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VERTEBRATE HISTORY IN THE LATE SILURIAN

Project 216
Global Bioevents

Project 328
Palaeozoic
Microvertebrates

Abstract. The last agnathans occurring in the Wenlock and the lower Ludlow (incl. the Himmiste Beds of the Paadla Stage) disappear in the Uduvere Beds of the Ludlow Paadla Stage. In these beds the first vertebrates, particularly characteristic of the Upper Ludlow (Kuressaare Stage) and Pridoli (Kaugatuma and Ohesaare stages) appear. The paper concentrates on the *hedei* event, i. e. the replacement of the fauna that took place in the marginal areas of the East European Platform (East and West Baltic, Timan-Pechora Region, the Central Urals), on the British Isles (South Wales), and Severnaya Zemlya. The changes that occurred on that level (Lower Ludfordian) were not simple environment-based appearances-disappearances, but rather extinction, innovation, and radiation events in the evolution of vertebrates.

Attention is also paid to the later development of the vertebrate fauna, that is to acanthodian, heterostracan-osteichthyan, and thelodont events that occurred in the Pridoli.

Analysing the bioevents of some Silurian faunal groups, Kaljo and Märss (1991) concluded that two major innovations had occurred among the vertebrates (particularly agnathans): the first in the late Wenlock (at the beginning of the *nassa-ludensis* Zone) and the second in the mid-Ludlow (at the beginning of the *leintwardinensis* Zone or a little earlier). Both innovations were followed by rapid and strong radiation during the *nassa-ludensis* and *leintwardinensis* zones. Extinctions were the most vigorous at the end of the late Wenlock (at the end of the *nassa-ludensis* Zone) and in the Ludlow (approximately at the end of the *leintwardinensis* Zone); diversity was the highest on the levels of the *nassa-ludensis* and *leintwardinensis* zones and in the Pridoli. Gnathostomes had strong radiation in the Pridoli.

In this context both graptolite zones comprise several events. In the present paper attention is focused on the event representing the most conspicuous change in the taxonomic composition of Silurian vertebrates — an almost complete turnover of the early Silurian ichthyofauna that took place in the Ludlow, Ludfordian. In the East Baltic the period under study covers the middle and late Paadla age and early Kuressaare age (Fig. 1).

The development of the Pridoli vertebrate fauna is touched upon with the aim of finding criteria for the subdivision of the corresponding beds.

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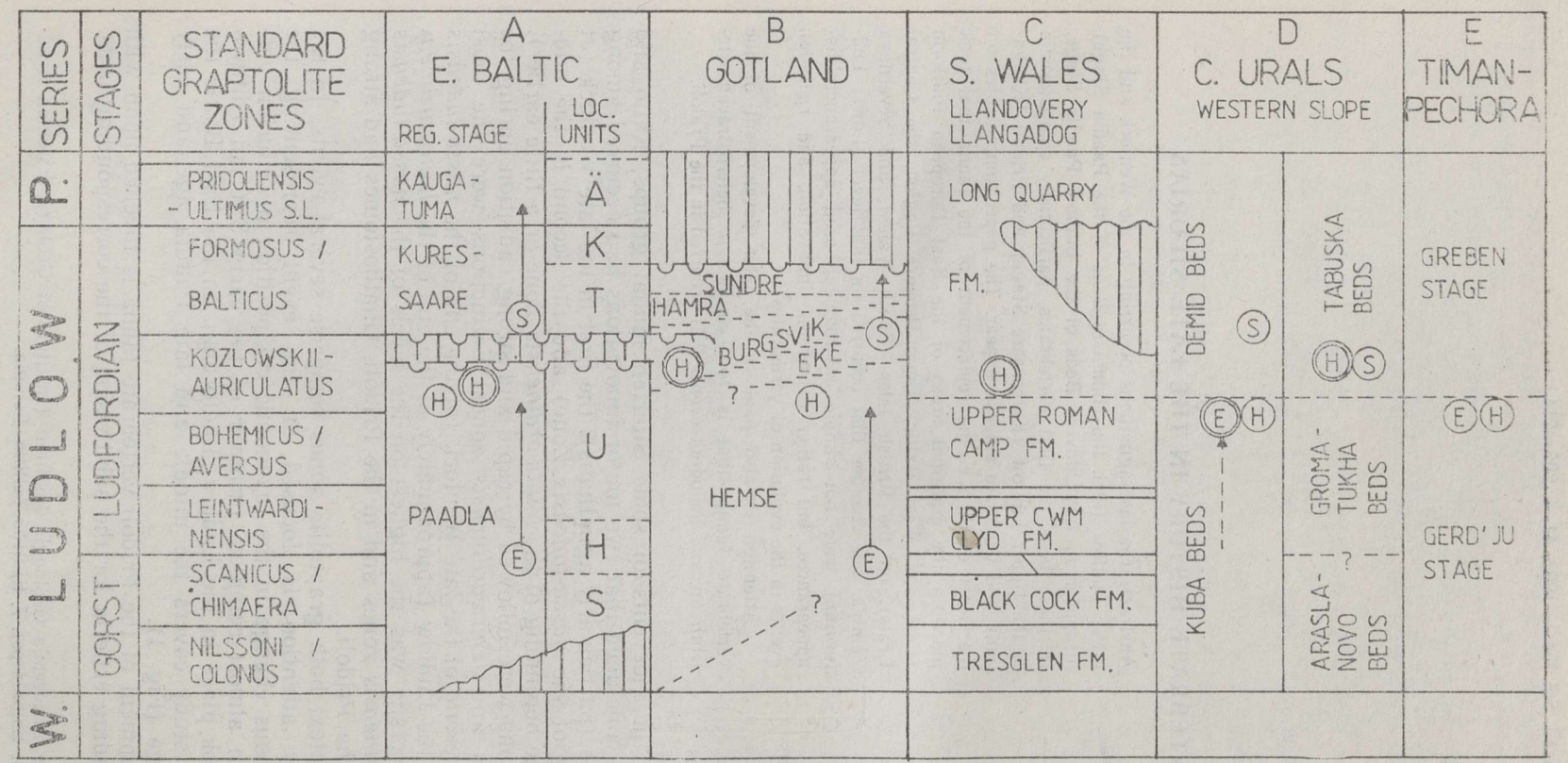

Fig. 1. Ludlow stratigraphy of some regions and location of the selected index-species in sections.
A — by Kaljo, 1990. Note the hiatus in the uppermost Paadla Stage; *B* — vertebrate identifications from Fredholm, 1988, 1989 and author; *C* — by Siveter et al., 1989. Note that the base of the Long Quarry Formation has been defined on a lower level; *D* — by Модзалевская and Мярсс, 1991; Шурыгина et al., 1981; *E* — vertebrate identifications from Валюкявичюс et al., 1983; Талимаа and Мельников, 1987; stratigraphy by Модзалевская and Мярсс, 1991.
Letters in circles: E — *Phlebolepis elegans*, H — *Andreolepis hedei*, S — *Thelodus sculptilis*. A circle marks the older vertebrate assemblage, double circle — the younger one. Arrows show the range of species.

The Paadla age with a marked regression maximum at the Himmiste Beds level was characterized by the flourishing of osteostracans (Fig. 2) that had started in the Wenlock, at the beginning of the Rootsiküla age. Rare osteostracan fragments have also been recovered from the earlier, Jaagarahu Stage and later, Kuressaare, Kaugatuma, and Ohesaare stages. Anaspids, which occurred abundantly in the Viita, Vesiku, and Himmiste beds, reveal a quite similar evolution pattern. In the Wenlock—Ludlow boundary beds their diversity decreases to some extent. As in the Wenlock and Ludlow the osteostracan species dominate over the anaspid ones, the appearance-disappearance levels are more distinct in the first group. In Estonia and western Latvia the upper boundary of the Himmiste Beds (or a somewhat lower level) shows the disappearance of *Trematas-pis milleri* Patten, *Tr. mammillata* Patten, *Dartmuthia gemmifera* Patten, *Oeselaspis pustulata* Patten, *Witaaspis schrenkii* (Pander), *Thyestes ver-rucosus* Eichwald, and *Procephalaspis oeselensis* (Robertson) among osteostracans and of Birkeniida sp. C, Birkeniida sp. C?, Birkeniida sp. D, and Birkeniida sp. D? among anaspids (see Мярсс, 1986). This is the late Himmiste disappearance level (Himmiste event) of osteostracans and anaspids whereas the higher ones in our area are already character-ized by new species and genera (Fig. 2). Of agnathans this level is crossed only by the thelodonts *Thelodus laevis* (Pander), *Th. carinatus* (Pan-der), *Thelodus* sp., *Loganellia martinssoni* (Gross), and *Phlebolepis ele-gans* Pander and of gnathostomes by two acanthodians (*Nostolepis striata* Pander and *Gomphonchus sandelensis* (Pander)). All these taxa have a micromeric exoskeleton.

Outside the Baltic area, beds with abundant anaspids have been recovered already in the Llandovery and Wenlock of Scotland (the Priesthill and Waterhead Groups and their coeval analogues), although there anaspids are represented by different species and genera, co-occur-ring with osteostracans in the Wenlock (Ritchie, 1985). The same has been noted in the Ringerike Group (Wenlock) in Norway (Kiaer, 1924; Ritchie, 1964). A thelodont *Loganellia* with a micromeric exoskeleton appears in the Llandovery and spreads over a very extensive area: North Greenland, Ireland, British Isles, Norway, East and West Baltic, Timan-Pechora Region, Severnaya Zemlya, Tuva, and locally possibly also in North America (see literature cited in Мярсс, 1986; Blieck and Janvier, 1991). The specimens recorded from the Ordovician (Caradoc), Harding Sandstone, and *Tesakoviaspis* of the Siberian Llandovery, mentioned in Blieck and Janvier (1991), are not thelodonts, but constitute tubercles of the heterostracan exoskeletons. Heterostracans, however, appeared already in the mid-Ordovician (Denison, 1967; Ritchie and Gilbert-Tomlinson, 1977).

Here it should be mentioned that in Estonia thousands of Ordovician limestone samples, studied on chitinozoans and conodonts for over 20 years, have for some reason yielded no vertebrates. The author concurs with Blieck and Janvier (1991) in that the absence of vertebrates in the Upper Ordovician cannot be explained by glaciation. For example, the Estonian area is characterized by bioherms referring at warm conditions during the Caradoc Keila and Oandu stages, Ashgill Pirgu and Porkuni stages, and also in the Silurian, Llandovery, Juuru Stage and higher (Rõõmusoks, 1983).

In Estonia the Himmiste Beds are succeeded by the Uduvere Beds, which are up to 10 m thick in Kingissepa core (recently renamed into Kuressaare). These beds are relatively poor in vertebrates. The sediments of vertebrates accumulated partly in the conditions of a transgressive,

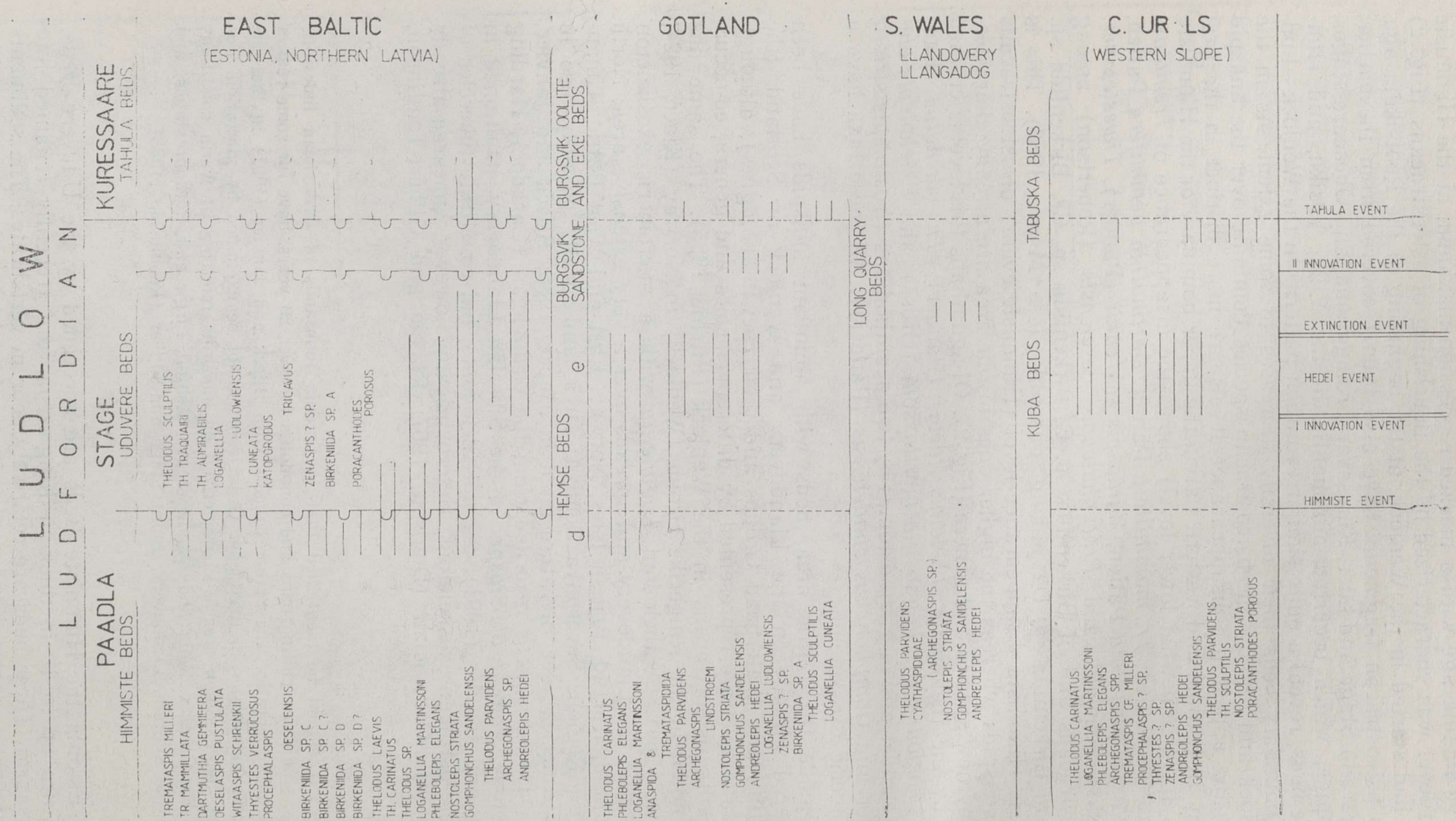

Fig. 2. Ludlow vertebrate succession in some regions. Data on the vertebrate distribution of Gotland by Fredholm, 1988, 1989 and author.

partly during the regressive phases of the development of the sea. The Ludlow transgression maximum was in Uduvere time (Эйнасто in Мярсс, 1986, p. 77). The extinction of the Wenlock and early Ludlow agnathan thelodonts *Thelodus laevis* (Pander), *Th. carinatus* (Pander), *Thelodus* sp., *Loganellia martinssoni* (Gross), and *Phlebolepis elegans* Pander and an innovation, represented by the appearance of *Thelodus parvidens* Agassiz, the earliest cyathaspidid heterostracan *Archegonaspis* sp. and the first osteichthyan *Andreolepis hedei* Gross, coincided with the formation of Uduvere Beds. In several Estonian sections (Sakla, Tahula-709, Suurlahe-738) the younger assemblage does not contain any forms of the older one. In the Ventspils and Ohesaare cores the species of both assemblages occur together. Such a situation has been recorded from the upper part of the Hemse *d* and Hemse *e* beds on Gotland (Fredholm, 1988, 1989), in the Kuba Beds near Mikhailovsk pond of the Ufa region in the Central Urals, in the Ust-Spokoinaya Formation of Severnaya Zemlya (author's identifications; Fig. 2), and in the Velikoretskaya Formation of the Gerd'ju Stage in North Timan (Валюкявичюс et al., 1983).

The younger assemblage is well exemplified on the Uddvide outcrop of Gotland (this part of the Burgsvik Sandstone correlates with the Uduvere Beds of the Paadla Stage; see Fig. 1), where *Andreolepis hedei* Gross occurs with *Loganellia ludlowiensis* (Gross), *Zenaspis?* sp. and two acanthodians. In South Wales the lower Long Quarry Beds of the Capel Horeb Main Quarry outcrop have yielded together with two long-ranging acanthodians also *Thelodus parvidens* Agassiz, Cyathaspididae (*Archegonaspis* sp.), and *Andreolepis hedei* Gross. In the Central Urals, the Tabuska Beds, located close to the mouth of the Tabuska River on the right bank of the Ufa River, have shown the occurrence of *Andreolepis hedei* in the same assemblage with *Thelodus parvidens*, *Th. sculptilis* Gross, *Archegonaspis* spp., *Nostolepis striata* Pander, and *Poracanthodes porosus* Brotzen.

Thus, the short-ranging *A. hedei* event (Fig. 2) constitutes the replacement of taxa in the Ludlow which started with the innovation at the beginning of the *A. hedei* Biozone and ended in an extinction event inside this Zone. A complex of sedimentary rocks comprising old and new forms corresponds to the event. The underlying beds contain only old taxa, the overlying beds only new ones (except two acanthodians).

The Ludlow of Euro-America is characterized by the occurrence of cyathaspidids and their radiation over a large area: Greenland, the British Isles, East and West Baltic, Vaigach Island, Timan-Pechora Region, the Central Urals, Severnaya Zemlya, North-West Territories, north-eastern Canada, and the Canadian Arctic Archipelago. In the last region the earliest cyathaspidids have been recorded already from the Upper Wenlock (Blieck and Janvier, 1991).

The other faunal groups also underwent big changes in the Ludfordian, just on the same level. For example, the lower boundary of the *Collarothyris canaliculata* brachiopod Zone displays the extinction of the *Didymothyris didyma* assemblage and mass appearance of new brachiopods progressively developing in the Pridoli. The faunal change on the western slope of the Urals coincides with the beginning of a new sedimentary cycle (Модзалевская and Мярсс, 1991).

In the East Baltic the taxonomically relatively poor younger Uduvere vertebrate assemblage is succeeded by the invasion of abundant agnathans and gnathostomes in early Kuressaare age. The initiation of this event is very sharp, being in many cores marked by a bone bed (Kuressaare, Tahula-709, Sakla, Sutu, etc.). The lower part on the Kuressaare Stage, the Tahula Beds, deposited in the regressive sea conditions of the late Ludlow. On the lower boundary of the Tahula Beds or slightly higher

the thelodonts *Thelodus traquairi* Gross, *Loganellia cuneata* (Gross), and *Katoporodus tricavus* (Gross) appear in our sections. This is the lowermost stratigraphical level known for these species. *Thelodus admirabilis* Märss appears somewhat higher, in several core sections on the lower boundary of the Kudjape Beds of the Kuressaare Stage. The Tahula Beds have revealed the first appearance of *Loganellia ludlowiensis*, osteostracan *Zenaspis*? sp., anaspid Birkeniida sp. A, and acanthodian *Poracanthodes porosus* in Estonian sections. In the Gotland and Central Urals sections, however, these species have been recorded on an earlier level. In the Virbalis core of Lithuania *Loganellia ludlowiensis* occurs simultaneously with *Thelodus sculptilis* and *Th. parvidens* in the top part of the Pagegiai Formation (Каратаюте-Талимаа et al., 1987).

The analysis of the younger Uduvere and Tahula assemblages has allowed of the conclusion that in the East Baltic the co-occurrence of *Thelodus sculptilis* and *Andreolepis hedei* falls within a stratigraphical hiatus in the uppermost part of the Paadla Stage. The break of sedimentation at about this level has been also noted by Einasto (1991). The single find of *Loganellia ludlowiensis* near the lower boundary of the Tahula Beds suggests that the appearance and a part of the vertical range of this species, as well as the innovation of fauna took place during this break, whereas the lower boundary of the Tahula Beds shows a radiation event (Tahula event, Fig. 2). The hiatus correlates with a part of the Eke and Burgsvik beds of Gotland and a part of Tabuska Beds of Central Urals (Fig. 1). In the Welsh Borderland of the British Isles (Turner, 1973) *L. ludlowiensis* has been attributed to a very long vertical range — from the Woolhope Limestone, Wenlock, up to the Temeside Bone Bed, Downton.

The very diverse and rich vertebrate fauna of early Kuressaare age becomes somewhat poorer in late Kuressaare and early Kaugatuma, Pridoli, ages (Ludlow—Pridoli boundary is indistinct by vertebrates). To some extent this was influenced by the beginning of a new transgressive phase in the development of the Paleobaltic basin when the high rate of the deposition reduced the frequency of scales in sediments. *Thelodus sculptilis* and *Th. admirabilis* become extinct and acanthodians gain predominance in early Kaugatuma age. The appearance of new taxa in this relatively continuous section is slow. In the late Äigu time the acanthodians *Nostolepis striata* and *Gomphonchus sandelensis* are supplemented by *Nostolepis gracilis* Gross. Sporadically the samples have yielded also specimens of other groups known already from the Kuressaare Stage. Therefore the overall number of species is rather high in the Kaugatuma Stage. The high predominance of acanthodians during most of the Kaugatuma time may be called the acanthodian event. Acanthodians continued to prevail until the end of the Silurian, although other vertebrate groups were also more numerous in that interval.

The acanthodian event is observable also on the British Isles (Holdgate Groub; Turner, 1973), Timan-Pechora Region (Greben Stage; Талимаа and Мельников, 1987), in Kaliningrad District (Minija Formation), and probably also in Poland (*Acastopyge* Biozone; only scarce material available to the author).

Several East Baltic core sections (Ohesaare, Kaavi-568, Sõrve-514, Ruhnu-500, Kolka-54, Ventspils) show always a definite successive upwards appearance of the cyathaspidid heterostracan *Tolypelepis undulata* Pander, the eriptychiid heterostracan *Strosipherus indentatus* Pander, and the osteichthyan *Lophosteus superbus* Pander in the higher Kaugatuma Stage. *T. undulata* and *S. indentatus* appear at an interval from 12 m in the Kaavi-568 core up to 40.3 m in the Ventspils core, whereas for *S. indentatus* and *L. superbus* the corresponding numbers are 5 m in

Sõrve-514 and 10.8 m in the Ventspils core. Stratigraphically these finds belong to the top part of the Lõo Beds of the Kaugatuma Stage and the upper and lower parts of the coeval Minija and Targale formations, respectively. This entrance can be called the heterostracan-osteichthyan event. These vertebrates pass on to the lower Lower Devonian.

The distribution of the above-listed vertebrates outside the East Baltic area is poorly known as the researchers have focused their attention on thelodonts. In the Timan-Pechora Region *Strosipherus indentatus* and *Tolypelepis* sp. have been identified (Валюкявичюс et al., 1983; Талимаа and Мельников, 1987) in the lower and upper ichthyofaunal complexes of red-coloured sandy sediments of the Greben Stage; for carbonate sediments, however, an assemblage of *Strosipherus indentatus*, *Lophosteus superbus*, and acanthodians has been distinguished.

The transition to the Ohesaare Stage is either distinctly marked by the appearance of vertebrates (the core sections Kaavi-568, Sõrve-514, Ruhnu-500, Kolka-54, etc.) or gradual (Ventspils core). The first case suggests the occurrence of a certain break in sedimentation. In the Ohesaare cliff section fish remains have concentrated in the bone beds, which give the most complete picture about the taxonomic composition of the ichthyofauna of the early Ohesaare time. In the Kaugatuma Stage the bone beds are missing. The lower part of the Ohesaare Stage shows the reappearance of several thelodonts of the Kuressaare Stage, which in the Kaugatuma Stage were absent or occurred sporadically. The renewal of the vertebrate fauna continues here: there appear Birkeniida sp. B and Birkeniida sp. E among anaspids, *Nostolepis alta* Märss among acanthodians, and *Tylodus deltoides* of uncertain systematic position. This genus and species need thorough investigation as they may lower considerably the first appearance level of some higher taxon.

In the latest Silurian the representatives of the genus *Thelodus* become extinct. The thelodont *Katoporodus tricavus* is replaced by *K. timanicus* (Kar.-Tal.) and *Loganellia kummerowi* (Gross) appears. Quite frequent is *Goniporus alatus* (Gross). This is the latest Silurian, pre-Devonian thelodont event, observable in the East Baltic, Timan-Pechora Region, and British Isles.

In non-graptolite sections the Silurian—Devonian boundary is marked by the appearance of the heterostracan genus *Traquairaspis*. On the same level a new innovation took place characterized by the incoming of thelodonts *Turinia pagei* (Powrie), *Boreania minima* Kar.-Tal., *Nikolivia elongata* Kar.-Tal., and other heterostracans (*Tesseraspis* sp., *Corvaspis* sp., etc.) in western Byelorussia, East Baltic, the Urals, Timan-Pechora Region, Severnaya Zemlya, and British Isles.

Beside *Traquairaspis*, thelodont researchers have used as a marker of the Devonian boundary the appearance of the thelodont *Turinia pagei* (Turner, 1973; Каратаюте-Талимаа, 1978). This view is completely supported by the present author. The *Traquairaspis* is very hard to identify on the species level, as in the insoluble residue its shields occur only as tiny fragments and more rarely than thelodont scales. On the basis of the latter it is possible to define species, moreover, thelodonts were good swimmers and their geographical distribution was more extensive.

Summary

In the Silurian the evolution of vertebrates was still on the initial stage (the first specimens recorded from the Middle Ordovician), therefore innovation and radiation events prevailed over extinctions.

The most distinct change in the taxonomic composition of East Bal-

tic vertebrates took place in the Ludlow, Paadla age. Because of the changeful character of sedimentary rocks, the structure of the stage is complicated: it comprises the beds, deposited during the Ludlow regression (Himmiste Beds) and transgression (Uduvere Beds) maxima.

In Estonia an event of local significance has been recorded on the upper boundary of the Himmiste Beds. Here the disappearance of osteostracans and anaspids from the sections was caused by facies changes and erosion of sediments. Extensive extinction of Wenlock and early Ludlow fauna in the whole European (subglobal) biogeographical faunal province took place in the late Uduvere time (late Paadla age). The subglobal innovation of late Ludlow vertebrate fauna (the first Uduvere innovation event), however, started earlier, at the beginning of the *Andreolepis hedei* Biozone. This is remarkable because of the appearance of the earliest taxa of cyathaspidid heterostracans and osteichthyans.

The following second innovation, the incoming of new anaspids of the order Birkeniida and acanthodians (genus *Poracanthodes*) is observable in the Gotland and Central Ural sections. In Estonian sections the corresponding assemblage is missing, suggesting the presence of a hiatus in the uppermost Paadla Stage. The beginning of the Kuressaare age, Tahula time, however, shows already a radiation event.

In the Pridoli (the Kaugatuma and Ohesaare stages) three events might be distinguished which can also be traced outside the Paleobaltic basin: (1) the practical predominance of acanthodians from above the Kuressaare—Kaugatuma boundary up to the top of the latter (acanthodians prevailed over other groups until the end of the Silurian); (2) the beginning of a new stage in the development of heterostracans and osteichthyans (*Tolypelepis*, *Strosipherus*, *Lophosteus*) in late Kaugatuma age; (3) the latest Silurian thelodont event, preceded by the extinction of the *Thelodus* species and the appearance of thelodonts transitional to the Early Devonian (*Loganellia kummerowi*, *Katoporodus timanicus*).

The most significant innovations in the evolution of the Silurian vertebrate fauna studied were (see also Blieck and Janvier, 1991):

- — appearance of thelodonts in the Llandovery;
- — incoming of cyathaspidid heterostracans in the Ludlow, reappearance of eriptychiid ones in the Pridoli after an interregnum which started in the late Ordovician;
- — emergence of anaspids in the Llandovery and osteostracans in the Wenlock and their flourishing in the Wenlock and Ludlow;
- — origination of acanthodians in the Llandovery (or in Upper Ordovician?), increase in their diversity during the Ludlow and prevalence in the Pridoli;
- — entrance of osteichthyans in the Ludlow and their taxonomic diversification in the Pridoli.

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Tiiu MÄRSS

SELGROOGSETE AJALOOLINE ARENG HILISSILURIS

Andreolepis hedei biotsooni tasemel Ludlow's Paadla lademe Uduvere kihtides toimus kalafauna asendumine uuega. See asendumine, nn. *hedei* sündmus haarab nii väljasuremise kui ka uuenemise sündmuse. Seda on võimalik jälgida Ida-Euroopa platvormi äärealadel (Baltikumis, Gotlandil, Timaani-Petšoora alal, Kesk-Uraalis), Briti saartel (Lõuna-Walesis) ja Severnaja Zemljal.

Pridolis eraldatakse välja akantoodide, heterostraakide-osteihtüiidide ja devonieelne telodontide sündmus.

Тийу МЯРСС

ИСТОРИЧЕСКОЕ РАЗВИТИЕ ПОЗВОНОЧНЫХ В ПОЗДНЕМ СИЛУРЕ

Установлено, что обновление фауны позвоночных в лудлове произошло на уровне биозоны *Andreolepis hedei*. Это событие (*hedei*) включает в себя как вымирание, так и обновление определенных таксонов позвоночных и прослеживается в разрезах краевых регионов Восточно-Европейской платформы (Прибалтика, о-в Готланд, Тимано-Печорская провинция, Средний Урал), Британских островов и Северной Земли.

В пржидоли выделены три события, касающиеся акантод, гетероstраков-остеихтид и позднесилурийских телодонтов.