

## Revision of Silurian vertebrate biozones and their correlation with the conodont succession

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**Abstract.** The first vertebrate-based subdivisions of Silurian strata were mainly drawn on material from outcrops in Britain and drill cores from the southern Baltic. Nearly twenty years ago the first vertebrate biozonal scheme was developed on the basis of vertebrate distribution in several continuous drill core sections in the northern Baltic. This paper presents a new scheme in which many new data on vertebrate distribution from the Baltica (Baltic region, NW Russia), Avalonia (southern Britain, eastern Canada), Laurentia (northern Canada, Greenland, Scotland) and Kara (Arctic Russia) palaeocontinents have been used. All the zones have been defined, and the geographical distribution and the reference stratum and locality for each zone have been given. The Llandovery part of the succession contains the *Valyalepis crista*, *Loganellia aldridgei* and *L. scotica* zones; the Wenlock part is represented by the *Archipelepis bifurcata*/*Arch. turbinata*, *L. grossi*, *Overia adraini*, *L. einari* and *Paralogania martinssoni* zones. The *Par. martinssoni* Zone continues in the Ludlow and is followed by the *Phlebolepis ornata*, *Phl. elegans*, *Andreolepis hedei*, *Thelodus sculptilis* and *T. admirabilis* zones. The last zone continues in the lower Pridoli and is followed by the *Nostolepis gracilis*, *Poracanthodes punctatus* and *Trimerolepis timanica* zones. The *L. aldridgei* and *Arch. bifurcata* zones are new, and the *Arch. turbinata* and *O. adraini* faunas have been raised from ‘faunal succession units’ to zones. The geographically widely distributed *L. grossi* Zone in the upper Sheinwoodian and the *Par. martinssoni* Zone in the upper Homerian–lowermost Gorstian allow the integration of regional successions into one Generalized Vertebrate Zonal Scheme. Possible correlations of conodont and vertebrate biozones, and gaps in sedimentation in the northern East Baltic Silurian sequence have been discussed, the most extensive hiatus being between the Paadla and Kuressaare stages.

**Key words:** agnathans, fishes, conodonts, biostratigraphy, Silurian, Baltic region, British Isles, Canada, Russian Arctic.

### INTRODUCTION

The first vertebrate-based subdivisions of Silurian strata were mainly drawn on material from outcrops in Britain (Turner 1973) and drill cores from Lithuania and Latvia (Karatajūtė-Talimaa 1978). Soon after, the first vertebrate biozonal scheme was compiled based on detailed studies of the vertebrate distribution in several continuous drill core sections from Estonia and Latvia (Märss 1982a, 1982b). New data obtained during later studies prompted some modifications of the original zonation, whereby the scheme became applicable to parts of the northern hemisphere (Märss 1989). Activities under IGCP Projects 328 and 406 provided additional information about Silurian vertebrates from many parts of the world, particularly from remote Arctic regions, which resulted in further revisions of the zonation and the proposal of the first standard scheme (Märss et al. 1995, 1996). New data subsequently became available from North Greenland (Blom 1999a, 1999b, 2000), Arctic Canada (Märss et al.

1998a, 1998b, 2006) and Russia (Karatajūtė-Talimaa & Märss 2002; Märss & Karatajūtė-Talimaa 2002). All the Silurian vertebrate-bearing localities in northwestern Canada (the Selwyn Basin) were revised (Soehn et al. 2000), biostratigraphically valuable thelodonts were described, a faunal succession scheme for the Avalanche Lake region (Mackenzie Mountains) was developed and correlations were made (Soehn et al. 2001). Additionally, studies of vertebrates from southern Britain (Turner 2000; Märss & Miller 2004) and Belarus (Plax & Märss 2011) have provided further taxonomical and biostratigraphical information about that group.

The first Silurian conodont zonation was published by Walliser (1964). Because a number of Walliser’s zones were not recognizable outside Cellon (Austria), several alternative zonations have been proposed (e.g., Aldridge 1972; Helfrich 1975; Barrick & Klapper 1976). In addition, Aldridge & Schönlaub (1989) attempted to work out a global zonation. Over the last two decades, the Silurian conodont zonation has been revised considerably, many

new units have been described and their applicability in regional and global correlations have been discussed (e.g., Jeppsson 1997; Corradini & Serpagli 1999; Viira 1999; Calner & Jeppsson 2003; Jeppsson et al. 2006; Männik 2007a, 2007b). A simplified version of the zonation was published by Cramer et al. (2011) to encourage its wider use.

Despite the many studies on conodonts and vertebrates, only a few publications have analysed co-occurrences of vertebrates and conodonts. In the southern East Baltic, in Lithuania, studies of thelodonts and conodonts in samples from several drill core sections allowed direct comparison of their distribution and the dating of the vertebrate assemblages recognized in terms of conodont biostratigraphy (Karatajūtė-Talimaa et al. 1987; Karatajūtė-Talimaa & Brazauskas 1995). In several samples from the Severnaya Zemlya Archipelago, vertebrates were found together with conodonts (Matukhin et al. 1999). The distributions of vertebrates and conodonts in samples from Arctic Canada (Franklin Basin) were compared with data from Europe (Märss et al. 1998b). That paper also presented the first carbon isotope data from the region and correlated  $\delta^{13}\text{C}$  variations with those in the Baltic area. The taxonomy and distribution of agnathans and fishes in southern Britain have been investigated, the regional vertebrate zonal scheme has been updated and characteristic vertebrate assemblages have been correlated with the conodont zonation (Miller & Märss 1999; Turner 2000; Märss & Miller 2004).

In the present study we have re-examined vertebrate distribution data from the Baltic region and have added new information from several other regions of the northern hemisphere (British Isles, Greenland, Canada, Russia, Belarus). Our aim is to give an updated Silurian vertebrate biozonation, to correlate the vertebrate and conodont biozones and to update datings and correlations of strata in the regions discussed.

The following abbreviations are used in the text and figures:

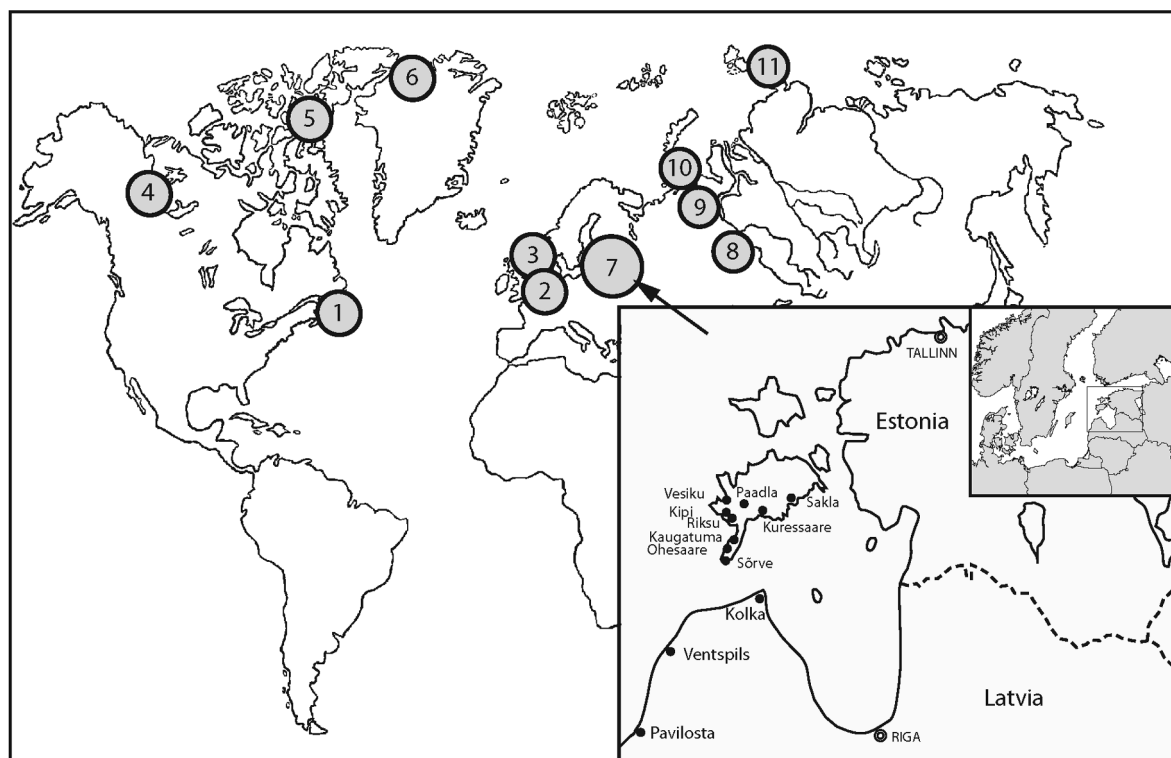
- (a) zonation – CZ, Conodont Zone; CSZ, Conodont Superzone; FAD, First Appearance Datum; GVZ, Generalized Vertebrate Zonation; GZ, Graptolite Zone; VZ, Vertebrate Zone;
- (b) northern East Baltic stratigraphical units – Ä, Äigu Beds; H, Himmiste Beds; J<sub>1</sub>P, Paramaja Member of the Jaani Formation; J<sub>2</sub>, Jaagarahu Stage; JG, Jaagarahu Formation; JM, Jamaja Formation; K, Kudjape Beds; K<sub>1</sub>, Rootsiküla Stage; K<sub>2</sub>, Paadla Stage; K<sub>3a</sub>, Kuressaare Stage; K<sub>3b</sub>, Kaugatuma Stage; K<sub>4</sub>, Oheesaare Stage; Kn, Kuusnõmme Beds; L, Lõo Beds; M, Maasi Beds; Ms, Mustjala Beds; N, Ninase Beds; R, Rumba Formation; RKs, Riksu Formation; RK, Raiküla Formation; S, Sauvere Beds; Sn, Soeginina Beds; SR, Sõrve Formation; T, Tahula Beds; Tg, Tagavere

Beds; TM, Tamsalu Formation; TR, Torgu Formation; U, Uduvere Beds; V, Vilsandi Beds; Vents., Ventspils Formation; VL, Velise Formation; VR, Varbola Formation; Vs, Vesiku Beds; Vt, Viita Beds;

- (c) names of taxa – *A.*, *Andreolepis*; *absid.*, *absidata*; *Am.*, *Amydrotaxis*; *amorph.*, *amorphognathoides*; *Anc.*, *Ancoradella*; *Arch.*, *Archipelepis*; *Asp.*, *Aspelundia*; *b.*, *bohemica*; *c.*, *confluens*; *Cor.*, *Coryssognathus*; *Ct.*, *Ctenognathodus*; *D.*, *Distomodus*; *e.*, *elegans*; *eopenn.*, *eopennatus*; *G.*, *Goniporus*; *I.*, *Icriodella*; *K.*, *Kockelella*; *L.*, *Loganellia*; *murch.*, *murchisoni*; *Neth.*, *Nethertonodus*; *N.*, *Nostolepis*; *o.*, *ortus*; *O.*, *Overia*; *Oul.*, *Oulodus*; *Oz.*, *Ozarkodina*; *Oz. r.*, *Ozarkodina remscheidensis*; *Oz. s.*, *Ozarkodina sagitta*; *p.*, *pennatus*; *Pand.*, *Panderodus*; *Par.*, *Paralogania*; *Phl.*, *Phlebolepis*; *Pol.*, *Polygnathoides*; *Por.*, *Poracanthodes*; *Pran.*, *Pranognathus*; *Ps.*, *Pseudooneotodus*; *Pt.*, *Pterospathodus*; *Pt. a.*, *Pterospathodus amorphognathoides*; *r.*, *remscheidensis*; *rhen.*, *rhenana*; *s.*, *sagitta*; *sn.*, *snajdri*; *staurog.*, *staurogathoides*; *v.*, *variabilis*; *wall.*, *walliseri*; *T.*, *Thelodus*; *Tr.*, *Trimerolepis*; *Tu.*, *Turinia*; *V.*, *Vahylepis*.

## VERTEBRATE BIOZONATION

The vertebrate biozonation (hereafter zonation) described below is a summary of data from the Baltica, Avalonia, Kara and Laurentia palaeocontinents. The zonation for the lower part of the Silurian succession (Llandovery and lower part of the Lower Wenlock) is mainly based on data from Avalonia (eastern Canada and southern Britain; Fig. 1: 1, 2) and Laurentia (Scotland, northern Canada, Greenland; Fig. 1: 3–6). The upper part of the zonation, which corresponds to the upper part of the Lower Wenlock to Přidoli (incl.), is mainly drawn on information from Baltica (Fig. 1: 7–10) and Kara (Severnaya Zemlya Archipelago) (Fig. 1: 11). Some zones in these large and geographically remote areas overlap in the upper Sheinwoodian, Homerian and lowermost Gorstian, which enables us to use them for compilation of the Generalized Vertebrate Zonal Scheme. Generally, the lower boundary of each zone is defined by the first appearance of a nominal species, and its upper boundary is defined by the first appearance of the succeeding nominal species. Thus, these zones are partial range zones. The lower boundary of acanthodian zones in the Přidoli has been defined either at the level where the taxon becomes abundant or where it obtains certain specific features. The total range of the nominal taxon can extend above the upper limit of the zone or even cross one or more zones (Fig. 2A, B). Note that in this paper the lateral replacement of taxa/zones is marked by a slash in the zone names.



**Fig. 1.** The General Vertebrate Zonal Scheme is based on material from the following regions. *Avalonia*: 1, eastern Canada (Quebec and New Brunswick), 2, southern Britain (Welsh Borderland); *Laurentia*: 3, Scotland, 4, northern Cordillera (Mackenzie Mountain area), 5, Canadian Arctic islands (Cornwallis, Baillie-Hamilton), 6, northern Greenland; *Baltica*: 7, Baltic Sea region, Skåne, Ringerike, eastern Poland, Belarus, 8, Central Urals, 9, Timan-Pechora Region, northern Urals, 10, Novaya Zemlya; *Kara*: 11, Severnaya Zemlya islands. Inset shows the locations of the core sections from Estonia and Latvia from where the data have been used in the text and/or Fig. 4A, B.

### The *Valyalepis crista* Zone Märss et al., 1996

**Definition.** The lower boundary of the zone is defined by the FAD of *V. crista* (Fig. 2A).

**Reference stratum and locality.** Clemville Formation, Chaleurs Group, Rhuddanian, Lower Llandovery; Petit Port Daniel River section, west of Clemville, Gaspé Peninsula, Québec, eastern Canada.

**Characteristic fauna.** *Valyalepis crista* co-occurs with *Loganellia scotica*-type and *L. sibirica*-type thelodonts.

**Distribution elsewhere.** Not recognized outside the type region.

**Reference.** Turner & Nowlan 1995.

**Remark.** The index species does not reach the lower boundary of the overlying zone.

### The *Loganellia aldridgei* Zone (established herein)

**Definition.** The lower boundary of the zone is defined by the FAD of *L. aldridgei* (Fig. 2A).

**Reference stratum and locality.** Purple Shales Formation, Telychian, Llandovery; calcareous beds in the middle part of the sequence at the Devil's Dingle locality, Buildwas, Shropshire, Welsh Borderland, Britain.

**Characteristic fauna.** *Loganellia aldridgei* occurs sporadically together with another *L. scotica*-type loganelliid.

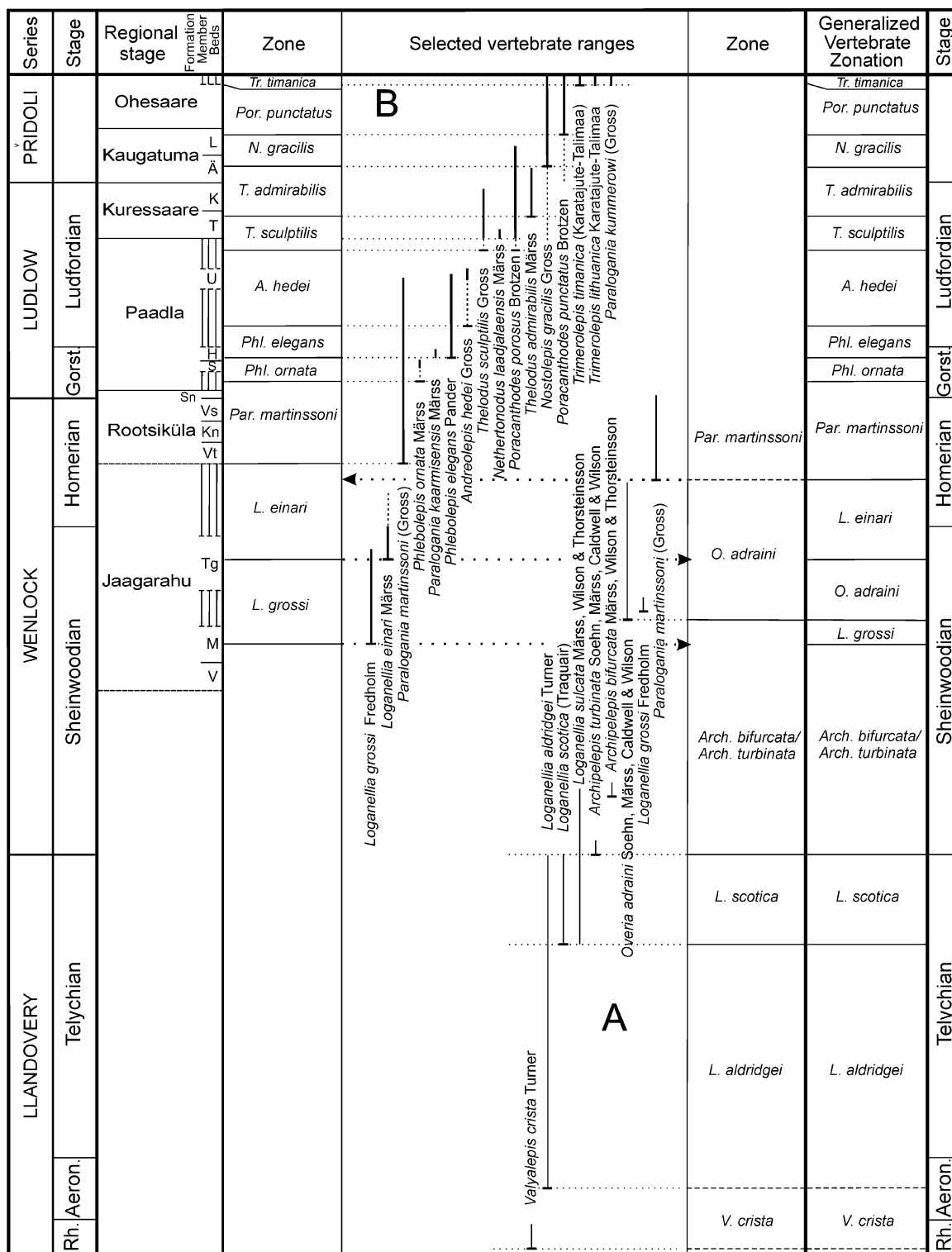
**Distribution elsewhere.** Venusbank and Minsterley formations, middle and upper Aeronian; Purple Shale Formation, lower Telychian, Shropshire, Welsh Borderland, Britain.

**Reference.** Turner 2000, tables 1, 2.

**Remark.** We exclude from *L. aldridgei* the specimens shown by Aldridge et al. (1996, figs 2 and 3) as *L. ex gr. scotica* in the Upper Telychian Kilbride Formation of Coolin Lough, western Ireland.

### The *Loganellia scotica* Zone Ritchie, 1985

**Definition.** The lower boundary of the zone is defined by the FAD of *L. scotica* (Fig. 2A).



**Fig. 2.** Ranges of selected vertebrate taxa: **A**, in the Avalonia and Laurentia palaeocontinents; **B**, in the Baltica palaeocontinent. The Baltic regional stratigraphy is modified from Nestor (1997). Vertical striping in the regional stratigraphic column indicates the main gaps, i.e., their known maximum extent in the outcrop area of the Silurian sections in Estonia. The horizontal line at the lower end of the vertical distribution of a taxon indicates the beginning of its range, i.e., the first appearance datum (FAD) and/or the zone boundary; dotted line – range of a taxon outside Estonia; solid line – known range in Estonia; horizontal lines with arrows in the transitional Sheinwoodian–Homerian interval show the shift of zone boundaries in an adjacent palaeocontinent. Rh., Rhuddanian; Aeron., Aeronian; Gorst., Gorstian. For abbreviations of northern East Baltic stratigraphical units and names of taxa see p. 182.

*Reference stratum and locality.* Patrick Burn Formation, Priesthill Group, upper Telychian, Upper Llandovery; Logan Water section, Lesmahagow, Scotland.

*Characteristic fauna.* In Scotland, the associated faunal list includes the protochordate *Ainiktozoon loganense* Scourfield and the agnathan *Jamoytius kerwoodi* White in addition to *L. scotica*.

*Distribution elsewhere.* Ree Burn Formation, Hagshaw, Scotland; Lafayette Bugt Formation, North Greenland; Wych Formation and upper part of the Purple Shale Formation, Worcester and Hereford, Welsh Borderland; Anse aux Cascons and Anse à Pierre Loiselle formations, Québec, eastern Canada; Cape Phillips Formation, Cornwallis and Baillie-Hamilton islands, Arctic Canada.

*References.* Ritchie 1985; Turner & Nowlan 1995; Märss & Ritchie 1998; Märss et al. 1998a, 1998b, 2006; Blom 1999a; Turner 2000; Soehn et al. 2001.

*Remarks.* (1) Ritchie (1985, fig. 5) was the first to recognize the range of *L. scotica* in the Patrick Burn and Kip Burn formations in Lesmahagow Inlier, Scotland. (2) The total range of *L. scotica* in the type region of the zone in Lesmahagow includes the Patrick Burn, Kip Burn and Dunside formations (Priesthill Group, upper Telychian, Upper Llandovery). (3) The zonal taxon does not enter the overlying zone, as exemplified in the Baillie-Hamilton BH1 section. (4) *Loganellia* sp. (cf. *L. scotica*), which was identified from the Avalanche Lake section AV4 (Märss et al. 1998b), was renamed *Loganellia* sp. nov. 2 by Soehn et al. (2000) and *L. cf. sulcata* herein. Its relationships, especially with *L. sulcata*, still need to be clarified. (5) The *L. sibirica* Zone, which was a constituent of the compound *L. scotica*/*L. sibirica* Zone in the Middle–Upper Llandovery interval in the first standard scheme, is hereby excluded from the scheme for two reasons. First, the total range of *L. sibirica* (= *L. sibirica* Zone) in the Siberian Platform corresponds to the entire Llandovery (Žigaitė & Blicek 2006) and therefore cannot be treated as coeval with the *L. scotica* Zone. Second, the interval is a single separate ‘hanging’ interval and does not have any vertebrate zones above or below it.

#### **The *Archipelepis bifurcata*/*Arch. turbinata* Zone Soehn et al., 2001, modified herein**

*Definition.* The lower boundary of the zone is defined by the FAD of *Arch. turbinata* or *Arch. bifurcata* (Fig. 2A).

*Reference stratum and locality.* Cape Phillips Formation, lower Sheinwoodian, lower Wenlock; sample at 90.0 m in the Baillie-Hamilton BH1 section, which corresponds to a level in the *Monograptus riccartonensis*–*Monograptus*

*belophorus* GZ as determined by the carbon isotope curve pattern (Märss et al. 1998a).

*Characteristic fauna.* *Archipelepis bifurcata* co-occurs with thelodonts *L. sulcata*, *Shiella parca* Märss, Wilson & Thorsteinsson, *S. gibba* Märss, Wilson & Thorsteinsson, *Phillipsilepis crassa* Märss, Wilson & Thorsteinsson, putative chondrichthyan *Frigorilepis caldwelli* Märss, Wilson & Thorsteinsson and *Lanarkia* cf. *horrida* Traquair in the Baillie-Hamilton BH1 section; *Arch. turbinata* occurs with *Lanarkia* cf. *horrida* and a yet undescribed *Loganellia* (*L. cf. sulcata* herein) in the Avalanche Lake sections.

*Distribution elsewhere.* Cape Phillips Formation, Sheinwoodian, Cornwallis Island, and the north shore of Baumann Fiord on Ellesmere Island; Road River Formation, 1 R Member, Sheinwoodian, lower Wenlock, Avalanche Lake sections, Mackenzie Mountains, northern Canada.

*References.* Märss et al. 1998a, 1998b, 2006; Soehn et al. 2000, 2001.

*Remarks.* (1) In 1995, the IGCP 328 thelodont working group established the *L. avonia* Zone for the lower Sheinwoodian. A preliminary study concluded that the *Loganellia* that occur in the Wenlock strata in Estonia and the Welsh Borderland are the same species. However, later research revealed that the scales from these two regions possess several different features; as a result, two species, *L. einari* (Märss 1996), which occurs in the Tagavere Beds of the Jaagarahu Stage in Estonia (see below), and *L. avonia* (Turner 2000), which occurs in the Brinkmarsh Beds, lower Sheinwoodian, Lower Wenlock of Tortworth Inlier, Avon, were established. Because of the restricted distribution of *L. avonia* (found only in one locality), the zone was removed from the zonal scheme (Märss & Miller 2004). (2) In the original regional thelodont succession, three units were introduced for the Upper Llandovery and Wenlock in the Avalanche Lake sections: *turbinata*, *adraini* and *martinssoni* (Soehn et al. 2001). The *Archipelepis turbinata* fauna has been determined to be a zone and is combined with the *Arch. bifurcata* Zone herein. Both *Arch. bifurcata* and *Arch. turbinata* disappear much below the upper boundary of the zone.

#### **The *Loganellia grossi* Zone Märss et al., 1995**

*Definition.* The lower boundary of the zone is defined by the FAD of *L. grossi* (Fig. 2A, B).

*Reference stratum and locality.* Maasi Beds (except their lower part) of the Jaagarahu Stage, upper Sheinwoodian, Lower Wenlock; interval 68.4–79.0 m of the Sakla core, Saaremaa, Estonia.

**Characteristic fauna.** *Loganellia grossi* occurs together with the thelodont *Thelodus* sp. and sometimes with the anaspid *Rhyncholepis parvula* Kiaer.

**Distribution in the Baltic.** Units f and g, Slite Beds, Gotland Island, Sweden; Maasi Beds (except the lower part) of the Jaagarahu Stage, upper Sheinwoodian, Saaremaa, Estonia; middle part of the Wenlock, East Lithuania.

**Distribution elsewhere.** Sundvollen Formation, Lower Ringerike Group, Wenlock, Ringerike Area, Norway; lower part of the Kap Morton Formation, mid-Wenlock, Kap Lucie Marie, Washington Land, North Greenland; Cape Phillips Formation, upper Sheinwoodian of Baillie-Hamilton Island, Arctic Canada; Wenlock, Timan-Pechora Region and northern Urals; upper half of the Samojlovich Formation, Matusевич River, October Revolution Island, Severnaya Zemlya Archipelago.

**References.** Turner & Turner 1974; Fredholm 1990; Märss 1996; Blom 1999a; Talimaa 2000; Nestor et al. 2001; Märss & Karatajūtė-Talimaa 2002; Märss et al. 2006; Plax & Märss 2011.

**Remarks.** (1) Märss (1982a) defined the *Logania taiti* Zone in the Maasi and Tagavere beds of the Jaagarahu Stage, and Märss (1982b) indicated its stratotype. The taxon and two stratigraphically following species were restudied later, and the corresponding zones *Loganellia grossi* and *L. einari* were described. For that reason, a new stratotype has been chosen for both the *L. grossi* and *L. einari* zones. (2) On the Baillie-Hamilton Island BH1 section, *L. grossi* appears shortly after *Overia adraini* (*L. grossi* occurs between 144.5 and 163.5 m in only one sample), which might mean that these two zones are present in a similar stratigraphic time interval. (3) In several sections of the Baltic region, *L. grossi* enters into the *L. einari* Zone.

#### **The *Overia adraini* Zone Soehn et al., 2001**

**Definition.** The lower boundary of the zone is defined by the FAD of *O. adraini* (Fig. 2A, B).

**Reference stratum and locality.** Cape Phillips Formation, upper Sheinwoodian, Wenlock; interval 140.0–144.5 m in the Baillie-Hamilton 1 section, Arctic Canada, which corresponds to an interval in the *Cyrtograptus rigidus*–*Cyrtograptus perneri* GZ based on the carbon isotope curve pattern (Märss et al. 1998a).

**Characteristic fauna.** *Frigorilepis caldwelli* Märss, Wilson & Thorsteinsson, *Lanarkia horrida* Traquair.

**Distribution elsewhere.** Delorme Formation (Member 1D) of Avalanche Lake, Mackenzie Mountains, northern Canada.

**References.** Soehn et al. 2000, 2001; Märss et al. 2002, 2006.

**Remark.** This interval was treated as a unit in the thelodont fauna (Soehn et al. 2001) but is raised to the status of the zone herein.

#### **The *Loganellia einari* Zone Märss, 1990**

**Definition.** The lower boundary of the zone is defined by the FAD of *L. einari* (Fig. 2A, B).

**Reference stratum and locality.** Tagavere Beds of the Jaagarahu Formation (Jaagarahu Stage), Sheinwoodian, lower Wenlock; interval 58.20–62.7 m in the Sakla core, Saaremaa, Estonia.

**Characteristic fauna.** *Thelodus* sp. and *L. grossi* occur together with *L. einari* in the Riksu-803 and Vesiku-507 drill cores.

**Distribution in the Baltic.** The *L. einari* Zone is recognized in the Saaremaa (Estonia) sections and in the uppermost Slite beds (Samsungs 1 locality) of the Gotland Island (Sweden) section.

**Distribution elsewhere.** Sundvollen Formation, Lower Ringerike Group, Wenlock, Ringerike Area, Norway. In the Ostrovets sections 7ts, 73 and 195 in Belarus, *L. grossi* and *L. einari* have been found together.

**References.** Turner & Turner 1974; Märss 1996; Nestor et al. 2001; Plax & Märss 2011.

**Remarks.** (1) The *L. einari* Zone was initially established as a regional zone (Märss 1996). Because of the wide distribution of the species, the zone was later recognized elsewhere and included in the Standard Scheme (Märss et al. 1996). (2) In the Sakla core section, the boundaries of the Jaagarahu and Rootsiküla regional stages, which are based on cyclostratigraphy (Einasto in Märss 1986), are in need of revision. In light of the faunal evidence found in many other cores, the boundary between the stages is situated above the last occurrence (sample 58.20 m) of the thelodont *L. einari*. The vertical distributions of *L. einari* and the next index species, *Paralogania martinssoni*, do not overlap in the Estonian sections or elsewhere.

#### **The *Paralogania martinssoni* Zone Karatajūtė-Talimaa, 1978**

**Definition.** The lower boundary of the zone is defined by the FAD of *Par. martinssoni* (Fig. 2A, B).

**Reference stratum and locality.** Viita Beds, Rootsiküla Stage, upper Homeric, uppermost Wenlock; interval 143.67–153.20 m in the Ohesaare core section, Estonia.

*Characteristic fauna.* In this zone, *Par. martinssoni* occurs together with the thelodont *Thelodus laevis* (Pander), the osteostracans *Tremataspis schmidti* Rohon, *Tremataspis milleri* Patten, *Saaremaaspis mickwitzii* (Rohon), *Oeselaspis pustulata* Patten, *Witaaspis schrenkii* (Pander), *Thyestes verrucosus* Eichwald, and the anaspids *Rhyncholepis parvula* Kiaer, *R. butriangula* Blom, Märss & Miller, *Birkenia robusta* Blom, Märss & Miller, *Pterygolepis nitida* (Kiaer), *Vesikulepis funiforma* Blom, Märss & Miller and *Rytidolepis quenstedtii* Pander.

*Distribution in the Baltic.* Rootsiküla and lower Paadla stages, respectively upper Homerian (uppermost Wenlock) and lower Gorstian (lowermost Ludlow), Estonia; Halla, Mulde and Klinteberg beds, and Hemse unit a, Homerian (upper Wenlock) and lower Gorstian (Ludlow), Gotland.

*Distribution elsewhere.* 1D Member of the Delorme Group in the Avalanche Lake sections, Mackenzie Mountains, Cape Phillips Formation, Homerian, on Baillie-Hamilton Island, the uppermost Wenlock or lowermost Ludlow, Prince of Wales Island, Northern Canada; Bed 10, upper Wenlock, Ringerike, Norway; upper Voron'ya Beds, upper Wenlock Mikhajlovsk Pond area, Central Urals, Russia; lower part of the Ust'-Spokojnaya Formation, Wenlock, Matusevich River section, October Revolution Island, Severnaya Zemlya, Russia; middle Elton Formation, lower Gorstian, lower Ludlow of Welsh Borderland, southern Britain.

*References.* Turner & Turner 1974; Karatajūtė-Talimaa 1978; Märss 1982a; Fredholm 1990; Talimaa 2000; Soehn et al. 2001; Märss & Miller 2004.

*Remarks.* The zone corresponds to the lower part of the *Par. martinssoni* total range within the Homerian (upper Wenlock) and lower Gorstian (lower Ludlow). The species reaches the lower half of the Ludfordian in northern Europe and northern North America.

#### **The *Phlebolepis ornata* Zone Fredholm, 1988**

*Definition.* The lower boundary of the zone is defined by the FAD of *Phl. ornata* (Fig. 2B).

*Reference stratum and locality.* Sauvere Beds (excluding the lowermost part) of the Paadla Stage, Gorstian, lower Ludlow, interval 111.80–112.25 m in the Ohesaare core section, Saaremaa, Estonia.

*Characteristic fauna.* *Phlebolepis ornata* occurs sporadically together with other thelodonts, such as *Thelodus* sp. and *Par. martinssoni*.

*Distribution in the Baltic.* The zone has been recognized only in the sections on Saaremaa and Gotland islands, in the middle and upper parts of the Sauvere Beds, Paadla Stage, and in units b and c of the Hemse Beds, respectively.

*Distribution elsewhere.* Not established outside the Baltic.

*References.* Märss 1986, 1990; Fredholm 1988.

*Remarks.* (1) A *Phl. ornata* fauna was described by Fredholm (1988) in the interval corresponding to units b and c of the Hemse Beds on Gotland. Later, a regional *Phl. ornata* Zone was established in the same interval (Märss 1990, 1996) and included in the Vertebrate Standard Scheme (Märss et al. 1996). (2) *Phlebolepis ornata* does not reach the level of appearance of *Phl. elegans*.

#### **The *Phlebolepis elegans* Zone Märss, 1982a**

*Definition.* The lower boundary of the zone is defined by the FAD of *Phl. elegans* (Fig. 2B).

*Reference stratum and locality.* Himmiste Beds (except their lower half) of the Paadla Stage, upper Gorstian–lower Ludfordian, Ludlow, interval 105.03–108.30 m in the Ohesaare core section, Saaremaa.

*Characteristic fauna.* Rich thelodont, osteostracan and anaspid fauna with *Phl. elegans* contains *Thelodus laevis*, *T. carinatus* (Pander), *Par. martinssoni*, *Tremataspis mammillata* Patten, *Tremataspis milleri*, *Dartmuthia gemmifera* Patten, *Oeselaspis pustulata*, *Witaaspis schrenkii*, *Thyestes verrucosus*, *Procephalaspis oeselensis* (Robertson), *Vesikulepis funiforma* Blom, Märss & Miller, *Silmalepis erinacea* Blom, Märss & Miller and *Rytidolepis? quenstedtii* Pander.

*Distribution in the Baltic.* Saaremaa, western mainland of Estonia (middle and upper Himmiste Beds and lower Uduvere Beds of the Paadla Stage), Gotland, Sweden (the uppermost part of unit c and the lower half of unit d of the Hemse limestones and the corresponding interval of the Hemse marls in NW Gotland).

*Distribution elsewhere.* Upper Bringewood and lower Leintwardine formations, Gorstian and Ludfordian of the Welsh Borderland, southern Britain; upper Mielnik Stage, Ludlow, eastern Poland; middle Gerd"yu Stage, upper Gorstian and lower Ludfordian, western slope of the North and Central Urals; Velikaya River Formation, Ludlow, Timan-Pechora Region; middle part of the Ust'-Spokojnaya Formation, Ludlow, Matusevich River, and lower part of the same formation in the Spokojnaya River section, October Revolution Island, Severnaya Zemlya.

*References.* Karatajūtė-Talimaa 1978; Märss 1986; Fredholm 1988; Märss 1990; Modzalevskaya & Märss 1991; Talimaa 2000; Turner 2000; Karatajūtė-Talimaa & Märss 2002; Märss & Miller 2004.

*Remarks.* (1) The *Phl. elegans* Zone embraces the middle part of the Paadla Stage, uppermost Gorstian–lower Ludfordian, Ludlow, but the species continues upwards into the next zone. (2) The Himmiste Quarry was indicated as a stratotype for the *Phl. elegans* Zone (Märss 1982b). However, during later studies, *Phl. ornata* was separated from *Phl. elegans* and, accordingly, two zones were recognized. The new stratotypes for both zones are indicated herein.

#### The *Andreolepis hedei* Zone Märss, 1982a

*Definition.* The lower boundary of the zone is defined by the FAD of *A. hedei* (Fig. 2B).

*Reference stratum and locality.* Mituva Formation, Paadla Stage, Ludfordian, Ludlow, interval 472.4–484.5 m in the Ventspils-D3 core section, western Latvia.

*Characteristic fauna.* Thelodonts *Thelodus laevis*, *T. carinatus*, *Par. martinsoni*, *Par. kaarmisensis*, *Phl. elegans*; heterostracan *Archegonaspis* sp.; osteostracan *Osteostraci* gen. et sp.; acanthodians *Nostolepis striata* and *Gomphonchus sandelensis*. The vertebrate fossils are strongly depauperate in the upper part of the zone.

*Distribution in the Baltic.* Middle and upper Uduvere Beds of the Paadla Stage, middle Ludfordian, Ludlow, Saaremaa, Estonia; upper half of units d and e of the Hemse limestones, Hemse marls and Burgsvik Sandstone (Uddvide section), Ludfordian, Ludlow, Gotland.

*Distribution elsewhere.* Upper (excluding the uppermost part) of the Ust'-Spokojnaya Formation, Ludlow, October Revolution, Pioneer and Komsomolets islands, Severnaya Zemlya; uppermost part of the West Khatanzej Formation, Ludlow, Khatanzej Peninsula, Novaya Zemlya; Velikaya River Formation, Gerd"yu Stage, Ludlow, Velikaya River, northern Timan; upper part of the Kuba Beds, lower Ludfordian, Ludlow, of the southern Mikhajlovsk Pond section, Mikhajlovsk Subzone, Central Urals.

*References.* Märss 1982a, 1982b, 2001; Valiukevičius et al. 1983; Fredholm 1988; Matukhin et al. 1999.

*Remarks.* (1) After the revision of *A. hedei*, a new species, *A. petri*, was described from the Tabuska Beds in the scattered Silurian bedrock blocks located on the right bank of the Ufa River, Serga Subzone in the Central Urals (Märss 2001). The beds are thought to be either late Ludlow (Modzalevskaya & Märss 1991) or early Pridoli (Shuiskij 1981; Shurygina et al. 1981) in age. (2) *Andreolepis* (identified as *A. hedei*? Gross by Märss 1986, pl. 34, figs 2, 5), found in the Long Quarry Beds (lower Pridoli) in the Chapel Horeb Main Quarry section, southern Wales, may belong to a new and yet undescribed species. (3) The ranges of *A. hedei* and *T. sculptilis* do not overlap in the Baltic.

#### The *Thelodus sculptilis* Zone Märss, 1982a

*Definition.* The lower boundary of the zone is defined by the FAD of *T. sculptilis* (Fig. 2B).

*Reference stratum and locality.* Lower part of the Tahula Beds of the Kuressaare Stage, upper Ludfordian, Ludlow; interval 83.10–95.17 m in the Ohesaare core section, Saaremaa.

*Characteristic fauna.* Other thelodonts, including *T. parvidens* Agassiz, *T. traquairi* (Gross), *Loganellia cuneata* (Gross), *Par. ludlowiensis* (Gross), *Par. perensae* Märss, *Nethertonodus laadjalaensis* Märss, *Trimerolepis tricava* (Gross), *Longodus acicularis* Märss; heterostracan *Archegonaspis* sp.; osteostracan *Zenaspis*? sp.; anaspid *Tahulalepis elongituberculata* Blom, Märss & Miller; acanthodians *Nostolepis striata* Pander, *Gomphonchus sandelensis* (Pander), *Poracanthodes porosus* Brotzen.

*Distribution in the Baltic.* Lower part of the Tahula Beds of the Kuressaare Stage, upper Ludfordian in western Latvia and Estonia; upper Pagegiai Formation, upper Ludlow, Lithuania; Burgsvik Formation, Ludfordian, Gotland, Sweden.

*Distribution elsewhere.* Öved Sandstone Formation, Öved-Ramsåsa Beds, Skåne, southern Sweden; uppermost Gerd"yu Stage, upper Ludlow, Timan-Pechora Region, Tabuska Beds; upper Ludlow or lower Pridoli (see above about the Tabuska Beds), Central Urals; Greben' Stage, upper Ludlow, Novaya Zemlya Archipelago, Russia.

*References.* Märss 1982a, 1982b, 1986, 1990; Karatajūtė-Talimaa et al. 1987; Modzalevskaya & Märss 1991; Karatajūtė-Talimaa & Brazauskas 1995; Märss et al. 1996; Talimaa 2000.

*Remarks.* (1) The species is present in the overlying *T. admirabilis* Zone. (2) The stratotype for the *T. sculptilis* Zone, as given in Märss (1982b), is divided herein to represent stratotypes of two zones, *T. sculptilis* and *T. admirabilis*.

#### The *Thelodus admirabilis* Zone Märss, 1990

*Definition.* The lower boundary of the zone is defined by the FAD of *T. admirabilis* (Fig. 2B).

*Reference stratum and locality.* Uppermost part of the Tahula and Kudjape beds of the Kuressaare Stage, uppermost Ludfordian, upper Ludlow; interval 64.65–83.10 m in the Ohesaare core section, Saaremaa.

*Characteristic fauna.* As for the *T. sculptilis* Zone; however, the specimens are less numerous, and *Nethertonodus laadjalaensis* and *Longodus acicularis* are missing.

*Distribution in the Baltic.* Upper Tahula and Kudjape beds, Kuressaare Stage, upper Ludlow, and the lower



Äigu Beds, Kaugatuma Stage, lower Pridoli, Latvia and Estonia; upper Pagegiai Formation, upper Ludlow, Central Lithuania.

*Distribution elsewhere.* Öved Sandstone Formation, Öved Ramsåsa Group, lower Pridoli, Skåne, southern Sweden.

*References.* Märss 1982a, 1982b, 1990; Karatajūtė-Talimaa & Brazauskas 1995; Vergoossen 1999; Talimaa 2000; Märss & Miller 2004.

*Remarks.* (1) The *T. admirabilis* Zone was originally established as a regional zone (Märss 1990; Märss & Miller 2004). Its geographically rather wide distribution and usefulness in correlations allow it to be included in the generalized scheme. (2) The *Poracanthodes porosus* Zone described in the deeper shelf deposits and used in a parallel zonation for the upper Ludlow–lower Pridoli interval (Märss 1997) corresponds to the *T. sculptilis*, *T. admirabilis* and *N. gracilis* zones in shallow shelf deposits.

#### **The *Nostolepis gracilis* Zone Märss, 1982a**

*Definition.* Corresponds to the interval between the level at which *N. gracilis* Gross begins to dominate the vertebrate fauna below and the domination of *Poracanthodes punctatus* with definite characteristic features (*sensu* Märss 1986, pl. 32, fig. 1) above (Fig. 2B).

*Reference stratum and locality.* Upper Äigu and Lõo beds (excluding the uppermost part) of the Kaugatuma Stage, Pridoli, interval 55.6–94.8 m in the Sõrve-514 drill core, Saaremaa.

*Characteristic fauna.* Abundant *N. gracilis* scales with rare scales of *T. parvidens*, *T. traquairi*, *L. cuneata*, *Trimerolepis tricava* and fragments of *Tolypelepis undulata*, *G. sandelensis*, *Por. porosus* and *Lophosteus connexus*.

*Distribution in the Baltic.* Upper Äigu and Lõo beds (excluding the uppermost part) of the Kaugatuma Stage, Pridoli, Estonia and Latvia; most of the Kaugatuma Stage (excluding the lower part), Kaliningrad District; upper Minija and lower Jūra formations, Lithuania.

*Distribution elsewhere.* Middle Downton (Holdgate Group), Welsh Borderland, southern Britain.

*References.* Turner 1973; Märss 1982a, 1982b, 1997; Valiukevičius 2005, 2006.

*Remarks.* In his summarized biozonal chart, Valiukevičius (2006, fig.1) gave a slightly different succession of Lithuanian acanthodians than was presented in Valiukevičius (2005, figs 7, 8) with *N. gracilis* appearing in the upper Ludfordian. In our opinion, the scales in the lower Kaugatuma Stage and older beds in the northern

Baltic differ from the characteristic *N. gracilis* because they have fewer ridges on the crown and are smaller.

#### **The *Poracanthodes punctatus* Zone Märss, 1982a**

*Definition.* Corresponds to the interval starting at the level where *Por. punctatus* obtains the definite characteristic features (*sensu* Märss 1986, pl. 32, fig. 1) below and the FAD of *Trimerolepis timanica* (Fig. 2B) above.

*Reference stratum and locality.* Uppermost Kaugatuma Stage and most of the Ohesaare Stage, interval 276.2–325.2 m in the Ventspils-D3 drill core, Latvia.

*Characteristic fauna.* Very rich vertebrate fauna including many taxa characteristic of the Kuressaare Stage, such as *T. parvidens*, *T. traquairi*, *L. cuneata*, *Tr. tricava*, *N. striata* and *G. sandelensis*, as well as those of the Ohesaare (uppermost Silurian) and Tilže (Lower Devonian) stages, (*Goniporus alatus* (Gross), *Tolypelepis undulata* Pander, *Oniscolepis dentata* Pander, *Gomphonchus hoppei* Gross, *Lophosteus superbus* Pander, *Tylodus deltooides* Rohon).

*Distribution in the Baltic.* Uppermost Kaugatuma Stage and most of the Ohesaare Stage, Estonia, Latvia, Lithuania and the Kaliningrad District.

*Distribution elsewhere.* Barlow Inlet Formation, Pridoli, Read Bay southern section, Cornwallis Island, Arctic Canada.

*References.* Märss 1982a, 1982b, 1986, 1997; Märss et al. 1998a; Valiukevičius 2005, 2006.

*Remarks.* According to Valiukevičius (2006), *Por. punctatus* appears in the Minija Formation in the Kaugatuma Regional Stage in Lithuania. This level is slightly lower than the level of appearance in the northern East Baltic but is also lower than indicated in the generalized zonal scheme. We treat *Por. punctatus* in the same manner as in Märss (1986, pl. 32, fig. 1), with very fine pores only on the crown.

#### **The *Trimerolepis timanica* Zone (= *Katoporodus timanicus*) Karatajūtė-Talimaa, 1978**

*Definition.* The lower boundary of the zone is defined by the FAD of *Tr. timanica* (Fig. 2B).

*Reference stratum and locality.* Uppermost Ohesaare Stage, Pridoli; interval 269.5–276.2 m in the Ventspils-D3 drill core, Latvia.

*Characteristic fauna.* Thelodonts *L. cuneata*, *Goniporus alatus*, heterostracans *Tol. undulata*, *Oniscolepis dentata*, acanthodians *N. striata*, *N. alta* Märss, *Gomphonchus sandelensis*, *Por. punctatus*.

*Distribution in the Baltic.* Uppermost Ohesaare Stage, Latvia (*Tr. timanica*) and Lithuania (*Tr. lithuanica*); in Estonia, the sedimentary rocks of this age are missing.

*Distribution elsewhere.* Uppermost Pridoli in the Timan-Pechora region, NW Russia (with both *Tr. timanica* and *Tr. lithuanica* present); Ledbury Formation, Welsh Borderland, southern Britain (*Tr. cf. timanica*, see remarks below).

*References.* Karatajūtė-Talimaa 1978; Märss 1982a, 1982b, 1986; Turner 1984; Karatajūtė-Talimaa & Brazauskas 1995; Talimaa 2000; Märss & Miller 2004.

*Remarks.* (1) Karatajūtė-Talimaa (1978) first identified the *Katoporus lithuanicus*/*K. timanicus* assemblage that occurs in the uppermost Downtonian (= Pridoli) strata in the European biogeographical province. Talimaa (2000, table 7) described the *Par. kummerowi* Zone below the combined *Tr. Timanica*–*Tr. lithuanica* Zone. (2) In the Welsh Borderland, the uppermost Pridoli is characterized by the occurrence of *Par. tarranti*, which is followed upwards by *Par. kummerowi*. The scales of *Tr. timanica* recognized in this region were later re-identified as *Tr. cf. timanica* (Märss & Miller 2004). In the Anglo-Welsh region, *Tr. cf. timanica* occurs in the interval from the Ledbury Formation below up to the St Maughan's Group? strata above (uppermost Pridoli to middle Lochkovian) (Turner 1984; Märss & Miller 2004).

### The *Turinia pagei* Zone Gross, 1967

The lower boundary of this zone, as well as the lower Devonian, is marked by the FAD of the thelodont *Turinia pagei* (Turner 1973, 1984; Karatajūtė-Talimaa 1978; Märss 1986, 1997; Talimaa 2000; Märss & Miller 2004).

## CONODONT ZONATION

The conodont zonation (with ranges of index species) used in this paper is shown in Fig. 3. The Llandovery–Wenlock part of the zonation is discussed in Männik (2007b). The zonation in the Ludlow interval (excluding the uppermost Ludfordian) corresponds to that in Cramer et al. (2011), and the uppermost Ludfordian–Pridoli zonation comes from Viira (1999). Because all major revisions of the Silurian conodont zonation have been published previously, only brief comments on the distribution of some key taxa and/or faunas are provided below (Figs 4, 5).

In general, the Rhuddanian is characterized by long-ranging simple cone conodonts (e.g. *Panderodus* and *Walliserodus*). Rich fauna, including several new lineages, appears in the uppermost Rhuddanian and is more charac-

teristic of the Aeronian. The possibility of establishing a universal (global) zonation for the Rhuddanian–Aeronian strata has been discussed, e.g., in Nowlan (1995), Männik (2001), Cramer et al. (2011). Two lineages, *Aspelundia?* and *Distomodus*, appear to have the highest potential for such zonation. However, *Distomodus* is very rare in many regions and occurs sporadically in strata older than the Telychian. Instead, *Aspelundia?* appears to be more common in the Rhuddanian–Aeronian sections in the East Baltic region as well as in other regions (see below). In the northern Baltic, *Aspelundia?* appears in the lowermost Raikküla Stage in the *Coronograptus cyphus* GZ (Loydell et al. 2003, 2010). In the sections on Canadian Arctic islands, *Aspelundia?* appears in the Allen Bay Formation (Uyeno 1990) and in the Mackenzie Mountains in Member 1W of the Whittaker Formation (Over & Chatterton 1987). The level of the FAD of *Pranognathus tenuis* (Aldridge) is more problematic, but it most likely does not lie below the lower boundary of the Aeronian (Aldridge 1972). This conclusion agrees with the data from Estonia, where *P. tenuis* has been found in the Jõgeva Beds (Põltsamaa and Heimtali core sections) and in the topmost Kolka Beds (Ikla core section) (Nestor et al. 2003).

A revised conodont zonation with six zones, which is based on the evolution of *Pterospathodus*, has been proposed for the Telychian (Männik 2007a; Fig. 3). For ecological reasons, the *Pterospathodus*-based zonation cannot be applied in some regions (e.g., the Timan-northern Ural region and Severnaya Zemlya). Still, several general faunal characteristics (e.g., high frequencies of specimens, a large number of taxa, occurrence of *Apsidognathus* together with other taxa) allow the Telychian strata to be recognized without major problems even in these regions. *Apsidognathus* proved to be particularly useful because it has a worldwide distribution, and its elements are morphologically very distinct. Because the *Apsidognathus* lineage appears in the lower Telychian (in the *Pterospathodus eopennatus* ssp. n. 1 Zone of Männik 2007a) and becomes extinct at Datum 2 of the Ireviken Event (corresponding to the Llandovery–Wenlock boundary in its type section at Leasows; Aldridge et al. 1993; Jeppsson 1997), *Apsidognathus* can be used as the most universal indicator for the Telychian. On Severnaya Zemlya and in the Timan–northern Ural region, the strata corresponding to the interval from the *Pt. eopennatus* ssp. n. 1 Zone to Datum 2 of the Ireviken Event can be recognized by the occurrence of *Apsidognathus* and are identified in the conodont sequence as the ‘*Apsidognathus*-interval’ (Fig. 5A, B). In both regions, the uppermost Telychian and Sheinwoodian strata are evidently missing (Männik & Martma 2000; Männik et al. 2000; Männik 2002).

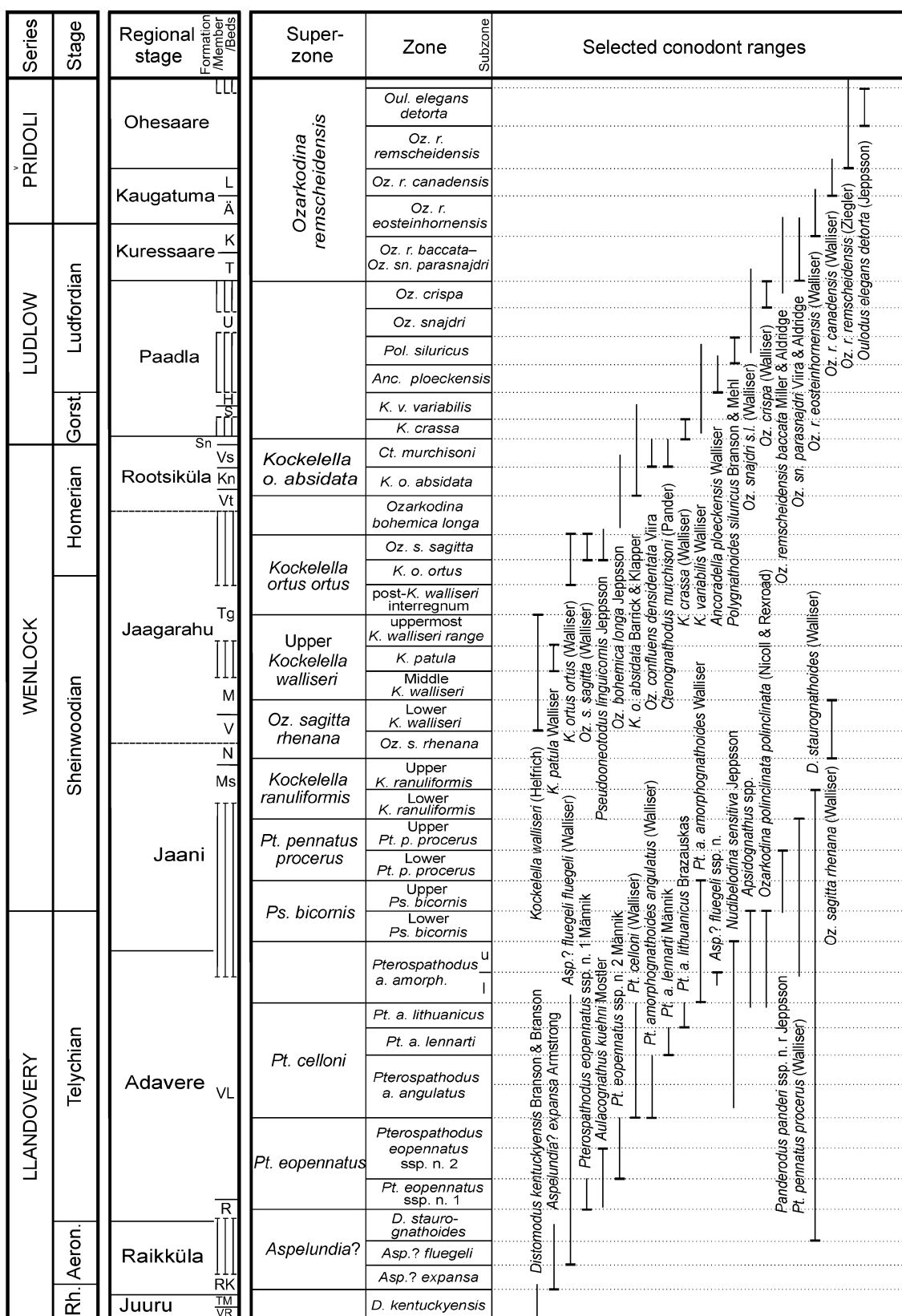
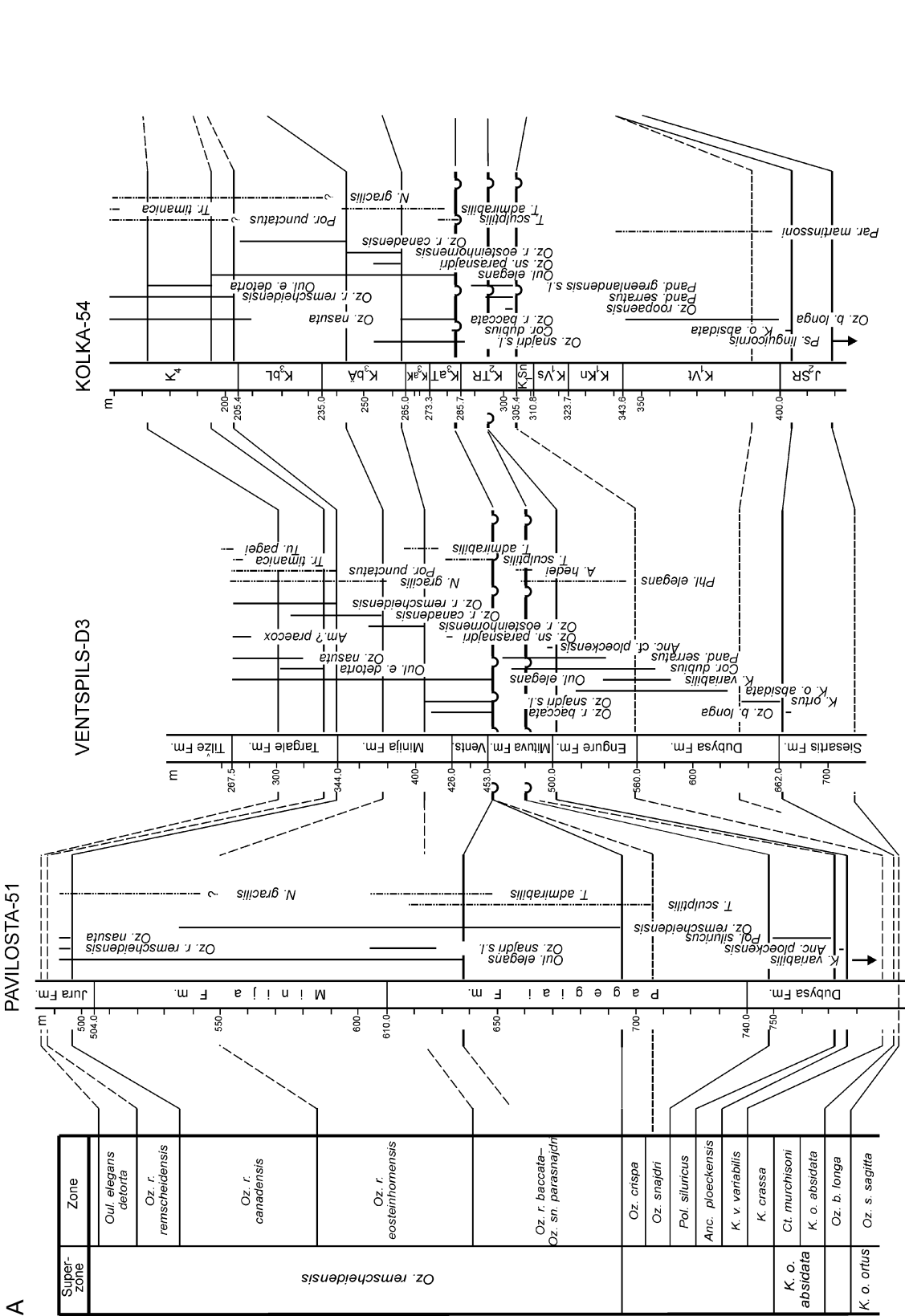


Fig. 3. Ranges of selected conodont taxa. Only the known total ranges of the taxa are indicated; u, upper subzone; l, lower subzone. For abbreviations of northern East Baltic stratigraphical units and names of taxa see p. 182.



**Fig. 4.** Distributions of selected conodont and vertebrate species in some studied core sections in Latvia (A) and Estonia (B); vertical solid line – distribution of conodonts, vertical dotted line – distribution of agnathans and fishes. Boundaries of stratigraphic units (stages, formations, beds) of sections and distributions of recognized conodont zones are indicated. Arrows mean that a taxon is also known from strata below the interval shown in the figure. Solid horizontal line – reliable location and correlation of zonal boundaries; dotted line – possible location and correlation of zonal boundaries. Thick dented lines correspond to main (dated) gaps in the sections. Stratigraphic subdivisions of the sections are mainly based on lithostratigraphy (after Einasto in Märss 1986) and not on fossil data. Conodont distribution data are from Viira & Männik (1997) (conodont collection revised herein by P. M.). For abbreviations of northern East Baltic stratigraphical units and names of taxa see p. 182.

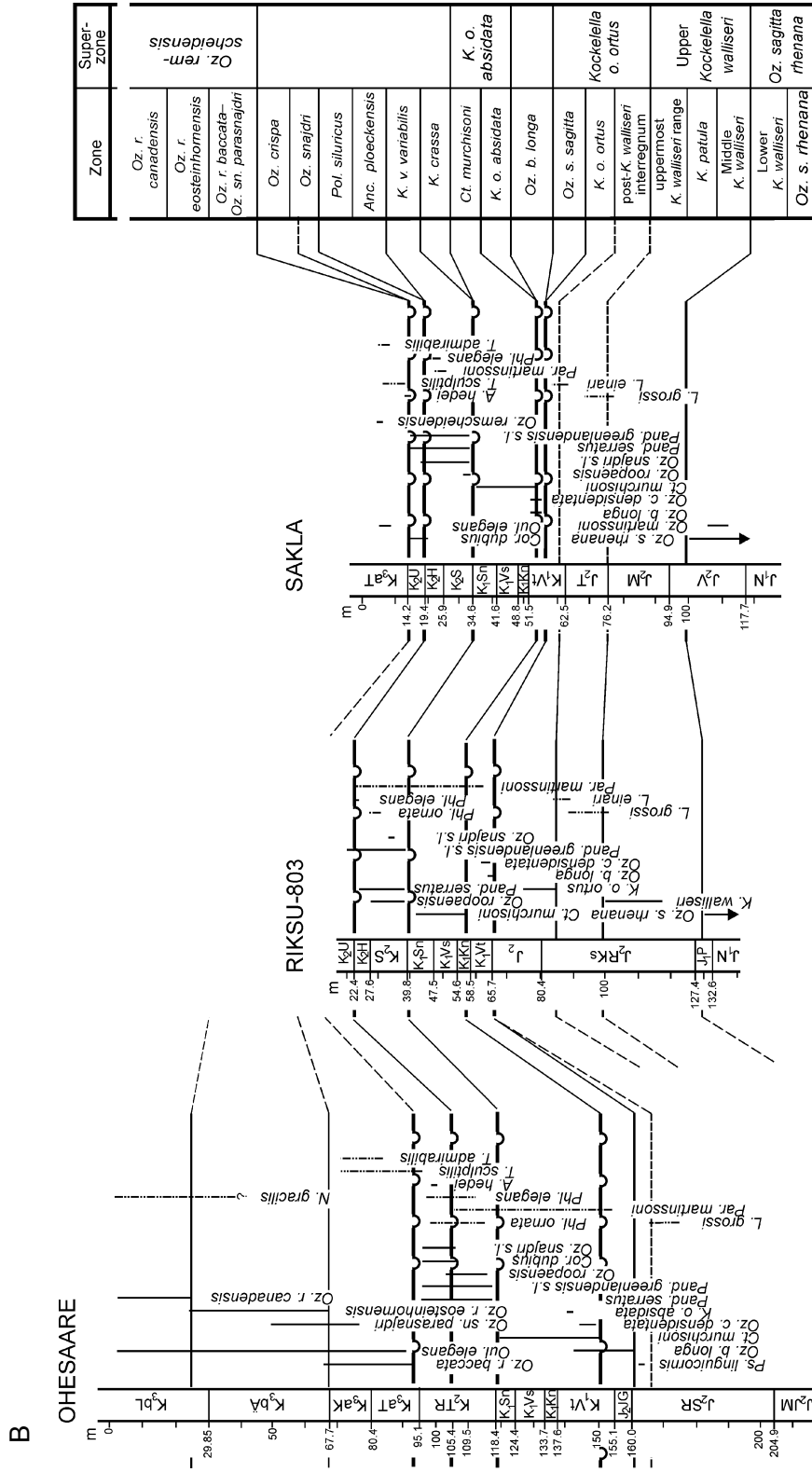
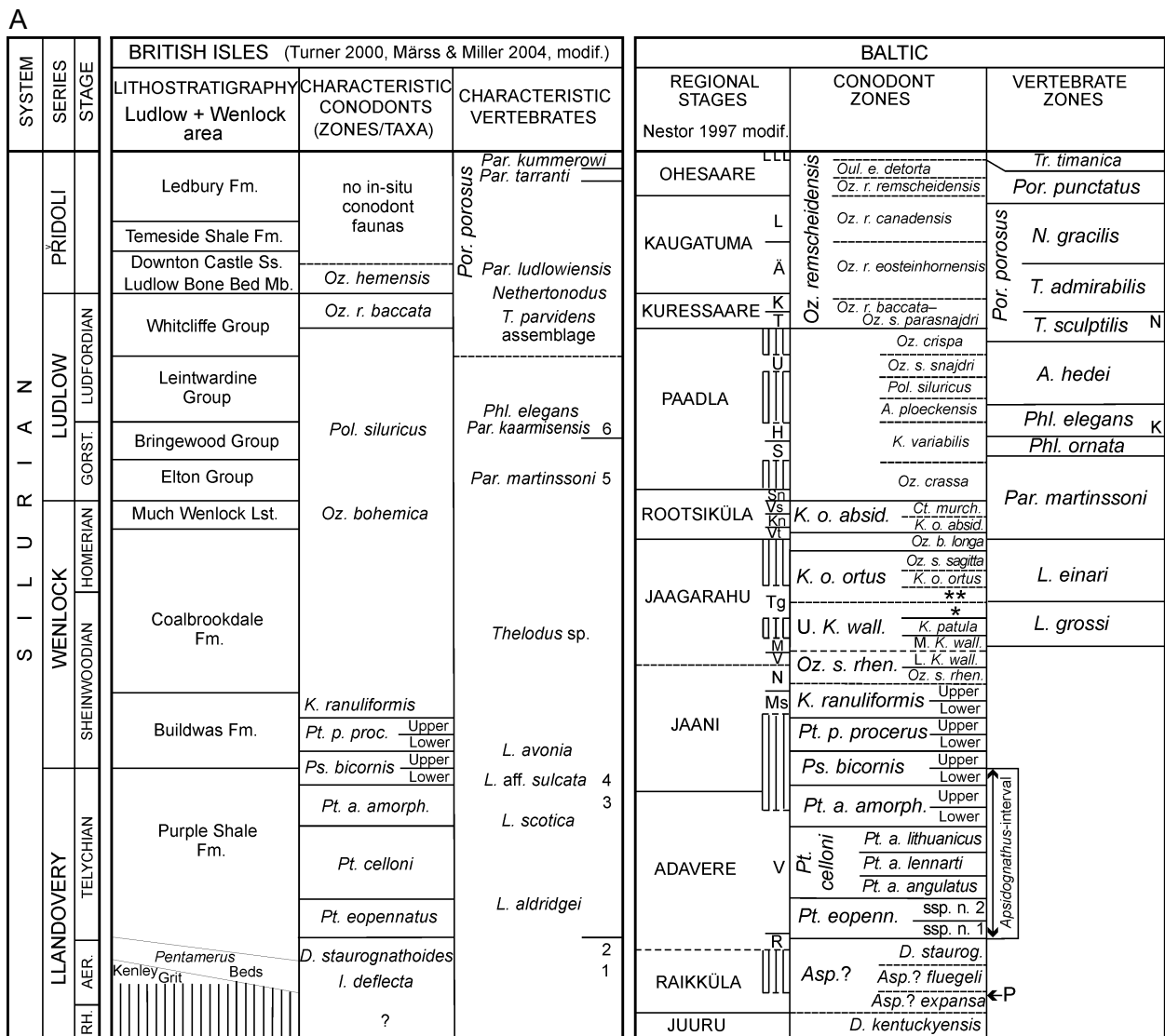


Fig. 4. Continued.



**Fig. 5.** Correlation of Silurian successions on the British Isles and in the Baltic region (A) and in Severnaya Zemlya, Arctic Canada and the Mackenzie Mountains (Canada) (B) based on the recognized biozones and characteristic faunas. An asterisk (\*) indicates the *Ozarkodina sagitta rhenana* CZ; two asterisks (\*\*) indicate the Lower *Kockelella walliseri* CZ; P indicates the level of appearance of conodont *Pranognathus tenuis*; K indicates the level with *Paralognathia kaarmisensis*; N indicates the level with *Netherptonodus* in Estonia. 1, Venusbank Formation; 2, Minsterley Formation; 3, Wych Formation; 4, Kilbride Formation (Ireland); 5, Ludlow Shale; 6, Aymestrey Formation. A.B.F., Allen Bay Formation; Barl. Inl., Barlow Inlet Formation; Gol., Golomyannyj Formation; Sam., Samojlovich Formation; Vod., Vodopad Formation; L., Lower; M., Middle; U., Upper. For abbreviations of northern East Baltic stratigraphical units and names of taxa see p. 182.

A detailed conodont zonation has been worked out for the uppermost Llandovery and Wenlock, and its applicability to different regions has been discussed (Jeppsson 1997; Calner & Jeppsson 2003). Most of these zones can be recognized in the East Baltic (Männik 2007b; Loydell et al. 2010). Seventeen zones were defined in the interval from the uppermost Telychian (Lower *Pseudooneotodus bicornis* Zone) to the topmost Homerian (*Ctenognathodus purchisoni* Zone). The lower six zones (Lower *Ps. bicornis* Zone to the Upper *Kockelella*

*ranuliformis* Zone; Fig. 3) and their boundaries can easily be identified in the northern East Baltic. *Ozarkodina sagitta rhenana* is also quite common. *Kockelella walliseri* is less common, most likely due to the small size of samples from the core sections. The *Oz. bohemia longa* Zone corresponds to the upper Wenlock (middle Homerian) interval (Calner & Jeppsson 2003). *Ozarkodina b. longa* is widespread, and most reports of *Oz. bohemia* and *Oz. b. bohemia* are based on this subspecies.

B

SEVERNAYA ZEMLYA		ARCTIC CANADA		MACKENZIE MOUNTAINS		GENERALIZED VERTEBRATE ZONATION	STAGE	SERIES
VERTEBRATES Märss 1982a, Märss & Karatajütë-Talimaa 2002 Karatajütë-Talimaa & Märss 2002	CONODONTS Männik 1999; Männik et al. 2009	VERTEBRATES Märss et al. 1998a, 2006 and new data herein	CONODONTS Uyeno 1990; Märss et al. 1998a and new data herein	VERTEBRATES Soehn et al. 2000, 2001	CONODONTS Over & Chatterton 1987 and new data herein			
Krasnaya Bukhta <i>Por. porosus</i>		Bari. Inl. <i>G. alatus</i> <i>Por. punctatus</i> <i>Por. ?porosus</i> <i>Tr. tricava</i>	Oz. remscheidensis			<i>Tr. timanica</i> <i>Por. punctatus</i>		
Samojlovich <i>L. grossi</i>	<i>O. adraini</i> <i>L. grossi</i>	<i>Par. martinsoni</i>	1D <i>Par. martinsoni</i>	Mb 1D - 2D <i>Oz. bohemia</i> <i>K. o. ortus</i> <i>U. K. wall.</i> <i>K. patula</i>	<i>A. hedei</i> <i>Phl. elegans</i> <i>Phl. ornata</i>			
								Srednij+Sam. <i>L. matura</i>
Vod. + Gol. <i>L. matura</i>	<i>Pt. a. amorph.</i> <i>Pt. celloni</i> <i>Pt. eopennatus</i>	<i>Arch. bifurcata</i> <i>L. sulcata</i> <i>L. scotica</i>	3W <i>Arch. turbinata</i> <i>L. cf. sulcata</i>	Mb 3W <i>Pt. p. procerus</i> <i>Ps. bicornis</i> <i>Pt. a. amorph.</i> <i>Pt. celloni</i>	<i>L. einari</i> <i>O. adraini</i> <i>L. grossi</i>			
								A.B.F. <i>D. kentuckyensis</i>
	<i>Aspelundia?</i> <i>D. kentuckyensis</i>	<i>Whittaker Fm.</i>	Mb 1W-2W <i>Aspelundia?</i> <i>D. kentuckyensis</i>	<i>L. aldridgei</i> <i>V. crista</i>				

Fig. 5. Continued.

As in the Late Wenlock, the distribution of conodont faunas in the northern East Baltic during the Ludlow was greatly affected by variable ecological conditions. Additionally, the correlation between the deep-water (northwestern Latvia; Fig. 4A) and shallow-water (Saaremaa; Fig. 4B) facies are complicated by a number of gaps in the outcrop area (e.g., Jeppsson et al. 1994; Kaljo et al. 1997). The *Kockelella variabilis*, *Ancoradella ploeckensis* and *Polygnathoides siluricus* zones in the Ludlow are only recognized in cores from western Latvia. *Kockelella variabilis* and *A. ploeckensis* have been found in the Ventspils-D3 and Pavilosta-51 core sections, while *Pol. siluricus* has only been found in the Pavilosta-51 core section (Fig. 4A). On Saaremaa, the intervals with the *A. ploeckensis* and *Pol. siluricus* zones most likely correspond to a gap between the Himmiste

and Uduvere beds (Fig. 5A). In Arctic Canada, the *Pol. siluricus* Zone was recognized in the Douro Formation on Devon Island and in the Cape Phillips Formation of Ellesmere Island (Uyeno 1990; Fig. 5B).

The *Oz. snajdri* Zone corresponds to the upper Paadla Stage in Estonia (= middle Ludfordian; Fig. 3). *Ozarkodina crispa* has also been reported from several sections (Viira & Aldridge 1998; Viira 1999). However, restudy of collections demonstrated that (1) the specimens identified as *Oz. crispa* in Estonia are morphologically different from those described and illustrated by Walliser (1964, pl. 21: 7–13) from Cellon and (2) *Oz. crispa*-type specimens are rare in samples, have sporadic distribution and always occur together with specimens of *Oz. snajdri*. Hence, it is possible that, in reality, they represent some specific morphs in the *Oz. snajdri* lineage. Further detailed

taxonomical studies of these specimens and direct comparison of them with type material from Cellon are needed to prove the occurrence/absence of *Oz. crista* in Estonia. In this paper, the *Oz. crista*-type specimens are considered as elements of *Oz. snajdri s.l.* As our *Oz. crista*-type specimens differ morphologically from the type material, we think that the strata yielding this species are missing in Estonia and the *Oz. crista* Zone *sensu* Walliser (1964) corresponds to a gap between the Paadla and Kuressaare stages.

Traditionally, only one zone has been identified in the Pridoli, based on the distribution of the *Ozarkodina remscheidensis*–*Oz. eosteinhornensis* Group. Different names have been used for this zone (e.g., *Oz. remscheidensis* Interval Zone in Nowlan 1995; *Oz. r. eosteinhornensis* Zone in Aldridge & Schönlaub 1989; *Oz. steinhornensis s.l.* Interval Zone in Cramer et al. 2011). In the uppermost part of the Pridoli, the *Oulodus elegans detorta* Zone was introduced by Jeppsson (1988). The abundant *Ozarkodina* fauna in the northern East Baltic has allowed four zones in the *Oz. remscheidensis* Superzone to be recognized (from below): *Oz. r. baccata*–*Oz. s. parasnajdri*, *Oz. r. eosteinhornensis*, *Oz. r. canadensis* and *Oz. r. remscheidensis* (Viira 1999). The lowermost of these zones, the *Oz. r. baccata*–*Oz. s. parasnajdri* Zone, is latest Ludlow in age. *Oulodus e. detorta* occurs in a short interval in the uppermost (excluding the topmost portion) *Oz. r. remscheidensis* Zone (Viira 1999, 2000; Fig. 3). The *Oz. remscheidensis* Superzone has also been recognized in Arctic Canada (identified as the *Oz. eosteinhornensis* Zone in Uyeno 1990), where it lies in the Devon Island Formation on Devon Island and in the Cape Phillips Formation on Ellesmere and Baillie-Hamilton islands and corresponds to the uppermost Ludlow and Pridoli (Uyeno 1990).

## CORRELATIONS OF VERTEBRATE AND CONODONT ZONES

### The *Valyalepis crista* Zone

In the type region of the zone (Gaspé Peninsula, Québec, eastern Canada), *V. crista* occurs in a number of localities in strata corresponding to the *Distomodus kentuckyensis* CZ (the A3–A4 brachiopod zones; Turner & Nowlan 1995) (Fig. 5B).

### The *Loganellia aldridgei* Zone

The *L. aldridgei* Zone is found in several localities in Wales and the Welsh Borderland in the middle and upper Aeronian Venusbank and Minsterley formations and in the lower part of the Telychian Purple Shales Formation (Turner 2000, table 1, pl. 1). The zone most

likely correlates with an interval extending from the middle *Aspelundia?* conodont Superzone (CSZ) to the *Pt. a. amorphognathoides* CS (Fig. 5A, B).

### The *Loganellia scotica* Zone

On Baillie-Hamilton Island (Arctic Canada), *L. scotica* appears together with another *Loganellia*, *L. sulcata*, in the strata that yield the conodonts *Apsidognathus lobatus* Bischoff, *Ozarkodina paraconfluens* Jeppsson and *Pterospathodus cf. rhodesi* Savage (Märss et al. 1998a, 1998b, 2006; in the first two papers, *L. sulcata* was treated among *L. scotica*) (Fig. 5B). This conodont assemblage is characteristic of the *Pt. a. amorphognathoides* and Lower *Ps. bicornis* CZs and indicates the late Telychian age of these strata. In the Kilbride Formation (Co. Galway, western Ireland), scales similar to those of *L. sulcata*, which were identified earlier as *L. aldridgei* (Turner 2000; Märss et al. 2007) but are reidentified here as *L. aff. sulcata*, co-occur with the conodonts *Icriodella aff. I. deflecta* Aldridge, *Panderodus* sp., *Ozarkodina ex gr. excavata* (Branson & Mehl), *Ozarkodina* sp. and *Distomodus* sp. (Aldridge et al. 1996). The fauna comes from a bed packed with shells of the brachiopod species *Eocoelia curtisi curtisi* Ziegler, suggesting a late Telychian age for this level. The conodont fauna does not identify the zone unequivocally, but the data indicate that this fauna also comes from strata not older than the *Pt. celloni* CSZ (Fig. 5A). In the Avalanche Lake section AV 4 from the Mackenzie Mountains in Canada, some thelodont scales similar to *L. scotica* and identified as *L. cf. scotica* (Märss et al. 1998b) were found in the upper(most) *Pt. a. amorphognathoides* CZ. These specimens were later considered to belong to a new, yet undescribed *Loganellia* sp. nov. 2 (Soehn et al. 2000). However, it is possible that these scales might belong to *L. sulcata* (herein as *L. cf. sulcata*; Fig. 5B), which is also found in Arctic Canada (Märss et al. 2002, 2006).

### The *Archipelepis bifurcata*/Arch. *turbinata* Zone

In the Avalanche Lake sections from the Mackenzie Mountains, the lowermost *Arch. turbinata* was reported from strata corresponding to the upper half of the *Ps. bicornis* CZ (Soehn et al. 2001), which today is treated as the Upper *Ps. bicornis* CZ. This interval corresponds to the lowermost Sheinwoodian. The genus *Archipelepis* is also known from the sections on Canadian Arctic islands (Baillie-Hamilton, Cornwallis and Ellesmere) and is represented here by another species, *Arch. bifurcata* (Thelodonti gen. et sp. nov. 1 in Märss et al. 1998a), which occurs there in the *Pt. pennatus procerus* CSZ (Fig. 5B).



### The *Loganellia grossi* Zone

In the Riksu-803 core section (Estonia), *L. grossi* appears in the uppermost part of the *Kockelella walliseri* range but occurs in the interval between the *K. walliseri* range and the lowermost *K. ortus ortus*. This suggests a correlation between the *L. grossi* Zone and the uppermost Upper *K. walliseri* and the lowermost *K. o. ortus* CSZs (Fig. 4B). On Gotland (Sweden), *L. grossi* is known from units f and g of the Slite Beds (Fredholm 1990, p. 63). Because the lower part of unit f corresponds to the Middle *K. walliseri* CZ (the lower part of the Upper *K. walliseri* CSZ; Jeppsson 1997), the lower boundary of the *L. grossi* Zone likely lies within this conodont zone.

*Loganellia grossi* occurs in samples 5-2-62 to 5-2-68 from section 2 of the Matusевич River succession (October Revolution Island, Severnaya Zemlya Archipelago, Russia) together with abundant specimens of the conodont *Ozarkodina confluens bucerus* Viira and less frequently with poorly preserved specimens identified as *Kockelella* cf. *ortus* (Walliser) (Männik 2002; Märss & Karatajūtė-Talimaa 2002, Fig. 5B).

### The *Overia adraini* Zone

In the Avalanche Lake region of the Mackenzie Mountains, *O. adraini* occurs in the interval 242–331 m of section AV 2 (Soehn et al. 2001). *Overia adraini* first appears in the lower part of Member 1D of Over & Chatterton (1987) in the interval of *Kockelella patula* Walliser (i.e., the *K. patula* CZ of Jeppsson 1997, Fig. 5B). *Overia adraini* was also found on Baillie-Hamilton Island in a thick complex in samples at 140.0 and 144.5 m in the BH1 section (Sheinwoodian) and upwards to 28.5 m in the BH2 section (Homerian), but diagnostic conodonts are absent. The carbon isotope curve pattern allows the correlation of its lower occurrence with the *Cyrtograptus rigidus*–*Cyrtograptus perneri* GZ level and the upper occurrence with the *Pristiograptus parvus*–*Gothograptus nassa* GZ level (Märss et al. 2006, text-figs 3 and 6).

The data from Gotland, in which the thelodont *L. grossi* appears in Slite beds f, the conodont *K. patula* occurs in Slite beds g, and *O. adraini* occurs together with *K. patula* in the Avalanche Lake section AV2, indicate that the lower boundaries of the *L. grossi* and *O. adraini* zones are rather close to each other.

### The *Loganellia einari* Zone

In Estonia, *L. einari* is found in the Kipi, Paadla, Riksu-803 and Sakla core sections from Saaremaa (Märss 1996; Nestor et al. 2001). Conodonts have been studied

from the Riksu-803 and Sakla core sections (Nestor et al. 2001 and herein). In both sections, *L. einari* has a short range below the level of appearance of *Oz. bohémica longa* Jeppsson (Fig. 4B). In the Riksu-803 core section, *L. einari* appears above the *K. walliseri* range in the interval corresponding to the ‘post-*K. walliseri* interregnum’ according to Jeppsson (1997), and reaches the lower part of the *K. o. ortus* range; this suggests that the *L. einari* Zone most likely correlates with the *K. o. ortus* CSZ (Figs 4B, 5A). On Gotland, *L. einari* occurs in the Samsungs 1 locality in the uppermost Slite beds, which is correlative with the upper(?) part of the *K. o. ortus* CSZ.

### The *Paralogania martinssoni* Zone

In the Kolka-54 core section (Latvia), *Par. martinssoni* appears in a sample at 396.7–397.0 m, which is 6.1 m above the level of appearance of *Kockelella ortus absidata* Barrick & Klapper at 402.8–403.1 m (i.e., the *K. o. absidata* CZ; Loydell et al. 2010; Fig. 4A). The lowermost *Oz. b. longa* in that section comes from a sample at 399.8–400.0 m. In the Kaugatuma and Riksu-803 core sections (Estonia), *Par. martinssoni* appears above the level of appearance of *Oz. confluens densidentata* Viira in the *Ctenognathodus murchisoni* CZ. The oldest (based on conodont biostratigraphy; see also Viira 1982a, 1982b) known *Par. martinssoni* in the studied region comes from the *Oz. b. longa* CZ in the Ohesaare core section. In the Sakla core section, *Par. martinssoni* is present only in the middle part of the Paadla Stage. Based on these data, the level of appearance of *Par. martinssoni* and the lower boundary of the *Par. martinssoni* Zone lie in the *Oz. b. longa* CZ.

In the Avalanche Lake region, *Par. martinssoni* occurs in section AV 4 (Soehn et al. 2001) with *Oz. bohémica* (Over & Chatterton 1987) (Fig. 5B). On Baillie-Hamilton Island in the Canadian Arctic Archipelago, the level with *Par. martinssoni* lies within the Cape Phillips Formation in the interval of *Erika* range (Märss et al. 1998a). On Gotland, *Erika* occurs in the unzoned interval above the *C. murchisoni* CZ and in the lower part of the *K. crassa* CZ (upper Klinterbeg Formation and lower Hemse Group; Jeppsson et al. 2006).

### The *Phlebolepis ornata* Zone

In Estonia, *Phl. ornata* appears in the lower part of the Paadla Stage, below the level of appearance of *Oz. snajdri s.l.* in the Ohesaare core section and above it in the Riksu-803 core section (Fig. 4B). *Phlebolepis ornata* and *Oz. roopaensis* occur together in these two sections. On Gotland in Sweden, *Phl. ornata* is present in units b and c of the Hemse Beds (Fredholm 1988). In

terms of conodont biostratigraphy, these strata correspond to a transition interval between the *K. crassa* and *K. variabilis* CZs, which is characterized by *Oz. excavata* n. spp. S, post-*Oz. excavata* n. spp. S and *Oz. e. hamata* faunas (Jeppsson et al. 2006). These strata evidently correspond to a gap in Estonia, and only the upper parts of the *Phl. ornata* range and the *Phl. ornata* Zone are observed. Based on the data from Gotland, the lower boundary of the *Phl. ornata* Zone lies in the *K. variabilis* CZ.

### The *Phlebolepis elegans* Zone

The lowest (in terms of conodont biostratigraphy) *Phl. elegans* in the East Baltic was discovered from the Ventspils-D3 core section (Fig. 4A). Here, *Phl. elegans* occurs in an interval below the level of appearance of *Oz. snajdri s.l.* *Kockelella* cf. *variabilis* has also been identified from the interval with *Phl. elegans*. In the Ohesaare and Kaugatuma core sections, *Phl. elegans* appears in the *Oz. snajdri s.l.* range. In the more proximal section (Riksu-803, Sakla), *Phl. elegans* occurs above the interval with *Oz. snajdri s.l.* (Fig. 4B). In the Goldap drill core from eastern Poland, *Phl. elegans* occurs at 1184.6–1202.0 m in the upper Mielnik Stage, Ludlow (pers. observation by T. M. in the collection of Dr K. Małkowski, Warsaw). This interval lies in the *Polygnathoides siluricus* CZ (Männik & Małkowski 1998). These data indicate that the lower boundary of the *Phl. elegans* Zone lies in the *K. variabilis* CZ but certainly not higher than the basal *Pol. siluricus* CZ. In southern Britain, the lowermost *Phl. elegans* has been found together with *Pol. siluricus* from the Aymestrey Formation (uppermost Gorstian; Märss & Miller 2004). This level is unusual for *Pol. siluricus*, as this taxon is mainly found in strata of early Ludfordian age. However, rare specimens of *Pol. siluricus* are known to occur in strata older than the *Pol. siluricus* CZ and even older than the underlying *Ancoradella ploeckensis* CZ (Jeppsson & Aldridge 2000; Jeppsson 2005).

### The *Andreolepis hedei* Zone

In Estonia, *A. hedei* has been found in the Sakla and Ohesaare core sections (Fig. 4B). It appears above the interval with *Oz. snajdri s.l.* in the Sakla core section and with *Oz. snajdri s.l.* in the Ohesaare core section. In the Ventspils-D3 core section (Latvia), *A. hedei* lies below the level of the FAD of *Oz. snajdri s.l.* (Fig. 4A). On Gotland, *A. hedei* is present in the upper part of unit d and in unit e of the Hemse Beds (Fredholm 1988). In the Gogs section (located near Lau, SE Gotland), *A. hedei* was recovered from strata corresponding to the *Monograptus leintwardinensis* GZ (Gross 1968), which

correlates with the *Anc. ploeckensis* and lower *Pol. siluricus* CZs (Cramer et al. 2011). *Andreolepis hedei* is also known from the Uddvide section (Burgsvik Sandstone), which corresponds to the lower *Oz. snajdri* CZ (Jeppsson et al. 2006). *Andreolepis hedei* appears slightly below the *Pol. siluricus* CZ and disappears above this zone on Gotland.

### The *Thelodus sculptilis* Zone

In several sections (Kaugatuma, Ohesaare, Kolka-54, Ventspils-D3) (Fig. 4A, B), *T. sculptilis* appears at almost the same level as *Oz. remscheidensis baccata*, whereas in the Pavilosta-51 core section its level of appearance lies about 15 m below the lowermost occurrence of *Oz. remscheidensis* (Fig. 4A). In the Ohesaare core section, the level of appearance of *T. sculptilis* lies below *Oz. remscheidensis*, but it appears to correlate with the base of the *Oz. r. baccata*–*Oz. s. parasnajdri* CZ in the Kaugatuma, Ventspils-D3 and Kolka-54 sections (Fig. 4A, B). In Lithuania, the range of *T. sculptilis* is within the upper Pagegiai Formation (Karatajūtė-Talimaa et al. 1987; Karatajūtė-Talimaa & Brazauskas 1995), the lower part of which (an interval below the appearance of *Oz. remscheidensis*) most likely corresponds to at least a part of the *Oz. crispa* CZ. The data from Lithuania suggest that *T. sculptilis* appears in the *Oz. crispa* CZ. Accordingly, the *T. sculptilis* Zone correlates with the *Oz. crispa* CZ and with the lower *Oz. r. baccata*–*Oz. s. parasnajdri* CZ. In Estonia, only the upper part of the *T. sculptilis* Zone is preserved. Its lower part, which corresponds to the *Oz. crispa* CZ, is missing due to a hiatus between the Paadla and Kuressaare stages, noticed earlier by Märss (1992).

### The *Thelodus admirabilis* Zone

In the Ventspils-D3, Ohesaare and Kaugatuma core sections (Fig. 4A, B), *T. admirabilis* appears in the middle part of the *Oz. r. baccata*–*Oz. s. parasnajdri* CZ. It appears somewhat earlier, in the lower part of the zone, in the Kolka-54 core section (Fig. 4A). However, in all the studied sections, *T. admirabilis* begins within the *Oz. r. baccata*–*Oz. s. parasnajdri* CZ below the level of appearance of *Oz. r. eosteinhornensis*. According to Karatajūtė-Talimaa & Brazauskas (1995), *T. sculptilis* and *T. admirabilis* appear together in the upper Pagegiai Regional Stage in some sections in Lithuania.

### The *Nostolepis gracilis* Zone

In most of the sections discussed in this paper, *N. gracilis* appears in the middle or upper part of the *Oz. r. eosteinhornensis* CZ and is abundant in the

samples (Fig. 4A, B). In eastern Lithuania, it begins in the upper Pagegiai Regional Stage, Upper Ludfordian (Valiukevičius 2005). The beginning of abundant occurrence in the sections is treated here as the lower boundary of the *N. gracilis* VZ.

### The *Poracanthodes punctatus* Zone

In the studied sections, *Por. punctatus* (*sensu* Märss 1986) has been found in the Ventspils-D3 and Kolka-54 core sections. In both sections, the lowermost specimens occur slightly below the appearance of *Oz. r. remscheidensis* (Fig. 4A), which indicates that the lower boundary of the *Por. punctatus* Zone lies in the uppermost *Oz. r. canadensis* CZ (Fig. 5A).

### The *Trimerolepis timanica* Zone

*Trimerolepis timanica* has been identified in the Ventspils-D3 and Kolka-54 core sections, where it occurs together with *Oz. r. remscheidensis* above the range of *Oulodus elegans detorta* (Fig. 4A). Accordingly, the *Tr. timanica* VZ corresponds to the topmost *Oz. remscheidensis* CSZ, to the interval above the *Oul. e. detorta* range (Fig. 5A).

## REMARKS ON SOME TAXA POTENTIAL FOR CORRELATIONS

*Loganellia aldridgei* scales from the upper Telychian of western Ireland (Turner 2000) are morphologically similar to loganelliid scales that were identified as *L. sulcata* in the Llandovery–Wenlock boundary beds from Baillie-Hamilton and Cornwallis islands in Arctic Canada (Märss et al. 2006). The Ireland scales are identified here as *L. aff. sulcata* (Fig. 5A). The scales similar to *L. sulcata* from the Mackenzie Mountains are named herein as *L. cf. sulcata*. These scales need to be studied in detail and identified to determine the biostratigraphical value of this taxon.

*Phlebolepis elegans* co-occurs with *Paralogania kaarmisensis* Märss in Estonia (in the Himmiste Beds of the Paadla Stage; Fig. 5A, letter 'K') and the Welsh Borderland (Upper Bringewood, Gorstian, and Lower Leintwardine Group, Ludfordian) (Märss 2003; Märss & Miller 2004). In the Matusevich River section in the Severnaya Zemlya Archipelago, *Par. kaarmisensis* was found in sample MF 11-1 (Ust'-Spokojnaya Formation, Ludlow; Karatajūtė-Talimaa & Märss 2002, fig. 3G–I, L) from a level just above the interval with *Phl. elegans* (samples 2-10, 2-11 and 2-19) and within the same formation (Fig. 5B). It appears that within these three

regions, *Par. kaarmisensis* with *Phl. elegans* is useful for correlations of the Gorstian/Ludfordian strata.

Two species of the genus *Nethertonodus* have been described by Märss & Miller (2004) and Märss (2006). One of them, *Neth. prodigialis*, is known from the uppermost Ludfordian and lowermost Pridoli in the Welsh Borderland. The other, *Neth. laadjalaensis*, occurs in the lower part of the Tahula Beds (Kuressaare Stage, upper Ludfordian) in the *Thelodus sculptilis* Zone in Estonia. In Britain, the interval with *Nethertonodus* is dominated by *Par. ludlowiensis*, which is extremely rare in Estonia (only one scale from the basal Tahula Beds is known from the Ohesaare core at depths of 94.45–94.48 m). *Nethertonodus* and *Par. ludlowiensis*, which are characteristic of the Ludlow and Pridoli boundary beds, provide additional criteria for correlation of this interval in the East Baltic and Britain.

Because acanthodians are most common in the strata of Pridoli age in the East Baltic (Märss 1986; Karatajūtė-Talimaa et al. 1987), vertebrate zonation for this interval was mainly based on these fossils. The *Nostolepis gracilis* and *Poracanthodes punctatus* zones were established based on acanthodians but the suitability of these zones was proved later. The scheme was complemented with *Por. porosus* (upper Ludlow–lower Pridoli) and *N. alta* (uppermost Pridoli) zones, which are both characteristic of sediments formed in deep-shelf environments (Märss 2000). Detailed studies of acanthodians with several new taxa described demonstrated that the group had high diversity in the Upper Silurian in the Ludlow and particularly in the Pridoli strata of Lithuania and Latvia (Valiukevičius 2003, 2004a, 2004b). Investigations of acanthodian biostratigraphy resulted in two different zonal schemes: one for the deeper shelf, mainly composed of argillaceous graptolitic facies, and another for the shallow shelf to lagoonal calcareous facies (Valiukevičius 2005, 2006). The *N. gracilis* Zone was recognized in both environments, whereas the *N. alta* Zone is only applicable to deeper shelf strata. According to the scheme of Valiukevičius, *N. gracilis* and *Por. punctatus* appear slightly earlier than in the northern East Baltic sections (Valiukevičius 2006). In our (T. M.) opinion, the morphology of scales of *N. gracilis* differs between the northern and southern Baltic.

Criticism of the Vertebrate Biozonal Standard (Märss et al. 1995, 1996) has mainly been directed against the acanthodian zonation in its Pridoli part. The main argument is that the zonation must be based on the evolutionary lineage(s) of only one group (genus or family). Pure thelodont zonation was preferred, for example, by Talimaa (2000, table 7). She proposed a subdivision of Pridoli age strata into two zones: the *Trimerolepis tricava* (= *Katoporodus timanicus*) and

*Goniporus alatus* zones. However, in Estonia and Latvia, these two thelodont species occur at some levels only; *Tr. tricava* occurs in the lowermost Kuressaare Stage, Ludlow, and in the Ohesaare Stage, upper Pridoli, while *G. alatus* is abundant in the Ohesaare Stage, upper Pridoli, and in the Lochkovian, Lower Devonian. *Trimerolepis tricava* and *G. alatus* were also discovered in the Barlow Inlet Formation, Pridoli, on Cornwallis Island in the Canadian Arctic Archipelago (Märss et al. 1998a, 2006; Fig. 5B), but their very rare occurrence in samples complicates their use in the dating of strata. Therefore, for the time being, we retain our acanthodian zonation, although we realize that acanthodians require further investigation.

## RESULTS

Over the last several decades, many new taxa of Silurian vertebrates and conodonts have been described and their distributions in time and space have been characterized. On the basis of the new data, the Generalized Vertebrate Zonation has been presented. The zonation is mainly based on data from the Avalonia (eastern Canada and southern Britain) and Laurentia (Scotland, northern Canada, Greenland) palaeocontinents, in the Llandovery and lower Sheinwoodian, Lower Wenlock, but on data from the Baltica (Baltic Sea region, Timan, Novaya Zemlya) and Kara (Severnaya Zemlya) palaeocontinents in the upper Sheinwoodian to the end of the Pridoli.

- Two previously informal units, the *turbinata* and *adraini* faunas in the thelodont faunal succession of the Mackenzie Mountains, have been raised to the rank of zones. The *Arch. turbinata* Zone has been combined with the *Arch. bifurcata* Zone.
- Our study resulted in the revision of several vertebrate zones. Some boundaries were re-defined (*Andreolepis hedei*, *Thelodus sculptilis*), index species were named for some new zones (*Loganellia aldridgei*), and reference stratum and locality were selected for new zones and zones in which the index species were divided (*L. grossi* and *L. einari*; *Phlebolepis ornata* and *Phl. elegans*; *T. sculptilis* and *T. admirabilis*).
- The Llandovery part of the zonation contains the *Valyalepis crista*, *Loganellia aldridgei*, *L. scotica* zones; the Wenlock part is represented by the *Archipelepis bifurcata*/*Arch. turbinata*, *L. grossi*, *Overia adraini*, *L. einari* and *Par. martinsoni* zones. The *Par. martinsoni* Zone continues in the Ludlow and is followed by the *Phl. ornata*, *Phl. elegans*, *A. hedei*, *T. sculptilis* and *T. admirabilis* zones. The last zone continues into the lower Pridoli and is followed by the *N. gracilis*, *Por. punctatus* and *Tr. timanica* zones.

- The *L. grossi* Zone in the upper Sheinwoodian and the *Par. martinsoni* Zone in the upper Homerian–lowermost Gorstian are geographically widely distributed in the Baltica, Laurentia and Kara palaeocontinents and allow uniting regional zonations into one Generalized Vertebrate Zonation.
- Vertebrate zones were correlated with conodont zones, and the ages of the lower boundaries were specified (noticeably in the *A. hedei* and *T. sculptilis* VZs) based mainly on co-occurrences of taxa. In Estonia, the *Oz. crispa* CZ probably corresponds to a gap between the Paadla and Kuressaare stages.
- Acanthodians are the most common taxa in Pridoli age strata, and the zones based on this group are easily recognizable in the Baltic region. Some acanthodians, including *Poracanthodes porosus* and *Por. punctatus*, have wider distributions; they have been found in Arctic Canada as well. *Poracanthodes porosus* is found in Severnaya Zemlya. Although the taxonomy and distribution of some acanthodian taxa need to be studied in more detail, it is evident that this group has good potential in biostratigraphy.

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## Siluri selgroogsete biotsoonide revisjon ja nende korrelatsioon konodontide järjestusega

Tiiu Märss ja Peep Männik

Siluri selgroogsete (agnaatide ja kalade) leviku uute andmete alusel on koostatud uus, üldistatud biotsonaalne skeem, mis on kasutatav Baltica (Baltikum, Loode-Venemaa), Avalonia (Briti saarte lõunaosa, Ida-Kanada), Laurentia (Kanada põhjaalad, Gröönimaa, Šotimaa) ning Kara (Severnaja Zemlja) paleokontinentidel. Kõik tsoonid on defineeritud ja on näidatud tsoonide levik ning iga tsooni stratotüüp. Llandovery on eraldatud *Valyalepis crista*, *Loganellia aldridgei* ja *L. scotica* tsoonid; Wenlock on esindatud *Archipelepis bifurcata*/*Arch. turbinata*, *L. grossi*, *Overia adraini*, *L. einari* ning *Paralogania martinssoni* tsoonidega (viimane esineb ka Ludlow's). *Paralogania martinssoni* tsoon jätkub Ludlow's ja sellele järgnevad *Phlebolepis ornata*, *Phl. elegans*, *Andreolepis hedei*, *Thelodus sculptilis* ning *T. admirabilis*, kusjuures viimane siseneb ka Pridolisse. Pridolis jätkub *T. admirabilis*'e tsoon ja lisanduvad *Nostolepis gracilis*'e, *Poracanthodes punctatus*'e ja *Trimerolepis timanica* tsoonid. *Loganellia aldridgei* ja *Arch. bifurcata* tsoonid on uued ning *Arch. turbinata* ja *O. adraini* 'faunad' on tõstetud tsooni kategooriasse. Laia geograafilise levikuga *L. grossi* tsoon Ülem-Sheinwoodis ja *Par. martinssoni* tsoon Ülem-Homeris–Alam-Gorstis võimaldavad regionaalseid järjestusi integreerida üheks üldistatud selgroogsete tsonaalseks skeemiks. On antud võimalikud korrelatsioonid kalade ja konodontide tsoonide vahel ning näidatud lüngad Põhja-Baltikumi läbilõigetes, millest ulatuslikem on Paadla ja Kuressaare lademe vaheline lünk.