian material corresponds to the early activity of the Variscan Orogeny. The geographical origin of this allochthonous Silurian unit would have been situated north of the area from which the 'nappes' themselves were derived. The latter are presently devoid of any Silurian deposits but Silurian black shales are known from

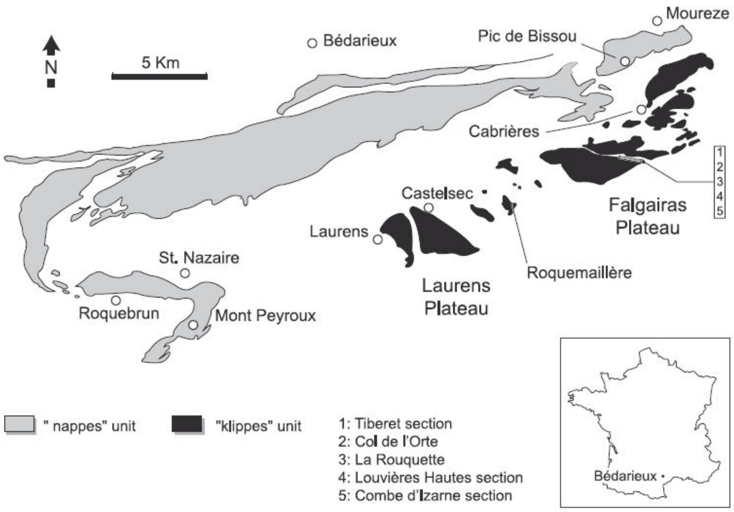

Fig. 6.25. Map of the Silurian of the Montagne Noire (after De Bock 1982).

localities further west in the subsurface of Aquitaine (Paris & Le Pochat 1994).

In the klippes of the Cabrières area, the Silurian succession commences with the Roquemaillère Black Shale (*c.* 50–70 m thick). These condensed anoxic deposits include limestone nodules and are fossiliferous. The Roquemaillère Black Shale ranges from mid-Llandovery to early Wenlock in age, with the oldest recorded graptolites in the area of late Aeronian age. The limestones and shales of the Falgairas Formation (50 to 60 m) overlie these fairly deep-water black shale deposits. The Falgairas Formation begins with platy to nodular limestone beds of Wenlock age including minor rare calcareous black shale interbeds. Ludlow strata are less fully developed. They are represented by rare metres of black calcareous mudstones and nodules with rare bedded or nodular limestones. Sedimentation was more active during the Přídolí (Feist 1977; De Bock 1982) as limestones and dolostones progressively replaced the black shales. The upper part of the Falgairas Formation records a shallowing trend, concomitant with the progressive input of detrital quartz (Feist 1977). Sandy limestones passing upward into calcareous sandstones replace the lower Přídolí limestones or dolomitic limestones. The local Silurian succession ends with the upper Přídolí Falgairas Sandstone (9 m) (Fig. 6.26). This nearshore sandy body is exposed on the Falgairas Plateau, in the Tiberet and Louvières Hautes sections (De Bock 1982) (Fig. 6.25).

Correlation

In addition to the numerous benthic fossils including trilobites, brachiopods, bivalves, ostracods and crinoids (Feist 1977), the Silurian strata of the Montagne Noire also yield a nectic and pelagic fauna (e.g. nautiloid orthocones, graptolites, conodonts, chitinozoans and acritarchs). Several Silurian graptolite biozones, i.e. *Stimulograptus sedgwickii*, *Neodiversograptus nilssoni*, *Lobograptus scanicus*, *Bohemograptus bohemicus* and *Monograptus ultimus,* in the Cabrières area (e.g. in the Roquemaillère and Combe d'Izarne sections) have been identified by Centène & Sentou (1975). Diagnostic conodont assemblages are also present all along the Silurian sequence in the Cabrières Klippes. Most of the conodont zones of the late Llandovery (i.e. *Pterospathodus celloni*, *Pterospathodus amorphognathoides),* Wenlock (e.g. *Kockelella patula*, *Ozarkodina sagitta*), Ludlow (i.e. *Ancoradella ploeckensis*, *Polygnathoides siluricus*, *Ozarkodina snajdri, Ozarkodina crispa*) and Přídolí (*Ozarkodina remscheidensis eosteinhornensis*) have been documented by Feist & Schönlaub (1974), and by Centène & Sentou (1975) in the calcareous beds and nodules of the Roquemaillère and Falgairas strata (Fig. 6.25). Deflandre (1942, 1946) reported organic-walled microfossils from the Roquemaillère Limestone (calcareous nodules of Wenlock age and undifferentiated limestone samples from the Roquemaillère section, and from the Ribouryrel Brook). These pioneer studies of acritarchs and chitinozoans gave no accurate age assignment, but later investigations by De Bock (1982) on other sections in the Falgairas and Laurens plateaus recorded chitinozoan assemblages with *Urnochitina urna* and *Eisenackitina bohemica.* These two species are the chitinozoan index fossils for the Přídolí (Verniers *et al.* 1995) and for the early Lochkovian (Paris *et al.* 2000) respectively. Thus, they allow the Silurian–Devonian boundary to be fairly precisely located in the Cabrières Klippes succession (De Bock 1982) (Fig. 6.26).

Among the benthic fauna recorded in the Silurian of the Montagne Noire, special attention has been paid to the numerous and diverse bivalves recovered from Wenlock to Přídolí strata. These bivalves allowed accurate correlation at a specific level with contemporaneous assemblages of the Prague Basin (Kříž 1996). Moreover, five distinct bivalve-dominated communities (i.e. *Cardiola* community group) have been identified in the Silurian of the Cabrières Klippes. These are also recognized in the Prague Basin and the Carnic Alps as well as in Sardinia, and the Armorican Massif (Kříž & Paris 1982). This similarity would suggest that there were close palaeobiogeographical relationships between these different regions during the Silurian. The closest relation, however, was with Sardinia, which shared three bivalve communities with the Montagne Noire (Kříž & Serpagli 1993). The bivalve diversity was higher in the Prague Basin than in Sardinia or the Montogne Noir region which were typical northern Gondwana areas (Kříž 1999*a*, *c*).

In contrast to numerous other French Silurian localities, which are devoid of trilobites (Paris in Kříž *et al.* 2003), is the occurrence of a fairly diverse trilobite fauna in the Falgairas Formation limestones and shales (see Feist 1977). The trilobites are well represented in the Wenlock part of the formation, and to a lesser extent in the Ludlow and Přídolí beds.

Lithofacies and biofacies

No sequence stratigraphical analysis is available for the Silurian of the Cabrières Klippes and therefore the regional sea-level fluctuations can only be broadly evaluated based on the lithological evidence, and on the composition of the recorded faunal assemblages (Paris, fig. 18 in Kříž *et al.* 2003). Black shales are usually regarded as representing condensed sedimentation, under low energy conditions, and probably in fairly deep marine environments. This is consistent with the prevailing occurrences of the pelagic and epipelagic faunas in these black shales from the late Llandovery to the early Přídolí. However, limestones with bivalve-dominated communities (Kříž 1996) indicate episodic shallowing events, and/or the occurrence of temporary currents interrupting or ameliorating the anoxic to highly dysaerobic conditions prevailing on the local sea bottom. As in many other northern or peri-Gondwana regions, the late Silurian regression is recognized in the sedimentary record of the Montagne Noire. The progressive shallowing is recorded by the fauna with dominantly benthic assemblages, and for the conodonts by the replacement of the ozarkodinid species with the icriodontid species, which are regarded as representative of more shallow-marine environments (Feist 1977). Hydrodynamic energy increased significantly during the Přídolí, corresponding with increased input of clastic material; the acme was the deposition of the Falgairas Sandstone in a high-energy environment.

Avalonia

In Central Europe, the Silurian rocks of Avalonia only crop out in the Brabant Massif and in the Condroz Inlier of Belgium, in the Ebbe and Remscheid inliers of Germany and in one location in the Boulonnais Inlier, northern France. In the subsurface, the Silurian is more widely present, with many boreholes in the Brabant Massif (Legrand 1969; De Vos *et al*. 1993), in northernmost France in the Artois-Boulonnais structural high (CFP. *et al.* 1965, 1966; Legrand 1969), in the subsurface of East Anglia, UK (see Molyneux 1991) and in the Dutch sector of the Southern Bight of the North Sea (Van Adrichem, pers. comm. 1994; Cocks *et al.* 2003).

Belgium

The **Brabant Massif** is a mostly concealed basement unit with outcrops only in its southeastern part (Fig. 6.27). The Brabant Massif forms a part of the larger Anglo-Brabant foldbelt

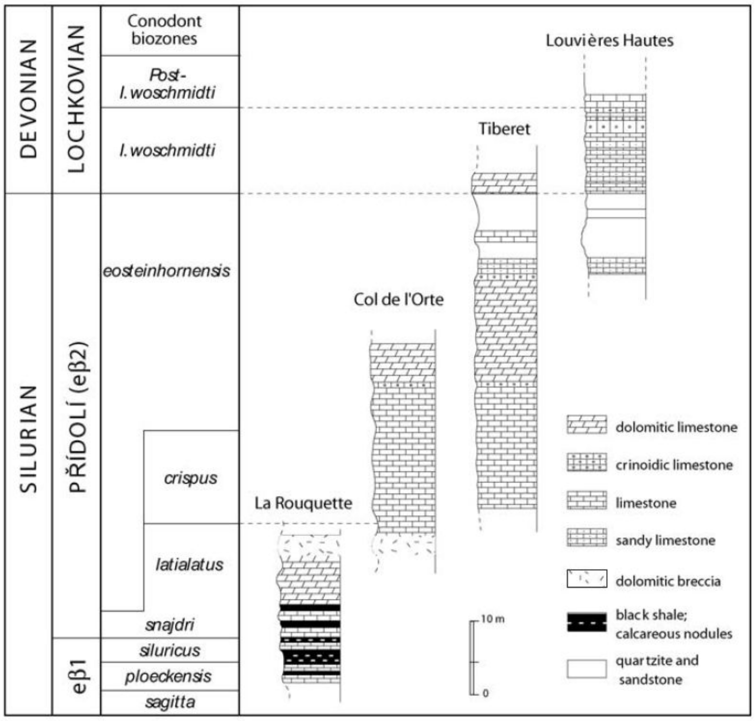

Fig. 6.26. Lithostratigraphy of the Silurian of the Montagne Noire (after Feist 1977).

(Pharaoh *et al*. 1993) later called the Anglo-Brabant Deformation Belt (Winchester *et al*. 2002) The rocks were folded, cleaved and faulted during the Silurian to early Eifelian Brabantian Orogeny (a late phase of the large Caledonian Orogeny) and metamorphosed to the zeolite or greenschist facies. One area escaped cleavage formation and metamorphism, namely the SW subcrop part. The orogeny resulted in the formation of an anticlinorial structure for the Brabant Massif (Van Grootel *et al*. 1997; Verniers *et al*. 2002). Silurian rocks are present along the southern rim: cropping out in the eastern part and in the west in numerous boreholes in southern Flanders (southern part of the provinces of East and West Flanders) and northern France. There is also poorly documented Silurian in a subcrop area with few boreholes in the NW, called the central rim, and in the north of the Brabant Massif (i.e. the northern rim). Further north, one borehole is reported in the Dutch sector of the North Sea and several extending below the upper Palaeozoic cover: Loenhout, Booischot and Kortgene (Legrand 1969; Verniers & Van Grootel 1991). The Silurian of the Brabant Massif was extensively reviewed by Verniers & Van Grootel (1991) and its lithostratigraphy formally revised in Verniers *et al.* (2001) (Fig. 6.27).

Graptolites are almost the only macrofauna present in the Llandovery to lower Ludfordian rocks. Most of the graptolite biozones as defined by Rickards (1976) have been recognized (Martin 1969). Organic microfossils, such as acritarchs and chitinozoans, have been used to date thick units when graptolites are missing. The following chitinozoan biozones have been demonstrated: *Belonechitina postrobusta*, *Spinachitina maennili*, *Eisenackitina dolioliformis*, *Angochitina longicollis*, *Margachitina margaritana*, *Cingulochitina cingulata*, *Sphaerochitina lycoperdoides* and *Angochitina elongata* (Martin 1969; Verniers 1983; Van Grootel 1990; Louwye *et al.* 1992; Verniers *et al.* 1995). These biozones were calibrated in relation to the graptolite biozonation by Verniers (1999).

Two different sedimentary environments are present in the Brabant Massif: (1) a deep shelf with graptolitic shales in the western part of the southern rim, and (2) a slope environment with proximal and distal turbidites in the outcrop area and along the central and northern rims. The Condroz Inlier (see below) is situated in the prolongation of the first area. Together they could have formed a large gently subsiding shelf basin with a highly subsiding slope basin filled with turbidites to the north (Verniers *et al*. 2002).

The Deerlijk and Lust formations are redorded in the subsurface of southern East and West Flanders. The Deerlijk Formation (more than 83 m thick) contains greenish and dark grey, homogenous or laminated shales or mudstones and clayey sandstones, interpreted as alternating distal turbidites and/or (laminated) hemipelagites. The sediments are often rich in graptolites with rare orthocone nautiloids, sponge spicules, foraminifers and benthic algae (Martin 1974). The Lust Formation (more than 54 m thick) is similar but contains up to 45% clayey fine-grained sandstones.

The Silurian (Rhuddanian to Gorstian) lithostratigraphy of the slope environment with proximal and distal turbidites is best studied in the outcrop area (see reviews in Verniers *et al*. 2001;

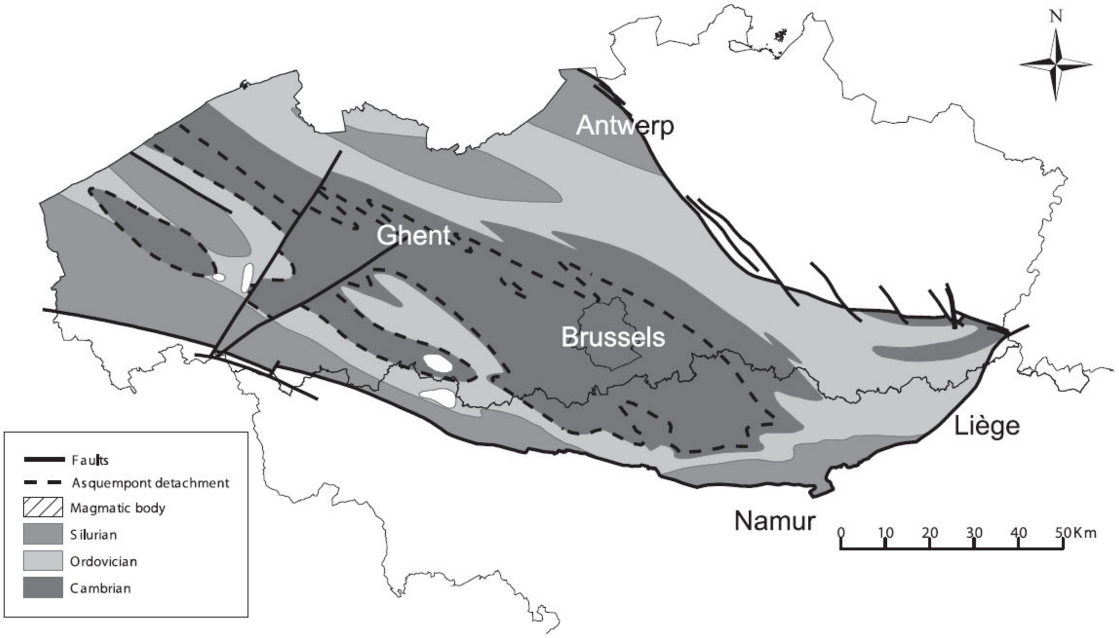

Fig. 6.27. Geological subcrop map of the Brabant Massif (Belgium) (modified after De Vos *et al*. 1993 and Piessens *et al*. 2005).

Herbosch *et al*. 2002). The lithology is mostly clayey to sandy siltstones or mudstones with rare sandstones. The colour is greenish and grey in the Llandovery and medium to dark grey in the Wenlock and Ludlow. Dark grey laminated hemipelagites, which may contain graptolites, are often intercalated. The Silurian comprises a non-turbiditic facies up to the mid-Telychian and above a Bouma-type turbiditic facies up to the Přídolí.

The Silurian succession commences with the greenish to dark grey mudstones of the Brûtia Formation (80 to 100 m thick), with some bioturbated levels; this is capped at the top by a white quartzitic tuff, locally weathered into kaolinite, with graptolites of the *Cystograptus vesiculosus* Zone in shales just above. These shales are finely bedded and together with laminated siltstones or fine sandstones form the Bois Grand-Père Formation (between 200 and 500 m thick), which is poorly dated to being mid-Rhuddanian to mid-Telychian in age. Bouma-type turbidites are first recorded in the mid-Telychian greenish grey to dark grey Latinne Formation (*c.* 180 m thick) and continue into the overlying medium to dark grey Hosdin Formation (*c.* 150 m thick) and the more than 626 m thick green Fallais Formation, all of which are late Telychian in age based on chitinozoans. The latter formation comprises several members, one which is a 26 m thick fining-upward volcaniclastic layer (Pitet Member). The overlying coarser-grained unit of the Corroy Formation is observed in many valleys, has a thickness of between 100 and 140 m and contains centimetre- to decimetre-scale sandstones, siltstones and shales (Herbosch *et al*. 2002). Graptolites from the *Cyrtograptus centrifugus*, *Cyrtograptus murchisoni, Monograptus riccartonensis* and *Cyrtograptus rigidus* zones have been reported (Legrand 1961; Verniers & Rickards 1978), together with rare *Conularia, Cardiola* sp., *Orthoceras* sp. and burrows (see Verniers & Van Grootel 1991). Thicker-bedded but lower-energy turbidites, always alternating with laminated hemipelagites, occur in the Les Vallées (more than 225 m), Vissoul (more than 30 m), Fumal (330 m) and Vichenet (more than 350 m) formations. These units are mostly composed of fine silty slate, clayey siltstones, and rare very fine-grained sandstones. The Vissoul Formation has a greater amount of siltstones or sandstones and the Vichenet Formation includes very thick, slightly calcareous slate units in between the laminated hemipelagites. These four formations are dated as mid-Wenlock to Homerian with chitinozoans (post-*Cingulochitina burdinalensis* interzone, *Eisenackitina lagena*, *Conochitina pachycephala*, *subcyatha* and *Sphaerochitina lycoperdoides* zones; Verniers 1999). Further to the west in the Senne valley the Petit Roeulx, Steenkerque and Froide Fontaine formations represent the lateral equivalents.

The lower Ludlow (Gorstian) is contained within the Ronquières Formation. It is more than 538 m thick and includes turbidites with intercalated laminated hemipelagites. Near the base of the formation 30 m of laminated hemipelagites with six metabentonite levels may represent the highest sea-level part of a megacycle. The top part of the Ronquières Formation is the only place in the Silurian of the Brabant Massif where complete Bouma sequences (Tabcde) occur. Graptolites and chitinozoans date the formation clearly as Gorstian, with the *Neodiversograptus nilssoni*, *Lobograptus scanicus* and possibly the *Pristiograptus tumescens* zones represented (Louwye *et al*. 1992).

One uppermost Gorstian to lower Ludfordian unit (the Bellegem Formation) and one unit (the Rekkem Formation) tentatively dated as Přídolí were described from a few boreholes in the SW part of the massif. They contain grey thin-bedded turbidites, often with burrowed horizons and fragments of the archaeostracan *Ceratiocaris* sp. (Van Grootel 1990).

To produce the observed pre-Givetian cleavage Michot (1978), Debacker (2001) and Verniers *et al*. (2002) suggested that sedimentation continued in the Brabant Massif after the Gorstian with deposition of another 4 to 6 km of upper Silurian sediments. Using reworked palynomorphs in the Lower Devonian south of the massif, Steemans (1989) postulated that sedimentation in the Brabant Massif could have continued until early in the Lochkovian.

Several parts of the lithostratigraphy in outcrops and boreholes are still insufficiently known in detail; this is especially true for much of the Llandovery, Ludfordian and Přídolí. The six boreholes along the northern rim contain distal turbidites alternating with laminated hemipelagites. These were dated as Wenlock and Ludlow using chitinozoans, but no formal lithostratigraphy has been applied.

The **Condroz Inlier** (Belgium), previously called the Condroz Ridge or the Sambre and Meuse Belt or Strip, is a 69 km long and 0.5 to 2 km wide belt situated south of the Sambre river from east of Charleroi to Namur, and south of the Meuse river from Namur to SW of Liège. The Variscan anticlinorial fold and fault structure, including the important Midi Thrust Fault between the Namur and Dinant synclinoria, brought discontinuous sections of Ordovician and Silurian strata in tectonic wedges to the present-day surface in this area. An overview of the older literature is given in Michot (1954) and Martin (1969). The Silurian part of the inlier was gently folded, without a clear cleavage development in Přídolí to early Lochkovian times, and later deformed during the Variscan Orogeny with faulting, folding and local cleavage development.

In contrast to the Brabant Massif, the Llandovery to Ludlow sedimentary rocks are much thinner, non-turbiditic, and richer in macrofauna (mostly graptolites with rare brachiopods, trilobites, crinoids, ostracods, conularids and *Orthoceras* sp.). The most recent graptolite study was by Maes *et al*. (1979). Most of the graptolite biozones, as defined by Rickards (1976), have been found, with the exception of the *Atavograptus atavus*, *Coronograptus cyphus*, *Gothograptus nassa* and the *Pristiograptus? ludensis* zones. However, a new study to establish recently defined biozones is necessary. Acritarch studies have elucidated a few of the previously undated sections (Martin 1969), and unpublished chitinozoan studies show the presence of the *Eisenackitina dolioliformis*, *Angochitina longicollis*, *Margachitina margaritana*, *Cingulochitina cingulata* and *Angochitina elongata* zones. A recent stratigraphical study by Vanmeirhaeghe and co-workers on the Llandovery indicated the presence of a hiatus from the Hirnantian to the lower Aeronian in the SW part of the Condroz Inlier (Puagne area and around Fosses), while in the central and NE part the succession appears to be continuous (Vanmeirhaeghe 2006).

The rocks are mostly siliciclastic and include shales, siltstones, some fine-grained sandstones and calcareous shales. They were deposited in an outer shelf environment (Verniers *et al*. 2001) (Fig. 6.28). A recently defined unit (Tihange) consists of greenish fine shales with Rhuddanian graptolites (Vanmeirhaeghe 2006). The dark grey or greenish Dave Formation (*c*. 280 m) contains silty shales with sandstones within the *Lituigraptus convolutus* and *Spirograptus turriculatus* zones. Several purple-red coloured intervals occur in the *Monoclimacis griestoniensis* and *Monoclimacis crenulata* zones and in the lower Sheinwoodian. The Criptia Group is a poorly studied possible lateral equivalent of the Dave Formation in the SW of the Condroz Inlier (Puagne area). This contains thick dark grey, greenish or yellowish fine and rather uniform shales. The Naninne Formation (more than *c*. 90 m) shows a rapid change to green or grey laminated, locally calcareous silty shales, fine sandstones, and shales (Maes *et al*. 1979). The Jonquoi Formation (*c*. 300 m) marks a return to homogenous or laminated greyish brown or green shales and mudstones with some levels of calcareous nodules (Maes *et al*. 1979). Lateral equivalents in the westernmost end of the inlier are the Longues Royes and Moncheret formations dated as Ludlow and/or Přídolí on the basis of trilete spores (Steemans in Delcambre & Pingot 2000). The Thimensart Formation (*c*. 100 m) contains grey laminated fine-grained sandstones and olive-green shales. The poorly studied, and supposedly thick, Colibeau Formation contains dark shales with rare sandstone beds. In the Telychian part of the Dave Formation and in the Naninne Formation, 11 acid volcanic or volcanosedimentary layers of approximately 1 m thick are present (Maes *et al*. 1979).

Northern part of Rhenish Massif (= Rheinisches Schiefergebirge)

The fairly restricted Silurian strata outcropping in the Ebbe and Remscheid anticlines, as well as in the Müsener Horst, are considered to be situated on the southern rim of eastern Avalonia (Verniers *et al*. 2002) (Fig. 6.4). A considerable gap exists in the Ebbe anticline between the Upper Ordovician (mid-Caradoc) of the Herscheid Group (Eiserhardt *et al*. 2001) and the Upper Silurian of the Köbbinghausen Formation. The uppermost unit of the Herscheid Group, the Solingen Shale Formation, contains chitinozoans of Caradoc age (Maletz 2000; Samuelsson *et al*. 2001). A stratigraphical gap, ranging from the late Caradoc (Upper Ordovician) to the Přídolí (late Silurian), has been noted, since fossils in the overlying Silurian Köbbinghausen Formation indicate a Přídolí age. The Köbbinghausen Formation is virtually identical in terms of its lithology to the underlying Solingen Shale Formation. Both are poor in fossils and it is possible that a considerable time interval may be present in the strongly condensed succession of the Köbbinghausen Formation, although without fossil evidence it is difficult to prove.

The Köbbinghausen Formation is estimated to be *c*. 300 m thick, including the Ocker Limestone. The lower part of the formation contains monotonous shales, grading upwards into more carbonaceous and fossil-rich layers, the *Dayia* beds (with *Dayia shirleyi,* formerly identified as *Dayia navicula* and with the trilobite *Acaste dayiana*) and the widely distributed *Scyphocrinus* horizon. The *Scyphocrinus* horizon contains *Scyphocrinites elegans* in the Ebbe anticline and can be correlated widely into the German Silurian. The units of the formations are, however, identified mostly by their fossil content and not in terms of their lithology. The upper part of the Köbbinghausen Formation consists of an alternating carbonate and carbonaceous shale succession, 200 m thick, formerly identified as the Ockrige Kalke (not to be confused with the Ockerkalk of the Thuringia Forest). The Silurian–Devonian boundary lies within this unit, as proven by trilobites and conodonts (see Timm 1981; Luppold 1995).

Far eastern Avalonia

No Silurian sediments have yet been recognized in boreholes from this completely subsurface terrane. Radiometric age dating of North Sea boreholes attests to intrusive, metamorphic or deformation events during the Silurian (Frost *et al*. 1981; Pharaoh 1999; Katzung 2001). A review of the Rügen Caledonides is also provided by Katzung *et al*. (2004) and Katzung & Feldrappe (2004).

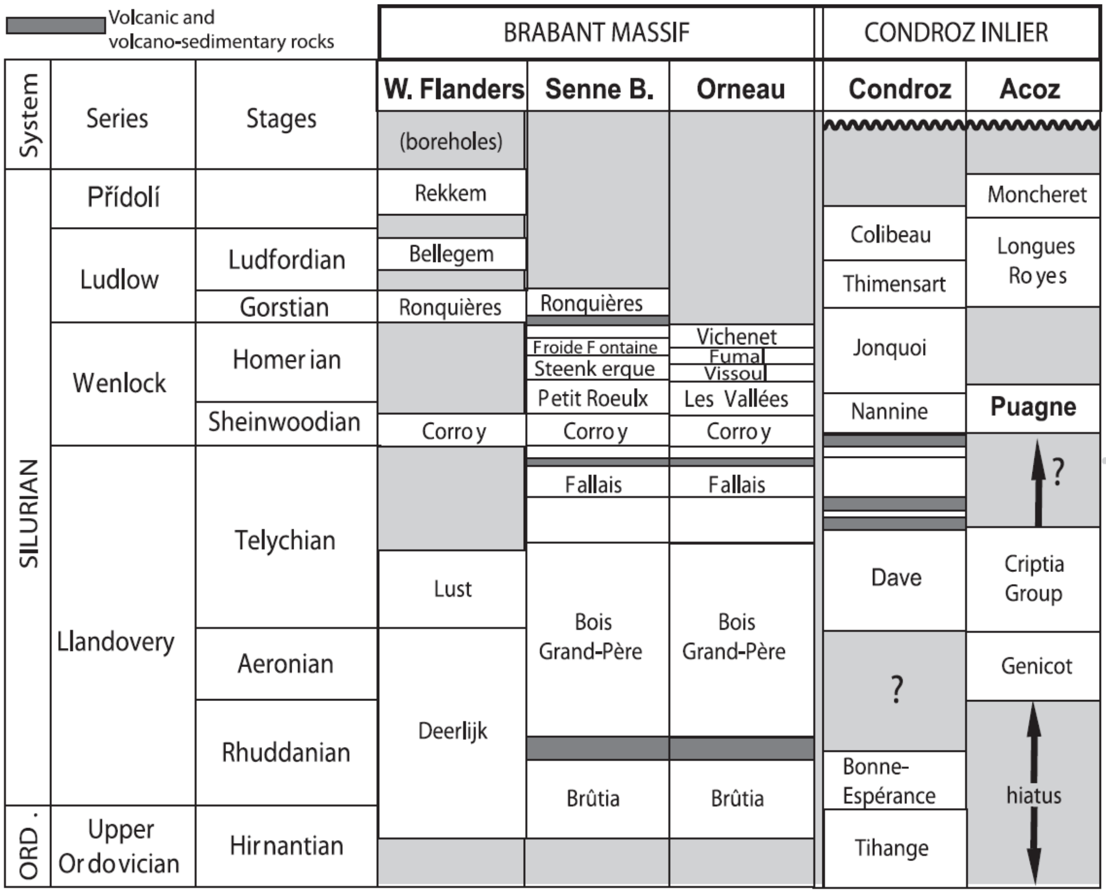

Fig. 6.28. Silurian lithostratigraphy of the Brabant Massif and the Condroz Inlier (Belgium) (modified after Verniers *et al.* 2001).

Areas of unclear palaeogeographical affinity

Carpathian Foreland

Dozens of deep boreholes have been drilled in the Silurian succession of the Carpathian Foreland (Tomczyk 1963, 1970; Moryc 1992, 1996; Maksym *et al.* 2003). The sediments are mainly monotonous graptolitic shales interbedded with thin radiolarian shales, assigned to the Llandovery, and marly mudstones of early Wenlock age which include the *rigidus* and *belophorus* graptolite zones (Maksym *et al.* 2003). The thickness of the Silurian deposits varies from a dozen metres in the northern Carpathian Foredeep to over 180 m in the southern part. The thickest, most complete and representative Silurian core was recovered from the Hermanowa-1 borehole (Maksym *et al.* 2003) (Fig. 6.7). The region possibly represents the easternmost part of the Małopolska Massif and indicates a similar but more variable depositional environment to that in the neighbouring central and western part of that massif (Nida Region). During the Llandovery and Wenlock, the graptolitic claystone facies was deposited in the pelagic, deep-water basin, with periodically oxygen-deficient conditions occurring at the bottom. The sediment accumulation rate was low and, thus, favourable for the deposition of a condensed radiolarian unit with sedimentary gaps (Maksym *et al.* 2003).

Sudetes (Polish part)

The Silurian in the Polish part of the Sudetic Mountains occurs in two areas: the Bardo Mountains (Góry Bardzkie) and the Kaczawa Mountains (Góry Kaczawskie) (Fig. 6.7). A historical review of Silurian research in the Sudetes has been published by Oberc (1970). All of the Palaeozoic successions in the Sudetes including the Silurian have been assigned to the Variscan Saxothuringian Zone, part of the structural mosaic of the European Variscides. The relationship the Saxothuringian Zone and the Barrandium Region as well as with other units of the Bohemian Massif has long been debated (Kryza *et al.* 1994; Żelaźniewicz 1997; Cymerman *et al.* 1997; Aleksandrowski 2003). There is agreement among Polish geologists that the Silurian in the Sudetes mountains (Bardo Mountains and Kaczawa Mountains) belong to Peri-Gondwana and Gondwana. Moreover, in the last year, archaeocyothids were found in the Cambrina of the Kaczawa Mountains that are very similar assemblages to those known from the neighbouring Goerlitz Synclinorium in Saxony.

The Silurian deposits of both regions in the Sudetes are developed in the Bavarian facies, one of the five northern or peri-Gondwana facies. As mentioned above it consists of greenish-grey shales interbedded with black graptolitic cherts and alum shales. The main difference with the Thuringian facies is the absence of carbonate sedimentation during the Ludlow and Přídolí. The sediments were deposited in the pelagic zone of a basin developed on oceanic-type crust. They probably represent fragments of an accretionary prism (Wajsprych 1986; Baranowski *et al.* 1987; Franke *et al.* 1993; Kryza & Muszyński 2003; Żelaźniewicz 2003), located in the southern part of the subtropical Rheic Ocean (Porębska & Sawłowicz 1997; Porębska & Koszowska 2001; Aleksandrowski *et al.* 2000). These accretionary tectonostratigraphic units finally coalesced during the Variscan Orogeny (Kryza & Muszyński 2003; Żelaźniewicz 2003).

The Silurian deposits in the Bardo Mountains are known from many small outcrops, but the most complete section is exposed at Żdanów (Fig. 6.29). The section commences with Ordovician shales intercalated with thin sand and silt turbidites overlain by Silurian shales which are increasingly interbedded up-section with light-coloured radiolarian cherts (Porębska 1982; Wyżga 1987; Porębska & Sawłowicz 1997; Porębska & Koszowska 2001). The Silurian part of the section is *c.* 48 m thick and is divided informally into the Lower and Upper Graptolitic Shales with the Green Shales in between (Fig. 6.29). The lithology of the units is characterized by bedded radiolarian cherts, siliceous and clayey shales with phosphate nodules and thin tuff layers. The shale units are finely laminated without any bioturbation, and yielding only planktonic fossils including abundant graptolites and acritarchs and rare conodonts and radiolarians. These deposits pass into Lower Devonian deposits represented by two highly condensed units of black graptolitic shales separated by grey-greenish shales.

The well-documented section with rich graptolite assemblages forms the basis for the biostratigraphy and chronostratigraphy of the Silurian–Lower Devonian interval in the Bardo Mountains (Malinowska 1955; Porębska 1982). Graptolite biozones from the Llandovery *Parakidograptus acuminatus* Zone up to the Pragian *craigensis* Zone can be recognized. The Silurian–Devonian boundary beds in the Bardo Mountains contain the uppermost Přídolí index graptolites *Monograptus transgrediens transgrediens* Perner and the first Lochkovian graptolites *Monograptus uniformis uniformis* Pribyl (Porębska 1982; Porębska & Sawłowicz 1997).

The Silurian rocks in the Kaczawa Mountains are deformed by folding or overthrusting (Baranowski *et al.* 1990, 1998). They are exposed as part of the Kaczawa Complex in small isolated outcrops, and it is often difficult to establish a continuous section. These variably thick sequences (up to several tens of metres) are mainly black siliceous and clayey slates with graptolites, cherts, quartzites and volcanogenic rocks, underlain by a thick complex of slates and phyllites, probably of Ordovician age. They are usually black in colour or rarely brown and grey. They were probably deposited in a pelagic setting. The rocks contain abundant graptolites with biozones assigned to the Llandovery, Wenlock and lower Ludlow (Jerzmański 1965; Kornaś 1977; Haydukiewicz 1987; Baranowski *et al.* 1987, 1990). Fossils diagnostic for the base of the Silurian, the *Coronograptus gregarius* Zone and the *Demirastrites triangulatus* Subzone (Llandovery) are recorded (Kornaś 1974), but there are none for the upper Ludlow and Přídolí. However, sedimentation was probably continuous from the Silurian into the Lower Devonian, since the latter is also represented by graptolite-bearing pelagic deposits (Baranowski *et al.* 1987). The lithology indicates the Bavarian facies. Ordovician low-grade metamorphic rocks of sedimentary and volcanic origin represent deposits developed during the initial rifting processes within a continental crust environment, while the Silurian–Devonian graptolitic shales and cherts (locally called lydites) with related T-MORB to N-MORB type lavas, represent oceanic-trench-type deposits of a mature basin developed on an oceanic-type crust (Furnes *et al.* 1994).

Summary

The Silurian is a relatively short period of approximately 28 Ma, but important in the history of life because it records the Llandovery recovery in biodiversity following the latest-Ordovician Hirnantian extinction event, the second most important one in the Phanerozoic. This recovery was followed by a peak in biodiversity for several groups in the Wenlock, Ludlow and Přídolí. The uppermost Wenlock and Ludlow witnessed the conquest of the continental realm with the first vascular land plants. Warm and increasing temperatures throughout the Silurian in a greenhouse climate, with some short icehouse intervals, went in tandem with low oxygen levels in the atmosphere and ocean surface waters. Low levels of organic matter were enough to cause anoxic conditions in the sea below 100 m depth, more than in any other period, leading to the characteristic anoxic and dark Silurian sediments. Strong anomalies in the global carbon cycle closely related to sea-level changes have recently been shown to influence the biodiversity of the marine faunas with radiations and extinctions.

During the Silurian Central Europe was more widely spread out over the globe than at present, with at least two intervening oceans which have since disappeared. Several large palaeocontinents such as Baltica in the NE and the northern part of Gondwana in the south were present, together with smaller palaeoplates such as Avalonia in the west, Far Eastern Avalonia in the north and NW and peri-Gondwana terranes such as Perunica in the centre. These were separated by the two oceans: the Tornquist Sea and the Rheic Ocean. These palaeocontinents were brought together by subduction of oceanic crust, closing of the oceans and the subsequent orogenic collisions, respectively termed the Caledonian and Variscan orogenies. The Alpine Orogeny also brought pieces of peri-Gondwana into the study area. They are included in the basement of the Alps in several tectonic windows (e.g. Carnic Alps) and are called the Proto-Alps.

Some palaeocontinents such as Baltica were situated in subtropical latitudes where locally small reefs could develop on shallow platforms. Other palaeocontinents such as northern Gondwana or peri-Gondwana were situated at high latitudes and characterized by the occurrence of glacial or glaciomarine diamictites in the Hirnantian, immediately preceding the Silurian. Avalonia and Far Eastern Avalonia were situated at temperate or low latitudes. The latter had collided with Baltica in the Ashgill and the former collided with Laurentia and Far Eastern Avalonia during the Silurian (see also Krawczyk *et al.* 2008).

Outcrop areas are rather scarce in Central Europe, but some subcrop areas have been drilled, thus providing additional information. The Silurian on Baltica is present in outcrops in the two parts of the Holy Cross Mountains, on Bornholm and in many boreholes of northern Poland NE of the Trans-European Suture Zone and in Lithuania. The Silurian of Far Eastern Avalonia is only recognized in boreholes from western Pomerania in the Koszalin-Chojnice Zone. Avalonia in the study area has outcrops in Belgium (Brabant Massif, Condroz Inlier) and Germany (Ebbe

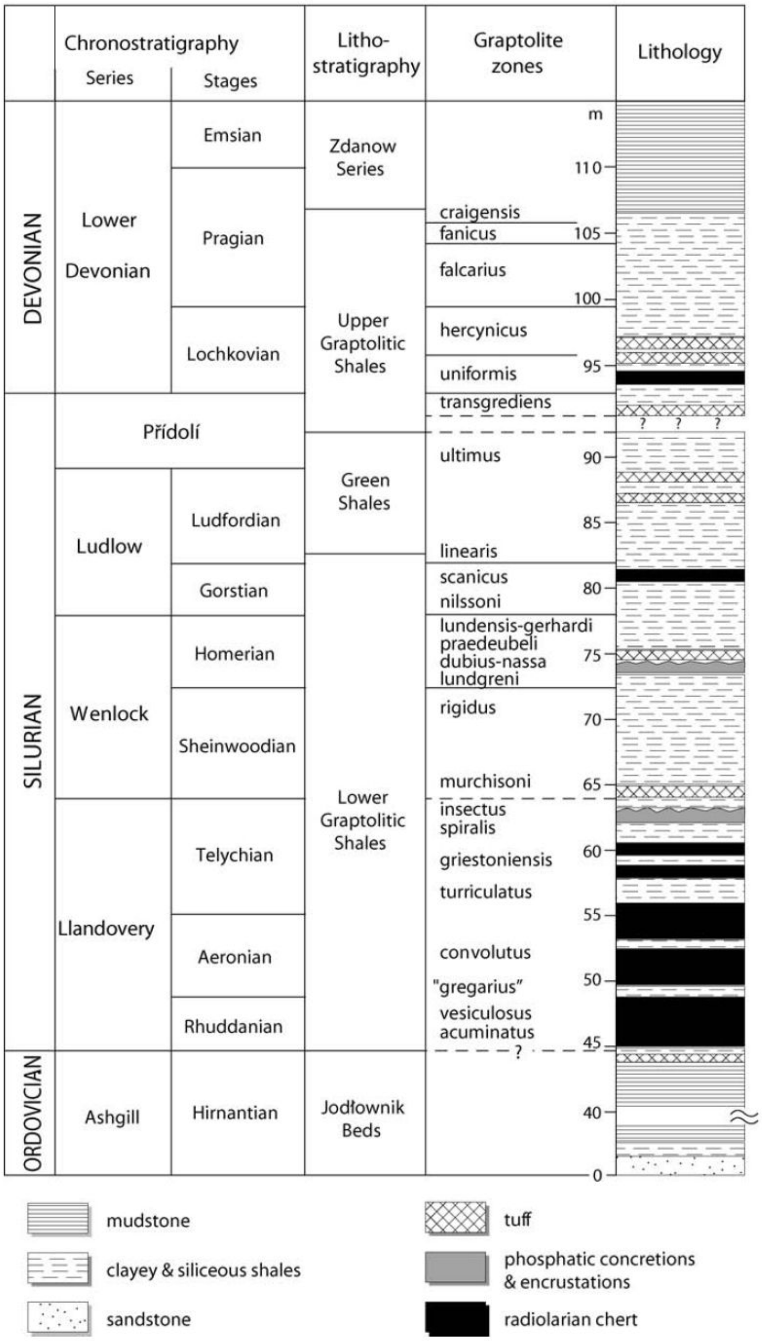

Fig. 6.29. Synthetic section of the Silurian strata in the Bardo Mountains with graptolite biostratigraphy after Malinowska (1955), Porębska (1982), Sawłowicz & Porębska (1998) and Porębska & Koszowska (2001).

anticline) and is recorded from boreholes in the Brabant Massif, North Sea and East Anglia. Peri-Gondwana terranes, within the Variscan structures of Franconia, the Mid-German Crystalline High, Saxothuringian Zone and the Moldanubian Zone, are found in many small outcrop areas of central Germany with complete successions in the Thüringer Wald, and in the Czech Republic particulary in the large, well-known outcrop area of the Prague Basin. Other peri-Gondwana terranes are found in Alpine tectonic units such as the Apulia/Italia Terrane and smaller outcrop areas, often deformed, north and south of the Periadriatic Line in Austria, northern Italy and Croatia. A well-studied outcrop area is present in the Carnic Alps succession. Another Alpine terrane, the Hellenic/Bosnian-Noric Terrane, contains small outcrop areas in Croatia and Serbia. Moesia is another peri-Gondwana terrane with Silurian present in several boreholes. In the study area, Silurian outcrops of northern Gondwana are only found in the Montagne Noire and the Maures Massif.

The depositional facies, often containing anoxic sediments such as black shales or calcareous shales and limestones, varies according to three factors: (1) local water depths are modulated by eustasy, and vary from lagoonal, shallow, middle or deep shelf environments and down the continental slope to deep marine units with turbidites or radiolarites; (2) the facies are also controlled by palaeolatitude, for example carbonates with occasional small reefs were only formed in shallow and middle shelf environments at low latitude, i.e. on Baltica and in the upper Silurian of Avalonia; (3) different tectonic settings, such as passive or active margins, result in important differences in sediment thickness. For example, Baltica (except along its SW margin) peri-Gondwana and northern Gondwana did not suffer crustal mobilization during the Silurian hence sedimentation occurred mainly on a passive margin, distal to the emergent land masses south of the study area. The low terrigenous influx and reduced subsidence resulted in successions of only a few tens to hundreds of metres in thickness. However, in faulted areas with active half-graben structures and sometimes intraplate volcanism, there were marked thickness variations as is the case in the Prague Basin and the Grauwacke Zone of Austria.

In the many peri-Gondwana outcrop areas, five main facies developed. The most common is the low energy, relatively deep shelf Thuringian facies with thin sequences of dysaerobic or anoxic dark shales and cherts in the lower Silurian with no current indicators, and typically thick aerobic limestones with interbedded thin quartzite beds in the upper Silurian (termed Ockerkalke in Germany). This facies type is found in Saxothuringia, parts of the Prague Basin and the Carnic Alps (where it is called the Bischofalm facies). The Bavarian facies is similar to the Thuringian facies and contains grey-green shales with interbedded graptolitic shales and alum shales. However there are no limestones in the upper Silurian. It is sometimes interpreted as having been deposited on a very deep shelf with radiolarites. It occurs in narrow bands in the Saxothuringian Zone.

The shelly fauna facies contains thick calcareous shales with limestone nodules and lenses rich in shelly fauna (cephalopod limestones) and was supposedly deposited on a moderately shallow to shallow shelf. It occurs in Saxothuringia, the Prague Basin, the Montagne Noire and the Carnic Alps, where it is subdivided into a shallower Wolayer facies and a less shallow Plöcken facies. There is also a facies intermediate between the shelly fauna facies and the Thuringian facies termed the Findenig facies. The Prague Basin facies formed in very shallow water on the gentle slopes of the Wenlock–Ludlow volcanic archipelago in the Prague Basin, and contains thick units of basic volcanics and macrofauna-rich bioclastic carbonates. The facies also developed in Austria. A fifth facies developed in Austria proximal to continental areas with a high input of siliciclastic material. This facies is sometimes turbiditic in nature.

The two Silurian active margins of Central Europe: the Heligoland-Pomerania Deformation Zone between Baltica and Far Eastern Avalonia, and the Anglo-Brabant Silurian Basin and Deformation Zone between Far Eastern Avalonia and Avalonia were areas of pronounced subsidence as recorded in the sometimes kilometre thick successions which were deposited. Due to subsequent Variscan or Alpine deformation and metamorphic overprinting with greenschist or amphibolite metamorphic facies in several areas, it is not always possible to deduce the original composition of the rocks.

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Article VIII

δ^{18}O composition of conodont apatite indicates climatic cooling during the middle Pridoli sea level fall in the Baltic Basin

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ABSTRACT

Phosphatic microfossils, such as conodonts and early vertebrate microremains (fish teeth and scales), originating from Upper Silurian (Pridolian) sections in Lithuania, have been studied for their oxygen isotope composition. $\delta^{18}O_{apatite}$ analyses of early vertebrate fossil apatite have been performed for the first time, using the corresponding method to conodont apatite analysis. The conodont colour alteration index did not exceed 1.5 in the material studied, reflecting minor thermal alteration of the Upper Silurian strata in this part of the Baltic Basin. Conodont $\delta^{18}O_{apatite}$ values range from 17.7 to 19.2‰ V-SMOW, perfectly fitting in the general δ^{18}O value range of 17.5 to 19.5‰ V-SMOW for the Silurian conodont apatite, and have been used for palaeosea-water temperature reconstruction. The analysis of early vertebrate remains from the same samples as the conodonts gave values lower by 2.5‰ in comparison to δ^{18}O of conodont apatite. This vertebrate data offset translate into about 10°C higher paleotemperatures in comparison to those estimated from conodont apatite. The general trend of the early vertebrate $\delta^{18}O_{apatite}$ curve resembles that of conodont $\delta^{18}O_{apatite}$. We present the first $\delta^{18}O_{apatite}$ curve from a Pridolian section in the eastern Baltic Basin (Gėluva-99 borehole), which is located in the central facies belt of the Silurian of Lithuania. The position of a positive shift in the curve perfectly matches a facies change between the lower Pridoli (Vievis Fm.), and the upper Pridoli (Lapės Fm.). The positive excursion, indicating drop of palaeoseawater temperature, also corresponds to an abrupt sea level drop in between Vievis and Lapės Formations in the middle Pridoli of the Baltic Basin. This formational boundary, biostratigraphically interpreted as a significant change in the faunal composition as well, is now supported by the δ^{18}O record indicating a cooling event in the middle Pridoli.

Key words: Biogenic apatite, chemostratigraphy, sea-level fall, palaeoclimate, Silurian.

INTRODUCTION

Recent studies on Ordovician, Silurian and Devonian conodonts (WENZEL et al., 2000;

JOACHIMSKI & BUGGISH, 2002; JOACHIMSKI et al., 2003, 2004; LEHNERT et al., 2007b) showed that conodont apatite can be a reliable proxy for high-resolution palaeotemperature curve reconstruction. The major advantage of the oxygen in phosphate isotope palaeothermometry is that it is a system which records temperatures with great sensitivity while phosphatic-tissue (dentine, bone, conodont crown tissue) building organisms are alive, and the record is nearly perfectly preserved after organism death, thus the post-depositional exchange can be neglected (KOLODNY et al., 1983). In this way oxygen isotopic composition of conodont biogenic apatite can be used to unravel the oxygen isotope ratio of ancient oceans and, with certain limitations (KOLODNY et al., 1983; see discussion below) to reconstruct oceanic palaeotemperature and salinity.

The possibility of using a phosphate oxygen isotope palaeothermometry method was first proposed in the middle of the 20th century (UREY et al. 1951). Conodonts are one of the most common Palaeozoic phosphatic microfossils, and apart of being important biostratigraphic indicators because of their morphological diversity, conodont apatite shows potential for retaining primary chemical information of palaeoseawater. The very important point in palaeoeclimate estimations is also the supposed entirely marine habitats of conodont animals (SANSOM et al, 1992; DONOGHUE et al., 2000).

Although the ubiquity of conodont fossils throughout marine sedimentary sequences makes them particularly attractive for palaeoseawater studies, issues of post-depositional chemical overprinting of primary compositions remain a significant problem. The oxygen isotopic composition of conodont apatite is supposed to be minimally affected by increasing burial temperatures and no prominent difference in the oxygen isotopic ratios between conodont taxa have been observed occurring preferentially in shallow water or pelagic deposits (JOACHIMSKI et al., 2003). The physical properties, crystalline structure, and inherent permeability of the component conodont tissues determine their susceptibility to diagenesis (TROTTER et al., 2007). Recent comprehensive investigations by transmission electron microscopy (TEM) and parallel geochemical studies suggest that cancellate albid crown of conodonts is the most resistant apatite tissue to diagenetic modification (TROTTER & EGGINS, 2006; TROTTER et al., 2007).

Conodonts possessed a complex feeding apparatus of elements composed of carbonate-fluor apatite, or francolite: $Ca_5[(F,O)(PO_4,CO_3)_3]$ (PEITZNER et al., 1968). The dense microcrystalline ultrastructure of conodont apatite is comparable in its consistence to tooth enamel (JOACHIMSKI et al., 2004). It has been shown that tooth enamel is relatively resistant to any diagenetic modification of the primary isotopic composition (QUADE et al., 1992; SHARP et al., 2000).

Attempts in using conodont apatite for oxygen isotopic analysis were hampered in the past by the very small size of individual conodont elements, often 0.1 – 0.2 mm, barely reaching 0.5 mm in length in the Early Palaeozoic. Laser-based microsampling or high-temperature reduction techniques (TC-EA) have made it possible to measure the oxygen isotopic composition of conodont microsamples, not exceeding ≤ 1 mg (JOACHIMSKI & BUGGISH, 2002). Nevertheless, it is still quite difficult to get 1 mg of conodont fossils in Silurian, sometimes more than 100-200 conodont elements are required. While contemporaneous early vertebrate fossils, which are presented by larger, more massive and robust exoskeletal microremains (dentine scales), can reach 1 mg sample with only a few scales. The early vertebrate exoskeleton microremains (dermal scales) possess homologous teeth histology, with compact surface layer of diagenetically-resistant enamel covering the dentine scales (MÄRSS et al., 2007). Moreover, the oxygen isotope composition of fossil fish biogenic apatites have been used initially to reconstruct past seawater temperature variations (KOLODNY & LUZ, 1991). This is why biogenic apatite of vertebrate (early fish) microremains have been chosen for comparative $\delta^{18}O$ analysis.

This study focuses on oxygen isotope composition of conodonts and early vertebrate (fish) phosphatic microremains from the Late Silurian (Pridoli) of the Baltic Basin (Lithuania).

The aim of this contribution is to first produce the $\delta^{18}O$ curve on conodont biogenic apatite for the Pridoli of the Baltic Basin, on example of Gėluva-99 borehole, as well as to examine early vertebrate biogenic phosphate usability for $\delta^{18}O$ analyses and palaeotemperature calculations in comparison to the conodonts, based on the experimental method of fish bone and teeth phosphate oxygen isotope thermometry (KOLODNY et al., 1983; JOACHIMSKI & BUGGISCH, 2002).

The Pridolian sequence of the Upper Silurian of the Baltic Basin has been chosen for the early vertebrate and conodont $\delta^{18}O$ analyses for several reasons: 1) The phosphatic fossil material (both conodonts and early vertebrates) is supposed to be minimally diagenetically altered, if to compare with the other Late Silurian sedimentary basins worldwide, due to the tectonic stability and unalteration of the Silurian strata of the Baltic Basin (VERNIERS et al., 2008) as well as conodont element CAI being less than ≤ 1.5, and early vertebrate microremains with minimal colour alteration; 2) Conodont elements and early vertebrate microremains are very abundant fossils in the late Silurian sediments of the Baltic Basin of Lithuania, even if considering relatively small core samples, so it was easy to collect the required quantity of phosphatic remains in the choosen stratigraphical points; 3) Neither the $\delta^{18}O_{apatite}$ nor $\delta^{18}O_{calcite}$ isotope curves have yet been made for the Pridoli of the Baltic Basin.

MATERIAL AND ANALYTICAL METHODS

Conodonts and early vertebrates have been collected from the following core samples of the Upper Silurian (Pridoli) of the Lithuania (Baltic Basin): Gėluva-99, Gėluva-119, Ledai-179, Liepkalnis-137, Kurtuvėnai-162, Nida-44, Stoniškiai-7, and Tauragė-11 boreholes, and processed using standard preparation techniques. Conodont elements and early vertebrate microremains have been picked-up manually from the insoluble residues after dissolving limestone of the core samples.

The classical evaluation of conodont element thermal alteration by the Colour Alteration Index (CAI) has been used as primary criterion for selecting conodonts for $\delta^{18}O$ analysis. Only pristine conodonts with CAI ≤ 1.5, according to the preservation quality recomended for oxygen isotopic palaeowater studies in conodont phosphate (HOLMDEN et al., 1996), and early vertebrate microremains of translucent dark brown colour, following the assumptions on the least thermal alteration of phosphatic vertebrate microremains (TWAY et al., 1986), have been used in this work. The majority of conodont elements revealed from the core samples possessed colour alteration index of ≤ 1.5, which is a reflection of very minor thermal alteration of the Upper Silurian strata in this part of the Baltic Basin.

Conodont elements and vertebrate microremains (0.8 to 1 mg) were dissolved in nitric acid and chemically converted into Ag_3PO_4 using a slightly modified method described by O'NEIL et al. (1994). The oxygen isotope composition was measured on

CO generated by reducing trisilverphosphate using a high-temperature conversion-elemental analyzer (TC-EA) connected online to a ThermoFinnigan Delta plus mass-spectrometer. Most samples were measured in triplicate. Accuracy and reproducibility were monitored by multiple analyses of trisilverphosphate prepared from Merck© hydroxyl apatite A and NBS120c trisilverphosphate standards (VENNEMANN et al. 2002). The average oxygen isotope composition of Merck© hydroxyl apatite A was 17.19‰ of Vienna Standard Mean Ocean Water (V-SMOW), and the mean δO^{18} value of NBS120c was 22.37‰ V-SMOW, which is 0.7‰ higher than values reported in the literature by CROWSON et al. (1991) and LÉCUYER et al. (1996), but relatively close to the value of 22.58‰ V-SMOW determined by VENNEMANN et al. (2002). The overall reproducibility determined by replicate analyses of trisilverphosphate standards as well as replicate sample analysis was better than ±0.2‰ (1 σ). Palaeotemperatures were calculated using the equations for apatite, given by KOLODNY et al. (1983).

RESULTS

The oxygen isotopic record of the Late Silurian (Pridoli) conodonts and early vertebrates of the Baltic Basin are shown in Fig. 1.

Pridolian conodonts have $\delta^{18}O_{apatite}$ values range from 17.7 to 19.2‰ V-SMOW with average values around 18.3‰. The early vertebrates have lower oxygen isotope ratios compared to those of conodonts from the corresponding samples: their $\delta^{18}O_{apatite}$ values range from 15.2 to 17.4‰ V-SMOW, giving average values around 16.3‰ V-SMOW. The $\delta^{18}O$ measurements of conodont apatite have been made through all the Pridoli section (90 m) in Gėluva-99 borehole, in the central facies zone of the Silurian basin of Lithuania (LAZAUSKIENĖ et al., 2003). The $\delta^{18}O$ curve on biogenic conodont apatite for the Pridolian of the Baltic Basin has been produced. A significant shift to lower $\delta^{18}O_{apatite}$ values in the Pridolian section of the Gėluva-99 borehole, is observed between the samples of 696 m and 687 m depth, with oxygen isotope ratios decreasing in 1.1‰, from 18.1 to 19.2‰ V-SMOW respectively, to the minimum $\delta^{18}O_{apatite}$ value for the Pridolian conodonts analysed in this work. The maximum negative $\delta^{18}O_{apatite}$ value is recorded 0.2 m. below the Vievis Fm. – Lapės Fm. boundary, at 687 m depth (Fig. 1). The negative shift corresponds to facies change from Vievis Formation to Lapės Formation, and to the middle-Pridolian sea-level drop in the Baltic Basin (PAŠKEVIČIUS, 1997; LAZAUSKIENĖ et al., 2003, ŽIGAITĖ et al., 2008).

The conodont $\delta^{18}O_{apatite}$ values of the Silurian (Pridolian) of southern Baltic Basin (Lithuania) fit in the general Silurian conodont apatite $\delta^{18}O$ value range of 17.5 – 19.5 ‰ V-SMOW, proposed by JOACHIMSKI et al. (2003).

DISCUSSIONS

Preservation of primary palaeoseawater oxygen isotope composition

The biogenic apatites have the properties required for an ideal geochemical recorder: they respond sensitively during their formation to the aqueous environment, and then preserve perfectly their record after death of the organism (KOLODNY et al., 1983). Oxygen isotope composition of phosphate remnant (PO_4^{3-}) in fossil apatite of marine ectotherm organisms (fish, conodonts, lingulids) depend on ambient palaeoseawater temperature and composition (KOLODNY et al., 1983; PUCÉAT et al., 2004). The important advantage in using phosphate for the oxygen isotope palaeothermometry is a system which records temperatures with great sensitivity while phosphatic-tissue (dentine, enamel, bone, albid) building organisms are alive, keeping the record nearly perfectly preserved after death, and the post-depositional exchange can be neglected (KOLODNY et al., 1983). It has been shown in number of works on phosphate geochemistry, that the isotopic exchange between aqueous inorganic solutions and PO_4^{3-} ions is so slow as to be negligible even over geological time scales, except if exposed to high temperatures (TUDGE, 1960; WINTER et al., 1940; BRODSKII & SULIMA, 1953), though on the other hand it has been demonstrated repeatedly (TUDGE, 1960; DAHMS & BOYER, 1973) that in enzyme-catalysed reactions the exchange of O^{18} between water and PO_4^{3-} is extremely rapid. Mechanisms which have been suggested for the biological formation of apatites would result in a rapid exchange of oxygen isotopes between water and phosphate (LEONARD & SCULLIN, 1969).

The conodont apatite has been distinguished of biogenic apatites as the one to be secreted in the most near-isotopic equilibrium with ambient seawater (KOLODNY et al., 1983), and better preserve an unaltered oxygen isotope ratio compared to commonly analysed brachiopod apatite or brachiopod calcite (JOACHIMSKI et al., 2003). Even encountering diagenetically very stable brachiopod low magnesium calcite, which oxygen isotope values result in significantly higher palaeotemperatures in comparison to those derived from conodont apatite (WENZEL & JOACHIMSKI, 1996; WENZEL at al., 2000, JOACHIMSKI & BUGGISH, 2002; JOACHIMSKI et al., 2004). Conodont apatite susceptibility to the pH variations of the ambient sea water is also close to a negligible margin, contrary to the brachiopod calcite, which is highly affected by sea-water pH change (JOACHIMSKI et al., 2004). The $\delta^{18}O$ values of brachiopod apatite also give significantly lower $\delta^{18}O$ values than coeval conodont apatite, and varies widely (13.0 to 17.5‰ V-SMOW) compared to homogeneous $\delta^{18}O$ values of conodonts, which have variation close to the analytical precision (± 0.2‰), (WENZEL et al., 2000). Moreover, the $^{18}O/^{16}O$ of conodont biogenic apatite is similar to the $\delta^{18}O_{apatite}$ values of modern and Mezozoic tropical biogenic apatites, and gives comparatively realistic palaeotemperatures by assuming a modern 'ice-free' oxygen isotope composition of the contamporaneous palaeoseawater (WENZEL et al., 2000). Thus the fact that the $\delta^{18}O$ values of conodont apatite translate into realistic palaeotemperatures serve as a basis to assume conodont apatite record of Palaeozoic temperatures as more reliable than that of coeval brachiopod calcite or apatite record (JOACHIMSKI et al., 2003, 2004).

The contamporaneous early vertebrate fossil apatite is composed of high density phosphatic tissues as dentine and enamel, which are comparable in its physico-chemical properties to conodont crown tissues; however it has not yet been properly tested for $\delta^{18}O_{apatite}$ composition and palaeotemperature calculations. The aim of this work is to prove vertebrate fossil apatite as a $\delta^{18}O$ recorder and palaeoenvironmental proxy in comparison to coeval conodont apatite.

The suitability of early vertebrate and conodont apatite as a geochemical archive

The biogienic apatite tissue properties of both early vertebrate and conodont fossil remains are of great importance as concerned with their potential to retain primary isotopic composition. The extreme differences in crystal sizes of conodont crown tissues together with their contrasting trace element composition has been considered to be important to conodont geochemical studies in the context of palaeoseawater reconstructions (TROTTER & EGGINS, 2006). Conodont hard apatite tissues have been recently differentiated by crystal size and shape, their inter- and intracrystalline porosities have been determined, giving insights in conodont histology, palaeobiology, and determining their chemical integrity, crucial in characterizing palaeoseawater composition and palaeoenvironmental changes (TROTTER et al., 2007). For instance, in porous bone tissue, pore connectivity and crystal size are key controls of permeability, which has significant implications for its inherent succeptibility to diagenetic alteration. Tissues with high pore connectivity will have greater hydraulic conductivity, thus enhancing pore-fluid migration, and large crystal surface areas will promote the diffusion and adsorption of secondary ions onto apatite crystallites. This kind of extensive porosity has been recognized in all conodont crown tissues, nevertheless the assessment of pore connectivity and consequent tissue permeability remain complex (TROTTER et al., 2007). Conodont cancellated albid crown comprises large (100' μm) apatite crystals, much larger than those in hyaline and basal body tissues of conodonts, and is not fine-grained aggregate as previously believed. These extraordinarily large crystals are presumed to reflect an *in vivo* crystallization event, and served as a less-permeable barrier to fluid exchange during diagenesis. The extraordinary large crystals, and apparent lack of pore connectivity of cancellate single crystal albid tissue would inhibit chemical exchange with impurities from diagenetic pore fluids (TROTTER et al., 2007), thus making it resistant to after-depositional changes in isotopic composition. Moreover, conodont albid crown in general is well recognized as being significantly more resistant to acid etching, and minimal post-mortem uptake REE, than other conodont crown tissues, implying to comparatively restricted permeability, thereby offering greater potential for retaining primary geochemical signatures (TROTTER et al., 2007). Subsequently it can be concluded that albid crown most likely represents the least permeable conodont tissue and thereby offers the greatest potential for retaining primary geochemical signatures.

Early vertebrate microremain tissue studies claim their exoskeleton microremains (dermal scales) possess homologous teeth histology, with compact surface layer of diagenetically-resistant enamel covering the dentine scales (e.g., MÄRSS et al., 2007). Vertebrate tooth enamel and dentine tissues are considered to be relatively resistant to any diagenetic modification of the primary isotopic composition (QUADE et al., 1992; SHARP et al., 2000). Different dentine tissue patterns and properties should be taken in consideration when analysing particular taxonomic groups of early vertebrates.

In addition to the oxygen isotopic composition of biogenic apatites, other isotope compositions, such as $^{87}Sr/^{86}Sr$ isotope ratio, rare earth element (REE) compositions may be taken as an argument of conodont apatite suitability as a geochemical archive, useful for palaeoseawater and palaeoclimate studies (HOLMDEN et al., 1996). Most of the apatitic fossils have Sr isotope ratios that are more radiogenic than the enclosing rock, indicating general susceptibility of biogenic apatites to post-depositional Sr exchange (BERTRAM et al., 1992). The largest isotopic shifts are measured in brachipods, and basal body material of conodont elements, whereas conodont crown material exhibited the smallest effects (HOLMDEN et al., 1996). A color alteration index (CAI) threshold, below which conodonts may be considered as unaltered for Sr isotope composition, has been accepted for a long time (BERTRAM et al., 1992). Nevertheless high resolution X-ray mapping reveals that even conodont crowns exchange Sr, which concentrations being gradually decreasing from the crown to the rim core even in the very pristine conodonts, CAI ≤ 1.5 (HOLMDEN et al., 1996). The recent studies of TROTTER et al. (2007) show that the conodont crown albid tissue (with low Ca / P ratios) has the least permeable histology and is less prone to isotopic disturbance relative to other types of fossil biogenic apatites, being more resistant to postmortem uptake of Sr, Y, Th, U, and REE, and this way more closely approaching primary conodont compositions (TROTTER et al., 2006). Thus conodont crown albid tissue apatite is considered in many aspects as a suitable material for investigating isotope ratios and reconstructing palaeoseawater, with the preservation of unaltered isotopic composition depending more on favorable diagenetic circumstances and on the crystallochemical attributes of conodont crown apatite (HOLMDEN et al., 1996).

Diagenesis tends to lower $\delta^{18}O$ values as a consequence of increasing burial temperatures and/or post-depositional interactions of meteoric waters depleted in $\delta^{18}O$. In addition to changes in geochemical composition, diagenesis and alteration can produce a modification of the overall material crystallinity (e.g. crystal size, lattice defects). It has been suggested that the shift in oxygen isotope composition of biogenic apatites, with respect to their pristine compositions, could be related to changes in crystallinity (SHEMESH, 1990). Since most of biogenic phosphate tissues (except tooth enamel) are originally poorly crystallized, it was concluded that well crystallized apatites are the result of recrystallization processes during diagenesis (SHEMESH, 1990). Thus the crystallinity index has been related to the $\delta^{18}O$ values, proposing that only samples with low crystallinity indices should be considered as well-preserved apatites suitable for geochemical studies. Recently, Raman spectroscopy has enabled precise investigations of biogenic apatites in order to determine the relationships between their structure (cristallinity) and geochemistry (e.g. oxygen isotope $\delta^{18}O$ content), and to determine additional Raman crystallinity index, CI_{Raman} (PUCÉAT et al., 2004). As a result, the crystallinity index appeared to be a poor criterion for determining if a sample has been altered since deposition: geochemical signatures of the biogenic apatites can be well preserved independently of the CI_{Raman}, as well as strongly alterated (as in terms of $\delta^{18}O$) without detectable recrystallization (PUCÉAT et al., 2004). Thus crystallinity index cannot be used as a criterion to identify biogenic apatites whose original oxygen isotope compositions have been modified during post-depositional isotopic exchange, and there is no simple relationship between the chemistry and crystallinity of apatites (PUCÉAT et al., 2004).

To summarize, the relationship between sample histology (crown albid tissue properties) and sample geochemistry, especially in the context of diagenetic overprinting, must be taken into consideration when reconstructing palaeoseawater compositions (TROTTER & EGGINS, 2006; TROTTER et al., 2007). The oxygen isotope compositions of conodonts may be considered as the best apatite-proxy for estimating Palaeozoic sea-water temperatures and climate history. However, the primary biogenic apatite composition both of the conodonts and early vertebrates may still be strongly modified by diagenetic proceses and alterated samples can provide erroneous temperature estimates. It is thus critical for palaeoenvironmental interpretations to distinguish between pristine and alterated phosphatic remains.

Palaeoseawater temperatures calculation from $\delta^{18}O_{apatite}$ and isotope stratigraphy

The palaeoseawater temperatures can be estimated from the $\delta^{18}O$ composition of the PO_4^{3-} remnant of conodont, and presumably vertebrate biogenic apatites. The Late Silurian (Pridolian) palaeoseawater temperature calculations presented in this study are based on the assumption that the oxygen isotopic composition of seawater during the Silurian was –1 ‰ V-SMOW, the same as it is assumed for the Devonian greenhouse period, considering the low latitudes of the Baltic Basin in Late Silurian (JOACHIMSKI et al., 2003, 2004). Absence of recorded tillites since Early Silurian Gondwanan glaciation argues any post-Wenlock Silurian glaciation hypotheses, and favoures warm climate persistence during succeeding middle and Late Silurian (LEHNERT et al., 2007a). However, according to the most recent studies, several glaciations have been suggested to cause Silurian Ireviken, Mulde and Lau Events, based on their similarity with the Late Ordovician glaciation (KALJO et al., 2003), and thus arguing Silurian climate underwent several cool periods. The most evident glaciation has been supposed to occur in the late Silurian (Ludfordian) and correspond to the prominent Lau Event, distinctly recorded as major $\delta^{13}C$ excursion in several late Ludlow sections of the Baltic Basin, together with regressive facies development (MARTMA et al., 2005; LEHNERT et al., 2007a; ERRIKSON & CALNER, 2008). Although the Pridoli is reported as a warm period with global greenhouse conditions, preceding the Silurian – Devonian boundary climate cooling, marked by less prominent $\delta^{13}C$ excursion known as Klonk Event (MUNNECKE et al., 2003; ERRIKSON & CALNER, 2008).

The palaeoseawater temperatures have been calculated using $\delta^{18}O$ values from the PO_4^{3-} remnant of both conodont and early vertebrate biogenic apatite, and the following equation:

$$T\,[°C] = 113.3 - 4.38\,(\delta^{18}O_{apatite} - \delta^{18}O_{sea\text{-}water})$$

(KOLODNY et al., 1983) (1)

Temperatures derived from the conodont apatite for the Pridolian section of the Gėluva-99 borehole range from 24.8 – 31.5 °C. Temperatures derived from the early vertebrate apatite range from 33.6 – 38.0 °C for the Gėluva-99 borehole, and from 32.6 – 38.1 °C for all the different borehole early vertebrate samples of the Pridolian section (Fig. 2). The palaeotemperature curves show reverse negative shifts in estimated palaeoseawater temperatures, corresponding to cooling events (Fig. 1 and 2). This negative excursion of both vertebrate and conodont apatite curves goes in a noteworthy accordance with middle Pridolian sea-level drop, which may be interpreted on a well-defined facies change from marginal (dolomites with gypsum), to the shallow shelf ones (organogenic detrital limestones) corresponding to the formation boundary (see Fig. 1 and 2) (LAZAUSKIENĖ et al., 2003; ŽIGAITĖ et al., 2008): top of the Vievis Fm., and bottom of the Lapės Fm. in the central facies zone of the Silurian basin of Lithuania (PAŠKEVIČIUS, 1997; LAZAUSKIENĖ et al., 2003.) This also well reflect a significant change in

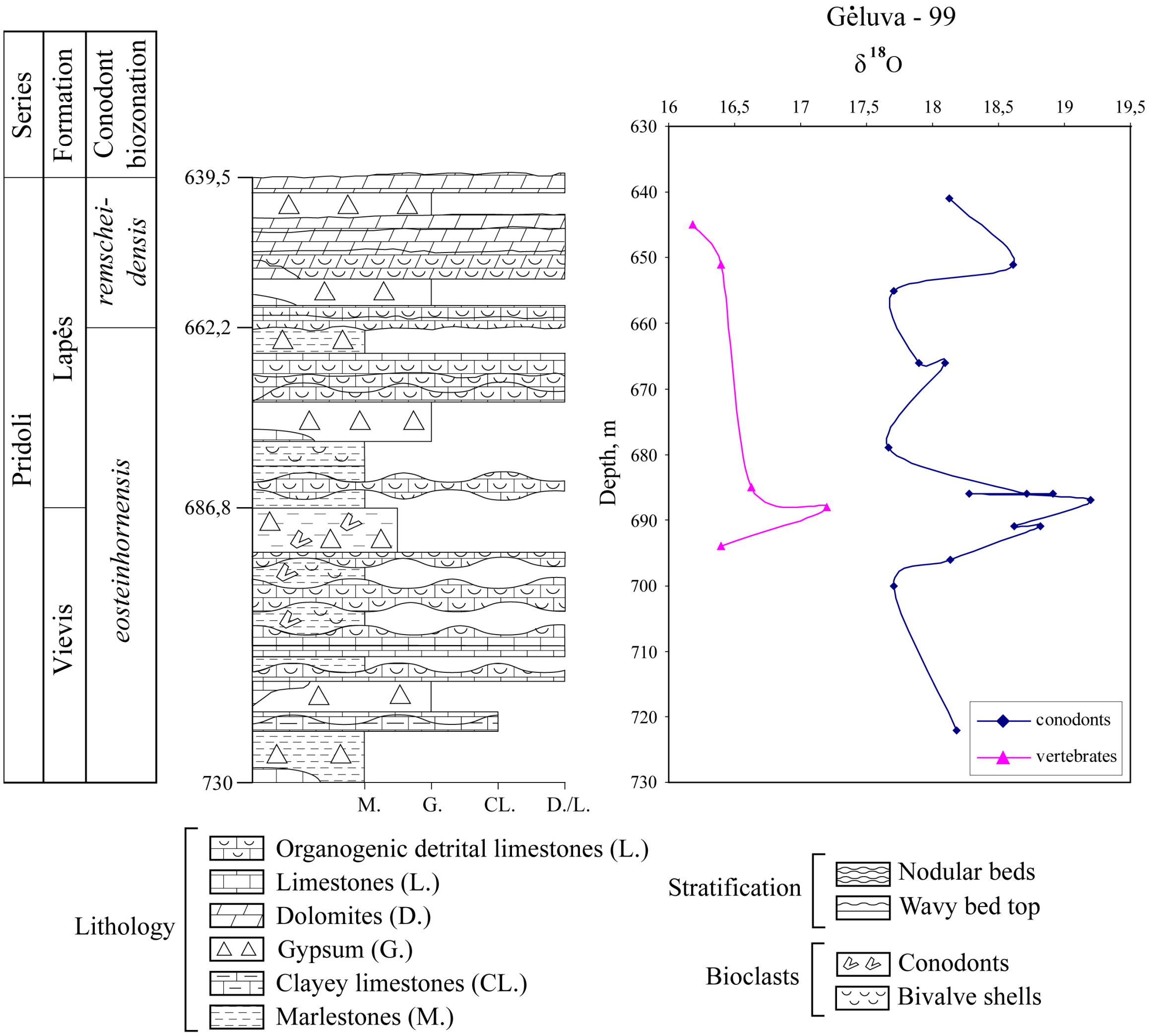

Fig. 1. The $\delta^{18}O_{apatite}$ values measured on early vertebrates and conodonts from the Upper Silurian Pridolian section of the Gėluva-99 borehole, the Silurian central facies zone of Lithuania (Baltic Basin, Lithuania). observed between the samples of 696 m (29.5 °C), and 687 m depth (24.8 °C), and therefore corresponding climate cooling is suggested.

vertebrate faunal associations, from *Goniporus alatus* and *Thelodus trilobatus* in Vievis Fm., to *Loganellia cuneata*, *Paralogania kummerovi*, *Thelodus sculptilis*, *Trimerolepis (=Katoporodus) tricavus*, and *Trimerolepis (=Katoporodus) lituanicus* in Lapės Fm. (KARATAJŪTĖ-TALIMAA & BRAZAUSKAS, 1994).

Global sea-level drop would be associated with climatic cooling if regional tectonic activity control is not considered (LAZAUSKIENĖ et al., 2003). As a consequence, we tend to interpret the observed shift in $\delta^{18}O_{apatite}$ as a change in temperature. Precizing to the $\delta^{18}O$ results of conodont apatite revealed in this work, a significant palaeoseawater temperature drop in almost 5 °C can be estimated for the Vievis Fm. – Lapės Fm. boundary, Early vertebrate oxygen isotope values are lower, and follow the conodont data offsetting regularly in approximately 2.5 ‰ V-SMOW, which gives palaeotemperatures of 10°C higher (ΔT range from 9,4°C to 11,6°C). This can be compared to the Late Devonian fish teeth $\delta^{18}O_{apatite}$ values from the Rhenish Slate Massif (Germany), shifting negatively from the conodont oxygen isotope ratios (see JOACHIMSKI & BUGGISH, 2002, fig.1). The temperatures revealed here from the conodonts of Pridoli, are a bit higher than those derived from conodonts of the Middle Devonian (Eifelian to early Givetian), but lower that those of the Late Devonian (Frasnian), the latter being close to or above the lethal termal limit for at least marine invertebrates (JAOCHIMSKI et al., 2004). The temperatures calculated in this work from the early vertebrate $\delta^{18}O_{apatite}$, are even higher, and thus translate into unrealistic warm palaeotemperatures, if using the equation (1) proposed by KOLODNY et al. (1983).

Nevertheless the oxygen isotope ratios of early vertebrate apatite are lower than those revealed from the conodont apatite, the general trends of $\delta^{18}O_{apatite}$ shifts of conodonts and early vertebrates appear to be comparable despite of the 2.5 ‰ offset, and show similar trends in the Pridolian sequence in the Upper Silurian of the Baltic Basin. The fact that we observe a stable offset and similar trends in both conodont and vertebrate $\delta^{18}O_{apatite}$ values, suggests that both groups of organisms record the same environmental change. With this consideration, the $\delta^{18}O$ value curves of contamporaneous vertebrate and conodont apatites can be used in sequence stratigraphy, interregional correlations, and palaeoclimate reconstructions. The variations in the isotopic signals correlate negatively with changes in sea level (WENZEL & JOACHIMSKI, 1996, fig. 8). Heavy oxygen signals coincide with sea-level lowstands, whereas light signals are recorded during sea-level highstands. Sea-level highstands were probably characterized by the formation of warm saline waters on subtropical epicontinental shelves, including oxygen-deficiency in the basins. The low $\delta^{18}O$ values are attributed to ^{18}O depletion in surface waters owning to the storage of ^{18}O-enriched saline waters in the basins (WENZEL & JOACHIMSKI, 1996). The unknown primary $\delta^{18}O_{water}$ composition of the palaeo-oceans, which depended on general palaeoclimate, water temperature and salinity, is the main limitation in the palaeoseawater temperature estimations. KOLODNY et al. (1983) have well-founded a possibility of palaeotemperature analysis using fossil fish from the geological record, which can be applied both to marine and fresh water fish bone, with reservation to assume the isotopic composition of the palaeowater prospectively. For the fresh water fish apatites (and carbonates as well) estimations of $\delta^{18}O_{water}$ possess a difficult problem (SHEMESH et al., 1983). An ideal case would be if one could independently obtain a value for $\delta^{18}O_{water}$ in each case.

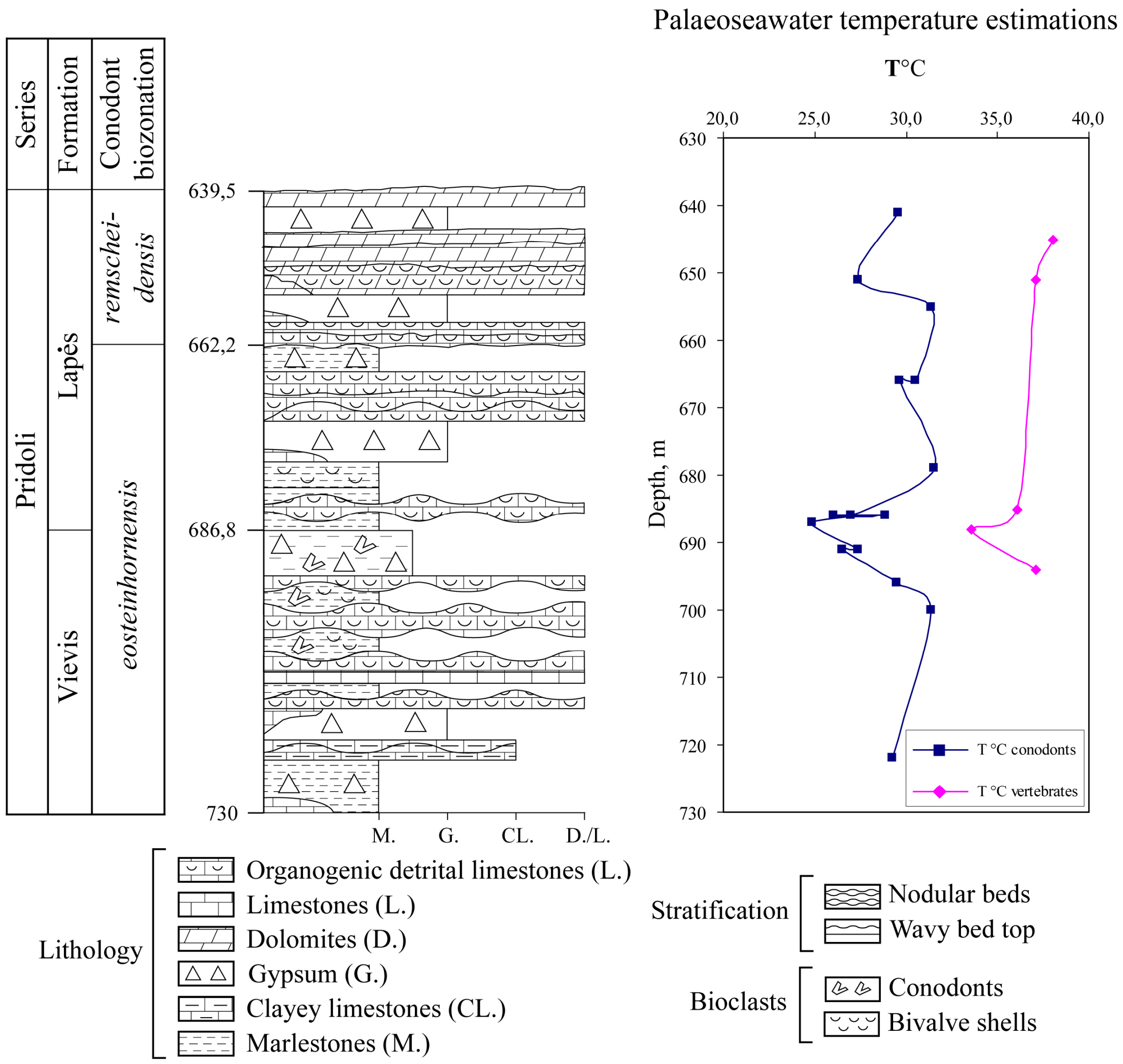

Fig. 2. Palaeotemperatues (T °C) estimated early vertebrates and conodonts from the Upper Silurian Pridolian section of the Gėluva-99 borehole, the Silurian central facies zone of Lithuania (Baltic Basin, Lithuania).

The palaeoclimate influenced greatly the $\delta^{18}O_{water}$ of the palaeo-oceans, as well as the salinity. Global cooling and glaciations at the Earth poles deplete ocean water from light ^{16}O, which is easier to evaporate as meteoric water, and get stored in the extensive ice-caps. Conversely, the equatorial ocean water goes in the same equilibrium during high warming periods, and is depleted from light ^{16}O as well, since an increase in evaporation eliminates light ^{16}O easier as meteoric wapour (HOEFS, 1997). Moreover, water salinity reflect an important control on the oxygen isotopic composition of sea-surface waters, as the same increase in evaporation will enrich such waters in ^{18}O. Contrary, fresh water dilution will result in an enrichment in ^{16}O (GROOTES, 1993).

Discrepancy between early vertebrate and conodont apatite $\delta^{18}O$ values

The early vertebrate $\delta^{18}O_{apatite}$ values are significantly lower than those of the conodonts from the coeval Pridolian samples, though causes to this offset is not unequivocal.

The offset in the $\delta^{18}O$ shifts of early vertebrates if compared to conodonts, can hardly be explained by different life habitats of conodonts and early vertebrates, and/or diagenetic alteration of the primary isotope signals. The 2.5 ‰ V-SMOW lower $\delta^{18}O_{apatite}$ values of early vertebrates can be interpreted either as a temperature increase, a salinity decrease or as the combined effect of increasing temperature and decreasing salinity. However, a strong decrease in surface water salinity would be required if the 2.5 ‰ V-SMOW decrease in early vertebrate $\delta^{18}O_{apatite}$ is to be explained exclusively by a lower salinity. This assumption seems implausible since conodonts and early vertebrates come from the same carbonate samples, which overall faunal composition do not show any brackish water influence. Different life habits of conodonts and early vertebrates might be another possible explanation for the observed varying offset in conodont and early vertebrate $\delta^{18}O$ values, although the particularities of the life habitats of conodont animal have not been firmly established inbetween different taxa. Some conodont specialists suggest they were living close to the sediment surface, others favour a fully nektonic life style within the water column (SWEET, 1988). Early vertebrates had mostly nektonic life habits (MÄRSS et al., 2007). Since temperatures decrease with water depth, the deviation from the expected offset between early vertebrate $\delta^{18}O_{apatite}$ and conodont $\delta^{18}O_{apatite}$ might be interpreted as an effect of different palaeowater depths (JOACHIMSKI et al., 2004). However, investigated early vertebrate phosphates record warmer palaeotemperatures in comparison to conodonts, though the vertebrates tested (thelodonts, acanthodians) are assumed to have nektonic life style (MÄRSS et al., 2007), and should record similar or lower temperatures in comparison to conodonts. Thus the observed discrepancy can be hardly explained by a difference in habitat in water-column of these two groups.

Other possibility might be a difference in ultrastructure of mineralized tissues of conodonts and vertebrates, which govern the differences in $\delta^{18}O_{apatite}$ preservation (TURNER et al., *in press*). Conodont elements consists of large, flat, oblong crystals, arranged in layers that run parallel to the long axis of the conodont. Within the layers, crystals of conodont hyaline tissue are positioned across the layer, perpendicular to the surface of the element, or are arranged obliquely in line with the layer. Enamel in the dentition or scales of living vertebrates has crystals, arranged in layers. The crystals are slender, elongate spicules, perpendicular to the surface of the tooth or scale. The crystals in conodont hyaline tissue are exceptionally large, with no trace of prisms, unlike the protoprismatic enamel of fish teeth and scales, or the highly organised prismatic enamel of mammals (KEMP & NICOLL, 1996; TROTTER & EGGINS, 2006; TROTTER et al., 2007; TURNER et al., *in press*).

In summary, we are unable to give a satisfactory explanation for the observed discrepancy in the $\delta^{18}O_{apatite}$ records of early vertebrates and conodonts. The fact that oxygen isotope values of conodont apatite give more realistic palaeotemperatures for tropical and subtropical surface waters lets us assume that conodont apatite records Palaeozoic palaeotemperatures more reliable than coeval early vertebrate apatite. This is why $\delta^{18}O_{apatite}$ values of conodont apatite remains the best proxy for estimating Palaeozoic sea surface temperatures or ice volume history in the Palaeozoic (JOACHIMSKI et al., 2004).

CONCLUSIONS

Pridolian conodonts of the Baltic Basin have $\delta^{18}O_{apatite}$ values ranging from 17.7 to -19.2‰ V-SMOW with average values around 18.3‰. The early vertebrates from the same Pridolian samples have lower $\delta^{18}O_{apatite}$ values ranging from 15.2 to 17.4‰ V-SMOW, giving average values around 16.3‰ V-SMOW. Palaeoseawater temperatures derived from the conodont apatite range from 24.8 – 31.5 °C, and those derived from the early vertebrate $\delta^{18}O_{apatite}$ are approximatelly in 10 °C higher, and range from 32.6 – 38.1 °C.

The first $\delta^{18}O$ curve on biogenic apatite for the Pridolian of the Baltic Basin has been produced on the example of Gėluva-99 borehole, showing a significant negative shift in $\delta^{18}O_{apatite}$ values at the Vievis Fm. – Lapės Fm. boundary, going along with strong sedimentary facies change, which corresponds to the mid-Pridolian sea-level drop (LAZAUSKIENĖ et al., 2003; ŽIGAITĖ et al., 2008), and the palaeotemperature drop (result of this work) all indicating palaeoseawater cooling.

The discreapancy in the $\delta^{18}O_{apatite}$ values of early vertebrates and conodonts in the coeval Pridolian samples of the Baltic Basin can not currently be explained satisfactorily. The fact that the $\delta^{18}O$ values of conodont apatite translate into more realistic palaeotemperatures suggests that conodont elements record Palaeozoic temperatures more faithfully than coeval early vertebrate exoskeleton microremains. Though the fact that the stable offset of 2.5 ‰ V-SMOW has been observed between conodont and vertebrate $\delta^{18}O_{apatite}$ values, together with similar curve trends, suggests that both groups of organisms record the same environmental changes. The calculated palaeotemperatures from conodont $\delta^{18}O_{apatite}$ values, indicate that (1) the assumption of a Pridolian seawater $\delta^{18}O_{water}$ value of –1 ‰ V-SMOW results in relatively realistic equatorial surfacewater temperatures, and (2) a significant cooling event occured during the middle Pridoli, coinciding with a facies change and formation boundary in the Baltic Basin.

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