Silurian acanthodian biostratigraphy of Lithuania

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ABSTRACT
Silurian acanthodian associations from western Lithuanian deep shelf graptolite facies and eastern Lithuanian shallow shelf and lagoonal carbonate facies are described and biozonation (Interval range zones) based on stratigraphic ranges of 45 taxa deduced. The Wenlock Series is characterized by the species-poor *Arenaceacanthus arcuatacanalis-Gomphonchus*? *minutus* Acanthodian Zone in east Lithuania, whereas in west Lithuania both of these zonal species occur later, in the Ludfordian (Ludlow). The *Nostolepis gracilis* and *Rohonilepis breviornatus* acanthodian zones occur at the end of the Ludlow in these two areas. The *Fecundosquama basiglobosa* Acanthodian Zone is distinguished in the formations of the Upper Minija Regional Stage (Pridoli) and has a wider regional distribution (discovered also in Latvia, Estonia and former East Prussia). The latest Pridolian Jūra Formation is subdivided into four acanthodian zones (from lowest to highest), the *Nostolepis alta*, *Cheiracanthoides planus*, *Vesperalia perplexa* and *Endemolepis inconstans* zones, and its eastern correlative the Lapės Formation into three, the *Monospina erecta*, *Cheiracanthoides planus* and *Endemolepis inconstans* zones. The acanthodian associations are the most abundant microvertebrates and are distinguished by the dominance of *Nostolepis*-derived taxa.

KEY WORDS
Silurian,
Wenlock,
Ludlow,
Pridoli,
acanthodian microremains,
faunal associations,
biostratigraphic zones,
Lithuania.

RÉSUMÉ
Biostratigraphie des acanthodiens du Silurien de Lituanie.
Les associations d'acanthodiens du Silurien dans des faciès à graptolites de plateau continental profond en provenance de l'ouest de la Lituanie sont décrites ainsi que celles trouvées dans des faciès carbonatés lagunaires et de plateau continental peu profond de l'est de la Lituanie. La biozonation fondée sur les extensions stratigraphiques de 45 taxa est établie. Les séries du Wenlock sont caractérisées par la zone à acanthodiens pauvre en espèces à *Arenaceacanthus arcuatacanalis-Gomphonchus* ? *minutus* dans l'est de la

Lituanie, alors que dans l'ouest de la Lituanie, ces deux espèces de zones apparaissent plus tard, dans le Ludfordien (Ludlow). Les zones à acanthodiens à *Nostolepis gracilis* et *Rohonilepis breviornatus* sont connues à la fin du Ludlow dans ces deux régions. La zone à acanthodiens à *Fecundosquama basiglobosa* est retouvée dans les formations de l'étage régional de la partie supérieure de Minija (Pridoli) ; elle a une distribution régionale plus vaste (découverte aussi en Lettonie, Estonie et dans l'est de l'ancienne Prusse). La Formation Jūra datée du Pridoli terminal est subdivisée en quatre zones à acanthodiens (de la plus ancienne à la plus récente) : les zones à *Nostolepis alta*, à *Cheiracanthoides planus*, à *Vesperalia perplexa* et à *Endemolepis inconstans*. Son équivalent oriental, la Formation Lapės, est, quant à elle, partagée en trois zones : à *Monospina erecta*, à *Cheiracanthoides planus* et à *Endemolepis inconstans*. Les associations d'acanthodiens constituent les microvertébrés les plus abondants et elles se remarquent par la prédominance des taxa dérivés de *Nostolepis*.

MOTS CLÉS
Silurien,
Wenlock,
Ludlow,
Pridoli,
microrestes d'acanthodiens,
associations fauniques,
zones biostratigraphiques,
Lituanie.

INTRODUCTION

Silurian rocks of Lithuania are a classic example of multifacial sediments with marine deep shelf (western part) and marine shallow shelf and lagoonal (eastern and easternmost part) facies. Alongside these, is an intermediate strip containing interfingering of beds from both principal facies fields. This strip occupies a submeridional area incorporating localities (from south northwards) Vilkaviškis-128, Sutkai-87, Gėluva-99, Kunkojai-12 boreholes (Fig. 1B) and continues farther north to the Latvian border. A clearcut subdivision of the territory into facies areas is complicated because of the water depth and type of deposition changing over time. The distribution shown in Figure 1B follows published opinions of Silurian researchers who have interpreted lithology and facies according to the structural-tectonical development of different parts of the sedimentary basin (Paškevičius 1973, 1979, 1994; Paškevičius *et al.* 1986; Paškevičius & Brazauskas 1987; Lapinskas 2000). It is principally based on the Late Silurian deposits which yielded most of the acanthodian assemblages summarized in this study. The western Lithuanian area is dominated by the maximally thick series of black argillaceous and carbonate clays, plus marls, and contains rare limestone interbeds. The black, graptolitic sediments are considered to have formed on an open deep shelf in the Ludlow. Borehole cores from the eastern part of this area are only characterized by graptolites in the lower Ludlow. Upwards, carbonate clays and clayey limestones prevail. This part of the basin was a deep shelf in the early Ludlow, then a shallow shelf in the late Ludlow and Pridoli.

The shallow shelf and lagoonal sediments (carbonate clays, dolomitic marls, nodular limestones, dolomites) dominant in eastern Lithuania lack graptolites, but yield diverse shelly benthic and nektonic faunas. Lagoons existed here during the entire Ludlow with short-time exceptions. For example, the Sudervė limestones of the Neris Formation accumulated on the shallow shelf. Later, in the Pridoli, shallow shelf sedimentation prevailed, with formation of nodular-detrital carbonate facies, as exemplified by the red-colored dolomitic marls and dolomites of the upper part of the Lapės Formation. Numerous sedimentary gaps distinguish the easternmost stratigraphical sections comprising the lagoonal dolomites and dolomitic marls of the Pabradė Formation.

The biostratigraphical zonations of different fossil groups are the basis for the dating geological formations and their assignment to the International stratigraphical scheme. In Lithuania, this is most completely achieved by graptolites

FIG. 1. — Map of Europe showing position of Lithuania (**A**) and a sketch with location of Lithuanian boreholes yielding the majority of the material studied (**B**). Borehole and its original number; **1**, Stoniškiai; **7**, Krekenava; **8**, Stačiūnai; **11**, Šešuvis; **12**, Kunkojai; **44**, Nida; **61**, Viduklė; **87**, Sutkai; **99**, Gėluva; **128**, Vilkaviškis; **137**, Liepkalnis; **162**, Kurtuvėnai; **179**, Ledai; **241**, Butkūnai; **252**, Svėdasai; **299**, Jočionys; **323**, Gražutė. Legend: **1**, outcrop-boundary of Silurian rocks; **2**, borehole and its original number; **3**, boundary between the west and east Lithuanian facies of Silurian rocks.

(Paškevičius 1965, 1973, 1979, 1994), conodonts (Brazauskas 1987, 1989, 1993), ostracodes (Sidaravičienė 1986, 1997; Sidaravičienė *in* Paškevičius *et al.* 1994; Paškevičius 1994), brachiopods (Paškevičius 1958, 1963, 1965; Musteikis & Puura 1983; Musteikis 1985, 2002; Musteikis & Paškevičius 1999) and vertebrates (Karatajūtė-Talimaa 1962, 1968, 1970, 1978; Karatajūtė-Talimaa *et al.* 1987; Karatajūtė-Talimaa & Brazauskas 1994; Talimaa 2000). However, trilobites, bivalves, gastropods and cephalopods are also known, but are less useful for detailed zonations.

Previously, Lithuanian acanthodians have not been used for stratigraphical purposes. Usually they were mentioned in studies of other vertebrate groups, e.g., thelodonts or heterostracans, but these preliminary and incomplete records presented only a few taxa assigned to genera known worldwide, *Nostolepis* Pander, 1856, *Gomphonchus* Gross, 1971 and *Poracanthodes* Brotzen, 1934.

Silurian acanthodians of the Baltic basin are best known from Estonia and west Latvia. Märss (1982, 1986, 1997, 2000) first used acanthodian taxa for a zonal subdivision of the Pridoli in the Baltic. The *Nostolepis gracilis* Vertebrate Zone (VZ) was established in the upper part of the Kaugatuma Regional Stage, and the *Poracanthodes punctatus* VZ in the uppermost Kaugatuma and Ohesaare stages (the shallow shelf facies). For the deep shelf, Märss (1997) added two more zones, the *Poracanthodes porosus* VZ in the Kuressaare and lower part of the Kaugatuma stages, and the *Nostolepis alta* VZ in the upper Ohesaare Stage.

All of these zonal units are less applicable in Lithuania. *Poracanthodes porosus* Brotzen, 1934 has not been found yet in Lithuania in the late Ludlow Ventspils Formation and Sudervė Beds, the correlatives of the Kuressaare. Its range is shorter here and restricted to the Jūra Stage. Lithuanian localities have yielded only rare specimens and fewer morphovarieties of *Poracanthodes* scales (pers. obs. and comm. with T. Märss) as compared with Estonia. *Nostolepis gracilis* Gross, 1947, however, has a wider range than in Estonia. Its first occurrence in east Lithuania is in the upper Pagėgiai Stage of the Ludlow, the Sudervė Beds of the Neris Formation, which corresponds to its entry point into the sequence in the upper part of the Ventspils Formation in the Lūžni-4 borehole core in west Latvia (Valiukevičius 2003b, 2004b). Thus, the regional lower boundary of the *N. gracilis* VZ should be lowered in the Baltic to the late Ludfordian. In Lithuania, *Poracanthodes punctatus* Brotzen, 1934 occurs through all of the Pridoli, and a correction of its position as a regional and standard Silurian zonal fossil is also needed. *Nostolepis alta* Märss, 1986 occurs through the entire Jūra Formation in west Lithuania, where the lower Girdžiai Beds correlate with the uppermost Kaugatuma Stage in Estonia (Paškevičius *et al.* 1994). This zonal index species has not been discovered yet in east Lithuania.

The acanthodians in this study are in more than 300 samples from geological formations spanning the Wenlock to Pridoli in east Lithuania. Wenlock samples from the western area were unfossiliferous. The Wenlock faunas are sparse, taxonomically restricted and found only at dispersed points in the cores. The dating of the first occurrence horizons of taxa are still considered preliminary through the Wenlock and also the Gorstian Stage of the Ludlow (Dubysa Regional Stage). The Ludfordian acanthodians of the later Ludlow are more diverse and species-rich, particularly in east Lithuania, and their stratigraphical ranges are better established because of the larger numbers of fossiliferous localities. Unfortunately, additional material is still needed, e.g., for pinpointing the entry into the sequence of the important index species *Nostolepis gracilis* and *Rohonilepis breviornatus* Valiukevičius, 2004. Acanthodians are abundant through the Pridoli in Lithuania and the entire Baltic with numerous short-range zonal units distinguished, based on the most diversified associations.

This study of Lithuanian acanthodians collected from all available localities plus revisions of the earlier stored samples have allowed a stricter lithostratigraphical control and correlation of taxa with distinct geological horizons or formations and their smaller units. Taxon numbers have increased, particularly for the genus *Nostolepis*

(Figs 2-6). Three new climatiiform and two more ischnacanthiform acanthodian genera were recently erected (Valiukevičius 2003a, 2004a).

ABBREVIATIONS
AZ Acanthodian Zone;
CZ Conodont Zone;
GZ Graptolite Zone;
OZ Ostracode Zone;
TZ Thelodont Zone;
VZ Vertebrate Zone.

LITHOLOGICAL AND BIOSTRATIGRAPHICAL BACKGROUND

The Birštonas Formation, which yielded the most ancient acanthodians, is distributed in the east and is composed of marls with interbeds of nodular limestones, formed on the shallow shelf. Its early or mid-Wenlockian age is based on the *Monograptus testis* GZ of central Lithuania (Paškevičius 1994) and the *Kockelella ranuliformis* CZ established in eastern Lithuania (Karatajūtė-Talimaa *et al.* 1987). In the Butkūnai-241 borehole, conodonts and acanthodians occur in the same samples. The lower part of the Verknė Formation, composed of marls and dolomites with interbeds and lenses of gypsum indicating lagoonal deposition, is possibly coeval. The Wenlockian age of these rocks is additionally based on occurrence of the graptolite *Monograptus flemingi* and the *Loganellia grossi* TZ (Talimaa 2000). The gypsiferous, mainly dolomitic lower Dukstyna Formation (Lapinskas 2000), former Nevėžis Formation (Paškevičius & Brazauskas 1987; Karatajūtė-Talimaa *et al.* 1987; Paškevičius 1994), represented by shallow marine marls and limestones in central Lithuania, is dated by conodonts as mid- to late Wenlockian and attributed to the *Kockelella amsdeni* CZ and *Loganellia grossi* TZ. The upper member of this Formation, composed of lagoonal marls and gypsiferous dolomites and attributed to the *Ozarkodina bohemica* CZ, is dated as topmost Wenlock to earliest Ludlow. This age is also given for the upper part of the Gėluva and the lower part of the Dubysa formations in central and west Lithuania. The Gėluva Formation is composed of marls, nodular limestones and dolomitic marls at the top. The *nassa-ludensis* GZ date this unit as Wenlock. The bi-folded Dubysa Formation (Ludlow) is characterized by marls and nodular limestones in the lower part (Šešupė Beds) and dominated by limestones in the upper part (Nova Beds), and is displaced in the west of the territory. Its eastern correlatives are the upper member of the Nevėžis Formation and the Širvinta Formation (frequently red-colored dolomitic clays and marls with lenses of gypsum and dolomite interbeds), which were formed in an extremely shallow lagoonal basin. The Šešupė Beds of the Dubysa Formation are in the *nilssoni-scanicus* GZ (Gorstian), and the Nova Beds are in the Gorstian-Ludfordian *tauragensis* GZ (Paškevičius 1994; Paškevičius *et al.* 1994). The *Kockelella variabilis* and *Polygnathoides siluricus* CZ and the nearly coeval *Paralogania martinssoni* TZ (Talimaa 2000) cover this time span. In central and eastern Lithuania, the facies correlatives, the mid-Dubysa and Trakai Beds of the Neris Formation (Lapinskas *et al.* 1985a, b), belong to the *Ozarkodina tillmani* CZ (mid-Ludlow). Acanthodians are found in this zone in the Gėluva-99 borehole at the 752-806 m level.

Ludfordian deposits are represented by the Pagėgiai Formation in the west, the Mituva and Ventspils formations centrally, and the Neris Formation in the east of Lithuania. The western area is dominated by maximally thick clays with only rare limestone interbeds. The central area has marls and dolomitic marls with more frequent interbeds of limestones predominating (Mituva Fm.); upwards they are replaced by nodular limestones containing black marl interbeds (Ventspils Fm.). The Neris Formation is composed of basal conglomerates, dolomites and dolomitic marls (the lower, Trakai Beds) and nodular limestones, dolomites and dolomitic marls (the upper, Sudervė Beds).

The Mituva Formation is dated by the *balticus* GZ, the *Rotundacodina dubia* CZ (embracing also the lower part of the Ventspils Formation) as shown in the Viduklė-61 and Kurtuvėnai-162 boreholes in this acanthodian study, and the

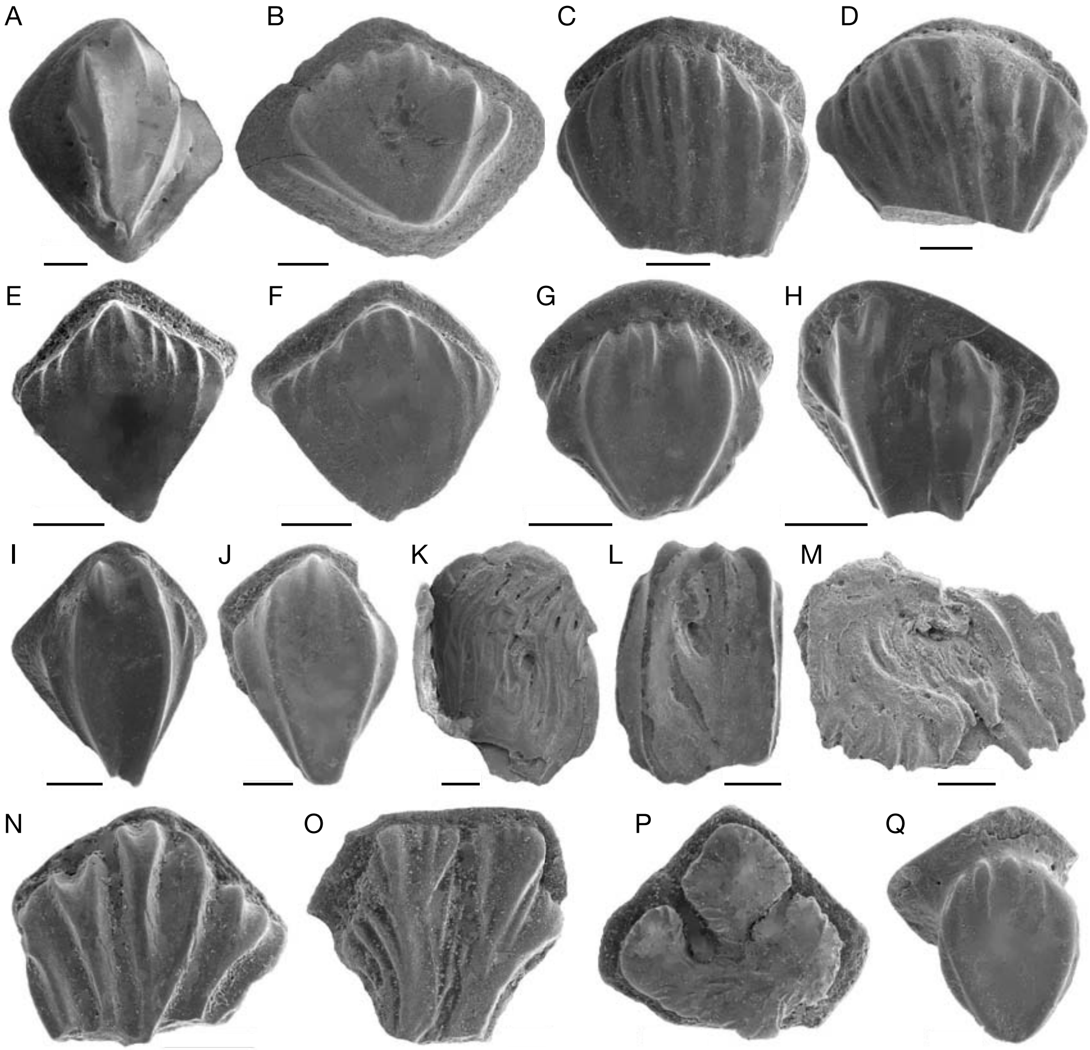

FIG. 2. — Silurian climatiiform acanthodians of Lithuania, flank scales, crown views, anterior upwards; **A**, **B**, *Nostolepis amplifica* Valiukevičius, 2003, Ledai-179 borehole, depth 535.0 m, Lapės Formation; **A**, LIGG-25-A-2397; **B**, LIGG-25-A-2400, holotype; **C**, **D**, *Nostolepis magnicostata* Valiukevičius, 2003, Nida-44, 1213.0 m, Jūra Fm.; **C**, LIGG-25-A-2537, holotype; **D**, LIGG-25-A-2538; **E**, **F**, *Nostolepis consueta* Valiukevičius, 2003, Ledai-179, 508.5 m, Lapės Fm.; **E**, LIGG-25-A-2427, holotype; **F**, LIGG-25-A-2428; **G**, **H**, *Nostolepis musca* Valiukevičius, 2003; **G**, morphotype 1, LIGG-25-A-2435, Nida-44, 1213.0 m, Jūra Fm.; **H**, morphotype 2, LIGG-25-A-2493, Ledai-179, 541.7 m, Lapės Fm.; **I**, **J**, *Nostolepis elegans* (Brotzen, 1934); **I**, LIGG-25-A-2426, Gėluva-99, 679.3 m, Jūra Fm.; **J**, LIGG-25-A-2442, Nida-44, 1213.0 m, Jūra Fm.; **K**-**M**, *Nostolepis linleyensis* Miller & Märss, 1999, Kurtuvėnai-162, 1063.4 m, Jūra Fm.; **K**, LIGG-25-A-2464; **L**, LIGG-25-A-2465; **M**, LIGG-25-A-2468; **N**, Nostolepidida indet., LIGG-25-A-2449, Ledai-179, 547.6 m, Vievis Fm.; **O**, **P**, *Nostolepis* sp. cf. *N. robusta* (Brotzen, 1934); **O**, LIGG-25-A-2462, Nida-44, 1221.0 m, Jūra Fm.; **P**, LIGG-25-A-2507, Nida-44, 1213.0 m, Jūra Fm.; **Q**, *Nostolepis alta* Märss, 1986, LIGG-25-A-2471, Kurtuvėnai-162, depth 1043.0 m, Jūra Fm. Scale bars: 0.2 mm.

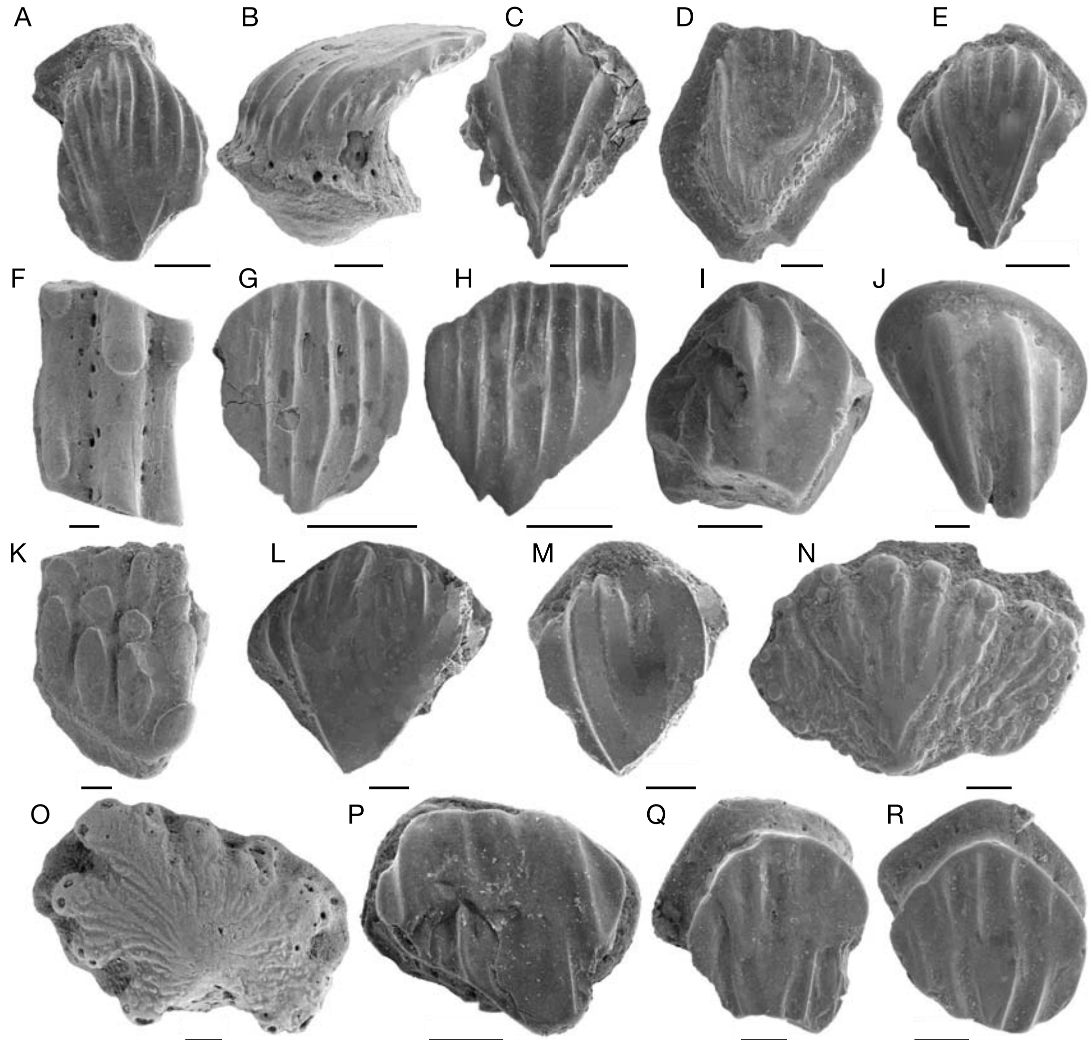

FIG. 3. — Silurian climatiiform acanthodians of Lithuania, flank scales and head *tesserae margaritatae* (**N**, **O**), crown views, anterior upwards and lateral view (**B**), and fin spine fragments (**F**, **K**), base downwards; **A**, **B**, *Nostolepis alta* Märss, 1986; **A**, LIGG-25-A-2504, Nida-44 borehole, depth 1213.0 m; **B**, LIGG-25-A-2497, Kurtuvėnai-162 borehole, depth 1063.4 m, Jūra Formation; **C**-**F**, *Nostolepis alifera* Valiukevičius, 2004; **C**, LIGG-25-A-2472, Kurtuvėnai-162, 1043.0 m, Jūra Fm.; **D**, LIGG-25-A-2475, Nida-44, 1273.8 m, Jūra Fm.; **E**, LIGG-25-A-2481, Stoniškiai-1, 1211.0-1217.0 m, Jūra Fm.; **F**, LIGG-25-A-2642, Stoniškiai-1, 1211.0-1217.0 m, Jūra Fm.; **G**, **H**, *Nostolepis gracilis* Gross, 1947; **G**, LIGG-25-A-2487, Kurtuvėnai-162, 1063.4 m, Jūra Fm.; **H**, LIGG-25-A-2523, Gėluva-99, 690.0 m, Vievis Fm.; **I**, **J**, *Nostolepis* sp. cf. *N. athleta* Valiukevičius, 1994; **I**, LIGG-25-A-2506, Nida-44, 1213.0 m, Jūra Fm.; **J**, LIGG-25-A-2529, Ledai-179, 537.4 m, Lapės Fm.; **K**, *Nostolepis elegans* (Brotzen, 1934), LIGG-25-A-2478, Nida-44, 1273.8 m, Jūra Fm.; **L**, **M**, *Nostolepis striata* Pander, 1856; **L**, LIGG-25-A-2554, Lūžni-4, 182.8 m, Targale Fm.; **M**, LIGG-25-A-2587, Lūžni-4, 260.0 m, Targale Fm.; **N**, **O**, *tesserae margaritatae* of *Nostolepis*; **N**, LIGG-25-A-2620, Lūžni-4, 197.2 m, Targale Fm.; **O**, LIGG-25-A-2635, Lūžni-4, 207.0 m, Targale Fm.; **P**-**R**, *Vesperalia perplexa* Valiukevičius, 2004, Nida-44, 1213.0 m, Jūra Fm.; **P**, LIGG-25-A-2419; **Q**, LIGG-25-A-2420; **R**, LIGG-25-A-2413, holotype. Scale bars: 0.2 mm.

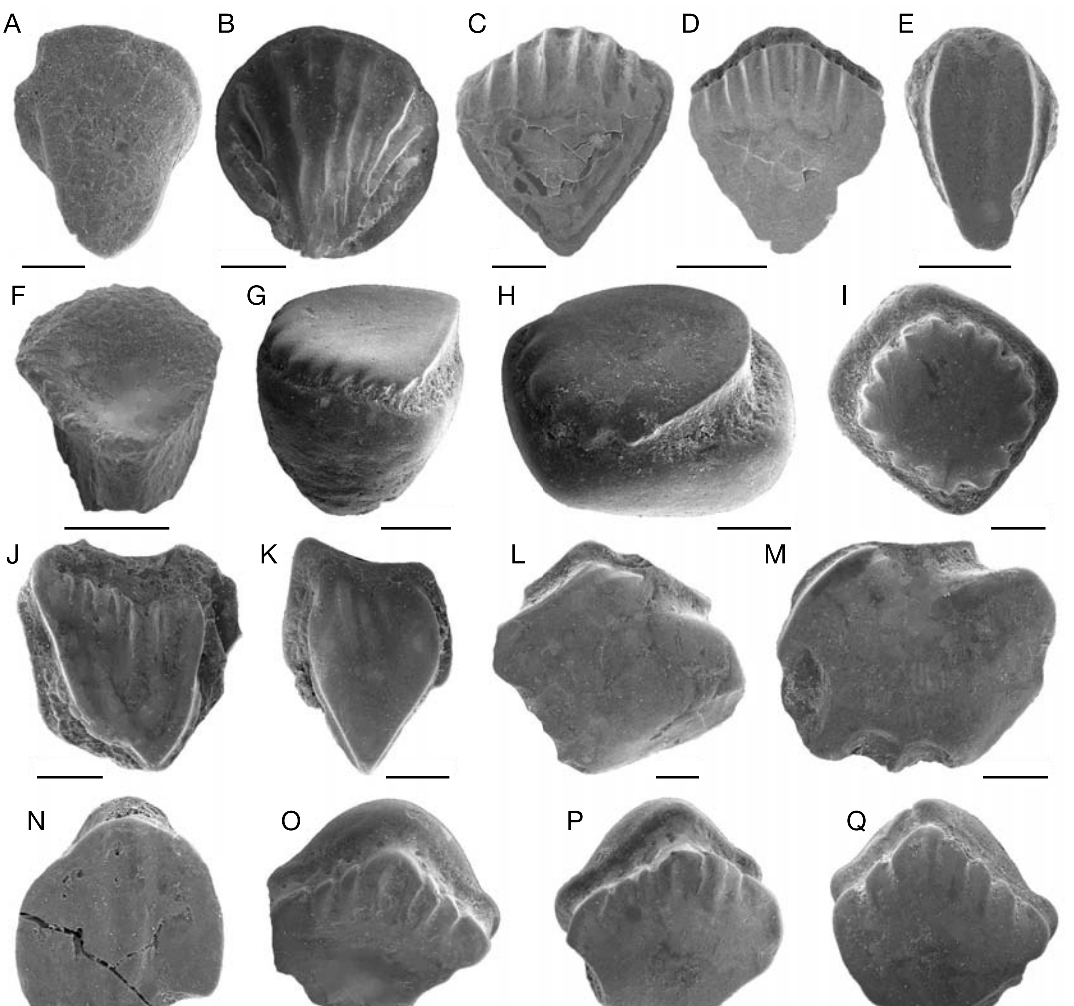

FIG. 4. — Silurian (**A**-**N**) and basal Lower Devonian (**O**-**Q**) climatiiform (**A**-**N**) and ischnacanthiform (**O**-**Q**) acanthodians of Lithuania. All flank scales, except for I, which is a head scale, crown views, anterior upwards, except for F, scale basal view, and G, H, antero-lateral scale view, anterior to left; **A**, **B**, *Monospina erecta* Valiukevičius, 2003, Nida-44 borehole, 1273.8 m, Jūra Fm.; **A**, LIGG 25-A-2474; **B**, LIGG 25-A-2477; **C**, **D**, *Cheiracanthoides planus* Valiukevičius, 1998, Kurtuvėnai-162, 1063.4 m, Jūra Fm.; **C**, LIGG 25-A-2488; **D**, LIGG 25-A-2489; **E**, **F**, *Nostolepis* sp. cf. *N. fragilis* Valiukevičius, 2003, Gėluva-99, 639.4 m, Lower Devonian, Tilžė Fm.; **E**, LIGG 25-A-2521; **F**, LIGG 25-A-2520; **G**-**I**, *Fecundosquama basiglobosa* Valiukevičius, 2004, Gėluva-99, 681.6 m, Vievis Fm.; **G**, LIGG 25-A-2405, holotype; **H**, LIGG 25-A-2406; **I**, LIGG 25-A-2409; **J**, **K**, cf. *Canadalepis linguiformis*, Nida-44, 1213.0 m, Jūra Fm.; **J**, LIGG 25-A-2510; **K**, LIGG 25-A-2511; **L**, **M**, "*Pruemolepis wellsi*" Vieth-Schreiner, 1983, Nida-44, 1213.0 m, Jūra Fm.; **L**, LIGG 25-A-2512; **M**, LIGG 25-A-2513; **N**, *Endemolepis inconstans* Valiukevičius, 1998, Nida-44, 1213.0 m, Jūra Fm., LIGG 25-A-2639; **O**-**Q**, *Bracteatacanthus assiduus* Valiukevičius, 2004, Nida-44, 1213.0 m, Jūra Fm.; **O**, LIGG 25-A-2450; **P**, LIGG 25-A-2452; **Q**, LIGG 25-A-2453, holotype. Scale bars: 0.2 mm.

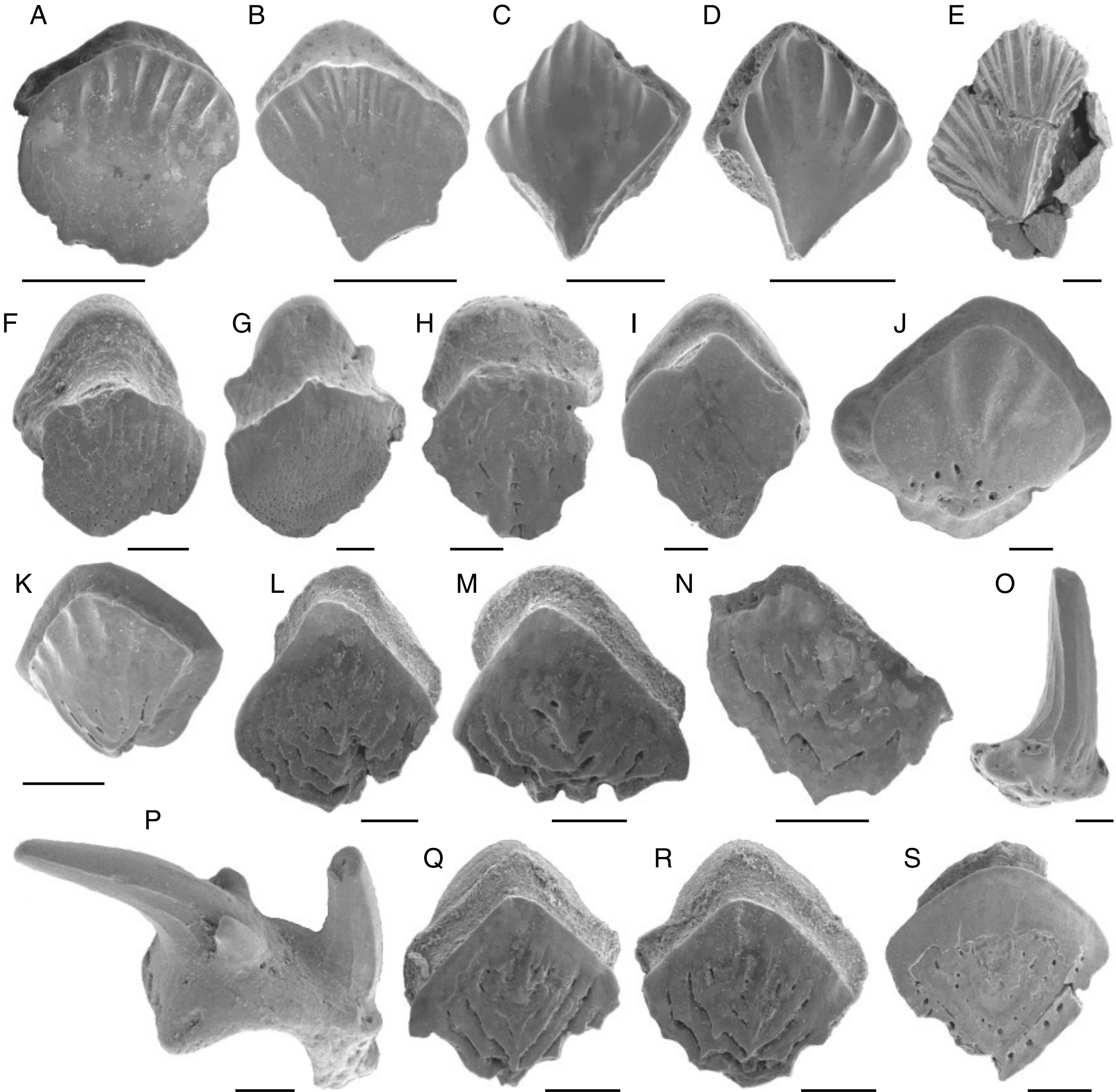

FIG. 5. — Silurian ischnacanthiform (**A**-**D** and **F**-**S**) and diplacanthiform (**E**) acanthodians, flank scales, crown views, anterior upwards, except for O, P, single teeth (**O**) and tooth whorl (**P**) in lateral view; **A**, **B**, *Arenaceacanthus arcuatacanalis* Valiukevičius, 2004, Ledai-179 borehole, depth 547.6 m, Vievis Fm.; **A**, LIGG 25-A-2443, holotype; **B**, LIGG 25-A-2447; **C**, **D**, *Rohonilepis breviornatus* Valiukevičius, 2004, Gėluva-99, 659.7 m, Jūra Fm.; **C**, LIGG 25-A-2458; **D**, LIGG 25-A-2459, holotype; **E**, *Diplacanthus* sp., LIGG 25-A-2463, Nida-44, 1221.0 m, Jūra Fm.; **F**, **G**, *Poracanthodes punctatus* Brotzen, 1934; **F**, LIGG 25-A-2448, Ledai-179, 547.6 m, Vievis Fm.; **G**, LIGG 25-A-2496, Kurtuvėnai-162, 1063.4 m, Jūra Fm.; **H**, **I**, *Poracanthodes subporosus* Valiukevičius, 1998, Nida-44, 1213.0 m, Jūra Fm.; **H**, LIGG 25-A-2498; **I**, LIGG 25-A-2500; **J**, *Poracanthodes* sp. cf. *P. stonehousensis* (*sensu* Vergoossen 2000), LIGG 25-A-2535, Ledai-179, 537.4 m, Lapės Fm.; **K**, *Poracanthodes porosus*?, LIGG 25-A-2404, Ledai-179, 535.0 m, Lapės Fm.; **L**-**N**, *Poracanthodes porosus* Brotzen, 1934; **L**, LIGG 25-A-2546, Gėluva-99, 667.7 m, Jūra Fm.; **M**, LIGG 25-A-2547, Gėluva-99, 667.7 m, Jūra Fm.; **N**, LIGG 25-A-2548, Šešuvis-11, 1006.0 m, Jūra Fm.; **O**, **P**, *Gomphonchus sandelensis* Gross, 1971, Kurtuvėnai-162, 1007.0 m, Jūra Fm.; **O**, LIGG 25-A-2528; **P**, LIGG 25-A-2527; **Q**, **R**, *Poracanthodes menneri* Valiukevičius, 1992, Nida-44, 1213.0 m, Jūra Fm.; **Q**, LIGG 25-A-2544; **R**, LIGG 25-A-2545; **S**, cf. *Gomphonchoporus*, specimen LIGG 25-A-2491, Kurtuvėnai-162, 1063.4 m, Jūra Fm. Scale bars: 0.2 mm.

Phlebolepis elegans TZ. The Ventspils Formation is tentatively correlated with the *formosus* GZ (Paškevičius 1994) and the *Thelodus sculptilis* TZ (Paškevičius *et al.* 1994). Deposits in the overlying *Ozarkodina crispa* CZ are distributed through almost the entire territory of Lithuania, and include the upper part of the Ventspils and the lowermost Minija formations, and the Sudervė Beds of the Neris Formation (Karatajūtė-Talimaa *et al.* 1987). This conodont zone is characteristic of the uppermost Ludlow.

The Pridoli is represented by the bi-folded Minija and tri-folded Jūra formations in west and central Lithuania, corresponding to the Vievis and Lapės formations respectively or an undivided Pabradė Formation in the easternmost area. The Minija Formation is composed of marls containing interbeds of nodular, rarely biomorphic limestones (the lower, Šilalė Beds), and clays and highly clayey marls (the upper, Varniai Beds). The lower part of the Šilalė Beds is dated by the *parultima-ultima* GZ and the *margaritae-alia* OZ which extends for the complete volume of the beds (Sidaravičienė 1997), whereas the Varniai Beds are tentatively assigned to the *lochkovensis* GZ and the *tuberculata* OZ. Conodonts of the *Ozarkodina steinhornensis eosteinhornensis* CZ (embracing also the principal part of the overlying Girdžiai Beds and the lower part of the Lapės Formation) and the *Goniporus alatus* TZ cover the Minija Formation time span, and consequently also the Vievis Formation of central and east Lithuania, where it is composed of nodular limestones with marl interbeds. The dominant dolomites of the Pabradė Formation (Svėdasai-252, Butkūnai-241, Jočionys-299, etc., cores) have yielded the same faunal associations.

The Jūra Formation is represented by carbonate clays, marls and limestones in thin interbeds; the relative percentages of the different rocks form the basis for subdivision of the formation into the Girdžiai, Kelmė and Rietavas Beds (lowermost to uppermost). However, this subdivision only applies in the western area. Eastwards, the rocks are undifferentiated. The Rietavas Beds are represented by a member several meters thick of red-colored carbonate clays in extreme southwestern Lithuania. The Girdžiai Beds are dated by the *pustulosa* OZ and the Kelmė Beds by the *leptosoma* OZ, whereas the Kelmė and Rietavas Beds and the uppermost Girdžiai Beds are dated by the *Paralogania kummerowi* and *Katoporodus lithuanicus* TZ and the *Ozarkodina steinhornensis remscheidensis* CZ. The transitional facies belt has yielded different ostracode associations, named according to the dominant representatives of *Amygdalella*: *A. comma* and *A. geluvensis* in the Girdžiai Beds, and *A. ariogalensis* in the Rietavas Beds (Sidaravičienė 1997). The Lapės Formation is composed of limestones that sometimes are of nodular texture, containing marl interbeds and topped by reddish clayey dolomites and dolomitic marls showing characteristic undulate surfaces of sedimentation gaps. The lower part of Lapės Formation is in the *O. steinhornensis eosteinhornensis*, and the remainder in the *O. steinhornensis remscheidensis* CZ (Paškevičius & Brazauskas 1987; Karatajūtė-Talimaa *et al.* 1987).

ACANTHODIAN ZONALITY

The biozonal scheme of Silurian acanthodians is based on the stratigraphic ranges of 45 taxa, of which most are scale-based taxa, with a few based on fin spines or teeth. The term "taxon" is also sometimes used here for different skeletal elements of an animal presumed to be from the particular genus, when the correct and substantiated attribution to distinct species is not possible, e.g., *Gomphonchus* teeth, tooth whorls or fin spines, *Nostolepis* fin spines and head *tesserae margaritatae*. "*Pruemolepis wellsi*" Vieth-Schreiner, 1983 is treated as a separate taxon even though it is considered by many fish workers of different regions (and myself) as a morphovariety of specialized scales of all nostolepids.

Acanthodian zonality is conditional on the first occurrence horizons of nominated species and is mainly based on climatiiform taxa. Most zones are Interval range zones, occupying a part of the range of the index-species, until the next index in the stratigraphical sequence occurs. This approach is directly related to the low number of characteristic species per zone.

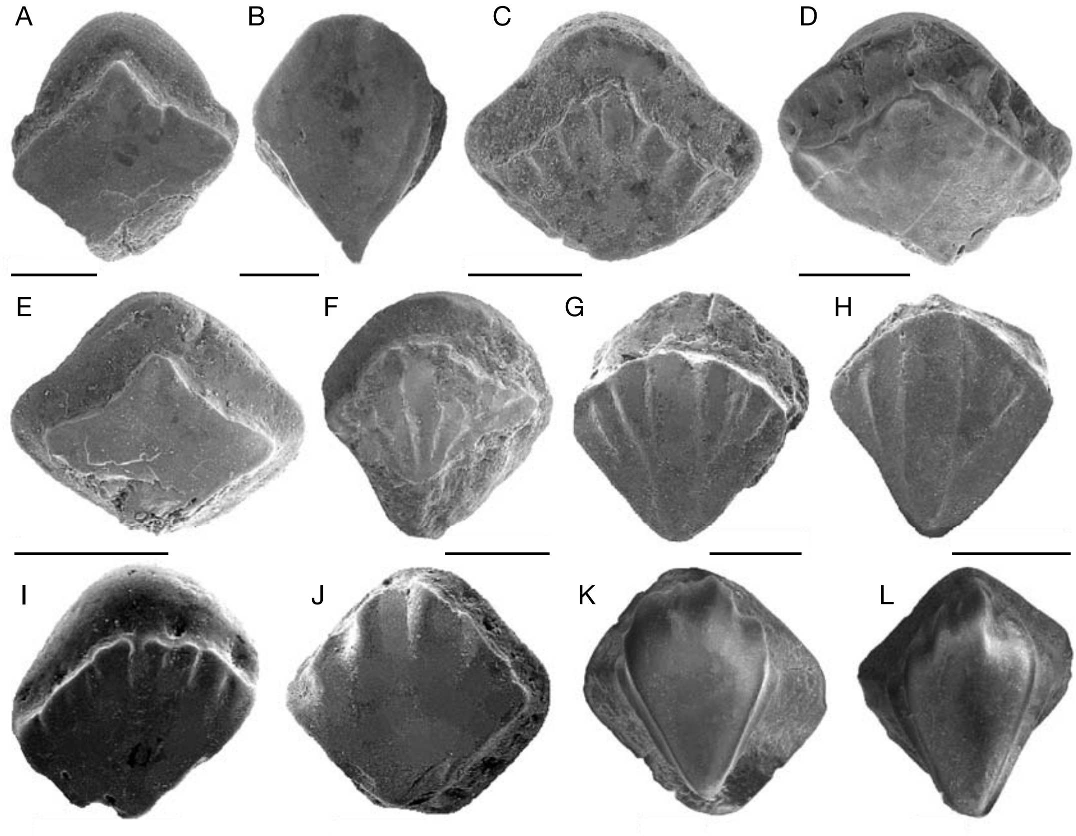

FIG. 6. — Silurian ischnacanthiform (**A**-**J**) and climatiiform (**K**, **L**) acanthodians of Lithuania, flank scales, crown views, anterior upwards; **A**, **B**, *Gomphonchus sandelensis* Gross, 1971, Nida-44, 1213.0 m, Jūra Fm.; **A**, LIGG 25-A-2502; **B**, LIGG 25-A-2501; **C**, **D**, *Gomphonchus* sp. cf. *G. hoppei*; **C**, LIGG 25-A-2479, Gėluva-99, 656.9 m, Jūra Fm.; **D**, LIGG 25-A-2495, Ledai-179, 535.0 m, Lapės Fm.; **E**, **F**, *Gomphonchus hoppei* (Gross, 1947), Nida-44, 1213.0 m, Jūra Fm.; **E**, LIGG 25-A-2644; **F**, LIGG 25-A-2643; **G**, **H**, *Gomphonchus mediocostatus* Vergoossen, 1999, Gėluva-99, 650.0 m, Jūra Fm.; **G**, LIGG 25-A-2646; **H**, LIGG 25-A-2648; **I**, **J**, *Gomphonchus*? *minutus* Valiukevičius, 2004, Lūžni-4, 307.5 m, Minija Fm.; **I**, LIGG 25-A-2584; **J**, LIGG 25-A-2581, holotype; **K**, **L**, *Nostolepis amplifica* or *N. elegans*, a transitional scale variety; **K**, LIGG 25-A-2482, Kurtuvėnai-162, 1060.8 m, Jūra Fm.; **L**, LIGG 25-A-2483, Nida-44, 1213.0 m, Jūra Fm. Scale bars: 0.2 mm.

Differences in taxonomical diversity and asynchrony in the first occurrence horizons of faunas in the west and east areas of Lithuania, probably related to their facies dependence, led to compilation of two acanthodian zonal schemes.

WEST LITHUANIA

Seven borehole cores provided the basic information for study of the acanthodians in west Lithuania (Fig. 1B). About 200 samples from these cores, plus some others previously studied from Silurian/Devonian boundary beds (Valiukevičius 1998), yielded acanthodian microremains from 42 taxa (Fig. 7). Unfortunately, they are all from the Upper Silurian only; no acanthodians are known yet from the Lower Silurian in this area.

The Ludlow acanthodian faunas are rare and impoverished, and are only known from two boreholes, Kurtuvėnai-162 and Viduklė-61 (Appendix 1). The Dubysa Formation, correlated with the Gorstian (Karatajūtė-Talimaa & Brazauskas 1994) or extending also to the lowermost Ludfordian and embracing the *nilssoni* to *tauragensis* GZ (Paškevičius *et al.* 1994), has yielded scarce tiny scales of an indeterminate nostolepid. The Mituva Formation spans the rest of the Ludfordian, corresponding to the lower part of the Pagėgiai Regional Stage, and is in the ***Gomphonchus*? *minutus* AZ**, dated by the *Rotundacodina dubia* CZ, *balticus* GZ (Paškevičius *et al.* 1994) and *Paralogania martinssoni-Phlebolepis elegans* TZ (Talimaa 2000). As well as the index fossil *Gomphonchus*? *minutus* Valiukevičius, 2004, this oldest acanthodian association is characterized by *Arenaceacanthus arcuatacanalis* Valiukevičius, 2004, and by the disappearance of the above-mentioned indeterminate nostolepid and incoming of *Gomphonchus sandelensis* Gross, 1971, a member of all the later Upper Silurian (Fig. 7) and Lower Devonian associations.

The uppermost part of the Mituva Formation in the Kurtuvėnai-162 borehole is the first occurrence horizon of *Rohonilepis breviornatus* Valiukevičius, 2004, the single index species defining the next zone. *Gomphonchus sandelensis* continues through this ***Rohonilepis breviornatus* AZ**. The documented acme of *R. breviornatus* occurs here in the lower part of the overlying Ventspils Formation (Appendix 1), dated by the *Ozarkodina crispa* CZ (Brazauskas pers. comm.) which is a correlative to the *valleculosus-formosus* GZ and *Thelodus sculptilis* TZ (Talimaa 2000).

Acanthodians flourished during the Pridoli in west Lithuania. They are represented here by the richest assemblages as compared to the rest of the country. Two faunal renewal horizons are recognized in the Minija Formation. The first is thought to correspond with the lower boundary of the Minija Formation and is based on occurrences in the Liepkalnis-137 borehole (Appendix 2). Unfortunately, the lithology and biostratigraphy of this borehole core have not been completely studied yet, but the thelodont and heterostracan (vertebrate) associations (the *Goniporus alatus* TZ) allow recognition of the lower Jūra Formation at a depth of 884.4 m (Karatajūtė-Talimaa & Brazauskas 1994). This fact, and also the occurrence of *Fecundosquama basiglobosa* Valiukevičius, 2004, the next index acanthodian (of the upper Minija Formation) high in the sampled sequence (892.1-893.9 m), indicate that the lower part of the Minija Formation occurs deeper in the profile. The ***Nostolepis gracilis* AZ** is defined here by the index fossil *N. gracilis* and the entry into the sequence of *Poracanthodes punctatus*, *Nostolepis musca* morphotypes 1 and 2, and *N. amplifica* (Valiukevičius 2003a). *Rohonilepis breviornatus* and *Gomphonchus sandelensis* continue from the earlier association. The zone is correlated with the *Ozarkodina steinhornensis eosteinhornensis* CZ, *Frostiella groenvalliana-Nodibeyrichia incerta* OZ and the *parultima-ultima* GZ (Paškevičius *et al.* 1994).

The second influx of a new acanthodian fauna characterizes the ***Fecundosquama basiglobosa* AZ** found in the upper Minija Formation and well illustrated in the Kurtuvėnai-162 and Stoniškiai-1 (Appendix 3) boreholes. In the latter, which is the stratotype for all the stratigraphic units of the Pridoli, the zone corresponds to the upper part of the Varniai Beds and is based on the uninterrupted and statistically dominant findings of the nominative species through the entire series of samples. The first occurrence of the association of *Fecundosquama basiglobosa* Valiukevičius, 2004, *Monospina erecta* Valiukevičius, 2003, *Nostolepis amplifica* and *Gomphonchus* sp. cf. *G. hoppei* is at 1072.4 m in the Kurtuvėnai-162 borehole. Notably, *Gomphonchus* fin spines, teeth and tooth whorls are often found in this zone and in most samples of the later Pridoli. The total number of taxa in this zone increases to 14, in comparison with seven in the previous *Nostolepis gracilis* AZ. The zone is correlated with the *Nodibeyrichia tuberculata* OZ and the *lochkovensis* GZ.

The next four acanthodian zonal associations from the Jūra Formation (latest Pridoli) are distinguished by the dominance of representatives of the genus *Nostolepis*.

The ***Nostolepis alta* AZ** is seen in the Girdžiai Beds of the Jūra Formation. The association comprises 30 taxa, of which 15 belong to the genus *Nostolepis*. *N. alta*, *N. striata* Pander, 1856, *N. elegans* (Brotzen, 1934), *N.* sp. cf. *N. athleta* Valiukevičius, 1994, *N. alifera* Valiukevičius, 2004, *N. amplifica* or *N. elegans* (transitional variety of scales), *N. linleyensis* Miller & Märss,

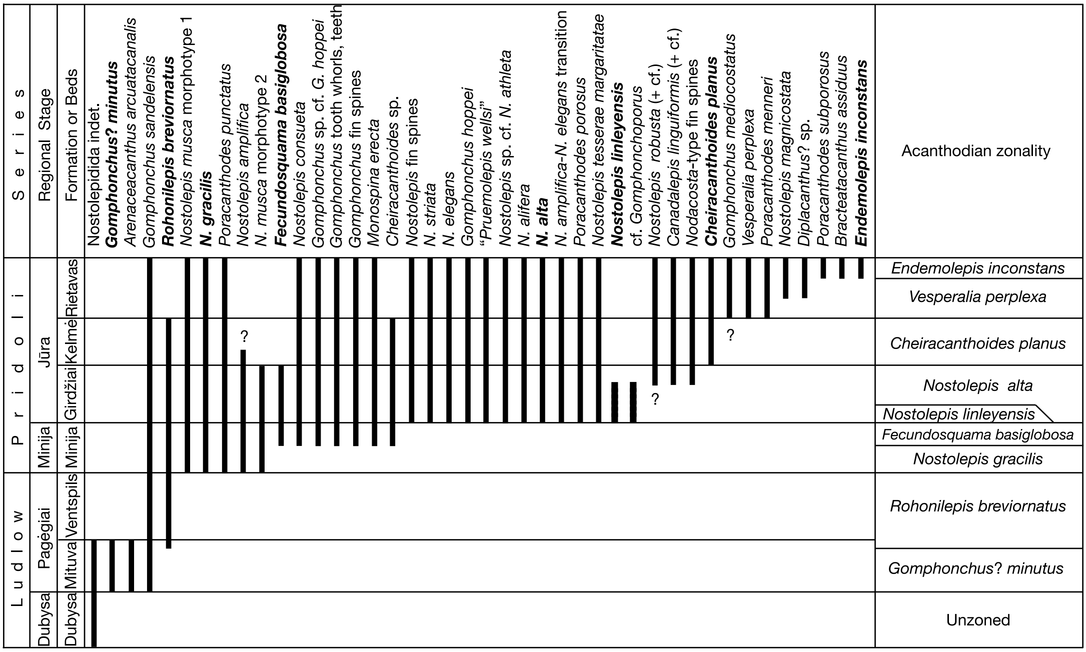

FIG. 7. — Stratigraphic ranges and zones of Silurian acanthodians in the western area of Lithuania. Zonal species in bold.

1999, and "*Pruemolepis wellsi*" occur here for the first time. As well as these, *Gomphonchus hoppei* Gross, 1947 and *Poracanthodus porosus* enter the sequence; they are the most widely distributed taxa regionally. Two representatives, *Fecundosquama basiglobosa* and *N. musca* morphotype 2, disappear at the upper zonal boundary. Of special interest are findings of *Nostolepis linleyensis* and cf. *Gomphonchoporus* sp. (Vergoossen 1999) which have short-time ranges in the basal part of this zone, and are possible correlatives for the dating of rocks in the Baltic, Great Britain and the Netherlands. The acanthodian association of the upper part of the zone is enriched by the incoming *Nostolepis robusta* (Brotzen, 1934), *Canadalepis linguiformis* Vieth, 1980 (or varieties resembling *C. linguiformis*) and *Nodacosta*-type fin spines (Gross 1940) (Fig. 7). The zone is coeval with the *Nodibeyrichia pustulosa* OZ (Paškevičius 1994) and the uppermost *Ozarkodina steinhornensis eosteinhornensis*-lowermost *O. steinhornensis remscheidensis* CZ interval.

Only two taxa of a total 27 forming the next association define the ***Cheiracanthoides planus* AZ**. These are the incoming *Cheiracanthoides planus* Valiukevičius, 1998 and the disappearing *Rohonilepis breviornatus*. The zone is exemplified in the Kelmė Beds of the Jūra Formation and is characterized by the dominance of transitional species (23 of 27, Fig. 7). Most of the earlier mentioned *Nostolepis* spp., including those which occurred at the start of the Pridoli, e.g., *Nostolepis gracilis* and *N. musca*, as well as subsequent entries *N. consueta*, *N. alta*, *Poracanthodes punctatus*, *P. porosus*, *Monospina erecta*, etc., survived and ranged through to the topmost Pridoli. The zone correlates with the *Ozarkodina steinhornensis remscheidensis* CZ which extends until the end of the Pridoli, the *Paraloganía kummerowi* TZ (Karatajūtė-Talimaa & Brazauskas 1994) and the *Kloedenia leptosoma* or *Amygdalella ariogalensis* associations of ostracodes.

The ***Vesperalia perplexa* AZ** is distinguished by the incoming *V. perplexa* Valiukevičius, 2004, *Nostolepis magnicostata* Valiukevičius, 2003, *Gomphonchus mediocostatus* Vergoossen, 1999, *Poracanthodes menneri* Valiukevičius, 1992 and *Diplacanthus*? sp. The numbers of predominant *Nostolepis* (13) and transitional taxa (24) remain stable as compared to the previous zone. The zone is defined in the lower part of the Rietavas Beds of the Jūra Formation, in the extreme west of Lithuania only, and is well illustrated in the Šešuvis-11 (Appendix 4) and Nida-44 (Appendix 5) boreholes.

The nominative species of the latest Pridoli ***Endemolepis inconstans* AZ** survived across the Silurian/Devonian boundary and ranges into the Lochkovian (Valiukevičius 1998). The zone is also based on the occurrence of *Poracanthodes subporosus* Valiukevičius, 1998 and *Bracteatacanthus assiduus* Valiukevičius, 2004 in the upper part of the Rietavas Beds of the Jūra Formation. The total number of taxa reaches a maximum (32) here, and transitional species (21) are still dominant. Of all Silurian species listed in the generalized Figure 7, only *Monospina erecta*, *Vesperalia perplexa*, *Nostolepis alifera*, *N. magnicostata*, *tesserae margaritatae* of *Nostolepis* sp., *Nodacosta*-type spines and *Bracteatacanthus assiduus* do not cross the Silurian/Devonian boundary. The zone is coeval with the *Katoporodus lithuanicus* TZ (Karatajūtė-Talimaa & Brazauskas 1994; Talimaa 2000) and the upper parts of the *Nodibeyrichia jurassica-Kloedenia leptosoma* or *Amygdalella ariogalensis* OZ.

East Lithuania

Acanthodians studied from 10 borehole cores yielded identifiable specimens in about 120 samples. The most ancient acanthodians are of Wenlockian Sheinwood age as dated by conodonts. The Birštonas and Verknė formations, facies correlatives assigned to the Jaani Regional Stage, yielded the two species which characterize the ***Arenaceacanthus arcuatacanalis-Gomphonchus*? *minutus* AZ**, accompanied by *G. sandelensis*, *Gomphonchus* sp. and *Nostolepis consueta* (Fig. 8). The rocks are dated in the Butkūnai-241 section (Appendix 6) by the *Kockelella ranuliformis* CZ (Karatajūtė-Talimaa *et al.* 1987). This acanthodian zone appears to span the entire Wenlock. No other acanthodian species occurs in the Dukstyna and Nevėžis formations of the Homerian Stage, the *Kockelella amsdeni* and *Oulodus siluricus* CZ (Paškevičius & Brazauskas 1987; Karatajūtė-Talimaa *et al.* 1987). The dating of rocks is doubtful in some cases as redeposited Ludlowian specimens occur together with the distinct conodonts of the *K. amsdeni* association. Acanthodians have slightly magnified these doubts about the later dating, firstly because of the distinct differences in the occurrence horizons of both index fossils when comparing west and east Lithuania, and secondly, because Lithuanian Wenlock acanthodians seem too advanced in their development (morphological elements of scale crowns are more relief, clearly expressed, what is characteristic of the phylogenetically later taxa) as compared to those best known in Estonia (pers. obs. and T. Märss pers. comm. 2003).

The basal Ludlow (Gorstian) Dubysa Formation and its correlatives remain unzoned by acanthodians. A single sample of the Gėluva-99 borehole (Appendix 7) yielded *Arenaceacanthus arcuatacanalis* and *Gomphonchus*? *minutus*.

The lowest Ludfordian (Trakai Beds of the Neris Formation) is also acanthodian-poor. The ***Nostolepis musca* AZ** is proposed here on the entry of the first morphotype of the nominative species and the last occurrences of *Gomphonchus*? *minutus*. *Arenaceacanthus arcuatacanalis*, *Gomphonchus sandelensis*, *Gomphonchus* sp. and *Nostolepis consueta*, the transitional members, compose the principal part of the association.

The ***Nostolepis gracilis* AZ** begins earlier than in the west, in the Sudervė Beds of the Neris Formation and is characterized by a more diverse acanthodian association. As well as the index fossil, *Cheiracanthoides* sp., *Acanthoides*? sp., *Nostolepis amplifica* and *Gomphonchus* sp. cf. *G. hoppei* occur for the first time. The reference section is Jočionys-299 borehole, depth 115.8 m. (Appendix 6), where the age of the zone is controlled by the *Thelodus sculptilis* TZ and *Ozarkodina crispa* CZ (Karatajūtė-Talimaa *et al.* 1987).

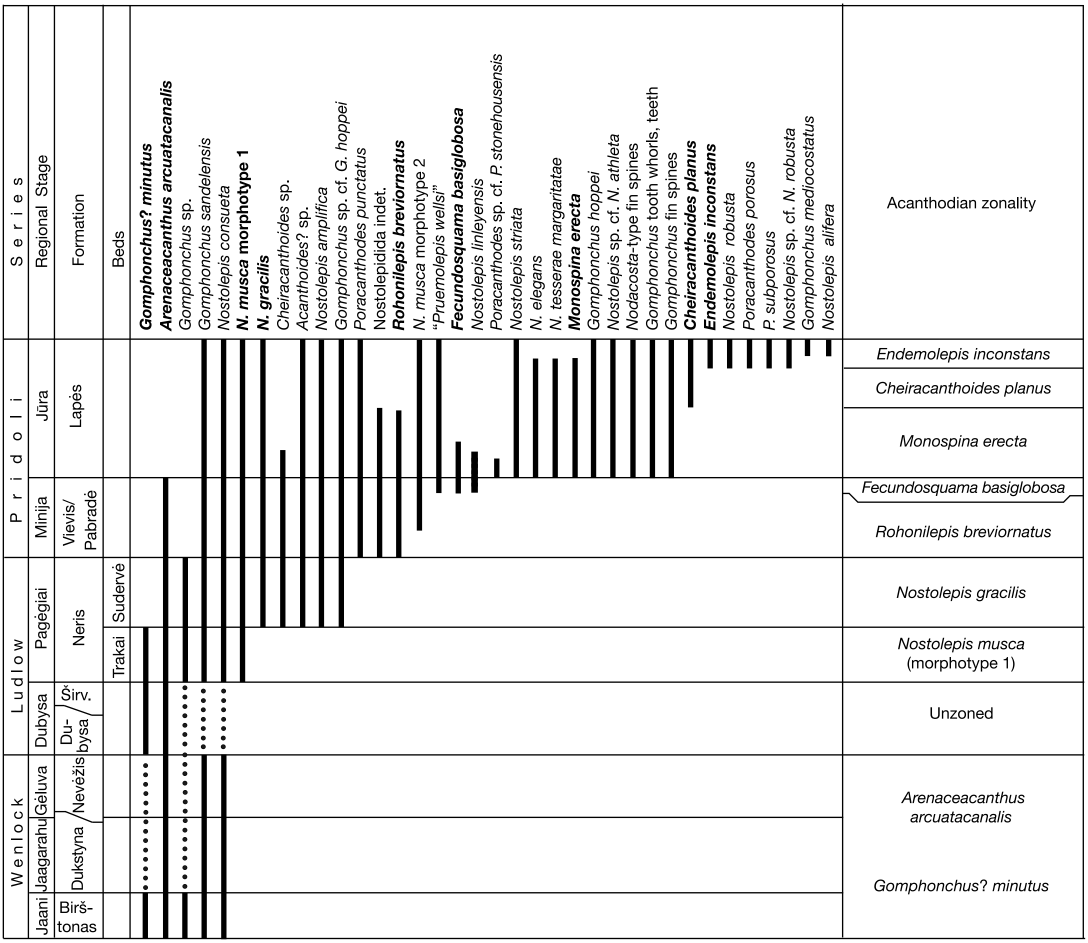

FIG. 8. — Stratigraphic ranges and zones of Silurian acanthodians in the eastern area of Lithuania. Taxa are not established yet in the dotted parts of stratigraphic range. Zonal species in bold.

Further diversification of acanthodian associations and distinct dominance of nostolepids characterize the Pridoli. The Vievis Formation and its facies correlative, the Pabradė Formation (perhaps extending higher, equivalent to the lower part of the Jūra if compared to the west) are ascribed to the next two acanthodian zones. The ***Rohonilepis breviornatus*** **AZ** spans the principal thickness of both formations. It is based on the entry of the index fossil and also on *Poracanthodes punctatus* and *Nostolepis musca* morphotype 2. *Arenaceacanthus arcuatacanalis* as well as the other taxa of the previous two zones continue, and thus the total number of taxa is increased to 13, of which six belong to *Nostolepis*. Sutkai-87 and Ledai-179 borehole cores are the reference sections (Appendices 8; 9). The zone correlates with the partial (lower) range of the *Ozarkodina steinhornensis eosteinhornensis* CZ defined widely in most localities.

Fecundosquama basiglobosa and *Nostolepis linleyensis* are the two most important taxa defining the ***Fecundosquama basiglobosa*** **AZ** in the uppermost Vievis Formation. Notably, *Arenaceacanthus arcuatacanalis* occurs for the last time. Transitional taxa (12 of 16) prevail.

The next three zones are seen in the Lapės Formation, the topmost unit of the Pridoli, and are characterized by an increased number of taxa. The ***Monospina erecta*** **AZ** correlates with the lower part of the Formation. Its association is distinguished by a majority of incoming taxa (nine) comprising *Monospina erecta*, *Nostolepis striata*, *N. elegans*, *Nostolepis* sp. cf. *N. athleta*, *tesserae margaritatae* of *Nostolepis* sp., *Gomphonchus hoppei*, *Gomphonchus* fin spines, teeth and tooth whorls, and *Nodacosta*-type fin spines. *Poracanthodes* sp. cf. *P. stonehousensis* (*sensu* Vergoossen 2000) possibly has a short range in the basal part of the zone. Four taxa have their last occurrences here (Fig. 8), of which *Fecundosquama basiglobosa* and *Rohonilepis breviornatus* are the most important. *Gomphonchus sandelensis*, *Gomphonchus* sp. cf. *G. hoppei*, *Nostolepis consueta*, *N. musca*, *N. gracilis*, *N. amplifica* and *Poracanthodes punctatus* continue through the zone as stable transitional members. The zone is correlated with the upper part of the *Ozarkodina steinhornensis eosteinhornensis* CZ and the *Nodibeyrichia pustulosa* OZ (Sidaravičienė 1986).

The ***Cheiracanthoides planus*** and overlying ***Endemolepis inconstans*** **AZ** are recognized in the upper part of the Lapės Formation. The first is based on the entry of the nominative species and the disappearing *Nostolepis elegans*, *Monospina erecta* and *tesserae margaritatae* of *Nostolepis* sp. The zonal acanthodian association is characterized by a preponderance of transitional taxa (15 of 19).

The latest Pridolian ***Endemolepis inconstans*** **AZ** is composed of 26 taxa, the maximum number, with transitional taxa (15) prevailing. *Endemolepis inconstans*, *Nostolepis robusta*, *Nostolepis* sp. cf. *N. robusta*, *N. alifera*, *Poracanthodes porosus*, *P. subporosus* and *Gomphonchus mediocostatus* enter the sequence. Of them, only *N. alifera* does not cross the Devonian boundary. All others range into the Devonian. Only three of the old transitional taxa, *Nostolepis amplifica*, *N. musca* (morphotype 2) and the *Nodacosta*-type fin spines disappear at the Silurian/Devonian boundary.

The last two zones are tentatively correlated with the *Ozarkodina* aff. *steinhornensis remscheidensis* CZ (Karatajūtė-Talimaa *et al.* 1987) and *Nodibeyrichia jurassica* OZ (Paškevičius 1994).

COMPARISON OF ACANTHODIAN ASSOCIATIONS OF WEST AND EAST LITHUANIA

Differences in the stratigraphical distribution of Silurian acanthodians of western and eastern Lithuania, shown by the first occurrence horizons and stratigraphical ranges of taxa, might be caused by insufficient data, as only a few localities provide applicable information. Also, the living conditions of taxa could have influenced the development of different taxa and associations. The latter cause is reflected by the different facies and might also depend on the evolutionary and/or migrational patterns of fauna.

The Wenlock-Ludlow Series shows differences in the occurrence horizons of all zonal species. *Arenaceacanthus arcuatacanalis* and *Gomphonchus*? *minutus* enter the section earlier in the east, in the Sheinwoodian (early Wenlock) Birštonas and Verknė formations, whereas in the west they occur in the Ludfordian (late Ludlow) Mituva Formation (Figs 9; 10). In contrast, *Rohonilepis breviornatus* appears earlier in the west (Ventspils Formation, late Ludfordian), whereas in the east it is first found in the basal Pridoli. The acanthodian association in the latter case is much more diverse when compared to the western association (13 taxa against two), and even if compared to the tentatively coeval basal Pridolian *Nostolepis gracilis* association of west Lithuania (13 taxa against seven, Fig. 11). The latter lacks the earlier *Arenaceacanthus arcuatacanalis*, and also the later appearing *Nostolepis consueta*, *Chiracanthoides* sp., *Acanthoides*? sp., *Gomphonchus* sp. cf. *G. hoppei*.

The *Fecundosquama basiglobosa* associations of both areas (the upper part of the Minija Regional Stage) are similar. *Arenaceacanthus arcuatacanalis* and *Nostolepis linleyensis* are additional representatives in the east, but *Monospina erecta* is lacking.

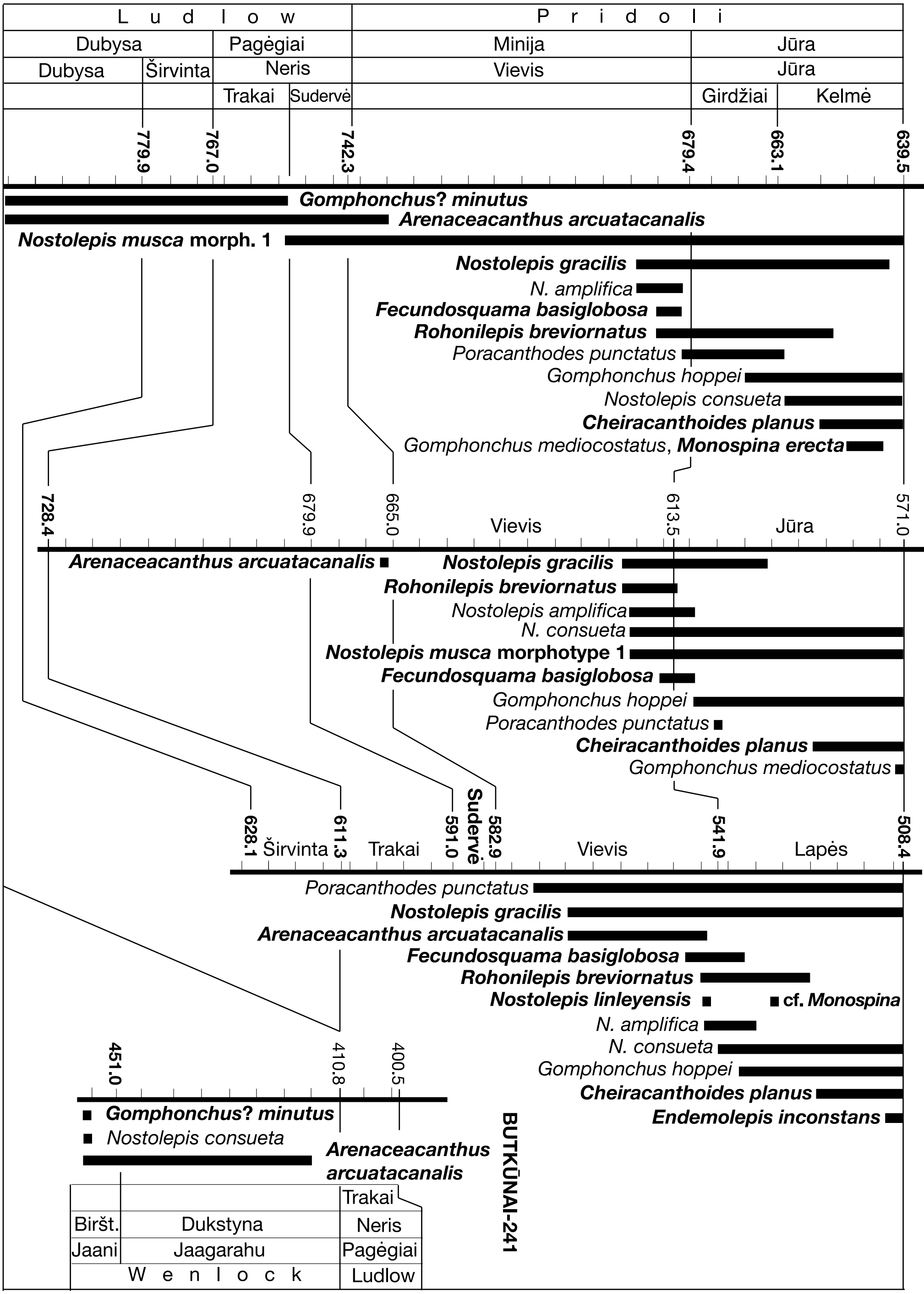

FIG. 9. — Distribution of the most valuable acanthodian taxa superimposed on the local stratigraphical units in the selected boreholes of east Lithuania. Zonal species in bold.

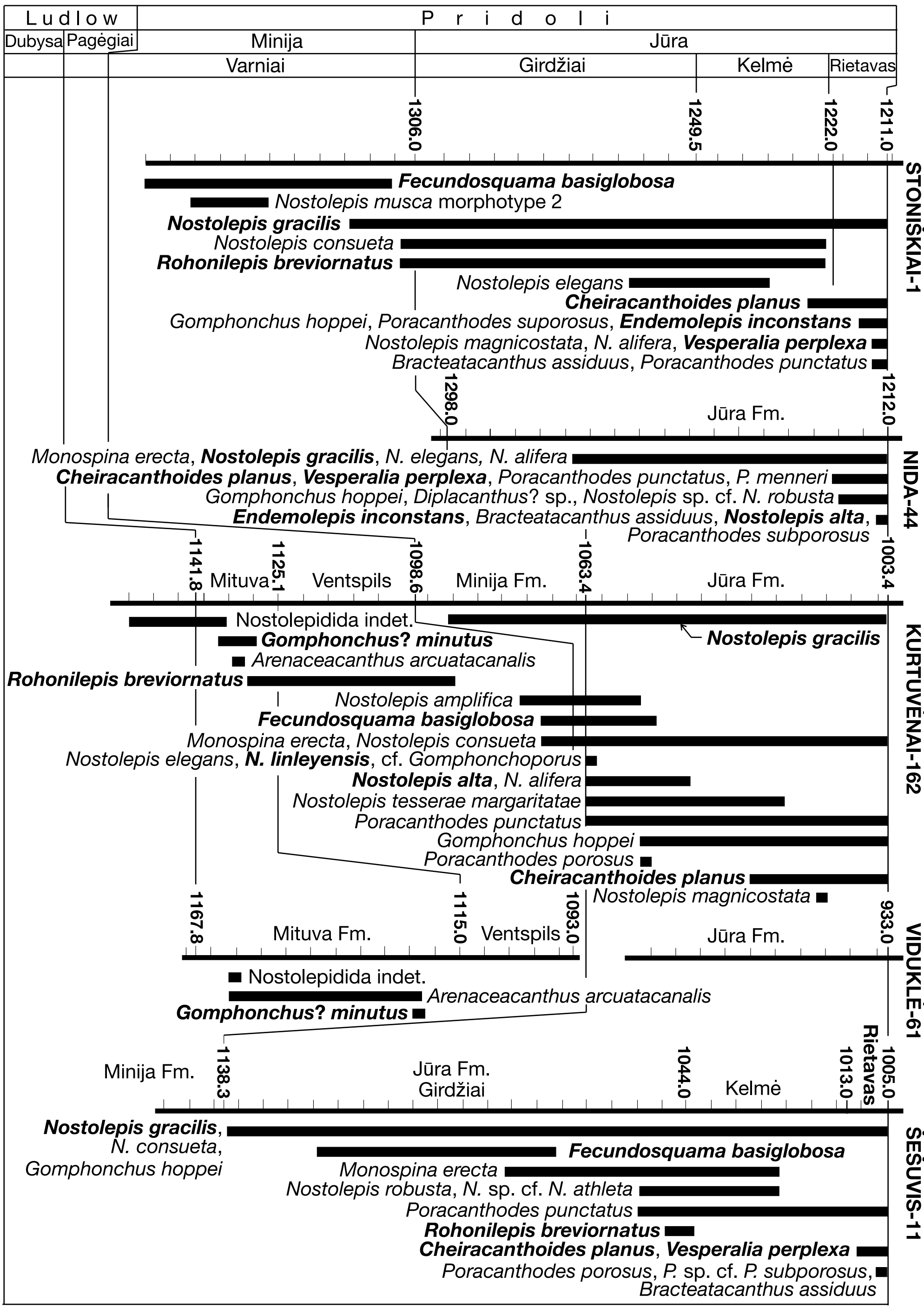

FIG. 10. — Distribution of the most valuable acanthodian taxa superimposed on the local stratigraphical units in the selected boreholes of west Lithuania. Zonal species in bold.

West Lithuania. Deep shelf facies

Series	Stage	Regional Stage	Formation or Beds	Acanthodian zonality	Species: Characteristic	Species: Appearing	Species: Disappearing	Species: Transitional	Species: Total	*Nostolepis*	*Gomphonchus*	*Arenaceacanthus*	*Rohonilepis*	*Poracanthodes*	*Fecundosquama*	*Monospina*	*Cheiracanthoides*	*“Pruemolepis”*	*Gomphonchoporus*	*Canadalepis*	*Nodacosta*	*Vesperalia*	*Diplacanthus*	*Bracteatacanthus*	*Endemolepis*
Pridoli		Jūra	Rietavas	*Endemolepis inconstans*	1	3	7	21	32	13	6	0	0	4	0	1	1	1	0	1	1	1	1	1	1
Pridoli		Jūra	Rietavas	*Vesperalia perplexa*	0	5	0	24	29	13	6	0	0	3	0	1	1	1	0	1	1	1	1	0	0
Pridoli		Jūra	Kelmė	*Cheiracanthoides planus*	0	1	3	23	27	13	5	0	1	2	0	1	2	1	0	1	1	0	0	0	0
Pridoli		Jūra	Girdžiai	*Nostolepis alta* / *Nostolepis linleyensis*	2	14	2	12	30	15	5	0	1	2	1	1	1	1	1	1	1	0	0	0	0
Pridoli		Minija	Minija	*Fecundosquama basiglobosa*	0	7	0	7	14	5	4	0	1	1	1	1	1	0	0	0	0	0	0	0	0
Pridoli		Minija	Minija	*Nostolepis gracilis*	0	5	0	2	7	4	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0
Ludlow	Ludfordian	Pagėgiai	Ventspils	*Rohonilepis breviornatus*	0	1	0	1	2	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Ludlow	Ludfordian	Pagėgiai	Mituva	*Gomphonchus? minutus*	2	1	1	0	4	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Ludlow	Gorst.	Dubysa	Dubysa	Unzoned	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Wenlock	Homerian	Gėluva	Gėluva	Unzoned																					
Wenlock	Sheinwood. / Homerian	Jaani / Jaagarahu	Riga	Unzoned																					

East Lithuania. Shallow shelf facies

Series	Formation	Beds	Acanthodian zonality	Species: Characteristic	Species: Appearing	Species: Disappearing	Species: Transitional	Species: Total	*Nostolepis*	*Gomphonchus*	*Arenaceacanthus*	*Rohonilepis*	*Poracanthodes*	*Fecundosquama*	*Monospina*	*Cheiracanthoides*	*“Pruemolepis”*	*Acanthoides?*	*Endemolepis*	*Nodacosta*
Pridoli	Lapės		*Endemolepis inconstans*	1	7	3	15	26	11	6	0	0	3	0	1	1	1	1	1	1
Pridoli	Lapės		*Cheiracanthoides planus*	0	1	3	15	19	8	5	0	0	1	0	1	1	1	1	0	1
Pridoli	Lapės		*Monospina erecta*	1	9	4	10	24	10	5	0	1	2	1	1	1	1	1	0	1
Pridoli	Vievis		*Fecundosquama basiglobosa*	1	2	1	12	16	7	2	1	1	1	1	0	1	1	1	0	0
Pridoli	Vievis		*Rohonilepis breviornatus*	0	4	0	9	13	6	2	1	1	1	0	0	1	0	1	0	0
Ludlow	Neris	Sudervė	*Nostolepis gracilis*	0	5	1	4	10	4	3	1	0	0	0	0	1	0	1	0	0
Ludlow	Neris	Trakai	*Nostolepis musca* morphotype 1	0	1	1	4	6	2	3	1	0	0	0	0	0	0	0	0	0
Ludlow	Dubysa / Širv		Unzoned	0	0	0	2	2	0	1	1	0	0	0	0	0	0	0	0	0
Wenlock	Birštonas / Dukstyna / Nevėžis		*Arenaceacanthus arcuatacanalis* / *Gomphonchus? minutus*	0	5	0	0	5	1	3	1	0	0	0	0	0	0	0	0	0

FIG. 11. — Comparison of biostratigraphical zonality of Silurian acanthodians and taxonomical diversity of zonal associations in the deep shelf (west Lithuania) and shallow shelf (east Lithuania) facies.

Acanthodian associations of the Jūra Regional Stage, the Jūra and Lapės formations of the west and east areas respectively, are also characterized by several differences (Fig. 11). First, four zonal units are distinguished in the western area, with only three in the east. It is supposed that the two uppermost units of the west correspond to a single uppermost unit in the east. Second, the taxonomic composition of associations going upwards through the comparative zones demonstrates the following discrepancies. The initial Jūra zones, *Nostolepis alta* in the west and *Monospina erecta* in the east, show a major renewal of acanthodian associations, with the first occurrence horizons of some valuable taxa (*Nostolepis elegans*, *Gomphonchus hoppei*, *tesserae margaritatae* of *Nostolepis* sp., both index fossils, etc.) being nearly coeval. *Fecundosquama basiglobosa*, the nominative species of a previous zone, disappears also at a similar stratigraphic horizon. *Nostolepis linleyensis*, unlike in the east, appears a little later, in the basal part of the *N. alta* AZ. Notably, *N. alta*, *Canadalepis linguiformis* and cf. *Gomphonchoporus* are lacking in the east, whereas *Poracanthodes* sp. cf. *P. stonehousensis* is missing in the west.

The largest differences comparing the western and eastern acanthodian associations concern the *Vesperalia perplexa* AZ, recognized in the extreme southwest of Lithuania (boreholes Nida-44, Stoniškiai-1 and Šešuvis-11). *Vesperalia perplexa*, *Poracanthodes menneri*, *Nostolepis magnicostata* and *Diplacanthus*? sp. have not yet been found in the east. Distinctly shortened ranges of *Nostolepis alifera*, *Gomphonchus mediocostatus* and *Poracanthodes porosus* in east Lithuania perhaps also reflect the absence of part of the geological series.

The topmost *Endemolepis inconstans* AZ is recognized in both areas. The nominative species and *Poracanthodes subporosus* are the most characteristic taxa common to both. Otherwise, the east lacks *Bracteatacanthus assiduus* and all species distinguishing the *Vesperalia perplexa* AZ, which survive until the Silurian/Devonian boundary in the west. Thus, an earlier opinion (Karatajūtė-Talimaa & Brazauskas 1994; Paškevičius *et al.* 1994; Karatajūtė-Talimaa *et al.* 1999) that the most stratigraphically complete Late Silurian geological sequence occurs in southwest Lithuania, in the deepest part of the Baltic Syneclise, is supported by acanthodian faunas showing missing taxa in the two latest faunal zones and by the shorter thickness of the Lapės Formation in the east Lithuanian area.

CONCLUSIONS

Silurian rocks of Lithuania have yielded acanthodian associations of slightly different taxonomical composition in the west compared with east. The first occurrence horizons of most biostratigraphically valuable taxa also often differ and occur in different parts of local formations. Thus, exact zonal boundaries are often still indeterminate. Faunas of the Wenlock and part of the Ludlow are inadequate, and thus a study is still underway with further refinements expected towards a better substantiated and unified biozonal scheme.

The Wenlock lagoonal formations of east Lithuania are ascribed to the *Arenaceacanthus arcuatacanalis-Gomphonchus*? *minutus* AZ (all zones are qualified Interval range zones) with an impoverished taxa association. The west Lithuanian area remains still unzoned through the Wenlock and the Gorstian in the Ludlow. The first appearance of *Arenaceacanthus arcuatacanalis* and *Gomphonchus*? *minutus* is later here, in the Ludfordian (clayey Mituva Formation). The overlying *Rohonilepis breviornatus* Acanthodian Zone of the Ludfordian (black argillite clays and nodular limestones of the Ventspils Formation) is still poorly represented, whereas its facies equivalent in the east (Sudervė Beds of the Neris Formation), the *Nostolepis gracilis* AZ, is characterized by a more diverse acanthodian association (10 taxa).

The *Nostolepis gracilis* association (*N. gracilis*, *N. amplifica*, *N. musca*) enters the sequence later in the west, in the basal Pridoli, embracing the lower part of the argillaceous Minija Formation. In the carbonate facies of the east (Vievis/Pabradė formations), its correlative is the *Rohonilepis breviornatus* AZ with a late entry of the nominative species as compared to the west. The zone is dominated by *Nostolepis* spp. The *Fecundosquama basiglobosa* AZ approximates the upper part of the Minija Regional Stage in both areas, and is regionally important and represented by almost the same numbers of taxa (14 in the west and 16 in the east), but of different species content. Entry of *Nostolepis consueta*, *Gomphonchus* sp. cf. *G. hoppei*, *Monospina erecta* and *Cheiracanthoides* sp. characterize the zone in the west, whereas in the east all of these species enter the sequence earlier except for *Monospina*, which appears slightly later. Three characteristic species, *Nostolepis linleyensis*, cf. *Gomphonchoporus* sp. and *Poracanthodes* sp. cf. *P. stonehousensis*, which have a short range across the boundary of the Minija and Jūra regional stages, could aid broad interregional biostratigraphical correlations (Great Britain, Canada, Baltic). The topmost Pridolian Jūra Formation of the deep shelf and Lapės Formation of the shallow shelf are distinguished by the numerically richest acanthodian associations (19-32 taxa) and dominance of *Nostolepis* spp. (8-15 taxa). Four zones (lower to upper), the *Nostolepis alta*, *Cheiracanthoides planus*, *Vesperalia perplexa* and *Endemolepis inconstans* AZ are distinguished in the west, and only three, *Monospina erecta*, *Cheiracanthoides planus* and *Endemolepis inconstans* AZ in the east. Of these, the *Nostolepis alta* and *Monospina erecta* zones are probably age correlatives representing similar acanthodian associations (except for *Nostolepis alta* which has not been discovered yet in the east) based on composition of the incoming *Nostolepis* species (common *N. striata*, *N. elegans*, *N.* sp. cf. *N. athleta*, *tesserae margaritatae* of *Nostolepis*) and *Gomphonchus hoppei* as the most valuable taxa.

The *Vesperalia perplexa* acanthodian association is developed in the restricted territory of southwest Lithuania and appears to have no correlatives in the east reflecting the shortened geological series of the Lapės Formation. *Poracanthodes menneri*, *Nostolepis magnicostata*, *Diplacanthus*? sp. and *Bracteatacanthus assiduus* which are associated with *V. perplexa*, are not found outside an area confined by the Nida-44, Stoniškiai-1 and Šešuvis-11 boreholes.

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REFERENCES

BRAZAUSKAS A. 1987. — Konodontovye zony silura Litvy [= Silurian conodont zones of Lithuania]. *Geologija* 8: 40-58 (in Russian).

BRAZAUSKAS A. 1989. — Granitsa Ludlova i Pridoli po konodontam v razrezakh Litvy [= The conodont-based boundary of the Ludlow and Pridoli in Lithuania]. *Geologija* 10: 31-42 (in Russian).

BRAZAUSKAS A. 1993. — *Konodonty i biostratigrafia silura Litvy* [= *Silurian Conodonts and Biostratigraphy of Lithuania*]. Doctoral dissertation thesis, Vilnius University, Lithuania, 23 p. (in Russian).

BROTZEN F. 1934. — Erster Nachweis von Unterdevon in Ostseegebiet durch Konglomeratgeschiebe mit Fischresten. II. Teil (Paläontologie). *Zeitschrift für Geschiebeforschung* 10: 1-65.

GROSS W. 1940. — Acanthodier und Placodermen aus *Heterostius*-Schichten Estlands und Lettlands. *Annales Universitas Tartuensis* 46: 1-89.

KARATAJŪTĖ-TALIMAA V. 1962. — Opisanie ostatkov dauntonskoi ichtiofauny Litvy [= Description of the Downtonian ichthyofauna of Lithuania]. [*Institute of Geology Proceedings*] 14: 45-58 (in Russian).

KARATAJŪTĖ-TALIMAA V. 1968. — O stratigraficheskom polozhenii i korreliatsii dauntonskikh otlozhenyi (minijaskie i jūraskie sloi) Yuzhnoi Pribaltiki [= On the stratigraphical position and correlation of the Downtonian deposits (Minija and Jūra Beds) of South Baltic], *in* GRIGELIS A. (ed.), [*Stratigraphy of the Lower Palaeozoic of the Baltic and Correlation with Other Regions*]. Mintis, Vilnius: 273-285 (in Russian).

KARATAJŪTĖ-TALIMAA V. 1970. — Ichthyofauna dauntona Litvy, Estonii i Severnogo Timana [= The Downtonian ichthyofauna of Lithuania, Estonia and North Timan], *in* GRIGELIS A. (ed.), [*Palaeontology and Stratigraphy of the Baltic and Byelorussia*]. Mintis, Vilnius: 33-66 (in Russian).

KARATAJŪTĖ-TALIMAA V. 1978. — *Telodonty silura i devona SSSR i Spitsbergena* [= *Silurian and Devonian Thelodonts of the USSR and Spitsbergen*]. Mokslas, Vilnius, 336 p. (in Russian).

KARATAJŪTĖ-TALIMAA V. & BRAZAUSKAS A. 1994. — Distribution of vertebrates in the Silurian of Lithuania. *Geologija* 17: 106-114.

KARATAJŪTĖ-TALIMAA V., VALIUKEVIČIUS J. & BRAZAUSKAS A. 1987. — Rasprostranenie konodontov i pozvonochnykh v siluryiskikh otlozhenyiakh Litvy [= Distribution of conodonts and vertebrates in the Silurian of Lithuania]. *Geologija* 8: 59-71 (in Russian).

KARATAJŪTĖ-TALIMAA V., BRAZAUSKAS A. & VALIUKEVIČIUS J. 1999. — Vertebrate assemblages of the Silurian/Devonian boundary beds and the section completeness in the Baltic Syneclise, *in* LUKŠEVIČS E., STINKULIS G. & KALNINA L. (eds), Problems and methods of modern regional stratigraphy. *The Fourth Baltic Stratigraphical Conference. Abstracts.* University of Latvia, Riga: 42-43.

LAPINSKAS P. 2000. — *Structure and Petroliferosity of the Silurian in Lithuania*. Institute of Geology, Vilnius, 203 p.

LAPINSKAS P., PAŠKEVIČIUS J. & BRAZAUSKAS A. 1985a. — Ob utochnenii stratigrafii siluryiskikh otlozhenyi v srednei i vostochnoi Litve [= On the stratigraphy precision of Silurian deposits in the mid- and eastern Lithuania], *in* JUODKAZIS V. (ed.), [*Studies of Geology and Mineral Resources of Lithuania*]. Institute of Geology, Vilnius: 98-99 (in Russian).

LAPINSKAS P., PAŠKEVIČIUS J. & JACYNA J. 1985b. — Novoe v stratigrafii i korreliatsii venloka i ludlova (silur) Yugo-Vostochnoi Pribaltiki [= Discoveries in the stratigraphy and correlation of the Wenlock and Ludlow (Silurian) in Southeastern Baltic]. *Geologija* 6: 29-40 (in Russian).

MÄRSS T. 1982. — *Thelodus admirabilis* n. sp. (Agnatha) from the Upper Silurian of the East Baltic. *Eesti Teaduste Akadeemia Toimetised. Geoloogia* 31 (3): 112-116.

MÄRSS T. 1986. — Pozvonochnye silura Estonii i zapadnoi Latvii [= Silurian vertebrates of Estonia and West Latvia]. *Fossilia Baltica* 1: 1-104 (in Russian with English summary).

MÄRSS T. 1997. — Vertebrates of the Pridoli and Silurian-Devonian boundary beds in Europe. *Modern Geology* 21: 17-41.

MÄRSS T. 2000. — Silurian vertebrate studies during 1990-1997, *in* BLIECK A. & TURNER S. (eds), Palaeozoic vertebrate biochronology and global marine/non-marine correlation. *Courier Forschungsinstitut Senckenberg* 223: 81-90.

MUSTEIKIS P. 1985. — *Nadsemeistvo Enteletacea i soobschestva brachiopod silura Litvy* [= *The Super-Family Enteletacea and Silurian Brachiopod Communities of Lithuania*]. Doctoral dissertation thesis, Vilnius University, Lithuania, 24 p. (in Russian).

MUSTEIKIS P. 2002. — The development of Silurian brachiopod communities in Lithuania, *in* SATKŪNAS J. & LAZAUSKIENĖ J. (eds), Basin stratigraphy – modern methods and problems. *The Fifth Baltic Stratigraphical Conference. Extended Abstracts.* Geological Survey of Lithuania, Vilnius: 137-140.

MUSTEIKIS P. & PAŠKEVIČIUS J. 1999. — Brachiopod communities of the Lithuanian Silurian, *in* BOUCOT A. J. & LAWSON J. D. (eds), *Paleocommunities: a Case Study from the Silurian and Lower Devonian*. Cambridge University Press, Cambridge: 305-326.

MUSTEIKIS P. & PUURA I. 1983. — Brachiopody roda *Dicoelosia* iz silura Pribaltiki [= Silurian brachiopods of the genus *Dicoelosia* of the Baltic]. *Eesti Teaduste Akadeemia Toimetised. Geoloogia* 32 (4): 138-146 (in Russian).

PAŠKEVIČIUS J. 1958. — Viršutinio silūro (ludlovio) stratigrafijos klausimu Lietuvoje [= On the question of the Upper Silurian (Ludlow) stratigraphy in Lithuania]. [*Institute of Geology and Geography Proceedings*] 7: 115-130 (in Lithuanian).

PAŠKEVIČIUS J. 1963. — Stratigraficheskaya reviziya siluryiskikh otlozhenyi Yuzhnoi Pribaltiki [= The stratigraphical revision of Silurian deposits of South Baltic], *in* GRIGELIS A. & KARATAJŪTĖ-TALIMAA V. (eds), [*Questions on the Geology of Lithuania*]. Pergalė, Vilnius: 385-405 (in Russian).

PAŠKEVIČIUS J. 1965. — Zonalnoe raschlenenie nizhnesiluryiskikh otlozhenyi Litvy [= Zonal subdivision of the Lower Silurian deposits of Lithuania] [*Institute of Geology Proceedings*] 1: 40-49 (in Russian).

PAŠKEVIČIUS J. 1973. — *Biostratigrafia, korreliatsia i graptolity ordovikskikh i siluryiskikh otlozhenyi Yuzhnoi Pribaltiki* [= *Biostratigraphy, Correlation and Graptolites of the Ordovician and Silurian Deposits of South Baltic*]. Doctoral Habilitation dissertation thesis, Vilnius University, Lithuania, 66 p. (in Russian).

PAŠKEVIČIUS J. 1979. — *Biostratigrafia i graptolity silura Litvy* [= *Biostratigraphy and Graptolites of Lithuanian Silurian*]. Mokslas, Vilnius, 267 p. (in Russian).

PAŠKEVIČIUS J. 1994. — Silūras [= Silurian], *in* GRIGELIS A. & KADŪNAS V. (eds), [*Geology of*

Lithuania]. Institute of Geology, Vilnius: 67-97 (in Lithuanian).

PAŠKEVIČIUS J. & BRAZAUSKAS A. 1987. — Obosnovanie stratigrafii melkovodnykh morskikh i lagunnykh siluryiskikh otlozhenyi vostochnoi Litvy [= Substantiation of a stratigraphy of the shallow marine and lagoonal Silurian rocks of east Lithuania]. *Geologija* 8: 10-28 (in Russian).

PAŠKEVIČIUS J., BRAZAUSKAS A., LAPINSKAS P., KARATAJŪTĖ-TALIMAA V., MUSTEIKIS P., SALADŽIUS V. & SIDARAVIČIENĖ N. 1986. — Zakonomernosti rasprostranenia fauny i korreliatsia raznofatsialnykh siluryiskikh otlozhenyi Yugo-Vostochnoi Pribaltiki [= Regularities in the distribution of faunas and correlation of multifacial Silurian deposits of the Baltic], *in* KALJO D. L. & KLAAMANN E. R. (eds), [*Theory and Practice of Ecostratigraphy*]. Valgus, Tallinn: 55-64 (in Russian).

PAŠKEVIČIUS J., LAPINSKAS P., BRAZAUSKAS A., MUSTEIKIS P. & JACYNA J. 1994. — Stratigraphic revision of the regional stages of the Upper Silurian part in the Baltic basin. *Geologija* 17: 64-87.

SIDARAVIČIENĖ N. 1986. — Rasprostranenie ostrakod v fatsiakh przhidolskogo yarusa Litvy [= Distribution of ostracodes in the facies of the Pridoli of Lithuania], *in* KALJO D. L. & KLAAMANN E. R. (eds), [*Theory and Practice of Ecostratigraphy*]. Valgus, Tallinn: 116-126 (in Russian).

SIDARAVIČIENĖ N. 1997. — Nauji *Amygdalella* genties ostrakodai iš Lietuvos viršutinio silūro [= New ostracodes of the genus *Amygdalella* from the Upper Silurian of Lithuania]. *Geologija* 21: 12-23 (in Lithuanian with English summary).

TALIMAA V. 2000. — Significance of thelodonts (Agnatha) in correlation of the Upper Ordovician to Lower Devonian of the northern part of Eurasia, *in* BLIECK A. & TURNER S. (eds), Palaeozoic vertebrate biochronology and global marine/non-marine correlation. *Courier Forschungsinstitut Senckenberg* 223: 69-80.

VALIUKEVIČIUS J. 1998. — Acanthodians and zonal stratigraphy of Lower and Middle Devonian in East Baltic and Byelorussia. *Palaeontographica* A 248: 1-53.

VALIUKEVIČIUS J. 2003a. — New Silurian nostolepids (Acanthodii, Pisces) of Lithuania. *Geologija* 42: 51-68.

VALIUKEVIČIUS J. 2003b. — Silurian acanthodian succession of the Lūžni-4 borehole (Latvia), *in* SCHULTZE H.-P., LUKŠEVIČS E. & UNWIN D. (eds), The Gross Symposium 2: advances in palaeoichthyology. *Ichthyolith Issues, Special Publication* 7: 51.

VALIUKEVIČIUS J. 2004a. — New Wenlock-Pridoli (Silurian) acanthodian fishes from Lithuania. *Acta Palaeontologica Polonica* 49 (1): 147-160.

VALIUKEVIČIUS J. 2004b. — Silurian acanthodian succession of the Lūžni-4 borehole (Latvia). *Acta Universitatis Latviensis. Earth and Environment Sciences* 679: 120-147.

VERGOOSSEN J. M. J. 1999. — Late Silurian fish microfossils from an East Baltic-derived erratic from Oosterhaule, with a description of new acanthodian taxa. *Geologie en Mijnbouw* 78: 231-251.

VERGOOSSEN J. M. J. 2000. — Acanthodian and chondrichthyan microremains in the Siluro-Devonian of the Welsh Borderland, Great Britain, and their biostratigraphical potential, *in* BLIECK A. & TURNER S. (eds), Palaeozoic vertebrate biochronology and global marine/non-marine correlation. *Courier Forschungsinstitut Senckenberg* 223: 175-199.

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APPENDIX 1

Acanthodian occurrence in the Kurtuvėnai-162 and Viduklė-61 borehole cores. Zonal species are given in bold. **+**, up to one hundred of scales; ●, up to one thousand of scales; ■, thousands of scales.

Depth (m)	*Gomphonchus sandelensis*	*Nostolepis consueta*	***Cheiracanthoides planus***	***Nostolepis alta***	*N. musca* morphotype 1	*Gomphonchus* sp. cf. *G. hoppei*	*G. hoppei*	*Gomphonchus* tooth whorls	*Gomphonchus* teeth	*Gomphonchus* fin spine fragments	***Nostolepis gracilis***	cf. *Fecundosquama basiglobosa*	?*Monospina erecta*	*Nostolepis* sp. cf. *N. gracilis*	***Rohonilepis breviornatus***	*Poracanthodes punctatus*	*P. porosus*	?*Cheiracanthoides* sp.	***Fecundosquama basiglobosa***	*Gomphonchus* sp. or *Poracanthodes* sp.	*Nostolepis amplifica*	*Gomphonchus* sp.	*Arenaceacanthus arcuatacanalis*	*Nostolepis striata*	"*Pruemolepis wellsi*"	*Nostolepis musca* morphotype 2	*Nostolepis* sp. cf. *N. athleta*	*Nostolepis* fin spine fragments	cf. *Canadalepis linguiformis.*	*Nostolepis magnicostata*	***N. linleyensis***	Nostolepidida indet.	*Nostolepis elegans*	cf. *Gomphonchoporus*	*Nostolepis alifera*	*N. amplifica* or *N. elegans*	*Nostolepis* tesserae margaritatae	***Gomphonchus? minutus***	Formation or Beds	Regional Stage
Kurtuvėnai-162																																								
1007.0	■	■	●		■	●	●	+	+	+	+		+			+									●		+	+	+										Jūra	Jūra
1014.0	+	+				+																																		
1016.0	●	+			+	+	+		+			●													+					+										
1017.4	●	●			+	+	+																																	
1022.0	●	●			●	+	+	+	+																															
1024.5	■	■			■	■	+	+	+		+		+					+							+		+										+			
1025.5	●	●			+	+	+				+																													
1028.0	■	■			●	●		+	+									+							+		+													
1030.0	■	■	+			●	+	+	+	+	+		+															+												
1038.0	+							+	+																															
1043.0	●			+	●	+	+	+	+		+													+	+			+							+					
1046.0	+	+			+	+								+																										
1052.2	■	●					+	+	+	+	+	+					+	+	●						+			+												
1054.5	+					+													●		+																			
1056.0	●	+			+						+							+	●		+				+															
1060.8	●	●			+	+					+							+		+	+				+			+					+			+	+			
1063.4	■	+		+	●	+			+		■		+			+		+			●			+	+	+	+	+			+			+	+		+			
1067.5																						+																	Minija	Minija
1072.4	●	●			●	+		+	+		+		+					+	+																					
1076.0	+																				+																			
1082.0																						+																		
1091.3											+				+																									
1097.2															+							+																		
1103.0															+																								Vent-spils	Pagė-giai
1117.8															●																									
1132.0															+							+	+															+	Mituva	
1136.0																																+								
1137.5																						+										+						+		
1154.9																																+							Dubysa	
Viduklė-61																																								
1124.0	+																						+															+	Mituva	Pagė-giai
1161.6																							+									+								

APPENDIX 2

Acanthodian occurrence in the Liepkalnis-137 borehole core. For legend see Appendix 1.

Depth (m)	*Gomphonchus sandelensis*	*Nostolepis consueta*	***Cheiracanthoides planus***	*"Pruemolepis wellsi"*	*Nodacosta*-type fin spine	*Nostolepis musca* morphotype 1	*Gomphonchus* sp. cf. *G. hoppei*	*G. hoppei*	*Gomphonchus* teeth	*Gomphonchus* fin spine fragments	*Nostolepis* sp. cf. *N. athleta*	***N. gracilis***	*Gomphonchus* tooth whorls	***Rohonilepis breviornatus***	*Poracanthodes punctatus*	***Fecundosquama basiglobosa***	*Nostolepis*-type fin spine fragments	*N. amplifica*	Formation	Regional Stage	Series
879.8	+	+			+	+		+											Minija-Jūra	Minija-Jūra	Pridoli
880.2	+	+	+					+													
880.6	●	+		+		+	+	+	+	+			+								
881.0	+	+				+		+													
881.8	+								+												
882.9	+											+									
883.5	+	+				+		+													
884.4	+	+		+		+		+			+	+									
886.5		+		+																	
886.7		+				+						+									
887.3	+	+					+					+									
887.6	+						+														
889.1	+	+										+									
892.1	+	+		+		+										+					
892.3	+	+		+												+					
893.9	+	+		+								+				+					
894.2	+	+				+						+					+				
895.3	+	+																			
896.5						+															
897.2	+	+		+		+															
897.5	+																				
898.0	+	+		+								+			+						
899.5	●	●				+		+				+						●			
900.1	+	+		+		+						+		+			+				
900.5	+			+		+						+		+							
901.8	+			+		+								+							
902.1	+	+																			
902.2	+					+						+									
902.3	+																				
903.2	+	+										+									
903.4	+					+															
904.5	+											+									
907.2	+					+															
907.4	+											+									
907.9	+																				
908.2	+																				
908.4	+																				
909.2														+							
909.9	+			+		+						+			+						
910.0	+											+									
915.9	+			+		+						+									

APPENDIX 3

Acanthodian occurrence in the Stoniškiai-1 borehole core. For legend see Appendix 1.

Depth (m)	*Nostolepis* sp. cf. *N. magnicostata*	*N. striata*	***Vesperalia perplexa***	***Nostolepis gracilis***	*"Pruemolepis wellsi"*	*Nostolepis consueta*	*Gomphonchus sandelensis*	*Gomphonchus* sp. cf. *G. hoppei*	*Poracanthodes punctatus*	***Endemolepis inconstans***	*Nodacosta*-type fin spines	*Nostolepis musca* morphotype 1	*N. elegans*	*Gomphonchus* tooth whorls	*Gomphonchus* teeth	*Poracanthodes subporosus*	*Nostolepis* sp. cf. *N. athleta*	*Gomphonchus hoppei*	***Cheiracanthoides planus***	*Gomphonchus* fin spine fragments	cf. *Canadalepis linguiformis.*	***Rohonilepis breviornatus***	***Fecundosquama basiglobosa***	*Bracteatacanthus assiduus*	*Nostolepis magnicostata*	*N. musca* morphotype 2	*N. alifera*	Beds	Formation, Regional Stage
1211.0-1217.0	+	+	+	+	+	●	■	+	+	+	+													+	+		+	Rietavas	Jūra
1214.0	+					+	+	+		+		+				+	+	+	+	+									
1216.0				+	+	+	+	+		+		+				+		+											
1217.0-1219.3				+	+	+	+	+				●							+										
1217.0-1222.3				+	+	●	●	+				+		+	+														
1220.0						+									+														
1222.0-1224.0						+	+																					Kelmė	
1224.0-1227.0												+							+		+	+							
1229.7												+																	
1231.0						+																							
1233.8						+						+										+							
1237.4												+	+																
1245.1						+						+																	
1250.8-1251.2								+				+																Girdžiai	
1263.2												+	+	+								+							
1267.4												+										+							
1271.5												+																	
1273.0							+					+																	
1275.8								+				+										+							
1289.1												+																	
1308.9						+						+										+						Varniai	Minija
1311.0				+								+											+						
1315.7				+			+					+											●						
1318.8				+			+					+											●						
1322.8																							+						
1325.4																							+						
1328.9																							+						
13348							+																+						
1338.8												+											+			+			
1341.0																							+						
1343.0							+																+						
1347.0																							+						
1351.0							+					+											+			+			
1355.0																							+						
1359.0																							+						

APPENDIX 4

Acanthodian occurrence in the Šešuvis-11 borehole core. For legend see Appendix 1.

Depth (m)	*Gomphonchus sandelensis*	*Nostolepis consueta*	*N. consueta* prepectoral spine	*N. consueta* teeth	***Cheiracanthoides planus***	***Vesperalia perplexa***	*Nostolepis musca* morphotype 1	*Gomphonchus* sp. cf. *G. hoppei*	*G. hoppei*	*Gomphonchus* tooth whorls	*Gomphonchus* teeth	*Gomphonchus* fin spines	***Nostolepis gracilis***	*Fecundosquama* sp.cf.*F. basiglobosa*	*Monospina* sp. cf. *M. erecta*	***Endemolepis inconstans***	***Rohonilepis breviornatus***	*Poracanthodes punctatus*	*P. porosus*	*P.* sp. cf. *P. subporosus*	***Fecundosquama basiglobosa***	*Nostolepis robusta* (+ cf.)	*Gomphonchus* sp.	*Nostolepis magnicostata*	*"Pruemolepis wellsi"*	*Nostolepis* teeth	*N.* sp. cf. *N. athleta*	*Nostolepis* fin spine fragments	cf. *Canadalepis linguiformis*	*Monospina erecta*	*Nodacosta*-type fin spines	*Nostolepis* sp.	Nostolepidida indet.	*Bracteatacanthus assiduus*	Beds	Formation, Regional Stage
1005.0	+	+				+	+				+		+			+			+	+		+												+	Rietavas	Jūra
1006.0	+	+				+	+				+		+			+			+	+		+												+		
1007.3	+	+				+	+																													
1007.8	●	+			+	+	+	+		+	+		+			+		+						+	+								+			
1009.5		+																																		
1010.8	+	+			+	+	+						+																							
1010.9	+	+				+		+	+				+												+								+			
1011.3	+	+					+																													
1012.0		+											+																							
1013.0	+	+					+																													
1013.5	+	+											+																						Kelmė	
1014.0		+																																		
1015.2	+	+	+										+																							
1016.9	+	+																																		
1017.8	+	+					+			+	+	+																								
1018.0	+	+					+	+																												
1019.0		+					+																													
1020.3		+																																		
1022.6		+																																		
1023.3	●	●					+	+	+	+	+		+												+											
1024.2	■	■	+	+			●	+		+	+		+					+							+											
1026.3	■	■					●	+		+	+		+		+										+		+						+			
1027.2	+	+					+			+																										
1028.4	●	●					+	+		+	+		+																							
1035.2	+	+						+		+															+				+							
1038.0	+	+					+	+	+	+			+												+											
1038.3	+	+					+																													
1047.0	+	+					+		+	+							+																		Girdžiai	
1049.5	+	+					+	+	+		+		+				+									+										
1051.5	●	●					●	+	+	+	+	+	+		+			+				+			+			+								
1053.5	+	+					+		+	+															+											
1054.3	■	■					■	+	+	+	+		●					+				+			+	+	+		+		+					
1056.0	+	+					+	+	+	+	+		+																							
1057.0	■	■						+	+	+	+		+		+							+			+											
1057.6	●	●						+	+	+	+		+												+											
1059.4	●	●					+	+	+	+	+		+																	+						
1072.9	+																				+															
1079.0	+	+					+		+	+	+		+																							
1082.8	+	●					+		+		+		+																	+						
1091.4	+						+							+							■															
1095.0																					+		+													
1095.2																					+		+													
1117.9								+						+							+															
1119.5														+							+		+													
1131.8																																+			Minija	Minija
1135.9	+								+				+																							
1137.8	+	+					+						+																							

APPENDIX 5

Acanthodian occurrence in the topmost Silurian of some borehole cores. For legend see Appendix 1.

Borehole	Depth (m)	*Gomphonchus sandelensis*	*Nostolepis consueta*	*Vesperalia perplexa* prepectoral spine	***Cheiracanthoides planus***	***Vesperalia perplexa***	***N. musca* morphotype 1**	*Gomphonchus* sp. cf. *G. hoppei*	*G. hoppei*	*Gomphonchus* tooth whorls	*Gomphonchus* teeth	*Gomphonchus* fin spine fragments	***Nostolepis gracilis***	*N. musca* morphotype 2	*N. elegans*	***Endemolepis inconstans***	*Poracanthodes punctatus*	*P. subporosus*	*Gomphonchus* sp. cf. *G. mediocostatus*	*Nostolepis magnicostata*	*Nostolepis* sp.	*"Pruemolepis wellsi"*	*Nostolepis* fin spine fragments	***Monospina erecta***	*Nodacosta*-type fin spine fragments	*Nostolepis striata*	*Poracanthodes menneri*	*Diplacanthus*? sp.	*Bracteatacanthus assiduus*	*Nostolepis* sp. cf. *N. robusta*	cf. *Canadalepis* sp.	*Nostolepis* sp. cf. *N. athleta*	***Nostolepis alta***	*N. amplifica* or *N. elegans*	*N. alifera*	Formation	Regional Stage
Nida-44	1213.0	■	●	+	+	●	●	+	+			+	+	+	+	+	+	+	+	+		+	+			+	+		+	+	+	+	+	+	+	Jūra	Jūra
	1213.8	●				●						+	+				+					+				+											
	1221.0	●	●			+		+	+	+	+		+				+					+		+				+		+					+		
	1221.3	+	+			+		+														+															
	1221.4	+	+		+	+		+		+			+				+					+					+										
	1230.6	■	■				●			+	+		+									+	+		+												
	1273.8	●	●				●			+	+		+		+							+		+		+									+		
Krekenava-7	540.6	+	+		+		+		+																											Lapės	Jūra
	541.4							+																													
	544.3	+							+																												
	545.0	+	+																																		
	545.8	+							+												+																
	546.5	+	+						+																												
	547.8	+	+				+	+	+		+																										
	548.3							+																													
	550.2	+	+						+			+																									
	552.8	+	+																																		
	553.5	+	+						+																												
Stačiūnai-8	856.5	+	+				+	+	+	+	+	+																							+	Lapės	Jūra
	858.8	+	+									+																									
	859.2	+	+								+																										
	859.5	+	+				+				+																										
	860.6	+	+					+	+		+		+									+															
	861.5	+	+				+	+			+																										
Kunkojai-12	898.0	+	+					+																												Jūra	Jūra
	900.5	+																																			
	901.5	+	+										+																								
	901.8	+	+																																		
	903.0	+	+				+	+	+	+	+		+									+															
	904.0	+																																			
	905.7	+	+				+																														
	906.0	+	+						+																												
	907.2	+	+				+	+	+	+	+											+															
	908.7	+	+				+		+		+																										
	910.0	+	+				+	+														+															
	912.0		+																																		

APPENDIX 6

Acanthodian occurrence in some of the borehole cores of eastern Lithuania. For legend see Appendix 1. *****, Sudervė Beds.

Borehole	Depth (m)	***Arenaceacanthus arcuatacanalis***	***Nostolepis gracilis***	*Gomphonchus sandelensis*	*Nostolepis consueta*	*Acanthoides* sp.	*N. musca* morphotype 1	*Poracanthodes punctatus*	***Cheiracanthoides planus***	*Nostolepis amplifica*	*Gomphonchus* sp. cf. *G. hoppei*	*Gomphonchus* sp.	*Cheiracanthoides* sp.	*Gomphonchus hoppei*	*Nodacosta*-type fin spine fragments	*Gomphonchus* tooth whorls	*Poracanthodes subporosus*	*"Pruemolepis wellsi"*	***Monospina erecta***	*Nostolepis elegans*	*N.* sp. cf. *N. athleta*	***Fecundosquama basiglobosa***	***Gomphonchus? minutus***	Formation	Regional Stage	Series
Butkūnai -241	416.4	+																						Dukstyna	Jaagarahu	Wenlock
	417.5											+														
	427.6			+																						
	457.0	+		+	+																		+	Birštonas	Jaani	
Jocionys -299	102.8			+		+	+	+																Pabradė	Minija	Pridoli
	115.8		+	+	+	+	+			+	+	+	+											Neris*	Pagėgiai	Ludlow
Svėdasai -252	365.6			+	+	+	+				+			+										Lapės	Jūra	Pridoli
	366.0			●	+	+	+	+		+	+			+	+	+	+									
	368.1			+					+																	
	367.9-368.6			■	+		●	+		+	+			+		+		+	+	+	+					
	373.6			+			+				+						+									
Gražutė	335.0	+										+											+	Verknė	Jaani	Wenlock
Vilkaviskis-128	706.2																					+		Vievis	Minija	Pridoli
	714.0																					+				

APPENDIX 7

Acanthodian occurrence in the Gėluva-99 borehole core. For legend see Appendix 1. 746.2 m, Sudervė Beds; 752.0 m, Trakai Beds.

Depth (m)	*Gomphonchus sandelensis*	*Nostolepis consueta*	***Cheiracanthoides planus***	*Nostolepis* sp.	*Nostolepis* sp. cf. *N. fragilis*	***N. musca* morphotype 1**	*Gomphonchus* sp. cf. *G. hoppei*	*G. hoppei*	*Gomphonchus* tooth whorls	*Gomphonchus* teeth	*Gomphonchus* fin spine fragments	***Nostolepis gracilis***	*Gomphonchus mediocostatus*	***?Monospina erecta***	*Nostolepis* sp. cf. *N. gracilis*	***Rohonilepis breviornatus***	*Poracanthodes punctatus*	*P. porosus*	*?Cheiracanthoides* sp.	***Fecundosquama basiglobosa***	*Poracanthodes* sp. cf. *P. porosus*	*Nostolepis amplifica*	Acanthodii indet.	***Arenaceacanthus arcuatacanalis***	*N. musca* morphotype 2	*N. elegans*	***Gomphonchus? minutus***	Formation	Regional Stage	Series
639.1	+	+	+																									Lower Devonian		
639.4	+	+		+	+																							Jūra	Jūra	Pridoli
639.6	●	+				+	+																							
640.0	●	+				+	+	+	+	+																				
641.6	●					+	+	+			+																			
643.0	●	+	+			+	+	+	+	+		+													+					
645.8	+	+				+				+																				
647.2	●	●				+	+	+	+			+	+																	
648.6	+	+				+	+		+					+																
650.0	●		+			+	+				+		+																	
651.3	●	+	+			+	+	+	+	+	+		+																	
652.7	+					+	+			+					+															
654.1	+					+	+			+		+				+														
655.5	+	+	+				+	+	+	+						+														
656.9	●	+				+	+	+		+						+														
659.7	+					+	+	+	+	+		+				+														
661.0	●	+				+	+	+	+	+						●	+													
662.2	+					+	+	+		+						+	+													
663.6	+						+	+								●														
666.4	●					+	+	+	+	+		+				+	+													
667.7	+					+	+	+		+	+							+												
669.2	+					+	+									+	+													
673.4	+											+				+														
676.9	+						+									+														
678.0	+					+	+					+				+			+											
679.3	●					+	+								+	●										+				
681.6	■	+				+	+								+		+			■	+	+	+					Vievis	Minija	
685.3	●					+										+														
690.0	+												+		●							+								
696.0	●					+									+															
735.2	+																							+	+					
738.0	+																													
746.4	+																							+				Neris	Pagėgiai	Ludlow
752.0	+	+				+																		+			+			
806.0																								+			+	Dubysa	Dubysa	

APPENDIX 8

Acanthodian occurrence in the Sutkai-87 boreholecore. For legend see Appendix 1. 666.6 m, Sudervė Beds.

Depth (m)	*Gomphonchus sandelensis*	*Nostolepis consueta*	***Cheiracanthoides planus***	*"Pruemolepis wellsi"*	*Nostolepis* sp. cf. *N. amplifica*	***N. musca* morphotype 1**	*Gomphonchus* sp. cf. *G. hoppei*	*G. hoppei*	*Fecundosquama* sp. cf. *F.basiglobosa*	*Gomphonchus* fin spine fragments	*Nostolepis* sp. cf. *N. athleta*	***N. gracilis***	*Gomphonchus mediocostatus*	***Rohonilepis breviornatus***	*Poracanthodes punctatus*	***Fecundosquama basiglobosa***	*Nostolepis amplifica*	***Arenaceacanthus arcuatacanalis***	*Nostolepis musca* morphotype 2	Formation	Regional Stage	Series
571.0	+	●		+							+		+							Jūra	Jūra	Pridoli
571.8	●	●	+	+		+	+	+														
571.9	+	●	+	+		+	+	+														
572.7	+	+																				
577.3		+				+																
578.4	+	●	+	+		+	+															
580.0		+																				
582.4		+																				
584.2						+																
586.0	+	+																				
587.4	+	+	+	+		+	+	+														
591.4	+	+						+														
593.0	+	+					+	+														
594.4	+	+					+	+		+	+											
595.8	●	●				+	+	+				+										
597.3	+	+			+		+															
598.5	+	+																				
600.8	+	+																				
602.3	+	+						+														
603.8	+	+																				
605.0	+	+						+				+			+							
606.5		+																				
608.1		+																				
609.3	●	●		+		+	+	+	+			+				+	+					
611.9	+	+					+									+						
612.9	●	+				+								+		●	+					
615.3	+	+										+		+		+	+			Vievis	Minija	
617.3	+	+																				
620.7						+													+			
622.0	●	+										+		+			+					
623.6	+											+		+								
666.6																		+		Neris	Pagėgiai	Ludlow

APPENDIX 9

Acanthodian occurrence in the Ledai-179 borehole core. For legend see Appendix 1.

Depth (m)	*Gomphonchus sandelensis*	*Nostolepis consueta*	***Cheiracanthoides planus***	*"Pruemolepis wellsi"*	*Acanthoides* sp.	***N. musca* morphotype 1**	*Gomphonchus* sp. cf. *G. hoppei*	*G. hoppei*	*Gomphonchus* tooth whorls	*Gomphonchus* teeth	*Gomphonchus* fin spine fragments	***Nostolepis gracilis***	*N.* sp. cf. *N. robusta*	cf. ***Monospina***	***Endemolepis inconstans***	***Rohonilepis breviornatus***	*Poracanthodes punctatus*	*P. porosus*	? *Cheiracanthoides* sp.	***Fecundosquama basiglobosa***	*Poracanthodes* sp. cf. *P. subporosus*	*Nostolepis amplifica*	***N. linleyensis***	***Arenaceacanthus arcuatacanalis***	*Nostolepis* sp. cf. *N. athleta*	*Gomphonchus?* sp.	Nostolepidida indet.	*Nostolepis elegans*	*N. striata*	*N. musca* morphotype 2	*N. tesserae margaritatae*	*Poracanthodes* sp. cf. *P. stonehousensis*	*P.* sp. cf. *P. porosus*	Formation	Regional Stage	Series
508.3	+				+	+					+						+																			
508.5	●	+	+	+		●	+	+	+	+		+	+		+																					
509.7	■	■	+	+		●	+	+	+	+		+			+		+	+			+															
511.7	■	■	+	+		■	+	+							+										+											
513.7		●	+	+		●	+	+				+																								
515.7	+	+				+	+																													
517.7	●	●	+			+	+	+				+																								
519.7	●	●	+	+		●	+	+	+			+																								
521.7	●	+				+	+	+	+																											
523.7	■	■	+	+		■	+	+									+														+					
525.7	+	+														+																		Lapės	Jūra	
527.0	+	+																																		
527.7	●	+				+	+																													
529.7	+	+					+									+																				
531.7	+	+					+					+				+	+																			
533.7	■	■		+		+	+	+				+		+		+	+												+		+					Pridoli
535.0	●	●		+			+	+	+	+		+					+					●			+			+					+			
535.7	●	●		+		+	+					+				+	+																			
537.4	■			+				+	+	+		+					+			■		●			+		+					+				
537.7	+	+				+	+					+								+									+							
539.7	●	+				+						+				+			+																	
541.7	■	●		+			+					+								+		+								+						
543.7	■						+					+										+	+							+						
544.1	+								+							+			+					+												
545.7	+																					+		+												
547.6	●											●					+		+	+				●			+									
551.6	+																							+										Vievis	Minija	
561.6	+																																			
567.6												+												+												
573.6																	+									+	+									
575.6																			+							+										