Several attempts have been made to subdivide the Silurian and the lowermost part of the Devonian using various vertebrates: osteostracans (Böllau, 1949), heterostracans and osteostracans (White, 1950), and thelodonts/(Gross, 1947, 1967; Karagače-Talimaa, 1968, 1974 (in Gašparčík, 1974), 1978; Turner, 1973/). As these zonal schemes were largely based on the material from outcrops representing only small parts of the continuous sections the zonations appeared to be insufficient for a detailed correlation within a paleobasin and/or for an interregional correlation.

Recent study of rich material from 17 borings and 9 outcrops of the East Baltic area demonstrates the great stratigraphical value of vertebrates. Nine zones (Fig. 1, 2) are established in an interval from the Lower Wenlock (in Estonia) to the Upper Downton (in Latvia). Here the Downton/Ditton boundary has been used according to H. W. Ball and D. L. Dineley (1961). The lower limit of a biostratigraphical zone is

<table>
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<th>STRAT. UNITS</th>
<th>BORING/OUTCUP (A)</th>
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<th>SAHLA</th>
<th>TAHULA</th>
<th>KINNO</th>
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**Fig. 1.** The tailzones of index-species in borings and outcrops. For indexes of stratigraphical subdivisions see Table in Preface.
Vertebrates were used for establishing of the lower boundary of the Kuresaare Stage, but not those of other ones.
defined by the earliest occurrence of the index-species (Hedberg, 1976). Usually the
index-species extends into the succeeding zone. The representatives of various verte-
brates (thelodonts, acanthodians, a heterostracan, an osteichthystid) are used as index-
species.

Vertebrate zones

In Estonia the earliest known vertebrates, i.e. thelodont and acanthodian scales
have been discovered from the Late Llandovery Rumba Formation, and from the upper part
of the Early Wenlock Jaani Stage (Fig. 2). The latter contains conodont Oszarkodina sa-
gitta rhemana (Walliser) (Viiru, personal communication). The scarcity of vertebrates
has not enabled to distinguish the zones on these levels. Higher up in sections the
vertebrate fossils are more numerous but in the earliest, Logania taiti zone they are
still rare.

The Logania taiti Zone (Fig. 2) corresponds to the Maasi (except their base) and
Tagavere Beds of the Jaagarahu Stage, the Wenlock of Estonia. Though the scales of
Logania are known from the upper part of the Jaani Stage, they cannot be referred with
certainty to those of L. taiti. In view of this, the lower limit is defined by the
earliest appearance of scales which definitely belong to L. taiti. Of the other spe-
cies, Thelodus laevis, Thelodus sp. ind., Osteostraci gen. et sp. ind. and Saarolepis
oeselensis? are represented. The acanthodians of Nostolepis striata and Comphochus
sandelsonis type are known from the Vesiku-507 boring, where the zone has a maximum
thickness (22.5 m). In the Sakla and Laimjala-515 borings L. taiti ranges above the
upper boundary of the zone (Fig. 1) (to our mind stratigraphy of the Wenlock part of
these sections needs a revision). The vertebrates of the L. taiti Zone occur in lagoon,
shoal and open-shelf deposits.

In Scotland the strata with Logania taiti are referred by A. Ritchie (1967) to the
Upper Wenlock or Lower Ludlow. Recently some scales of this thelodont have been found
by the author from the Slite Beds from Nygård 1 and Atlingbo localities on Gotland. Loga-
nia taiti and L. martinsoni have been listed from 9g and 10 beds in Norway (Turner,
Turner, 1974). According to J. Bockelie (1973) the greater part of the Whole Stage 9
belongs to the Wenlock, the lowermost part of the Stage 10 to the Lower Ludlow, or pos-
sibly to the uppermost Wenlock. The data on the distribution of vertebrates in Esto-
nia seem to confirm the Wenlock age of 9g beds and partly 10 beds, the Sundvollen For-
mation. On Severnaya Zemlya scales of L. taiti have been found from the section of the
Maturevich River in the middle part of the Samoichov Formation.

The L. taiti Zone corresponds to the upper part of the level with loganids from the
L. scottica group according to V. Karatajüté-Talimaa (Karatajüté-Talimaa, 1978).

The Logania martinsoni Zone (Fig. 2) occupies the Rootsiküla Stage and the Sau-
vere Beds of the Paadla Stage (excluding the uppermost part of these beds). For the
first time the zone was distinguished by V. Karatajüté-Talimaa (Karatajüté-Talimaa,
1978) for the uppermost Wenlock and Ludlow of the European biogeographical province.
At present, more detailed zonation, the Logania martinsoni Zone is restricted to the
level indicated above. This zone was previously named after two species, Thelodus
schmidtii and Logania martinsoni (Mapp, 1978). As Th. schmidtii appears already in the
underlying strata, it is better to avoid the double name. By the way, Th. schmidtii is
considered as a junior synonym Th. laevis. L. martinsoni is accompanied by thelodonts
Th. laevis, Th. cf. marginatus, osteostracans Trematospis schmidtii, T. milleri, Oes-
laspis putulata, Thyeses verrucosus and anaspid Saarolepis oeselensis. In the Laim-
java-515 and Sakla’borings in the Viita Beds only scales of L. taiti occur. The whole
listed vertebrate assemblage (except L. taiti) ranges into the succeeding zone. The
maximum thickness of the strata corresponding to the *Logania martinsoni* Zone is 44.9 m in the Ohesaare boring. Facial distribution of *L. martinsoni* coincides with that of *L. taiti*.

Outside Estonia *L. martinsoni* is listed from the Halla Beds of Gotland (Martinson, 1966; Gross, 1967, 1968a), and from 9g and 10 beds of the Ringerike district, Norway (Turner, Turner, 1974). The identification of *L. martinsoni* from the beds 9g needs a revision. From the Mortimer outcrop area, (loc. 314 of Silurian Subcommission localities), the Middle Eltonian of Welsh Borderland have been found both *L. martinsoni* and *Thelodus laevius*. In the Canadian Arctic they occur in the Upper Wenlock and Lower Ludlow of the Prince of Wales Island (Turner, Dixon, 1971; Dixon, Williams, Turner, 1972), in North Timan in the Velikoretskaya Formation (Ludlow) (Kossovoy, Kapataev-Talimaa, 1977), and in the Ust-Spokoinaya Formation, Ludlow of Severnaya Zemlya (author's identifications).

<table>
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<th>SERIES</th>
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Fig. 2. Subdivision of Silurian deposits based on vertebrates. • - finds of single scales of *Thelodus sp.* and *Gomphonchus sp.*, **•** - the same + *Logania sp*. DCSF - Downton Castle Sandstone Formation, TSF - Temeside Shale Formation. Stratigraphy and (partly) paleontological data after Ball, Dinley, 1961; Turner, 1973; Turner, Turner, 1974; Kaljo, 1978; Holland, 1980; Галляре, Ульст, 1974; Ненер и др., 1979; Пашковичус, 1979.

The *Phlebolepis elegans* Zone (Fig. 2) evidently occupies the topmost part of the Sauvere Beds, Himmiste Beds and lowermost part of the Uduvere Beds of the Paadla Stage. Ch. Pander (1856) in his description of *Phlebolepis elegans* gave for type-locality "Rootsiküla". Numerous samples from stratotype outcrops and from the cores of more than 10 boreholes representing the same stage, have not revealed a single scale from the Rootsiküla level. Maximum thickness of the strata corresponding to the *Phlebolepis elegans* Zone is 68.0 m in the Ventspils boring. The other thelodonts, osteostracans,
anaspids and acanthodians coincide with those of the preceding zone. However, *Th. marginatus* has been identified from the *P. elegans* Zone with certainty (and not with some doubt as in the preceding zone). *Phlebolepis* n. sp., and osteostracans *Tremataspis mammillata* and *Dartmouthia gemmifera* make their first appearance in this zone. Index-species ranges into the succeeding zone. Facial range of *Phlebolepis elegans* is somewhat wider than those of *L. taitii* and *L. martinssoni*. It has been found in the deposits of lagoon, shoal, open-shelf and slope belts of the Paleobaltic Silurian basin.

The *Phlebolepis elegans* Zone has been established in the Paadla Formation (Ludlow) of Estonia in numerous boring sections, in the Pagėgiai Formation of Latvia in the Kolka-4 (= Lužni) boring (see Šukys, 1974). In the Ventspils boring (at the depth 484.5-552.5 m) the zone corresponds to the most of the Dubysa Formation and the lower part of the Pagėgiai Formation. The Kuba Beds in the Mikhailovsk section, western slope of the Central Urals, and a part of the Ust-Spokoinaya Formation of the October Revolution Island, Severnaya Zemlya may be equivalent to the *Phlebolepis elegans* Zone of the East Baltic area.

The *Andreolepis hedei* Zone (Fig. 2) has been determined in the Uduvere Beds (excl. lowermost part) of the Paadla Stage of the Ludlow. The lower boundary of the zone is defined by the appearance of *Andreolepis hedei*. The zonal assemblage includes Upper Wenlock-Lower Ludlow elements, as well as the earliest Downton ones. The core section of the Ohesaare boring at the interval 98.9-99.5 m contains *Thelodus parvidens*, *Phlebolepis elegans*, *Cyathaspidae* (Archegonaspis?) sp., *Nostolepis striata* and *Andreolepis hedei*. In Tahula-709 boring two more agnathans: Osteostraci gen. et sp. ind. and Anaspida n. sp. A. occur. In the Central Baltic the maximum thickness of the strata corresponding to this zone is 28.5 m (in Ventspils boring). The index-species comes from the deposits of shoal, open shelf and slope belts.

*Andreolepis hedei* has been identified by the author from the Ust-Spokoinaya Formation of the Pioneer Island of Severnaya Zemlya together with *Th. marginatus*, *L. martinssoni*, a heterostracan, an anaspid and an acanthodian of Gomphonochus sandelensis type, and from the Long Quarry Beds, Capel Horeb Main Quarry, South Wales, together with *Th. parvidens?*, *Cyathaspidae* gen. et sp. ind., *Nostolepis striata* and *Gomphonochus sandelensis*. W. Gross (1968b) described *Andreolepis hedei* from the Upper Hemse Beds of Gotland. According to V. Katarajuté-Talimaa (Kosovoy, Katarajuje-Talimaa, 1977) *A. hedei* occurs in North Timan, together with *Th. marginatus*, *L. martinssoni*, *P. elegans*, etc. in the Velikoretskaya Formation, correlated in recent paper with the upper part of the Paadla Stage of the East Baltic.

The *Thelodus sculptilis* Zone (Fig. 2) is rather distinct in the Upper Ludlow and lowermost Downton. The zone occupies the whole Kuressaare Stage, and extends into the Xigu Beds of the Kaugatum Stage. V. Katarajute-Talimaa (in Šukys, 1974) for the first time distinguished this zone in Latvia in the section of the Kolka-4 boring at the base of the Minija Beds. Later on, however, she has not mentioned the zone. But, as *Th. sculptilis* appears in many borings at the same level and is abundant, it is worth using this thelodont as an index-species. The maximum thickness of the strata occupied by the zone is known in the Pavilosta boring, Latvia, (more than 155 m). Northwards the thickness decreases. In the lower part of the zone the fish assemblage is very variable and abundant. Almost at the same level with *Th. sculptilis* appear in Ohesaare boring thelodonts *Th. traquairi*, *Logania owenata* and *L. ludlowiensis*. In the lowermost part of the zone in the Sakla boring appears *Katoporus tricousus*, and in Varbla-502 boring *Logania owenata*. Scales of an acanthodian which may belong either to *Gomphonohus hoppei* or *Foracanthodes poroaua* (see Gross, 1971) have been found in many borings. Somewhat higher occurs *Th. admirabilis*. A number of forms, such as *Cyathaspidae* (Archegonaspis?) sp., Osteostraci gen. et sp. ind., *Nostolepis striata* and *Gom-
pomphonchus sandelsonis range into the Thelodus sculp tilis Zone from the preceding one. More characteristic of the zone are Th. sculp tilis, Th. admirabilis, L. ludowi ensis and the acanthodian of the uncertain systematic position (Gomphonchus hoppei or Pora canthodes porosus). The lower boundary of the zone can be defined by the appearance of these forms (except Th. admirabilis). There is an interval before the succeeding zone (up to 69.6 m thick in the Pavilosta boring), poor in the characteristic vertebrates. Th. sculp tilis has been found in deposits of all facies belts of the Baltic basin except the depression one. It is especially numerous in the first two nearshore belts. In the other regions of the East Baltic Thelodus sculp tilis has been found in the upper part of the Upper Ludow Pagėgiai Formation and at the base of the Minija Formation, Downton of Lithuania (Virbalis boring, depth 843.6 m), and Latvia (Kolka-4, depth 336.5-338.6 m; Engure, depth 468.5-471.5 m) see Karatajūtė-Talimaa, 1978; it is also known from borings Sutkai-89, depth 839.7-875.1 m, and Jurbarkas-36, depth 1034.0-1062.1? m (Karatajūtė-Talimaa, pers. comm.). The scales of Th. sculp tilis have been discovered by the author also from the Upper Ludow of the Kunkoiai section (depth 1055.1 m) Lithuania, and from the Demid Beds (Downton) of the Mikhalovsk section, West Urals. Gross (1967) noted Th. sculp tilis from Ramsösa Beds, South Sweden.

V. Karatajūtė-Talimaa (Karatajute-Talimaa, 1978) distinguished an assemblage with Logania ludowi ensis for the Early Downton of Europe biogeographical province. This assemblage is characteristic of the Lower Downton of Britain. However, the first finds of Logania ludowi ensis are recorded from the Lower Wenlock (Turner, 1973). Evidently, in the Wenlock and Ludow of Welsh Borderland, a number of Logania-species occur (see Fig. 2). This is confirmed by finds of L. martinssonii in the Mortimer Forest outcrop area, Middle Eltonian (see above) and Logania sp. B in the Sunnyhill Quarry, Upper Brinewoodian. Scales similar to those of Logania sp. B and L. ludowi ensis (but not identical with the latter ones) have been found from the uppermost beds of the Samoilovich Formation or the lowermost beds of the Ust-Spokoinaya Formation of Severnaya Zemlya (collections of V. Karatajūtė-Talimaa). Five scales of Logania ludowi ensis have been found on Gotland Källstede locality in the Eke Beds, together with corals. In the Kuressaare Formation of Estonia, upper part of the Pagėgiai Formation of Lithuania and Latvia, also in boulders of North German lowland L. ludowi ensis is rare, and so it is difficult to use this thelodont as an index-species.

The No stolepis gracilis Zone is approximately equivalent to the upper half of the Kaugatuma Stage (Fig. 2). The acanthodians are especially characteristic of the zone. Rare specimens of Thelodus parvidens occur together with No stolepis gracilis, N. striata, and Gomphonchus sandelsonis. In the Ohesaare and Ventspils borings Th. traquairi, Katopor sus tricavus, heterostracans Tolypelepis undulata and Strosipherus indentatus appear at this level. No stolepis gracilis ranges into the succeeding zones. This acanthodian occurs in the first four facial belts.

The vertical distribution of Silurian acanthodians in the North and Central East Baltic shows, that besides theiodont some representatives of this group may be well used for biostratigraphical purposes. They are especially valuable for the lower part of the Downton where the theiodonts and other vertebrates are rare. W. Gross, V. Karatajūtė-Talimaa and S. Turner have indicated in their papers a Downton level rich in acanthodians. This level, by author, corresponds in Latvia and Lithuania to the upper part of the Minija and lower part of the Jūra Beds, in Britain partly to Holdgate sandstones containing only acanthodians. For the middle part of the Baltic Downton V. Karatajūtė-Talimaa (Karatajute-Talimaa, 1978) distinguished an assemblage with Katopus tricavus. However, finds of K. tricavus are so rare that it is hardly possible to use this thelodont as a zonal species.
The *Poracanthodes punctatus* Zone (Fig. 2) corresponds to the uppermost beds of the Kaugatuma and to the greater part of the Ohesaare Stage. The establishment of the lower boundary of the zone is sometimes complicated, as it is not always easy to tell the difference between *Poracanthodes punctatus* and the acanthodian of uncertain systematic position (*Poracanthodes porosus* or *Gomphonchus hoppei*). The strata at the depth of 325.2-276.2 m of the Ventspils boring, and at the depth of 205.9(?) -161.6 m of the Kolka-54 boring represent the zone entirely. The index-species ranges into the succeeding zone. The zone is characterized by a very variable and rich vertebrate assemblage. It includes, on the one hand, species, which occur in the Kuressaare Stage, and on the other hand species, ranging into the Devonian. Thus, beginning with the Låde time in Estonia, the assemblage with *Por. punctatus* includes *Goniporus alatus*, *Gomphonchus hoppei*, *Lophoesteus superbis* and *Tylodus deltoidees*. In the uppermost part of the zone all the *Thelodus* species disappear. *Poracanthodes punctatus* has been found from the deposits of lagoon, shoal and open shelf facial belts.

The zone evidently corresponds to the upper part of the *Kaptoporus tricavus* assemblage level distinguished by V. Karatajüté-Talimaa (Karatajuté-Talimaa, 1978).

The *Kaptoporus timanicus* Zone occurs in the Upper Downton of Latvia (Fig. 2) and North Timan. It corresponds to the *Kaptoporus lithuanicus* Zone of Lithuania, established by V. Karatajüté-Talimaa (Karatajuté-Talimaa, 1978). The author of the present paper has identified scales of *K. timanicus* from four samples of the Ventspils boring (depth 276.2-269.5 m), and from the Kolka-54 boring (depth 161.6-158.3 m). Zonal assemblage contains besides the index-species a small number of thelodont scales, fragments of hetrostracans, numerous acanthodian scales and remains of osteichthyid *Lophoesteus superbis*, and skeletal fragments of *Tylodus deltoidees*. They are all known from the preceding *Poracanthodes punctatus* Zone. *Kaptoporus timanicus* and associated species have been found from deposits of lagoon, shoal and open-shelf belts.

Vertical distribution of *Logania kummerowi*, distinguished by W. Gross (1967) as zonal species for the assemblage lacking *Thelodus parvidens*, is not fully known. V. Karatajüté-Talimaa (see Gajlīte, Uļļst, 1974) identified from the Kolka-4 boring together with *Kaptoporus sp. (? lithuanicus)* also *Logania kummerowi ?* and *Traqauraspis sp.* ind. The first one of these three species occurs somewhat lower in the section. V. Karatajüté-Talimaa (Karatajuté-Talimaa, 1978) changed in the Kolka-4 boring the identification of the *Logania kummerowi ?* to *L. borealis ?* and noted (p. 180) that some scales of *Logania borealis ?* in the number and size of lateral spines are reminiscent to the scales of *L. kummerowi*. In the Nida and Stoniškiai borings, Lithuania, *L. kummerowi* appears earlier than *K. lithuanicus*. According to the data from the Ventspils boring, two types of *Logania* scales can also be distinguished, and *L. kummerowi* occurs higher the monolithic scales of *K. timanicus*. By S. Turner (1973, p.566) the *Goniporus - Kaptoporus* assemblage, containing *L. kummerowi*, is distributed in conglomerates of the Upper Red Downton Group. Higher, in the "Psammosteus" Limestones Group this fauna is associated with *Traqauraspis pocoki*. Evidently, we are dealing with two species of *Logania*: (1) *Logania cuneata*, which is of wide vertical distribution (ranging from the Kuressaare Stage into the lowermost beds of the Tilžė Stage) and (2) *Logania kummerowi* with a limited stratigraphical distribution (from the uppermost beds of the Ohesaare Stage up to the lowermost beds of the Tilžė Stage incl.). As biozones of *L. kummerowi*, *K. timanicus* and *K. lithuanicus* possibly coincide, but *K. timanicus* is geographically more widespread (North Timan, Latvia, evidently also in Britain, see Turner, 1973, Fig. 7c), the last has been chosen as an index-species. As to *Logania borealis ?* indicated by Karatajüté-Talimaa (Karatajuté-Talimaa, 1978), it must be considered as junior synonym of *L. cuneata*.  

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The *Traquairaspis* Zone has been distinguished in the Upper Downton by E. White (1950). In the Ventspils boring *Traquairaspis* sp., *Tesseraspis* ? sp. and *Turinia pagei* are associated with *Logania cuneata*, *L. kummerowi*, *Goniporus alatus*, etc., the Silurian forms of preceding zone. The *Traquairaspis* Zone has not been completely studied by the author so far.

**Facies and cyclic distribution of vertebrates**

The facies distribution of Silurian vertebrates is rather wide. The majority of species has been found from lagoon, shoal and open-shelf deposits, but some of them /*Phlebolepis elegans*, *Logania* sp. ind., *Thelodus parvidens*, *Th. sculptilis*, *Th. admiralabilis*, *Cyathaspidaeae* (Arhegonaspis ?) sp., *Nostolepis vtriata*, *N. gracilis*, *Gomphonchus sandelensis*, *Andreolepis hedei*/ also from the slope facies belt which increases the correlative value of these vertebrates. It must be taken into account that from the Late Downton slope facies we have a small number of samples. Thus, data on the distribution of some species are incomplete, e. g. those of the *Poracanthodes punctatus* Zone. And so is the case with the assemblage of the *Andreolepis hedei* Zone (lagoon deposits corresponding to the latter are not known).

The comparison of the environmental changes during the Silurian in Estonia (see diagram by Эйнасто et al., 1978) with the vertical distribution of vertebrates has revealed an interesting coincidence between the appearance of many new genera and species and transgressions of higher rank. This coincidence is especially clear by the maximum phase of Ludlow transgression during the Uduvere time when first elements of a new, Downton vertebrate fauna appear. The next transgression of a higher rank took place in the Downton in the Kaugatuma time. This transgression is connected with the appearance of vertebrates ranging into the Devonian. The data from the Wenlock are more limited, particularly from its lower part. But the appearance of *Logania martinsoni* in the Early Viita (Late Wenlock) and *Phlebolepis elegans* in Late Sauvere (Early Ludlow) time seem to confirm this rule. As to *L. taiti*, it might appear even during an earlier transgression in the Late Llandovery or Early Wenlock. It must be kept in mind that it is not always possible to fix exactly the first appearance of a new vertebrate species in transgressive deep-water rock where scales are highly scattered (Мясс,Эйнасто, 1978). G. Lindberg (Линдберг, 1978, p. 19) writes about the influence of the change of phases of transgression and regression on the evolution of fish and fish-like animals as follows: "We have a full right to consider a sudden transgression after a long lowering of the ocean level as one of possible reasons for the existence of stages in the development of organic world". Recently it has been demonstrated that extensive transgressions in the Silurian have been caused by fluctuations of the level of the world ocean (see Антюшкина et al., 1976). Thus, if G. Lindberg's presumption is valid, the appearance of new contemporary vertebrate genera and species must have taken place in vast territories.

I thank Dr. E. Kurik for discussions and Dr. V. Viira, M. Pärmamae and P. Männik for the specimens of agnathans and fish discovered among conodonts from Estonia and Severnaya Zemlya.

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ЗОНЫ ВЕРТЕБРАТ В СИЛУРЕ ПРИБАЛТИКИ

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Для выяснения последовательности и предела распространения видов бесчелюстных и рыб в силуре и силуре - нижнем девоне Северной и Центральной Прибалтики с большой детальностью опробовались разрезы 17 буровых скважин /рис. 1/. Начиная с юагарахуского горизонта, нижнего венлака до тильжеского горизонта нижнего девона установлено 9 зон позвоночных. Нижние границы зон определены по первому появлению вида - индекса.

Самая нижняя, зона Logania taiti соответствует маазиским /без основания/ и тагвереским слоям яагарахуского горизонта Эстонии /рис. 2/. Зона Logania martii охватывает роотсикюлаский горизонт и саувереские слои паадлаского /за исключением верхов этих слоев/. Зона Phlebolepis elegans занимает, вероятно, верхи саувереских, химистеских и ниши удверересских слоев паадлаского горизонта. Зона Andreolepis hedei выделяется в удверереских слоях /без низов/ паадлаского горизонта. Зона Thelodus sculpillis охватывает весь курессаареский и большую часть эйгуских слоев каугатумаского горизонта. Зона Nostolepis graciilis выделена в верхах эйгуских и в лыоских /за исключением самых верхов/ слоев каугатумаского горизонта. Зона Poracanthodes punctatus охватывает верхи каугатумаского и большую часть окесаареского /без верхов/ горизонтов. Зону Katoporus timanicus можно выделить в верхах окесаареского горизонта. Зона Trachipartaspis sp. /зона Trachipartaspis sp./ определено в разрезе скв. Вентспилс в низах тильжеского горизонта. В полном объеме она не изучалась.

Большинство видов силурийских вертебрат связано с лагунарными, отмелыми и открыто-шельфовыми отложениями. Некоторые виды найдены и из отложений склоновой зоны. Однако, необходимо иметь в виду, что в верхнем даунтоне мы не имеем отложений склоновой зоны, а в лудлове /в удверереских слоях/ - лагунной зоны, и поэтому данные о фашиальном распределении некоторых видов не полны.