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The Second Gross Symposium "Advances of Palaeoichthyology"

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Otrais Grosa simpozijs “Paleoihtioloģijas sasniegumi”

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ERVĪNS LUKŠEVIČS un ĢIRTS STINKULIS

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2003. gada nogalē paleontologu saime atzīmēja 100 gadus kopš dzimis izcilais paleozoologs Valters Roberts Gross (*Walter Robert Gross*). Viņa liktenis ļoti raksturīgs dinamiskajam un dramatisku pārmaiņu pilnajam XX gadsimtam. V. Gross bijis vairāku izzudušo valstu pilsonis – dzimis Krievijas impērijas Livlandes guberņā, dzīvojis Veimaras republikā, Trešajā reihā, Vācijas Demokrātiskā republikā; ilgu laiku bijis arī jaundzimušās Latvijas republikas pilsonis, bet muža beigās kļuvis par Federatīvās Vācijas pilsoni (Schultze 1996). Dzimis 1903. gada 20. augustā Katlakalnā, baltvācu luterāņu mācītāja Ervina Johanna Grosa ģimenē. No 1907. līdz 1918. gadam Grosu ģimene, kurā bija 9 bērni, dzīvojusi Straupē, pastorātā netālu no Straupes pils un baznīcas. Krāšņā daba Straupes apkaimē jau bērnībā modinājusi Valtera dvēselē dabaspētnieku. Viņš interesējies par augiem un dzīvniekiem, vācis herbārijus, vērojis putnus. Savos memuāros V. Gross (1974) atcerējies, ka jau piecu gadu vecumā nolēmis kļūt par zoologu. Pusaudža gados interešu lokā nonākuši izmirušie dzīvnieki, kuru atliekas V. Gross atradis Braslas krastu atsegumos un jau 17 gadu vecumā sācis veidot nopietnas paleontoloģiskas kolekcijas.

Būdams vēl ļoti jauns, 1921. gadā Valters iestājies Rīgas Dabaspētnieku biedrībā. Nodibinājās kontakti ar biedrības muzeju, kuram V. Gross vēlāk nodevis paleontoloģiskos materiālus un kuri joprojām glabājas Latvijas Dabas muzeja krājumā (Lukševičs 2002). Kā lojāls Latvijas valsts pilsonis 1923.-24. gadā V. Gross dienējis Latvijas bruņotajos spēkos. Pēc dienesta pārcēlies uz Vāciju, kur pavadījis visu atlikušo mūžu, izņemot īsākus vai garākus ceļojumus.

Sekoja studijas Mārburgas universitātē, kur viņam bija jāizdara grūta izvēle starp zooloģiju un paleontoloģiju, bet 1929. gadā nācās pārcelties uz Berlīni un turpināt studijas A. Humbolta Universitātā. Studiju gados Gross turpinājis vākt un pētīt mugurkaulnieku atliekas no devona nogulumiežu atsegumiem Gaujas un tās pieteku krastos. Būdams tikai IV kursa students, 1928. gada 24. septembrī Rīgas Dabaspētnieku biedrības sēdē viņš ziņojis par savu pētījumu rezultātiem (Lukševičs 2002). Savācis visai reprezentatīvu bruņuzivs *Asterolepis ornata* atlieku kolekciju, Gross samērā precīzi rekonstruējis vairākas bruņu plātnes un bruņu "kārbu" kopumā, izlabojot dažu iepriekšējo pētnieku kļūdas (Gross, 1931). 1931. gadā par šo darbu V. Grosam piešķirts filozofijas doktora grāds; viņš kļūst arī par Rīgas Dabaspētnieku biedrības korespondētājlocekli.

Pētījumu turpinājumam saņemts finansējums grantu veidā no Vācijas zinātnes "glābšanas asociācijas" (vēlāk – Vācijas Zinātnes fonds). Pateicoties tam, varēja iegādāties mikroskopu histoloģiskiem pētījumiem, kā arī publicēt virkni nozīmīgu darbu, kuri iznākuši no 1931. līdz 1935. gadam. Lielākoties šīs publikācijas veltītas devona zivīm, galvenokārt no Baltijas. Apkopojis savas 1931. gada ekspedīcijas materiālus, kā arī izmantojot latviešu ģeologa un paleontologa Nikolaja Delles un viņa igauņu kolēģa Kārļa Orviku vākumus, V. Gross (1933) publicējis plašu un ļoti nozīmīgu darbu par Baltijas devona zivīm, kurā izdalījis 12 jaunas sugas.

Kopš 1936. gada Gross ieņēma docenta vietu Humbolta Universitātē, bet kopš 1943. gada – asociētā profesora vietu (Schultze 1996). Arī tolaik viņš uzturēja kontaktus ar Baltijas ģeologiem un Rīgas Dabaspētnieku biedrības vadību, šajā laikā iznākušas vairākas Grosa publikācijas, kurās viņš apraksta Igaunijas un Latvijas bruņuzivis, akantodes un daivspurzivis (Gross 1940, 1941). Otrā pasaules kara vidū profesoru Grosu iesauca reiha armijā, kurā viņš dienējis līdz kara beigām; ticis internēts kā kara gūsteknis, atbrīvots 1946. gadā. Tikai 1949. gadā V. Gross atgriezies Berlīnes Humbolta Universitātē, jau Vācijas Demokrātiskajā republikā, kur 1950. gadā kļuvis par paleontoloģijas profesoru, ģeoloģijas-paleontoloģijas institūta un Dabas muzeja paleontoloģijas sekcijas direktoru.

Pēc bēdīgi slavenā Berlīnes mūra uzcelšanas 1961. gada augusta beigās Valters Gross ar kundzi Ursulu ieradās Hamburgā, kur notika Vācijas paleontoloģijas biedrības gadskārtējā sanāksme. Tā kā Grosu bērni jau atradās Rietumos, tika akceptēts profesora Šindevolfa priekšlikums V. Grosam ieņemt asociētā profesora amatu Tībingenē (Schultze 1996). Viņa zinātniskā aktivitāte ir saglabājusies, publicēta virkne rakstu par zivju un bezžokļeņu mikroskopiskajām atliekām – zobiem un zvīņām, veltot uzmanību ne tikai to ārējai morfoloģijai, bet arī histoloģiskajai uzbūvei. V. Gross pensionējās 1969. gadā, tad arī viņam konstatēja vēzi. Tomēr viņš aktīvi turpināja zinātnisko darbu līdz pat 1973. gada beigām. V. Gross miris 1974. gada jūnijā.

Daudzas publikācijas (to kopskaits sniedzas pāri par 90) jau 1950. gados padarījušas V. Grosa vārdu pazīstamu plašās paleontologu aprindās, īpaši mugurkaulnieku pētnieku vidū Zviedrijā, Lielbritanijā, Francijā, ASV, Krievijā un it īpaši Baltijā. 1973. gada žurnāla *Palaeontograhica* 143. sējums tika pilnībā nokomplektēts no V. Grosa 70 gadu jubilejai veltītiem rakstiem paleoihtioloģijas jomā, kuros atspoguļojas viņa saiknes ar kolēģiem Eiropā un Ziemeļamerikā.

Agrīno mugurkaulnieku paleontoloģijas simpozijā, kas notika 1987. gadā Pekinā, paleoihtiologu grupa nolēma uzsākt paleozoja mugurkaulnieku mikroskopisko atlieku izpētes programmu. Austrāliete Sjūzena Tērnere (*Susan Turner*) vērsās pie potenciāliem sadarbības partneriem ar priekšlikumu organizēt mugurkaulnieku mikroatlieku pētījumiem veltītu starptautisku simpoziju, vēlams Eiropas centrālajā daļā (Turner 1988: p. 2). Starp daudzu pētnieku atsauksmēm bija arī Igaunijas Ģeoloģijas institūta pētnieces Dr. Tiju Mjarss (*Tiiu Märss*) vēstule ar vairākiem priekšlikumiem (skat. *Ichthyolith Issues* 1988, Nr. 1, 9.-10. lpp). Viena no akadēmiķa Dimitrija Kaljo (*Dimitri Kaljo*) idejām – organizēt mugurkaulnieku mikroatlieku izpētes programmu kādas starptautiskās organizācijas, piemēram UNESCO un Starptautiskās ģeoloģijas zinātņu savienības (IUGS) paspārnē. To drīzumā arī izdevās realizēt kā IUGS Starptautisko ģeoloģisko korelāciju programmas (IGCP) 328. projektu "Paleozoja mugurkaulnieku biohronoloģija un globālā jūras/kontinentālo nogulumu korelācija" Dr. Alana Blika (*Alain Blieck*) un Dr. S. Tērneres vadībā. Otras idejas autore Tiju Mjarss ieteica saistīt pirmo "mikromugurkaulnieku" simpoziju ar V. Grosa 90 gadu jubileju un organizēt to Vācijā. Pateicoties profesoru Otto Valizera (*Otto Wallizer*) un Hansa-Petera Šulces (*Hans-Peter*

Schultze) pūlēm, 1993. gada Getingenē notika Valtera Grosa simpozijs, kurā piedalījās vairāk nekā 80 dalībnieku no 20 valstīm, arī viens no šo rindu autoriem (E. L.).

Godinot V. Grosa piemiņu un ievērojot viņa ieguldījumu mūsdienu paleoihtioloģijā, 2003. gadā no 7. līdz 14. septembrim Rīgā, Latvijas Dabas muzejā notika Otrais V. Grosa piemiņai veltītais starptautiskais simpozijs "Paleoihtioloģijas sasniegumi", aizsākot tradīciju atzīmēt izcilā zinātnieka jubilejas ar lasījumiem zemāko mugurkaulnieku paleontoloģijā. Simpozija organizācijā piedalījās Latvijas Universitātes Ģeoloģijas institūta, Ģeogrāfijas un Zemes zinātņu fakultātes un Latvijas Dabas muzeja speciālisti. Turpinot jau pirmā Grosa simpozijā aizsākto sadarbību, arī otrais Grosa simpozijs notika IUGS IGCP 491. projekta "Viduspaleozoja mugurkaulnieku bioģeogrāfija, paleoģeogrāfija un klimats" ietvaros. Viens no simpozija mērķiem bija iepazīstināt tā dalībniekus ar Latvijas un Igaunijas devona un silūra fosilo mugurkaulnieku atradnēm lauka ekskursijas laikā, kura norisinājās pēc simpozija zinatniskās sesijas.

Mutiskie un stenda ziņojumi bija, nu jau var teikt, tradicionāli veltīti zemākajiem mugurkaulniekiem, sākot no telodontiem līdz primitīviem četrkājiem, aptverot galvenokārt ievērojamu evolūcijas posmu no silūra līdz karbonam, bet daži ziņojumi skāra arī ordovika, perma, mezozoja un kainozoja zivju izpētes rezultātus. Lielākā uzmanība tika pievērsta skrimšļzivju, daivspurzivju un tetrapodu, telodontu un bruņuzivju morfoloģijai, evolūcijas aspektiem, bioģeogrāfijai un stratigrāfiskajai nozīmei. Daži ziņojumi bija veltīti arī mugurkaulnieku kompleksu stratigrāfiskajai nozīmei, kā arī silūra un devona biostratigrāfiskajai iedalīšanai. Simpozija laikā notika vairāku darba grupu sēdes, bet daivspurzivju un tetrapodu pētnieki nodibināja jaunu darba grupu, kurā vienojās koordinēt šo mugurkaulnieku evolūcijā īpaši nozīmīgu taksonu pētniecību, lai noskaidrotu zivju-tetrapodu savstarpējās radniecības attiecības, kā arī veicinātu to paleoekoloģijas un paleoģeogrāfisko aspektu izpēti. Simpozijā pārstāvētie 27 mutiskie ziņojumi un 32 stenda referāti uzskatāmi parādīja, ka V. Grosa ietekme nav mazinājusies arī pēc zinātnieka nāves, bet viņa sasniegtie mugurkaulnieku mikroatlieku aprakstīšanas augstie standarti vēl ilgi ietekmēs gan mikropaleontoloģijas nozari, gan paleoihtioloģiju kopumā.

Šis Latvijas Universitātes rakstu sējums aptver tos darbus, kurus iesniedza simpozija dalībnieki. Ceru, ka lasītājam šie raksti liksies interesanti un svarīgi, jo daļa no tiem satur jaunu taksonu aprakstus no samērā maz vai nepietiekami pētītām grupām, kā arī aptver ilgstošu pētījumu rezultātus, kas veikti Baltijas vai tās kaimiņvalstu teritorijā.

Pateicības. Esam ļoti pateicīgi Latvijas Universitātes vadībai par simpozija finansiālo atbalstu un iespēju publicēt simpozijam sagatavotus darbus kā Latvijas Universitātes rakstu speciālo sējumu. Ievērojamu finansiālo atbalstu sniedza arī IUGS IGCP 491. projekts (vadītājs Dr. Zu Mins (*Zhu Min*) un Latvijas Dabas muzeja vadība. Simpozijs nevarēja notikt bez Organizācijas komitejas locekļu A. Ceriņas (LU), L. Lukševičas (LDM), E. Lukševiča (LU, priekšsēdētājs), T. Mjarss (Tallina), H.-P. Šulces (Berlīne), Ģ. Stinkuļa (LU), I. Upenieces (LU), A. Zabeles (LU), I. Zupiņa (LDM) aktīvas darbības. Lielu ieguldījumu rokrakstu vērtēšanā snieguši Alens Bliks (*Alain Blieck*), Hennings Bloms (*Henning Blom*), Kerola Burova (*Carole Burrow*), Edvards Dešlers (*Edward Daeschler*), Deivids Eliots (*David Elliott*), Gevins Jangs (*Gavin Young*), Aleksandrs Ivanovs, Valentīna Karatajūte-Talimā (*Valentina Karatajūte-Talimaa*), Dženifera Klaka (*Jennifer A. Clack*), Tiju Mjarss (*Tiiu Märss*), Ģirts Stinkulis, Sjūzena Ternere (*Susan Turner*), Marks Vilsons (*Mark V.H. Wilson*), Filips Žanvje (*Phylipp Janvier*).

The Gross Symposium 2: Advances in Palaeoichthyology

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At the end of 2003 the community of palaeontologists celebrated centennial anniversary since has born outstanding palaeozoologist Walter Robert Gross. His destiny has been characteristic for 20th century being dynamic and changeable. W. Gross has been a citizen of several now extinct countries – born in Livland, Russian Empire; lived in Weimar Republic, III Reich, Democratic Republic of Germany; long time has been a citizen of a new-born Republic of Latvia; during last period of his life became a citizen of Federative Germany (Schultze 1996). He has born in 20th August of 1903, in Katlakalns, in family of Baltic German Lutheran pastor Ervin Johann Gross. From 1907 to 1918 the Gross family lived in Straupe, pastorate close to the Straupe Castle and Church. Beautiful nature in the vicinity of Straupe already in childhood has aroused a spirit of natural scientist in Walter's soul. He has been interested in plants and animals, collected herbaria and observed birds. In his memoir W. Gross (1974) remembered that already 5 years old he decided to become a zoologist. In teenage years W. Gross started to interest about extinct animals, which fossils he has found in outcrops at the Brasla River banks, and at age of 17 he already started to create serious palaeontological collections.

Being very young, in 1921, W. Gross entered the Naturforsher Vereins zu Riga. He has established contacts with the museum, and later he consigned to this museum his palaeontological materials, which are still kept at the Natural History Museum of Latvia (Lukševics 2002). After the military service in armed forces of Latvia he resettled to Germany, where has spent all the rest of his life, except shorter and longer journeys.

Studies in the Marburg-am-Lane University followed, and he had to do a difficult choice between zoology and palaeontology, but in 1929 he needed to move to Berlin, where the studies continued in the A. Humboldt University. During study years, Gross continued to collect and study the Devonian vertebrate fossils from Gauja River and its tributaries. Based on the work on placoderm fish *Asterolepis ornata* (Gross 1931) the degree of Doctor of Philosophy was assigned to W. Gross in 1931; he became also a corresponding member of the Naturforscher Vereins zu Riga. Several important papers were written between 1931 and 1935, which were focused mostly on the Devonian fishes, mainly from the Baltic.

Since 1936 Gross became a docent at Humboldt University, since 1943 an associate professor at the same university (Schultze 1996). Also during this time he maintained contacts with Baltic geologists and the Naturforscher Vereins zu Riga administration; during this time several publications of Gross were issued on Estonian and Latvian placoderms, acanthodians and sarcopterygians (Gross 1940, 1941). In middle of the 2nd World War professor Gross has been enrolled in the Reich Army, where he served until the end of war; he was interned as prisoner of war, released in 1946. Only in 1949 W. Gross has returned to the Berlin, Humboldt University, where became a professor of palaeontology, director of the Geologische-Paläontologische Institut and Palaeontological Section of the Museum.

After building of the notorious Berlin Wall, at the end of August of 1961, Walter Gross together with wife Ursula arrived in Hamburg, where annual meeting of the German Palaeontological Society took place. As the Gross children were already in Western Europe, W. Gross accepted proposal of professor Schindenwolf to become an associate professor in Tübingen (Schultze 1996). His scientific productivity has not decreased, he published several papers on the fish and agnathan microremains, where not only their external morphology, but also histology was characterized. W. Gross retired in 1969, and in this year his illness with cancer was identified. Nevertheless, he actively continued scientific studies until the end of 1973. W. Gross deceased in June of 1974.

Many publications (total number more than 90) already in 1950-ties have made name of W. Gross famous among wide community of palaeontologists, especially vertebrate researchers from Sweden, Great Britain, France, U.S.A., Russia and particularly from Baltic States. In 1973 the 143rd volume of the journal *Palaeontographica* has been formed completely of papers on palaeoichthyology devoted to 70th jubilee of W. Gross; papers displayed his contacts with colleagues in Europe and North America.

In the Symposium on the Early Vertebrate Palaeontology, held in Beijing in 1987, a group of palaeontologists decided to begin a research programme on the Palaeozoic vertebrate microremains. Australian Dr. Susan Turner wrote a letter to potentially interested partners with proposal to hold an International Symposium on Vertebrate Microremains probably at a centre of Europe (Turner 1988: p. 2). Among many responses there was also a reply from Dr. Tiiu Märss, researcher of the Institute of Geology, Estonia, with several proposals (see *Ichthyolith Issues* 1988: Nr. 1, p. 9-10). The idea of Academician Dimitri Kaljo was to organise the programme of vertebrate microfossils research under auspices of some international organization such as UNESCO or International Union of Geological Sciences (IUGS). This idea has been quite soon realised as the IUGS IGCP Project no. 328 “Biochronology of Palaeozoic Vertebrates and Global Marine/Non-marine Correlation”, leading by Drs Alain Blieck and Susan Turner. Second idea of Tiiu Märss was to relate first “Microvertebrate” Symposium with 90th Jubilee of W. Gross and organise it in Germany. Thanks to efforts of professors Otto H. Wallizer and Hans-Peter Schultze, in Göttingen in 1993 the W. Gross Symposium took place, and more than 80 participants from 20 countries, including one of the authors of this paper (E.L.), attended it.

In honour of W. Gross and considering his contribution in modern palaeoichthyology, the Second International Symposium in Honour of W. Gross “Advances in Palaeoichthyology” has been held in Riga, Natural History Museum of Latvia, in 7-14th September of 2003, giving a start to tradition to celebrate jubilees of great scientist by presentations on the early vertebrate palaeontology. Institute of Geology, University of Latvia, Faculty of Geographical and Earth Sciences, and Natural History Museum of Latvia organized the Symposium. Tradition of the Gross Symposium was continued, and the Second Symposium also took place under auspices of the IUGS IGCP Project 491 “Middle Palaeozoic Vertebrate Biogeography, Palaeogeography and Climate”. One of aims of the symposium was to introduce its participants with the Devonian and Silurian fossil vertebrate sites in Latvia and Estonia during the field trip held after the scientific session.

The oral and poster presentations were, already traditionally, focused on the early vertebrates, mostly from the Silurian to Carboniferous, but some presentations touched also the Ordovician, Permian, Mesozoic and Cenozoic fish study results. Emphasis was put on morphology, aspects of evolution, biogeography and stratigraphic importance of chondrichthyans, sarcopterygians and tetrapods, thelodonts, and placoderms. Some presentations were focused on stratigraphic importance of the vertebrate assemblages, as well as on biostratigraphic subdivision of the Silurian and Devonian. Several workshops took place during the symposium, and researchers of sarcopterygians and tetrapods established a new research group to coordinate studies of these organisms particularly important in evolution of vertebrates, to find out fish-tetrapod relation links and to promote studies of their palaeoecology and palaeogeography. 27 oral presentations and 32 posters clearly showed that authority of W. Gross has not been decreased after his passing away, but his highly put standards on description of the vertebrate microfossils will have an effect on the micropalaeontology and palaeoichthyology for long time.

This volume of *Acta Universitatis Latviensis* comprises the papers submitted by participants of the symposium. I hope that the reader will find the papers interesting and important, because a part of them include descriptions of new taxa from insufficiently studied groups, as well as include results of continuous studies carried out in the Baltic States and their neighbouring countries.

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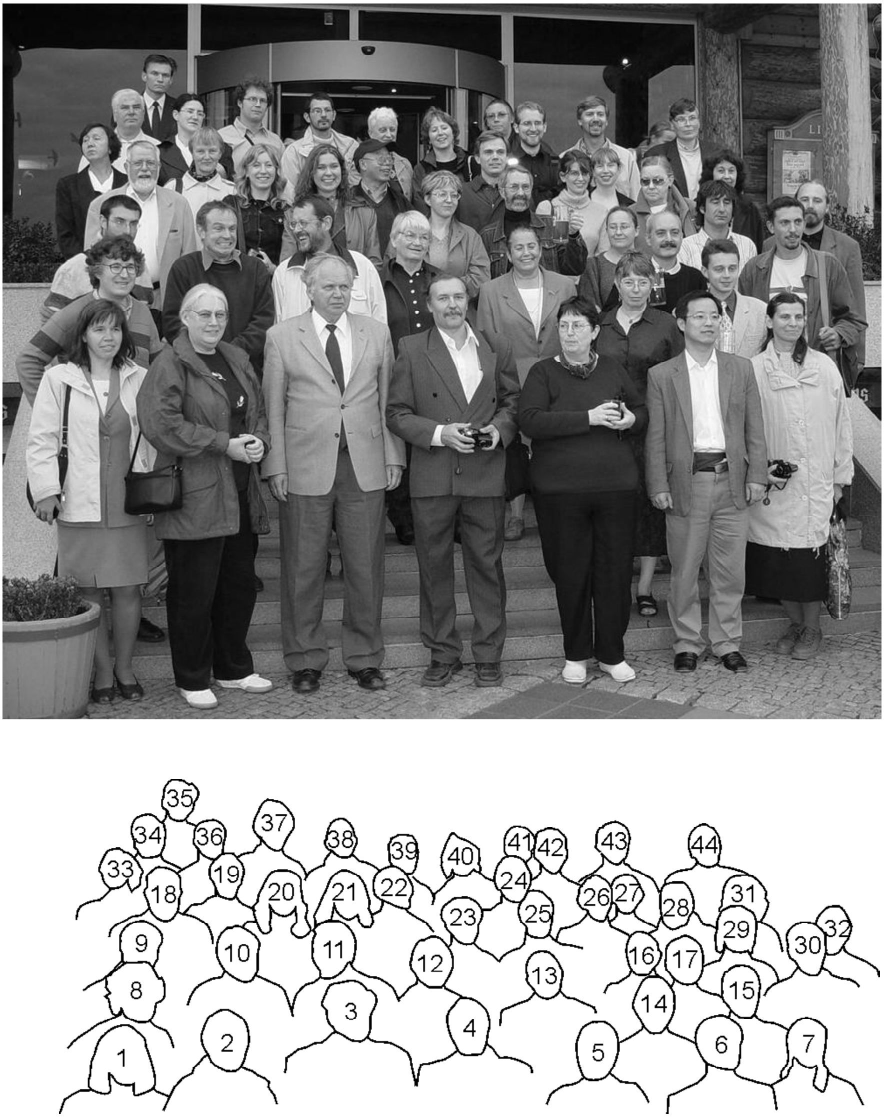

Fig. 1. Simpozija dalibnieki. Participants of the meeting. 1, I. Upeniece; 2, K. Bryan; 3, H.-P. Schultze; 4, E. Lukševics; 5, S. Turner; 6, Zhao Wen-Jin; 7, L. Lukševica; 8, R. Soler-Gijón; 9, Vincent Dupret; 10, C.G. Miller; 11, A. Blieck; 12, V. Karatajute-Talimaa; 13, G. Arratia; 14, J.A. Clack; 15, P. Szrek; 16, G. Zakharenko; 17, M. Ginter; 18, G. Johnson; 19, T. Märss; 20, M. Niit; 21, Ž. Žigaite; 22, Wang Nian-Zhong; 23, O. Afanassieva; 24, P.E. Ahlberg; 25, G.C. Young; 26, R. Wade; 27, E. Sharp; 28, E. Kurik; 29, H. Botella; 30, P. Beznosov; 31, S. Young; 32, D. Plaksa; 33, Z. Yurieva; 34, J. Valiukevicius; 35, I. Zupinš; 36, Ts. Tonashka; 37, H. Blom; 38, G. Clement; 39, C. Burrow; 40, C. Derycke-Khatir; 41, M. Duncan; 42, M. Friedman; 43, E. Daeschler; 44, A. Ivanov. Photo by O. Lebedev.

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Microrelief on the exoskeleton of some early osteostracans (Agnatha): preliminary analysis of its significance

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The surface of the osteostracan exoskeleton has been studied using the SEM on isolated microremains, and small fragments taken from complete cephalothoracic shields. The material comes from the Silurian and Lower Devonian deposits of Severnaya Zemlya Archipelago, Russia, and Saaremaa Island, Estonia. Imprints of epidermal cells on the exoskeleton surface are described for the first time in osteostracans. It is concluded that the sculpture on the osteostracan exoskeleton, both macrosculpture and microsculpture, reflects processes of the probable mode of ossification of the osteostracan hard cover. On the other hand, various types of microsculpture (microtubercles, fine ribs or stripes, microapertures) in general are related to the functional peculiarities responsible for animals' adaptation to the ambient environment, and were necessary for the implementation of metabolic processes in different covering tissues of early vertebrates.

Key words: Palaeozoic agnathans, osteostracans, exoskeleton, surface sculpture.

Introduction

In the last few decades considerable progress has been made in the study of the dermal skeleton of Palaeozoic vertebrates. Use of the scanning electron microscope (SEM) produced new interesting data on the exoskeleton microstructure of different groups, including the fine sculpture of the exoskeleton surface (Smith 1977; Schultze 1977; Deryck and Chancogne-Weber 1995; Märss 2002; Beznosov 2003; also see references in Märss 2002). For instance, fine sculptural elements, about ten microns in diameter, were found on the exoskeleton surface in different groups (in chondrichthyans, acanthodians, and dipnoans) and were explained as imprints of the epidermal cells of integument. However, for osteostracans little is known about the exoskeleton microrelief, and there are no special papers on the subject. The present paper attempts to analyze some of the relevant data for the osteostracan exoskeleton.

Material and methods

Isolated microremains of exoskeleton, extracted by V.N. Karatajute-Talimaa from rock samples by dissolving with formic acid, were determined as *Oeselaspis pustulata* (Patten), *Tremataspis obruchevi* Afanassieva et Karatajute-Talimaa, *Tremataspis* cf. *schmidti*, *T.* cf. *milleri*, and *Tremataspis* sp. (Afanassieva and Märss 1999; Afanassieva 2000). The material comes from the Ust'-Spokojnaya Formation, Ludlow, Upper Silurian of October Revolution Island, Severnaya Zemlya Archipelago, Russia.

Ungulaspis arctoa, described by Afanassieva and Karatajute-Talimaa (1998), occurs in the upper part of the Severnaya Zemlya Formation deposits of the Lower Devonian of October Revolution Island. Exoskeleton microfragments belonging to the holotype of *Ungulaspis arctoa* were taken from the anterolateral and marginal parts of the dorsal shield.

All fragments were studied by the present author using the SEM technique. Complete and fragmented shields of osteostracans from the collections of the Paleontological Institute of the Russian Academy of Sciences in Moscow (mainly, Tremataspidoidei from Silurian of Saaremaa Island) were used for comparison.

Material described in this paper is housed in the Paleontological Institute of the RAS (PIN) and in the Institute of Geology and Geography of Lithuania in Vilnius (LIGG).

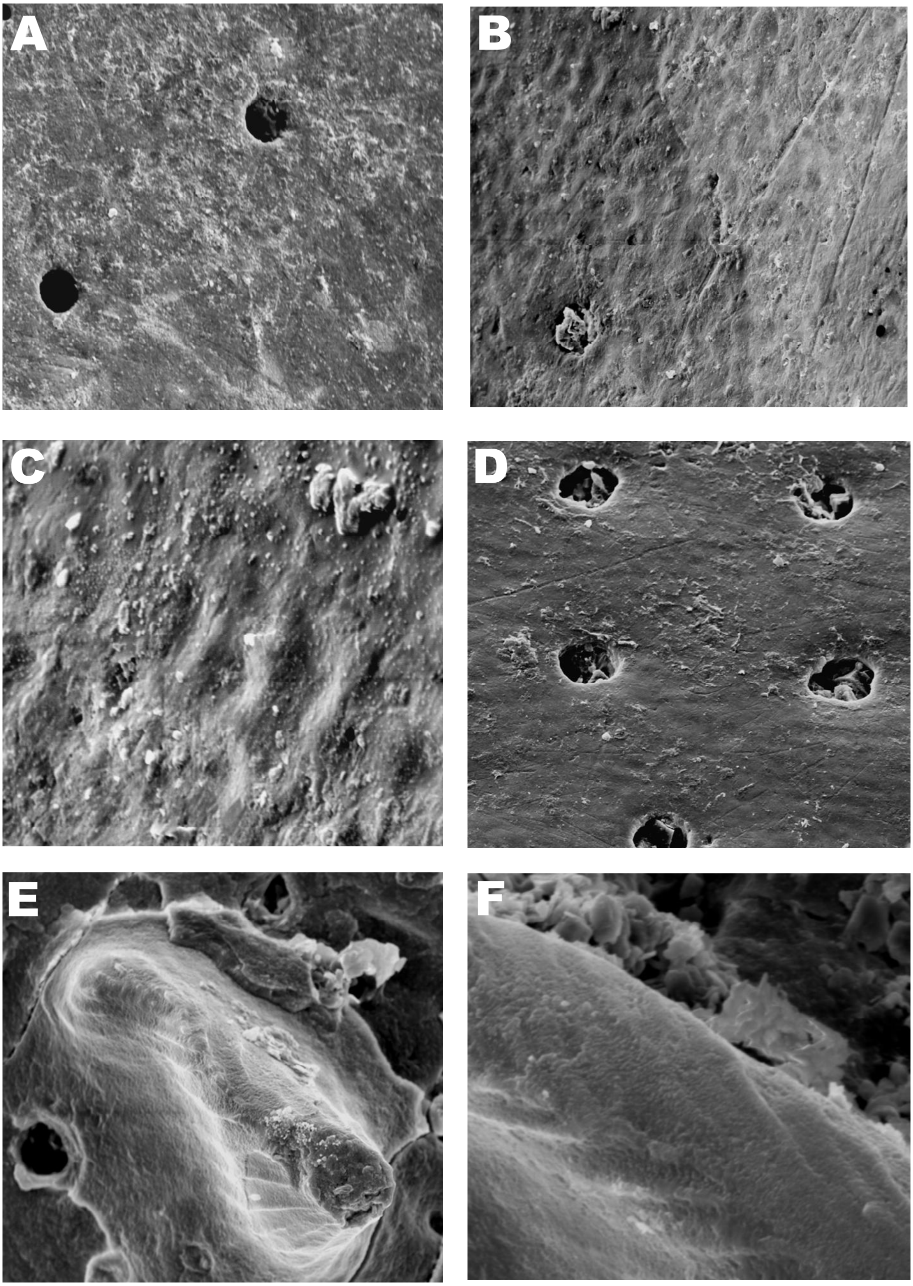
Description and discussion

The surface of the cephalothoracic shields of *Tremataspis* species is smooth and shiny (Robertson 1938; Denison 1951a; Afanassieva and Karatajute-Talimaa 1998). There are only a few, low tubercles on the dorsal side of the interzonal part of the shield. The tubercles have smooth, non-perforated walls and tops. The sensory-line system opens on the surface through the relatively wide pores. The diameter of the pores varies from 10-15 microns (*T. milleri* Patten) up to 40 microns (*T. obruchevi* Afanassieva et Karatajute-Talimaa).

The surface of trunk scales of *Tremataspis* is usually shiny and smooth (Fig. 1 A). The scales are thick, with all three layers of exoskeleton well developed. The basal layer has a typical cross-laminated structure and forms a significant part of the exoskeleton. No fragments and scales with tubercles were found. Some scales demonstrate an infrequent type of fine sculpture. On the surface of the scale (specimen PIN 4765/20) irregular polygons reminding a honeycomb pattern are clearly visible (Fig. 1 B, C). Their diameter is about 10 microns. Similar ultrasculpture has been found on the surface of cephalothoracic shields, and of several scales of *Tremataspis* species from the Silurian deposits of Saaremaa Island, Estonia (Fig. 1 D).

The surface of the cephalic shield of *Ungulaspis arctoa* in the anteromedial parts of the dorsal side are covered with small rounded and elongated tubercles (Afanassieva and Karatajute-Talimaa 1998; Afanassieva 1999, pl. 1, fig. 1). The tubercle sides are composed of relatively compact tissue without any foramina. The surface of the tubercles is covered with fine ribs which form a peculiar microrelief (Fig. 1 E, F). The distance between the ribs is about 5 microns. The ribs usually meet at the top of the rounded tubercle and at the apical part (ridge) of the elongated one. Similar ribbing is found on the side surfaces of the large (about 1 mm in length) elongated tubercles situated along the anterior and lateral edges of the cephalic shield of *Ungulaspis arctoa* (Afanassieva 1999, pl. 1, fig. 4).

To clarify the significance of the thin ribbing of the osteostracan exoskeleton we should focus our attention on the external skeleton of *Thyestes verrucosus* Eichwald. The surface of the *Thyestes* shield is covered with numerous tubercles (Stensiö 1932; Denison 1951b) that can be divided into three types: large tubercles with curved tips,


A
B
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E
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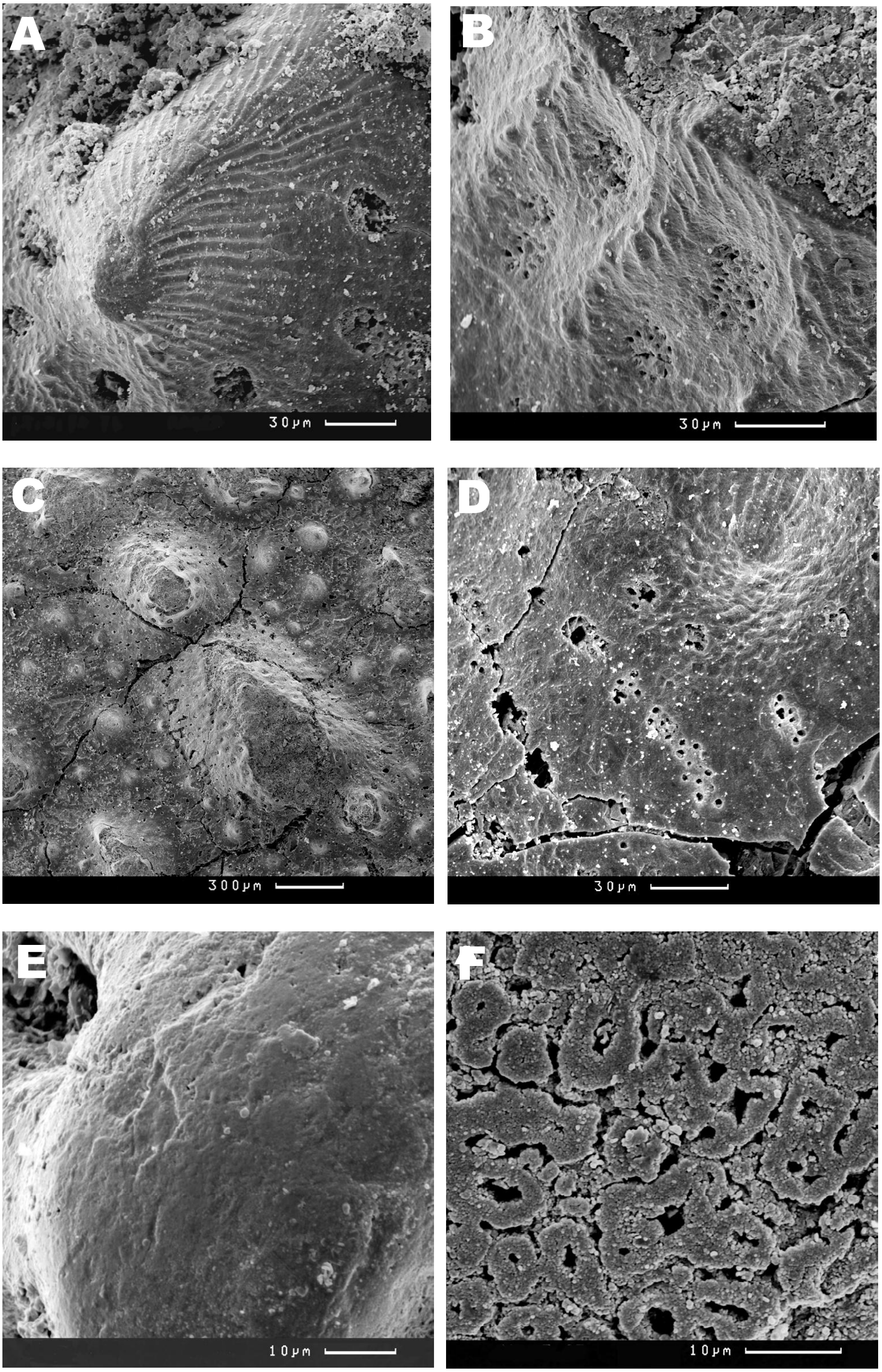
arranged in longitudinal rows (diameter at the base about 1 mm), tubercles of medium size with straight tips (about 0,3 mm), and numerous small (0,03-0,15 mm) ribbed tubercles (Afanassieva 1985). A row (sometimes two or three rows) of shiny flattened tubercles is arranged along the anterior and lateral edges of the cephalic shield. As in *Ungulaspis arctoa*, thin ribbing of *Thyestes verrucosus* is located on the surface of the tubercles of small size, in the lower parts of medium-sized tubercles, and on the surface of the marginal tubercles. The hypermineralized tissue of the superficial layer is present only in the apical parts (tips) of the large tubercles, of medium-sized tubercles, and of marginal ones. The basal layer is poorly developed. The exoskeleton mainly consists of relatively friable bony tissue of the middle layer, with numerous cavities of various sizes.

The assumption that the exoskeleton of this type was covered by soft tissue (Stensiö 1927, 1932) is supported by the position of the elements of the sensory system in the covering of *Thyestes verrucosus* (Denison 1951a, b). In my opinion, the arrangement of the main sensory lines in the exoskeleton of this species is marked by the elongated tubercles of medium size, disposed in pairs along the conjectural sensory canals (Afanassieva 1985, 1991, pl. VI, fig. 6). The set of the main sensory lines and their distribution pattern, marked by the tubercles of that type, are characteristic of this osteostracan group. It is possible to identify the infraorbital, postorbital, transversal and main lateral sensory lines in the *Thyestes* exoskeleton. The sensory lines of *Thyestes* were located between the "sensory" tubercles, i.e. superficially to the exoskeleton. In addition, I suppose that variously sized cavities at the bases of marginal flattened tubercles in *Thyestes verrucosus* and *Aestiaspis viitaensis* contained soft tissues of the cutaneous covering.

Thus an analysis of mutual arrangement of the exoskeletal structures in *Thyestes verrucosus* reveals that the external skeleton was covered by soft tissue. In this connection it is important to note that the fine ribbing is found on the surface of the exoskeletal structures that were surrounded by soft tissue (small tubercles, lower parts of medium-sized tubercles and of marginal ones). I suppose the fine ribbing was used for optimal conjunction between the layers of the soft and hard tissues within the cover. The same assumption stands for the external skeleton of *Ungulaspis*, *Aestiaspis, Septaspis* and other osteostracans, and early vertebrates, with the similar type of exoskeleton microrelief.

As is known, numerous microapertures (2-5 microns in diameter) are located on the surface of the exoskeleton of some early osteostracans. They are often grouped in pore

Fig. 1. A-D, surface of the *Tremataspis* exoskeleton: A, smooth surface of *Tremataspis* cf. *milleri* Patten, specimen PIN 4765/30, Ust'-Spokojnaya Formation, Ludlow, Upper Silurian; 14, locality 47, Spokoinaya River, October Revolution Island, Severnaya Zemlya Archipelago, Russia; B, C, *Tremataspis* sp., specimen PIN 4765/20, Ust'-Spokojnaya Formation, Ludlow, Upper Silurian; locality 31 (talus), Ushakov River, October Revolution Island; D, *Tremataspis milleri*, fragment of the specimen PIN 4219/ 7, Kuusnymme Beds of Rootsiküla Regional Stage, Upper Wenlockian, Lower Silurian; Elda Cliff, Saaremaa Island, Estonia. E, F, *Ungulaspis arctoa* Afanassieva et Karatajute-Talimaa, Severnaya Zemlya Formation, Lochkovian, Lower Devonian; Pod'emnaya River, October Revolution Island, Severnaya Zemlya Archipelago, Russia; microfragment (PIN 4766/1) of the holotype LIG 35-670; tubercles with fine ribbing on the surface of the cephalic shield.


A
30µm
B
30µm
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30µm
E
10µm
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fields. These structures (or perforated septa in species with a well-developed exoskeleton), connected with the sensory system, are typical for most of the members of the suborder Tremataspidoidei (*Tremataspis*, *Dartmuthia*, *Saaremaaspis*, *Oeselaspis*, *Procephalaspis*, *Thyestes*, *Aestiaspis*, *Septaspis*). It should be noted that exoskeletal microstructure of *Sclerodus* and *Tyriaspis* (possible Tremataspidoidei) has never been investigated, and in *Witaaspis* similar structures were not found (Afanassieva 1991). In my opinion their absence in *Witaaspis* is probably due to incomplete exoskeletal development in this form (the thin cephalothoracic shield is composed only of a part of the middle and basal layers).

In *Thyestes verrucosus* a large number of pore fields is located on the surface of the shield and on the slopes of large and medium-sized tubercles. As a rule, no trace of the polygonal pattern typical of osteostracans is observed. I studied the cephalothoracic shield of *Thyestes verrucosus* (specimen PIN 1628/31), in which, as supposed, the processes of dermal ossification have not been completed. The material comes from the Viita or the Vesiku Beds of the Rootsiküla Regional Stage. In the posterolateral parts of the dorsal side of the shield radiating canals were found opening on the surface of the exoskeleton (Fig. 2 C). It has been determined that pore fields on the slopes of large tubercles are aligned in rows along radiating canals (Fig. 2 D). Distal parts of these canals, open from above, form a pattern, typical of osteostracans, and determine approximate borders of "tesserae" of various sizes. It is assumed that the large tubercles of longitudinal rows (along the ribs of rigidity of the dorsal shield) emerged first. The formation of the exoskeleton began with the laying of dentine tips of the tubercles, and proceeded centripetally. Middle-sized tubercles with thin tips were formed between them. Every tubercle was laid in the center of an individual "tessera". Finally, small tubercles emerged last in ontogenesis, which is proved by their location on the slopes of larger tubercles. The exoskeleton of *Thyestes verrucosus* developed relatively rapidly but slower than in species of *Tremataspis*. The existence of a system of units (tesserae), gradually increasing in size, allowed the individual to grow during a longer period of time up to complete consolidation of the shield, and also distributed the burden on the organism resulting from a rapid process of shield formation (Afanassieva 2002).

In *Oeselaspis pustulata* (Patten) the tops of large tubercles are capped with a thick layer of enameloid tissue and mesodentine (Denison 1951b). Usually the surface of large tubercles is smooth (Fig. 2 E). The microfragment of the cephalothoracic shield of *Oeselaspis pustulata* (specimen PIN 4765/65) is distinguished from the others by the surface sculpture of one of the large tubercles (Fig. 2 F). A part of the largest tubercle

Fig. 2. A-D, *Thyestes verrucosus* Eichwald, specimen PIN 1628/31, dorsal part of cephalothoracic shield; Viita or Vesiku Beds of Rootsiküla Regional Stage, Upper Wenlockian, Lower Silurian; Saaremaa Island, Estonia; A, fine ribbing on the surface of small tubercle; B, fine ribbing on the lower part of the medium-size tubercle with broken apical part; C, tubercles of different sizes and open radiating canals on the surface of the shield; D, pore fields on the slope of the large tubercle lining up along radiating canals. E, F, *Oeselaspis pustulata* (Patten), specimen PIN 4765/65, microfragment of cephalothoracic shield; ?upper part of the Samojlovich Formation, Upper Wenlock, Lower Silurian; sample 5D/76, locality Sosednii, Jungsturm Strait, Pioneer Island, Severnaya Zemlya Archipelago, Russia; E, smooth surface of the large tubercle; F, surface of the horizontal section of the large tubercle as a result of acid-etching (or/and abrasion).

surface demonstrates a complicated pattern, composed of pits of different sizes (1-5 microns) and diversely directed grooves. In the present case the enameloid and (partly) mesodentine tissue are missing as a result of acid-treatment (or/and abrasion), and the odontocyte cavities and narrow grooves of canaliculi branching off from them become visible at the horizontal section of the superficial layer (Afanassieva 2000). M.M. Smith has also described a similar type of tissue in *Griphognathus whitei* Miles (Smith 1977: pl. 2, fig. 28-31; pl. 3, fig. 32; the surface of the tooth ridge after acid-treatment). Thus in osteostracans the characters of the exoskeleton, including fine sculpture, can be used for taxonomic purposes, and are necessary for the identification of fragmentary material; however we must take into consideration that an abrasion or acid-etching can cause the appearance of unusual microrelief on the exoskeletal surface.

The information presented above leads to the conclusion that the sculpture on the osteostracan exoskeleton, both macrosculpture and microsculpture, reflects processes of the probable mode of ossification of the osteostracan hard cover. On the other hand, various types of microsculpture (microtubercles, fine ribs or stripes, microapertures) in general are related to the functional peculiarities responsible for the animals' adaptation to the ambient environment, and were necessary for the implementation of metabolic processes in different layers (and between the layers) of covering tissues of early vertebrates.

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Dažu agrīno kaulvairodžu ārējā skeleta mikroreljefs: tā nozīmīguma sākotnējā analīze

OLGA B. AFANASJEVA

Kaulvairodžu (Osteostraci) ārējais skelets pētīts skanējošā elektronmikroskopā, izmantojot atseviškas mikroskopiskas atliekas un nelielus fragmentus no veseliem galvkrūšu vairogiem. Izmantots materiāls no Severnaja Zemļas arhipelāga (Krievija) un Sāmsalas (Igaunija) silūra un apakšējā devona nogulumiem. Pirmo reizi ir apraksīti epidermālo šūnu nospiedumi kaulvairodžu ārējā skeleta virsmā. Secināts, ka kaulvairodžu ārējā skeleta ornamentējums, gan makro-, gan mikroskulptūra, iespējams, ataino kaulvairodžu cietā apvalka pārkaulošanās procesu īpatnējo veidu. No otras puses, dažādu mikroskulptūras paveidu daudzveidība (mikropauguri, smalkas ribas vai švīkas, mikroskopiskas atveres un poras) kopumā ir saistīta ar tām organismu funkcionālām īpatnībām, kas nosaka dzīvnieku pielāgošanos mainīgiem vides apstākļiem, un tā ir nepieciešama vielmainas procesu nodrošināšanai agrīno mugurkaulnieku ārējā apvalka dažādos audos.

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A revision of *Obruchevia* (Psammosteida: Heterostraci) and a description of a new obrucheviid from the Late Devonian of the Canadian Arctic

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Psammosteids are the youngest heterostracans, surviving until the end of the Frasnian in western Europe where their faunal succession is well known. Recent collections made by the 1999-2002 Nunavut Paleontological Expeditions from the Devonian clastic wedge across Melville, Bathurst, Devon, and Ellesmere islands now show a similar psammosteid faunal succession in the Canadian Arctic. Some very thick psammosteid plates from southern Ellesmere lack dentine tubercles but do have an increased amount of the hard tissue pleromin infilling the spongy aspidin at the surface. This feature is otherwise known only in the psammosteid *Obruchevia,* described from the Lovat′ River, Novgorod District, northwestern Russia. The dorsal plates of *Obruchevia* are large, notably thick, and cardiform and appear to have grown by the addition of lateral flanges that developed from the lower surface of the margins. The surface is ornamented with radial furrows and pits. The branchial plates have a vertically directed lateral margin that would have functioned as a runner. Previously undescribed specimens from the Lovat′ River, housed in the collections of the Natural History Museum of Latvia, Riga, confirm the structure of the branchial plates and show that the ventral plate, not known before in *Obruchevia*, had a deep posterior notch similar to that found in *Schizosteus*, *Pycnolepis, Pycnosteus, Ganosteus*, and *Tartuosteus*. The almost complete specimens of the branchial plates from the Palaeontological Institute, Russian Academy of Sciences, Moscow, allow this plate to be more fully described. Although the obrucheviid from the Canadian Arctic is incomplete and shows an ornament of large elongated blisters and irregular ridges rather than pits and grooves, it also possessed a ventral plate with a well-developed posterior notch. In addition a well-developed dorsal sensory canal system is present as open surface grooves, an unusual feature in psammosteids. This species is clearly related to *Obruchevia* within the Obrucheviidae.

Key words: Heterostraci, Psammosteida, Arctic Canada, Late Devonian, *Obruchevia*.

Introduction

Psammosteids (Suborder Psammosteida) are a group of heterostracans, extinct jawless vertebrates (Agnatha) in which the head and body are covered by a series of plates that form a bony carapace. Heterostracans are characterized by a pair of common branchial openings on either side of the head armor and are known to range from the Wenlock (Lower Silurian) to the Late Frasnian (Late Devonian). Psammosteids are known from the Early Devonian (Pragian) up to the Late Devonian (Frasnian), and are particularly characteristic of the Middle Devonian where they have been used as zonal indicators (Mark-Kurik 2000; Weddige 2000). Species of some genera (*Tartuosteus*, *Pycnosteus*) reached almost 2 m in length and breadth making them by far the largest heterostracans known; however, only the Early Devonian forms are preserved in articulation (Gross 1963), while later forms are known only from isolated plates. Early Devonian psammosteids are found in Germany, South West England, and Luxembourg (one genus) and Poland (two genera); in the Middle Devonian they are particularly common in the Baltic area (Estonia, Latvia) and the adjacent parts of Russia, the Leningrad and Pskov regions (seven genera). In the Middle and Late Devonian psammosteids also occur in Scotland, the Timan region and the Severnaya Zemlya Archipelago (Russia), Spitsbergen, Greenland, and Arctic Canada. In the Late Devonian their numbers significantly diminished (represented mainly by two genera) and at the end of the Frasnian psammosteids died out over almost their entire range, the last representatives occurring in late Frasnian deposits in the Canadian arctic.

Psammosteids have been studied since the first half of the 19th century. However, the most important work on them was carried out in the 1960's resulting in two monographs being published practically at the same time (Halstead Tarlo 1964, 1965; Obruchev and Mark-Kurik 1965). The work by Obruchev and Mark-Kurik contains the description of well preserved psammosteid material from the territory of the former Soviet Union, particularly from the Baltic area. Halstead Tarlo's monograph is an overview of the entire suborder and includes a short overview of the taxa described by Obruchev and Mark-Kurik. Since the publication of the above monographs, a number of papers has been published on psammosteid morphology and taxonomy (Halstead Tarlo 1967a, Halstead 1974; Lyarskaya 1971; Mark-Kurik 1968, 1984, 1993, 1999; Obruchev 1967); nevertheless, the overall taxonomy of the group has not been reviewed since it was presented in the monograph by Obruchev and Mark-Kurik (1965). It has been generally accepted that psammosteids were derived from another heterostracan taxon, the Pteraspidida (Elliott 1984; Blieck *et al.* 1991); however, this view has yet to be tested by modern phylogenetic analysis using computer-assisted methods (Janvier 1996).

The Canadian Arctic record of psammosteids has been based on a small collection from southern Ellesmere Island along Goose Fiord. This area was visited first during the explorations of The Second Norwegian Arctic Expedition in the Fram (1898-1902) under the command of Otto Sverdrup. At that time fossil vertebrates, including a few psammosteid fragments, were collected by Per Schei, geologist to the expedition, from strata referred to as "Series E," but now designated as the Fram Formation within the Okse Bay Group (Mayr *et al.* 1994). The psammosteid fragments were described as two species of *Psammosteus* by Kiaer (1915) and revised by Halstead Tarlo (1965), but no further work was carried out until 1999, 2000, and 2002, when expeditions led by one of us (Daeschler) made a large collection of vertebrates, including psammosteids, from the Devonian clastic wedge that stretches from Melville across Bathurst, Devon, and Ellesmere islands. The psammosteid material ranges in age from the Frasnian (Fram Formation, Okse Bay Group) into possibly the early Famennian (Parry Islands Formation) (Mayr *et al.* 1994, 1998; Trettin 1978) although the Famennian age attribution seems doubtful as little stratigraphic control is available. Regardless, the collection appears to include some of the youngest known psammosteids (and heterostracans) as well as greatly extending the area from which these animals are known. The collection is currently being described by two of us (Elliott and Mark-Kurik) and includes some of the same species that occur in the Baltic (Elliott *et al.* 2003), thus allowing the development of a correlation scheme (Obruchev and Mark-Kurik 1968).

Included within the collection are plate fragments from the Late Devonian Clastic Wedge that are extremely thick and that do not have a surface ornament of dentine tubercles. This feature is otherwise only described in the aberrant psammosteid *Obruchevia* (Obruchev 1936) from the Lovat′ River, northwest Russia. In this paper we describe the new Canadian material and also add to the knowledge of *Obruchevia* by the description of additional material from the collections of the Latvian Natural History Museum, Riga, and the Palaeontological Institute, Russian Academy of Sciences, Moscow.

Stratigraphy

Most of the Canadian Arctic obrucheviid material in this report was collected from a single site near Okse Bay on southern Ellesmere Island (Fig. 1). The site, designated as field site NV2K11, is within the lower to middle part of the Nordstrand Point Formation exposed on the northern limb of the Schei Syncline. The fossil site is located within 2km of the type section of the Nordstrand Point Formation as designated by Embry and Klovan (1976). Most of the Nordstrand Point Formation is middle Frasnian in age based on palynomorph samples, although the upper 100 to 200 meters of the 675-meter-thick type section are late Frasnian (Embry and Klovan 1976). The Nordstrand Point Formation is the uppermost unit of the Okse Bay Group. On southern Ellesmere Island the Okse Bay Group is a 3000-meter-thick succession of fluvial sediments derived from tectonic highlands to the east that fed several fluvial systems prograding generally to the southwest (Mayr *et al.* 1994).

The fossiliferous horizon at the NV2K11 site is a dark, carbonaceous siltstone. The obrucheviid and other fossil material is abundant in the fissile siltstone as well as an underlying ironstone layer. The total thickness of this fossiliferous zone is 120 to 150 mm. The sediments suggest a low energy overbank depositional setting rich in organic material. Fossil plant material occurs as large compressed stems and as three-dimensional stems up to 100 mm in diameter. Associated vertebrate fauna from the NV2K11 site includes *Psammosteus* sp., *Bothriolepis* sp., and *Holoptychius* sp.

An additional fragment of obrucheviid plate was recovered in 1999 from the sequence of Late Devonian clastic sediments near the southern coast of Ile Vanier (Bathurst Island Group). This locality is designated NV9918, and is 400 km west of the NV2K11 site (Fig. 1). The stratigraphic position of the NV9918 site is problematic, although currently mapped as within the Cape Fortune Member of the Parry Islands Formation by Harrison and de Freitas (1998). The Cape Fortune Formation is mainly early Famennian in age (Embry and Klovan 1976). Harrison's mapping was based on lithostratigraphic markers; however, the obrucheviid specimen, as well as psammosteid material from other localities on Ile Vanier, suggest that it is in error. It is more likely that the psammosteids on Ile Vanier are from the upper part of the Beverly Inlet Formation and therefore Frasnian in age. The Beverly Inlet Formation is considered to be distal facies

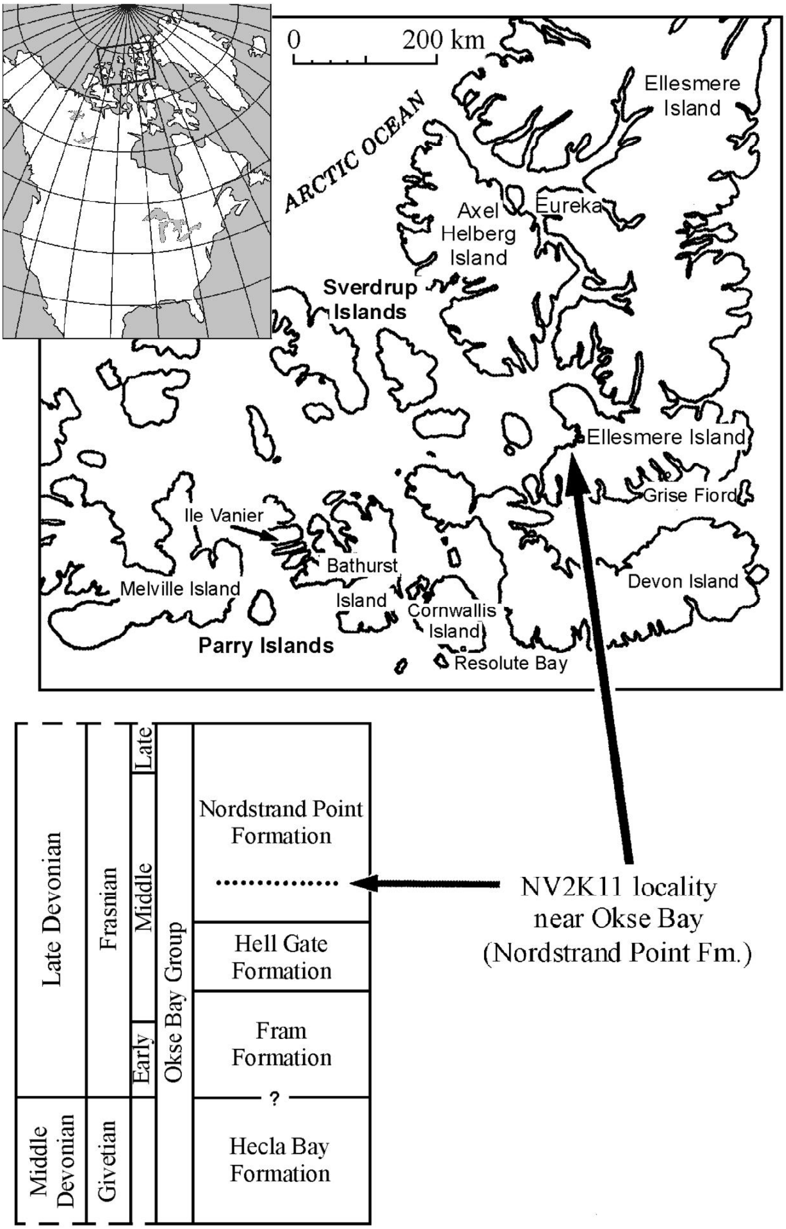


Fig. 1. Map of the central Arctic Islands showing the fossil locality and the Late Devonian stratigraphic section on southern Ellesmere Island.

of the Okse Bay Group, and the lower part of the Nordstrand Point Formation correlates with the upper part of the Beverly Inlet Formation (Embry and Klovan 1976). Thus, the obrucheviids from the Canadian Arctic can be a valuable biostratigraphic tool for intrabasinal, as well as interbasinal correlations.

Material and methods

The material both from the Canadian Arctic and Russia was collected in a weathered condition, and preparation has been minimal beyond that needed for repair. The *Obruchevia* material is held in the collections of the Natural History Museum of Latvia, Riga (prefixed Pl), and the Palaeontological Institute, Russian Academy of Sciences, Moscow (prefixed PIN), and the Canadian Arctic material is held in the collections of the Canadian Museum of Nature, Ottawa (prefixed CMN).

Systematic palaeontology

Order PTERASPIDIFORMES Berg, 1940
Suborder PSAMMOSTEIDA Tarlo, 1962
Family OBRUCHEVIIDAE Tarlo, 1964
Genus *Obruchevia* Whitley, 1940

Discussion. The generic name problem. In 1941 D. Obruchev described a peculiar Late Devonian heterostracan under the name *Aspidosteus heckeri* gen. nov. sp. nov. He considered it to be a member of the family Cardipeltidae of the suborder Psammosteida. Based on this description, Berg (1955) established the family Aspidosteidae in the order Psammosteiformes. In 1964 Obruchev accepted both the above family and generic names, and mentioned as a synonym the name *Obruchevia*, given by Whitley (1940). Whitley, however, establishing that the name *Aspidophorus*, preliminarily used by Obruchev for the heterostracan, was preoccupied, changed the name *Aspidophorus* (not *Aspidosteus*) into *Obruchevia*. It appeared that Obruchev's first publication on this heterostracan appeared in 1936, when in a paper of the popular-scientific journal Priroda (Nature), he gave a description and figure of the dorsal shield under the name *Aspidophorus heckeri* n.gen. n.sp. Obruchev later (1941, 1964) did not refer to his paper of 1936, and he also did not mention his own usage of the name *Aspidophorus heckeri* (*nomen nudum*) in a stratigraphical paper by Hecker *et al.* (1935).

Whitley (1940) established that the generic name *Aspidophorus* was preoccupied for recent cottoid fishes. In 1940 (or earlier?) Obruchev may have discovered this for himself, as he renamed the heterostracan *Aspidophorus heckeri* as *Aspidosteus heckeri.* It is not impossible that Whitley did not know of Obruchev's paper of 1940, published in a sedimentological symposium volume in October 1940 (in imprint [impressum] the date is 7th October 1940). Whitley's paper was published in May of 1940, thus having firm priority.

Halstead Tarlo (1964, p. 20; 1965, p. 149) explained in detail the problems concerning the generic name. He published the family name, Obrucheviidae Tarlo, 1964, generic name *Obruchevia* Whitley, 1940, and species name *Obruchevia heckeri* (Obruchev, 1936) as the valid ones (Halstead Tarlo 1965); however, he did not refer to Obruchev's paper of 1940. Obruchev and Mark-Kurik (1965, p. 19, 78) used the name *Aspidosteus*, and mentioned Obruchev's paper of 1940. They did not, however, describe the genus *Aspidosteus* as the monograph concerned only the representatives of the family Psammosteidae Traquair.

Obruchev could not and did not consider the name *Obruchevia* Whitley, 1940 as a *nomen nudum* as Whitley correctly followed the Article 13 of the International Code of Zoological Nomenclature (1964), referring to Obruchev's paper of 1936. Obruchev (1964) did not ignore Whitley's (1940) corrections of fish names in other cases, either. For example, he recognized Whitley as the author of the generic name *Cyrtaspidichthys* for the genus *Cyrtaspis* Bryant, 1932. Whitley anticipated White and Moy-Thomas (1940), who published a new name, *Eucryptaspis,* for Bryant's genus only one month later (in June 1940).

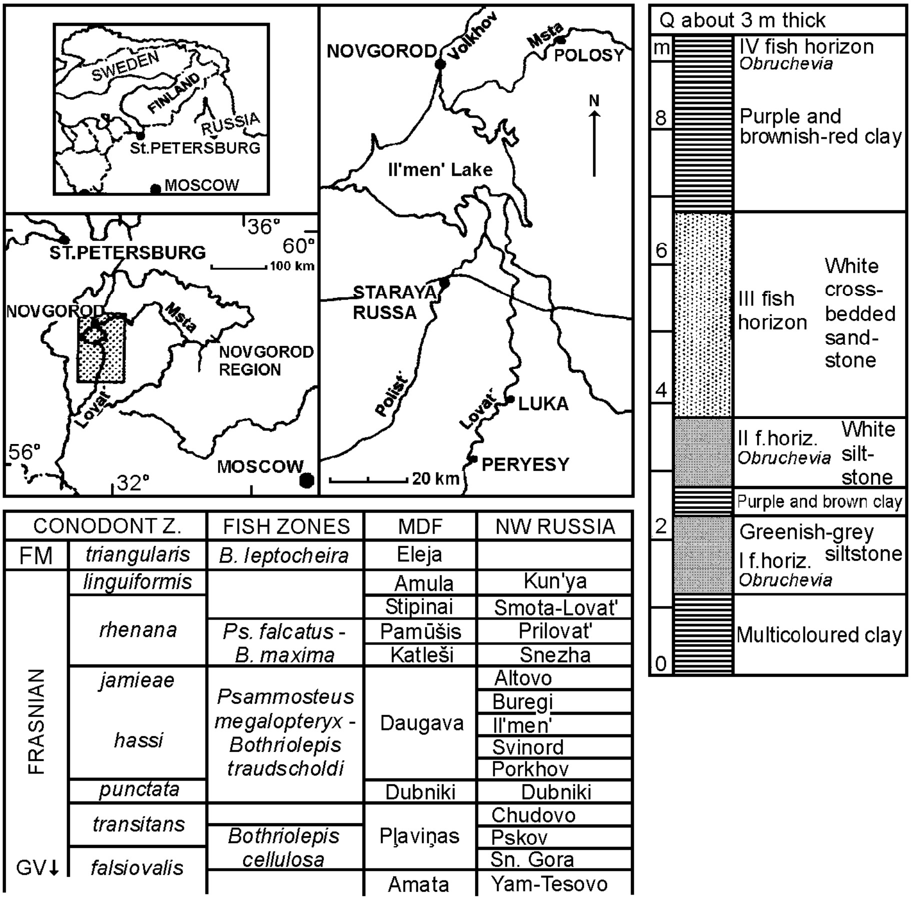
In many papers published after 1941 on Devonian biostratigraphy (e.g., Blieck *et al.* 1988) and fish paleontology of the NW of the East European platform, including Obruchev's own papers (e.g., that of 1967), the name *Aspidosteus* (not *Obruchevia*) was commonly used. It was, however, not the case with Halstead Tarlo who regularly used the name *Obruchevia* in his publications (Halstead Tarlo 1963, p. 3; 1967b, p. 1233; Halstead 1969, p. 22; 1974, p. 61 *etc.*) but not yet in Halstead Tarlo 1962 (p. 261). Therefore, in relation to the priority problem, the stability or universality criteria cannot be applied (see Article 23 in the International Code of Zoological Nomenclature, 1999).

There seem to be two possibilities: (1), Obruchev considered his description of *Aspidophorus* (later called *Aspidosteus* or *Obruchevia*) in 1936 not valid as publication was in a popular science journal (Priroda); or (2), he published the name *Aspidosteus* in some paper before May of 1940, i.e. before the correction was made by Whitley (however we have not found such a paper). Halstead Tarlo (1964, p.124; 1965, p. 159) referenced two of Obruchev′s papers in press (Obruchev, D., 1965a, "On the branchial plates of *Aspidosteus*," and Obruchev, D., 1965b, "*Pycnosteus nathorsti* n. sp. from the Middle Devonian of Spitsbergen") but unfortunately, neither was ever published.

It is concluded here that as Obruchev (1964, p. 75 in the Russian edition) clearly indicated that the genus *Aspidosteus* was established by him in 1941, the priority belongs to the name *Obruchevia* Whitley, 1940, and the name *Aspidosteus* Obruchev, 1941 is its junior synonym.

Localities. Obruchev (1964) mentioned that *Aspidosteus* was known from the Novgorod Region, Russia, and from Latvia. According to Lukševičs (2001) *Aspidosteus* occurs in Latvia in the Pamūšis Regional Stage, whereas in Lyarskaya and Lukševičs (1992) it was mentioned as occurring in two units: the Katleši and Ogre (= Pamūšis) formations. Lukševičs (pers. comm. 2003) is of the opinion that the occurrences of *Aspidosteus* from Latvia were after all erroneously reported.

The main distribution area of *Obruchevia* is the Novgorod Region, NW Russia (Fig. 2, upper left). Six *Obruchevia* (*Aspidosteus*) localities have been reported on the River Lovat′ about 30 km upstream from the railway bridge of the connection between



CONODONT Z.		FISH ZONES	MDF	NW RUSSIA
FM	*triangularis*	*B. leptocheira*	Eleja	
FRASNIAN	*linguiformis*		Amula	Kun'ya
	rhenana		Stipinai	Smota-Lovat'
		Ps. falcatus - B. maxima	Pamūšis	Prilovat'
			Katleši	Snezha
	jamieae	*Psammosteus megalopteryx - Bothriolepis traudscholdi*	Daugava	Altovo
				Buregi
	hassi			Il'men'
				Svinord
				Porkhov
	punctata		Dubniki	Dubniki
	transitans		Pļaviņas	Chudovo
		Bothriolepis cellulosa		Pskov
GV↓	*falsiovalis*			Sn. Gora
			Amata	Yam-Tesovo

Fig. 2. Map of the Novgorod area to show the *Obruchevia* localities and the section of the Prilovat′ Formation at the Luka locality on the Lovat′ River, and the Frasnian biozones and subdivisions in the NW of the East European Platform (modified after Lukševics 2001). Abbreviations: FM, Famennian, GV, Givetian, MDF, Main Devonian Field, the Baltic part.

Staraya Russa and Bologoe (to the East), at Cherenchitsy, and about 20 km further upstream. One more locality is known from the Msta River at Polosy northeast of Novgorod. The type locality of *Obruchevia* (*Aspidosteus*) is at Kulakova, on the Lovat′ River (Obruchev 1941).

In 1958 an expedition led by Prof. D. Obruchev to the Novgorod Region yielded many *Obruchevia* plates upstream of Luka on the River Lovat′. A large dorsal shield and several branchial plates were excavated, and Halstead Tarlo briefly described the latter in 1965. The *Obruchevia* collection belonging to the Natural History Museum of Latvia was collected in 1998 and comes from the Peryesy locality (Fig. 2). It includes several fragments of dorsal plates, a large fragment of the right branchial plate and a ventral plate fragment.

Obruchev (1940) published the description of the Luka section in his paper on the Devonian river delta on the Lovat′ River. In 1958 about 10 m of the section was documented by Elga Mark. The Luka locality (Fig. 2, upper left) is an extensive outcrop, consisting of rather soft terrigenous rocks of the Frasnian Prilovat′ Formation (Fig. 2, lower left). It consists of purple, brown, red or greenish clay, and white, yellow or brownish siltstone and sandstone (Fig. 2, right). Fossil fishes were discovered in a clay bed (IV fish horizon) and three siltstone and/or sandstone beds in the lower part of the section, the II fish horizon being the richest. In both these horizons the same fishes occurred: *Obruchevia heckeri*, *Bothriolepis maxima* and the sarcopterygian *Platycephalichthys bishoffi*. The II horizon yielded an additional psammosteid, *Psammosteus falcatus*. According to Esin *et al.* (2000) the above mostly large or very large forms characterize the Snezha-Prilovat′ (or Katleši-Pamušis) interval of the Upper Frasnian of the NW of the East European Platform (Fig. 2, lower left). *Psammosteus falcatus* and *Bothriolepis maxima* are Late Frasnian index fossils (Lukševics 2001). The marine basin during the Pamušis (Ogre)-Prilovat′ time was shallow and dominated by clastic sedimentation. The main source area of rich detrital material was situated to the north and northwest in the area occupied by the modern Baltic Shield (Sorokin 1978, p. 236, fig. 50).

Obruchevia heckeri (Obruchev, 1936)

(Figs. 3-5)

Diagnosis. (Modified after Halstead Tarlo, 1965) Dorsal plate thick with wide, shallow re-entrant angle at anterior margin, and marked notch in posterior part of each lateral margin. Ornamentation of smooth, radial grooves and shallow, circular pits. Histological structure of spongy aspidin reinforced by pleromic dentine towards external surface. Branchial plates thin, long and narrow, and bent at right angles so that the lateral part is oriented vertically. Ventral plate thick with a long, posterior median notch.

Material. Six branchial plates (PIN 87/9-13; Pl 10/8); three dorsal plate fragments (Pl 10/9, 10/11, 10/12); ventral plate fragment (Pl 10/10).

Locality. Lovat′ River, near Peryesy and Luka, Novgorod, Region, Russia. Prilovat′ Formation, Upper Devonian, Frasnian.

Description. The description of *Obruchevia* (*Aspidosteus*) was based on its dorsal plates (Obruchev 1941, pl. I), the other plates only becoming known later. The dorsal plates are very large, notably thick, and cardiform. The length of the holotype (housed in the CNIGR Museum, St. Petersburg, coll. # 1/4680) is 510 mm and the maximum width is 480 mm. The ornament of the external surface of the plates varies: it consists either of radial furrows (Obruchev 1941; pl. I, fig. 1) or of pits or both (Obruchev 1941; pl. I, fig. 2; pl. II, fig. 3). Two fragments from the Riga collection show variations of the ornament (Fig. 3). One specimen (Pl 10/12, Fig. 3B) has strongly developed furrows, but in the other (Pl 10/11, Fig. 3A) the furrows are wider, wavy, and more delicate. The dorsal plates appear to have grown by the addition of lateral flanges that developed from the lower surface of the margins. In Pl 10/12 four such flanges can be counted (Fig. 3B). The visceral surface of the fragments has marginal zones, lacking the basal layer, that are 30-50 mm wide.

Specimen Pl 10/10 is a fragment of *Obruchevia* ventral plate (Fig. 4C, 4D) from the posterior portion of the right side; it is 110 mm wide, 105 mm long, and has a maximum thickness of 17 mm. The margins of the fragment are broken, except for the smooth and slightly convex mesial margin that shows the presence of a posterior notch. Five growth lines are visible on the external surface, the middle one being the strongest. They parallel the outer margin of the plate but successively die out against the inner margin. The two earliest growth zones are smooth but the later ones have short radial furrows. The fragment is thickest (about 20 mm) at its anterior margin and above the earliest two growth lines. The plate becomes gradually thinner towards the lateral margin. The ventral plate was probably rather flat. As in *Obruchevia* dorsal plates, the growth of the ventral plate took place along the outer edges under the margins in such a way that one or several flanges (actually growth zones) were formed. The center of the ventral plate and the flanges that were formed later are thinner. Due to this method of growth the spongy layer is laminated. Weathering of the plate has caused the thin basal layer on the visceral surface of the ventral plate to peel off and the spongy layer has also peeled off in patches (Fig. 4D). The ventral plate, not known before in *Obruchevia*, had a deep posterior notch similar to that found in *Schizosteus*, *Pycnolepis, Pycnosteus, Ganosteus*, and *Tartuosteus* (see Obruchev and Mark-Kurik 1965; Halstead Tarlo 1964, 1965) (Fig. 10B).

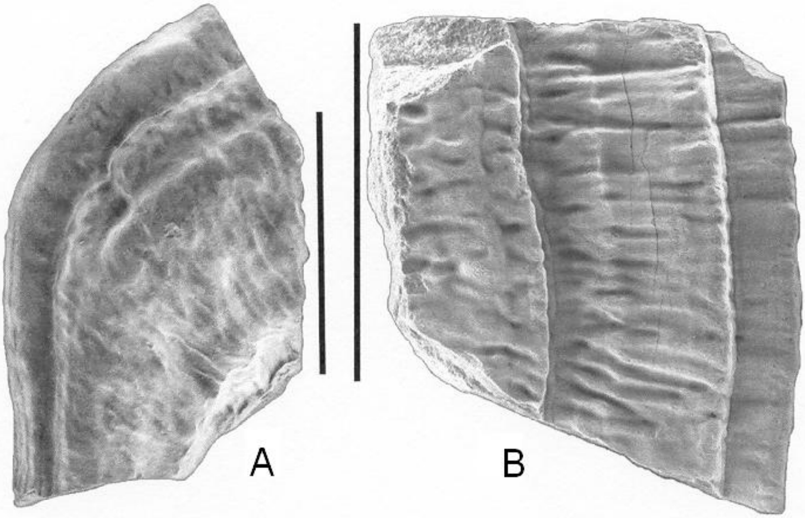


Fig. 3. Obruchevia heckeri. Fragments of the dorsal plate showing variations in dorsal surface ornament and the presence of growth lines. 1, PI 10/11; 2. PI 10/12. Scale bars equal 50 mm.

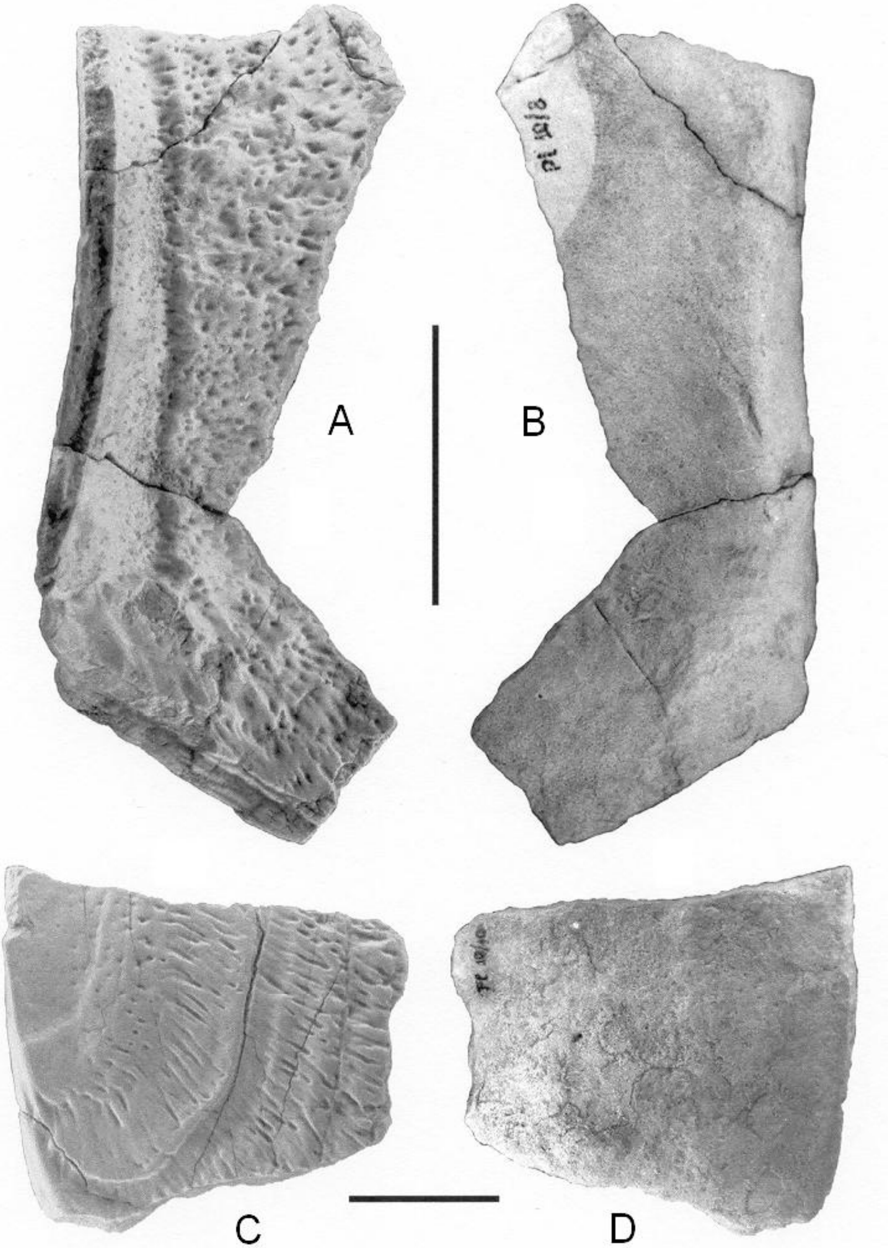


Fig. 4. *Obruchevia heckeri*. Branchial plate (PI 10/8) in ventral (**A**) and dorsal (**B**) views; posterior lateral fragment of a ventral plate (PI 10/10) in dorsal (**C**) and ventral (**D**) views. Scale bars equal 50 mm.

The branchial plates in *Obruchevia* were briefly described and schematically figured by Halstead Tarlo (1965, fig. 48). The Moscow collection contains five branchial plates (PIN # 87/9-13, O. Lebedev pers. comm., 2003), four of them fairly complete. The plates are of either a wider (Fig. 5C, 5D, PIN 87/11) or narrower type (Fig. 5A, 5B, PIN 87/10). In either case they are broadly triangular with a somewhat concave medial margin and convex lateral margin. Where preserved the posterior margin is transverse and shows a well-developed lobe towards the lateral edge of the plate. The dorsal surface is convex and generally unornamented, as it was mostly covered by soft tissue in life. In PIN 87/11 (Fig. 5C, a right branchial plate) some growth lines are visible on the dorsal side of the vertically oriented lateral portion of the plate, which was presumably exposed. The growth lines on the concave ventral side of the plate are more strongly developed. On this side the plate shows radially arranged furrows, similar to those on the external surface of the ventral plate (Fig. 5D). The branchial plates have strongly downturned lateral free margins, which would have functioned as runners. One of the Riga specimens is an incomplete right branchial plate (Fig. 4A, 4B, Pl 10/8). It includes part of the distal edge and posterior margin, although much of the proximal part of the plate is missing. It is 133 mm long, 70 mm wide, and 11 mm in maximum thickness and is 'j' shaped in cross-section. The concave ventral surface (Fig. 3A) is ornamented with irregular rounded pits and is shiny due to the addition of pleromin to the outer part of the spongy aspidin. A strongly developed growth line parallels the outer margin of the plate. Laterally the plate margin is slightly concave and strongly downturned. The margin is broken, revealing a cross section of the bone and showing that it has a central spongy layer (2.5-5 mm thick), covered on both sides by compact pleromin (2 mm thick). The margin is finely vertically striated, more strongly on the dorsolateral side, giving evidence of abrasion of the "runners" against the bottom sediment.

The microstructure of the *Obruchevia* dorsal plate (Obruchev 1941, pl. II) does not differ very much from that known in other psammosteids (except in the absence of dentine tubercles). The upper part of the spongy aspidin layer is compact and solidified by the deposition of pleromin; further down the spongiosa is coarser. The basal layer is comparatively thin and finely laminated (in Obruchev 1941, pl. II fig. 1 the laminated structure is not visible: in the photo the basal layer is completely black). Halstead Tarlo also figured pleromin in *Obruchevia heckeri* (1964, pl. VII, fig.1, 2, 4; pl. XII, fig. 5). His fig. 4 (pl. VII) shows pleromin in polarized light.

Discussion. Pleromin in the free margins of *Obruchevia* branchial plates shows the same phenomenon known in other psammosteids in which particularly the lateral corners of the branchial plates but also the central part of the ventral plates and the posterior ends of ventral ridge scales show additional deposition of this hard tissue. However, pleromin is not thought to have developed in obrucheviids as a tissue to counteract wear only. The tissue had several different functions, to counteract wear of the carapace and squamation, but also to reinforce the fabric of the carapace (Ørvig 1976; Mark-Kurik 1984). Ørvig established that pleromin started to appear between and below the tubercles before the exoskeletal plates were attacked by wear. This can be seen in several of the specimens described here in which pleromin can be seen on surfaces that were not subjected to wear (e.g. the growth lines visible on the lateral dorsal surface of PIN 87/11, Fig. 5C).

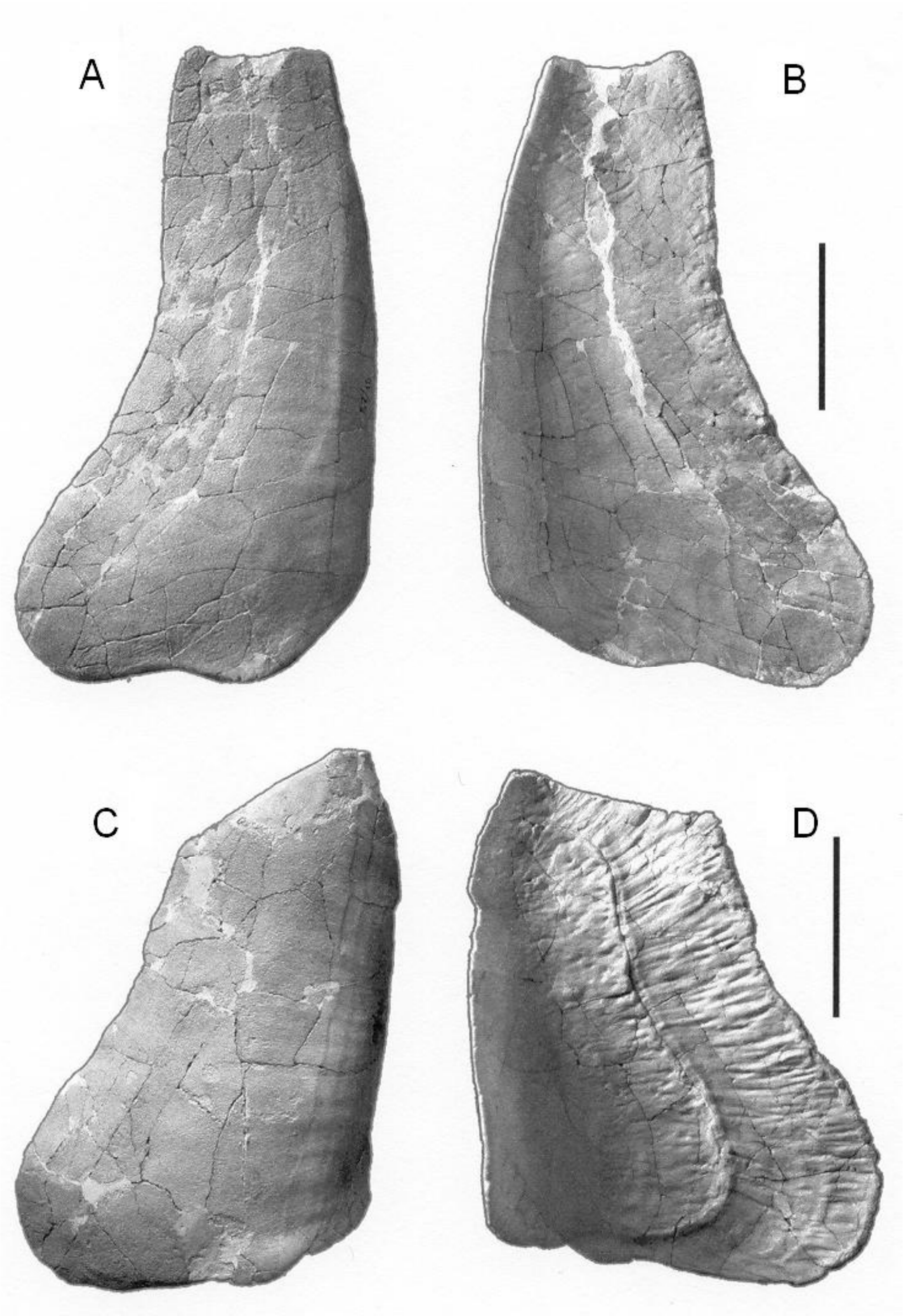


Fig. 5. *Obruchevia heckeri* . Branchial plates (PIN 87/10, 87/11) in dorsal (**A, C**) and ventral (**B, D**) views. Scale bars equal 50 mm.

Genus *Perscheia* gen. nov.

Etymology. In honor of Per Schei, the geologist on the 1898-1902 Fram Expedition, who collected the only previously known psammosteids from the Canadian Arctic.

Perscheia pulla sp. nov.

(Figs. 6-10)

Etymology. From the Latin, pullus, black, referring to the black color of the specimens.

Diagnosis. Dorsal plate thick and with surface ornamentation of well developed elongated blisters and irregular radial ridges. Histological structure of spongy aspidin reinforced by pleromin towards the outer surface. Ventral plate thick and with long posterior median notch.

Material. Six pieces of plate from the dorsal and ventral armor: CMN-NUFV 101-CMN-NUFV106.

Holotype. Posterior part of the dorsal plate (CMN-NUFV101).

Locality. Lower part of the Nordstrand Point Formation, southern Ellesmere Island, inland from Okse Bay. N77° 06.163' W87°09.064'. Field site number: NV2K 11.

Description. The material consists of five large pieces of dorsal or ventral plate and one small fragment that has been sectioned to show the histology.

The holotype, CMN–NUFV101 (Figs. 6A, 6B, 7A), is part of a plate showing a natural edge and three broken edges. It is convex on the outer and concave on the inner surfaces, roughly square (with about one quarter missing), and 180 mm in length and 210 mm in width. The thickness varies from 5 mm at the natural edge to 18.5 mm on the opposite edge. The external surface is finely pitted and ridged due to the presence of the spongy aspidin layer at the surface. It is covered by irregular blisters or excrescences on the more medial part of the plate; this ornament is replaced about 100 mm from the natural margin of the plate by low, round-topped, irregular, radial ridges. The change of ornament occurs at what appears to be a growth line delineated by a groove that runs parallel to the natural edge. A similar growth line is present about 45 mm from the plate edge. The ridges are generally about 3-5 mm wide, the blisters are mostly about 5 mm x 8 mm becoming larger and more pronounced towards the central part of the plate.

Two sensory canals run across the plate at right angles to the natural edge and parallel to the ridges (Fig. 7A). The more complete of these runs the entire length of the specimen. It forms a shallow groove 0.5-0.75 mm wide and has four short lateral branches in the zone of blisters, but only one in the ridged zone. A longer lateral branch runs parallel to the growth line that delineates the change in ornament. At the broken edge of the plate the longitudinal canal connects to a sensory canal running at right angles to it along the edge of the specimen. From this canal three additional short branches project. The longitudinal canals are probably the medial dorsal canals, the canal at right angles forming a dorsal transverse commissure.

The inner face of the specimen is smooth and shiny, and at least three growth lines, delineated by either shallow grooves or thickening of the bone, run parallel to the natural edge (Fig. 6B). The surface is formed of a dense laminar basal layer of aspidin that is up to 2 mm thick and tends to flake away from the spongy overlying layers. The surface shows small foramina related to narrow, shallow, radial grooves and large smooth blisters that are elongated radially. This specimen is assumed to be part of the median dorsal plate, probably the median posterior part based on the presence of the medial canals, the orientation of the ornament, and the shape of the natural margin.

CMN–NUFV102 (Figs. 6C, 7B) is a roughly pentagonal, concavo-convex fragment of plate in which all the edges are broken. Its maximum dimensions are 134 mm x 112 mm and the thickness varies from 15 mm to 10 mm. The outer surface of the plate is ornamented with large elongated blisters, apparently radially oriented. Several of these are ring shaped with a depressed center. Four sections of the sensory canal system can be seen, forming two parallel pairs almost at right angles to each other (Fig. 7B). One pair consists of a short section within the plate and a section along the right-hand edge. They run at an angle to the trend of the ridges, the canal on the plate edge does so almost at right angles to the ridges. The second pair consists of a canal that runs along the longest edge, almost at right angles to the first pair and a short section on the opposite edge. The longest section of canal is almost parallel to the trend of the ornament suggesting that it is part of the medial dorsal canal; the short section parallel to it may be part of the lateral dorsal canal, while the other two sections of canals are probably transverse commissures. The internal surface is concave, smooth, and shiny with a thick, dense, laminar, basal layer and no obvious growth lines.

CMN–NUFV103 (Figs. 6D, 7D) is an irregular fragment with maximum dimensions of 96 mm and 161 mm. It varies in thickness from 12 mm to 7 mm. The external surface is covered by large blisters and short ridges arranged roughly parallel to the long axis of the plate fragment. At about the midpoint of the specimen a sensory canal runs almost at right angles to the trend of the ridges (Fig. 7D). Six short lateral branches separate from the main canal and project between the surface ridges. Towards one end a short section of canal can be see running along one edge and parallel to the radial ornament. This canal is probably one of the transverse commissures while the longer section is part of one of the lateral or medial dorsal canals. The internal surface is weathered and the laminar basal layer is missing, exposing the spongy aspidin above it.

CMN-NUFV104 (Figs. 6E-G, 7C) is an irregular and thick piece of plate, 85 mm x 155 mm and up to 28 mm thick. It has broken margins on all edges except for one small section 55 mm long on one margin where there is a natural rounded edge to a shallow embayment. The curved margin adjacent to the embayment is probably close to the plate margin as it thins rapidly. The outer surface is concavo-convex with a suggestion of growth lines parallel to the curved margin (Fig. 6F). A single sensory canal is present running across the middle of the fragment for two-thirds of its width and then branching at right angles (Fig. 7C). One branch runs parallel to the embayment to the broken margin in one direction and for about 50 mm parallel to the plate margin in the other direction before petering out. Presumably this part of the sensory canal is the lateral dorsal canal. Although damaged the surface shows the same pattern of coarse blisters present on the other plates.

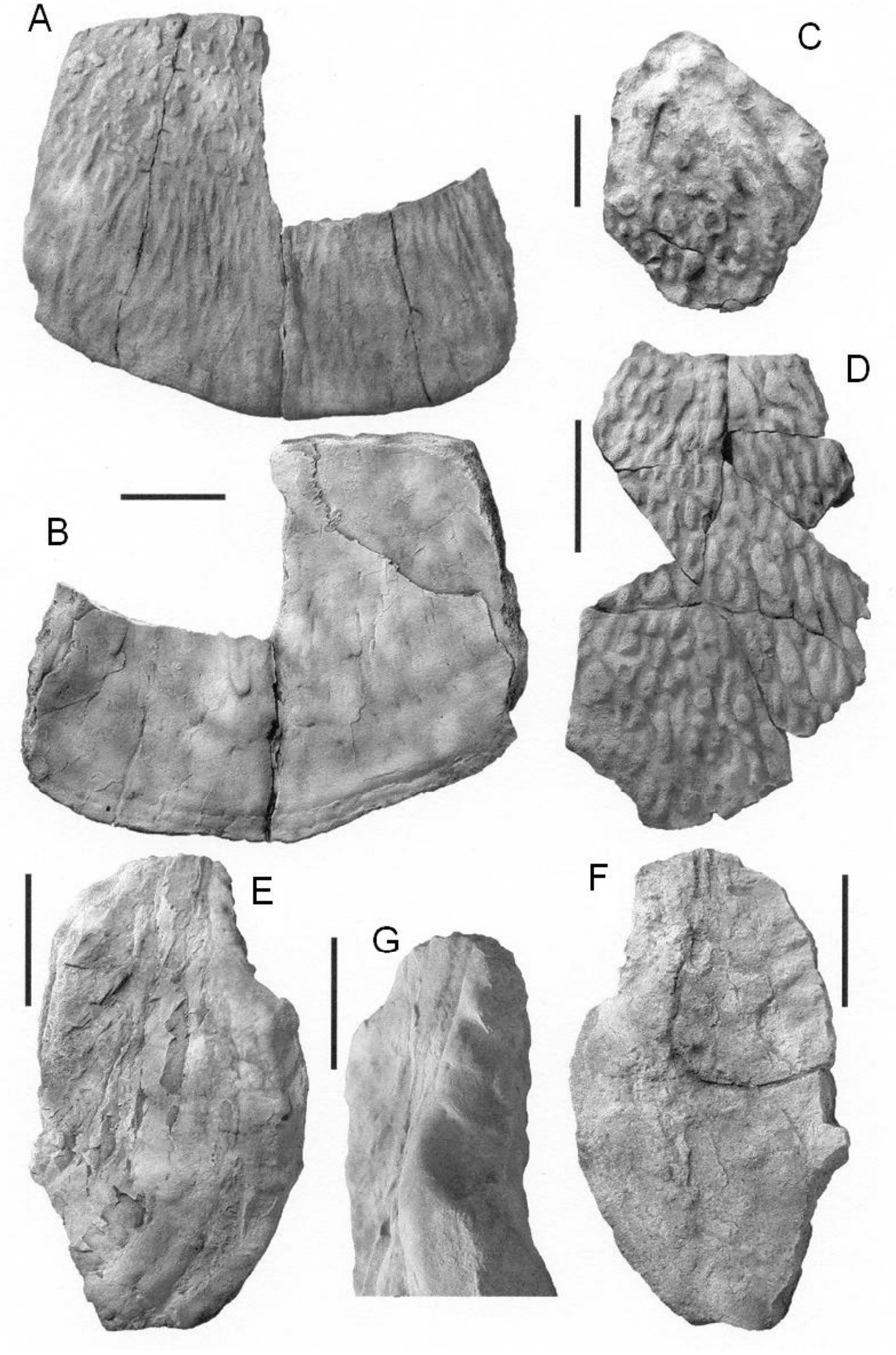


Fig. 6. *Perscheia pulla* gen. et sp. nov. Holotype (CMN-NUFV101), posterior part of the dorsal plate in external (**A**) and internal (**B**) view; **C**, dorsal plate fragment (CMN-NUFV102) in dorsal view; **D**, dorsal plate fragment (CMN-NUFV103) in dorsal view; posterolateral part of the dorsal plate (CMN-NUFV104) in ventral (**E**) and dorsal (**F**) views and a detail of the lateral notch showing posteriorly oriented ridges and grooves (**G**). Scale bars equal 50 mm (A-F) and 20 mm (G).

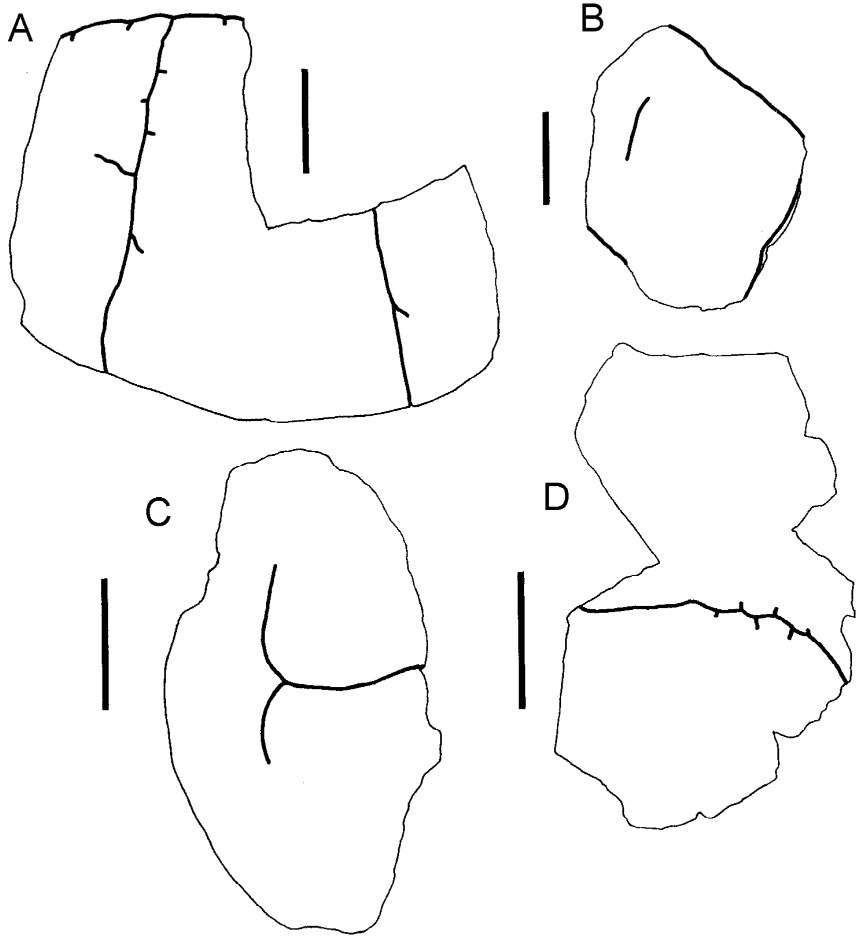


Fig. 7. Perscheia pulla gen et sp. nov. Outline of plates with canals accentuated. **A**, holotype, posterior part of the dorsal plate (CMN-NUFV 101); **B**, dorsal plate fragment (CMN- NUFV 102); **C**, dorsal plate fragment (CMN-NUFV 103); **D**, posterolateral part of dorsal plate (CMN-NUFV 104). Scale bars equal 50 mm.

The internal surface (Fig. 6E) is concavo-convex, shiny and smooth. Several growth lines are present parallel to the curved margin and a number of large smooth blisters are present towards what appears to be the lateral margin of the plate. The basal layer is dense, laminar, and up to 2 mm thick.

The embayment is about 55 mm long and has a rounded natural margin. At one end it curves towards the outer margin until truncated by the broken edge, in the other it meets the broken end of the plate. Although broadly rounded, the margin shows three well-developed rounded ridges, about 5 mm across, that run diagonally from the inner to the outer surface and terminate externally in a blister (Fig. 6G). Part of a fourth is visible at the broken edge. It seems probable that this embayment is the same as that seen on the postero-lateral part of the dorsal disc in *Obruchevia*, possibly indicating the position of the branchial duct.

CMN-NUFV105 (Fig. 8A, 8B) is almost flat and oval with one straight broken margin and with maximum dimensions of 140 mm x 207 mm. The two longest margins curve slightly, so that one is slightly concave, the other slightly convex. The thickness varies from 15 mm to 10 mm. The external surface (Fig. 8B) is slightly convex, and though heavily weathered, an ornament of small blisters can be seen in some places. No sensory canals are visible. The inner face (Fig. 8A) is smooth and shiny and a number of smooth, rounded blisters are present, generally elongated in a radial direction. A series of growth lines is visible. These seem to parallel the convex margin but are only sub-parallel to the concave margin, dying out successively against it. This specimen is interpreted as the left posterior part of the ventral plate. The concave margin forms one side of the median posterior notch.

The histology can be seen in thin section (CMN-NUFV106, Fig. 9) and in the weathered broken edges of some of the plates. The lamellar basal layer, up to 2 mm thick, is composed of thin horizontal lamellae through which pass roughly vertical vascular canals (Fig. 9C, **lam**). This is similar to the situation in *Obruchevia*, although it appears to be a thinner and less compact layer (Obruchev 1941, pl. 2-1). The main part of the plate consists of a spongy layer composed of aspidin, with openings varying in size from 0.5 mm near the base to 2-2.5 mm in the upper part. The outer 2.5 mm of the plate

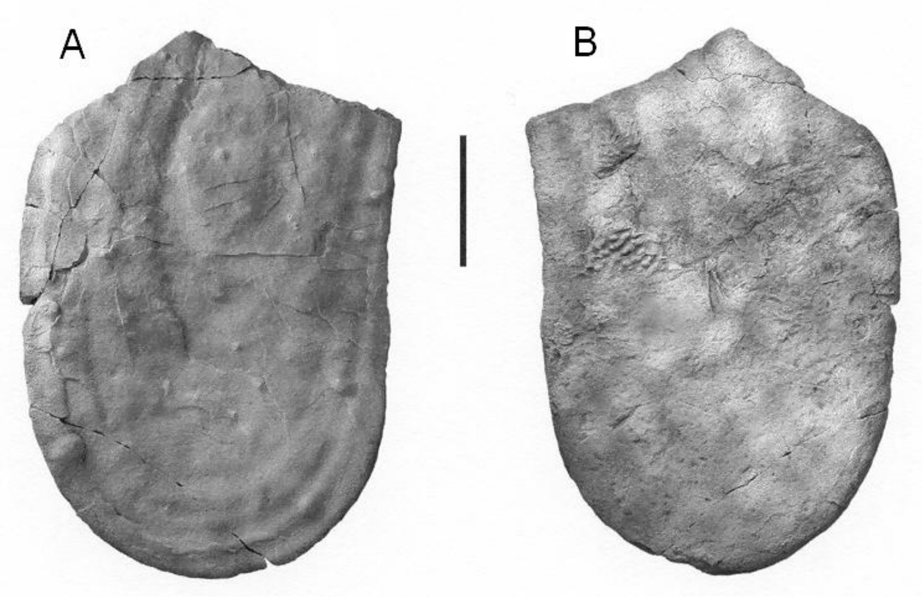


Fig. 8. Perscheia pulla gen. et sp. nov. Left posterior part of ventral plate (CMN-NUFV105) in dorsal (**A**) and ventral (**B**) view. Scale bar equals 50 mm.

forms a zone that is much more compact, and the openings reduce rapidly in size and number in the lower part of this layer (Fig. 9C, **pl**). At the external surface spongy aspidin has been strengthened by the addition of pleromin (Fig. 9A) the hypermineralized tissue characteristic of psammosteid heterostracans (Ørvig 1976, Mark-Kurik 1984). Polarized light reveals the characteristic dark "crosses" in the pleromin (Fig. 9B). Similar "crosses" have been illustrated in the dense pleromin of *Psammosteus megalopteryx* (Ørvig 1976, fig. 9). The pleromin in *Perscheia* appears to be less dense and shows narrower vascular canals than in *Obruchevia* (Obruchev 1941, pl. 2.1).

Discussion. Although the material consists of fragments, it is possible to use them to make a partial restoration of the dorsal and ventral plates (Fig. 10). Apart from CMN-NUFV105 (Fig. 8) all the fragments appear to come from the dorsal plate. Of these the

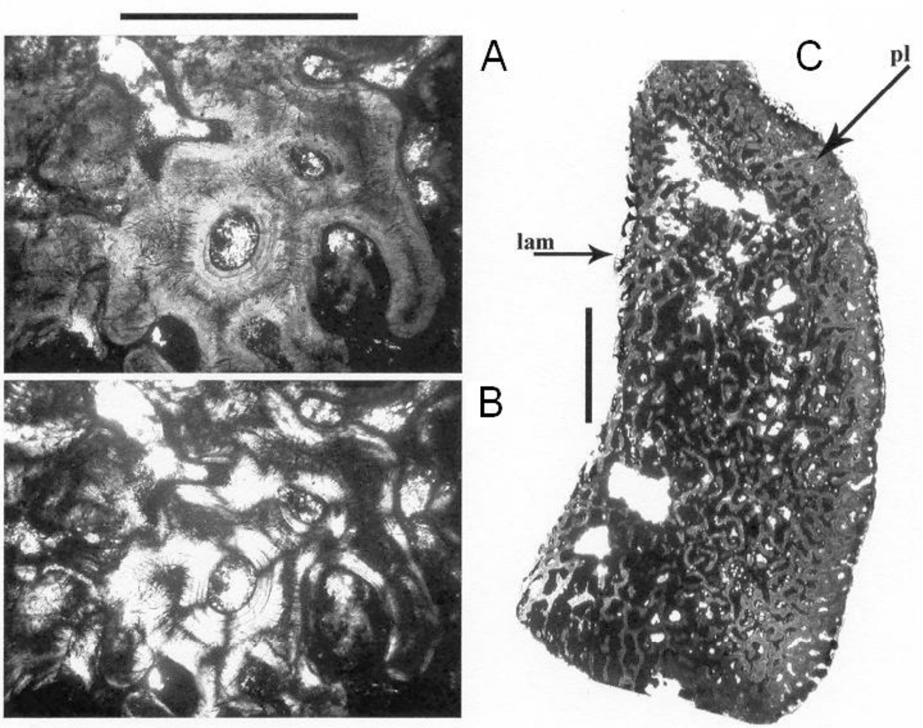


Fig. 9. Perscheia pulla gen et sp. nov. CMN-NUFV106. Vertical transverse thin section of the surface layer showing dense structure (**A**) and the characteristic cross developed under crossed polars (**B**); **C**, entire vertical transverse thin section (inner surface to the left) showing a thin, laminar, basal layer followed by a thick spongy layer and then a denser surface layer in which the aspidin has been reinforced by pleromin. Scale bars equal 0.5 mm (A, B) and 5 mm (C). Abbrev: **lam**, laminar basal layer; **pl**, pleromin strengthened outer layer.

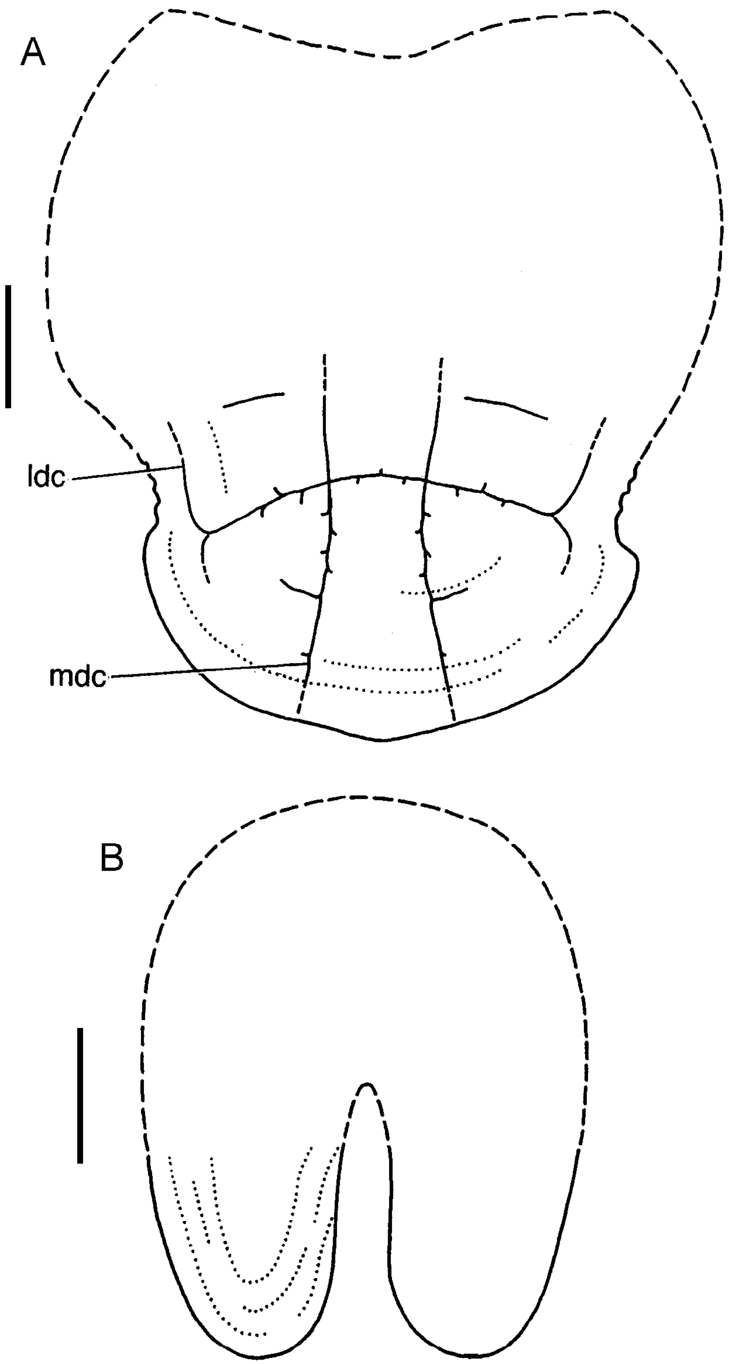


Fig. 10. Perscheia pulla gen. et sp. nov. Reconstruction of dorsal (**A**) and ventral (**B**) plates based on the new material. Dorsal plate outline based on the holotype of *Obruchevia heckeri* (Obruchev 1941; pl. I.1). Abbrev: **ldc**, lateral dorsal sensory canal; **mdc**, medial dorsal sensory canal. Scale bars equal 100 mm.

two most important in reconstructing the plate are the holotype CMN-NUFV101 (Figs. 6A, 6B, 7A), which is probably from the posterior margin, and CMN-NUFV104 (Figs. 6E-G, 7C), which is from the posterolateral margin. CMN-NUFV101 can be placed in the midline based on the presence of symmetrically placed longitudinal sensory canals that are probably the medial dorsal canals. They run parallel to the radial ornament and are joined by a transverse commissure that runs parallel to the growth lines. CMN-NUFV104 is a fragment of the lateral part of the plate and contains a shallow embayment that is probably equivalent to the lateral notch present in *Obruchevia*. It is suggested here that this fragment comes from the left side of the plate based on the fact that: (1), the sensory canal thought to be the lateral dorsal canal continues in one direction (anterior) while petering out in the other (posterior); (2), the growth lines suggest a very convex margin to the plate beyond the lateral notch and if this was the anterior part of the fragment then it would suggest a very anterior position for the notch which is not the case in *Obruchevia*; and (3), the diagonal ridges across the embayment, if related in some way to the branchial duct, are more likely to be oriented posteriorly.

Specimens CMN-NUFV102 (Figs. 6C, 7B) and CMN-NUFV103 (Figs. 6D, 7D) have no natural edges and can only be positioned on the dorsal plate based on their ornament and the sensory canals present. CMN-NUFV103 probably extends from the midline towards the lateral margin and contains a section of the lateral dorsal canal. CMN-NUFV102 may represent a more posterior part of the plate close to the postero-lateral notch and contains parts of the medial and lateral dorsal canals. Based on these interpretations the dorsal plate might be as much as 600 mm long and 550 mm wide, which is close to the size of the dorsal plate of *Obruchevia*.

The ventral plate is represented only by CMN-NUFV105 (Fig. 8), which clearly represents the left posterior part of the plate including the margin of the posterior median notch. It is difficult to estimate the overall size of the plate from this one fragment, but based on other species that have notched ventral median plates, it could have been as much as 450 mm long and 350 mm wide (Fig. 10B).

Remarks on the phylogenetic relationships of obrucheviids

The presence of a well-developed and apparently connected canal system on the dorsal plate of *Perscheia* is an unusual feature, as the psammosteid canal system is generally poorly known (Obruchev and Mark-Kurik 1968). Where it is known it normally consists of a pair of medial dorsal canals and one to three pairs of transverse commissures, all of which are present below the surface layer of dentine tubercles. The presence of this system as open grooves on the surface in *Perscheia* is also unusual, although not unexpected in a species in which the surface covering of dentine tubercles is missing. An intermediate stage can be seen in *Traquairosteus pustulatus,* a Frasnian species from Scotland in which the outer surface of aspidin is thrown up into conical mounds, each surmounted by a small crenulated dentine tubercle. The dentine tubercles are thus very sparse. In the holotype (BM P.8297; Halstead Tarlo 1965, pl. XVII, fig. 1) two canals can be seen as open grooves on the surface, indicating that as the dentine tubercles were reduced, the canals became exposed and were only covered by dermis. Given this situation it is surprising that none of the dorsal plates of *Obruchevia* show any indication of the presence of the sensory canal system.

Halstead Tarlo (1964) placed *Obruchevia* together with *Traquairosteus* in the Family Obrucheviidae, an arrangement that we agree with here. It is also clear that the new genus *Perscheia* should be included within this family. Higher level phylogenetic relationships are poorly understood, as no attempt has been made to assess relationships within the Psammosteiformes since the study by Halstead Tarlo (1964). This study was flawed somewhat by the inclusion of a number of early species that are now not considered to be psammosteids, such as *Tesseraspis*, *Corvaspis*, and *Psephaspis*. Halstead Tarlo used a variety of features such as the type of ornamentation, and the shape of the branchial and ventral plates to show that advanced psammosteids derive from *Guerichosteus,* from the Emsian of central Poland, which subsequently gave rise to two lineages. In one the posterior notch in the ventral plate was deepened and widened, and the branchial plate became broad and triangular (*Pycnolepis*, *Pycnosteus*). In the other lineage the posterior ventral notch was progressively eliminated, and the branchial plates became greatly shortened and broadened, forming spine-like plates in some forms (*Psammosteus*). *Obruchevia* and *Traquairosteus* were very incompletely known at the time Halstead Tarlo attempted his analysis of phylogeny; however, he placed them in a tentative relationship with psammolepids based on the fact that the branchial plates were strongly downturned, a feature that is present to a much lesser degree in the psammolepids, and despite the fact that the branchial plates of *Obruchevia* are long and narrow, not short and broad. The new information presented here shows that both *Obruchevia* and *Perscheia* had a ventral plate in which a well-developed posterior notch was present, therefore indicating that the obrucheviids are more likely to be connected to the group including *Pycnolepis*, *Pycnosteus*, and *Tartuosteus* in which this is a major feature. However, until a modern phylogenetic analysis of the Psammosteiformes has been carried out, a study that is beyond the scope of this paper, no firm conclusion can be reached as to the relationship of the obrucheviids.

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Ģints *Obruchevia* (Psammosteida: Heterostraci) revīzija un jauna obručevīdu suga no Arktiskās Kanādas vēlā devona

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Psammosteīdu kārtai pieder jaunākie dažādvairodži, kas Eiropā, kur to filoģenēze ir labi zināma, izdzīvojuši līdz Franas laikmeta beigām. Nunavutas paleontoloģiskās ekspedīcijas 1999.-2002. gadā ievāktie materiāli no devona klastisko nogulumu griezumiem Melvilas, Baturstas, Devonas un Ellesmeras salas parāda līdzīgu faunistisko sukcesiju Arktiskajā Kanādā. Dažas ļoti biezas psammosteīdu bruņu plātnes no Ellesmeras dienviddaļas ir bez dentīna pauguriņiem, bet tajās ir palielināts cieto audu – pleromīna – daudzums. Šie audi aizpilda tukšumus spongiozajā virsmas aspidīnā. Šī pazīme ir novērota tikai psammosteīdu ģints *Obruchevia* pārstāvjiem, kas sākotnēji aprakstīta no Lovates upes Novgorodas apgabala ziemeļrietumu Krievijā. *Obruchevia* muguras bruņu plātnes ir lielas, ievērojami biezas, sirdsveida; tās ir augušas, veidojot malu pieauguma joslas, kas attīstījās ārmalu apakšējā virsmā. Virsma ir ornamentēta ar radiālām vadziņām un bedrītēm. Vēdera bruņu plātnes ar vertikālām sānmalām, kuras pildījušas slieču funkciju. Iepriekš neaprakstītie paraugi no Lovates, kas glabājas Latvijas Dabas muzejā Rīgā, apstiprina branhiālo plātņu uzbūvi un parāda, ka vēdera plātne, kas iepriekš nebija zināma ģints *Obruchevia* pārstāvjiem, ir bijusi ar dziļu aizmugures izgriezumu, līdzīgu tai, kas atrasta ģinšu *Schizosteus, Pycnolepis, Pycnosteus, Ganosteus* un *Tartuosteus* pārstāvjiem. Gandrīz pilnīgi vesela branhiālā plātne, kas glabājas Krievijas ZA Paleontoloģijas institūtā Maskavā, ļauj detalizēti aprakstīt šo skeleta daļu. Kaut obručevīda atliekas no Arktiskās Kanādas ir nepilnīgas, bet kauliem raksturīgs ornamentējums no lieliem iegareniem pauguriem un neregulāriem valnīšiem, nevis bedrītēm un vadziņām, tā ventrālā plātne ir ar labi attīstītu aizmugures izgriezumu. Turklāt labi attīstītā sānu līnijas kanālu sistēma uz muguras ir pārstāvēta ar atvērtām vadziņām, kas psammosteīdiem ir neparasta pazīme. Šis taksons ir radniecīgs ģintij *Obruchevia* un ievietojams obručevīdu dzimtas ietvaros.

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New anaspid material from the Late Silurian of Britain and Estonia

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A new birkeniid anaspid *Trimpleylepis juncta* gen. et sp. nov. is described from the Prídolí, late Silurian at Man Brook, Welsh Borderland. *Trimpleylepis concatenata* gen. et sp. nov. is described from the Ohesaare Borehole, Ludlow, Silurian of Estonia. Histological sections show that *Trimpleylepis* has similar features to material previously described from the Family Septentrioniidae Blom, Märss and Miller, 2002. However, vascular canals have not been seen in sections of either species, and rare openings of canals have only been seen on one or two specimens of *T. concatenata*, so assignment to this family is tentative. *Silmalepis* cf. *erinacea* has been identified from Man Brook and extends the range of the genus into the Prídolí. New anaspid material from the late Silurian of Gardner's Bank, Welsh Borderland suggests that anaspids from the Family Rhyncholepididae Kiær, 1924 were present from the mid Wenlock to the late Prídolí.

Key words: Agnathans, anaspids, Welsh Borderland, East Baltic, late Silurian, Ludlow, Prídolí.

Introduction

The uppermost Silurian of the Welsh Borderland has yielded a rich microvertebrate fauna. The Man Brook locality is no exception, having produced well-preserved thelodont scales (Turner 1973, 1984; Vergoossen 1995, 1999; Märss and Miller in press), acanthodian scales, teeth and fin spines (Vergoosen 1995, 2000), anaspid scales and platelets (Blom *et al.* 2002) as well as many osteostracan and heterostracan scale and shield fragments (collections and documentation at The Natural History Museum). Anaspids are agnathans with a fusiform head, elongate body, a slanting row of branchial openings on either side of the body and a strongly hypocercal tail (see Miller *et al.* in press for review). Birkeniid anaspids appear in the geological record as disarticulated phosphatic scales with an external sculpture and a rib on the visceral surface; other closely related taxa have only spines and dorsal scales (e.g. *Lasanius* Traquair 1898) or are naked or with a weakly mineralised exoskeleton (e.g. *Jamoytius* White 1946). For the purposes of this article, the general term "anaspid" will be used in place of birkeniid anaspid. Blom *et al.* (2002) published a taxonomic scheme combining anaspid body features and scale morphology with histology. Anaspids were illustrated from Man Brook (ibid.) but the collection also contained many other fragments of scales, spines and platelets that were not described or illustrated because the histological structure was not known from the material available at the time. The external sculpture of these fragments was consistent with an anaspid affinity, but doubts remained concerning the histology of the material, because the scales were extremely cracked and difficult to section. Since the study of Blom *et al.* (2002), more material has become available from Man Brook, as well as comparative material at a slightly higher stratigraphic level from another Welsh Borderland locality at Gardner's Bank. These are compared herein to material from the Silurian of Saaremaa Island, Estonia, and the stratigraphic distribution of anaspids discussed.

Sampled localities

Gardner's Bank. Exposures on motorcross track, *c.* 1.5km S of Cleobury Mortimer, Shropshire, UK, GR SO 6815 7438, *c.* 7m below *Psammosteus* Limestone, U. Downton Group, Prídolí, Silurian. Collected by CGM and TM 15th June 1995.

Man Brook. Stream section between Coldridge and Birch woods, NE of fish farm, Shatterford, Hereford and Worcester, UK, GR SO 8026 8159, sample from the upper part of Prídolí Series, Upper Silurian (see discussion in Blom *et al.* 2002, p. 274 on the exact stratigraphic level of this material). Collected by CGM and TM 15th June 1995.

Ohesaare Borehole. Saaremaa Island, Estonia. Core section from 94.32-94.40m, Tahula Beds, Kuressaare Regional Stage, Ludfordian Stage, Ludlow Series, Upper Silurian. Collected by TM in 1968.

Materials and methods

All samples were processed using the standard acetic acid preparation techniques followed by Jeppsson *et al.* (1999). Material picked from Man Brook was photographed on the Hitachi S-2500 SEM at the Natural History Museum and the remainder of the material photographed on a JEOL JSM-840A in Tallinn. All illustrated thin sections were prepared and parts of them photographed in detail at a number of focal planes in Tallinn. The focal slices were amalgamated using Syncroscopy AutoMontage software at the Natural History Museum and composite parts spliced together using Adobe Photoshop. Specimens prefixed by NHM are deposited at the Department of Palaeontology at The Natural History Museum, London and those prefixed by GIT deposited at the Institute of Geology, Tallinn Technical University, Estonia.

Systematic Palaeontology

Class ANASPIDA Traquair, 1899
Order BIRKENIIDA Berg, 1937
Family ?SEPTENTRIONIIDAE Blom, Märss and Miller, 2002
Genus *Trimpleylepis* gen. nov.

Derivation of name. After Trimpley, Welsh Borderland, Shropshire, U.K., and *lepis* meaning scale.

Type species. *Trimpleylepis juncta* gen. et sp. nov., uppermost Prídolí, Upper Silurian, Man Brook, near Trimpley, Shropshire, U.K.

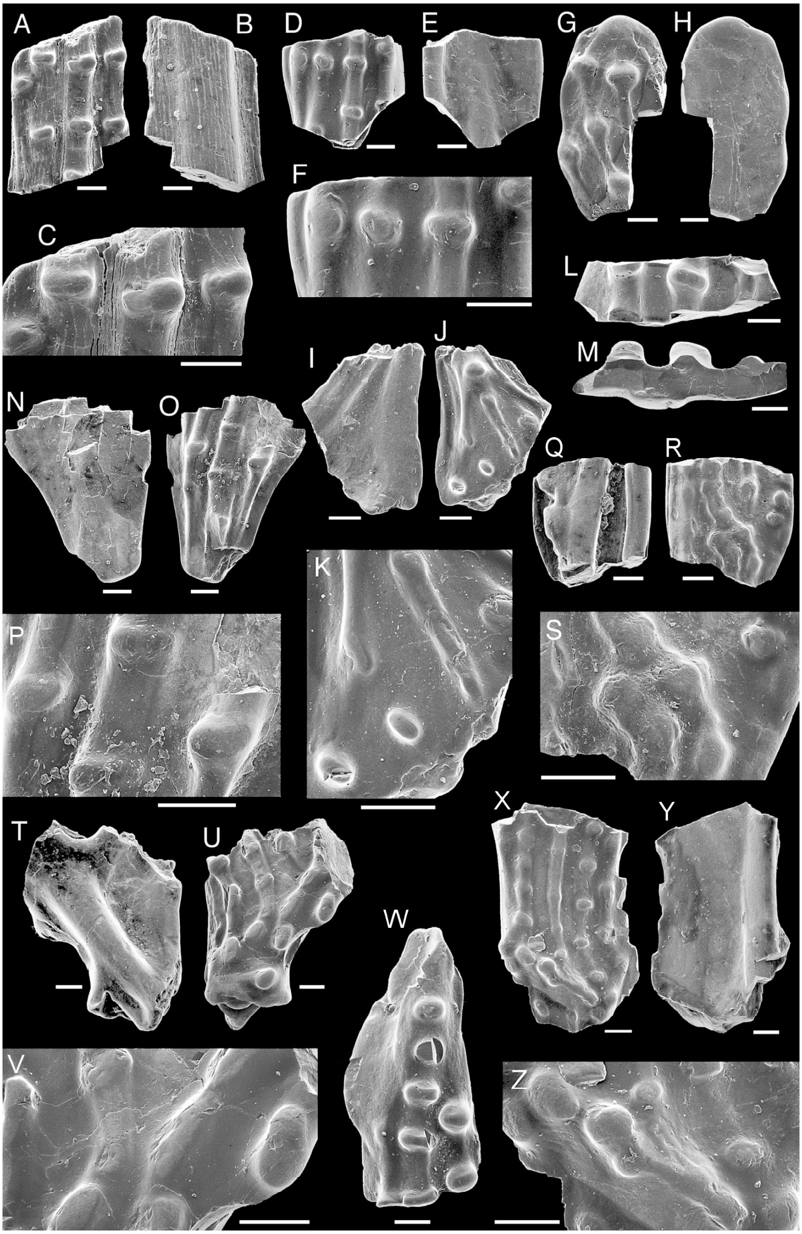

Fig. 1A-Z. Trimpleylepis juncta gen. et sp. nov. SEM pictures of fragments of scales and (?)platelets from Man Brook, upper part of Prídolí Series, Upper Silurian. All scale bars are 0.2 mm. A-C, holotype, scale NHM P 65593: A, external; B, visceral; C, close up of sculpture. D-F, scale NHM P 65601: D, external; E, visceral; F, close up of sculpture. G-H, scale NHM P 65594: G, external; H, visceral. I-K, scale NHM P 65597: I, visceral; J, external; K, close up of sculpture. L-M, scale NHM P 65600: L, external; M, cross section. N-P, scale NHM P 65595: N, visceral; O, external; P, close up of sculpture. Q- S, (?)platelet, NHM P 65612: Q, visceral; R, external; S, close up of sculpture. T-V, (?)platelet, NHM P 65604: T, visceral; U, external; V, close up of sculpture. W, scale NHM P 65606, external. X-Z, (?)platelet, NHM P 65602: X, external; Y, visceral; Z, close up of sculpture.

Diagnosis. Scales with a compact microstructure and well developed rounded to sub rounded tubercles joined by ridges parallel or sub-parallel to scale long axis; narrow to absent overlapped area.

Trimpleylepis juncta gen. et sp. nov.

Fig. 1; Figs 2A, C

Etymology. *Juncta* in Latin meaning connected or joined, because sculptural tubercles are connected to each other by well developed ridges.
Holotype. Figs 1A-C; scale NHM P 65593 from uppermost Prídolí, Upper Silurian, Man Brook, near Trimpley, Shropshire, U.K.
Material. About 200 broken scales and platelets from Man Brook.
Diagnosis. Scales with very narrow, smooth, anterior overlapped area which widens towards articulation processes; scales and (?)platelets with two to four rows of tubercles united with lower but well developed ridges. Vascular canals absent.
Description. Black scales (Figs 1A-P, W) of variable width (600-1200 µm) with fragments of ends of scales (Fig. 1O) and middle parts preserved (Figs 1A, D, L). Anterior overlapped area of scales smooth and very narrow (generally <50 µm but can be up to 100 µm) at mid scale but wider (up to 200 µm) on articulation processes (Fig. 1J, O, W). Main area of scale with two to four rows of circular (Fig. 1F) to slightly elongated (Fig. 1C) tubercles on ridges that run parallel or sub-parallel to anterior margin (Figs 1A, D). Tubercles are arranged in antero-posterior rows. On scales that taper towards articulation process, ridges converge (Fig. 1O). Smooth, broad and shallow grooves between ridges (Fig. 1M). Usually one broad and flat visceral rib (Fig. 1B) but scales can lack a visceral rib (Fig. 1H, N) at articulation process.
?Platelets (Figs 1O-V, X-Z) usually wider than 1000 µm with same tuberculated ridge sculpture as scales but ridges seldom parallel often coalescing and curving towards terminations of plates (Figs 1S, U, X). Visceral surface with one (Fig. 1T) or two (Fig. 1Q) well developed ribs.
Histology. Scales of compact structure with distinct thin growth layers, particularly in the visceral ribs (Fig. 2A, 4A). One sectioned scale (Figs 2A, 4A) does not contain any fibre tubules (=*Feinfasern in den Rippen und Skulpturen* of Gross, 1958). Very fine, bearly visible tubules occur in the anterior marginal rib and sculpture tubercles of the scale in Figures 2C and 4C. There are no Sharpey's fibre tubules.
Remarks. The histology of the scales figured here, especially in Fig. 4C, shows that *Trimpleylepis* is an anaspid. The compact structure and distinct thin growth lines are similar to both the first and the third anaspid histological types recognised by Blom *et al.* (2002, figs 17, 22, 41, 44, 49, 52). The structure is closer to the third histological type as seen in the Ludlow-Prídolí anaspids *Septentrionia*, *Tahulalepis*, *Liivilepis* and *Manbrookia*, but differs in the lack of vascular canals, although the other species described here *Trimpleylepis concatenata* gen. et sp. nov. shows evidence of possible vascular canal openings on the main scale area (Figs 3B, F). For this reason we tentatively place *Trimpleylepis* in the Family Septentrioniidae. The radiating tubules in the visceral ribs can be present (Figs 2C 4C) or absent (Figs 2A, 4A). The birkeniid anaspids *Trimpleylepis juncta* gen. et sp. nov., *Birkenia elegans* Traquair 1898, *Tahulalepis elongituberculata* Blom, Märss and Miller, 2002, *T. kingi* (Woodward) and *Manbrookia asperella* Blom,

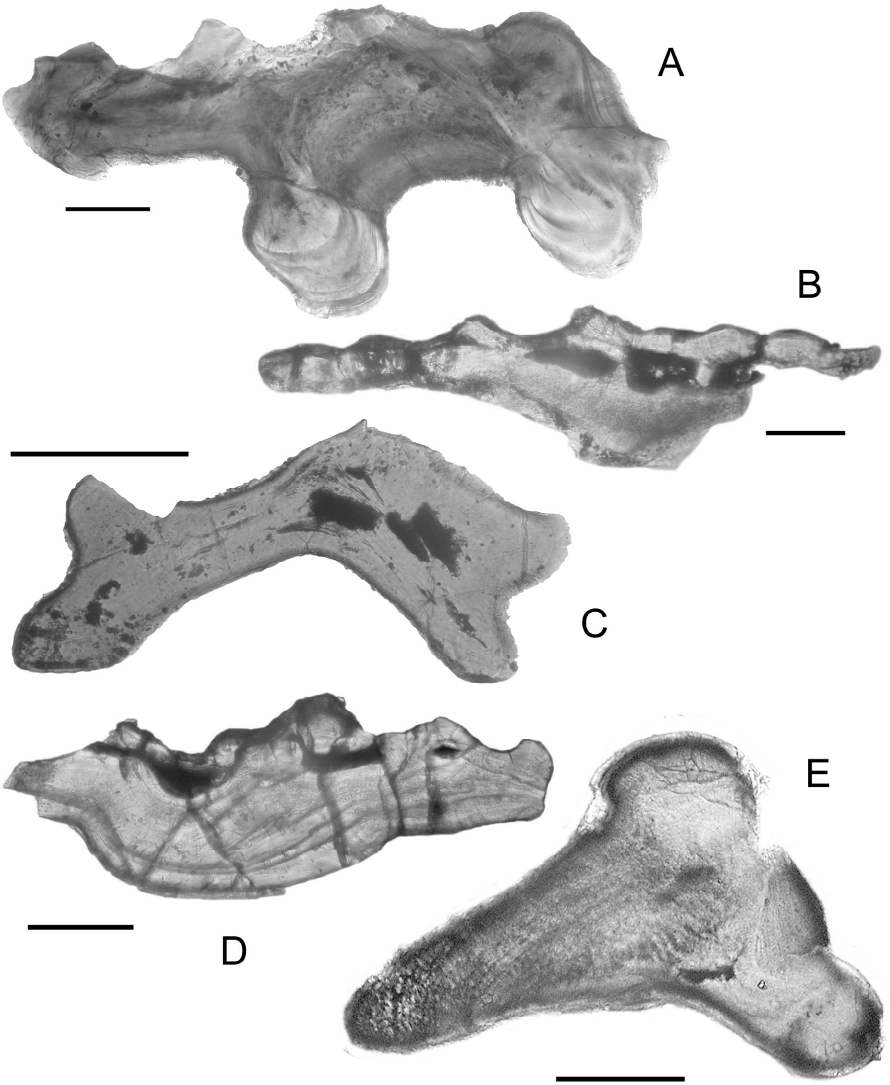

Fig. 2. Vertical cross-sections of scales with all scale bars 0.2 mm. A, C, *Trimpleylepis juncta* gen. et sp. nov. A, GIT 384-10, Man Brook, upper part of Prídolí Series, Upper Silurian; C, GIT 384-11, Man Brook. E, *Trimpleylepis concatenata* gen et. sp. nov. GIT 384-12, Ohesaare Borehole, Saaremaa, Estonia, depth 94.32-94.40 m, Ludfordian, Upper Silurian. B, D. Family Rhyncholepididae Kiær, 1924 gen. et sp. indet., scale, B, GIT 385-13, Gardner's Bank, *c.* 7 m below *Psammosteus* Limestone, U. Downton Group, Prídolí, Silurian; D, GIT 384-14, Gardner's Bank, *c.* 7 m below *Psammosteus* Limestone, U. Downton Group, Prídolí, Silurian.

Märss and Miller, 2002 all have a tuberculated sculpture (*M. asperella* having star-like tubercles). *Trimpleylepis juncta* differs from all of them in having tubercles joined by low ridges, which follow the long axis of scales/(?)platelets and because it has a narrower scale anterior overlapped area. For these reasons we consider that the material is different enough from other birkeniid anaspids for a new genus to be established. It is possible that the material referred here as platelets could represent terminations or articulation processes of scales (Fig. 1U) as some scales in articulated specimens of *Birkenia* Traquair have sculptures that converge and are not so regular towards terminations of scales (Blom *et al.* 2002, fig. 14g). However, because of their greater width, we prefer to describe them here as possible platelets. The tubercles on both scales and (?)platelets are remarkably regular in size (Fig. 1) which would suggest that they all belong to the same taxon. Some of the Man Brook material including the holotype (Figs 1A-C) appears striated under a light microscope, but these pseudo-striations are the result of microscopic cracks present in much of the material. HCl treatment of thin sections showed only that the etching preferentially dissolved the areas adjacent to cracks.

Trimpleylepis concatenata sp. nov.

Figs 2E; 3A-F

Etymology. The ridges that join the tubercles fade in the gap between tubercles and give the impression of a concatenation.

Holotype. Fig. 3C, scale GIT 384-3 from core section from depth 94.32-94.40m, Ohesaare Borehole, Saaremaa, Estonia, Tahula Beds, Kuressaare Regional Stage, Ludfordian Stage, Ludlow Series, Upper Silurian.

Material. 6 scales from the Ohesaare Borehole.

Diagnosis. Flattened and saddle-like scales with a single row of well developed tubercles of circular outline; ridge that joins tubercles parallel to long axis of scale becomes lower between each tubercle. Microstructure of scales relatively compact with tubules often diverging in a fan-shape; rare ?vascular canal openings on main scale area.

Description. Scales flattened to saddle shaped in section with a single row of rounded tubercles. Tubercles mostly arranged in a linear fashion, occasionally line is slightly disrupted (Fig. 3B). Ridge joining tubercles prominent but becomes lower between tubercles leaving either reduced ridge (Fig 3C) or almost flattened area (Fig 3D). Area either side of ridges smooth with occasional openings of vascular canals (Figs 3B, F). Overlapped area absent (Figs 3B, D, E), reduced (Figs 3A, C) or well developed near to articulation processes (Fig. 3F).

Histology. The material from the Ohesaare borehole, Saaremaa, Estonia (Figs 3A-F) is not so cracked; its histology (Fig. 2E) is similar to the British material (e.g. Fig. 2C). In thin section, no evidence was found for vascular canals despite the openings visible on the main scale area of some scales (Figs 3B, F). Fine tubules diverge in a fan-shape (Fig. 4E; cf. Gross 1958, fig. 3).

Remarks. The tubercles on the Estonian material are identical in diameter to the British specimens but in general are more rounded (Figs 1, 3). A poorly developed overlapped area in some scales is also common to both taxa. For these reasons the Estonian material can certainly be considered to be from the genus *Trimpleylepis*. *T. juncta* gen. et sp. nov. from Man Brook shows a wide variation in tubercle outline ranging from spherical

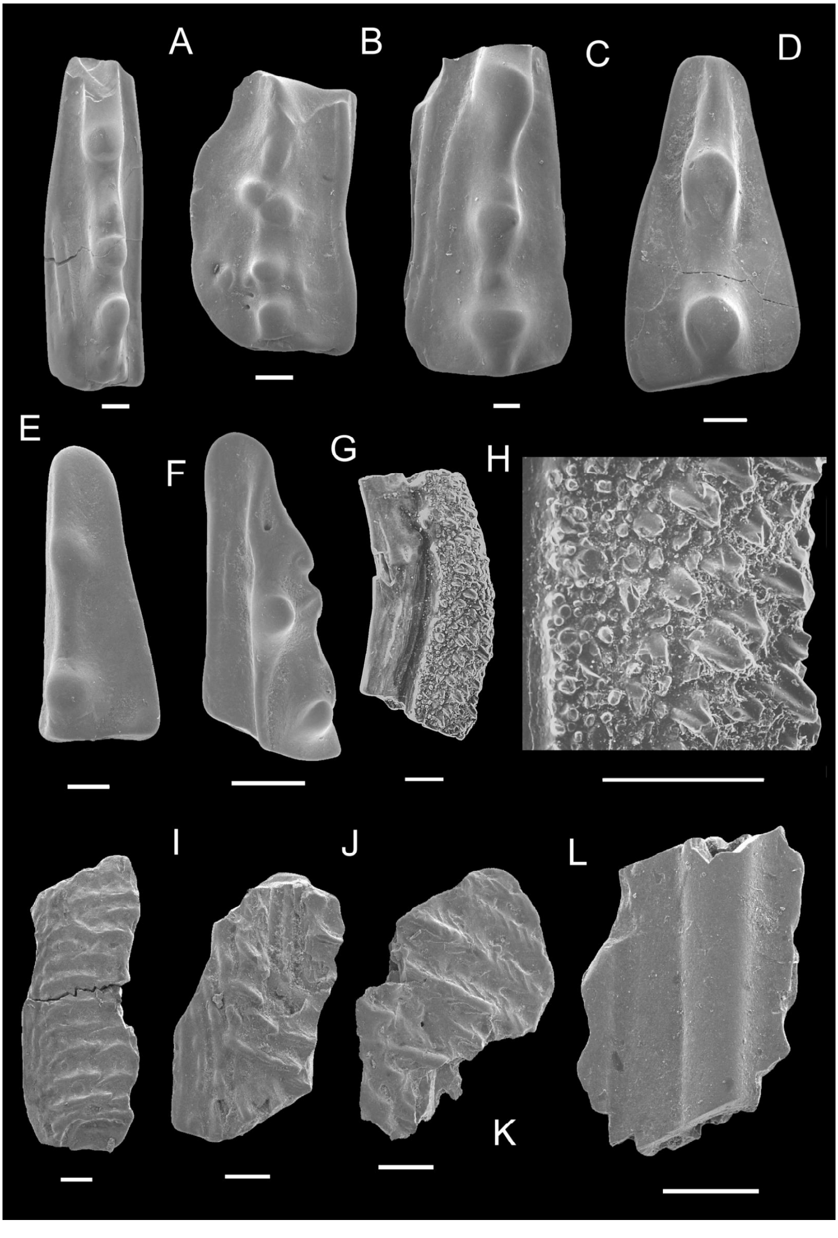

Fig. 3. SEM pictures of fragments of scales in external view unless stated. All scale bars are 0.2 mm. A-F, *Trimpleylepis concatenata* gen. et sp. nov., fragments of scales from Ohesaare Borehole, Saaremaa, Estonia, depth 94.32-94.40 m, Ludfordian, Upper Silurian. A, GIT 384-1; B, GIT 384-2; C, GIT 384-3, D; GIT 384-4; E, GIT 384-5; F, GIT 384-6. G-H. *Silmalepis* cf. *erinacea* Blom, Märss and Miller, 2002, scale fragment from Man Brook, upper part of Prídolí Series, Upper Silurian, NHM P 66018(1): G, scale in external view; H, close up of sculpture. I- L, Family Rhyncholepididae Kiær, 1924 gen. et sp. indet., fragments of scales from Gardner's Bank, *c.* 7m below *Psammosteus* Limestone, U. Downton Group, Prídolí, Silurian. I, GIT 384-7. J; GIT 384-8; K, scale now sectioned and illustrated in Fig. 2D; L. GIT 384-9, visceral view.

(Fig. 1F) to more elongate in the holotype (Fig. 1C) and the Estonian material certainly falls within these variations. However, we prefer to classify the Estonian material under *T. concatenata* gen. et sp. nov. which has only one row of tubercles per scale, and three of the six scales are saddle shaped in cross section (Fig. 2E), whereas *T. juncta* gen. et sp. nov. scales show two to four rows of tubercles joined by more prominent ridges (Figs 1, 2C). The Ludlow age of *T. concatenata* gen. et sp. nov. suggests that the range of the genus *Trimpleylepis* should be Ludlow-Prídolí.

Family RHYNCHOLEPIDIDAE Kiær, 1924

Silmalepis cf. *erinacea* Blom, Märss and Miller, 2003

Fig. 3G-H

Material. One broken scale from Man Brook from uppermost Prídolí, Upper Silurian, Man Brook, near Trimpley, Shropshire, U.K.

Description. Scale with wide smooth overlapped area; groove extends entire length of scale close and parallel to the sculpture margin on the main scale area. External sculpture of closely spaced fine tubercles of variable diameter followed by relatively closely spaced ridges that point into the gap between the following row. The ends of ridges are broken in this specimen but three distinct rows of ridges can be seen across the scale. Visceral side with single rib and no evidence of vascular canal openings. No histological sections have been made due to lack of material.

Remarks. Precise identification of this scale is not possible due to lack of material and the preservation of the scale, which has broken spine-like ridges. *Septentrionia mucronata* Blom, Märss and Miller, 2002 has spine-like ridges that point between the next set of ridges, as the spines do in the material figured here. *S. mucronata* is also similar as it has a wide overlapped area, but it differs in having a narrow well developed ridge with granular sculpture (Blom *et al.* 2003, fig. 45g-h) in the position where there is a groove developed in the scale illustrated here. In our opinion the scale figured here (Fig. 3G, H) is much closer to *Silmalepis erinacea* Blom, Märss and Miller, 2002 that also has a coarse tuberculated to granular sculpture to the anterior of the main area of the scale (Blom *et al.* 2002, fig. 34a). The long spines inclined at a low angle to the main scale area of *Silmalepis* (Blom *et al.* 2003, fig. 34b) look to have broken off in the material figured here. The broken spines also have a concave upper surface as they do in *S. erinacea*. As the spines are broken, and because the scale figured here has a much broader overlapped area than typical *S. erinacea*, we consider the material certainly belongs within *Silmalepis* but identify *S. erinacea* with doubt. The material figured here extends the range of *Silmalepis* from mid Ludlow (Blom *et al.* 2003, fig. 10) to mid Ludlow-late Prídolí.

RHYNCHOLEPIDIDAE gen. et sp. indet.

Figs 2B, D; 3I-L

Material. One intact scale, one small fragment, and two fragments that were used for thin sectioning, all from from Gardner's Bank.

Description. Scales with a narrow furrowed overlapped area that is incompletely preserved on most of specimens available. Low ridges on the main scale area are well-spaced with the ends nearest the anterior overlapped area slightly curved. Each ridge

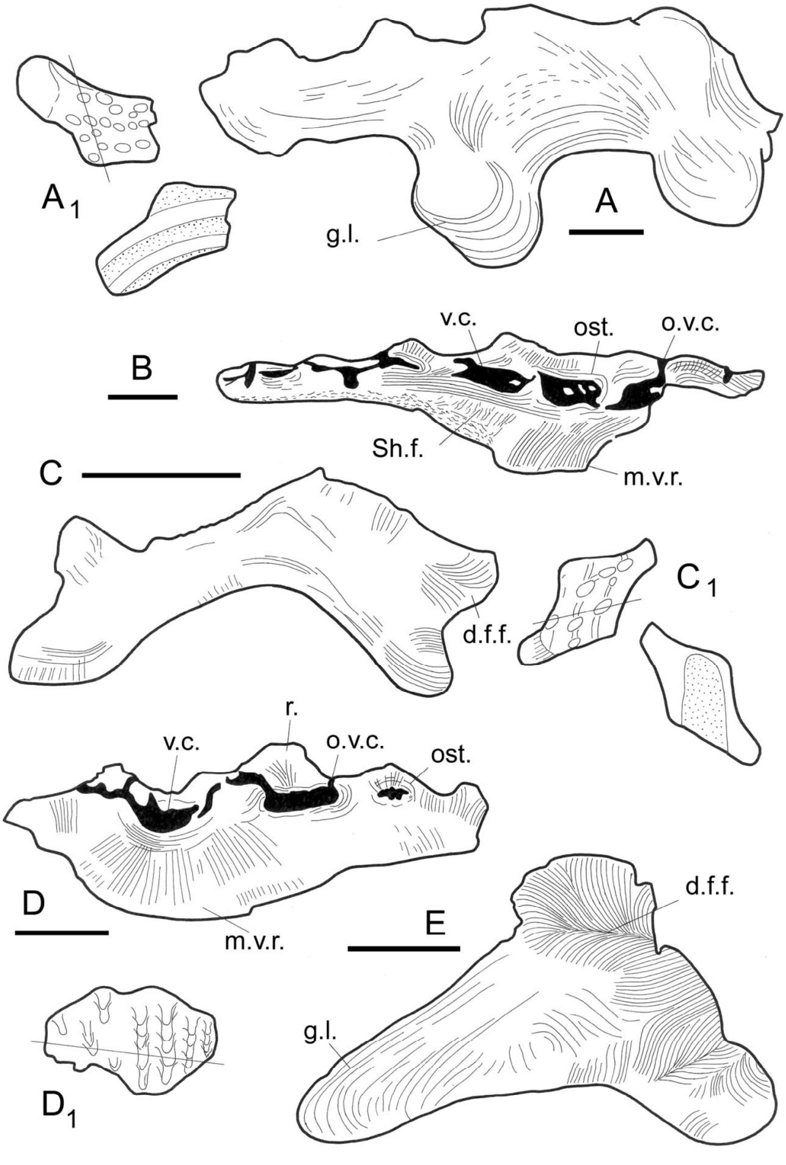

Fig. 4. Drawings of thin sections given in Fig. 2. Scale bars 0.2 mm. A, C, *Trimpleylepis juncta* gen. et sp. nov. A, GIT 384-10, Man Brook, upper part of Prídolí Series, Upper Silurian; C, GIT 384-11, Man Brook. B, D. Family Rhyncholepididae Kiær, 1924 gen. et sp. indet., scale, Gardner's Bank, *c.* 7 m below *Psammosteus* Limestone, U. Downton Group, Prídolí, Silurian; B, GIT 385-13; D, GIT 384-14. E, *Trimpleylepis concatenata* gen et. sp. nov. GIT 384-12, Ohesaare Borehole, depth 94.32-94.40 m, Saaremaa, Estonia, Upper Ludlow, Upper Silurian.
A_1, C_1 and D_1 are drawings of corresponding scales in external and visceral views which were thin sectioned. The line across the scale shows approximate position of the section. Abbreviations: d.f.f., diverging of fine fibres; g.l., growth lines; m.v.r., medial visceral rib; ost., osteon; o.v.c., opening of vascular canal; r., sculpture ridge; Sh.f., Sharpey's fibres; v.c., vascular canal.

follows the previous ridge; ridges slightly oblique (Fig. 3J) to perpendicular to the long axis of the scale (Fig. 3I). One specimen with main scale area of chevron-like, continuous ridges crossing whole of preserved part of scale (Fig 3K). Articulation facet visible on most complete scale (Fig. 3I). Single, well-developed, central visceral rib occurs on the smooth lower surface of the scale (Fig. 3L). On two scales, vascular canals exposed where sculpture of the main scale area has been worn away (Figs 3J, K).

Histology. Well developed vascular canal system present just below level of the main scale area (Figs 2B, D; 4B, D). Distinct parallel growth lines of compact structure in the visceral rib of one specimen (Figs 2D, 4D). Fine fibres present both in the sculpture ridges and visceral rib. Sharpey's fibres found in one scale (Figs 2B, 4B).

Remarks. Less material was available from Gardner's Bank than at Man Brook. The Gardner's Bank scales were also broken but it was easier to make thin sections of them. The broken external surface on one specimen that has now been sectioned (Figs 2D, 3K, 4D) suggests that there were a series of closely spaced fine elements forming each major ridge on the main scale area. These could have been similar to the ridges on *Rhyncholepis parvula* Kiær, 1924 (Blom *et al*. fig. 26m) or *Schidiosteus mustelensis* Pander, 1856 (Blom *et al*. 2002, fig. 30m). Histological sections (Figs 2B, D; 4B,D) show a well developed vascular canal system that suggest more of a similarity with the rhyncholepidids *Rhyncholepis*, *Silmalepis*, *Vesikulepis*, *Schidiosteus* or *Rytidolepis*. One specimen (Fig. 3J) also shows traces of vascular canals in a worn area below the sculpture on the main scale area. Well developed vascular canal systems are consistent with members of the Family Rhyncholepididae, which at present is confined to the late Wenlock to middle Ludlow (Blom *et al.* 2002). Identification of this material under the Family Rhyncholepididae extends the range of the family to the late Prídolí. More material from Gardner's Bank is certainly needed before the genus can be decided with any certainty.

Conclusions

1. *Trimpleylepis* gen. nov. is an anaspid that shows similarities to those from the Family Septentrionidae. However, there is some doubt that vascular canals are developed, so at present *Trimpleylepis* can only tentatively be assigned to this family.
2. Two species have been described; *Trimpleylepis juncta* gen. et sp. nov. from the Prídolí of the Welsh Borderland at Man Brook and *Trimpleylepis concatenata* gen. et sp. nov. from the Ludlow of Estonia.
3. Material described from Man Brook extends the range of the genus *Silmalepis* to Ludlow-latest Prídolí.
4. New material from Gardner's Bank, Welsh Borderland significantly expands the range of the Family Rhyncholepididae to mid Wenlock-late Prídolí.

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Jauns anaspīdu materiāls no Lielbritānijas un Igaunijas vēlā silūra

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Ir aprakstīts jauns birkenīdu dzimtas anaspīdu taksons *Trimpleylepis juncta* gen. et sp. nov. no Menbrūkas, Velšborderlanda, augšējā silūra Pršidolas nodaļas. *Trimpleylepis concatenata* gen. et sp. nov. ir izdalīta no Ohesāres urbuma, Igaunija, silūra Ludlovas nodaļas. Histoloģiskos plānslīpējumos redzams, ka *Trimpleylepis* ir raksturīgas īpatnības, kas iepriekš atrastas dzimtai Septentrioniidae Blom, Märss et Miller, 2002 piederīgajā materiālā. Tomēr vaskulārie kanāli abu sugu zvīņu plānslīpējumos nav saskatāmi, bet retās kanālu atveres ir novērotas tikai vienā vai divos *T. concatenata* paraugos, tāpēc šī ģints ievietota dzimtā tikai pagaidām. Taksons *Silmalepis* cf. *erinacea* ir atrasts materiālā no Menbrūkas, pagarinot ģints izplatību līdz Pršidolas nodaļai. Jauns anaspīdu materiāls no Gardnera krasta, Velšborderlanda, augšējā silūra, norāda uz to, ka anaspīdu dzimta Rhyncholepididae Kiær, 1924 ir eksistējusi no Venlokas vidus līdz Pršidolas beigām.

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Revisiting *Lophosteus*, a primitive osteichthyan

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Gross (1968) recognized one species of *Lophosteus, L. superbus,* from a single locality, Ohesaare Cliff, Saaremaa, and a single time interval, late Pridoli, Late Silurian. Today, six species are recognized and have a worldwide distribution from early Ludlow to early Pragian. We describe three new species from the type locality, the Canadian Arctic and the Urals. The systematic position of the genus is ambiguous. *Lophosteus* has been placed with sarcopterygians and with actinopterygians, or basal to both osteichthyan groups and in connection to acanthodians. Similarities to placoderms are superficial. We identify *Lophosteus* as a taxon close to acanthodians.

Introduction

Pander (1856) described *Lophosteus superbus* based on a small bone from the Ohesaare cliff, Saaremaa (German: Ösel). Rohon (1893) synonymised the species *Pterichthys elegans* Pander 1856 with *Lophosteus superbus* Pander, and treated *P. harderi* Pander 1856 as a distinct species, *L. harderi*. He placed *Lophosteus* in close relationship to sarcopterygians (*Holoptychius, Glyptolepis* etc.) based on its histology. A second species from the same locality (*L. harderi* (Pander), 1856) was synonymised with *L. superbus* by Gross (1969). Gross (1969, 1971) gave the most exhaustive description of the morphology and histology of *Lophosteus superbus* Pander 1856. Additional material has been described by Märss (1986) who proposed a new species, *Lophosteus? connexus*, from Vaivere, Saaremaa; Märss (1997) also identified similar Early Devonian scales from the Central Urals as Actinopterygii gen. et sp. A. Burrow (1995a) proposed another species, *L. incrementus*, from the Lower Devonian of Australia, and Märss (2000) shortly described *Lophosteus* sp. from Cornwallis Island, Arctic Canada.

Here, we synthesise all data on lophosteids, give diagnoses for all species and summarise current knowledge of their relationships.

Abbreviations: GIT, Institute of Geology at Tallinn University of Technology, Tallinn, Estonia; IGB, Institute of Geology, Beijing, China; MMM, Mining and Mineralogical Museum, Sydney, Australia; QMF, Queensland Museum fossil collection, S. Brisbane, Queensland, Australia; Tü, Geologisch-Paläontologisches Institut und Museum, Universität Tübingen, Germany; UALVP, Laboratory of Vertebrate Paleontology, University of Alberta, Edmonton, Alberta, Canada; UQY, Geology Department, University of Queensland, Brisbane, Queensland, Australia. All previous numbers of type specimens have been changed in the collections of the Institute of Geology at Tallinn Technical University during the process of creating the computerised database (for *Lophosteus* see Appendix 1).

Systematic description

OSTEICHTHYES Huxley, 1880
LOPHOSTEIFORMES Gross, 1969
LOPHOSTEIDAE Gross, 1969

Diagnosis (after Gross 1969): Osteichthyan fishes with rhombic scales that have a keel on the inner side, but lacking peg on dorsal margin (sometimes broad based "peg"); different sculpture on scales (with ridges) and head bones (with star-like tubercles); ridges formed by dentine (orthodentine) on bony base.
Included genera: *Lophosteus* Pander 1856.

Lophosteus Pander, 1856

Type species: *Lophosteus superbus* Pander 1856.
Geographic distribution: Arctic Canada, Baltic region, Central Urals, E-Australia, Timan-Pechora region.
Time: Ludlow-Pridoli, Late Silurian – Lochkovian, Early Devonian.
Diagnosis (after Gross 1969): Rhombic scales with broad based "peg"; free field of scales covered with elevated, obliquely arranged ridges which are widely separated. Ridges can be overgrown during size increase, but they rarely form a continuous dentine layer. They bear ridgelets oblique to the crest. – Long symmetrical spines triangular in cross-section without cavity and proximal with a smooth marginal area; ridges run parallel to its length, and are sometimes fused to a median ridge; posterior side furrow-like proximally whereas arched distally. Some asymmetrical long and flattened spines present. – Bones with ridge-like or star-like tubercles. Sensory lines in the form of open furrows on the bones.
Included species: *Lophosteus superbus* Pander, 1856; *Lophosteus* cf. *superbus* Burrow and Turner, 2000; *Lophosteus canadensis* n. sp.; *Lophosteus connexus* Märss, 1986; *Lophosteus incrementus* Burrow, 1995; *Lophosteus ohesaarensis* n. sp.; *Lophosteus uralensis* n. sp.; *Lophosteus* sp. indet. Turner, 2000.
Remarks: Species are distinguished mainly on the arrangement of ridgelets. The important characters are the angle between crest (= the highest line on the ridge) and ridgelets (= small ridges on the sides of the ridges), and the posterior extension of the ridges (= raised structures on the scale).

Lophosteus superbus Pander, 1856

Figs 1-2

1856 *Lophosteus superbus* — Pander: 62; pl. 6, fig. 23 a-c.
1856 *Pterichthys harderi* — Pander: 63; pl. 5, fig. 9.
1856 *Pterichthys elegans* — Pander: 63; pl. 5, fig. 10 a-d.
1858 *Lophosteus superbus* — Schmidt: 185.
1891 *Lophosteus superbus* — Woodward: 128.
1893 *Lophosteus superbus* — Rohon: 69-75; pl. 1, figs 38 + 39, pl. 3, figs 66 + 67.
1893 *Lophosteus harderi* — Rohon: 75-76; pl. 1, fig. 48.
1969 *Lophosteus superbus* — Gross: 16-46; 17 figs.
1971 *Lophosteus superbus* — Gross: 131-151; figs 1-7 + 9 A-H.
1977 *Lophosteus superbus* — Schultze: 152.
1977 *Lophosteus* — Schultze: 152-157; figs 1 + 2.
1978 *Lophosteus superbus* — Janvier: 90-91, 93-94.
1982 *Lophosteus* — Pearson: 54.
1986 *Lophosteus superbus* — Märss: 58, 90; text-fig. 24.2 a, b; pl. 35, figs 1-14, pl. 36, figs 3-6.
1987 *Lophosteus superbus* — Talimaa and Melnikov: 15.
1989 *Lophosteus superbus* — Märss: 285-286; fig. 176 G 5.
1991 *Lophosteus superbus* — Otto: 345-346; fig. 1.
1991 *Lophosteus* — Otto: 345-349.
1992 *Lophosteus* — Schultze: 239; fig. 11.
1995a *Lophosteus superbus* — Burrow: 327, 332.
1995 *Lophosteus superbus* — Turner *et al.*: 385.
1996 *Lophosteus* — Janvier: 183-184, 187-188; figs 4.65 D1,2 + 4.67 A.
1997 *Lophosteus superbus* — Märss: figs 2, 5.
1998 *Lophosteus superbus* — Märss *et al.*: 62, 70.
2000 *Lophosteus superbus* — Märss: 68.
2001 *Lophosteus* — Märss: 185-186.
2001 *Lophosteus superbus* — Märss: 186.

Neotype: scale Tü Pi 1359/1 (Gross 1969: fig. 1 A, B, 2 $\mathrm{H}_{1\text{-}3}$).
Additional material: many scales, spines and plates.
Type locality: Ohesaare cliff, Saaremaa (German: Ösel), Estonia.
Type horizon: *Ozarkodina remscheidensis remscheidensis* Conodont Subzone (Viira and Männik 1997), Ohesaare Regional Stage, upper Pridoli, Upper Silurian.
Localities: Loode cliff, Saaremaa, Estonia, and the following bore holes in Estonia: Ingelandi-615, depth 41.5 m; Ingelandi-618, depth 35.5 m; Kaavi-568, depth 9.2-42.2 m; Kaavi-571, depth 17.3-32.3 m; Mäebe-869, depth 51.7 m; Ruhnu-500, depth 148.1-171.9 m; Sõrve-514, depth 31.1-45.5 m; Tammuna-569, depth 1.1-10.5 m; Türju-620, depth 3.5-12.9 m; in Latvia: Ventspils, depth 271.3-325.5 m; Kolka-54, depth 158.3-205.9 m; and in Kaliningrad District: Kashino, depth 1005.4 m.
Diagnosis: ridgelets form an angle of 40°-65° to the crest; anterior overlapped field pustulate.
Description. *L. superbus* is common at Ohesaare Cliff. Gross (1969, 1971) gave extensive descriptions of scales, bony plates, tooth plates and spines. We will deal here only with the spines, add one unusual element, and re-describe a platelet from Märss (1986: pl. 35, fig. 1 a, b).

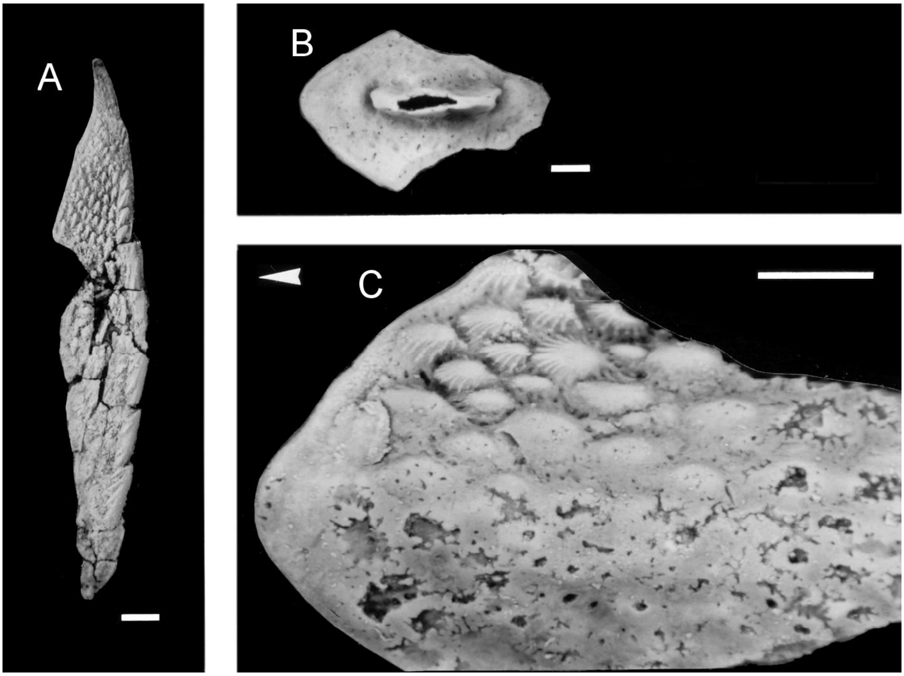

Fig. 1. Lophosteus superbus; upper Pridoli, Upper Silurian.
A, spine GIT 382-118, borehole Ruhnu-500, 152.2 m depth, Estonia; B, C, middorsal plate GIT 283-25, Ohesaare cliff, Saaremaa, Estonia. b, inner side; c, detail of external side with preserved tubercles. Dusted with NH_4Cl. Scale bars equal 1 mm.

One nearly complete spine (GIT 382-118, Fig. 1A) has been discovered in bore hole Ruhnu-500, Estonia, at 152.2 m depth. Its maximum length is 40 mm. It is flat. The anterior crest carries large elongate ridge-like tubercles on the lower half and much smaller tubercles (a third to a half in length) in the dorsal half of the anterior crest; there is an abrupt change in size. The elongate tubercles on the lateral sides are much smaller (one fourth the large tubercles) and are arranged in parallel rows. The base of the spine is remarkably long, reaching about half the length of the spine, so that one has to assume that the spine was attached at a low level to the body. Fragmentary material of such completely flat spines are found in acetic residues; these flat spines have a similar sculpture on both sides (see also Gross 1969: fig. 5 E).

We assume that specimens of *L. superbus* carry several spines and spine-like elements of very variable size, shape and sculpture, based on the occurrence of differently shaped spines with the same ornamentation. Altogether eight different types of spines and spine-like elements have been found (see also Rohon 1893: pl. 1, figs 38-39a; Gross 1969: figs 4 A, D, 5 B, D, E; Gross 1971a: fig 3 A, C; Otto 1991: fig. 1). Rohon (1893: pl. 1, figs 38-39 a) figured two spines of *Lophosteus superbus*, both are 7.1 mm deep and around 3 mm (3.3 and 2.8 mm) wide. Both have a triangular cross-section and a thicker proximal end. Smaller ridge-like tubercles form distinct longitudinal rows, whereas a row of larger ridge-like tubercles intersects the rows of finer ridge-like tubercles (Rohon 1893: pl. 1, fig. 38). It is not quite clear which is the leading edge of the spine (it should be the edge with coarser sculpture). The figure of the other spine(Rohon 1893: pl. 1, fig. 39 a) presents perhaps the posterior side of the spine.

Gross (1969) distinguished symmetrical and asymmetrical spines that precede median unpaired and paired fins respectively. They posses narrow, smooth overlapped areas at the base of the spines. Gross (1947, 1971b) also described acanthodian spines without such an overlapped area. Gross (1969: 25; text-figs 4 A-E, G-H, 5 A-E) figured symmetrical spines from the midline of the trunk; the anterior edge and both sides of the two spines described are sculptured, whereas on the posterior side of the third it is absent. A few spines also have sculpture on their distal posterior side. The largest spines although broken are 3.6 mm long and 1.5 mm wide, and their largest ridge-like tubercles are 0.9 mm long. The third spine has a length of 3.1 mm, a width of 1.15 mm, and 0.8 mm long ridge-like tubercles. Still, most spines are less than 2 mm long. The ridge-like tubercles are parallel to the longest edge of the spine, and the rows of ridge-like tubercles run parallel to each other. All ridge-like tubercles can be of uniform size, or they become smaller on the sides. The unsculptured side of the spines is more or less concave proximally, and flat or convex distally. In several spines the proximal end is narrower than the distal. Gross (1969: 25) did not find a narrow and smooth anterior margin in symmetrical spines. He (1969: text-figs 3 D, 4 I) also described some symmetrical spine-like elements. They are relatively wide with tightly packed tubercles, have a low depth and a convex lower side.

Asymmetrical spine-like elements are more common, and possibly represent the anterior margin of paired fins (Gross 1969: 25; text-figs 3 E, G, 4 F). Their proximal end has a smooth edge. The sculpture is less regular on such spines, the tubercles continue slightly onto the visceral side. Their wider side can be twice as broad as the narrower side.

Gross (1971: text-fig. 3 C) figured a fragment of a spine-like element which carries a very large ridge-like tubercle anteriorly, and ridge-like tubercles on the sides that are more than four times shorter. The fragment is 4.8 mm deep and 2.2 mm wide. Another asymmetrical spine-like element (Gross 1971: text-fig. 3 A, B) has ridge-like tubercles of different size, but all are relatively short. The estimated maximum length of this element is 7.5 mm, the width 3.6 mm. Big pores, which can open in pairs between the tubercles, are extraordinary for spines, and might belong to the lateral line system according to Gross (ibid.: 135). The pores better support an interpretation of the structure as a plate rather than as a spine.

Otto (1991: 348) described a mediodorsal fin spine, that is a ca. 4 mm deep, bilaterally symmetrical, pyramidal element with a broken basal part and a triangular cross-section. The posterior side lacks sculpture, which, however, is present on the two anterior sides. The largest ridge-like tubercles are arranged in a row along the anterior edge, whereas the tubercles on the lateral sides are of different size and not arranged in distinct rows. The spine has a cavity in its base. Otto (1991) expressed the opinion that this spine is a true mediodorsal fin spine, whereas the spine-like elements described by Gross (see above) are not fin spines.

The main visible difference between spines with a triangular cross-section as depicted by Rohon (1893) and Otto (1991) is in the arrangement of ridge-like tubercles, which are arranged either in rows or irregularly, and in the difference in depth.

The spine described by Gross (1969: text-fig. 5 E) is of the same type as that from the Ruhnu bore hole. They are flattened, sculptured on both flattened sides and distally around the whole spine. Proximally they have a cavity that extends one third of their length. This spine has some similarities with the cornual plate of placoderms.

Other spine-like elements described by Gross and also those in the Tallinn collection, were attached to tesserae-like elements in the skin. These have a concave visceral side and are not fin-spines.

The spine assigned to the sarcopterygian *Psarolepis* (Zhu and Schultze 1997) has a very narrow overlapped area. These spines are not inserted deeply in the skin in contrast to spines of sharks and most acanthodians. Zhu *et al.* (1999) emphasized the occurrence of spines in basal osteichthyans (including *Lophosteus*), acanthodians and sharks. Advanced sharks and the Early Devonian chondrichthyan *Leonodus* (Soler-Gijón and Hampe 2003) possess only symmetrical spines, whereas spines in front of paired fins are known in Early Devonian sharks (Sahney and Wilson 2001: putative chondrichthyan; Miller *et al.* 2003: *Doliodus*).

A convex plate (GIT 382-25, Fig. 1 B, C) represents a new element. Its maximum preserved length is 6.6 mm. The plate is convex externally and concave internally; the lateral margins are broken. It has a short anterior overlapped area. Oval, smooth, abraded tubercles are distributed in indistinct rows posterior to that area (Fig. 1 C); smaller tubercles are placed between larger ones. Fine ridgelets occur radially at the margin of each tubercle. The deeper part of an elongate narrow keel on the concave inner side is partly broken off (Fig. 1 B). Lineations that may represent growth lines are visible in front of the keel. The plate is symmetrical, belongs to the dorsal midline, and may be comparable to a fulcrum.

An interesting head plate (GIT 232-16 = Pi 6186, Fig. 2) of *L. superbus* was described and figured by Märss (1986: 58, pl. 35, fig. 1 a, b). The arched plate shows an open lateral line canal which bifurcates anteriad around the anterior invagination. The course of the lateral line nerve is picked out on the inner side by pores that transmitted branching nerves to the neuromasts in the lateral line canal. The course of the pores and thus the course of the lateral line nerve on the inner side from a posterior to an anterior invagination does not show the bifurcation of the canal on the outer side of the plate. Such plates with an open lateral line canal have already been described and figured by Gross (1969: figs 5 H, 6 D, 7 A, B).

Lophosteus cf. *superbus*

2000 *Lophosteus* sp. cf. *L. superbus* — Burrow and Turner: 170, 172; fig. 3.3.

Material: part of one scale UQY 8667 (Burrow & Turner 2000: fig. 3.3).
Locality: Bullock Creek, northern Queensland, Australia.
Horizon: *Ancoradella ploeckensis* Conodont Zone, Jack Formation, lower Ludlow, Upper Silurian.
Description: Burrow and Turner (2000) gave no description. The scale is reminiscent of those of *L. superbus* and have a pustulate anterior field and elevated oblique ridges

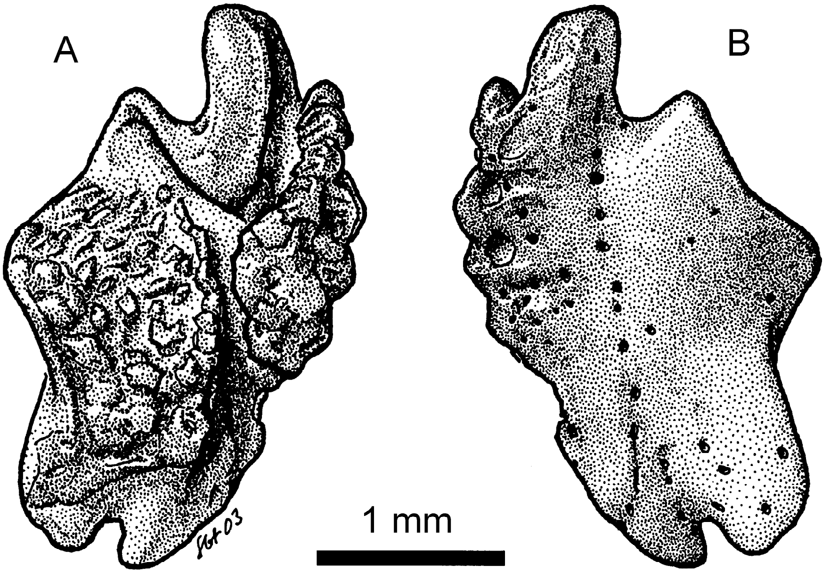

Fig. 2. Lophosteus superbus; head plate GIT 232-16; upper Pridoli, Upper Silurian; Ohesaare cliff, Saaremaa, Estonia. A, external side; B, inner side.

with strong ridgelets. The angle between crest and ridgelets at around 20° is lower than in *L. superbus*. – This is the oldest record of *Lophosteus*.

Lophosteus canadensis n. sp.
Fig. 3

1998 *Lophosteus* sp. — Märss *et al.*: 60, 62.
1998 *Lophosteus* spp. — Märss *et al.*: fig. 4.
2000 *Lophosteus* sp. — Märss: 68.

Holotype: scale UALVP 447 66 (Fig. 3 A, B).
Etymology: Named after region of origin (Canada).
Type locality: 141.0 m in the Read Bay southern section, Cornwallis Island, Arctic Canada (Märss *et al.* 1998).
Type horizon: Barlow Inlet Formation, Pridoli, Upper Silurian.
Additional material: two more scales, one scale is figured herein (UALVP 447 85; Fig. 3 C), one short spine (UALVP 447 90; Fig. 3 D), one plate (UALVP 447 65; Fig. 3 E, F), and head plate and tooth plate fragments.
Localities: Two samples at 87.0 m in the Read Bay southern section, Cornwallis Island, Arctic Canada (Märss *et al.* 1998).
Horizon: Barlow Inlet Formation, Pridoli, Upper Silurian. The material occurs together with conodonts *Ozarkodina confluens*, *Oz. excavata*, ?*Ligonodina confluens*, *Pelekysgnathus* sp,. and *Ctenognathodus* sp. (Männik in Märss *et al.* 1998: fig. 4).

Diagnosis: Scale ridges short, not reaching the posterior border, where they override older ridges. Alternating ridgelets cover the entire ridge and even the crest; anterior overlapped field pustulate. Tubercles of the plate have nodules at the base of the ridgelets.

Description: The holotype (Fig. 3 A) represents a deep scale from the left anterior flank of the fish. It is 3.0 mm deep and 0.7 mm wide. The ridges arising posteriad have convex surfaces and do not form a crest. The anterior overlapped field is wide and pustulate, the free field is covered with two generations of ridges. There are 16 ridges. The longer anterior (younger) ridges overlie posteriorly shorter (older) ridges; both cover only part of the free field. The ridges are covered by ridgelets that alternately reach the crest (Fig. 3 B). The dorsal margin of the scale forms a broad overlapped area ("peg"). The overlay of ridges is more intimate in other scales (Fig. 3 C), where the two or three generations are not so clearly separated as in the holotype. The inner surface of the scale carries an elongate elevation. Only a few ridges are present on the scale (0.9 mm deep and 0.6 mm wide); the ridges are more elongate than in the holotype, and the ridgelets are more distinct. The scale has a pillow-like elevation on the inner surface. The spine assigned to the species, clearly shows the overlay of flat ridges (Fig. 3 C) that are covered anteriorly with pronounced ridgelets. Fine pores of vascular canals open around the ridges in the basal plate.

A bony plate with star-like tubercles (Fig. 3 D, E) is assigned to *L. canadensis* on the basis of comparison with *L. superbus* and of the co-occurrence with the scales of *L. canadensis* at the same locality. Only one, the longest margin of the plate, is preserved intact, it is arched downwards; the other margins are broken, so that the position of the plate cannot be established. Its maximum measurements are: width 8.0 mm and length 4.0 mm. The plate is covered with closely packed stellate tubercles of different sizes; they are tiny on the arched margin. The middle area of the plate is covered by tubercles of 2 to 3 generations, older ones are partly covered by younger ones. Each stellate tubercle carries fine ridgelets converging towards its smooth apex. On the bony basal plate, the ridgelets terminate in small nodules; small nodules are also placed irregularly between the tubercles. The same is the case in *L. superbus* (Gross 1969: figs 8 A, D, 9 G). The concentric lines around the tubercles (on the ridgelets just above the basal plate) are a peculiar feature and reminiscent of growth lines (Fig. 3 E). Three deep open grooves of the sensory line system occur on the plate, two of them form an angle of about 45° on one side, and one short section is preserved on the opposite side (Fig. 3 D). The bony base appears rather compact with small canal openings as seen on the margins of the broken plate.

Comparison: *Lophosteus canadensis* n. sp. and *Lophosteus superbus* have scales of nearly the same size. The ridges on the free field of the scales are slightly closer to each other in *Lophosteus canadensis* n. sp. than in *L. superbus*. The ridges are smaller in *L. connexus*, and joined at the base on some elements. Alternating ridgelets reaching the top of the ridges are characteristic of *L. canadensis*. This feature distinguishes the species from all other species of the genus. A crest is not developed like in *L. incrementus*. Moreover, the bony pustules on the anterior overlapped area and between the ridges are lower and smaller in *L. superbus* and *L. canadensis* than in *L. incrementus*.

On the bony plates, nodules on the ridges of the stellate tubercles are present in four species of *Lophosteus* (Märss 1986: pl. 35, figs 1-14, for the nodules see fig. 13 a);

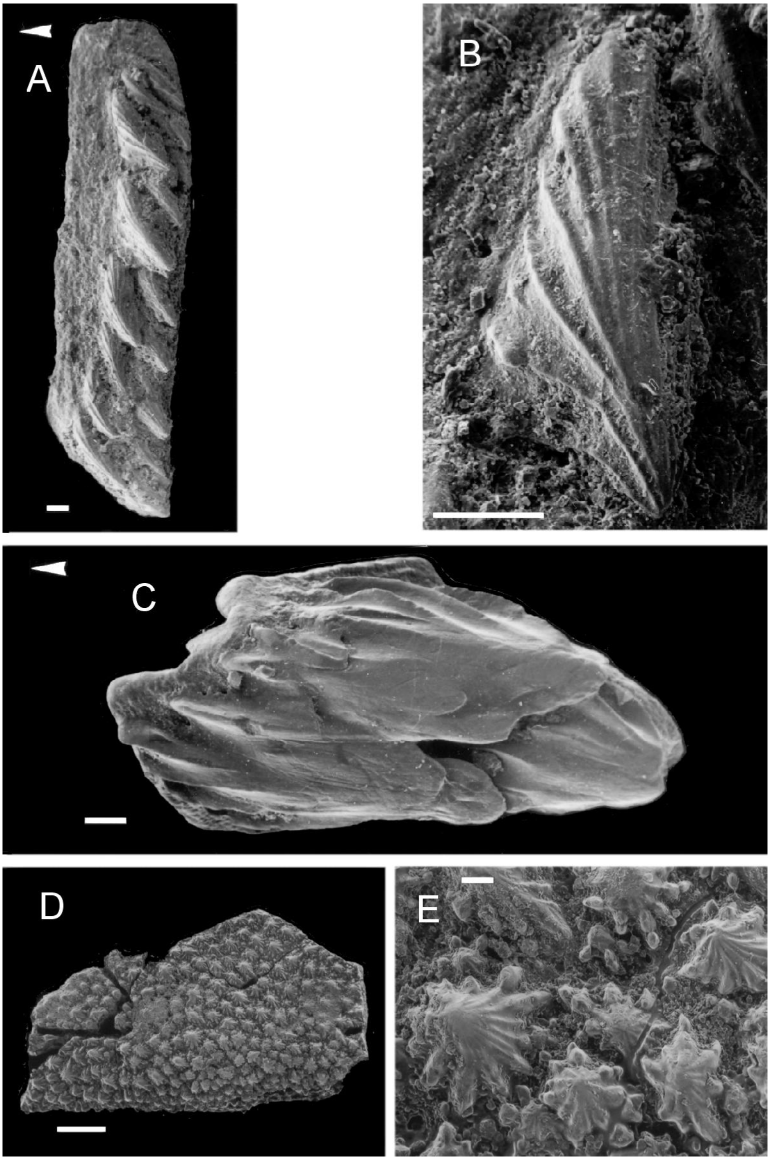

Fig. 3. *Lophosteus canadensis* n. sp.; Pridoli, Upper Silurian; Cornwallis Island, Arctic Canada. A, scale of left anterior flank, holotype UALVP 447 66; B, tubercle of A; C, spine, UALVP 447 90; D, bony plate, UALVP 447 65; E, detail from D. SEM pictures, scale bars equal 100 µm except D (1 mm).

they are also found in some placoderms and acanthodians. The tips of the stellate tubercles are smoothly convex in *L. superbus* and *L. canadensis,* whereas they are sharply pointed in the Australian taxon.

Lophosteus connexus Märss, 1986
Fig. 4

1986 *Lophosteus? connexus* n. sp. — Märss: 59, 90; pl. 34, figs 7-11.
1997 *Lophosteus? connexus* — Märss: 35; fig. 8.
2000 *Lophosteus? connexus* — Märss: 68.

Holotype: scale GIT 232-413 (= Pi 7042; Märss 1986: pl. 34, fig. 10).
Additional material: 15 scales and plates.
Type locality: Vaivere outcrop, Saaremaa, Estonia.
Type horizon: lowermost part of Äigu Beds, *Ozarkodina remscheidensis eosteinhornensis* Conodont Subzone (Viira and Männik 1997), Kaugatuma Regional Stage, Pridoli, Upper Silurian.
Localities: Äigu, Saaremaa, Estonia; the following bore holes in Estonia: Ohesaare, depth 64.65 m, and in Latvia: Kolka-54, depth 261.3-261.5 m; and north bank of Mikhailovsk Pond, Ufa amphitheatre, western slope of Central Urals, Russia.
Emended diagnosis: small scales (up to 1.5 mm deep and 0.3 mm long), curved and straight dentine ridges ending posteriorly in a pointed tip and reaching the posterior margin of the scale or beyond. The ridges carry very oblique, short, lateral ridgelets angled at 20° or less to the crest. The ridges have a narrow, smooth and flat crest. The posterior-most pair of ridgelets form a wider, flattened, wing-like structure.
Description: Märss (1986) figured five specimens and chose an elongated low scale as the holotype (Märss 1986: pl. 34, fig. 10). Specimen GIT 232-412 (Märss 1986: pl. 34, fig. 8) represents a typical scale (Fig. 4 A, B) with broad, dorsally overlapped area ("peg"); the scale has a weakly developed keel on the inner side. Vascular canals open as pores around the ridges as in *L. superbus*. A median ridge scale (probably from the dorsal midline) is shown in figure 11 (Märss 1986: pl. 34). Specimen GIT 232-415 (Märss 1986: pl. 34, fig. 9) looks like a scale, but it is a plate with a convex posterior border and a flat inner surface; it carries the typical ridges with oblique ridgelets and a wing-like posterior-most pair of ridgelets.

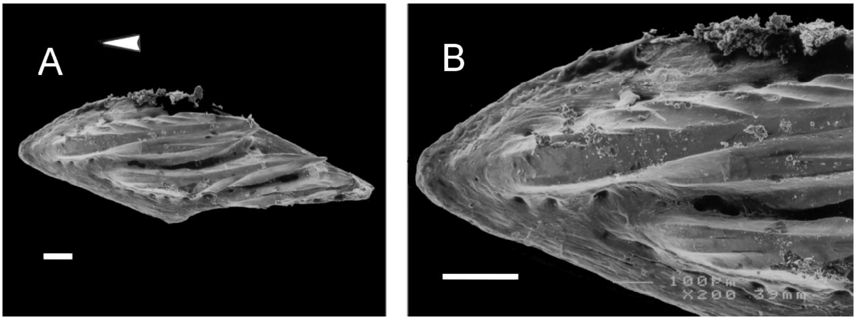

Fig. 4. Lophosteus connexus; Pridoli, Upper Silurian; Vaivere outcrop, Saaremaa, Estonia. A, scale GIT 232-412; B, detail of A. SEM pictures, scale bars equal 100 µm.

Comparison: Scales and sculpture elements of *L. connexus* are smaller, the ridges relatively longer and with more ridgelets than in *L. superbus*. The posterior-most wing-like pair of ridgelets distinguish this taxon from all other species of *Lophosteus*. The ridges fuse to form a united dentine cover on some scales of *L. connexus,* showing similarities to some scales of *Andreolepis hedei*.

Lophosteus incrementus Burrow, 1995

1995a *Lophosteus incrementus* nov. sp. — Burrow: 328-332; fig. 2, pl. 1, figs 1-6 + 8-9, pl. 2, figs 1-8.

Holotype: Scale MMM C01955 (Burrow 1995a: pl. 1, fig. 6).
Additional material: see Burrow (1995a).
Type locality: Site C661, Trundle beds, central New South Wales, Australia.
Type horizon: Base of Garra Formation, *Pedavis pesavis* Conodont Zone, upper Lochkovian, Lower Devonian.
Diagnosis: Short, tubercle-like ridges not running over the entire free (exposed) field, no crest, but many ridgelets, smaller ridges in-between larger ones, small triangular pustules on anterior overlapped field.
Description: see Burrow (1995a).
Comparison: The star-like tubercles of *L. incrementus* (Burrow 1995a: pls 1 and 2) are lower, the tip of the tubercles is sharply pointed, and the bony pustules on the anterior overlapped area are triangular and relatively larger and more strongly developed than in *L. canadensis* and *L. superbus*.

Lophosteus ohesaarensis n. sp.

Fig. 5

1986 *Lophosteus superbus* — Märss: pl. 34, fig. 6

Holotype: Scale GIT 382-87 (Fig. 5 A).
Etymology: Named after locality of origin (Ohesaare cliff).
Additional material: Scales GIT 382-82, 382-88-92, 382-121, -123 and tessera GIT 382-93, from Ohesaare Cliff, Saaremaa; scale GIT 232-42 (= Pi 6218; Märss 1986: pl. 34, fig. 6) from Ventspils, Latvia.
Type locality: Ohesaare cliff, Saaremaa, Estonia.
Type horizon: *Ozarkodina remscheidensis eosteinhornensis* Conodont Subzone, Ohesaare Regional Stage, upper Pridoli, Upper Silurian.
Localities: Bore holes Ventspils, depth 280,0 m and Kolka-54, depth 205.6 – 205.9 m in Latvia, Jura Formation, upper Pridoli, Upper Silurian.
Diagnosis: Scales with fine parallel ridgelets on crest, ridgelets change angle from 10° to nearly 90° to crest on lateral sides of the ridges; lower part of ridgelets with nodular serrations; anterior overlapped field weakly pustulate.
Description: *Lophosteus superbus* is the common species at Ohesaare cliff, Saaremaa; *L. ohesaarensis* is rare (10 scales and 8 pieces of bones and spines). A deep scale has been chosen as the holotype (Fig. 5 A); two elongate, steep and two smaller intercalated

ridges cover the scale, the ridgelets run nearly parallel on the crest, barely reaching the posterior end of the crest. The angle of the ridgelets on the lateral sides changes from 10° to nearly vertical to the crest posteriad on the lateral sides. The lower part of each of the ridgelets bears a nodular serration increasing in number with the size of the tubercles (Fig. 5 C). One tessera with a vertical tubercle (Fig. 5 B) is assigned to the species, because it shows fine ridgelets running to the tip in addition to stronger ridgelets with nodules located more basally. The ridges on the spines have parallel ridgelets on their anterior part.

Comparison: *L. uralensis* is closest to *L. ohesaarensis*; the ridgelets do not form chevrons in *L. ohesaarensis* in contrast to *L. uralensis* and *L. canadensis*. *L. superbus* has broader ridges with strong ridgelets that form a distinct angle to the crest. The serration of the lower part of the ridgelets is unique to *L. ohesaarensis.*

Lophosteus sp. indet.

2000 *Lophosteus*? sp. — Turner *et al.*: 492; fig. 3 F.

Material: A section of a single spine QMF35785 (Turner *et al.* 2000: fig. 3 F).

Locality: Between Gray Creek and Basalt Bore, Broken River district, north Queensland, Australia.

Horizon: *Pedavis pesavis - Eognathodus sulcatus* conodont zones, Shield Creek Formation, upper Lochkovian/lower Pragian, Lower Devonian.

Description: Turner *et al.* (2000) cited the specimen in connection with the description of microvertebrates from the Broken River district, Queensland. A short piece of one spine is preserved. It shows five arch-like tubercles with a smooth crestand with ridgelets on the sides; smaller pointed tubercles are present on the side of the spine.

Lophosteus uralensis n. sp.

Fig. 6

1997 Actinopterygii gen. et sp. A — Märss: pl. 5, figs 14-16.
1997 Osteichthyan — Märss: 35.

Holotype: scale GIT 297-62 (= Pi 7236; Märss 1997: pl. 5, fig. 15).

Etymology: Named after region of origin (Ural).

Additional material from the type locality: 2 scales (GIT 297-63 + 297-61 [= Pi 7237 + 7238; Märss 1997: pl. 5, figs 16 + 14])

Type locality: locality 67, Kuba River, Ufa amphitheatre, western slope of Central Ural.

Type horizon: lower Lochkovian, Lower Devonian.

Diagnosis: Ridgelets of ridges reach to top of the crest where they join and form chevrons; oblique angle between crest and ridgelets (around 10°); anterior overlapped field pustulate.

Description: Scales of the new species are only known from the Central Ural. They show the main features of *Lophosteus*, pustulate anterior overlapped field, separated ridges of different size on the free field and a narrow dorsal overlapped area without a

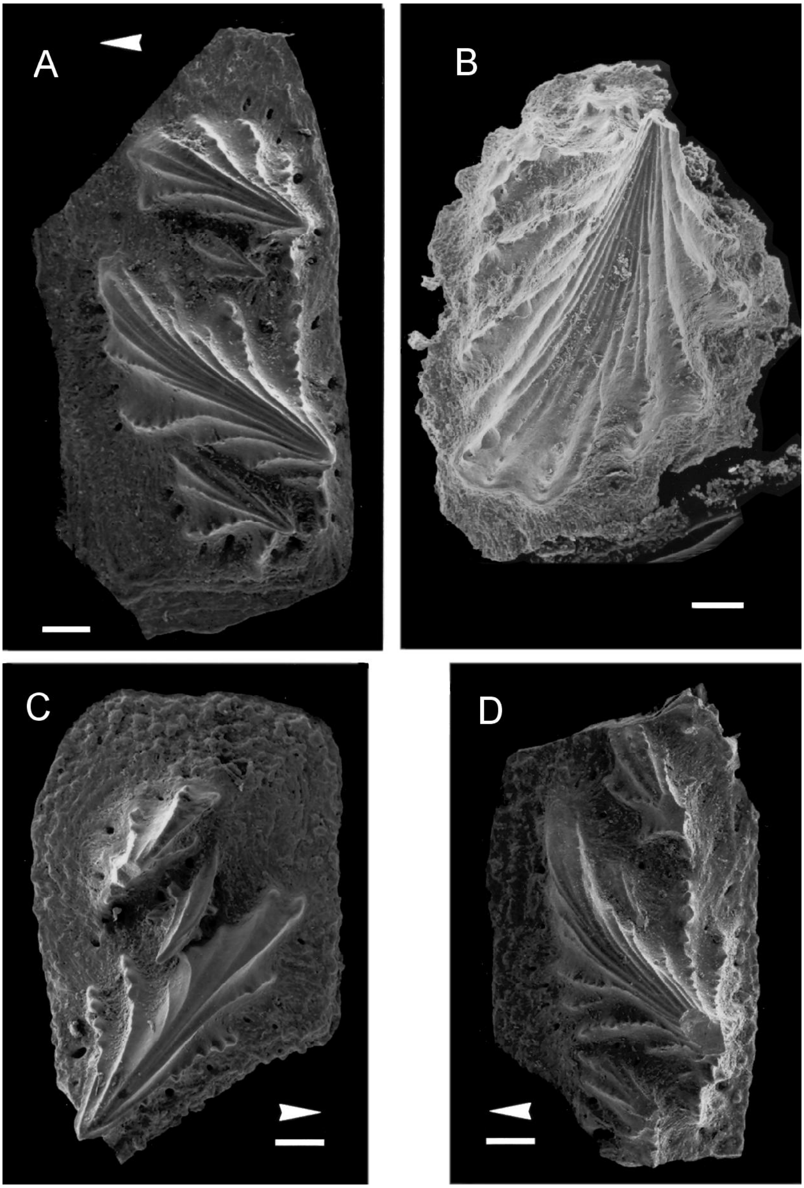

Fig. 5. Lophosteus ohesaarensis n. sp.; upper Pridoli, Upper Silurian; Ohesaare cliff, Saaremaa, Estonia.
A, Scale, GIT 382-122, holotype; B, tessera with one tubercle, GIT 382-89; C, scale, GIT 382-123. SEM pictures, scale bars equal 100 µm.

defined peg. The holotype, a scale of the right flank (Fig. 6 A), shows three long ridges that, notably, arise and partly extend beyond the posterior border of the scale. Three shorter ridges lie between the larger ridges. The ridgelets extend to the crest, forming

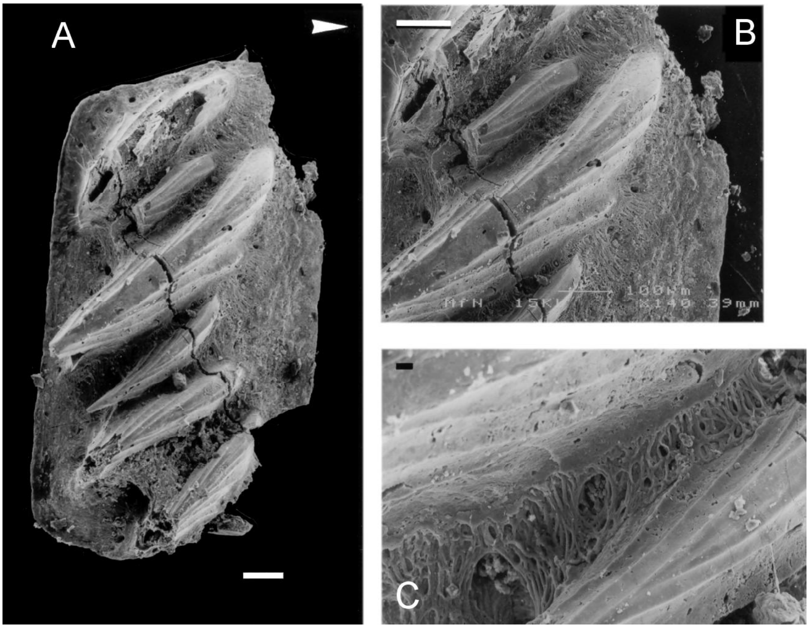

Fig. 6. *Lophosteus uralensis* n. sp.; lower Lochkovian, Lower Devonian; Kuba River, Ufa amphitheatre, western slope of Central Ural.
A, scale of right flank, holotype GIT 297-62; B, C, details of A. SEM pictures, scale bars equal 100 µm.

chevrons in the lower ridges; the ridgelets are separated by a distinct crest in the most prominent ridge. The angle between the crest and the ridgelets is around 10°. The pores between the ridges open in a meshwork of bone (Fig. 6 C) in contrast to the smooth bony surface evident in scales of other species. A second scale shows the same features, but the anterior pustulate area is more distinct; small pustules form rows parallel to the anterior margin of the scale, and more posteriorly they partially join with each other. The plate surface is also uneven posteriorly. Vascular canal pores are very small and hidden between the fine pustules of the basal plate.
Comparison: The species is distinguished from *L. canadensis* by the length of the ridges, the formation of a crest in adult ridges, ridgelets that form chevrons and well-developed, partially joined fine pustules on the anterior overlapped area.

Non *Lophosteus*

1995 lophosteiform or actinopterygian scale – Turner *et al.*: fig. 2.3 + 2.6.

Material: one scale (IGB B48-y2.1; Turner *et al.* 1995: fig. 2.3) and one spine (IGB 53-y1.4; Turner *et al.* 1995: fig. 2.3).
Locality: Longmenshan section, southern China.
Horizon: Ganxi and Xiejiawan formations, Emsian, Lower Devonian.
Description: The figured scale is that of the actinopterygian *Ligulalepis*.

Systematic position

Most researchers considered *Lophosteus* as a primitive osteichthyan, but difficult to be assigned systematically. Rohon (1893: 70) was the first to recognize its osteichthyan relationship; he placed the genus close to the "Cyclodipterinen" (*Holoptychius, Glyptolepis* etc.) of Pander (1856). Gross (1969, 1971) identified *Lophosteus*, together with *Andreolepis* as basal osteichthyan in the family Lophosteidae and order Lophosteiformes. This was based on plesiomorphic histological characters, and he left the question open, if the family and order are closer to the Actinopterygii or the Sarcopterygii. Schultze (1977) separated these genera and placed *Andreolepis* at the base of Actinopterygii, because he described ganoine in the latter genus, and identified *Lophosteus* as a basal osteichthyan between the actinopterygians and sarcopterygians. Janvier (1978) agreed with the placement of *Andreolepis* in Actinopterygii. He suggested assignment of the order Lophosteiformes at the base of the Actinopterygii, preceding the Palaeonisciformes; nevertheless he left open the question whether both genera belong „to a hitherto unknown class of fishes which became extinct at the end of the Silurian and possessed characters in common with the actinopterygians, the struniiformes and the acanthodians" (Janvier 1978: 94). Long (1989) considered the lophosteiforms as the probable sister group to all osteichthyans. Schultze (1992) employed *Lophosteus* as an outgroup to arrange early actinopterygians phylogenetically, whereas Janvier (1996) placed the genus at the base of the Actinopterygii. Märss (2001) agreed with Schultze (1977) that *Andreolepis* is an actinopterygian and that *Lophosteus* is different from that genus; she placed *Andreolepis* in the new family Andreolepididae because the lateral line canals are situated differently in the dermal skeleton in the genera *Andreolepis* and *Lophosteus*. *Lophosteus* has rather wide and deep open canals whereas in *Andreolepis* they are closed as in actinopterygians. Otto (1991) suggested an intermediary position between acanthodians and osteichthyans. Burrow (1995a) indicated similarities with placoderms, but those were considered superficial by Märss (2001).

A limited number of characters are known only in *Lophosteus* (Appendix 2). The main characters are those of the scales, their shape, ornament and histology. In addition, few characters can be extracted from spines, teeth and tesserae. We have analysed these characters in comparison with early osteichthyans, one acanthodian and one arthrodiran placoderm (Appendix 3). Phylogenetic analysis (PAUP 3.1.1: DELTRAN) with *Climatius* and *Sigaspis* as outgroups, and *Terenolepis, Naxilepis* and *Orvikuina* deleted because of missing characters, results in a shortest tree of 42 steps, a consistency index of 0.714 and a homoplasy index of 0.452. This analysis consistently places *Lophosteus* with *Climatius* in the outgroup outside the osteichthyans. The analysis separates the actinopterygians from the sarcopterygians within the osteichthyans (Fig. 7). *Andreolepis* forms a sister group of all other actinopterygians, and the Chinese sarcopterygians at the base to all other sarcopterygians except *Achoania*. Interrelationships within the sarcopterygians, including *Psarolepis* and *Achoania*, are unresolved. The database is too restricted to achieve a resolved cladogram for the sarcopterygians, which in any case is not the goal of this analysis. Interrelationships within actinopterygians are still resolved with the inclusion of *Orvikuina* and *Naxilepis*; only the additional inclusion of *Tenerolepis* results in an unresolved interrelationship of all actinopterygians above *Andreolepis*.

All actinopterygians are characterised by the presence of ganoine, all sarcopterygians by the presence of a broad based peg, cosmine and true enamel. The course of the lateral line canals in bone is the common character of all osteichthyans. The sister group relationship of *Lophosteus* and *Climatius* is the result of the presence of symmetrical and paired fin spines, and of tooth whorl. The presence of a spiny process on the shoulder girdle appears to be a basal character, lost within actinopterygians more derived than *Andreolepis* and within sarcopterygians in forms more derived than *Psarolepis*. This agrees with the analysis of Zhu *et al.* (1999), who placed special importance on the occurrence of spines and spiny processes in early osteichthyans. Tesserae appear as a unique character of *Climatius*, because *Lophosteus* is coded with tesserae or plates. All osteichthyans have a closed skull roof (plates), a feature not known from *Lophosteus*. Still there are plates larger than what is normally considered as tesserae.

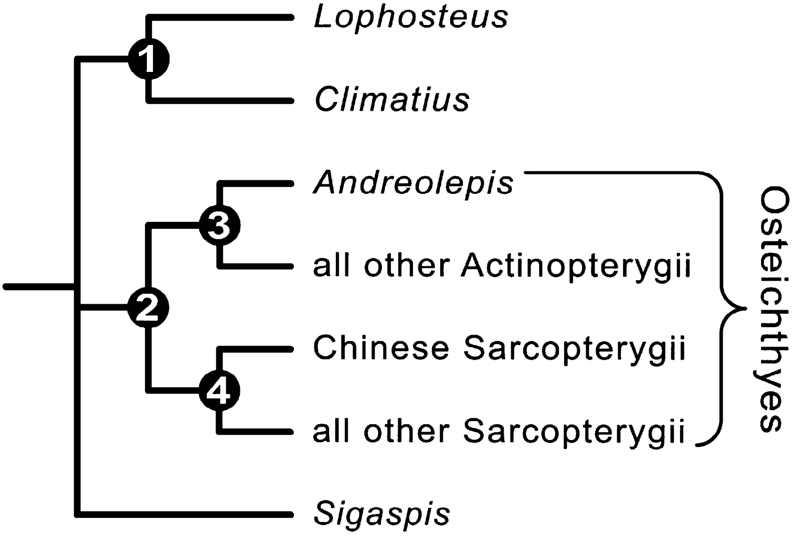

Fig. 7. Interrelationship of *Lophosteus*. Node 1: 8^1, $9^{2\text{-}1}$, 11^1; node 2: **17^1**; node 3: **5^1**; node 4: **2^1**, **6^1**, **14^1** [bold = unique character change; for explanations see Appendix 2 and text].

Characters of the ornament-like stellate tubercles (also found in *Sigaspis*) and ridges (also present in some actinopterygians and sarcopterygians) occur in parallel to *Lophosteus* in other gnathostomes. Nodules, another form of ornamentation, is known in arthrodires (Gross 1973), acanthodians (Gross 1971b) and *Lophosteus* (Gross 1969). That such a similar ornament can appear again and again, is very well established.

Conclusions

For over 100 years, *Lophosteus* Pander, 1856 was known only from the upper Pridoli of one locality, the Ohesaare Cliff on Saaremaa, Estonia. Märss (1986) described a second species from the lower Pridoli of a second locality on Saaremaa. About 10 years later, Burrow (1995a) and Märss (1997) extended the range of the genus to the Lochkovian of Australia and the Urals. Since the beginning of this century, the genus has been known from the lower Ludlow to the upper Lochkovian and from Australia to the Canadian Arctic and the Urals. The genus falls within the distribution, in time and paleogeography of the oldest actinopterygian scales (*Naxilepis,* upper Wenlock – upper Ludlow, China [Wang and Dong 1989]; *Andreolepis*, middle Ludlow – lower Pridoli, Scandinavia [Gross 1968], Baltic region, southern Britain, Asian part of Russia [Märss 2001] and China [Burrow *et al.* 2000]; *Ligulalepis*, upper Ludlow to Emsian, Australia [Schultze 1968, Burrow 1994] and China [Wang and Dong 1989]; *Terenolepis,* upper Lochkovian, Australia [Burrow 1995b]; *Dialipina,* Lochkovian – Emsian, Canadian Arctic, Siberia [Schultze 1968, 1977, 1992] and Sichuan, China [Burrow *et al.* 2000]). *Psarolepis* (upper Pridoli – upper Lochkovian, China [Zhu and Schultze 1997, Yu 1998]) and the sarcopterygians *Onychodus* (Pragian, China [Wang 1992], Emsian, China [Burrow *et al.* 2000]), and *Achoania* (Zhu *et al.* 2001), *Youngolepis* (Chang 1982), and *Diabolepis* (Chang and Yu 1984) appear later (upper Lochkovian, China) as do *Powichthys* (Jessen 1975, 1980) and the lungfish *Uranolophus* (Denison 1968) and *Speonesydrion* (Campbell and Barwick 1982).

The 17 characters, which can be collected from *Lophosteus*, place the genus outside all osteichthyans, whereas these characters separate actinopterygians and sarcopterygians within osteichthyans. *Lophosteus* is the sister group of the acanthodians as suggested by Otto (1991). One may place it between acanthodians and osteichthyans as a basal osteichthyan.

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Appendix 1

New collection numbers for *Lophosteus* species and Actinopterygii gen. et sp. A (= *L. uralensis* n. sp.) in the collections of the Institute of Geology at Tallinn University of Technology, Tallinn, Estonia

New number	Old number	Published data
GIT 232-5	Pi 6175	Märss, 1986, pl. 35, fig. 7
GIT 232-7	Pi 6177	Märss, 1986, pl. 35, fig.8
GIT 232-8	Pi 6178	Märss, 1986, pl. 35, fig. 6
GIT 232-9	Pi 6179	Märss, 1986, pl. 35, fig. 5
GIT 232-15	Pi 6185	Märss, 1986, pl. 5, fig. 3
GIT 232-16	Pi 6186	Märss, 1986, pl. 35, fig. 1 a, b; text-fig. 24.2 a, b
GIT 232-18	Pi 6188	Märss, 1986, pl. 35, fig. 4
GIT 232-23	Pi 6196	Märss, 1986, pl. 35, fig. 2 a, b
GIT 232-35	Pi 6211	Märss, 1986, pl. 35, fig. 13 a, b
GIT 232-36	Pi 6212	Märss, 1986, pl. 35, fig. 9 a, b
GIT 232-37	Pi 6213	Märss, 1986, pl. 35, fig. 12 a, b
GIT 232-38	Pi 6214	Märss, 1986, pl. 35, fig. 10; Märss 1989, fig. 176 G 5
GIT 232-40	Pi 6216	Märss, 1986, pl. 35, fig. 14
GIT 232-41	Pi 6217	Märss, 1986, pl. 35, fig. 11
GIT 232-42	Pi 6218	Märss, 1986, pl. 34, fig. 6
GIT 232-346	Pi 6950	Märss, 1986, pl. 36, fig. 6
GIT 232-365	Pi 6974	Märss, 1986, pl. 36, fig. 4
GIT 232-366	Pi 6975	Märss, 1986, pl. 36, fig. 5
GIT 232-367	Pi 6976	Märss, 1986, pl. 36, fig. 3
GIT 232-412	Pi 7041	Märss, 1986, pl. 34, fig. 8
GIT 232-413	Pi 7042	Märss, 1986, pl. 34, fig. 10
GIT 232-414	Pi 7043	Märss, 1986, pl. 34, fig. 7
GIT 232-415	Pi 7044	Märss, 1986, pl. 34, fig. 9
GIT 232-418	Pi 7047	Märss, 1986, pl. 34, fig. 11
GIT 297-61	Pi 7238	Märss, 1997, pl. 5, fig. 14
GIT 297-62	Pi 7236	Märss, 1997, pl. 5, fig. 15
GIT 297-63	Pi 7237	Märss, 1997, pl. 5, fig. 16

Appendix 2

List of characters for phylogenetic analysis:

Scale characters:

1. Shape: (0) rhombic, (1) small a. square, (2) round
2. Dorsal margin of rhombic scale: (0) broad overlap, (1) broad based peg, (2) short based peg
3. Anterodorsal process: (0) absent, (1) present
4. Free field: (0) ridges, (1) tubercles, (2) covered surface
5. Ganoine: (0) absent, (1) present
6. Cosmine: (0) absent, (1) present
7. Kind of dentine: (0) orthodentine, (1) semidentine, (2) mesodentine

Spine characters:

8. Symmetrical (dorsal, anal) fin spines: (0) absent, (1) present
9. Paired fin spine: (0) absent, (1) present, (2) spiny process

Tooth characters:

10. Marginal teeth: (0) absent, (1) present
11. Tooth whorl: (0) absent, (1) present
12. Tooth plates: (0) broad tooth field, (1) narrow tooth rows, (2) single tooth row
13. Acrodin: (0) absent, (1) present
14. True enamel on teeth: (0) absent, (1) present

Head characters:

15. Stellate tubercles: (0) absent, (1) present
16. Head with: (0) tesserae, (1) plates
17. Lateral line: (0) open, (1) in bone

Primitīvās kaulzivs *Lophosteus* revīzija

HANS-PETERS ŠULCE un TĪJU MJARSS

Gross (1968) izdalījis sugu *Lophosteus superbus* kā vienīgo ģinti, no vienas atradnes Ohesāres klintīs Sāmsalā un īsa laika intervāla – vēlā silūra Pršidolas epohas beigām. Pašlaik ir zināmas sešas sugas, kuras izplatītas visā pasaulē no Ludlovas nodaļas apakšdaļas līdz Prāgas stāva apakšdaļai. Mēs aprakstām trīs jaunas sugas no tipiskās atradnes Sāmsalā, Arktiskās Kanādas un Urāliem. Ģints sistemātiskā piederība ir neskaidra. Ģinti *Lophosteus* ievieto gan daivspurzivju, gan starspurzivju grupā, vai arī kā bazālo taksonu abām kaulzivju klases grupām saiknē ar akantodēm. Līdzība ar bruņuzivīm ir virspusēja. Mēs identificējam ģinti *Lophosteus* kā taksonu, kas ir tuvs akantodēm.

Appendix 3
Data matrix

Taxa/character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Lophosteus	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	0&1	0
Andreolepis	0	0	0&1	0&2	1	0	0	0	2	1	0	0	?	?	?	0&1	1
Terenolepis	0	0	1	0	1	0	?	?	?	?	?	?	?	?	?	?	?
Ligulalepis	0	2	1	0	1	0	0	?	?	?	?	?	?	?	?	1	1
Dialipina	0	2	1	0	1	0	0	0	?	1	0	0	0	0	0	1	1
Cheirolepis	1	0	0	2	1	0	0	0	0	1	0	0	0	0	0	1	1
Moythomasia	0	2	1	2	1	0	0	0	0	1	0	0	1	0	0	1	1
Psarolepis	0	?	?	2	0	1	0	1	2	1	1	1	0	1	0	1	1
Achoania	?	?	?	2	0	1	0	?	?	1	?	2	0	1	?	1	1
Onychodus	2	?	?	0&1	0	0	0	0	0	1	1	2	0	1	0	1	1
Youngolepis	0	1	0	2	0	1	0	?	?	1	0	1	0	1	0	1	1
Powichthys	0	1	0	2	0	1	0	?	?	1	0	2	0	1	0	1	1
Miguashaia	2	?	?	0&2	0	0	0	0	0	1	0	2	0	1	0	1	1
Speonesydrion	0	1	0	2	0	1	0	0	0	0	0	?	0	1	0	1	1
Uranolophus	0	1	0	2	0	1	0	0	0	0	0	0	0	1	0	1	1
Sigaspis	0	0	0	1	0	0	1	0	2	0	0	0	0	0	1	1	0
Climatius	1	0	0	2	0	0	2	1	1	1	1	1	0	0	0	0	0
Naxilepis	0	0	1	2	1	0	0	?	?	?	?	?	?	?	?	?	?
Orvikuina	0	0	1	0&2	1	0	0	?	?	?	?	?	?	?	?	?	1
Diabolepis	0	?	?	2	0	1	0	?	?	1	0	0	0	1	0	1	1
Porolepis	0	1	0	2	0	1	0	0	0	1	1	2	0	1	0	1	1
Kenichthys	0	1	0	2	0	1	0	?	?	1	0	0	0	1	0	1	1
Gavinia	2	?	?	0&1	0	0	0	0	0	1	0	2	0	1	0	1	1

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A new tetrapod *Jakubsonia livnensis* from the Early Famennian (Devonian) of Russia and palaeoecological remarks on the Late Devonian tetrapod habitats

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Skeletal remains of the earliest tetrapod *Jakubsonia livnensis* gen. et sp. nov. are described from the Lower Famennian, Upper Devonian of the Gornostayevka quarry (SW of the Livny Town, Oryol Region, Russia). A part of the skull roof, incomplete angular, the right cleithrum with scapulocoracoid and partial femur are described. The new genus demonstrates characters in the structure of the interorbital region and the cleithrum suggesting similarity to the *Ventastega* Ahlberg, Lukševics and Lebedev, 1994.

An analysis of early tetrapod sites indicates that these animals dwelled within a wide range of aquatic environments. The antiarch genus *Remigolepis* played an important role in Famennian tetrapod communities. The presence of more than one tetrapod in the communities indicates many more diverse tetrapod trophic adaptations than previously considered.

Key words: tetrapods, Russia, Oryol region, Devonian, Famennian, palaeoecology, *Jakubsonia*.

Introduction

Studies of Late Devonian tetrapods became especially intensive during the last decade of the 20th century. Apart from *Ichthyostega* Säve-Söderbergh, 1932 and *Acanthostega* Jarvik, 1952, new taxa from most continents of the world, of both Laurussian and Gondwanan origin, have recently been described. Most of these tetrapods (*Metaxygnathus* Campbell and Bell, 1977, from Australia, *Tulerpeton* Lebedev, 1984 from Russia, *Hynerpeton* Daeschler, Shubin, Thomson and Amaral, 1994 and *Densignathus* Daeschler, 2000 from Pennsylvania (U.S.A.), *Ventastega* Ahlberg, Lukševics and Lebedev, 1994 from Latvia, *Sinostega* Zhu, Ahlberg, Zhao and Jia, 2002 from China and an ichthyostegid tetrapod from Belgium) (Campbell and Bell 1977; Lebedev 1984; Lebedev and Clack 1993; Daeschler *et al.* 1994; Lebedev and Coates 1996; Ahlberg, Lukševics and Lebedev 1994; Daeschler 2000; Zhu *et al.* 2002; Lukševics, Ahlberg and Clack 2003; Clement *et al.* 2004) originate from the upper and middle Famennian deposits. Only *Elginerpeton pancheni* Ahlberg, 1995 is known from the upper Frasnian of Scotland (Ahlberg 1995, 1998). For that reason, each new find of tetrapod material in deposits older than middle Famennian make a contribution of special interest to our knowledge in this field of vertebrate palaeontology.

The first finds of vertebrates from the rich fossil vertebrate locality Gornostayevka quarry (sometimes previously called the Livny quarry) situated to the SW of the Livny

Town in Oryol Region (Central Russia) (Fig. 1) were made by crews of the Palaeontological Institute of the Russian Academy of Sciences, headed by V.V. Dobrokhotova in 1976 and N.I. Krupina in 1977 (Obrucheva and Obrucheva 1977; Moloshnikov 2001). Subsequently between 1997 and 2000 collecting was carried out by a field crew headed by the author in collaboration with a member of the Livny Town Natural History and Local Lore museum, O.L. Jakubson. During the 1999 season the first tetrapod remains were found in this locality.

Previously the only Devonian tetrapod from Russia was *Tulerpeton curtum* Lebedev, 1984, known from the Andreyevka-2 locality (Fig. 1) situated in the Tula Region (Khovanshchinian Regional Stage, uppermost Famennian, *praesulcata* conodont zone) (Lebedev 1984; Lebedev and Clack 1993; Lebedev and Coates 1996).

Postcranial remains of Devonian tetrapods and more specifically limb bones play an important role in the solution of the question whether tetrapod digited limbs were formed in an aquatic environment as a special kind of paddles used for swimming, or in terrestrial environments as specialised lever-type props used for walking (for example, Romer 1958). Clack and Coates (1995) argued that the earliest tetrapods acquired digited limbs while still dwelling in water and were primarily aquatic, based upon *Acanthostega* material. Newly described material provides further arguments in favour of the latter point of view.

Geological setting, sedimentology and taphonomy

The Gornostayevka industrial quarry exposes deposits of the Evlanovian, Livnian (Upper Frasnian) and Zadonskian Regional Stage (lower Famennian). Specimens of *Jakubsonia livnensis* gen. and sp. nov. were collected from the Gornostayevka locality situated within the limits of the upper part of the section within the Zadonskian Regional Stage (Moloshnikov 2001). This stage is correlated to the ?*triangularis-crepida* Zone of the Standard conodont scale (Alekseev *et al.* 1996). The lower part of the Zadonskian sandstones inconformably overlie the Livnian (Upper Frasnian) limestones.

In the west the part of the Zadonskian deposits exposed at the surface is dominated by terrigenous, sometimes coarse-grained rocks. To the east carbonates become dominant (Rodionova 1995), suggesting their outlying position from a denudation area (Voronezh Uplift). The locality under discussion is situated in the western part of the Zadonskian basin in which a terrigenous type of sedimentation prevailed.

Fossiliferous coarse-grained sands and sandstones intercalated with fine-grained clays and thin limestone layers occur in the middle of the Zadonskian Regional Stage section of the quarry. These deposits imply sedimentation in hydrodynamically active conditions (Moloshnikov 2001). However, preserved shells of rhynchonellid brachiopods in the layers immediately above and below the vertebrate fossiliferous layer suggest deposition in a marine environment.

The bone-bearing coarse-grained sands and gravels form a lens and a pocket about 15-30 cm thick and extending for several square meters. Bones demonstrate insignificant sorting by size or by weight and no orientation. A special feature of sorting is the complete absence of the smallest skeletal elements, like acanthodian scales, despite abundant presence of their fin spines. Probably, this reflects easy transport of scales by

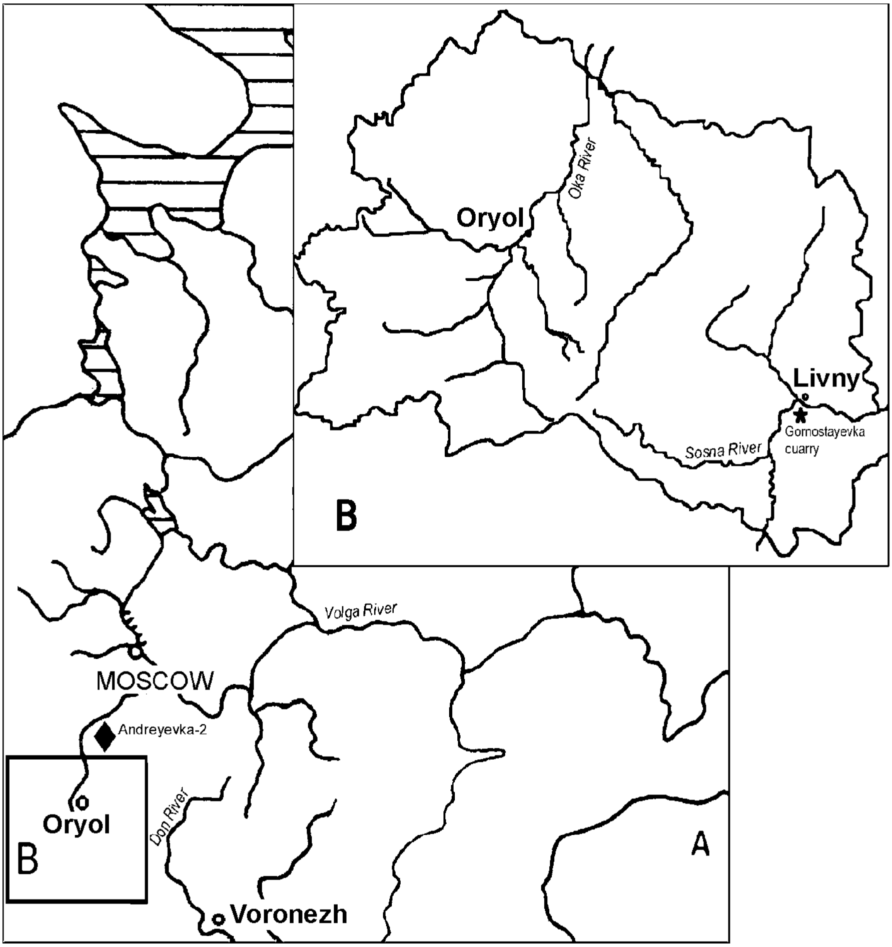

Fig. 1. Map showing location of the Gornostayevka quarry, marked by an asterisk. Location of previously known tetrapod site Andreyevka-2 marked by a black diamond.

currents to burial in different environments. The fossiliferous lens and pocket are overlain with a thin layer of plastic reddish-brown clay and fine-grained quartz, white and brownish sands containing rare and poorly preserved vertebrate fragments. Moloshnikov (2001) suggested that the site was formed as a result of temporary stream activity within the shallow-water near-shore zone of an epicontinental basin.

Most of the bones are to some extent eroded, however some of them are intact, implying different conditions of transport. Bone colour varies from white to brown and black depending on the rate of their impregnation with iron and manganese oxides and salts. The hardness of the bone is also influenced by mineral impregnation, making white and yellowish bone very fragile and dark-brown and black ones extremely solid. The amount of iron and manganese oxides and salts may suggest former proximity to denudation areas (Tolstikhina 1952). Thus, it is not clear how much of the bone was brought from uplands by streams and how much was deposited *in situ*.

The following vertebrate remains are preliminarily identified from the Zadonskian deposits of the Gornostayevka locality: abundant cranial and postcranial remains of antiarchs "*Bothriolepis*" *zadonica* H. Obrucheva, 1983, *Bothriolepis sosnensis* Moloshnikov, 2003, *B.* cf. *leptocheira* Traquair, 1893 and *Remigolepis* ? sp. (Moloshnikov 2001, 2003); numerous acanthodian fin spines of *Devononchus* cf. *laevis* (Gross, 1933); rare isolated bones of the ptyctodontid *Chelyophorus* sp. and pachyosteomorph arthrodires; abundant scales and bones of the porolepiform *Holoptychius* cf. *nobilissimus* Agassiz, 1839, osteolepiforms *Megapomus markovskyi* Vorobyeva, 1977 and *Glyptopomus* sp.; numerous tooth plates and rare cranial and postcranial bones of dipnoans *Conchodus* sp., *Holodipterus* sp. and *Dipterus* sp.

Material and methods

All skeletal fragments were found disarticulated, some of them were broken, while others, thin and fragile, are complete. The internal (visceral) surface is generally well preserved. Cranial materials include: the interorbital part of the skull roof, including the frontals, anterior part of the parietals and almost complete postfrontals preserved in natural contact (PIN 2657/346) and an incomplete angular (PIN 2657/347). Postcranial materials consist of the right cleithrum with partly preserved scapulocoracoid fused to it (holotype PIN 2657/343) and the distal part of the femur (PIN 2657/344). Specimen PIN 2657/346 is chosen as holotype, all the remaining cranial and postcranial materials are referred to it, as there is no certainty in whether all remains belong to the same taxon. The posterior part of the skull roof PIN 2657/348 is questionably assigned to *Jakubsonia livnensis* gen. and sp. nov. The material is stored in the collection 2657 of the Palaeontological Institute of the Russian Academy of Sciences (PIN).

All specimens were prepared manually with mounted needles.

Systematic palaeontology

Superclass TETRAPODA Goodrich, 1930
Family undesignated
Genus *Jakubsonia* Lebedev, gen. nov.

Derivation of name – to honour O.L. Jakubson, the member of the Livny town Natural history and Local Lore museum, who enthusiastically helped excavations.
Type species - *Jakubsonia livnensis* Lebedev, sp. nov.
Diagnosis. An early Famennian tetrapod characterised by short snout (estimated by frontals which are only 2.4 times longer than wide) and large orbits. The lateral side of the prefrontal adjoins the lateral margins of the frontal and postfrontal together, the dorsal process of the postorbital abuts the posterolateral part of the postfrontal, rather than wedges between it and the parietal.

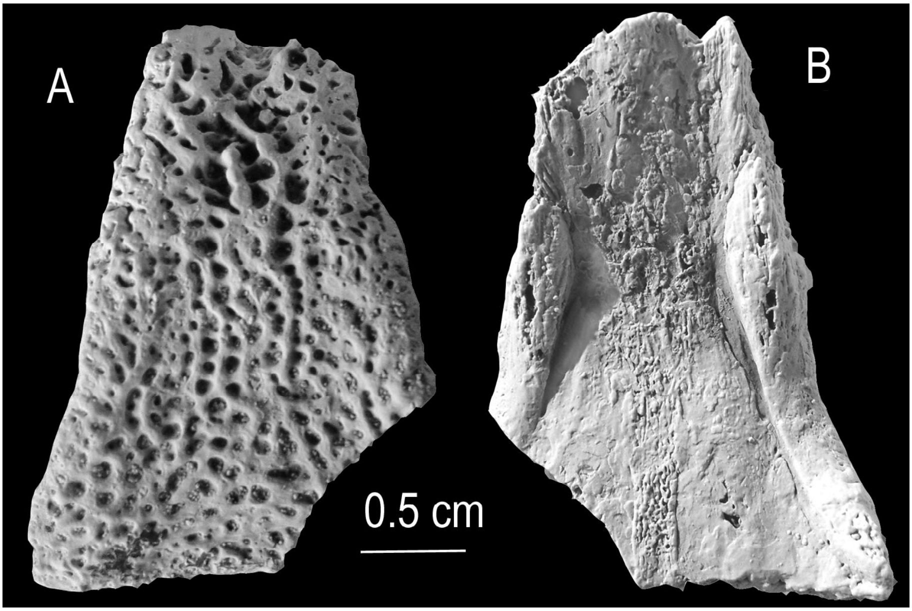

Fig. 2. Jakubsonia livnensis gen. and sp. nov., interorbital fragment of the skull roof, PIN 2657/346. A, dorsal view; B, ventral view.

Jakubsonia livnensis Lebedev, sp. nov.

Etymology. After the town of Livny.

Holotype. PIN 2657/346, the interorbital part of the skull roof, including the frontals, anterior part of the parietals and almost complete postfrontals preserved in natural contact.

Diagnosis. As for the genus.

Locality and horizon. Gornostayevka quarry, SW of the Livny Town, Oryol Region, Central Russia, ? *triangularis-crepida* Zone of the Standard conodont scale, Zadonskian Regional Stage, Lower Famennian, Upper Devonian.

Description and comparisons. *Skull.* The holotype PIN 2657/346, a fragment of the **interorbital part of the skull roof** (Fig. 2) includes the frontals, anterior part of the parietals and completely preserved postfrontal from the left side and its anterior half from the right side preserved in natural contact. The dorsal side of this fragment is ornamented with pit-and-ridges sculpturing characteristic of all known Devonian tetrapods. The pits are more uniform in size and isometric at the parietals and the postfrontals; in the central part of the frontals they are much deeper, and their outline is irregular. In the anterior part of the frontals these pits even partly merge forming a short deep groove.

The anterior, frontal part of the holotype slopes ventrally with respect to the parietal part at an angle of approximately 20°. The frontals and parietals are fused without any trace of medial suture. The frontals are short; they are only 2.4 times longer than wide. The posterior half of their lateral contact area is occupied by the postfrontal contact, the anterior part served for the prefrontal attachment (Fig. 3). This condition is not observed in the Devonian tetrapods *Ichthyostega* (Jarvik 1952), *Acanthostega* (Clack and Coates 1993) or *Ventastega curonica* (Lukševics, pers. comm.); however, it may be found in the long-snouted anthracosauromorphs, for example *Proterogyrinus scheelei* Romer, 1970 (Holmes 1984), *Eoherpeton watsoni* Panchen, 1975 (Smithson 1985) and *Anthracosaurus russelli* Huxley, 1863 (Panchen 1977). However, in these species the frontal is very long, because of the general elongation of the preorbital part of the skull. In *Jakubsonia*, on the contrary, a short frontal in combination with a long contact to the prefrontal might suggest large orbits, rather than a long snout. The anterior edge of the frontals shows no sutural contact; on the contrary, the bone becomes thinner here suggesting participation in the posterior margin of an internasal fontanelle as in *Tulerpeton* (Lebedev and Clack 1993) or in *Ventastega* (Lukševics *et al.* 2003). The lateral side of the left frontal, however, shows a rather deep notch, which houses the infraorbital canal opening. This notch might be interpreted as a contact for the left nasal. The lateral parts of the fronto-parietal suture are visible at the ventral side of the skull roof. Mesially a sheath of spongy matter of the connecting ethmosphenoid obscures the suture (Fig. 2B).

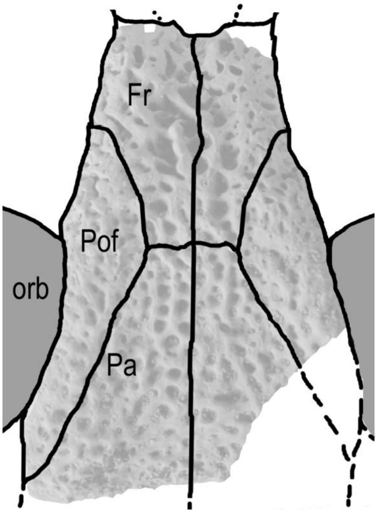

Fig. 3. Jakubsonia livnensis gen. and sp. nov., reconstructed interorbital fragment of the skull roof. Abbreviations: **Fr**, frontal; **Pa**, parietal; **Poc**, contact margin for the postorbital; **Pof**, postfrontal; **Prf**, position of prefrontal; **or**, orbit; **soc**, supraorbital canal; **son**, notch housing the anterior opening of the supraorbital canal in the frontal.

From the frontals the supraorbital canal turns laterally and enters the narrow, semilunate postfrontals. The shape of this bone is characteristic of the Devonian tetrapods *Ichthyostega* (Jarvik 1952), *Acanthostega* (Clack and Coates 1993) and *Tulerpeton* (Lebedev and Clack 1993). In the later Carboniferous tetrapods, for example

Proterogyrinus (Holmes 1984), *Crassigyrinus* (Panchen 1985; Clack 1998) and *Anthracosaurus* (Panchen 1977) the posteromesial part of the postfrontal widens, deeply wedging into the parietal. However, in contrast to the condition in *Acanthostega* and in accordance with that in *Ventastega* (Lukševics, pers. comm.) the lateral sides of the prefrontals must have adjoined the lateral sides of the frontal and postfrontal together, and the lateral process of the postorbital must have abutted the posterolateral part of the postfrontal, rather than wedged between it and the parietal. The contact surface for the postorbital is preserved at the posteriormost tip of the postfrontal on the left side of the specimen. The infraorbital canal leaves the bone shortly anteriorly to this contact area. A pronounced swollen ridge forms the orbital margin.

Only the anterior parts of the parietals are preserved. Posteromedially the parietals become thinner at its centre and form a depression on the dorsal side, probably running forwards from the pineal foramen. On the ventral side the most impressive features are deep grooves running alongside the parietal-postfrontal contact. These grooves bear blood vessel impressions, which lead to moderately large foramina opening into the canals inside the bone. The mesial part of the parietals is occupied with a narrow impression of the sphenethmoid.

The only lower jaw element preserved is an incomplete left **angular** (PIN 2657/347) (Fig. 4). In most respects it agrees with the corresponding bones in *Ichthyostega* (Jarvik 1952), *Acanthostega* (Clack and Coates 1993), *Ventastega* (Ahlberg *et al*. 1994),

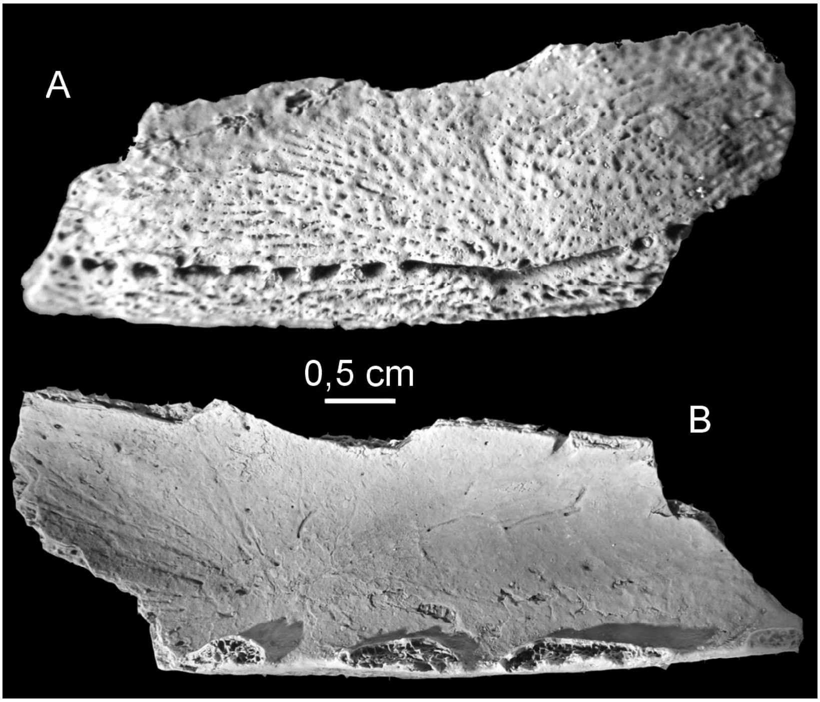

Fig. 4. *Jakubsonia livnensis* gen. and sp. nov., incomplete angular, PIN 2657/347. A, lateral view; B, mesial view.

Tulerpeton (Lebedev and Clack 1993) and *Densignathus* (Daeschler 2000). Its anterior and posterior edges are broken off; the dorsal margin shows small fused parts of the surangular. The ornament consists of shallow pits and anastomosing ridges, the pits become more elongated radially from the ossification centre in the area dorsal to the mandibular seismo-sensory canal groove (Fig. 4A). Ventral to it the ridges become more swollen and pits are deeper than above the canal. The canal is deep and wide, a short part of it close to the ossification centre is exposed to the surface, and the remaining course communicates to the surface with a single row of large rounded or elongated foramina. This pattern conforms to that in *Densignathus* (Daeschler 2000), but contrasts with that found in *Tulerpeton*, in which the canal is completely housed in an open groove (Lebedev and Clack 1993). In *Acanthostega*, on the contrary, most of the canal is enclosed in the bone and only its anterior and posterior sections at the angular are exposed in the grooves (Ahlberg and Clack 1998). In *Ventastega* the canal through this bone is not exposed at all (Ahlberg *et al.* 1994). The ventral edge of the preserved part of the bone is almost straight. The mesial lamina is narrow and smooth; its lateral edge is separated from the lateral lamina with a straight ridge of uniform width. The notches for the Meckelian foramina are shallow, and there are at least three of them seen in the preserved fragment (Fig. 4B).

Pectoral girdle. The **cleithrum** (PIN 2657/343) (Fig. 5) is generally well preserved, only its lateral surface and the anterior edge are slightly worn. On its mesial surface the posterodorsal corner of the dorsal lamina (Fig. 5B) bears a deep elliptical pit, which may be a trace of lifetime damage, as the edges of the bony bars at the pit bottom constituting the tissue are smooth, as happens in healed tissue. However, there are no traces of regeneration to support this suggestion.

In its general shape the cleithrum is very similar to the bones (LDM 81/522 and LDM 57A/1984) attributed to *Ventastega* (Ahlberg *et al.* 1994). The general outline of the cleithrum is feather-shaped; it is sigmoidally curved in the lateral aspect. In the anterior aspect (Fig. 5C) the bone is only very slightly curved laterally, its dorsal lamina is comparatively thin; the maximum thickness of the bone is attained at the contact with the supraglenoid buttress. The bone outline and thickness are most consistent with that of *Ventastega*, however it is significantly less curved laterally. In *Hynerpeton bassetti* Daeschler, Shubin, Thomson et Amaral, 1994 and *Acanthostega gunnari* Jarvik, 1952 (Coates 1996) the dorsal lamina is much more robust. The maximum length of the bone is 57 mm, maximum width across the ventral point of the anterodorsal edge is 17 mm.

The lateral surface of the bone (Fig. 5A) is covered with tiny pores of blood supply vessels in combination with longitudinally directed small anastomosing ridges. At the mesial surface similar sculpturing is observed only in the anterodorsal part of the bone; it marks here the contact area for the anocleithrum. The rest of the mesial surface dorsally from the scapulocoracoid bears numerous minute subparallel blood vessel grooves organised in a fan-shaped manner, which radiate from the dorsal edge of the scapulocoracoid attachment area.

The expanded dorsal blade occupies more than half of the bone length, as in *Ventastega* and in contrast to other known Devonian tetrapods (Ahlberg *et al.* 1994; Lebedev and Coates 1995; Jarvik 1996; Coates 1996; Daeschler *et al.* 1994). The anterodorsal edge of the cleithrum, forming the contact with the anocleithrum, is

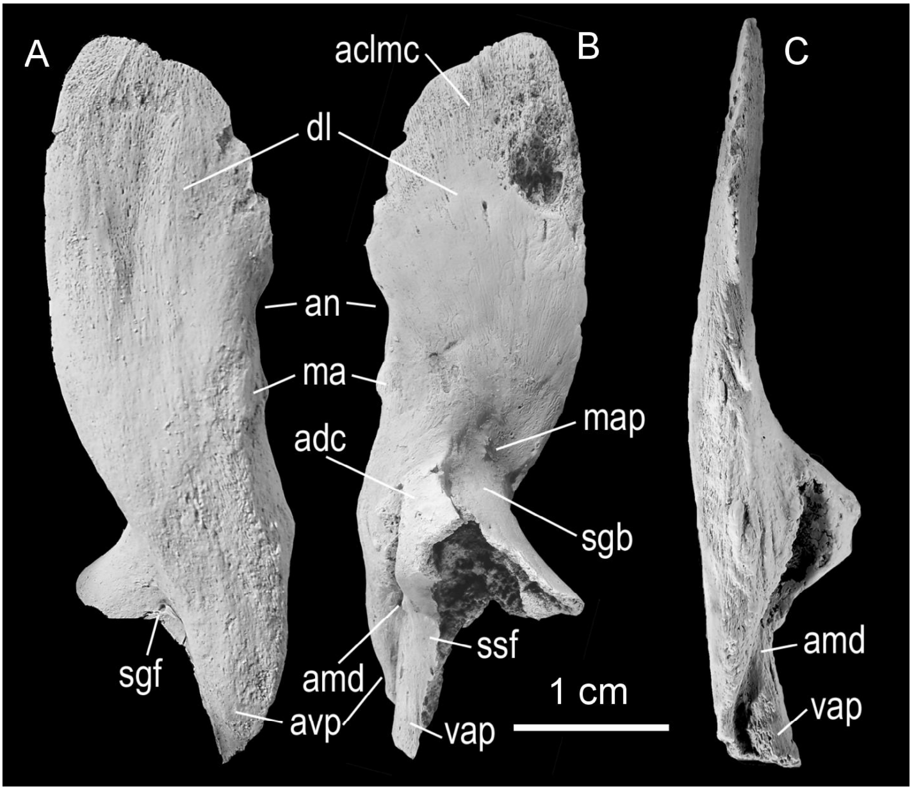

Fig. 5. Jakubsonia livnensis gen. and sp. nov., right cleithrum with partly preserved scapulocoracoid, holotype PIN 2657/343. A, lateral view; B, mesial view; C, anterior view. Abbreviations: **aclmc**, contact area for the anocleithrum; **adc**, anterodorsal crest; **amd**, anteromedial depression; **an**, anterior notch; **avp**, anteroventral process; **dl**, dorsal lamina; **ma**, muscle attachment tubercles; **map**, muscle attachment pits; **sgb**, supraglenoid buttress; **sgf**, supraglenoid foramen; **ssf**, subscapular fossa; **vap**, ventral anteromedial process.

subvertical and arched; more ventrally it forms a slight notch as in *Hynerpeton* (Daeschler *et al.* 1994) and *Tulerpeton* (Lebedev and Coates 1995). In the Carboniferous forms this notch is found in the cleithrum of, for example, *Proterogyrinus* (Holmes 1984). In *Ventastega*, *Ichthyostega* and *Acanthostega* this notch is unknown. As in *Ventastega*, *Elginerpeton* (Ahlberg 1998) and *Hynerpeton*, and in contrast to *Acanthostega* (Coates and Clack 1991; Coates 1996) and *Ichthyostega* (Jarvik 1980) the anterior edge ventrally forms no branchial lamina. Instead, in *Jakubsonia* this edge is rounded, thickened and bears massive elongated tubercles for the attachment of muscles directed anterodorsally, seemingly for the *m. cuccularis* or *m. depressor mandibulae*. The most prominent tubercle bearing rugosity is situated opposite the anterodorsal part of the supraglenoid buttress (Fig. 5B). Ventrally from it the anteroventral process tapers quickly. Laterally it limits the deep anteromedial depression, which housed the posterior lamina of the dorsal process of the clavicle (Figs. 5B, C). The ventral part of the anterior edge of the cleithrum is convex. Mesially from the anteroventral process and posteriorly from the anteromedial depression there is a process parallel to the former, named here the ventral anteromedial process. Its mesial surface is smooth; it is straight and the ventral tip projects below the apex of the anteroventral process.

The corresponding part of the posterior edge of the cleithrum is, on the contrary, concave and its outline almost follows in parallel that of the anterior edge. The contact with the scapulocoracoid can be easily traced; it follows the sharp ridge of the posteroventral edge. The posterodorsal edge of the bone is less acute and smoothly arched in plan view.

The **scapulocoracoid** (Fig. 5B) is incompletely ossified and only its scapular portion is partly preserved, in accordance with the condition noted by Holmes (1980) in *Proterogyrinus*. This bone is solidly fused to the mesial side of the cleithrum, however, in contrast to *Ichthyostega*, *Acanthostega* and *Hynerpeton* and in agreement with the condition in *Elginerpeton* (Ahlberg 1998) its sutures are fairly well discernible. As noted above, the posterolateral suture of the scapulocoracoid runs parallel to the posteroventral edge of the cleithrum. Posterodorsally it is obscured by three shallow muscle attachment pits, possibly for the analogue of the *m. levator scapulae*. These pits are separated anteriorly from the anterodorsal part of the supraglenoid buttress by a prominent transverse ridge. The anterodorsal crest at this point is robust, ventrally it reduces in height forming a concavity at the anterior edge of the subscapular fossa, which would have been large and comparable in configuration to that in *Hynerpeton* (Daeschler *et al.* 1994) and *Elginerpeton* (Ahlberg 1998). The anteroventral part of the anterior edge of the scapulocoracoid abuts the dorsal part of the ventral anteromedial process of the cleithrum. A small supraglenoid foramen is situated close to the scapulocoracoid-cleithrum suture in the same position as in *Hynerpeton* and foramen “C” in *Acanthostega* (Coates 1996).

Only the distal part of the left **femur** (PIN 2657/344) is preserved. The major feature distinguishing it from all other known Devonian tetrapods is the absence of an intercondylar fossa (Figs. 6, 7) and correspondingly distinctly expressed condyles. Instead, the dorsal (extensor) surface of the femur in its distal part is almost flat (Fig. 6B). Two shallow ridges, one running along the posterior edge of the dorsal surface and the other parallel to it roughly in the middle of the surface, form a shallow groove with uneven surface. The rest of the surface adjoining the tibial condyle is also flat and pierced with several large blood vessel foramina. Its anterior edge forms an abrupt bend to the condyle surface. More proximal part of the dorsal surface in the shaft area is rounded and passes smoothly into the shaft portion of the anterior surface of the femur. The massive adductor crest running obliquely towards the anterior bone surface delimits the ventral margin of the anterior surface (Fig. 6A). The distal part of the anterior surface is dominated by the bulky perichondral mass of the tibial condyle strongly overhanging and even partly enclosing ventrally the large and deep triangular-shaped popliteal fossa (Figs. 6A, C). The ventral surface of the bone enclosed between the adductor crest and a sharp ridge separating this surface from the posterior one is narrow distally but widens in the proximal direction. The latter ridge is situated topographically in the same position as a well marked unnamed ridge situated at the ventral side of the femur receiving the distal extremity of the adductor crest and separating

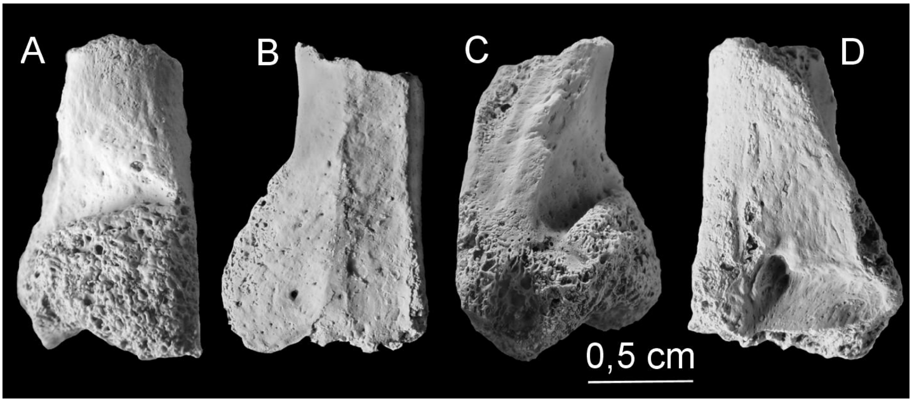

Fig. 6. Jakubsonia livnensis gen. and sp. nov., distal part of the left femur, PIN 2657/344. A, anteriorly, B, dorsally, C, ventrally, D, posteriorly.

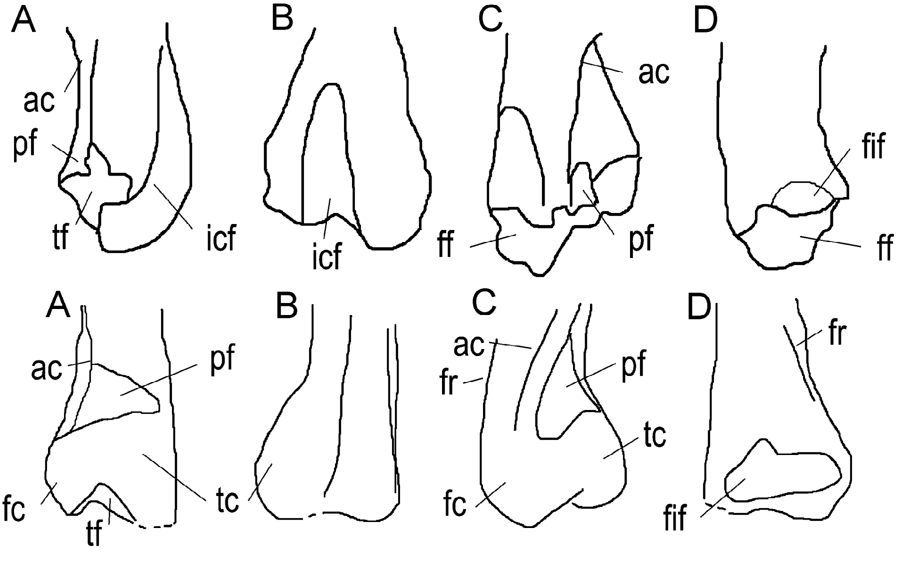

Fig. 7. Distal part of the femur in *Tulerpeton curtum* Lebedev, 1984 (upper row) and left femur in *Jakubsonia livnensis* gen. and sp. nov. (lower row). The drawings of *Tulerpeton curtum* femur reversed from the right to the left for the sake of comparison, distal part directed downwards. A, anterior view, B, dorsal view, C, ventral view, D, posterior view. Abbreviations: **ac**, adductor crest; **fc**, fibular condyle; **ff**, fibular facet; **fif**, fibular fossa; **fr**, fibular ridge; **icf**, intercondylar fossa; **pf**, popliteal fossa; **tc**, tibial condyle; **tf**, tibial facet.

the popliteal from the fibular fossa in *Tulerpeton* (Lebedev and Coates 1995). It supports the ventral corner of the fibular condyle and is termed here the fibular ridge (fr).

The fibular ridge limits the posterior face of the distal part of the femur ventrally (Fig. 6D). The ventral part of this surface distally is occupied by a very large triangular elongated fibular fossa, the size of which, as that of the popliteal fossa, exceeds the sizes of corresponding structures in all known Devonian tetrapods.

In cross-section the distal part of the femur is shaped roughly as an equilateral triangle, with its base slightly arched outwards (anteroventrally) at the expense of the overhanging tibial condyle. The distal articulating surface is very well ossified, but incompletely preserved. The only intact area is the central part of the tibial facet adjoining the crest, which separates it from the fibular facet. The latter is completely destroyed (Fig. 6).

Cranial bone questionably assigned to *Jakubsonia livnensis* gen. and sp. nov. (Fig. 8). **The posterior part of the skull roof** PIN 2657/348 includes an unpaired postparietal, the anterior part of the right tabular, right supratemporal, fragments of the right parietal and left supratemporal. The only well preserved margin of this specimen is the posterior. The feature which might suggest attribution of the specimen to tetrapods is the characteristic pit-and-ridges dermal sculpturing of the same type as found in the fragment of the interorbital part of the skull roof described above (PIN 2657/346). However, the

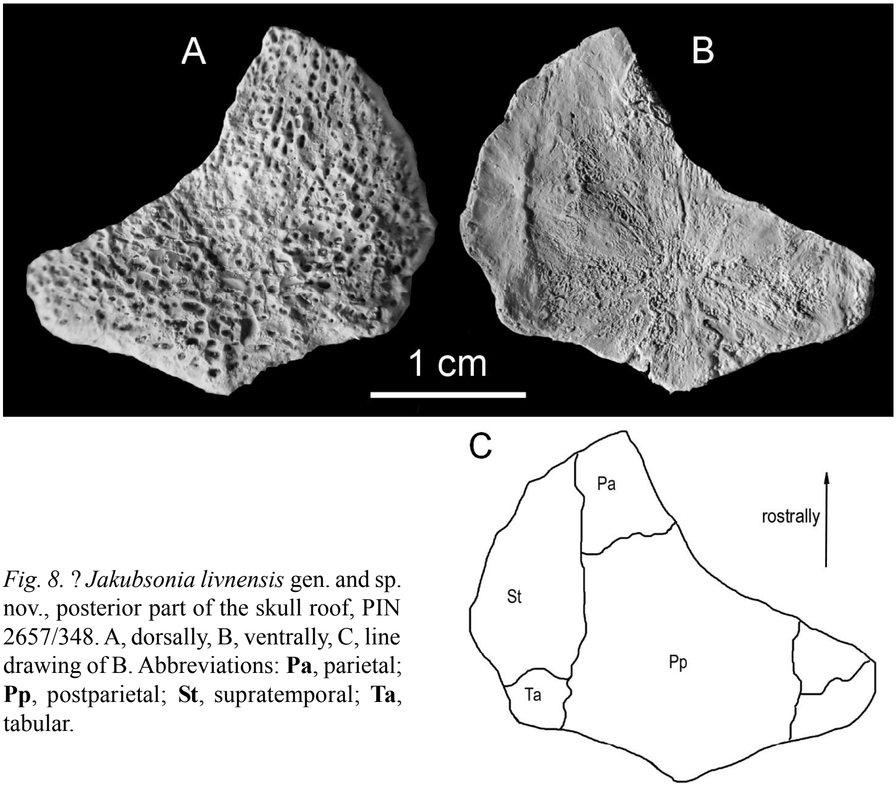

Fig. 8. ? *Jakubsonia livnensis* gen. and sp. nov., posterior part of the skull roof, PIN 2657/348. A, dorsally, B, ventrally, C, line drawing of B. Abbreviations: **Pa**, parietal; **Pp**, postparietal; **St**, supratemporal; **Ta**, tabular.

roofing bone pattern is unusual, and among Devonian tetrapods may be compared only to that in *Ichthyostega*, in which the postparietal is unpaired. In contrast to the condition in that animal, the posterior margin in PIN 2657/348 is convex rather than concave. More precisely, its shape is angular and the most conspicuous medial point is formed by the posteromesial process of the postparietal as in *Ventastega* (Lukševics, pers. comm.). The postparietal is hexagonal and occupies about half of the skull table width in this area. The lateral side contacts the tabular and the supratemporal, the anterolateral one the parietal.

Given the skull roof pattern of this specimen, which is characteristic of dipnoans, one could be skeptical of its attribution to a tetrapod. However, no Devonian dipnoan is known to possess pit-and-ridge dermal sculpturing.

Discussion

***Jakubsonia*, an aquatic tetrapod**

In order to support the hypothesis of the primary aquatic life mode of *Acanthostega* and *Ichthyostega*, Clack and Coates (1995) put forward a number of morphological arguments relating to limb structure, such as the absence of olecranon on the ulna, correspondence of radius and ulna length and polydactyly.

The femoral structure was never discussed from this point of view, as most of the previously known early tetrapod femora are more or less similarly built. In this respect the femur in *Jakubsonia* demonstrates probably the most unusual morphology in that there is no intercondylar fossa on its dorsal (extensor) surface distally and, respectively the condyles themselves are not expressed as well (Fig. 8). That means that the extensor muscles were not capable of pulling the epipodium forwards and the knee joint movements were more than limited. It is very probable that natural mobility in the joint was passive (that is, the muscles did not really act to deflect the knee effectively enough to reach significant limb bending) and instead of muscles, impeding of the surrounding matter (most likely, water!) was compensated only by exceptionally strong ligaments originating at the popliteal and fibular fossae. Thus, this animal was not capable of walking at all and paddling was the only function of its hind limb. This implies that the earlier the tetrapod is found in the Devonian, the more features support its primarily aquatic mode of life.

Palaeoecological remarks

Earlier attempts to study palaeoecology of Devonian tetrapods were undertaken by Spjeldnaes (1982) who focused on *Ichthyostega*, Bendix-Almgreen *et al.* (1990), Coates and Clack (1995) on *Acanthostega*, and Lebedev (1985, 1992) who considered *Tulerpeton* in the Andreyevka biota. Since those times several new localities have been discovered, which yielded previously unknown tetrapod remains (see Introduction). The palaeoecology and taphonomy of the Gornostayevka locality from where *Jakubsonia livnensis* gen. and sp. nov. originates were recently described by Moloshnikov (2001). This contributed much to our knowledge of the subject.

In order to evaluate palaeoecological data the primary taphonomical, environmental and assemblage structure information was assembled in the table (Table I). An attempt to synthesize this accumulated information is made here.

Table I. Taphonomical, environmental and assemblage structure data on the localities and assemblages of the Devonian tetrapods

Locality	**Scat Craig** (Ahlberg 1998)	**Red Hill** (Daeschler *et al.* 1994; Daeschler 2000)	**East Greenland** (Bendix-Almgreen *et al.* 1990; Coates and Clack 1995)	**Andreyevka-2** (Lebedev 1992; Lebedev and Clack 1993; Alekseev *et al.* 1994)	**Ketleri and Pavāri** (Lebedev, Lukševičs 1996; Lukševičs, pers. comm.)
Age	Upper Frasnian	Upper Famennian	Upper Famennian	Uppermost Famennian	Upper Famennian
Tetrapod	*Elginerpeton*	*Hynerpeton* *Densignathus*	*Ichthyostega* *Acanthostega*	*Tulerpeton* and "undetermined tetrapod	*Ventastega* and "second tetrapod?" (in Ketleri)
Remigolepis	-	-	+	+	-
Bothriolepis	+	-	+	+	+
Holoptychius	+	-	+	+	+
Eusthenodon	-	*Hyneria*	+	+	-
Dipnoi	+	+	+	+	+
Acanthodians	+	+	-	+	+
Dominant vertebrate	*Holoptychius* *Bothriolepis*	? groenlandaspidids	*Remigolepis*	*Andreyevichthys*	*Holoptychius* *Bothriolepis*
Missing group	*Remigolepis* *Eusthenodon*	*Holoptychius* *Bothriolepis* *Remigolepis*	Arthrodira Acanthodians	Arthrodira	Arthrodira ? *Remigolepis* *Eusthenodon*
Presence of macroflora	?	+	+	-	-
Palaeogeographical position	Laurussia	Laurussia	Laurussia	Laurussia	Laurussia
Environment	Fluvial	Coastal alluvial plain	Fluvial	Epicontinental sea	Near-shore
Basin salinity	? Fresh-water	? Brackish, inconstant salinity	Fresh-water	Brackish, inconstant salinity	? Brackish
Burial type	Allochtonous	Autochthonous	Autochthonous	Autochthonous	Autochthonous (Pavāri) Allochtonous (Ketleri)
Sediments	Coarse-grained terrigenous	Fine-grained terrigenous	Fine-grained terrigenous	Fine-grained carbonate	Coarse-grained terrigenous

Table I includes information on 8 known tetrapod localities and on two others in which tetrapods are unknown, used for comparative purposes (Rybnitsa in Oryol Region, Russia and Ala-Archa, Kirghizstan). The Rybnitsa locality is known to render a vertebrate assemblage very close to the Latvian Ketleri and Pavari localities (Lebedev 1995; Lebedev and Lukševics 1996). The Ala-Archa locality yielded the remains of an antiarch fish *Remigolepis*, which seems to play an important role in the structure of the Devonian tetrapod biota.

Continuation of the Table

Locality	**Rybnitsa** (Lebedev 1995)	**Gornostayevka quarry** (Tolstikhina 1952; Alekseev *et al.* 1996; Moloshnikov 2001)	**Ala-Archa (Tien Shan)** (Panteleyev 1992)	**Ningxia** Zhu *et al.* 2002	**Jemalong, N.S.W.** (Campbell, Bell 1977; Young 1993)
Age	Upper Famennian	Lower Famennian	Upper Devonian	Upper Famennian	? Middle-Upper Famennian
Tetrapod	None	*Jakubsonia*	None	*Sinostega*	*Metaxygnathus*
Remigolepis	-	+	+	+	+
Bothriolepis	+	+	-	*Sinolepis*	-
Holoptychius	+	+	-	-	-
Eusthenodon	-	?	-	-	-
Dipnoi	+	+	-	?	+
Acanthodians	+	+	-	-	-
Dominant vertebrate	*Holoptychius* *Bothriolepis* *Dipterus*	*Holoptychius* *Bothriolepis*	*Remigolepis*	*Remigolepis*	?
Missing group	*Remigolepis* *Eusthenodon*	? *Eusthenodon*	Arthrodira Dipnoi *Holoptychius* *Eusthenodon* Acanthodians	Arthrodira *Holoptychius* *Eusthenodon* Acanthodians	Arthrodira *Holoptychius* *Eusthenodon* *Bothriolepis* Acanthodians
Presence of macroflora	-	-	+	+	-
Palaeogeographical position	Laurussia	Laurussia	Kazakhstan	North China craton	East Gondwana
Environment	Deltaic near-shore	Deltaic near-shore	?Intramontane	Non-marine	Fluvial
Basin salinity	? Brackish, inconstant salinity	Marine, inconstant salinity	Fresh-water	? Brackish	? Brackish
Burial type	Allochtonous	Allochtonous	Allochtonous	?	?
Sediments	Coarse-grained terrigenous	Coarse-grained terrigenous	Fine-grained terrigenous	?	Fine-grained terrigenous

One of the problems of Palaeozoic biota reconstruction is determining whether fossil remains found in the oryctocoenosis are autochthonous or allochthonous. This is usually estimated by use of transportation traces on the skeletal elements, more precisely the degree of *post mortem* wear. If this wear is considerable, it almost certainly indicates long transportation and possible introduction of alien animal remains to the taphocoenosis. The most accurate approach towards this problem is to regard as autochthonous only articulated or at least semi-articulated skeletal parts. In Table I this regards only the East Greenland and Andreyevka localities. However disarticulated, the Red Hill remains were also regarded as autochthonous by Daeschler (2000). All the rest are formally regarded as allochtonous despite the possibility of long pebbling within the same basin and biotope which was the original dwelling place. This indeterminate situation especially refers to the near-shore environments of the Russian platform localities: Ketleri-Pavari, Rybnitsa and Gornostayevka. Coarse or fine-grained embedding rock may also provide information on the duration of transportation.

Before 1984 it was generally accepted that the earliest tetrapods dwelled exclusively in fresh-water basins. The discovery of *Tulerpeton* (Lebedev 1984; Lebedev and Clack 1993) demonstrated that the habitats of these animals were more diverse than thought earlier, and tetrapods could also live in the brackish-water conditions close to marine. As deduced from sedimentological and invertebrate information, analysed localities are separated by salinity level into presumably fresh-water (Scat Craig, Ala-Archa and East Greenland), that follows from their intramontane position and absence of geological information on connection to marine basins, and presumably brackish (most of the remaining ones). Gornostayevka is considered here as mostly marine with occasional fresh water influxes from nearby uplands. The presence of macrofloral remains in East Greenland, Red Hill, Ningxia and Ala-Archa might support their presumed fresh-water or almost fresh water environmental conditions.

At this time within Laurussia, epicontinental marine, deltaic near-shore and fluvial vertebrate assemblages are known. The poorly known East Gondwanan Jemalong locality is believed to be fluvial (Campbell and Bell 1977); the Kazakhstan Ala-Archa is supposed intramontane. Thus, the original idea of the rigid relation of tetrapods to fresh-water basins may be rejected, as tetrapod habitats show a great variety of environmental conditions. Tolerance of these animals to non fresh water corroborates Thompson's (1980) and Milner's (1993) idea of the possibility they might also live in the littoral zone that gave them wide possibilities of migration from one continent to another. This implies that the faunal exchange between the Laurussian, Gondwanan and North Chinese block was rather active, and the Tethys intercontinental basin was comparatively shallow, making possible migrations.

The second part of Table I deals with assemblages' composition. The most striking feature, as noted earlier by Lebedev (1985) is the presence of *Remigolepis* antiarch fishes in all Devonian tetrapod localities known at that time and his suggestion of the potential for a tetrapod find in Ningxia. Such a close association, as we now know, is not invariable. Examples of this are the absence of this genus from Scat Craig, Ketleri and Red Hill. The first of these localities dated as Frasnian that explains the situation, as *Remigolepis* is not yet recorded from such early deposits. At Red Hill, in contrast to the localities of the Russian platform and Greenland, the assemblage includes abundant groenlandaspidids, but no *Holoptychius* or *Bothriolepis* (Daeschler *et al.* 2003; Daeschler, pers. comm.), highly characteristic of these central and east Laurussian communities. Possibly, the biocoenosis structure at Red Hill was quite different from that of the Russian platform and Greenland or groenlandaspidids might in some respects substitute for *Remigolepis* in the community. The sarcopterygian *Sauripterus* might occupy the ecological niche of *Holoptychius* and *Hyneria* that of *Eusthenodon*.

At Ketleri the dominant members of the assemblage are *Holoptychius* and *Bothriolepis*. These genera are also highly characteristic of East Greenland tetrapod localities, but *Bothriolepis* is not the dominant antiarch there. Direct substitution of *Remigolepis* with *Bothriolepis* in the ecological niche does not seem convincing, as in many other cases these groups, which are rather different morphologically, coexist in the same community, obviously playing their own separate roles. On the other hand, Ketleri differs from the Greenland localities, on the one hand, and from Andreyevka, on the other, by the almost complete absence of dipnoans (it provided only a few isolated remains of *Orlovichthys*, see Lebedev and Lukševics 1996), which constitute one of the most substantial elements in two other communities.

Despite all these facts, *Remigolepis* is recorded in the majority of known Devonian tetrapod communities (at least five of 8), but the nature of this association is not yet understood and requires further study.

Interestingly, the assemblage composition of the locality Rybnitsa (Lebedev 1995; Lebedev and Lukševics 1996) is very close to that of Ketleri and differs in gross features only by the dominance of several dipnoan species (Krupina 2000). However, during almost 30 years of exhaustive exploration of this site, no traces of tetrapods have been found at Rybnitsa; the same also applies to the absence of *Remigolepis*. These differences cannot be explained by aspects of physical geography in this region, because as it was demonstrated above, they were very similar to those at Andreyevka and Gornostayevka.

One more interesting feature characterising Upper Devonian tetrapod assemblages is the absence of arthrodires. There are three exceptions; these are the Gornostayevka locality, Red Hill and Scat Craig. In the first one, pachyosteomorph arthrodire plates were found in the fossiliferous lens itself and in the overlaying clays and sands above it. This suggests that wherever the tetrapod and accompanying fish materials were brought, arthrodires dwelled both within this community and separately from it. The possibility of transportation of the tetrapod and fish materials from upland basins cannot be excluded.

The presence of the tristichopterid osteolepiform *Eusthenodon*, highly characteristic of the west Laurussia localities, is however not recorded in the Ketleri community. This genus is also missing from the Gondwanan, Chinese and Kazakhstan assemblages.

Daeschler (2000) noted that tetrapod morphological diversity in the Red Hill community suggests numerous morphological lineages, which specialised in a variety of ecological niches in Late Devonian ecosystems. This seems to be corroborated by data from other localities and from Red Hill itself. A classic example of that is the coexistence of *Ichthyostega* and *Acanthostega* in East Greenland (Bendix-Almgreen *et al.* 1990); *Ventastega* coexisted with a "second tetrapod ?" in Ketleri (Ahlberg *et al.* 1994) and *Tulerpeton* and "undetermined tetrapod" in Andreyevka-2 (Lebedev and Clack 1993), *Hynerpeton* and *Densignathus* in Red Hill Daeschler (2000). The presence of more than one tetrapod within the same community might argue for their much more diverse trophic specialisations than previously thought (for example, Lebedev 1992).

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Jauna tetrapodu suga *Jakubsonia livnensis* no Krievijas agrā Famenas laikmeta (devons) un piezīmes par vēlā devona tetrapodu paleoekoloģiju

OĻEGS ĻEBEDJEVS

Aprakstītas agrīnā tetrapoda *Jakubsonia livnensis* gen. et sp. nov. skeleta atliekas no Gornostajevkas karjera (DR no Livniem, Orlas apgabals, Krievija), kur atsedzas augšējā devona Famenas stāva apakšējās daļas nogulumi. Sniegts galvaskausa virsējās daļas, nepilnīga stūra kaula, labās puses kleitruma ar skapulokorakoīdu un augšstilba apraksts. Jaunā ģints demonstrē starporbītu daļas un kleitruma uzbūves pazīmes, kas liecina par līdzību ar *Ventastega* Ahlberg, Lukševičs et Lebedev, 1994.

Agrīno tetrapodu atradņu analīze parāda, ka šie dzīvnieki mituši dažādos ūdens vides biotopos. Antiarhu ģints *Remigolepis* spēlēja nozīmīgu lomu Famenas mugurkaulnieku asociācijās. Vairāk kā viena tetrapodu suga asociācijā norāda uz daudz plašākām tetrapodu trofiskām adaptācijām, nekā lēsts iepriekš.

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Sedimentology, fauna, and taphonomy of the Pavāri site, Late Devonian of Latvia

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The distribution, sorting, orientation, state of preservation, and wearing of vertebrate remains from the upper Famennian (Upper Devonian) Ketleri Formation of the Pavāri site, western Latvia, have been studied. The vertebrate fauna is dominated by the placoderm, *Bothriolepis ciecere,* and includes also acanthodians, several sarcopterygian taxa and the primitive tetrapod *Ventastega curonica.* Taxonomic composition, pattern of distribution, sorting, preferred orientation of vertebrate remains suggest that the assemblage was winnowed by water transport in a low concentration flow. Nevertheless, an almost total lack of wearing and the high degree of preservation, including many articulated skeletal parts, indicate short transportation of the remains before burial. An almost autochtonous character of the oryctocoenosis is, therefore, suggested. Sedimentological and taphonomic studies of the locality suggest that it was formed in relatively shallow sea conditions dominated by stream and weak wave influence, probably representing a low-tidal near-shore depositional environment. Most likely, vertebrates from the Ketleri Formation dwelled in a marine coastal environment, although the possibility that the remains have been transported for a considerable distance can not be excluded.

Key words: Palaeoecology, placoderms, sarcopterygians, tetrapods, Famennian.

Introduction

The environmental conditions in habitats of early tetrapods and the palaeoecological aspects of the origin of tetrapods are still disputable problems of vertebrate evolution (Thomson 1980; Spjeldnæs 1982; Bendix-Almgren *et al.* 1990; Coates and Clack 1995; Lebedev, this volume). Studies on taphonomy in fossil vertebrate sites using both sedimentological and bionomic data is one of the methods that can provide some clues to the problem. This study concerns the sedimentological, environmental and taphonomic context of the locality known as the Pavāri (or Ciecere) site in western Latvia. This is one of the well-known sites where the primitive tetrapod *Ventastega curonica* has been found together with abundant fish remains in a sandstone of the upper Famennian (Upper Devonian) Ketleri Formation.

The stratigraphy and fossils of the Ketleri Formation have attracted the interest of geologists and palaeontologists for more than 70 years (Gross 1942; Lyarskaya and Savvaitova 1974; Vorobyeva 1962, 1975; Lukševičs 1992; Lebedev and Lukševičs 1996). This interest has grown significantly in recent years after the discovery of the first tetrapod fossils from the Ketleri Formation (Ahlberg, Lukševičs and Lebedev 1994; Ahlberg and Lukševičs 1998; Lukševičs, Ahlberg and Clack 2003). Vertebrate fossils from the Pavāri site were for the first time excavated by Lyubov Lyarskaya in 1970, and the geological setting of the Ketleri Formation was defined and stratigraphical conclusions were made together with Lyudmila Savvaitova (Lyarskaya and Savvaitova 1974). In subsequent years excavations were organised by L. Lyarskaya (in 1973), and by E. Lukševičs in cooperation with palaeontologists from the Natural History Museum of Latvia, Museum of Natural History (London), Palaeontological Institute (Moscow), Cambridge University, Institute of Petroleum Geology (Novosibirsk), in 1988, 1989, 1991, 1995, and finally in 2001, adding significantly to the vertebrate material. Some palaeoecological clues analysing the faunal composition and taphonomical features of the Ketleri and Pavāri localities have been made previously (Lukševičs 1992), and notes on the faunal composition were published together with the first description of *Ventastega* (Ahlberg, Lukševičs and Lebedev 1994). The fossil assemblage of the Pavāri site is important for the understanding of palaeoecology of the Late Devonian vertebrates in the Baltic palaeobasin. Now the Pavāri locality is a Nature Monument still under active study; some sedimentological and taphonomical studies were carried out there in 2001, 2002 and 2004 by the authors of this article. The present paper provides a more complete description of the geology, taphonomy and faunal composition of the Pavāri site.

Material and methods

The Ketleri Formation is distributed only in southwestern Latvia and northwestern Lithuania, cropping out only along the northern margin of its distribution in Latvia. Two localities of the Ketleri Formation are particularly rich in vertebrate fossils: the Ketleri site at the river Venta near the former Ketleri hamlet and the Pavāri site at the river Ciecere opposite the former Pavāri hamlet. The Pavāri site is located in the southern corner of the Kuldīga district, in western Latvia (Fig. 1). The best fossils come from the Pavāri site, where more than a thousand specimens of fossil vertebrates were excavated during several field seasons. Vertebrate fossils were collected mainly to examine the faunal composition of the assemblage and the morphology of the various taxa, but in 1988 and 2001, also to collect taphonomic and sedimentological information. More than 900 specimens have been determined to the generic/species level. The distribution, sorting, orientation, state of preservation, and wearing of vertebrate remains have also been studied. Data on spatial distribution, sorting and azimuthal orientation of fossil bones and skeletal fragments were collected in 1988 and 2001; totally 325 measurements of the orientation of fossil bones were taken. More than 800 specimens stored at the Natural History Museum of Latvia were examined to detect the state of preservation and wearing of bones.

A complete grain size analysis of seven rock samples from the Ketleri Formation was carried out. The content of clay and silt was detected using the pipette method at the Laboratory of Quaternary Environment and Laboratory of Soil Research at the Faculty of Geographic and Earth Sciences of University of Latvia. Sand particles were sieved at the laboratory of the Institute of Silicate Technology at the Riga Technical University using a set of „Fritsch” sieves „Analysette 3PRO”. MS Excel was used to run the statistical analysis of the data. Variation and cumulative curves were drawn to illustrate the granulometric composition of the rocks, and the coefficient of sorting and

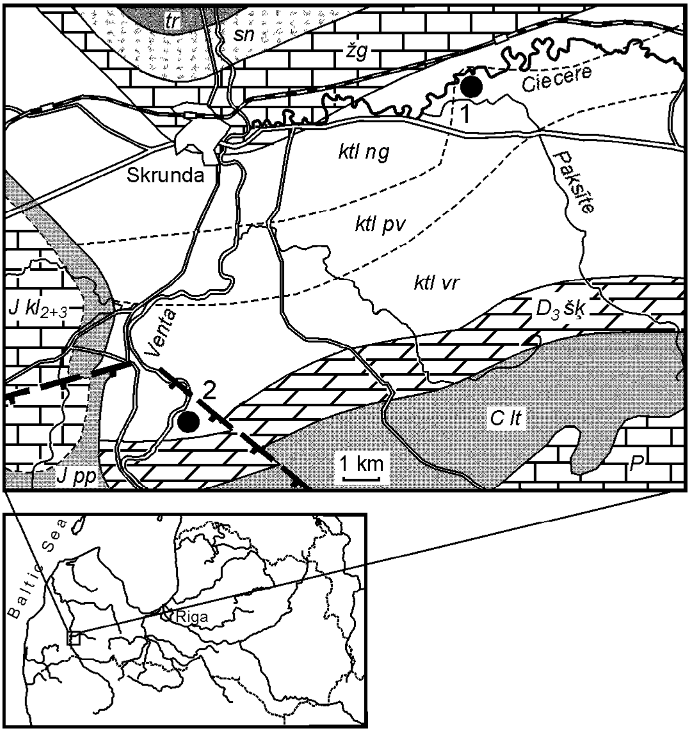

Fig. 1. Map of vicinities of Skrunda showing fossil sites (1, Pavari; 2, Ketleri) within the Ketleri Formation. Abbreviations for stratigraphic units: *ktl ng*, Nigrande Member; *ktl pv*, Pavari Member; *ktl vr*, Varkali Member; *sn*, Snikere Fm; *tr*, Tervete Fm; D_3 *šk*, Škervelis Fm; *žg*, Žagare Fm, all Upper Devonian, Famennian; *C lt*, Letiža Fm, Carboniferous; *P* – Naujoji Akmene Fm, Permian; *J* kl_{2+3}, Middle and Upper Callovian; *J pp*, Papile Fm, Lower Callovian?, Jurassic.

asymmetry and excess of the curves were calculated. These data were compared to Buller's-McManus's plot (Tucker 1988) of genesis of sandy rocks. Much attention was paid to the sedimentological structures of the rocks.

The main portion of the fossil material from both Ketleri and Pavāri is kept at the Natural History Museum of Latvia, Riga, collection No. 57 (Ketleri) and No. 81 (Pavāri), and some specimens were deposited at the Museum of Natural History (London). The abbreviation LDM is used in the text designating the collection of the Natural History Museum of Latvia.

Geological setting and lithology

Devonian deposits are widespread in the territory of the Baltics cropping out in a sub-Quaternary surface in southern and eastern Estonia, most of the territory of Latvia and northern Lithuania. They also lie below younger rocks in south-west Latvia and are exposed in most of Lithuania, apart from its very southern margin where the deposits have been eroded. The Devonian deposits are also spread throughout the territory of Latvia, in the Gulf of Riga and in the aquatorium of the Baltic Sea. Although not outcropping, the Lower Devonian deposits are to be found in the whole territory of Latvia, excluding the Viļaka tectonic rampart and the territory east of it. The Middle Devonian rocks are widely represented throughout the whole territory of Latvia and exposed in many sites in picturesque outcrops of the Old Red Sandstone facies rocks. The distribution of the Upper Devonian deposits corresponds to that of the Middle Devonian rocks, lacking only in areas where they have been destroyed by glacier. The Upper Devonian is represented by the Frasnian and the Famennian stages. Frasnian and Famennian deposits are rather various by origin and composition. At the very beginning of the Frasnian a new record of mixed carbonate and siliciclastic sedimentation started. Diversity of deposits is particularly characteristic for the Famennian, which is composed of sandstones, dolostones, dolomite marls, siltstones, clays, limestones and other rocks intercalating in a complicated pattern (Savvaitova 1977). The Famennian basin was situated in the Latvian-Lithuanian Depression, which in the west and south-west was periodically connected to the open sea. Hence, Famennian deposits are spread only in south-western Latvia and north-western Lithuania. During maximum transgressions the Baltic paleobasin was probably connected also with the sea of Middle Russia through the Pripyat' Deep (Savvaitova 1977).

The Ketleri Formation comprises sands, sandstones, clays, and dolomitic marls which overlie the carbonate deposits of the Žagare Formation. In Latvia the thickness of the Ketleri Formation reaches 45 m, while in Lithuania it is 41 to 56 meters thick. The formation is divided into three members separated from each other by the erosional surfaces (Lyarskaya and Savvaitova 1974). The lowermost, Nīgrande Member is characterized by 8 to 12 meters thick clayey carbonate deposits which overlie an eroded surface of carbonate rocks of the Žagare Formation. The lower part of the member is composed of greenish grey and brownish dolomite marls with a low content of silt. Among them several thin beds of greenish grey microcrystalline dolomite and clay occur.

Tiny poorly preserved fish remains have been found in the dolomite marls at the base of the member. P. Liepinš, E. Mark-Kurik and V. Talimaa have determined them as belonging to the taxa: *Chelyophorus* sp., *Bothriolepis ornata* Eichwald, *Devononchus* sp., *Holoptychius* cf. *nobilissimus* Agassiz, *Eusthenopteron* sp., Osteolepididae gen. indet., Dipnoi indet., Palaeoniscidae gen. indet. (Liepiņš 1959; Savvaitova and Žeiba 1981). However, the identification of a species may be inaccurate and causes some doubt. For example, the two species *Bothriolepis ornata* un *B. ciecere* Lyarskaja resemble each other in respect to the structure of the head shield and ornamentation, but they differ remarkably in the proportions of the trunk armour plates and character of dorso-lateral and ventro-lateral ridges (Lukševičs 2001). Quite often it is impossible to determine the species by small fragmentary remains. L. Lyarskaya mentions *Devononchus tenuispinus* (Gross) among the fish remains from the Nigrande Member (Lyarskaya and Lukševičs 1992).

The amount of carbonate in rocks decreases towards the upper part of the member, and dolomite marls are replaced by clay and clayey siltstone, in some cases by fine-grained sandy material. Spores of *Stenozonotriletes* sp. sp., *S. triangularis* Naum., *S. simplex* Naum., *Euryzonotriletes* sp., *Trematozonotriletes intermedium* (Waltz)

Naum., *Leiotriletes immanus* Isch., *Dictyotriletes* sp. have been identified by M. Stanichnikova from clayey interbeds (Savvaitova 1977). V. Talimaa has reported remains of following vertebrate taxa from the Nīgrande Member in the territory of Lithuania: *Chelyophorus* sp., *Panderichthys* sp., Rhizodontidae gen. indet., *Osteolepis*? sp., *Onychodus* sp., *Dipterus*? sp., Palaeoniscidae gen. indet. in the lower part of the member; *Bothriolepis* sp., Acanthodei gen. indet., Sarcopterygii gen. indet., *Panderichthys* sp., *Holoptychius* sp. in the upper part (Žeiba and Savvaitova 1981). In this case the identification of some taxa also causes doubt, as identifiable remains of the genus *Panderichthys* so far have been recorded only from the Givetian – Frasnian interval in the deposits of the Gauja, Lode, Amata, and Dubniki Formations, while the genus *Osteolepis* is known mainly from the Middle Devonian.

The eroded surface of the clay and clayey-silty rocks of the Nīgrande Member is overlaid by the yellowish grey fine-grained sandstone and sand of the Pavāri Member. In most of the distribution area sand and sandstones consist of quartz with admixture of feldspars, and in some places contain great amount of mica. In some levels sandstone is well cemented by dolomite. The content of fine-grained sand increases in the sections towards the northern part of distribution area (boreholes 27, 1-Priekule, 15-Sab-Nākotne); towards the north-western margin the amount of the medium sized grains also increases. The facies of the upper part of the Pavāri Member is more variable, being composed of thin beds of clay, clayey siltstone, dolomite marl and feldspar-quartzitic micaceous sand. The total thickness of the section is 16-21 meters. Sand and sandstones of the Pavāri Member contain a rich assemblage of fishes and tetrapods, the full content of which is described further below.

Sandstones of the upper Varkaļi Member overlie the eroded surface of the Pavāri Member. The lower part of the Varkaļi Member is composed of light greenish-grey very fine and fine-grained feldspar-quartz sands and weakly cemented sandstones, frequently containing large amounts of mica. Parallel cross-bedding is characteristic for the sandstones. In some beds, smooth horizontal bedding is accentuated by the distribution of muscovite scales, fish bones and their fragments, and clay pebbles. The lower part of the Varkaļi Member crops out on the right bank of the Venta River near the former Ketleri hamlet. The conglomerate in the fine grained sandstones of the lower part of this member is formed of well rounded blue-grey pebbles of microcrystalline dolomite marl of usually small, but sometimes quite large (up to 5 – 7 cm) size, dolomite marl interlayers and vertebrate remains. Mainly small remains of fishes and tetrapods as well as rounded and abraded fragments of larger bones are to be found in sandy rocks. During several excavations organized by D. Obruchev (1957), L. Lyarskaya (1970, 1973) and E. Lukševičs (1984, 1988) rather rich material of fossil vertebrates has been collected at the locality: fragments of the trunk armour and disarticulated bones of the head shield of placoderm *Bothriolepis ciecere*, acanthodian spines, scales of "*Devononchus*" *ketleriensis* Gross un "*D.*" *tenuispinus* (Gross), as well as scales of at least yet another acanthodian, scales and rare disarticulated bones of the head of the sarcopterygians *Holoptychius* cf. *nobilissimus*, *Ventalepis ketleriensis* Schultze, *Glyptopomus*? *bystrowi* (Gross), *Cryptolepis grossi* Vorobyeva, *Platycephalichthys* sp., parasphenoideum of a lungfish *Orlovichthys* cf. *limnatis* Krupina, remains of tetrapods *Ventastega curonica* Ahlberg, Lukševičs et Lebedev and Tetrapoda gen. indet. (Ahlberg *et al.* 1994). Comparison of the vertebrate assemblages from Ketleri and Pavāri sites enabled us to come to the conclusion that two oryctocoenoses most probably originated from the same palaeobiocoenosis, differing mainly in the character of transportation and burial conditions (Lukševičs 1992).

No spores or conodonts have been found in the Ketleri Formation, therefore the age of the formation (corresponding to the *expansa* conodont zone; Esin *et al.* 2000) could be judged only from its position above the Žagare Formation. Dolomite of the Žagare Formation yeilds conodonts providing the possibility to correlate it with the interval from *marginifera* to *postera* Zones (Esin *et al.* 2000). The underlying Švete Formation (in Lithuania; corresponds to the Sniķere and Tērvete formations in Latvia) contains conodonts of the *postera* Zone (Middle – Lower *styriacus* Zone of the previous conodont zonation; Žeiba and Valiukevičius 1972).

Results

Sedimentology. The detailed studies of the outcrop of the Ketleri Formation on the left bank of Ciecere River, opposite the former Pavāri hamlet, show a sandstone body with a total thickness of more than 3 m, most of which is only visible after major excavation and cleaning of the wall-shaped outcrop. The lithology of the section is shown in Figure 2. Very fine-grained to fine-grained white or light yellow almost unconsolidated quartzose sandstone dominates the sequence. An erosional surface, interpreted here as a relatively shallow (about 0,5 m deep) and at least 8 m wide erosional channel, is traced in the lower part of the section (Fig. 3). Measurements of dip suggest that a stream flowing from NNE to SSW formed this erosional channel. The same direction is characteristic for the whole cross-stratified deposits of the Ketleri Formation (Savvaitova 1974). In accordance with the results from a grain-size analysis (Fig. 4), the erosional channel was filled by a well-sorted fine-grained sand in the lower part (Fig. 3, layer 6, sample 6A) and more silty moderately sorted material in the upper part (sample 6), showing fining upward sequence which contains numerous vertebrate remains in the bottom part of infilling, but no admixture of dispersed clay particles. Vertebrate remains are unevenly spread in the rocks, mainly forming accumulations in the bottom part of the sandstone infilling of the erosional channel. Accumulations were found also below a thin clay layer (number 5 in Fig. 3) underlying the erosional surface.

Large-scale cross-bedding is characteristic for the lower and middle part of the channel infilling. Small-scale current(?) ripples are also noticed above the cross-stratified sandstone. Cross-stratified beds are rather thick in the lower part and very thin in the middle part, usually bearing layers of mica on their surfaces. Measurements of cross-stratified beds show their bipolar orientation (Fig. 5), and their dip azimuth is almost perpendicular to the axis of the erosional channel. Such orientation is usually explained by the influence of inter-tidal streams (Reineck and Singh 1980). Laminae of the cross-bedded layers show variable angle of dip, in some places the high angle reaches 37°. Deformations of sandstone bedding and intrabasinal conglomerate consisting of clay pebbles noticed mainly in the left side of the outcrop (along the right edge of the erosional channel) indicate the role of slump processes in the filling of sides of the channel. Another erosional surface (below the layer 7, Fig. 3) lies above the filling of the erosional channel, trapping animal remains. The azimuth and dip angle of the upper channel are

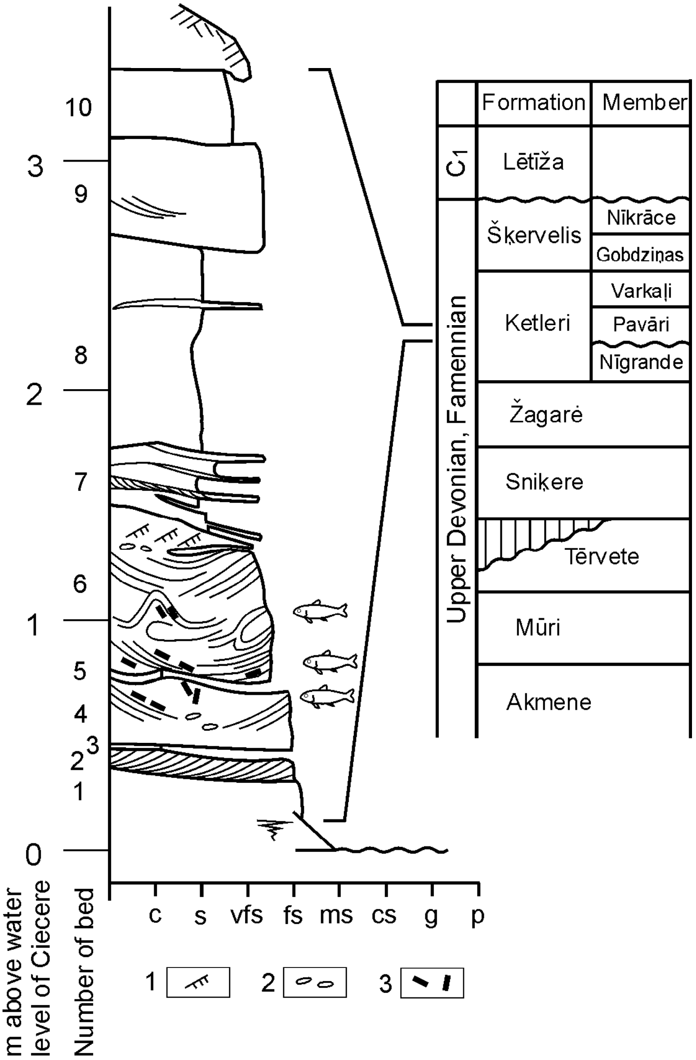

Fig. 2. Geologic section of the Pavari outcrop and a stratigraphic sequence of selected Devonian and Carboniferous lithostratigraphic units in Kurzeme. 1, ripple marks; 2, clay pebbles; 3, fish remains.

in general the same as parameters of the lower one. Higher up there is a bed of greenish clayey silt and very fine-grained sandstone of changeable thickness, which is overlaid by sandy-clayey silt (layer 8). This is a rather thick unit of changeable colour, greenish in the lower and uppermost part, and dark red in the middle part. It is obvious that the middle portion of the layer shows the primary red colour while it is secondarily changed along the underlying and overlaying sandstone. No clear structure is observed within the layer, apart from thin lenses of more sandy material and some lenses of more clayey

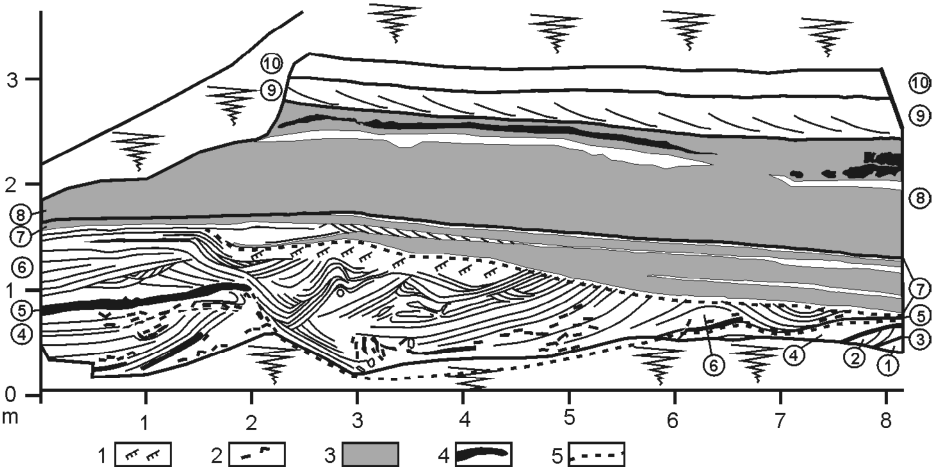

Fig. 3. Schematic plan of the outcrop wall at the Pavāri site. Numbers in circles refer to the numbers of layers mentioned in the text. 1, ripple marks. 2, fossil remains. 3, siltstone. 4, clay pebbles or layers. 5, erosional surface of supposed erosional channel.

rock in the uppermost part. Judging by the poor sorting (Fig. 4, samples 8, 8A, and 8B) these deposits were accumulated under calm water conditions. The uppermost part of the exposed section (layers 9 and 10) is formed by white, moderately well-sorted, fine-grained and very fine-grained sandstones (Fig. 4, samples 9 and 10), probably originated in a weak stream.

Vertebrate remains are usually represented by disarticulated plates of placoderms, isolated teeth or bones of sarcopterygians and tetrapods. Articulated portions of placoderm head shields, trunk and pectoral fin armour, complete lower jaws or portions

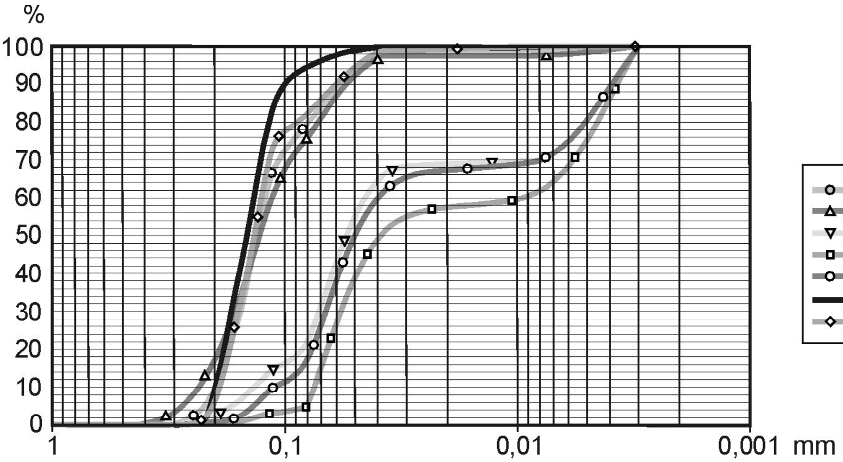

Fig. 4. Grain-size distribution cumulative curves for siliciclastic deposits of the Ketleri Formation. Numbers refer to the numbers of layers mentioned in the text and shown in the Fig. 3.

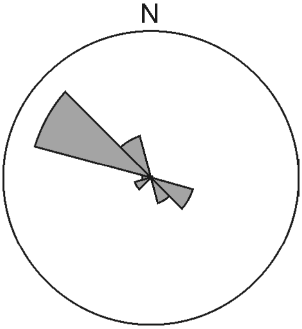

Fig. 5. Bipolar orientation of the cross-bedding of the infilling sandstone (layer No. 6). N = 30.

of skulls have also been found, particularly in slump depressions or close to slumping structures. Fossils are rarely found close to the margins of the supposed erosional canal; mainly scales of sarcopterygians have been collected there. Fish and tetrapod remains are usually brown or dark brown, rather soft and fragile, therefore many specimens kept in the museum collection bear cracks, as the results of breakage during transportation in the plaster jackets or during preparation.

Fossil assemblage. Of the more than 1000 specimens collected from the Pavāri site, 909 have been identified to the generic/species level. About 800 specimens are housed at the LDM. Identified taxa from the Pavāri site are listed in the Table 1, and persentages of each taxon are shown in the Table 2 and Figure 6.

Taxonomic representation. The fossils assemblage from the Pavāri site seems to be taxonomically incomplete, lacking the remains of arthrodires, ptyctodonts and chondrichthyans. Actinopterygian remains are extremely rare, including only one small incomplete scale ever found. Arthrodires are known from the underlying beds of the Žagare Formation, while ptyctodonts and actinopterygians have been found in the Nīgrande Member of the Ketleri Formation (Gross 1933, Lyarskaya and Savvaitova 1974). Chondrichthyan remains are in general rare in Baltic Devonian deposits (Ivanov and Lukševičs 1994; Mark-Kurik and Karatajūte-Talimaa 2004). From the Famennian deposits they have so far been found only in dolostones of the Kursa Formation and sandstones of the Mūri and Tērvete formation (both are older than the Ketleri Formation). Underrepresentation of small fish or small skeletal parts of fish bodies are common features of fossil assemblages and is usually interpreted as a combination of biotic and abiotic factors that destroy or remove small, delicate bones (Behrensmeyer 1991). Possibly the absence of ptyctodonts, chondrichthyans and actinopterygians in the material from Pavāri can be explained by the small size of the armour plates of ptyctodonts, scales and teeth of chondrichthyans and actinopterygian scales, although the possibility that this part of the Baltic sedimentary basin was not suitable for the existence of these fishes during the Ketleri time can not be excluded. Considering the presence of acanthodian scales one should note their much smaller size comparable with that of the sand grains.

Material from the Natural History Museum of Latvia (collection No LDM G 81), collected in 1970, 1973 and 1995, has been used for comparison of the percentage of

Table 1. List of identified taxa from the Pavāri site

- Placodermi
  - Euantiarcha
    - Bothriolepididae
      - *Bothriolepis ciecere* Lyarskaja
- Acanthodii
      - "*Devononchus*" *tenuispinus* Gross
      - "*Devononchus*" *ketleriensis* Gross
      - Acanthodii gen.et sp.indet.
- Osteichthyes
  - Palaeonisci
      - Palaeonisci gen. et sp. indet.
  - Sarcopterygii
    - Porolepiformes
      - *Holoptychius* cf. *nobilissimus* Agassiz
      - *Ventalepis ketleriensis* Schultze
    - Osteolepiformes
      - *Glyptopomus* ? *bystrowi* (Gross)
      - *Cryptolepis grossi* Vorobyeva
    - Dipnoi
      - *Orlovichthys* cf. *limnatis* Krupina
- Tetrapoda
      - *Ventastega curonica* Ahlberg, Lukševičs et Lebedev

vertebrate occurrence. In 1988 the number of remains for each taxon was documented already at the outcrop. These data are included in our analysis as well. Both the number of specimens for each taxa and minimum number of individuals (MNI) have been taken into account (Table 2, Fig. 6). The minimum number of individuals has been evaluated based on the maximum number of identical skeletal parts, e.g. jaws or individual plates of armour from the same side of the trunk, etc. Only macroremains, including acanthodian spines, were counted. Acanthodian scales are quite common; still their number has not been considered in further analysis as they underwent different regularities of sedimentation due to the small size of the scales equal to that of sand grains. The material from 1970 and 1973 expeditions has been used only for comparison, as the data on percentage were available only by counting the specimens in the collection No. LDM G 81. In 1988 all the specimens were counted, including those which have not been included in the museum collection after preparation. Also it is worth noting that during the 1995 and 2001 year expeditions special attention was paid to tetrapod remains. Therefore tetrapod or sarcopterygian fish remains could be slightly overestimated. As the preparation of the material collected in 2001 still goes on, the data from this expedition is not complete and therefore excluded from this analysis.

Placoderm *Bothriolepis ciecere* dominates the vertebrate assemblage of each individual expedition. All together, placoderms varies between different collection years in representation from 47% to 97% of the total number of remains. When estimating

Table 2. Number of specimens and minimum number of individuals of vertebrates from the Pavāri site. 1970, 1973, 1988, 1991, 1995, excavation of particular year. Total, number of specimens from all excavations. Perc., percentage of specimens. MNI, minimum number of individuals from all excavations. Unidentified specimens, paleoniscoid and acanthodian scales not included.

Taxon	1970	1973	1988	1991	1995	Total	Perc.	MNI
Bothriolepis ciecere	152	210	107	74	121	664	73,0	87
Acanthodians	0	0	1	0	1	2	0,2	2
Holoptychius cf. *nobilissimus*	39	3	13	7	34	96	10,6	4
Ventalepis ketleriensis	0	0	2	2	8	12	1,3	1
Glyptopomus ? *bystrowi*	0	1	0	0	1	2	0,2	1
Cryptolepis grossi	2	0	3	24	59	88	9,7	4
Orlovichthys cf. *limnatis*	1	0	0	1	1	3	0,3	2
Ventastega curonica	3	2	4	5	28	42	4,6	9

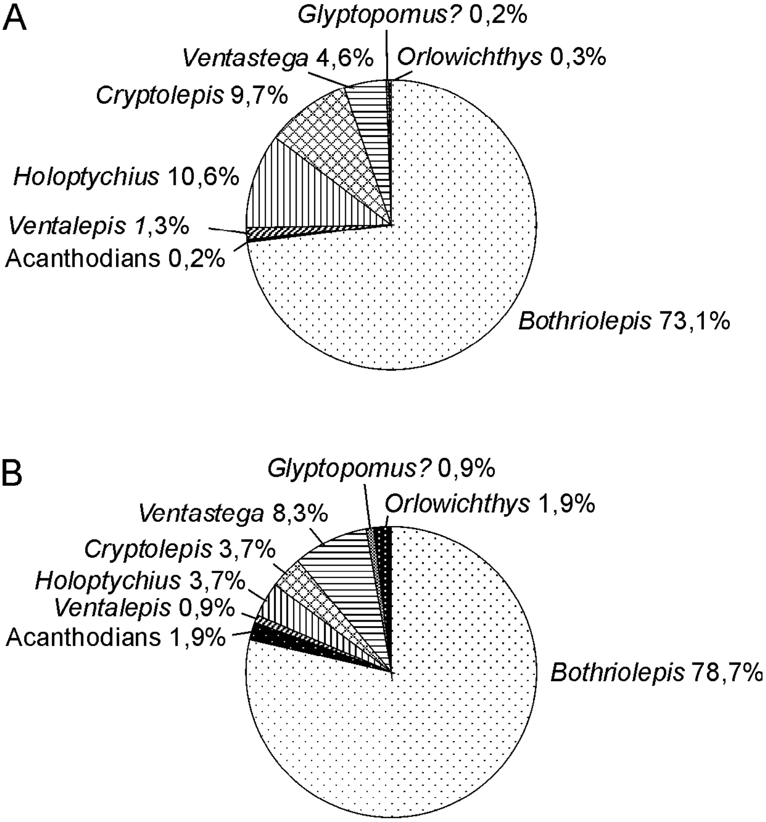

Fig. 6. A, percent representation of vertebrate specimens identified to at least generic level from Pavāri site (n = 909). B, percent representation of vertebrate taxa based on MNI from Pavāri site.

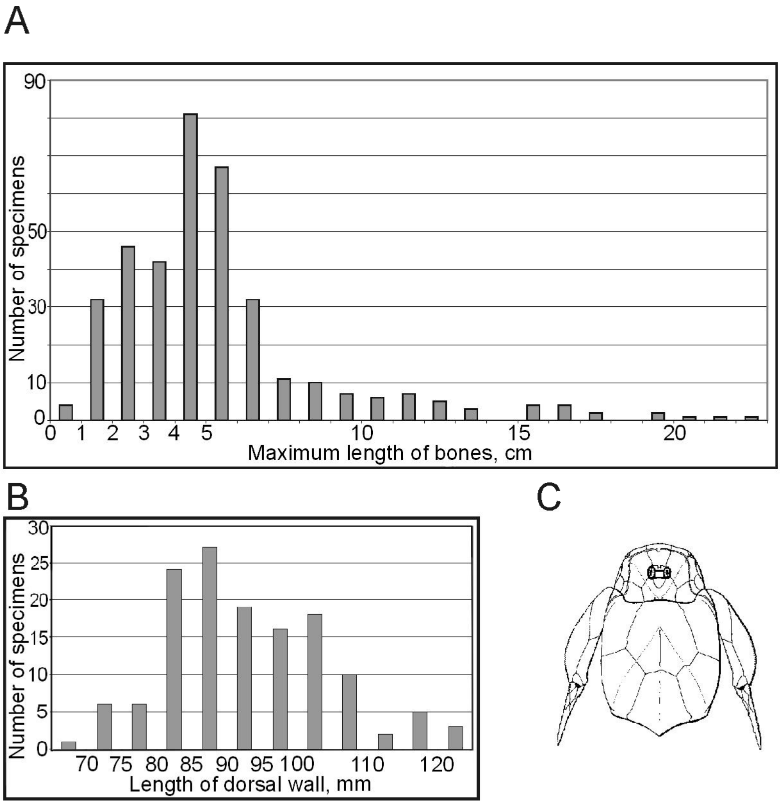

Fig. 7. Number of fossils of different size from the Pavāri locality. A, for all measured specimens. B, estimated for the dorsal wall of the trunk shield of *Bothriolepis*. C, generalized reconstruction of *Bothriolepis* in dorsal view.

the minimum number of individuals (MNI) of *Bothriolepis ciecere,* based on the number of left PVL's, their relative percentage is even higher. *Holoptychius* cf. *nobilissimus* is the second most widespread taxon according to specimen occurrence, which is more than one tenth of the total number. The minimum number of individuals based on the number of right clavicles, however, is smaller than in *Ventastega curonica*. The remains of *Cryptolepis grossi* are just slightly less common, while the estimated MNI based on the number of right lower jaws is the same as for *Holoptychius*. *Ventastega curonica* lies among the species which are comparatively common, and the estimated MNI based on the number of right lower jaws indicates that *Ventastega* individuals are the second most common taxa in the oryctocoenosis. It is possible that the differences between the total number of remains and the MNI can be explained by the fact that both *Holoptychius* and *Cryptolepis* are represented mainly by scales, while bones of the head, jaws and bones of the shoulder girdle are found more rarely if compared to those in *Ventastega*. The number of remains belonging to the rest of taxa is small.

Age specific distribution. The age of the fossil individuals by the time they died can be estimated only for taxa represented by a greater number of specimens, e.g.

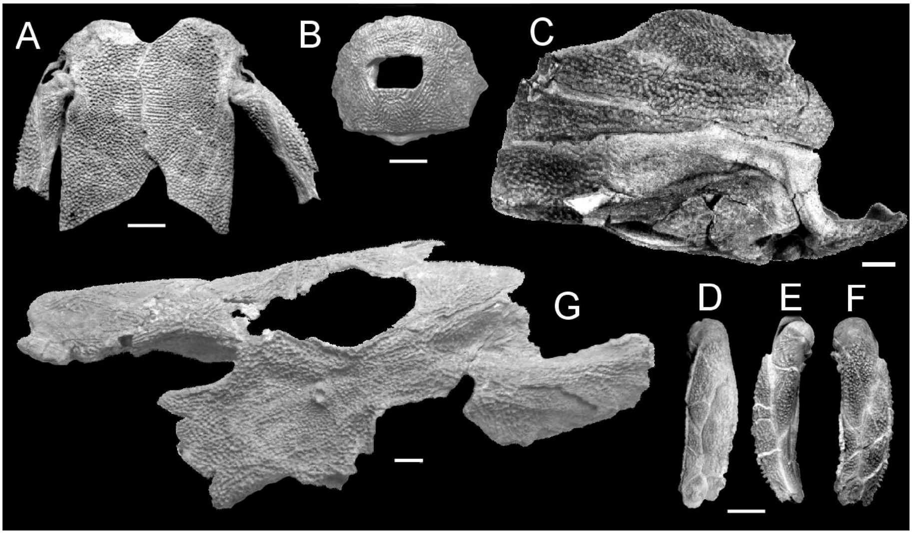

Fig. 8. Articulated specimens of *Bothriolepis ciecere* (A-F) and *Ventastega curonica* (G). A, anterior ventro-lateral bones with articulated proximal segments of pectoral fin LDM 81/716 in ventral view. B, head shield LDM 81/545 in dorsal view. C, articulated anterior dorso-lateral, anterior ventro-lateral, central dorsal 1 and partial central ventral 1 LDM 81/434 in right lateral view. D-F, proximal segments of pectoral fin: D, LDM 81/724 in dorsal view; E-F, LDM 81/723 in ventral and dorsal view. G, skull composed of two specimens, skull roof LDM 81/775 and left cheek LDM 81/776, supposedly from one individual; specimens were found in a distance of 45 cm. Scale bar: 10 mm.

Bothriolepis ciecere and *Ventastega curonica*. Judging from the size of the fossil bones, no remains of juvenile individuals at all have been found at the Pavari oryctocoenosis. Bones of small sized placoderms are disproportionately rare (Fig. 7 B). Large bones which could have belonged to older individuals are also comparatively rare as well. This is the case for *Ventastega* as well. Judging from the individual size range of vertebrates from the Pavāri oryctocoenosis, the assemblage is represented by young adult and fully adult individuals as well as a few elder individuals. There are two possible explanations for such age specific distribution of individuals. First of all, it is possible that younger individuals (or juveniles) dwelled elsewhere aside from the adult individuals as it use to be the case in aquatic animals. Secondly, a slightly delayed burial might have resulted in bones of smaller individuals getting selectively destroyed.

Skeletal disarticulation. At the Pavāri site vertebrate remains are usually represented by fully disarticulated plates of placoderms, separate teeth or bones of sarcopterygians and tetrapods, but articulated portions of placoderm head shields, trunk and pectoral fin armour, complete lower jaws or portion of skulls of sarcopterygians and tetrapod, have also been found (Fig. 8). Most of articulated specimens belongs to placoderm *Bothriolepis* and tetrapod *Ventastega*. There are at least twelve more or less complete head shields of *Bothriolepis ciecere* found among 664 specimens and 85 individuals belonging to this species. All complete head shields are preserved without pineal plate, orbital and jaw ossifications, since they are loosely attached to the head shield. Only three of the shields are complete consisting of unpaired Nu, Pp and Prm plates, as well as paired Pn, Pmg and La plates. Two head shields lack Pmg from one side, and four more shields are without Pmg plates from both sides. Three head shields have lost the anterior most portion, and the Prm plate is not present. In some cases (specimens LDM 81/283, 81/726) it seems that the head shield has been disarticulated after burial, since plates are displaced and situated at a distance of 1 to 3 mm from each other. One of the best preserved portions of the trunk shield is specimen LDM 81/434, consisting of articulated right ADL, AVL, Cd1 and Cv1. Besides this specimen, there are 18 examples of articulated AVL plates and proximal segments of pectoral fin. Specimen No. LDM 81/716, for example, shows articulated AVL plates on both sides with connected proximal segments. Another seven specimens are articulated proximal segments of pectoral fin alone. Only two specimens, LDM 81/58-60 and 81/83, have a partially preserved dorsal wall of the trunk shield. Three specimens (LDM 81/41, 81/81 and 81/82) constitute an incomplete ventral wall of the trunk shield. By counting articulated or partly articulated portions of shields of *Bothriolepis* one may infer that the disintegration of placoderm fish skeletons took place quite close to the place of burial, and that the final stages of disintegration continued even after transportation was finished.

Sarcopterygian and tetrapod remains are represented with some completely disarticulated bones of the shoulder girdle and skull, as well as rare scales or sometimes teeth, but more or less complete lower jaws have often been found, e.g. three partial lower jaws of *Holoptychius* cf. *nobilissimus*, five jaws of *Cryptolepis grossi*, and 14 complete or partially complete jaws of *Ventastega curonica*. There are two almost complete specimens representing tetrapod cheeks, and one skull roof of *Ventastega*, which was found at a distance of some 45 cm from the left side cheek. Judging from the size and shape of broken edges, both skull and cheek belong to the same individual.

Skeletal element representation. The sorting of remains according to their shape, size and weight has been observed. Among the remains, medium-sized (4-6 cm long) bones prevail, smaller remains such as scales of *Cryptolepis grossi* are disproportionally rare, but larger ones such as lower jaws of *Ventastega curonica* (about 21 cm long) are considerably more frequently found than the other skeletal elements of the animal (Fig. 7 A).

Voorhies assigned skeletal elements of some modern mammals to one of three categories in accordance with their ease of fluvial transport: Group I is the most readily transported and Group III the most resistant to transport (Behrensmeyer 1975). It is impossible to conduct the Voorhies Group analysis of the Devonian vertebrate assemblages for two reasons. Firstly, skeletons of different taxa in a mixed taxonomic assemblage yield different numbers of elements for each Voorhies Group, and sometimes homologous elements from even phylogenetically close taxa fall into different Voorhies Groups (Behrensmeyer 1975). Secondly, placoderms and ancient tetrapods have no direct analogues with homological skeletal elements among modern taxa. Therefore the abilities of different skeletal elements of vertebrates from the Pavāri oryctocoenosis to be transported and sorted by fluvial processes can only be evaluated. A most satisfactory analysis is possible only examining representation of *Bothriolepis ciecere*, from which almost all bones are represented in the assemblage. *Ventastega curonica* and *Cryptolepis grossi* could also give satisfactory results since they are represented by many skeletal elements. It is, however, impossible to use the other taxa due to the insufficient number of specimens.

Disarticulated bones of the trunk and head shield of *Bothriolepis ciecere* are represented in different numbers. Strongly convex dorsolateral and ventrolateral bones, particularly posterior ventral lateral plates from the left side (PVL) and mixilateral plates from the right side (MxL), dominate among the trunk shield bones (Tab. 3). Possibly these bones, along with the less convex anterior median dorsal (AMD), could belong to the Voorhies Group III, being the most resistant to transport. The number of the anterior ventro-lateral (AVL) and anterior dorso-lateral (ADL) plates is smaller, and the almost flat posterior median dorsal (PMD) and flat median dorsal (MV) are the rarest among the trunk shield bones, representing the Voorhies Group II, which is moderately readily transported. Besides that, the distribution of paired convex bones shows assymetry. The number of the right-sided MxL plates more than three times exceeds the number of the left-sided MxL, but the situation is opposite in the case of PVL plates. The number of the left-sided PVL two times exceeds the number of the right-sided PVL. The differences between various Voorhies groups and number of bones from the right and left side of the trunk suggest quite an important hydraulic sorting of skeletal elements of placoderms. Bones of the head shield are also represented in different numbers, always being more rare than the trunk shield plates. Thick and relatively large lateral (La) and nuchal (Nu, n = 17) plates, as well as complete head shields, are found comparably often. Still, articulated head shields, which supposedly could represent the Voorhies Group III, are disproportionally rare. Separate premedian (Prm, n = 2) and other small and thin bones are very rare. Such very thin and small bones as inferognathals and submarginals, as well as bones of sklerotic ossifications, were not found. Possibly the lightest bones were readily transported soon after death.

Table 3. Number of some skeletal elements of placoderm fish *Bothriolepis ciecere*

Number of specimens Plate	From the left side	From the right side	Totally	Expected number	Representation of plates (percent)
AMD*	-	-	68	87	78,2
PMD*	-	-	34	87	39,1
MxL	24	85	109	174	62,6
ADL	14	26	40	174	23,0
AVL	31	44	75	174	43,1
PVL	87	35	122	174	70,1
MV*			13	87	14,9
Head shield*	-	-	13	87	14,9
La	8	14	22	174	12,6
Cd1	17	20	37	174	21,3

* Unpaired bones and shield

Orientation of bones. The occurrence of preferred orientation of the fossils is also observed. Convex bones such as placoderm dorso-lateral or ventro-lateral plates of the trunk shield mainly lie in a hydrodinamically most stable position with the convex surface facing upwards (more than 86 per cent of all observed convex plates). Azimuthal orientation data were collected in 1988 and 2001; totally 325 measurements were taken.

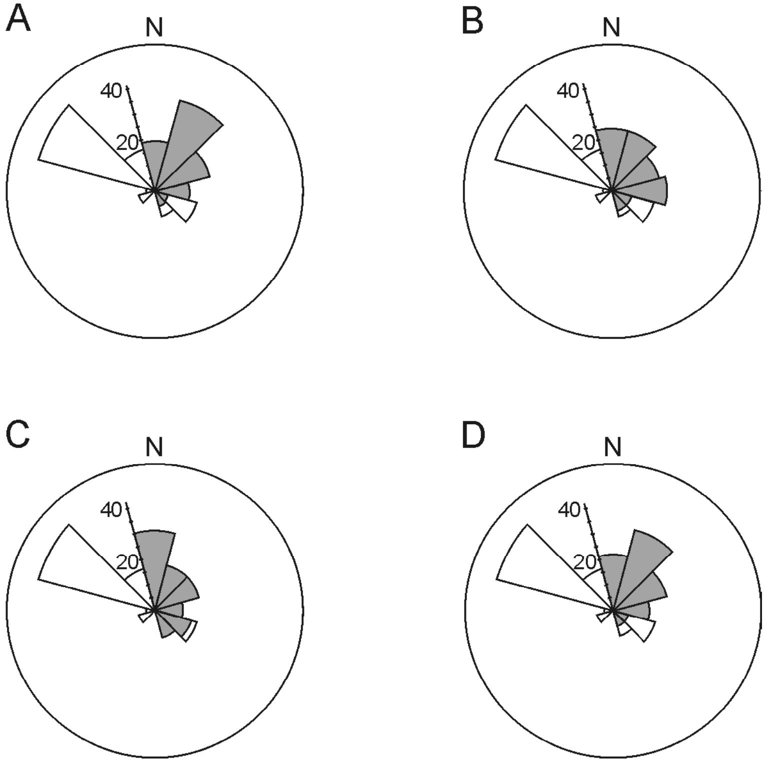

Fig. 9. Rose diagrams illustrating azimuthal orientation of fossils from the Pavāri site. A, posterior ventro-lateral bones (PVL) of *Bothriolepis ciecere* (n = 138). B, long bones with length/width ratio larger than 3 (n = 37). C, flat and almost isometric bones (n = 23). D, whole set of analysed fossils (n = 274). White sectors show orientation of cross bedding, grey sectors demonstrate orientation of fossils (in percent).

Three groups of fossil bones were selected: convex slightly elongated bones (mainly placoderm plates; 214 measurements), flat slightly elongated or almost isometric bones with slightly traced long axes (such bones as median ventral of *Bothriolepis*, gular plate, cleithrum or clavicle of *Holoptychius* etc.; 74 measurements) and long bones with length/width ratio larger than 3 (such as lower jaws of sarcopterygians and *Ventastega*, disarticulated pectoral fins of *Bothriolepis*, ribs, lepidothichia, and acanthodian spines; 37 measurements). Isometric and flat round elements such as *Holoptychius* scales were excluded from the analysis because they have no long axis suitable for measurement. Rose diagrams were prepared for each group of bones, and separately for the whole set (n = 274). The analysis of azimuthal orientation shows that convex bones are strongly oriented showing unidirectional distribution as exemplified by orientation of the posteror ventro-lateral plates (Fig. 9 A). A dominant NNE-SSW orientation is approximately parallel to the axis of the erosional channel, thus indicating deposition in one-way stream. Long bones and flat almost isometric fossils do not show obvious orientation (Fig. 9 B, C), which might indicate an insufficient strength of the stream, failing to lift the bones lying chaotically on the bottom of channel. It also should be mentioned that the comparison of a mean angle of azimuthal orientation of bones demonstrates that elongated, as well as flat and almost isometric bones are differently oriented in different parts of the channel, whereas convex bones lie almost parallel to the axis of erosional channel along the whole outcrop.

Breakage, wearing and abrasion of skeletal elements. Broken bones are comparatively rare, composing less than 2% of all specimens. On the other hand, only four of 14 lower jaws of *Ventastega curonica* are complete. The other ten are only partially articulated, or some skeletal elements are missing. It should be noted that the number of broken plates and bones could be underestimated due to selection of better preserved specimens for the collection, but it is not the case for material analysed in 1988. In most cases broken bones are still complete with detached portions separated by narrow fissures or cracks (usually not wider than 5 mm). Possibly breakage of skeletal elements might be explained mainly by diagenetic processes during compaction of rocks or even much later.

Only a few of about 800 fossils show traces of wearing, for example, the central dorsal plate 1 of the pectoral fin of *Bothriolepis* LDM 81/475 lacking ornamentation. Almost total lack of wearing and the high degree of preservation indicates that the remains were not transported for a long distance before burial.

Discussion

The sedimentation in the Baltic paleobasin during the Famennian took place mainly in the Latvian-Lithuanian Depression. This basin was periodically connected with an open sea in the west and southwest from Baltic area. During maximal transgressions in Kruoja and Joniškis time (early Famennian) and in Žagare time (late Famennian) the basin probably contacted also with the sea in Middle Russia through territory of Belarus (Savvaitova 1977). During significant regressions this basin became more isolated, smaller and more shallow, often turning into a semiclosed basin with changing water salinity. The last Devonian transgression in the Baltic took place during the Piemare time in the late Famennian, when sea waters flooded the Latvian-Lithuanian Depression after partial or even total erosion of the Tērvete deposits (Savvaitova 1995; Lukševičs *et al.* 1999). The widest transgression took place in the Žagare time when mainly carbonates were deposited and rather diverse marine fauna existed, including articulated brachiopods, crinoids, cephalopods, bivalves, gastropods, and fishes (Žeiba and Savvaitova 1981). At the very end of the Famennian, when deposits of the Pavāri and Varkaļi members, as well as Šķervelis Formation were formed, the basin was represented by a shallow brakish water bay almost completely surrounded by land. Palaeocarst phenomena in the middle part of the Šķervelis Formation and finds of dolocretes in the upper part of the formation, suggest that continental conditions similar to semidesert or desert prevailed at the very end of the Šķervelis time (Stinkulis 2004).

The results of the analysis of rocks of the Pavāri Member indicate their forming in alternating hydrodynamic regime. A powerful stream flowing from NNE to SSW formed the erosional channels. Some of them were filled by moderately or well-sorted very fine-grained to fine-grained sand containing no admixture of clay particles. Judging from the size and sorting of clastic particles, the material was probably transported in a low concentration flow. According to data of the grain-size analysis the clastic material has been sorted by stream and, possibly, also influenced by wave action. Deformations of sandstone bedding and intrabasinal conglomerate consisting of clay pebbles indicate the role of slump processes on sides of the erosional channels. Cross-bedding is characteristic for the infilling of the channels and clearly demonstrates high angle of dip and bipolar orientation, which is usually explained by the influence of inter-tidal streams (Reineck and Singh 1980). The structure and poor sorting of the overlaying beds of clayey silt and sandy-clayey silt suggest accumulation in calm water.

Fining upwards sequence of sedimentary structures is characteristic for the coarse-grained point bar deposits in fluvial systems (apart of bidirectional orientation of cross beds) or shallow channels in tidal inlets and tidal deltas in a coastal marine environment (Reineck and Singh 1980). The remarkable orientation of fossils indicate transportation in a medium-strong stream with velocity about 1-20 cm/sec, and deposition of remains on the bottom of an erosional channel at the moments of drastic decrease in stream power.

Considering the results of taphonomic and sedimentologic analysis of the Pavāri locality it is concluded that it formed in relatively shallow sea conditions dominated by stream, not wave influence. The deposits were not accumulated in continental or coastal freshwater environment, and there is not enough evidence to support the delta hypothesis regarded previously (Lebedev and Lukševičs 1996). Most likely, vertebrates from the Ketleri Formation existed in a coastal marine environment, although the possibility that the remains have been transported for a more considerable distance can not be excluded. Possibly, rocks of the Pavāri locality formed in a low-tidal terrigenous shelf environment between low islands where shallow channel might be formed in tidal processes. It is worth noting that *Acanthostega gunnari* from East Greenland, morphologically the most closely resembling *Ventastega curonica*, have been interpreted as a mainly aquatic animal dwelling in an active fluvial channels in a fluvial-dominated environment (Bendix-Almgreen *et al.* 1990). Comparison of the faunal composition of the Britta Dal (locality 'A') and Ketleri (Pavāri locality) formations shows clear taphonomic differences between these two localities. The fossil assemblage from the Britta Dal Formation is dominated by abundant remains of *Acanthostega* represented by isolated bones and articulated, sometimes exceptionally well-preserved material including skulls and even articulated postcranial parts in association with skulls. On the contrary, the fish material is poorly preserved, consisting only of disarticulated scales, teeth and placoderm trunk armour plates. The fish fauna of this particular fauna is represented only by some taxa including *Holoptychius*, lung-fishes *Soederberghia* and perhaps *Oervigia*, as well as rarely found placoderm *Remigolepis*. Probably, taphonomic peculiarities of the formation of Britta Dal oryctocoenosis resulted in the elimination of a significant part of information on the ancient biocoenosis. In contrast, composition of the fossil assemblage from the Pavāri locality is supposedly much more informative about the content of the palaeobiocoenosis, where dominant placoderms played the role of prey for diverse predators among sarcopterygians and tetrapod.

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Vēlā devona zivju un tetrapodu fauna no Pavāru atradnes un fosīliju sedimentoloģiski tafonomiskā izpēte

ERVĪNS LUKŠEVIČS un IVARS ZUPIŅŠ

Ir raksturota Ketleru svītas mugurkaulnieku atlieku, kas iegūtas Pavāru atradnē Kurzemē, izplatība, šķirojums, orientācija, saglabāšanās pakāpe un abrāzija. Mugurkaulnieku faunā dominēja bruņuzivis *Bothriolepis ciecere,* tajā bija pārstāvētas arī akantodes, vairāki daivspurzivju taksoni un primitīvs tetrapods *Ventastega curonica*. Taksonomiskais sastāvs, atlieku izplatības un šķirojuma īpatnības, kā arī izteikta azimutāla orientācija liecina par kompleksa pārveidi transportēšanas laikā zemas koncentrācijas ūdens plūsmā. Tomēr, abrāzijas pēdu trūkums un atlieku augsta saglabāšanās pakāpe, ieskaitot vairākas artikulētas skeletu daļas, norāda uz atlieku īsu transportēšanu pirms to apglabāšanas, tāpēc oriktocenozi var raksturot kā gandrīz pilnīgi autohtonu. Atradnes sedimentoloģiski tafonomiskā izpēte ļauj secināt, ka tā veidojusies relatīvi seklās jūras apstākļos, kur dominēja straumju un vāji izteikta viļņu darbība, iespējams, zema līmeņa plūdmaiņu sedimentācijas nogabalā tuvu krastam. Visticamāk, Ketleru laikposma mugurkaulnieki eksistējuši jūras apstākļos tuvu piekrastei, kaut gan nevar pilnīgi izslēgt iespēju, ka šo dzīvnieku atliekas pirms apglabāšanas ir transportētas tālu no dzīves vietām.

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Silurian acanthodian succession of the Lužni-4 borehole (Latvia)

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Acanthodians of the Lužni-4 borehole core include about 50 species and other dermal element forms distributed in the late Ludlow to the topmost Pridoli. Eleven acanthodian associations are obtained classified as the intervals (=intervals of partial ranges) of index species. Ranges of taxa which characterize the local and regional stratigraphical units are given, and most valuable species are distinguished. The earliest occurrence of *Nostolepis gracilis* in the Baltic region is reported from the late Ludlow, a lower stratigraphic level than previously recognized. Some taxa, such as *Nostolepis latvica* sp. nov., *N. alifera* sp. nov., *N.* cf. *linleyensis*, *Rohonilepis breviornatus, Arenaceacanthus arcuatacanalis, Fecundosquama basiglobosa, Poracanthodes marssae* sp. nov., have biozonal utility, and *Nostolepis linleyensis, Gomphonchus mediocostatus, Monospina erecta, Poracanthodes* spp., are significant for wide interregional correlations. The short-ranging topmost Pridolian acanthodian associations of the Lužni-4 lack some taxa characteristic of the deepest water Jura Formation as compared to southwestern Lithuania, perhaps indicating a shortened geological profile in this basin part.

Key words: Acanthodii, Climatiiformes, Ischnacanthiformes, histology, associations, biostratigraphy.

Introduction

The Lužni-4 borehole is on the shore of the Baltic Sea, in the northwestern part of the Kurzeme peninsula (west Latvia). The Silurian portion of the core has been used as a reference to characterise Latvian stratigraphical units and the palaeogeographical development of this part of the basin. I direct readers to publications of 1974-1987 (Gailite and Ulst 1974; Ulst 1974; Gailite 1978; Ulst and Gailite 1986; Gailite, Ulst and Yakovleva 1987; Karatajute-Talimaa 1978) for the geological and facies characteristics of this section and of the whole Kurzeme area, and for distribution of different faunal groups including ostracodes, brachiopods, conodonts and vertebrates.

The acanthodian-bearing stratigraphic sequence studied here embraces the late Ludlow (Ventspils Formation) and Pridoli (Minija and Targale formations). The geological profile is composed of biomorphic and detrital limestones (the main part of Ventspils Fm.), clayey marls with interlayers of detrital limestones (Šilale Beds of the Minija Fm.), clayey marls (Varniai Beds of the Minija Fm.), dominant nodular biomorphic limestones (Venzava Beds), marls (Garzde Beds) and dolomitized limestones and dolomitic marls (Lužni Beds) of the Targale Formation. The sediments were mostly accumulated in the near shore zone of the shallow shelf. This environment was replaced by a lagoonal one during the latest Pridoli, with deposition of the Lužni Beds in the gradual transition from Silurian to Devonian.

The first microvertebrate report of the Lužni-4 core was provided by Gailite and Ulst (1974) based mainly on thelodont identifications by V.Karatajute-Talimaa. In the Pagegiai Formation (of the old nomenclature, embracing modern Mituva and Ventspils formations), *Thelodus laevis* Thelodont Zone (TZ) was distinguished; *Th. sculptilis* TZ in the lower part of the Minija Fm.; and *Th. parvidens* TZ in the upper Minija and the principal part of the Targale Formation (until the depth of 195 m). Two following facts obtained from this core are of great interest in discussing the completeness of the Silurian profile in the basin, and in tracing the Silurian/Devonian boundary. These are the discovery of the *Katoporodus lithuanicus* TZ (195-176.6 m), a short-ranging topmost unit of the Silurian Vertebrate Standard Scheme (Karatajute-Talimaa 2000; Märss 2000), and the earlier entry into the sequence of *Turinia pagei*, which first occurs here about 4.6 m below the traditional Silurian/Devonian boundary drawn at the base of the red dolomitic marls. Both facts demonstrate the developmental peculiarities of this part of the basin, which became more isolated and lagoonal, but with the complete occurrence of index fossils which mark the Silurian/Devonian boundary beds with no stratigraphic gap.

Acanthodians of the Lužni-4 collection were reported in the publications of 1974, with only short biostratigraphical comments (Karatajute-Talimaa 1978). Only the widest spread, commonly known taxa were recognized - *Nostolepis striata* Pander, *N. gracilis* Gross, *Gomphonchus sandelensis* (Pander), *G. hoppei* (Gross) and representatives of *Poracanthodes.* The present study extends the list to about 50 taxa or skeletal elements of an animal (teeth, spines) which attribution to distinct taxa is uncertain (Table). The collection is housed at the museum of the Institute of Geology and Geography (abbreviated LIGG) in Vilnius and is numbered 25-A.

Systematic palaeontology

Class ACANTHODII Berg, 1922
Order CLIMATIIFORMES Berg, 1940
Family Climatiidae Berg, 1940
Genus *Nostolepis* Pander, 1856

Type species. *Nostolepis striata* Pander, 1856; Upper Silurian, Pridoli, Ohesaare Regional Stage. Ohesaare Cliff, Saaremaa, Estonia.

Nostolepis alifera sp. nov.
Fig. 1A-L, 2 A-D

Etymology. *Alifer* (Latin) - winged, referring to the lateral crown slopes on scale crowns.

Holotype. LIGG 25-A-2550, flank scale (Fig. 1 F).

Type horizon. Garzde Beds of the Targale Formation, Pridoli, Upper Silurian.

Range. Type horizon only.

Material. About 2500 scales.

Table. Acanthodian occurrence in the Lūžņi-4 borehole. ✖ - 1-20 scales, ○ - 20-50 scales,
● - 50-100 scales, ▣- hundreds of scales, ■ - up to one thousand of scales, ◆ - thousands of scales

Depth, m	*Monospina erecta*	*Nostolepis alta*	*N. gracilis*	*N.* cf. *robusta*	*N.* cf. *athleta*	*N. musca* morpha A	*N. musca* morpha B	*N. consueta*	*"Pruemolepis wellsi"*	*Poracanthodes punctatus*	*P.* cf. *porosus*	*Gomphonchus sandelensis*	*G. hoppei*	*G.* cf. *hoppei*	*Gomphonchus* teeth	*Gomphonchus* tooth whorls	*Cheiracanthoides planus*	*Gomphonchus* cf. *mediocostatus*	*Poracanthodes subporosus*	*Nostolepis amplifica*	*Gomphonchus mediocostatus*	*G.* sp.	*Gomphonchus* fin spines	*Nostolepis* fin spines	*N. elegans*	*N.* cf. *magnicostata*	*Poracanthodes sulcatus* sp. nov.	*Nostolepis* cf. *alta*	*Cheiracanthoides* sp.	*Endemolepis inconstans*	*Nostolepis striata*	*Nodacosta*-type fin spines	*Nostolepid* squamae margaritatae	*Poracanthodes porosus*	cf. *Cheiracanthus*	*Nostolepis alifera* sp. nov.	*Rohonilepis breviornatus*	*Nostolepis* teeth	cf. *Canadalepis linguiformis*	*Fecundosquama basiglobosa*	*Poracanthodes* cf. *stonehousensis*	*P. marssae* sp. nov.	? *Diplacanthus* sp.	*Arenaceacanthus arcuatacanalis*	*Fecundosquama* cf. *basiglobosa*	*Nostolepis latvica* sp. nov.	Nostolepidida indet. 1	*Nostolepis* cf. *linleyensis*	*Gomphonchus*? *minutus* sp. nov.	*Nostolepis* cf. *amplifica*	Nostolepidida indet. 2	Beds	Formation
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
172.2	✖	✖	✖	✖	✖	▣		▣	✖	✖	✖	▣	✖	✖	✖		✖																																			Lūžņi	Targale
172.5						○		○				○					✖	✖		✖																																	
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173.5	✖	✖	✖			◆	✖	◆	✖	✖		◆	✖	✖				✖	✖	✖	✖																																
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176.5						■		▣	✖	✖		■	✖		✖						○			✖	✖		✖	✖	✖																								
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178.8		✖				●		●	✖			●	✖	✖						✖	✖	✖					✖																										
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180.0		✖	✖			●		○		✖		●	✖	✖	✖	✖				✖	✖			✖							○	✖																					
182.7			✖		✖	○		○	✖			●	✖	✖						✖				✖			✖				○		✖	✖																			
182.8		✖	✖			◆	✖	◆	✖	✖		◆	✖	✖	✖	✖					✖			✖			✖				✖	✖		✖																			
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196.0	✖	✖			○	▣	●	◆	○			◆		○	✖	✖				✖				✖												■	○	✖	✖														
196.5	✖	✖	○		✖	◆	●	▣	✖	✖		◆	✖		✖	✖								✖	✖	✖	✖	✖				✖				●	✖																
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Diagnosis. *Nostolepis* with high-crowned scales having porose necks. Wide raised triangular medial area dominates on crowns, which bear five to eight sub-parallel anterior ridges that extend half of crown length, or reach its posterior part converging with the longest central ridges. The lateral crown slopes are ornamented by longitudinal or oblique ridges converging with the longest medial ridges posteriorly. Up to four superposed

Continuation of Table

1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
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lamellae in crowns are composed of *Stranggewebe* and simple networked bone-like mesodentine and contain a well developed main vascular system with particularly large radial vascular canals over the bases of scales. The *Stranglacunae* are long, dense, with numerous osteocytes interspersed. The *Stranggewebe* layers are enveloped in the lamellae by strips of highly cellular mesodentine.

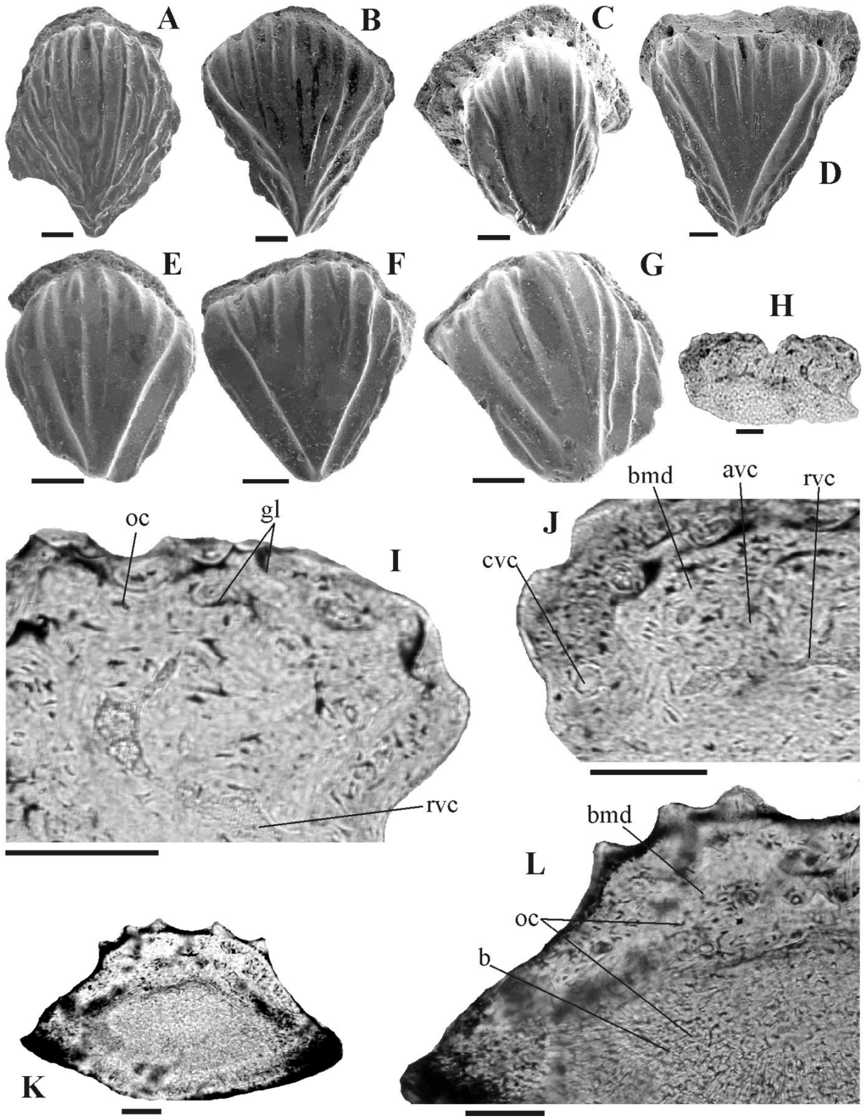

Fig. 1. Nostolepis alifera sp. nov. SEM micrographs of scales (A-G), crown views, anterior upwards, and thin section photos (H-L). A, LIGG 25-A-2570; B, LIGG 25-A-2568; C, LIGG 25-A-2632; D, LIGG 25-A-2571; E, LIGG 25-A-2549; F, holotype, LIGG 25-A-2550; G, LIGG 25-A-2553; H-J, vertical transverse section of a scale like that in Fig. 1G. Thin section 3758. H, general view; I, details of the right, and J, of the left crown and bordering base parts; K-L, vertical transverse section through the anterior part of a holotype-like scale. Thin section 3759. K, general view; L, the left part at higher magnification. Lūžņi-4 borehole, depth 197.0 (A-B, H-J), 197.2 (C), 207.0 (D, K-L) and 189.8 (E-G) m. m. Přidoli, Jūra Regional Stage, Garzde Beds of the Targale Formation. Abbreviations: ***avc***, ascending vascular canal, ***b***, bone, ***bmd*****,** bone-like mesodentine, ***cvc***, circular vascular canal, ***gl*****,** growth lamella, ***oc*****,** osteocyte cavity, ***rvc***, radial vascular canal. Scale bars: 0.1 mm.

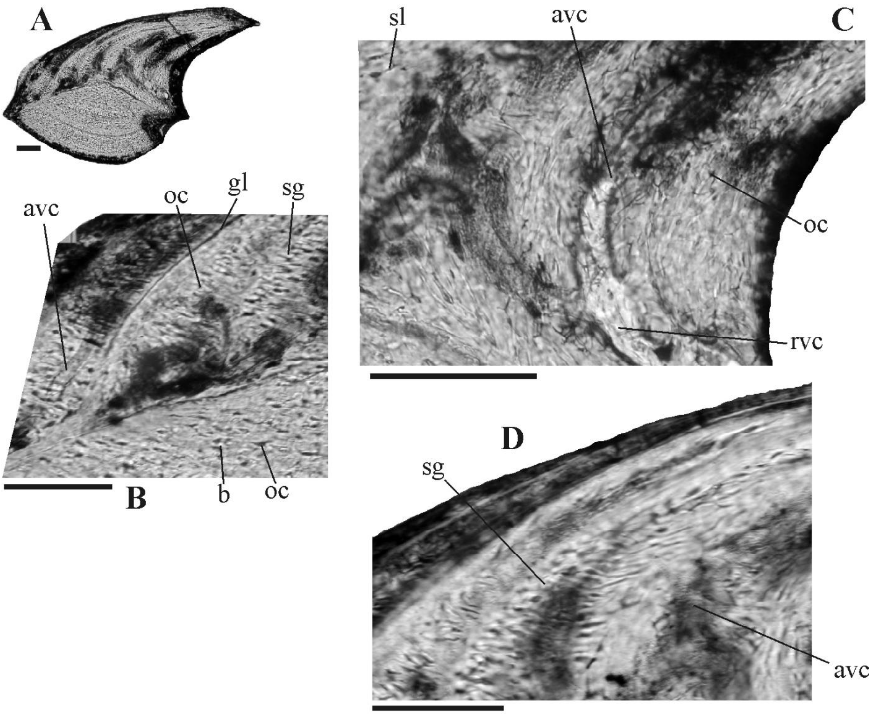

Fig. 2. Nostolepis alifera sp. nov. Histological structure of a scale like that in Fig. 1B. Vertical longitudinal section. Thin section 3760. A, general view; B, detail of the scale primordium; C, detail of the posterior part of neck with the neck/base junction; D, detail of the central part of crown. Lūžņi-4 borehole, depth 207.0 m. Přidoli, Jūra Regional Stage, Garzde Beds of the Targale Formation. Abbreviations: ***avc***, ascending vascular canal, ***b***, bone, ***gl***, growth lamella, ***oc***, osteocyte cavity, ***rvc***, radial vascular canal, ***sg***, *Stranggewebe*, ***sl***, *Stranglacuna.* Scale bars: 0.1 mm.

Description. *Morphology.* Most (flank) scales have posteriorly elongated rhomboidal to elipsoidal crowns from 0.28 to 0.85 mm long. Rare specialized varieties have triangular crowns. The crown plate slopes down slightly anteriorly. A clear elevated triangular medial area and lower lateral areas are distinguished on the crowns. The medial area carries five to eight sub-parallel anterior ridges with rounded crests that fade out at about half of crown length (Fig. 1 C, E-F). Some scales have unevenly long medial ridges of which some point to or converge with the longest central ridges at the posteriormost crown part (Fig. 1 B, G). Short anterior bifurcation of ridges occurs rarely. The medial crown area sometimes has a wide deep central groove (Fig. 1 G). The lateral crown areas contain one to two ridges extending the whole crown length (Fig. 1 D, G) or short, more numerous oblique ridgelets which converge with the longest medial ridges posteriorly (Fig. 1 A-B). The scale bases are rhomboidal (except for specialized varieties, see Fig. 1 D), slightly (Fig. 1 K) to moderately convex, and separated from the necks by a clear rim. The necks are short anteriorly because of the downsloping crown, and frequently contain large pores (up to five basally on each side, see Fig. 1 C).

Histology. Three or four superposed growth lamellae of scale crowns are composed of simple bone-like mesodentine and only poorly formed *Stranggewebe* (scales with medial groove, Fig. 1 H-J), and of *Stranggewebe* enveloped in each lamellae by a strip of simple networked mesodentine (holotype-like scales, Fig. 2 A-D). Both scale varieties contain large main radial, circular and ascending vascular canals positioned basally in the growth zones (Fig. 1 I-J, 2 C). Particularly long and wide radial vascular canals are displaced over the base, separating the different tissues of base and crown. The crown tissues are highly cellular up to the outer layer. Osteocyte cavities are multi-angular, large, and incorporated into a short-tubular mesodentine network or *Stranggewebe* distinguishing by dense and long *Stranglacunae* (Fig. 2 B, D). The cellular bone of bases is densely lamellar and contains plenty of multi-angular osteocyte cavities (Fig. 1 L).

Remarks. The sculpture characters of the crown, crown/neck/base proportions, as well as the histologic microstructure of tissues, including highly vascularized bone-like mesodentine and *Stranggewebe* in crowns and cellular bone in bases, suggest an attribution of scales to the genus *Nostolepis.* Among the known Silurian nostolepids, *N. alifera* sp. nov. seems most similar to *N. alta* (Märss 1986). One variety of the latter also has a raised medial area sculptured by sub-parallel ridges and the lowered lateral areas on scale crowns (Märss 1986: pl. 28, figs 12-14), but their neck and base features separate them distinctly. Unlike *N. alta*, no scales of N. *alifera* have tall necks or small and flat bases that sometimes are pierced by large vascular canals. The histologic structure of both species is similar except for the vascular canals in scale bases and reduced *Stranggewebe* area in crowns of *N. alta* (Märss 1986: pl. 31, figs 1-4), and the poorly developed mesodentine network strips in the outer layers of growth lamellae in *N. alifera*.

N. alifera resembles *N. amplifica* and *N. musca* (Valiukevicius 2003 b: fig. 2 A-H and fig. 5 J-R respectively), both from the Baltic Silurian in the development of the medial area on scale crowns. However, the ridge ornamentation is different: *N. amplifica* and *N. musca* have shorter, more rough and rounded ridges which are less uniformly arranged than in *N. alifera*. Converging ridges on the postero-medial crown part are not observed in both compared species. The histologic structure of all species is similar except for wider and more numerous vascular canals of the principal system in *N. alifera*, that are almost absent in *N. musca* (Valiukevicius 2003 b: fig. 8 A-G), and thicker layers of simple networked mesodentine enveloping the *Stranggewebe* in *N. amplifica* (Valiukevicius 2003 b: fig. 3 A-G). The *Stranggewebe* of *N. musca* shows longer and more uniform *Stranglacunae* distributed more evenly in the growth lamellae.

Several Devonian or Siluro/Devonian nostolepids recently described from the Old Red Sandstone Continent are similar to *N. alifera* in having medial areas on scale crowns. In *N. decora* (Valiukevicius 2003 a: fig. 17 C-G) this area is concave, carrying only one or two short central anterior riblets, whereas the lateral edges are often spiny with the spinelets directed obliquely upward. The principal histologic difference is that the *Stranggewebe* is not overlain by the mesodentinal network in the outer parts of growth lamellae in *N. decora* (Valiukevicius 2003 a: fig. 18 A, C, F). *N. adzvensis* (Valiukevicius 2003 d) is distinguished by characteristic posterior crown/neck structures comprising oblique ridges and oblique or vertical neck riblets. The crown tissues of the latter contain no enlarged vascular canals, and the networked mesodentine closely resembles bone in the density of osteocyte spaces and the short osteocyte processes. *N. terraborea* (Valiukevicius 2003 d) typically has four uniform, short and basally widened ridges with sharp crests on the raised medial area and unornamented lateral slopes. *N. valentinae* (Valiukevicius 2003 d) is distinguished by a highly raised elipsoidal to triangular medial area which is smooth or bears one to five very short sub-parallel rounded anterior riblets that never bifurcate. The lateral areas sometimes contain obliquely-upward, posteriorly directed riblets like in *N. alifera*. The *Stranggewebe* and simple mesodentine do not differ from those of *N. alifera* apart from absence of networked strips enveloping the *Stranggewebe* and the weakened system of principal vascular canals, particularly the radial canals, in crowns of both *N. terraborea* and *N. valentinae*.

Occurrence. See Table.

Nostolepis latvica sp. nov.

Fig. 3 A-M

2003 c *Nostolepis "prestriata"*; Valiukevicius, p. 51.

Etymology. The species is named from Latvia, the country of origin for the type material.

Holotype. LIGG 25-A-2574, flank scale (Fig. 3 A).

Type horizon. The lower part of the Venzava Beds of the Targale Formation, Pridoli, Upper Silurian.

Range. Šilale and Varniai Beds of the Minija Formation and the lower part of the Venzava Beds of the Targale Formation, Pridoli, Upper Silurian.

Material. About 850 scales.

Diagnosis. *Nostolepis* having scales with rhomboidal, posteriorly tapered and elongated crowns overhanging bases. Crowns are sculptured by four to eight uniform, wide anterior ridges extending a half of crown length or have a slightly raised medial area carrying few riblets of different lengths. Lateral crown areas are narrow, outlined by oblique, short neck ridges. Scale crowns composed of *Stranggewebe* and networked mesodentine. The *Stranggewebe* area of the posterior crown is reduced, replaced by simple bone-like mesodentine in the lower (neck) part; its strips are not covered by the mesodentinal network. Simple mesodentine of the anterior crown part is densely networked and highly cellular. The main vascular system is poorly developed.

Description. *Morphology*. The scales are mostly of medium size and only rarely reach 0.9-1.1 mm in crown length. Crowns are slightly downsloped anteriorly, flat, rarely medially concave, of rhomboidal to elipsoidal form, tapered and clearly elongated posteriorly. The posterior crown part (up to a half of total length) overhangs the base. Crowns are ornamented by four to eight uniform, low, basally widened ridges extending half of their length (Fig. 3 A-B, D). The lateral step-like lowered areas are frequently present (Fig. 3 C, E-F), but are narrow and sometimes very short. The medial area, occupying the main part of the crown, is only slightly raised, flat or side to side concave, and bears two to

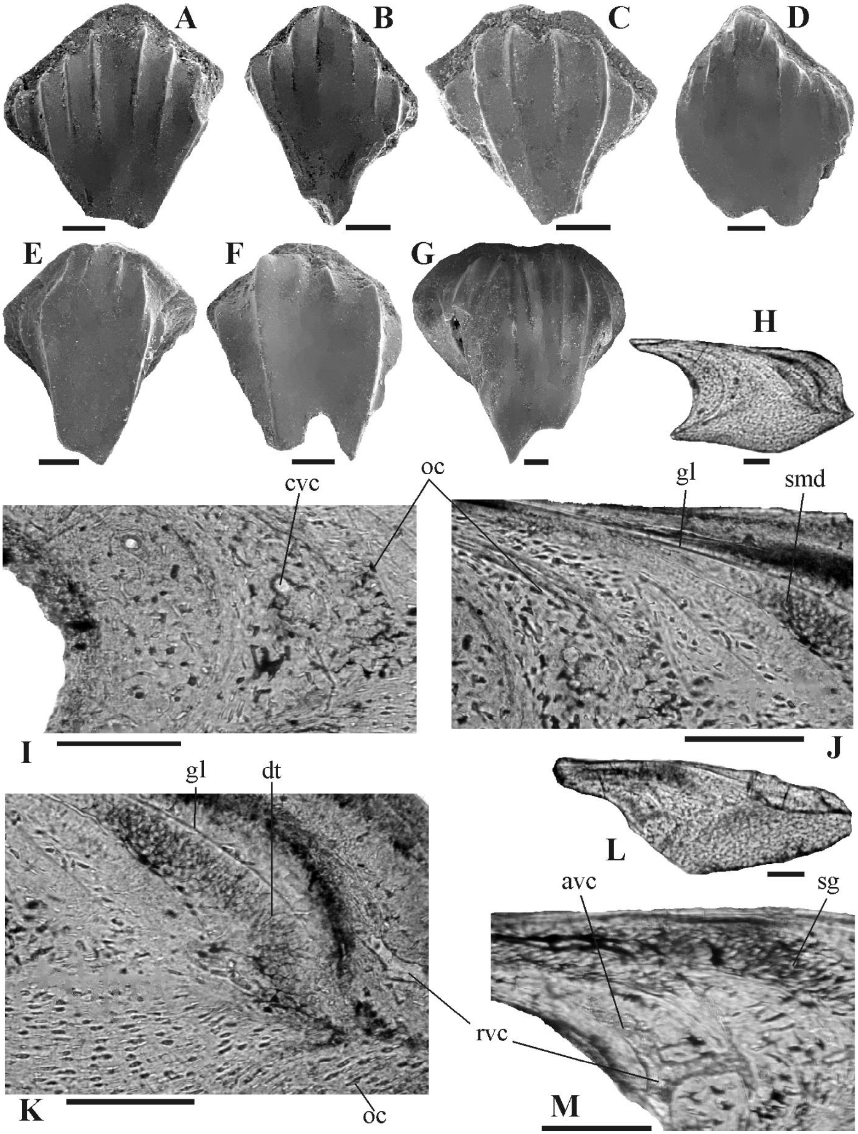

Fig. 3. *Nostolepis latvica* sp. nov. SEM micrographs of scales (A-G), crown views, anterior upwards, and vertical longitudinal thin section photos (H-M). A, holotype, LIGG 25-A-2574; B, LIGG 25-A-2575; C, LIGG 25-A-2576; D, LIGG 25-A-2578; E, LIGG 25-A-2609; F, LIGG 25-A-2610; G, LIGG 25-A-2655; H-K, thin section of a holotype-like scale. Thin section 3788. H, general view; I-K, details of the posterior (I), central (J) and anterior (K) crown parts and the bordering base portions at higher magnification; L-M, thin section of a scale like that in Fig. 3 F. Thin section 3763. L, general view; M, detail of the posterior crown part at higher magnification. Lūžņi-4 borehole, depth 272.7 m. (G-K), 280.3 m (A-D and L-M) and 330.4 m (E-F). Přidoli, Minija Regional Stage, Varniai (A-D and G-M) and Šilalė (E-F) Beds of the Minija Formation. Abbreviations: ***avc***, ascending vascular canal, ***cvc***, circular vascular canal, ***dt***, dentine tubule, ***gl***, growth lamella, ***oc***, osteocyte cavity, ***rvc***, radial vascular canal, ***sg***, *Stranggewebe*, ***smd***, simple mesodentine. Scale bars: 0.1 mm.

three short anterior riblets (Fig. 3 C, E-G). The ribbed crown slopes sharply down to the base anteriorly. The base is rhombic in outline and has clear anterior rims; it is shallow, centrally convex, often wider than long and protrudes beyond the antero-lateral margins of the crown. No pore or vascular canal openings are visible on the scales.

Histology. The microstructure of flank scales is mainly uniform despite the marked differences in crown sculpture. Four to six lamellae in crowns of the superpositional growth type are composed of *Stranggewebe* and networked mesodentine. The *Stranggewebe* area of the posterior crown part seems slightly reduced as compared to the classical "*Nostolepis*"-type histology. It is replaced by the bone-like cellular mesodentine in the basal crown parts (area of the posterior neck, Fig. 3 I-J), with plenty of large osteocyte cavities connected by short winding processes almost excluding space for the dentinal canaliculi here. The *Stranggewebe* strips are not covered by the mesodentinal network (Fig. 3 M). The anterior part of all crown lamellae except the scale primordium is entirely composed of very dense simple mesodentine incorporating frequent osteocytes among the interwoven dentine tubules (Fig. 3 J-K). The main system of wide vascular canals is poorly developed except for the ascending and radial canals basally in the neck (Fig. 3 M). The low-pyramidal base has large numbers of spindle-shaped osteocyte cavities of the cellular bone oriented along the thin-lamellar growth lines (Fig. 3 K). This pattern, combined with the lack of *Stranggewebe* in the lower areas of the crown, gives a sharp border between the crown and base tissues.

Remarks. In the crown sculpture characters (slightly concave medial area carrying short anterior riblets, presence of lateral steps formed by the oblique neck ridges), *N. latvica* sp. nov. resembles *N. striata* sensu Gross 1947 (pl. 26, figs 8-11), but distinctly differs from Pander's original *N. striata* (Pander, pl. 6, figs 7 a-c). This difference led to my prior definition of this species as *"prestriata"* (Valiukevicius 2003 c) according to its lower stratigraphic occurrence in the sequence. (*N. striata* is present only in the Garzde and Lužni Beds of the topmost Pridoli in the Lužni-4 borehole). *N. latvica*, judging by both morpho- and histological characters, belongs to the *N. striata* group of nostolepids. In this sense, it can be covered by the discussion of nostolepid species having medial crown area on scale crowns given by Valiukevicius (2003 d). The holotype-like scales of *N. latvica* differ from those of other nostolepids by the uniform sub-parallel, sharp and constant number of ridges fading out at the mid-length of crown, and also by details of the *Stranggewebe* and simple mesodentine structure (reduced area of the first tissue in the posterior crown part, density of the dentinal network of the second one in the anterior part, reduction of the system of main vascular canals higher in crowns).

Vergoossen (2002 a, pl. 6, fig. 63; 2002 b, pl. 3, fig. 36) recorded morphologically similar, but not histologically examined scales from the Late Silurian of Sweden which he assigned to *N. striata*. The Lužni scales, especially holotype-like ones, differ from those of Sweden by the uniformity and stable number of crown ridges.

Occurrence. See Table.

Nostolepis cf. *amplifica*
Fig. 4 A-M

2003 b *Nostolepis amplifica;* Valiukevicius, figs 2 A-H, 3 A-I.

Range. The lower part of the Šilale Beds of the Minija Formation, Pridoli, Upper Silurian.

Material. 72 flank scales.

Remarks. *N. amplifica* was originally defined on large trunk scales having a high robust median crown area ornamented with two to six short parallel ridges fading out at a quarter of crown length, and narrow lateral crown steps delimited by clear oblique neck ridges. Most of the Lužni scales are within the morphologic range of *N. amplifica*, differing only in having more pronounced, wider bases protruding beyond the antero-lateral edges of crowns, and scales generally being smaller (crowns 0.35-0.6 mm long and 0.3-0.85 mm wide). Two reasons preclude definite assignment of the scales to *N. amplifica*. First, the long stratigraphic gap that separates the isolated occurrence (338.6 m) of *N.* cf. *amplifica* from the range of definite *N. amplifica* (202.4-172.2 m); and second, histologic differences. The *Stranggewebe* in crowns of *N. amplifica* is covered by a mantle of highly cellular simple mesodentine and is distinguished by short and narrow *Stranglacunae*; osteocytes are present in the primordial lamella only; large principal vascular canals develop in each growth lamella (Valiukevicius 2003 b, fig. 3 A-I). These characters are almost opposite in the Lužni scales. The enveloping *Stranggewebe* mantle of the networked mesodentine is absent here or is very thin (Fig. 4 J-K), *Stranglacunae* are particularly long and osteocytes are present, though rare, in all growth lamellae (Fig. 4 H, M). The system of main vascular canals is less developed in *N.* cf. *amplifica*, and only narrow ascending and radial canals were observed.

Nostolepis elegans (Brotzen) 1934
Fig. 5 A-M

1934 *Diplacanthoides elegans*; Brotzen, pl. 1, fig. 11 a-c.
Diplacanthoides insignis; Brotzen, pl. 2, fig. 1 a-b.
? *Diplacanthoides crassus*; Brotzen, pl. 1, fig. 16 a-b.
1937 ? *Diplacanthoides unguiparatus*; Lehman, pl. 2, fig. 30.
? *Diplacanthoides trilobatus*; Lehman, pl. 2, figs 31; pl. 4, figs 64.
Diplacanthoides elegans; Lehman, pl. 3, fig. 57.
non 1980 *Nostolepis arctica*; Vieth, pl. 5, figs 1-9.
1998 *Nostolepis striata*; Valiukevicius, pl. 1, fig. 2 a-b.
1999 a *Nostolepis arctica*; Vergoossen, figs 2-4.
1999 b *Nostolepis striata, 'elegans'* form group; Vergoossen, pl. 2, figs 15-17.
2002 a *Nostolepis striata*; Vergoossen, fig. 59.
2002 b *Nostolepis striata*; Vergoossen, fig. 36.
2002 c *Nostolepis striata, 'elegans'* form group; Vergoossen, figs 93-99.

Holotype. Brotzen 1934 a: pl. 1, fig. 11 a-c; a flank scale.

Type horizon. The Lower Devonian erratics of the Baltic basin.

Range. From Upper Silurian, Ludlow Series to Lower Devonian, Lochkovian.

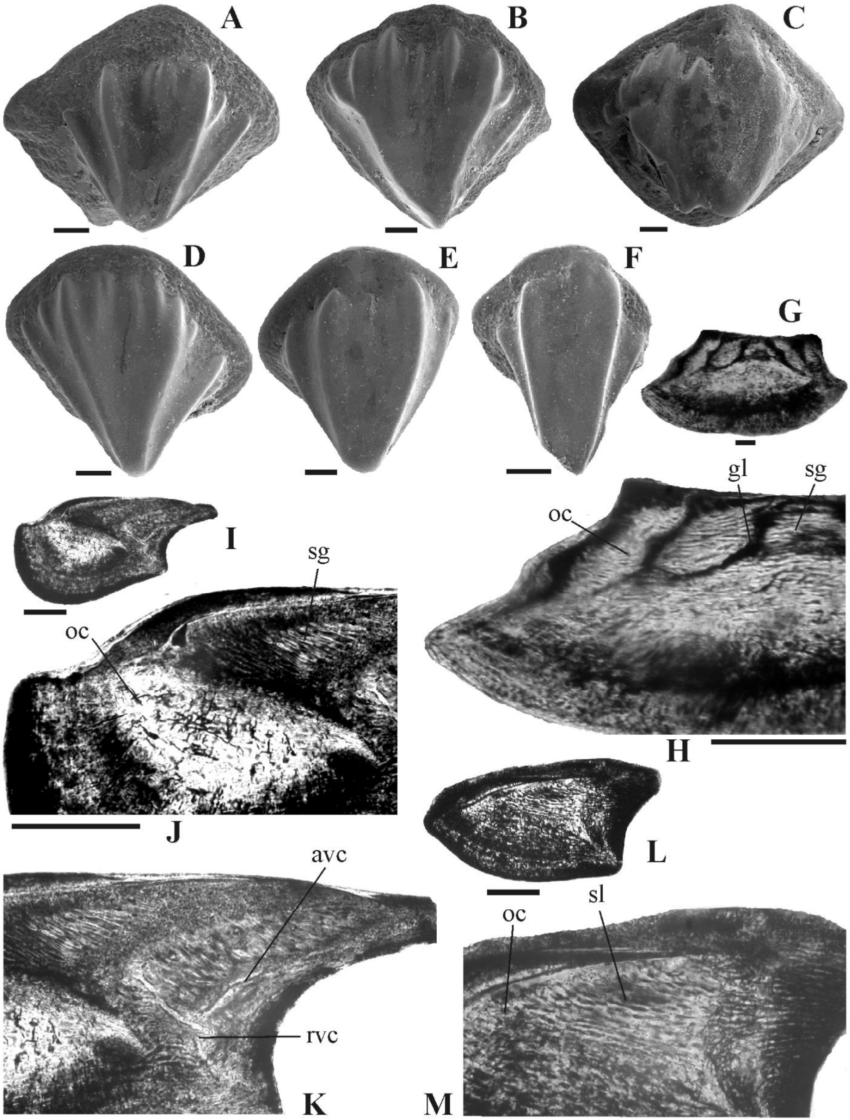

Fig. 4. Nostolepis cf. *amplifica*. SEM micrographs of scales (A-F), crown views, anterior upwards, and thin section photos (G-M). A, LIGG 25-A-2601; B, LIGG 25-A-2606; C, LIGG 25-A-2603; D, holotype, LIGG 25-A-2604; E, LIGG 25-A-2602; F, LIGG 25-A-2607; G-H, vertical transverse section of a holotype-like scale. Thin section 3775. G, general view; H, detail of the left crown part and the base portion at higher magnification; I-K, longitudinal section of a holotype-like scale. Thin section 3777. I, general view; J, detail of the anterior crown part and scale primordium at higher magnification; K, magnified detail of the posterior crown part; L-M, vertical longitudinal section of a scale like that in Fig. 4 C. Thin section 3778. L, general view; M, detail of scale primordium. Lūžņi-4 borehole, depth 338.6 m. Přidoli, Minija Regional Stage, Šilalė Beds of the Minija Formation. Abbreviations: ***avc***, ascending vascular canal, ***gl***, growth lamella, ***oc***, osteocyte cavity, ***rvc***, radial vascular canal, ***sg***, *Stranggewebe*, ***sl***, *Stranglacuna*. Scale bars: 0.1 mm.

Material. Approximately 170 scales.

Diagnosis. *Nostolepis* having mid-sized scales with highly raised dominant medial area on crowns ornamented by one to four short anterior ridges; narrow lateral areas are outlined by long oblique neck ridges pointed posteriorly. Scale crowns (maximum four growth lamellae) are composed of dense, finely-networked, cellular simple mesodentine (dominant tissue) and outer durodentine; no *Stranggewebe*; vascular canals are well developed; mesodentine grades into the cellular bone of scale bases without sharp border.

Description. *Morphology*. Scales have elongated triangular crown plates slightly sloping down anteriorly with the tapered posterior crown part far overhanging the base. Crown length varies from 0.38 to 1 mm; most frequently 0.6-0.8 mm. Crown width is 0.2-0.62 mm. A wide medial area forms most of the crown, which is highly raised compared to the narrow lateral slopes. Only the anteriormost strip of the medial area is sculptured by a few (one to four) short rounded ridges. The lateral areas are outlined by the oblique long neck ridges which converge with the medial ones extremely posteriorly (Fig. 5A-C). The posterior crown overhang can reach a half of its length. Scale necks are low and bases rhomboidal, of medium convexity, with the deepest point forward of centre. *Histology*. Three to four growth lamellae of the crown are composed of simple mesodentine and durodentine (canalless dentine) which is developed in thin strips superficially centrally (Fig. 5L). *Stranggewebe* is lacking in the posterior crown parts. Simple mesodentine forms a particularly dense and fine network of dentinal canaliculi (Fig. 5 E-F) incorporating numerous random, large, multi-angular osteocyte cavities. Mesodentine character in this respect is similar to the base bone pattern except for more regular orientation of osteocytes along the growth lines in bases (Fig. 5 E-G). There is no sharp border between the crown and base tissues; mesodentine and bone make a gradual transition. The system of principal vascular canals in crowns (ascending, radial and circular) is well developed forming long and wide branches in each lamella (Fig. 5 I, L).

Remarks. Gross (1947) regarded *Diplacanthoides elegans* as a junior synonym of *Nostolepis striata*. However, as proposed by Vergoossen (1999-2002), the '*elegans*' group of scales is distinguishable from *N. striata* by diagnostic morpho- and histological characters. *N. striata sensu* Gross (1947, 1971) can not compare with the other nostolepid taxa or any acanthodian in having so numerous and excessively diverse scale forms, and undoubtedly incorporates multiple biological species. For more extended morphological comments on *N. elegans* scales and comparisons with other nostolepids, I direct readers to Vergoossen's (1999-2002) remarks. *N. arctica* Vieth (1980: pl. 5, figs 1-9; fig. 20 A-E) differs from *N. elegans* in having more ornamented scales which crowns are highly inclined, longer and often longitudinally bent. Now, after a study of histologic structure of scales (*N. elegans* was not previously examinated), the differences from *N. arctica* are furtherly supported by the absence of *Stranggewebe* in crowns of *N. elegans*.

Occurrence. See Table.

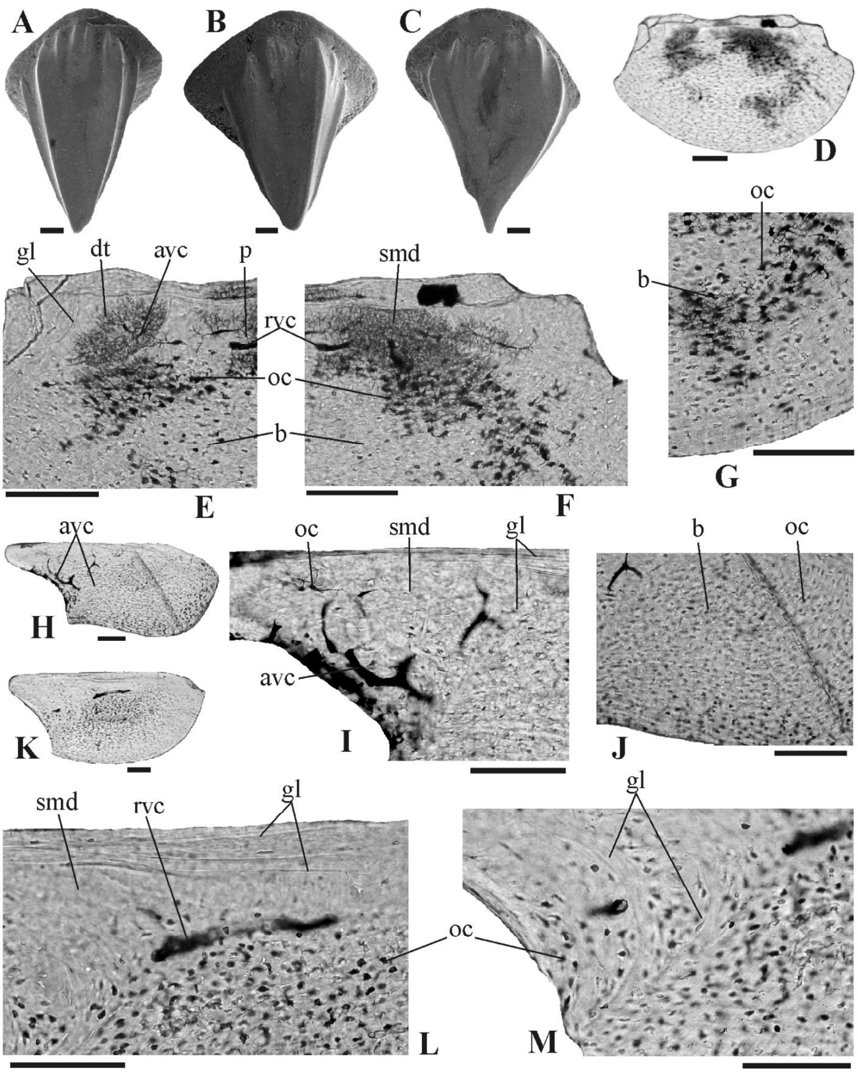

Fig. 5. Nostolepis elegans (Brotzen) 1934. SEM micrographs of scales (A-C), crown views, anterior upwards, and thin section photos (D-M). A, LIGG 25-A-2624; B, LIGG 25-A-2629; C, LIGG 25-A-2623; D-G, vertical transverse section of a scale like that in Fig. 5 A. Thin section 3743. D, general view; E, detail of the left crown part and the base portion; F, detail of the right crown part and base portion; G, detail of the right part of the base; H-M, vertical longitudinal sections of scales. H-J, thin section 3742. H, general view; I, detail of the posterior crown part at higher magnification; J, detail of the central base part at higher magnification; K-M, thin section 3740. K, general view; L, detail of the central crown part (scale primordium and the later growth lamellae) and the bordering base strip at higher magnification; M, detail of the crown/base junction from the left side at higher magnification. Lūžņi-4 borehole, depth 197.2 m. Přidoli, Jūra Regional Stage, Garzde Beds of the Targale Formation. Abbreviations: ***avc***, ascending vascular canal, ***b***, bone, ***dt*****,** dentine tubule, ***gl****,* growth lamella, ***oc***, osteocyte cavity, ***p***, scale primordium, ***rvc***, radial vascular canal, ***smd***, simple mesodentine. Scale bars: 0.1 mm.

Order ISCHNACANTHIFORMES Berg, 1940
Family ISCHNACANTHIDAE Woodward, 1891
Genus *Gomphonchus* Gross, 1971

Type species. *Gomphonchus* (pro *Gomphodus* Pander, 1856) *sandelensis* (Pander). Upper Silurian, Pridoli; Saaremaa, Estonia.

Gomphonchus? minutus sp. nov.
Fig. 6 A-K

Etymology. *Minutus* (Latin) - small.

Holotype. LIGG 25-A-2581, flank scale (Fig. 6 B).

Type horizon. Šilale Beds of the Minija Formation, Pridoli, Upper Silurian.

Range. Minija Formation, Pridoli, Upper Silurian.

Material. Total about 4500 scales.

Diagnosis. Ischnacanthid having tiny rhomboidal scales with deep bases which protrude slightly beyond the crowns on all sides. Crown ornament varies from almost smooth with only shallow anterior incisions, to short, low, flattened parallel ridges, that are rarely sub-radial and widened anteriorly. Scale crowns are composed of modified acellular networked mesodentine with neither lacunae nor outer durodentine present. Thin-lamellar acellular bone in bases contains long traces of Sharpey's fibres.

Description. *Morphology.* Scales are tiny; the length of crown rarely reaches 0.5 mm. Crowns are flat, without an anterior downslope, isometrically rhomboidal or slightly longitudinally stretched. A minority have crowns wider than long (Fig. 6 E). Crowns do not overhang bases. The crown sculpture varies from almost smooth, without ridges but with short, shallow incisions along the anterior edges (Fig. 6 A, C), to short, uneven, rounded parallel ridgelets fading out in the anterior part or a little longer (Fig. 6 B, D). Some scales have stout, rounded, sub-radially placed ridges that widen anteriorly and fade out at one-third of crown length (Fig. 6 E). The rest of the crown surface is smooth except on rare scales which have shallow slits on the posteriormost part (Fig. 6 B) reflecting the growth zones. Scale necks are well developed but short, porose on the anterior or all faces (Fig. 6 E and B-C), with from two to four pores per side. Bases are rhomboidal, extending slightly beyond the crown on all sides, deeply convex, with the deepest part centrally.

Histology. Six lamellae in crowns of the superpositional growth are composed of simple acellular ?mesodentine. Durodentine is absent or possibly present superficially in only the two outer lamellae. A fine mesodentinal network of canaliculi (Fig. 6 I) is developed among the ascending vascular canals, of which the main branches are distinguished well only in the lower (neck) crown part. Horizontal longitudinal dentine canals are also interwoven with many small canaliculi. No lacunae are visible in crowns. Radial vascular canals, of comparable width to the ascending canals, are positioned over the flat-pyramidal base that is composed of fine-lamellar acellular bone pierced by traces of long Sharpey's fibres.

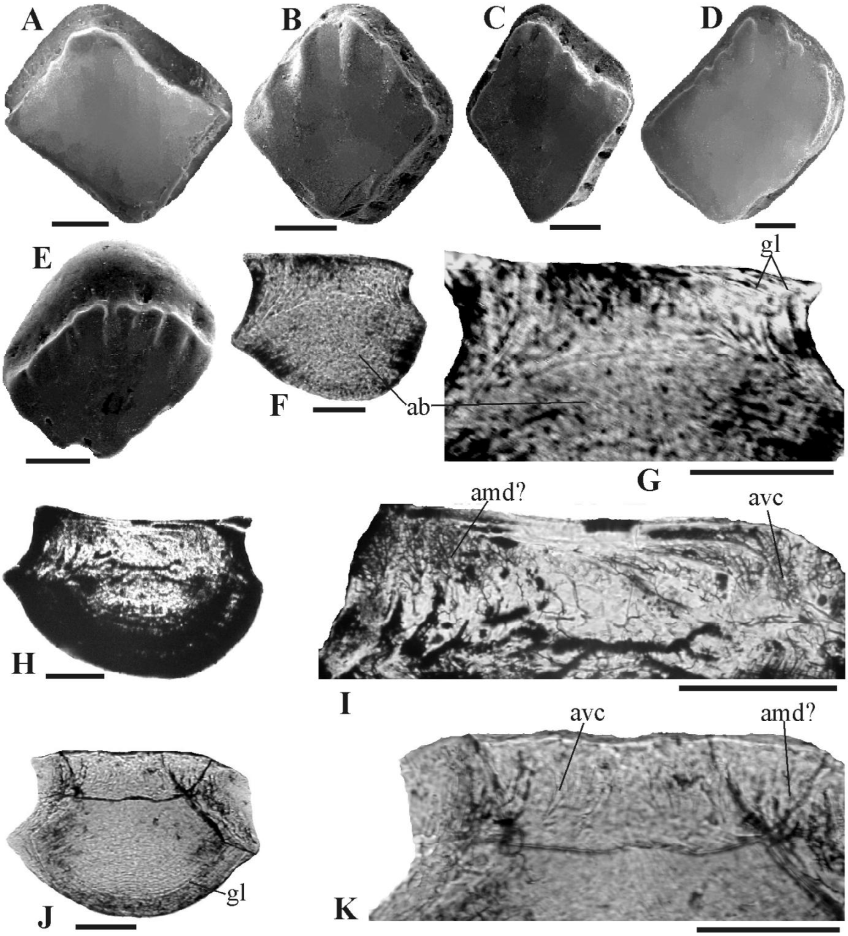

Fig. 6. Gomphonchus? minutus sp. nov. SEM micrographs of scales (A-E), crown views, anterior upwards, and thin section photos (F-K). A, LIGG 25-A-2580; B, holotype, LIGG 25-A-2581; C, LIGG 25-A-2582; D, LIGG 25-A-2583; E, LIGG 25-A-2584; F-I, vertical longitudinal sections of the holotype-like scales. F-G, thin section 3791. F, general view; G, crown and base portion at higher magnification; H-I, thin section 3790. H, general view; I, the main part of crown at higher magnification; J-K, vertical transverse section of scale. Thin section 3793. J, general view; K, the main part of crown and adjacent base strip at higher magnification. Lūžņi-4 borehole, depth 307.5 (A-E), 315.4 (H-I) and 319.9 (F-G and J-K) m. Přidoli, Minija Regional Stage, Varniai (A-E) and Šilalė (F-K) Beds of the Minija Formation. Abbreviations: ***ab***, acellular bone, ***amd?***, acellular mesodentine?, ***avc***, ascending vascular canal, ***gl***, growth lamella. Scale bars: 0.1 mm.

Remarks. Attribution of scales to the genus *Gomphonchus* is doubtful owing to the specified characters of the dentinal tissue in crowns, which differs distinctly from that of *G. sandelensis*, the genotype. The latter shows a classical *"Acanthodes"*-type histology: thick superficial durodentine in the outer crown part and orthodentine in the rest of the crown. The dentine has clear principal branches of ascending canals (Gross 1971, figs 20 A-E, 21 A-D) which branch differently compared to those in *G.? minutus*, and do not form a complicated network of canals of mesodentine-type. Horizontal canals in crowns of *G. sandelensis* form separate branches which are not interwoven with dentine canaliculi.

Scales of *Gomphonchus turnerae* (Burrow and Simpson 1995) from the Ludlow of northeastern Australia resemble those of *G? minutus* in several features - they are small scales, also with slits following the growth lines on the posterior crown surface. The preservation of the histological structure of *G? turnerae* scales is poor, but they also show an acellular base, and a crown tissue intermediate between non-lacunal mesodentine and orthodentine of the usual *Gomphonchus*-type.

Two further species of *Gomphonchus*, *G. mediocostatus* Vergoossen (1999 c, pl. 2, figs 18-23; see also Valiukevicius 1998, pl. 7, figs 23-24; pl. 8, figs 1-7) and *G. nordicus* Valiukevicius (2003 a, figs 23 N-P, 35 A-D) show *"Acanthodes"*-type histology in crowns concerning even small details, but their bases are formed of cellular bone. Sometimes the latter tissue does not differ from that in scales of the *"Nostolepis"*-type (Valiukevicius 2003 a, fig. 35 A-B). Based on sections of scales from the Lužni-4, *G. mediocostatus* also has cellular bone in scale bases. The outstanding dcharacteristic of *G. mediocostatus* is a pair of median crown ridges fading out half way along the crown, and shorter, often radial ridgelets that converge with the central ridges or one with another. Sometimes short ridges are uniform, sub-radial.

A variant of *G.? minutus* scales having more robust, rounded and anteriorly widened sub-radial anterior ridges (like in Fig. 6 E) resembles *G. volborthi* (Rohon 1893; also Lehman 1937, pl. 3, fig. 53; Vergoossen 1999 a, figs 10-12) in the general scale shape (flat crowns smaller than deep bases) and form of ridges (widened anteriormost edges), but differs in that they are not as marked and separated by wide, deep grooves forming deep incisions along the anterior crown edge as in *G. volborthi*.

Gomphonchus? sp. (Burrow *et al.* 1999, fig. 8 A-G) from the Pridoli of Arctic Canada, though different in scale shape (in my opinion, more *Acanthoides*-like), is comparable to the Lužni species in having short anterior ribs (though these are different in form) or being smooth, and in posterior slits on the crown surface which zig-zag are parallel to the growth zones. The histologic structure can not be compared as only a horizontal section of the upper crown of the Canadian *Gomphonchus?* sp. was figured giving little information.

Gomphonchus minicostatus and *G. abruptus* (Valiukevicius, 2003 d) provide controversial data in the problem of categorizing histologic structure and systematic position of this genus. *G. minicostatus* has scales ornamented with few parallel very flat anterior ridges and composed of orthodentine-like tissue in crowns and cellular bone in bases, whereas scales of *G. abruptus* are smooth, with vertically or obliquely cut posterior crown edges and have typical *"Acanthodes"*-type histology, containing acellular bone in bases and the crown orthodentine similar to that of *G. sandelensis.*

Some of the differences noted for *Gomphonchus* and *Gomphonchus?* possibly indicate that, based on the histological similarities, *G? minutus* and *G? turnerae* should be assigned to a new genus. The morphological and histological differences shown by "*Gomphonchus*" *hoppei* seem to support Vergoossen's (1999 c) creation of a new genus *Gomphonchoporus* for *G. hoppei* Gross.

Family PORACANTHODIDAE Vergoossen, 1997
Genus *Poracanthodes* Brotzen, 1934

Type species. *Poracanthodes punctatus* Brotzen, 1934. Upper Silurian, Pridoli, Ohesaare Regional Stage; Ohesaare Cliff, Saaremaa, Estonia.

Poracanthodes sulcatus sp. nov.
Fig.7 A-J

? 1986 *Poracanthodes punctatus*; Märss, pl. 32, fig. 2.
2003 c *Poracanthodes punctatus* var. "*sulcatus*"; Valiukevicius, p. 51.

Etymology. Named from the characteristic antero-median sulcus in scale crowns.

Holotype. LIGG 25-A-2613, flank scale (Fig. 7 A).

Type horizon. Garzde Beds of the Targale Formation, Pridoli, Upper Silurian.

Range. Upper Silurian, Pridoli, Targale Formation and its correlatives of Estonia.

Material. 42 scales.

Diagnosis. Punctatiform *Poracanthodes* having relatively large scales up to 1 mm long; pores on crowns are densely and randomly positioned; up to one-third of crown plate to the anterior is free of pores; well developed antero-median sulcus on crown; superficial winding "vermiculate" pore canals are visible through the thin transparent outer crown layer; histologic microstructure of *"Poracanthodes"*-type is identical to that in *Poracanthodes punctatus.*

Description. *Morphology.* Scale crowns are flat, without inclination, sub-rhomboidal, with an elongated and stretched posterior part. Their length is 0.36-1 mm; the larger varieties prevail. The part of the posterior crown overhanging base may reach one-third of crown length. The antero-median sulcus on crowns is shallow, kite-shaped (Fig. 7 A-B), with the deepest part projecting slightly in front of the rest of the anterior margins. Most of the numerous pores opening on the surface are placed randomly, or rarely in indistinct lines on the posterior crown part, following the growth zones. The anterior crown part (up to one-third of length) is usually free of pores, but the porose area can begin just behind the sulcus (Fig. 7 B). Superficial pore canals of a winding "vermiculate" form, directed obliquely upward at a low angle, are visible through the thin transparent outer layer of the posterior half of the crown, characterize the scales. Scale necks are high and porose on all faces. The anterior neck walls carry large pores basally, near to the base rim. They frequently open in vertical linear grooves that are visible all around the neck. Large radial pore canals open on the undersurface of the crown in the posterior part.

Histology. Six to eight lamellae of superpositional growth in scale crowns are composed of dentine with narrow, long, unbranched ascending and radial canals (Fig. 7 D-E). The porose posterior crown part contains only a few canals which are short, narrow, winding and mostly directed upwards. Durodentine is absent. Large radial pore canals, mostly eight, extend obliquely from the aperture on the posterior crown undersurface to the scale primordium (Fig. 7 E). They send ascending oblique, short, winding pore canals

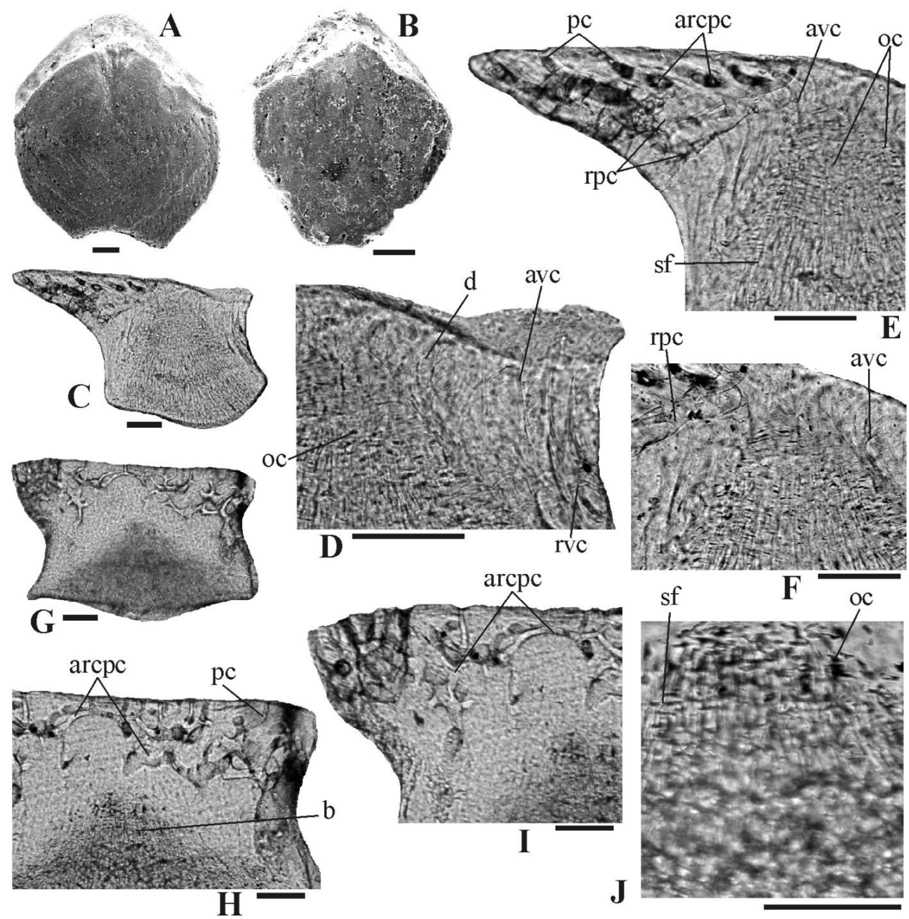

Fig. 7. Poracanthodes sulcatus sp. nov. SEM micrographs of scales (A-B), crown views, anterior upwards, and thin section photos (C-J). A, holotype, LIGG 25-A-2613; B, LIGG 25-A-2614; C-F, vertical longitudinal section of scale. Thin section 3776. C, general view; D, detail of the anterior crown part and base apex at higher magnification; E, magnified detail of the posterior crown part and base; F, detail of scale primordium at higher magnification; G-J, vertical transverse section of scale. Thin section 3790. G, general view; H, the right part of crown at higher magnification; I, the left part of crown and the adjacent base portion; J, detail of the base apex at higher magnification. Lūžņi-4 borehole, depth 176.5 m. Přidoli, Jūra Regional Stage, Lūžņi Beds of the Targale Formation. Abbreviations: ***arcpc*,** arcade pore canal, ***avc***, ascending vascular canal, ***b***, bone, ***d*,** dentine, ***oc***, osteocyte cavity, ***pc***, superficial pore canal, ***rpc***, radial pore canal, ***rvc*,** radial vascular canal, ***sf*,** Sharpey's fibre traces. Scale bars: 0.1 mm.

to open on the surface. The arcade pore canals (Fig. 7 H-I) are just as wide as the radial canals and connect the latter and superficial ones to form the complicated net piercing the crown tissue. The high-pyramidal base is composed of densely lamellar cellular bone incorporating varying numbers of osteocytes and pierced by long traces of Shapey's fibres. The osteocytes are densest in the apex of the pyramid, where they are largest and most clearly oriented along the almost horizontal growth lines, transforming into a *Stranggewebe*-like tissue(Fig. 7 E, F, J).

Remarks. This punctatiform *Poracanthodes* is closestly related to *P. punctatus* Brotzen discovered in many regions (Brotzen 1934; Lehman 1937; Gross 1947, 1956, 1971; Märss 1986; Valiukevicius 1998, 2003 a; Burrow *et al.* 1999; Vergoossen 1999 a, b, c; 2000; Burrow 2003). From typical *P. punctatus* it differs in having an antero-median sulcus, random arrangement of pores on crowns, and winding "vermiculate" oblique superficial pore canals seen through the thin transparent outer layer in the posterior crown part. The histological microstructure is generally uniform with the scales of *P. punctatus*.

Poracanthodes marssae sp. nov.

Fig. 8 A-E

1986 *Gomphonchus hoppei* (Gross); Märss, pl. 29, fig. 7.
2003 c *Gomphonchus boekschoteni* Vergoossen; Valiukevicius, p. 51.

Etymology. In honour of Dr T. Märss (Tallinn), the first discoverer of scales.

Holotype. LIGG 25-A-2559, flank scale (Fig. 8 A).

Type horizon. Venzava Beds of the Targale Formation, Pridoli, Upper Silurian.

Range. Targale Formation and its Estonian equivalent.

Material. 6 scales.

Diagnosis. Punctatiform *Poracanthodes* having scales with smooth, flat, pear-shaped crowns with a long, narrow posterior spine-like corner; symmetrical lateral projections in crowns placed at the beginning of its narrowing; very small pores visible on the posteriormost crown part; scale bases deep, protruding beyond crowns laterally and far anteriorly; necks of medium height and linearly porose on all faces; sharp keel on the posterior neck mirroring the crown shape. Scale crowns are composed of acellular mesodentine or dentine, and durodentine; ascending canals with rare branches; branches of radial canals extend down to the base; one? radial pore canal with few superficial pore openings running back from the scale primordium; high-pyramidal base is composed of dense, thin-lamellar cellular bone.

Description. *Morphology.* Scales are of medium to large size (crown length is 0.34-0.81 mm). Crown is smooth, flat, without inclination, pear-shaped, consisting of a rhomboidal main plate and very narrow, spine-like posterior part that may be as long as the main plate (Fig. 8 A). Two symmetrical lateral projections of triangular form occur in crowns of some scales at the place where the prominent narrowing of the crown begins (Fig. 8 C, see alo Märss, pl. 29, fig. 7). Crowns of most scales have a shallow medial concavity extending almost the entire length. A few ?linearly placed small pores, visible only at high magnification, open centrally on the posteriormost crown part (Fig. 8 B). Very deep rhomboidal bases protrude beyond crowns laterally and far anteriorly. The base is always deepest in advance of the crown. The base/neck junction is outlined by a clear anterior rim. Necks are well developed, of medium height and porose on all sides (Fig. 8 A). Pores are large, forming linear rows. A sharp vertical keel on the

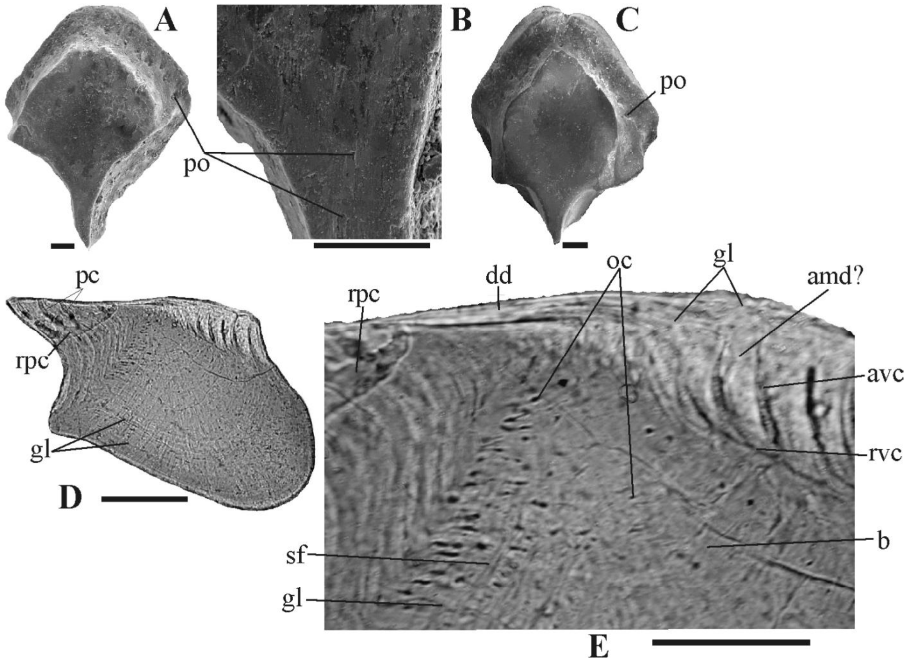

Fig. 8. *Poracanthodes marssae* sp. nov. SEM micrographs of scales (A-C), crown views, anterior upwards, and thin section photos (D-E). A, holotype, LIGG 25-A-2559; B, detail of the posterior crown part of the same scale at higher magnification; C, LIGG 25-A-2560; D-E, vertical longitudinal section of scale. Thin section 3757. D, general view; E, detail of the crown and base structure in the central part at higher magnification. Lūžņi-4 borehole, depth 210.4 (A-C) and 197.0 (D-E) m. Přidoli, Jūra Regional Stage, Garzde Beds of the Targale Formation. Abbreviations: ***amd?***, acellular mesodentine?, ***avc***, ascending vascular canal, ***b***, bone, ***dd*,** durodentine, ***gl***, growth lamella, ***oc***, osteocyte cavity, ***pc***, superficial pore canal, ***po***, pore, ***rpc***, radial pore canal, ***rvc***, radial vascular canal, ***sf*,** Sharpey's fibre traces. Scale bars: 0.1 mm.

posteriormost neck is characteristic (Fig. 8 A, C), thus the neck in this part distinctly follows the crown form.

Histology. Eight lamellae of superpositional growth in crowns are composed of acellular mesodentine or 'ortho'dentine, and durodentine superficially centrally, where lamellae are very thin (Fig. 8 E). Ascending canals positioned basally in each lamella are widest, with few branches in the lower neck part, whereas higher they are narrower, with more numerous branchings. Radial canals at the base/neck junction consist of long linear main branches sending side branchings, oriented along the growth lines, to the base. One radial pore canal pierces the posterior crown part behind the scale primordium (Fig. 8 D-E), with pore canals branching off and opening on the crown surface. The very high pyramidal base, which has minimized the thickness of the central crown part, is composed of dense cellular bone arranged in the finest growth lamellae. It contains medium numbers of large osteocyte cavities (more frequent in the topmost part) and long traces of Sharpey's fibres (Fig. 8 E).

Remarks. Crown pores were not visible on examination of scales under a binocular microscope, and they were considered possibly related to *Gomphonchus boekschoteni* Vergoossen (1999 c, pl. 2, figs 24-25; pl.3, figs 26-31). As for *Poracanthodes marssae*, most *G. boekschoteni* scales have large pores opening on all faces of the neck, pear-shaped crowns with strengthened and elongated posterior parts, and the similar neck characters including a prominent posterior keel. The grade of the base convexity and its position in advance of the crown in *P. marssae* were also within the range of the *G. boekschoteni* morphovarieties. Discovery of pores on crowns of *P. marssae* precluded assignment to *G. boekschoteni* and supported attribution of scales to the punctatiform *Poracanthodes.*

Occurrence. See Table.

Biostratigraphical potential of acanthodians

A single studied locality is insufficient to determine exact acanthodian zonality, but the Lužni-4 core fauna is interesting both in the subdivisional and correlational aspects of Silurian acanthodians in Latvia and the wider region. The series of the Ludlow and Pridoli is here acanthodian-based divided into eleven biostratigraphic **intervals** named by the chosen index species (Fig. 9, right column), and defined by the first occurrence of the nominative taxon. The intervals are neither interval zones nor partial range zones, because they occupy only some parts of the partial ranges of indices, until the next index appears in the sequence. This fact lowers the stratigraphic value of the interval units. However, the entry levels of the index or other first appearing taxa are significant to the regional record.

The most ancient acanthodian of the Lužni-4 borehole is a tiny indeterminable nostolepid (of the putative *N. striata*-group?) at the depth of 458 m (see Table).

The first, ***Nostolepis gracilis*** **interval** starts at the depth of 388 m, about 50 m below the top of the Ventspils Formation, that is coincident with the boundary of Ludlow/ Pridoli. The unit is based on only a few scales of *N. gracilis* at this single point, which has yielded no other taxon. The finds are significant (I have no doubts concerning their identification), because they mark the earliest occurrence of *N. gracilis* Gross (1947) ever defined in the Baltic. All prior data (Märss 1986, 1992, 1997, 2000; Märss *et al.* 1995, 1996) indicated that this species did not exist in the Ludlow, and it was introduced as the Pridolian index fossil of the Vertebrate Standard Scheme. Seemingly, its entry and the biozonal boundary must be lowered into the late Ludlow.

The next, ***Nostolepis latvica*** **sp. nov. interval** (338.6-306.2 m) is approximately attached to the Šilale Beds of the Minija Fm. The first occurrence of the index is about 1.3 m above the lower boundary of the Beds, and its range extends to the Venzava Bedss of the Targale Fm. This basal Pridolian acanthodian association is based on the entry of *Gomphonchus? minutus* sp. nov. and *Nostolepis* cf. *amplifica* as the most definitive species (for full list of taxa of this and further intervals see Fig. 9). Its correlational value is yet uncertain, as all three most significant taxa have not been discovered in Lithuania. Of note, *N. gracilis* starts its ongoing occurrences in samples in the upper part of the interval, above 319.9 m (see Table), about 20 m over the

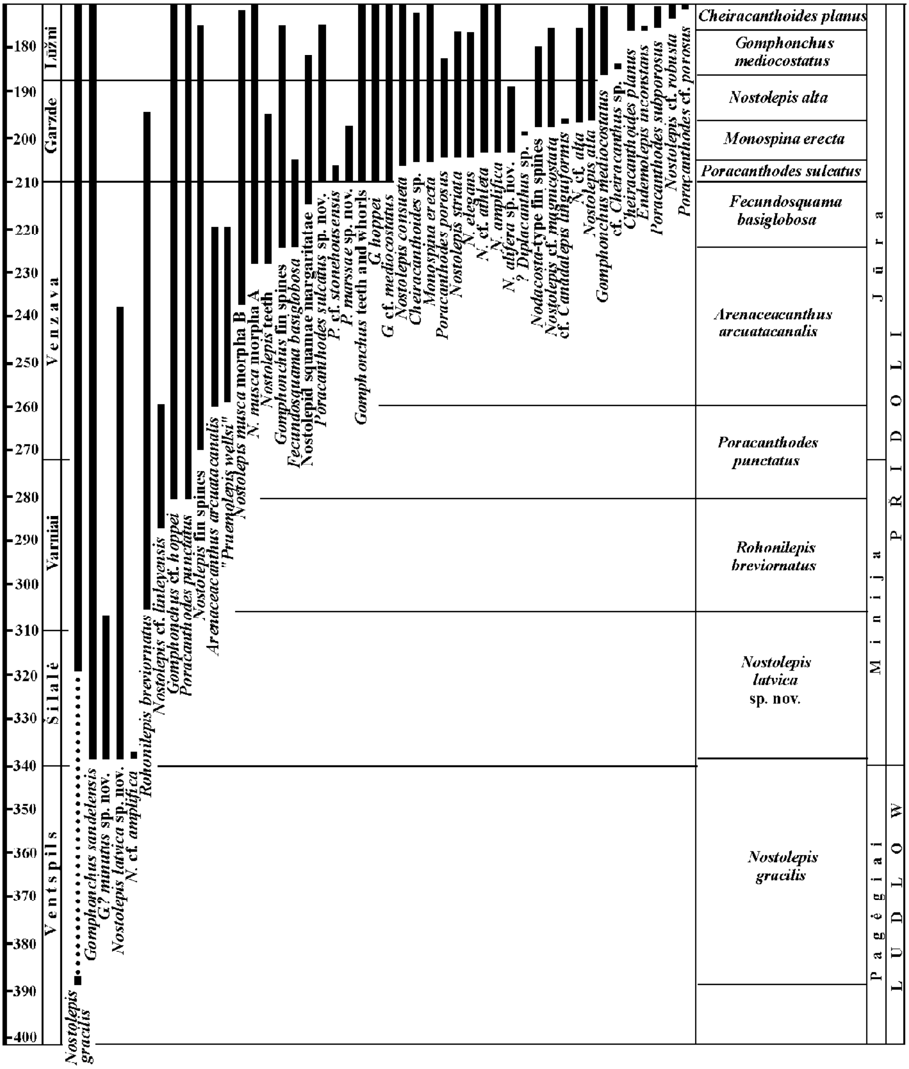

Fig. 9. Stratigraphic ranges of acanthodian taxa and designated biostratigraphic intervals through the late Ludlow and Přidoli of the Lūžņi-4 borehole.

Ludlow/Pridoli boundary, and perhaps this level corresponds to its entrance point into the sequence earlier referred to in publications.

The ***Rohonilepis breviornatus*** **interval** (306.2-280.3 m) embraces the main part of the Varniai Beds (Minija Fm.) and except for the nominative species (Valiukevicius 2004), includes one more characteristic acanthodian of short range in the Baltic, *Nostolepis* sp. cf. *N. linleyensis* (Miles and Märss 1999). *N. linleyensis* is certainly obtained at the Minija/Jura boundary in Lithuania, and at a nearly coeval horizon in the Lužni core (see Fig. 9). The stratigraphical potential of this taxon is high for the assignment of the biozonal unit and wider correlations, as in the type locality (Linley Brook near Much Wenlock, UK) it is only known from the Downton Castle Sandstone Fm., the lower part of Pridoli (Miles and Märss 1999).

Poracanthodes punctatus accompanied by *Gomphonchus* sp. cf. *G. hoppei* first appear at the same point, and distinguish the next interval (280.3-260 m). *P. punctatus* is the second acanthodian species of the Silurian Vertebrate Standard Scheme (SVSS), having its interval zone attached to the upper part of the Pridoli (Märss 1986, 1992, 1997, 2000; Märss *et al.* 1995, 1996). In the Lužni-4 core, the interval correlates to the Minija/Targale Fm. boundary beds, perhaps supporting the prior opinion on its first occurrence in Estonian localities. However, in Lithuania, particularly in the west area, which is characterized by the deepest marine sediments and most complete geological profile, it ranges for the entire Pridoli, in the Minija and Jura formations.

The ***Arenaceacanthus arcuatacanalis* interval** (260-223 m) comprises almost full ranges of the index species (Valiukevicius 2004) and *"Pruemolepis wellsi"* Vieth (1983) (the last being only a specialized morphological variety of nostolepids), and *Nostolepis musca* Valiukevicius (2003 b) appearing high at the top of the interval. Both most valuable taxa demonstrate distinctly later stratigraphical entry as compared to Lithuania, where *A. arcuatacanalis* appears in Wenlock? (with some doubt according to conodont dating of rocks) and *N. musca* in the Ludlow.

The next, ***Fecundosquama basiglobosa* interval** (223-210.8 m) is attached to the upper part of the Venzava Beds (Targale Fm.) and probably the previous showing a shorter range in comparison with Lithuania, where the nominative species makes the first occurrence in the Minija Fm. (Valiukevicius 2004). This species is of great interest in acanthodian biozonality as it is easy identifiable, with a restricted stratigraphic range and wide regional distribution. It is recognized in all Baltic republics and the Kaliningrad district of Russia. Of note, in this interval nostolepid *squamae margaritatae* (Gross 1971) first appear, possibly identifying a stratigraphic level useful for correlation over a wide area.

The Garzde and Lužni Beds of the Targale Fm. are connected with the flourishing time for acanthodians in the late Pridoli. The acanthodian associations (likely as in the whole Baltic region) have shorter ranges, and the new indices and characteristic taxa reach maximum numbers here and appear with the highest frequency.

The short-ranging ***Poracanthodes sulcatus* sp. nov. interval** (210.8-202 m) is distinguished at the base of Garzde Beds and marks a sequential dominance of ischnacanthid acanthodians in the taxa-rich associations. Alongside the index species, it is marked by the entry of two more *Poracanthodes, P.* cf. *stonehousensis* (*sensu* Vergoossen 2000) and *P. marssae* sp. nov., and also two representatives of *Gomphonchus, G.* cf. *mediocostatus* Vergoossen (1999 c) and *G. hoppei* (Gross 1947). Poracanthodids are not yet defined in Lithuania, but the stratigraphical level may be approximated by the representatives of *Gomphonchus* occurring in the Kelme Beds of the Jura Fm.

The ***Monospina erecta* interval** (202-196.5 m) marks an essential renewal of acanthodian associations with the entering of most valuable *Monospina erecta* Valiukevicius (2003 d), *Nostolepis elegans* (Brotzen 1934), *N. alifera* sp. nov., *N. amplifica* Valiukevicius (2003 b) and *?Diplacanthus* sp., whereas the overlying ***Nostolepis alta* interval** (196.5-186 m) yields only the index species of significance for biozonal purposes. *N. alta* is the topmost Pridolian vertebrate zonal fossil in the SVSS. However, a recent study, which includes the Lužni and Lithuanian boreholes, provides material (in preparation) for the revision of acanthodian zonality in this part. In the Lužni-4, ***Gomphonchus mediocostatus*** and ***Cheiracanthoides planus*** **intervals** are defined with the boundary between them at the depth of 176.3 m. In west Lithuania, all taxa of these two intervals (listed in Fig. 9) are recognized also, but the Pridolian zonal chart is captioned by the two other, presumedly younger associations of acanthodians, *Vesperalia perplexa* and *Endemolepis inconstans* characterizing the topmost profile part that appears absent? in Lužni-4.

Conclusions

1. Detailed results obtained from the well sampled Lužni-4 core are very useful for a further regional acanthodian study of the Baltic Silurian from taxonomical, biozonal, correlational, palaeogeographical, and palaeobiogeographical aspects.
2. Eleven biostratigraphic intervals of acanthodians proposed may form the basis for the forthcoming zonal scheme of Latvia following the reappraisal of the available sampled acanthodian collections (Ventspils-3 D, Kolka-54, *etc.* boreholes).
3. Lužni-4 core contributes to the correction of previous records of the regional occurrence of stratigraphically significant taxa, e.g., zonal *Nostolepis gracilis*, for which the range must be extended down to the Ludlow.
4. Most acanthodians are represented here by shortened stratigraphic ranges that are mainly caused by their later entry into the sequence as compared with Lithuania.
5. Nevertheless, some taxa, such as *Rohonilepis breviornatus, Nostolepis* (cf.) *linleyensis, Fecundosquama basiglobosa* and many others of the late Pridoli, are of great interest as the potential indices for more detailed regional biozonality; some are applicable for wider interregional correlations.
6. Lužni-4 core contributes to the understanding of regional taxonomic diversity and the facies dependence of Silurian acanthodians, e.g., the newly described species *Gomphonchus? minutus, Nostolepis latvica, N. alifera, Poracanthodes sulcatus, P. marssae* are not found in Lithuania.

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Silūra akantožu kompleksi no urbuma Lūžņi-4 (Latvija)

JUOZAS VAĻUKEVIČS

Urbumā Lūžņi-4 atrastās akantodes aptver apmēram 50 sugas un dermālo elementu formas, kuras izplatītas no Ludlovas apakšdaļas līdz Pršidolas nodaļas pašai augšai. Raksturoti 11 akantožu kompleksi, kas klasificēti kā vadfosīliju izplatības intervāli (=daļējas izplatības intervāli). Parādīti to taksonu izplatības intervāli, kuri ir raksturīgi vietējām un reģionālajām stratigrāfiskām vienībām, izdalītas nozīmīgākās sugas. Pirmā *Nostolepis gracilis* parādīšanās Baltijas griezumā atzīmēta vēlajā Ludlovas epohā, agrākā laikā nekā bijis zināms iepriekš. Dažiem taksoniem, tādiem kā *Nostolepis latvica* sp. nov., *N. alifera* sp. nov., *N.* cf. *linleyensis*, *Rohonilepis breviornatus, Arenaceacanthus arcuatacanalis, Fecundosquama basiglobosa, Poracanthodes marssae* sp. nov., ir liels potenciāls biozonēšanā, bet *Nostolepis linleyensis, Gomphonchus mediocostatus, Monospina erecta, Poracanthodes* spp., ir vērtīgi plašām reģionālām korelācijām. Īsmūžīgos akantožu kompleksos no Lūžņi-4 urbuma Pršidolas augšējās daļas trūkst dažu taksonu, kas raksturīgi dziļākā baseina Jūras svītai no Lietuvas dienvidrietumu daļas. Iespējams, tas norāda uz nepilnīgu griezumu šajā baseina daļā.

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Evidence of biostratigraphic correlations within the Wood Bay Formation (Lower Devonian, Spitsbergen)

Some paleontological results of the 1969 french expedition with geological considerations

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Until now, geologists and paleontologists who study the Wood Bay Formation (Lower Devonian, Spitsbergen) have been using different stratigraphic tables. The geological works are based on a lithostratigraphic scale defined in the Dicksonfjord–Austfjord area while paleontological works are based on a biostratigraphic scale established in the Woodfjord area.

A large amount of palaeontological material was collected in both cited regions during the 1969 French mission (CNRS-MNHN). This material is here used to establish the first correlation between the palaeontological divisions and the geological ones. Finally equivalencies are proposed as follows: the Sigurdfjellet and Kapp Kjeldsen faunal divisions are lateral equivalents of the Austfjord Member, while the Keltiefjellet and Stjørdalen divisions are equivalent to the Dicksonfjord Member at the Dicksonfjord-Austfjord area.

Introduction

The Wood Bay Formation (Lower Devonian, Spitsbergen) is commonly divided, for palaeontologists, into four faunal divisions: Sigurdfjellet, Kapp Kjeldsen, Keltiefjellet and Stjørdalen (Føyn and Heintz 1943; Friend *et al.* 1966; Goujet 1984; Fig. 1). These divisions are characterised by vertebrate associations, mainly pteraspidiform heterostracans (Friend et al. 1966). Recent works have increased our knowledge of the Wood Bay Formation biodiversity (Blieck *et al.* 1987; Pernegre 2002, 2003, 2004; and a still unpublished revision of the genus *Gigantaspis*).

An extensive study of material collected during the 1969 French expedition (CNRS-MNHN), makes it possible to establish biostratigraphic interpretations and correlations between the field localities. We establish here that two localities (from Mount Sigurd) bracket the Sigurdfjellet – Kapp Kjeldsen boundary. Some others (from Mount Wagner) characterise the boundary between the Kapp Kjeldsen - Keltiefjellet faunal divisions.

From these preceding data, a new scheme of correlation is proposed between the Woodfjord area, divided into biostratigraphic units (Blieck and Cloutier 2000), and the Dicksonfjord-Austfjord area, divided into stratigraphic units (Blieck and Cloutier 2000).

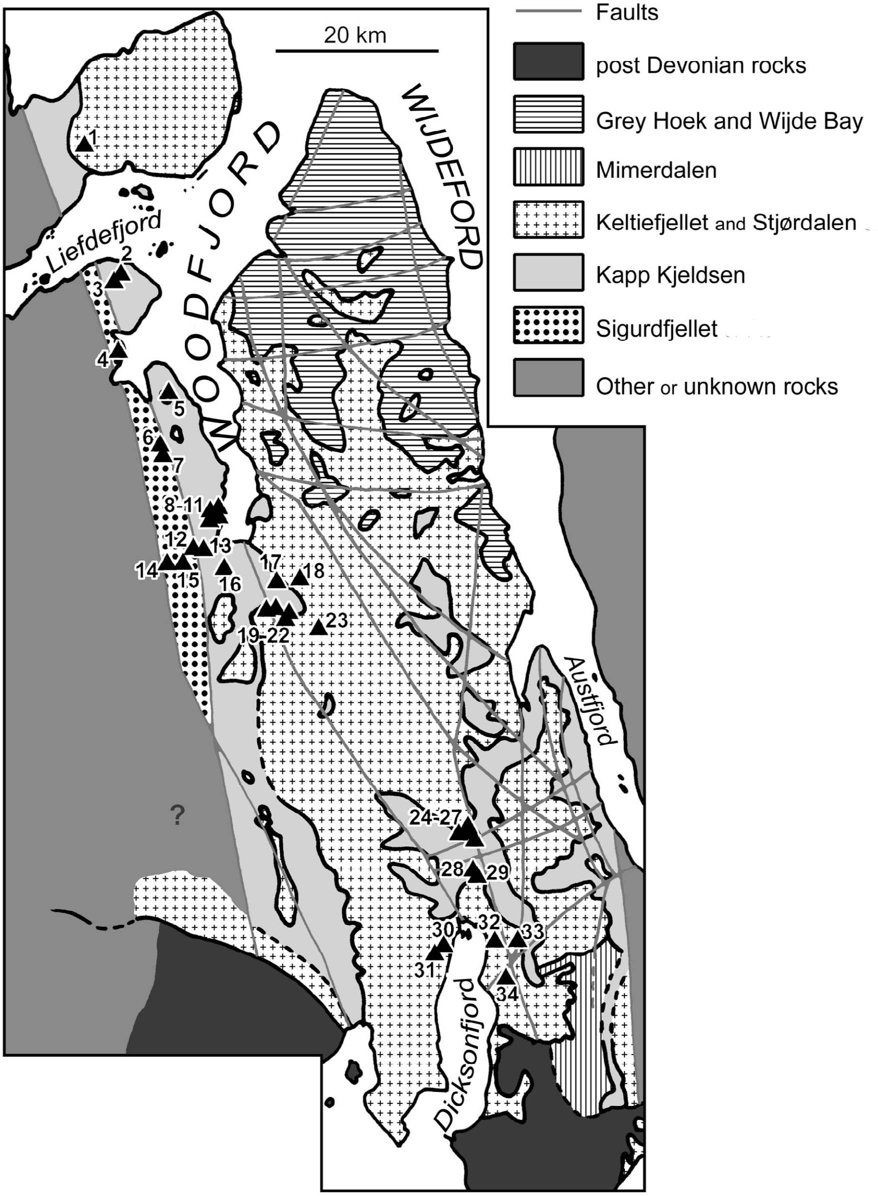

Fig.1. Geological map of the north Devonian graben. Detail of the Wood Bay Formation stratigraphy. Scale: 20 km. After Friend and Moody-Stuart 1972; Murashov and Mokin 1976; Goujet 1984. Locality map of the studied field sites. **1**: A_{16}; **2**: BL; **3**: BO; **4**: A_{11}; **5**: BH; **6**: BJ; **7**: Bi; **8-11**: $A_{1\text{-}4}$; **12**: B'I; **13**: BI; **14**: BII; **15**: BIV; **16**: BC; **17**: BG; **18**: BE; **19**: BD; **20-22**: $H_{1\text{-}3}$; **23**: C_4; **24-26**: $BR_{1\text{-}3}$; **27**: BS; **28**: BΔ; **29**: BΔ'; **30**: C_{18}; **31**: C_{17}; **32**: BT; **33**: C_{19}; **34**: BY.

This work is important to clarify the Wood Bay Formation subdivision. It is presently different for geologists, using the stratigraphic units, and palaeontologists who use the biostratigraphic units.

Brief history

A Wood Bay Formation stratigraphy was first proposed by Føyn and Heintz (1943). They divided the formation into three divisions (Kapp Kjeldsen, Lykta, and Stjørdalen) mainly based on the differing suites of pteraspidiforms.

Friend (1961) confirmed these divisions for the Woodfjord area. He tried to characterise them from a geological point of view based on colour, grain size, and alternations of beds. However, he replaced the Lykta name by Keltiefjellet. At the same time Friend proposed another geological scale for the Dicksonfjord-Austfjord region where he described two different units: the Austfjord Sandstone and Dicksonfjord Sandstone (Friend 1961, p. 90-92).

Friend *et al.* (1966) pointed out that the previous geological considerations for the Woodfjord area were unsatisfactory. They came back to the concept of faunal divisions, redefining them on the basis of their content of pteraspidiforms and placoderms. They also revised the lithostratigraphic units from the Dicksonfjord-Austfjord area and renamed them as members (Friend *et al.* 1966, p. 61). Finally, they proposed possible stratigraphic correlations between the Woodfjord and Austfjord-Dicksonfjord regions, without any faunal considerations.

The last revision of the biostratigraphy of the Wood Bay Formation was done by Goujet (1984). He enhanced it with the introduction of a new basal faunal division, the Sigurdfjellet, characterised by its peculiar but at that time undescribed faunal content.

Since the first subdivision of the Wood Bay Formation by Føyn and Heintz (1943), the ranges of the pteraspidiforms have been used as data for differentiation of the divisions. This choice is dictated by their abundance in terms of specimens and their easy recognition in the field outcrops (Føyn and Heintz 1943; Heintz 1962, 1967). Moreover their diversity is sufficient to characterise the divisions with successions of the different species (Pernegre 2002, 2003, and unpublished revision of the genus *Gigantaspis*).

The other known fauna possess less value for such a work due to the high diversity of forms, as for e.g. the osteostracans: 16 genera with 40 described species (Janvier 1985). Moreover, each taxon is only represented by a restricted number of specimens (often one specimen only), so it is impossible to establish precise range extensions. The placoderms are well represented (Heintz 1929; Goujet 1973, 1984) in terms of occurrence and specimens available, but many forms remain undescribed and others should be redescribed. At the same time, no global biostratigraphic works have been done with the placoderms. Therefore, our biostratigraphic correlations are mainly based, as for preceding authors, on the pteraspidiform associations.

Evidence for correlation in the Wood Bay Formation

Woodfjord area (Sigurdfjellet, Kapp Kjeldsen, Keltiefjellet, and Stjørdalen faunal divisions)

The major part of the material collected in 1969 comes from the Woodfjord area (Fig. 1). The four faunal divisions were described in this region and are used by paleontologists (Føyn and Heintz 1943; Goujet 1984). With information taken from recent works (Goujet 1984; Janvier 1985; Blieck *et al.* 1987; Pernegre 2002, 2003, 2004, and still unpublished data), we can now accurately correlate the field localities after identification of their faunal content.

By using their identified fauna (pteraspidiforms, placoderms and osteostracans), we can classify the field localities noted as **BIV, BII, Bi, BJ** and **A_{11}** (Fig. 1) into the Sigurdfjellet faunal division. The **BIV** locality is the richest collected site of the 1969 French mission and includes *Doryaspis arctica*, *Gigantaspis* sp. nov. and *Xylaspis prima* (pteraspidiforms) in association with *Sigaspis lepidophora*, *Arctaspis* sp. (placoderms) and *Boreaspis rostrata*, *B. intermedia*, *B. ceratops*, *B. ginsburi*, *Cephalaspis curta*, *Norselaspis glacialis*, and *Axinaspis whitei* (osteostracans). The **BII** samples contain *Doryaspis arctica*, *Gigantaspis* sp. nov., *Xylaspis prima* and *Arctaspis* sp. *Doryaspis arctica*, *Gigantaspis* sp. nov. and *Diademaspis* sp. are identified in the **Bi** locality. We only find *Gigantaspis* sp. nov. in our material from the **BJ** site and in the **A_{11}** area we only identify *Xylaspis prima*. The occurrence of these two last species, however, is sufficient to indicate the Sigurdfjellet faunal division (Fig. 2).

With the two close **BI'** and **BI** localities (Fig. 1), we can identify the Sigurdfjellet - Kapp Kjeldsen boundary. *Doryaspis arctica* and *Gigantaspis* sp. nov. are found in the **BI'** samples, two associated species which indicate the Sigurdfjellet faunal division. In the **BI** samples we identify *Gigantaspis isachseni*, the characteristic pteraspidiform of the Kapp Kjeldsen division. In conclusion, the Sigurdfjellet – Kapp Kjeldsen boundary is localised somewhere between these two close localities. This implies a quite rapid boundary without important transitional beds and fauna.

The characteristic fauna of the Kapp Kjeldsen division is identified in the **A_{1-4}, BO** and **BL** localities (Fig. 1). *Gigantaspis isachseni*, *Gigantaspis bocki* and *Doryaspis arctica* are found in the **A_{1-4}** and **BL** samples. The **BO** material contains *Gigantaspis isachseni* and *Doryaspis arctica* in association with *Diademaspis poplinae* and *Meteoraspis moythomasi* (osteostracans). *Gigantaspis isachseni* is considered to be a guide fossil for the Kapp Kjeldsen division (Fig. 2), and its identification alone is sufficient to characterise this division.

The Kapp Kjeldsen – Keltiefjellet boundary is exemplified in the Woodfjordalen, between the mounts Vaktaren and Wagner. In this region, many localities have been visited (**H_{1-3}**, **BG**, **BC** and **BE**, **C_4**, and **BD**; Fig. 1). The faunal identifications of the collected samples do not highlight a clear and precise boundary as for the Sigurdfjellet and Kapp Kjeldsen divisions. The fauna suggests a transitional boundary between Kapp Kjeldsen and Keltiefjellet faunal divisions.

In the **H_{1-3}** locality we find *Gigantaspis isachseni*, a huge unidentified *Doryaspis* sp. 1 (plate dimensions twice those of *Doryaspis nathorsti*) and another *Doryaspis*

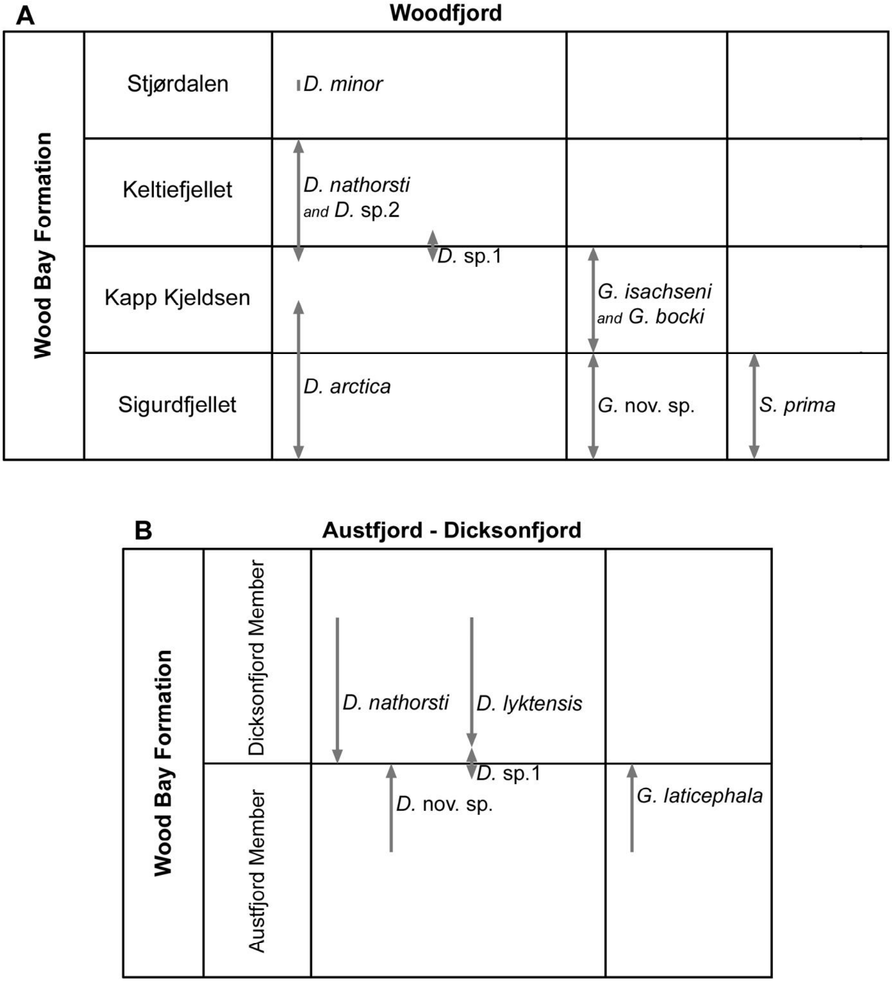

Fig.2. A, Wood Bay Formation biostratigraphical scale. It presents the distribution of the Pteraspidiformes in the Woodfjord region. B, Wood Bay Formation lithological scale. The distribution of the Pteraspidiformes into the Austfjord-Dicksonfjord region is shown.

sp. 2 which presents some *Doryaspis nathorsti* affinities. Daniel Goujet has identified *Heintzosteus* sp., and *Gigantaspis isachseni* and *Arctolepis* sp. are identified in the samples from the **BG** locality. The **BC** site contains *Gigantaspis* sp. and the same *Doryaspis* sp. 2 as in **H**$_{1\text{-}3}$. These three localities are considered to be members of the Kapp Kjeldsen division due to the occurrence of *Gigantaspis isachseni*. The presence of *Doryaspis* sp. 2 and of the identified placoderms suggests a very high position in the division, close to the top, because of the similarity between *Doryaspis* sp. 2 and *Doryaspis nathorsti* (present only in the upper division). It is the same for the placoderm *Arctolepis*, a genus which presents its acme in the upper Keltiefjellet faunal division.

The fauna of the **BE** locality is composed of *Doryaspis* sp. 1 and *Doryaspis* sp. 2 for the pteraspidiforms and *Arctolepis decipiens* and *Arctaspis maxima* as representatives of placoderms. In the **C4** site we recognise the same pteraspidiforms as in the **BE**, associated with *Arctolepis decipiens* and an osteostracans, *Meteoraspis lanternaria*. The faunal list of the **BD** samples comprises *Doryaspis* sp. 1, *Doryaspis* sp. 2, *Arctaspis maxima* and *Arctolepis* sp. Those three field localities belong to the Keltiefjellet basal layers due to the occurrence of *Arctolepis decipiens*, *Arctaspis maxima* and *Doryaspis* sp. 1. So, these localities follow stratigraphically the preceding Kapp Kjeldsen ones (**H**$_{1-3}$**, BG, BC**).

In conclusion, the new huge *Doryaspis* species can be used as a guide fossil for the transitional beds of the Kapp Kjeldsen - Keltiefjellet boundary (Fig. 2).

The characteristic Keltiefjellet pteraspidiform fauna is identified in the samples from the **A**$_{16}$ and **BH** localities (Fig. 1). The occurrence of *Doryaspis nathorsti* in all this material suggests this interpretation. We establish the presence of *Arctaspis* sp. in both localities and of *Arctolepis decipiens* in the **BH** site, thus confirming the Keltiefjellet age. Two osteostracans have been identified in the material from the **A**$_{16}$ locality, *Meteoraspis oblongata* and *Meteoraspis* sp. The presence of *Doryaspis nathorsti* associated with *Arctolepis decipiens* is sufficient to characterise the Keltiefjellet faunal division (Fig. 2).

Dicksonfjord and Austfjord area (Austfjorden and Dicksonfjorden Members) and comparison with the Woodfjord localities and fauna

Other Spitsbergen material is available in the paleontological collections of the Muséum National d'Histoire Naturelle, Paris. Part of it was collected in 1964 by J. P. Lehman at Grønhorgdalen and another part was collected in the Dicksonfjord-Austfjord area during the 1969 French expedition (Fig. 1).

Friend (1961) defines in this region two stratigraphic units based on their lithologic facies. The Austfjord Sandstone is composed of green-grey sandstones and conglomerates with intraclasts (Friend 1961). It is presented as the basal unit. The overlying unit named the Dicksonfjord Sandstone is similar lithologically to the upper northern divisions (red siltstones and sandstones). These units were revised by Friend *et al.* (1966) who renamed them as members. They considered the Austfjord Member as a lateral equivalent of the Kapp Kjeldsen faunal division and the Dicksonfjord Member as strictly similar to the Keltiefjellet and Stjørdalen divisions. This interpretation is only based on lithological conclusions without any faunal considerations.

We know three localities from the Austfjord Member: **BΔ, BΔ',** and **BS** (Fig. 1). We find in our samples from **BΔ** and **BΔ'** the pteraspidiforms *Doryaspis* sp. nov. and *Gigantaspis laticephala*, in association with the well preserved placoderms *Dicksonosteus arcticus*, *Heintzosteus brevis*, and *Lehmanosteus hyperboreus* (Goujet 1984). The same *Doryaspis* species with *Nectaspis areolata* and *Hildenaspis digitalis* is present in the **BS** samples. The fauna identified in this member (Fig. 2) is easily correlateable with the equivalent one of the Sigurdfjellet - Kapp Kjeldsen divisions (mainly the association *Doryaspis* – *Gigantaspis* with the occurrence of *Heintzosteus* for Kapp Kjeldsen). This faunal correlation confirms the Friend *et al.* (1966) geological

Table. Localities with vertebrate fossils and their stratigraphic position within the Wood Bay Formation

Wood Bay Formation	Stjordalen		C_{17-19} BY BT BR_{1-3}	Dicksonfjord Member
	Keltiefjellet	A_{16} BH BE C_4 BD		
	Kapp Kjeldsen	H_{1-3} BG BC A_{1-4} BO BL BI	BS BΔ BΔ'	Austfjord Member
	Sigurdfjellet	B'I BIV BII Bi BJ A_{11}		

correlations. Moreover, we suggest a high position in the member for the **BS** locality due to the occurrence of the osteostracan *Nectaspis areolata* (Janvier 1981).

The fauna from the base of the Austfjord Member remains unknown due to insufficient visited localities. So we cannot conclude if the peculiar fauna of the northern Sigurdfjellet faunal division possesses an equivalent at the base of the Austfjord member. However, the association of pteraspidiforms genera present in the southern member allows a possible equivalency with both Sigurdfjellet and Kapp Kjeldsen (Fig. 3).

The boundary between the Austfjord Member and Dicksonfjord Member is defined as in the Woodfjord localities. We identify in the **BR**$_{1-3}$ samples the huge *Doryaspis* sp.1 in association with *Meteoraspis lanternaria* (osteostracan) and *Arctaspis maxima* (placoderm). The occurrence of *Arctaspis maxima* suggests this locality should be placed in the Dicksonfjord Member. The presence of the huge *Doryaspis* sp.1 in this area is interpreted as for the northern localities and indicates the extreme base of the considered member (Fig. 2). According to a faunistic point of view, the Austfjord – Dicksonfjord Member boundary corresponds to the Kapp Kjeldsen – Keltiefjellet one, due to the occurrence of *Doryaspis* sp.1 in both cases (Fig. 3).

The Dicksonfjord Member is found at the **C**$_{17-19}$, **BY** and **BT** sites (Fig. 1). *Doryaspis nathorsti* and *Doryaspis lyktensis* are found in all the localities. They are associated with *Diademaspis poplinae* (osteostracan) in the **C18** site, with *Arctaspis maxima* in **C**$_{19}$, and with *Nectaspis peltata* and *Arctolepis decipiens* (placoderms) in the **BY** locality.

A great part of the fauna contained in the samples appears as strictly similar to what is found in the northern Keltiefjellet faunal division. This confirms the Friend et al. (1966) geological conclusions. We conclude that the Dicksonfjord Member is equivalent to the Keltiefjellet division. This interpretation is well supported by the occurrence of *Doryaspis nathorsti* and *Arctolepis decipiens* in both divisions (Fig. 3).

Conclusion

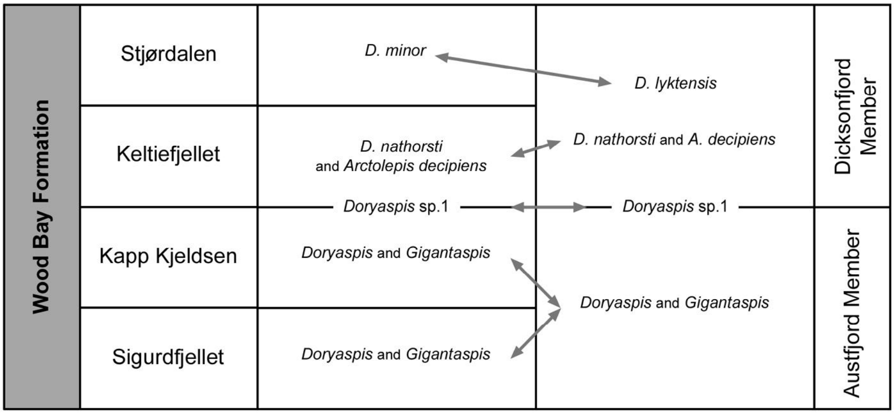

Fig.3. Comparison of the fauna present in the Woodfjord and Austfjord-Dicksonfjord areas. Implied correlation between biostratigraphic and lithologic scales.

The new data on the Wood Bay fauna allows us to propose the first biostratigraphic correlations between the two existing stratigraphic scales. On one hand, palaeontologists divide the Wood Bay Formation into four faunal divisions. On the other hand, geologists divide it into two members.

We have identified the pteraspidiform and placoderm content of the collected localities from the 1969 French mission. Each of them is located geographically (Woodfjord or Austfjord-Dicksonfjord region) and stratigraphically (faunal division or member).

Therefore, biostratigraphic correlations are made. The northern Sigurdfjellet and Kapp Kjeldsen faunal divisions are equivalent to the southern Austfjord Member. This is based on their *Doryaspis – Gigantaspis* association (Fig. 2). The southern Dicksonfjord Member is correlated with the northern Keltiefjellet faunal division due to the common occurrence of *Doryaspis nathorsti* and *Arctolepis decipiens* (Fig. 2).

The northern Stjørdalen faunal division is not clearly established due to the lack of recent faunal information. However the occurrence of *Doryaspis minor* (N. Heintz 1960) in this division is considered as equivalent of the presence of *Doryaspis lyktensis* in the southern Dicksonfjord Member (Fig. 2).

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Vūdbejas formācijas biostratigrāfiskā korelācija (apakšējais devons, Špicbergena)

Daži 1969. gada franču ekspedīcijas rezultāti

VINCENTS PERNĒ un VINCENTS DJUPRĒ

Līdz šim tie ģeologi un paleontologi, kas pētī Vūdbejas formāciju (apakšējais devons, Špicbergena), izmanto atšķirīgas stratigrāfiskās skalas. Ģeoloģijā tiek izmantota litostratigrāfisko vienību shēma, kas izstrādāta pēc griezumiem Diksonfjorda-Austfjorda rajonā, turpretī paleontoloģiskos pētījumos izmanto biostratigrāfisko shēmu pēc griezumiem Vudfjorda rajonā.

Plašu paleontoloģisko materiālu abos minētajos rajonos ieguva 1969. gada Francijas ekspedīcijas (CNRS-MNHN) dalībnieki. Šis materiāls izmantots šajā darbā pirmajai paleontoloģisko un litostratigrāfisko vienību korelēšanai. Ir piedāvāts šāds korelācijas variants: Sigurdfjelletas un Kapkjeldsenas faunas vienības ir Austfjorda ridas laterālie ekvivalenti, bet Keltiefjelletas un Stjerdalenas vienības Diksonfjorda-Austfjorda rajonā ir ekvivalentas Diksonfjorda ridai.

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

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

Key words: Central Asia, Lower Silurian, Thelodonti.

Introduction

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

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

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

Systematic palaeontology

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

Talimaalepis gen. nov.

Etymology. In honour of Habil. Dr. Valentina Karatajūtė-Talimaa; *lepis* (Greek), scale.
Type species. *Talimaalepis rimae* gen. et sp. nov.
Diagnosis. As for type species.
Remarks. The description of the new taxon is based on the isolated microremains of exoskeleton, the dentine scales. It has intermediate position between the two thelodont genera – *Loganellia* (Fam. Loganellidae) and *Helenolepis* (Fam. Phlebolepidae). *Talimaalepis* possesses one single pulp canal, which is typical to genus *Loganellia*. Though well-defined thick dentine canals opened into pulp canal are very specific to genus *Helenolepis*.

Talimaalepis rimae sp. nov.

Figs 1-3

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

Etymology. *Rima, ae*, f. (Latin) meaning a gap, a slot. Name emphasizes the type species of genus *Talimaalepis* gen. nov. placed between thelodont genera *Loganellia* and *Helenolepis*.
Holotype. LGI M-1/224, cephalo-pectoral scale, Fig. 1 herein.
Type locality and stratigraphy. South-east slope of mount Chargat, 80 km north from lake Khara-Ubs-Nuur, Lake Basin outcrop No 21, north-west Mongolia; Chargat Formation, Salhit Regional Stage, upper Llandovery – Wenlock, Silurian.
Material. About 800 scales stored in the Institute of Geology and Geography, Lithuania; collection numbers LGI M-1 and LGI T.
Diagnosis. Elongated scales of medium size, up to 1.4 mm long, 0.6 – 0.8 mm on the average. The elongate and flattened crown of most common cephalo-pectoral scales divided into main central and paired shorter lateral parts. Crown surface with longitudinal sculpture composed of central groove and lateral pairs of ribs. Wedge-shape base usually

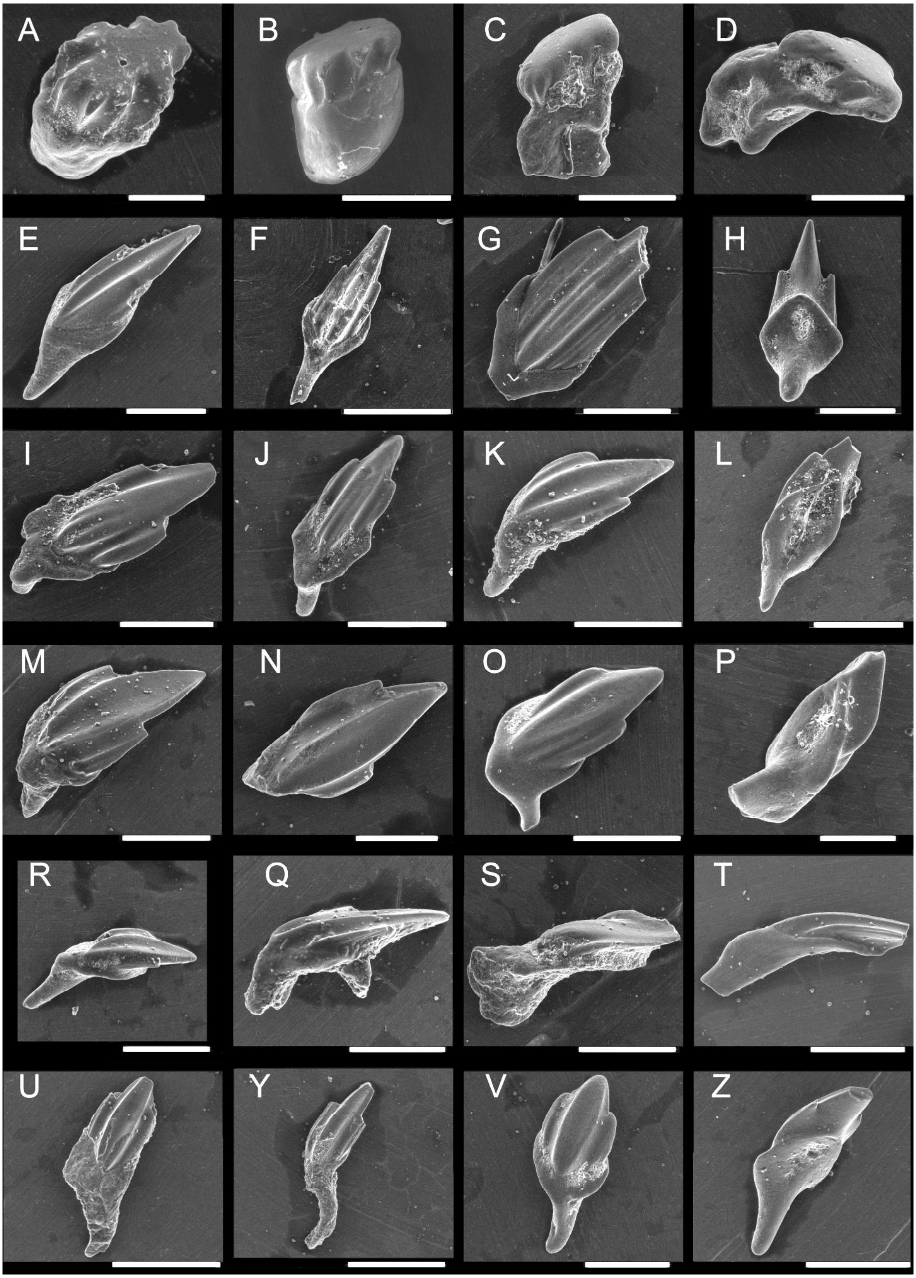

Fig. 1. *Talimaalepis rimae* gen. et sp. nov. scale morphological varieties. Lake Basin outcrop No 21, north west Mongolia; Chargat Formation, Salhit Regional Stage, Upper Llandovery – Wenlock, Lower Silurian. **A**, LGI M-1/201, oral scale; **B**, LGI M-1/254, oral scale; **C**, LGI M-1/203, oral scale;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

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

Description.

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

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

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

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

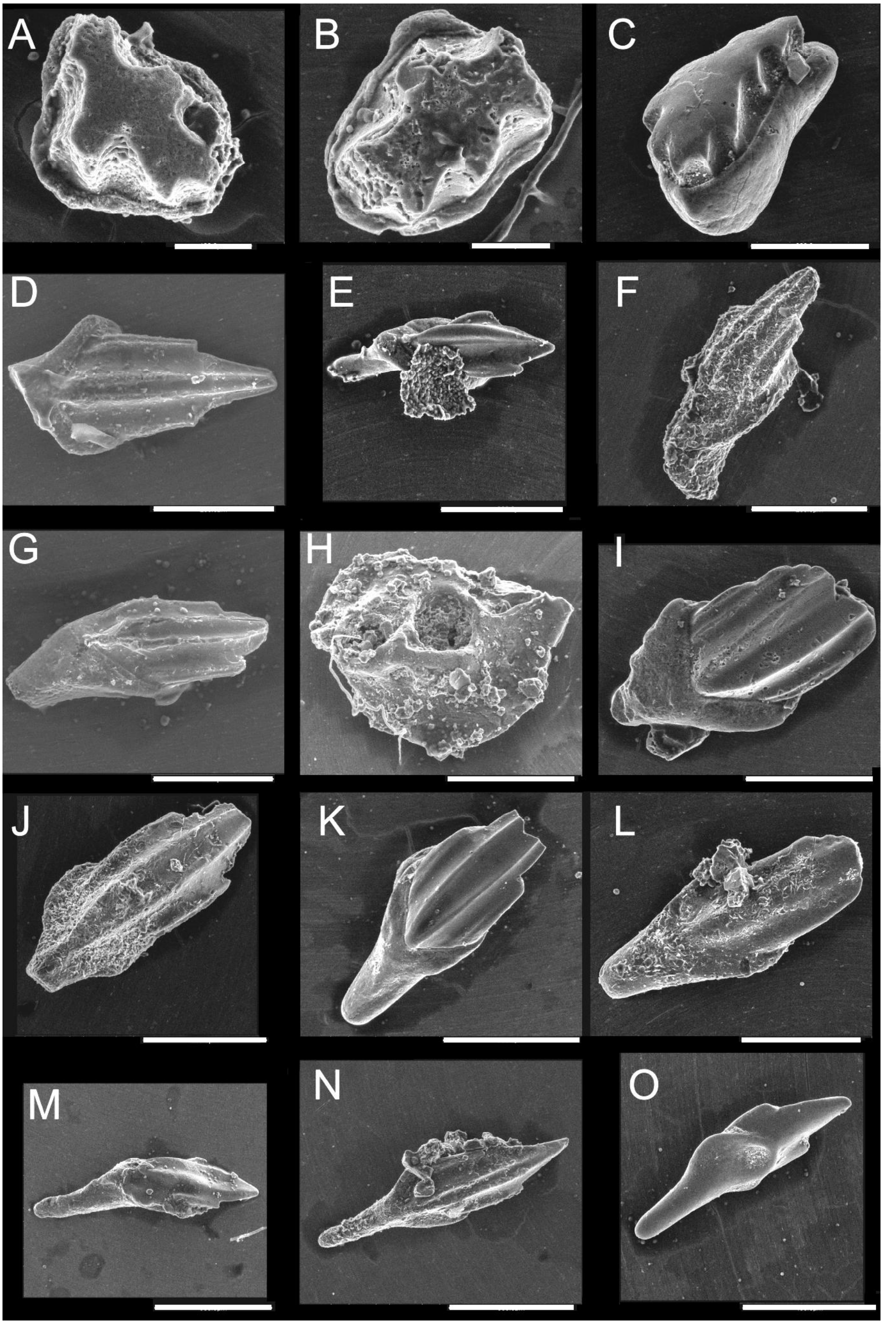

Fig. 2. *Talimaalepis rimae* gen. et sp. nov. scale morphological varieties. Kyzyl-Tchiraa outcrop, Central Tuva; Tchergak series, Kyzyl-Tchiraa Regional Stage, Upper Llandovery, Lower Silurian. **A**, LGI M-1/240, oral scale; **B**, LGI M-1/241, oral scale; **C**, LGI M-1/242, oral scale; **D**, LGI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

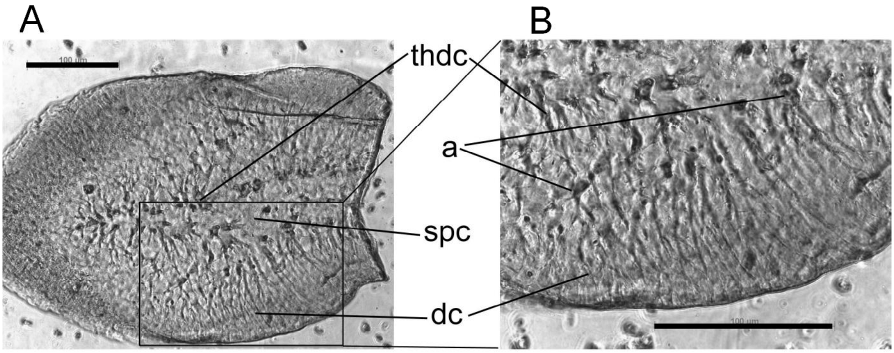

Fig. 3. *Talimaalepis rimae* gen. et sp. nov., cephalo-pectoral scale, horizontal longitudinal thin section (B is part of A). Lake Basin outcrop No 21, north west Mongolia; Chargat Formation, Salhit Regional Stage, Upper Llandovery – Wenlock, Lower Silurian. Thin section No 80, Institute of Geology and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

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

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

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

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

ŽIVILĖ ŽIGAITĖ

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

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