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783, SĒJUMS

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Astotā Baltijas stratigrāfijas konference

Ervīns Lukševičs, Ģirts Stinkulis, Laimdota Kalniņa

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Šis Latvijas Universitātes rakstu speciālais sējums aptver tos darbus, kurus iesniedza Astotās Baltijas stratigrāfijas konferences (BSK) dalībnieki. Cerams, ka lasītājam šie raksti liksies interesanti un svarīgi, jo tie aptver rezultātus ilgstošiem pētījumiem, kas veikti Baltijas vai tās kaimiņvalstu teritorijā. Baltijas stratigrāfijas konferences (BSK) jau sen, kopš 1976. gada Viļņas sanāksmes, ir kļuvušas par tradicionālām Baltijas un kaimiņvalstu pētnieku tikšanās reizēm, kad notiek domu apmaiņa par dažādiem stratigrāfijas, paleontoloģijas un ar šīm zinātnēm saistīto jomu jautājumiem (Grigelis, šis sējums; Kaljo un Hints 2009). Baltijas stratigrāfis sadarbība ir kļuvusi ļoti cieša kopš Baltijas reģionālas starpresoru stratigrāfiskās komisijas (BRSSK; pazīstama arī pēc abreviatūras BRMSK, pēc nosaukuma krievu valodā) dibināšanas 1969. gadā. Pirmā Baltijas stratigrāfijas konference tika sasaukta 1976. gadā Viļņā, un tās rezultāti ieviesti visu Baltijas republiku ģeoloģiskās kartēšanas un stratigrāfisko pētījumu praksē. Baltijas stratigrāfu sadarbība BRSSK ietvaros sekmīgi ir turpinājusies arī 20. gs. 80. gados (Grigelis, šis sējums), tomēr līdz otrajai konferencei pagāja ievērojams laiks.

Baltijas valstīm pakāpeniski atgūstot neatkarību, 1990. gadā BRSSK tika pārveidota par mazāk formālu organizāciju: triju Baltijas republiku stratigrāfijas komisijas vienojās par sadarbību Baltijas stratigrāfijas asociācijā (BSA), kuras statūtus katras valsts nacionālā stratigrāfijas komisija ratificēja 1991. gadā. BSA galvenais mērķis ir veicināt sadarbību starp pētniekiem Baltijas stratigrāfijas jomā, kā arī organizēt regulāras konferences. Otrā Baltijas stratigrāfijas konference notika 1993. gadā Viļņā, un kopš tā laika BSK ir kļuvušas patiesi starptautiskas. Tajās piedalās ne tikai Baltijas un tuvāko kaimiņvalstu, bet arī citu Eiropas valstu un pat aizjūras valstu viesi. Trešā BSK tika sarīkota 1996. gadā Tallinā, un galvenā uzmanība tika pievērsta augstas izšķirtspējas biostratigrāfijai un Baltijas reģionālajai stratigrāfijai. Ceturtās BSK, kas notika 1999. gadā Jūrmalā, tēma bija "Mūsdienu reģionālās stratigrāfijas problēmas un metodes", bet piektā BSK tika sasaukta 2002. gadā atkal Viļņā, tās tēma — "Baseinu stratigrāfija: mūsdienu metodes un problēmas".

Krievijas ziemeļrietumu daļas pētnieki ir saglabājuši ciešus kontaktus ar Baltijas kolēģiem un 2003. gadā T. Koreņas vadībā nolēma pievienoties BSA aktivitātēm, organizējot sesto BSK Sanktpēterburgā. Konferencē apskatītas ne tikai ar stratigrāfiju saistītās tēmas, bet arī skarts plašāks jautājumu loks, un jaundibinātā tradīcija radusi atspoguļojumu arī turpmākajās konferencēs. Septītā BSK tika organizēta Tallinā

2008. gadā, bet 2011. gadā kārtējo, jau astoto BSK ir uzņēmusi Rīga. Konferences organizācijā piedalījās BSA, Latvijas Universitātes Ģeogrāfijas un Zemes zinātņu fakultātes, Latvijas Dabas muzeja un Ziemeļvidzemes ģeoparka pārstāvji. Turpinot ceturtajā BSK iedibināto tradīciju, arī astotās BSK darbība risinājās, atbalstot divu IUGS IGCP projektu mērķus: tika organizētas sesijas, kas veltītas 591. projektam "Ordovika revolūcija" un 596. projektam "Viduspaleozoja klimata izmaiņas un biodaudzveidības modeļi (agrais devons — vēlais karbons)". Viens no konferences mērķiem bija iepazīstināt tās dalībniekus ar interesantākajiem Vidzemes devona un kvartāra nogulumu griezumiem, iežiem un fosilijām, kā arī pirmā Latvijas ģeoparka darbību lauka ekskursijas laikā, kura norisinājās pēc zinātniskās sesijas (Stinkulis un Zelčs 2011).

Konferences tēžu krājumā ir iekļauti 64 mutisko un stendu ziņojumu tēzes (Lukševičs u.c. 2011). Vairāk nekā trešā daļa ziņojumu ir veltīta dažādām paleontoloģijas tēmām, apmēram ceturtā daļa stratigrāfijai, nedaudz mazāk – sedimentoloģijai. Pārējos ziņojumos apskatīti kvartārģeoloģijas, hemostratigrāfijas, bioloģiskās daudzveidības un bioģeogrāfijas jautājumi, kā arī ģeoloģijas lietišķie aspekti un ģeoloģiskās datubāzes. Nedaudz mazāk nekā trešdaļa ziņojumu (27%) ir veltīti devonam, 24% kvartāram, 20% ordovikam un tikpat daudz – silūram, 5% (3 ziņojumi) kembrijam un pa vienam ziņojumam juras, krīta un paleogēna periodam. Šāds ziņojumu skaita sadalījums kopumā atbilst Baltijas un tuvāko teritoriju ģeoloģiskās uzbūves īpatnībām un pētījumu specifikai.

Konferences laikā notika ģeoloģiskajām datubāzēm veltīta darba grupas sēde, kā arī BSA plenārsēde, kurā apspriesti jautājumi par sadarbības padziļināšanas iespējām, nacionālo stratigrāfijas komisiju mājaslapu veidošanu vai pilnveidošanu, kā arī par nākamo BSK. Lietuvas stratigrāfijas komisija izteica vēlmi organizēt nākamo BSK 2014. gadā Viļnā.

Šis LU Rakstu speciālais sējums satur rakstus, kas balstās uz dažiem 8. BSK sniegtiem ziņojumiem un aptver galvenokārt paleontoloģijas un stratigrāfijas tēmas, kā arī lietišķās ģeoloģijas aspektus. Daži no ziņojumiem jau ir publicēti vai tuvākā nākotnē tiks iespiesti arī citos zinātniskos žurnālos.

Algimantas Grigelis (Viļņa), ilggadējs BRSSK vadītājs, atskatās nesenajā pagātne un analizē šīs komisijas sekmīgas darbības rezultātus, kā arī atzīmē visu triju Baltijas republiku vadošo ģeologu – stratigrāfu un paleontologu devumu Baltijas paleozoja un mezozoja stratigrāfisko shēmu un ģeoloģisko karšu sagatavošanā un publicēšanā.

Aleftina Jurina (Maskava) un Marina Raskatova (Voroņeža) apraksta senāko pirmkailsēkļu *Swalbardia bankssi* makroskopisko fosiliju atradumus devona mālos no Lodes karjera un apspriež šo atradumu paleobioģeogrāfisko un biostratigrāfisko nozīmi. Miosporu komplekss, kas atrasts līdzās augu makroatliekām, ļauj precizēt Lodes svītas ietvaros atrastās A tafocenozes vecumu un korelēt šo slāņkopu ar vidējā devona Živetas stāva augšējo daļu.

Larisa Norova (Sanktpēterburga) veltījusi rakstu tādiem sarežģītas uzbūves ģeoloģiskiem objektiem kā apraktajām ielejām Krievijas ziemeļrietumu daļas lielākās pilsētas teritorijā, īpašu uzmanību pievēršot dažāda vecuma morēnas iežiem, kas aizpilda apraktās ielejas. Aprakto ieleju teritorijas ir svarīgas kā būvniecībai derīgo

izrakteņu izplatības un potenciālās ieguves vietas, kā dzeramā ūdens horizonti, un ielejas aizpildošo iežu īpašības ir pamatā būtisku nosacījumu izvirzīšanu pilsētas transporta infrastruktūras un ēku celtniecībai.

Marina Raskatova (Voroņeža) un Aleftina Jurina (Maskava) pievērsušas uzmanību Franas stāva miosporu kompleksu izplatībai Latvijas centrālajā un austrumu daļā, kā arī kaimiņu teritorijā Pleskavas apgabalā, un to biostratigrāfiskajai nozīmei. Pētījumā tika nodalīti pieci miosporu kompleksi. Salīdzinājums ar miosporu kompleksu izplatību Centrālajā devona laukā un Baltkrievijā, kā arī vadfosiliju atradumi Latvijas un Pleskavas Franas stāva griezumā ļauj trasēt dažas zonas no Austrumeiropas platformas miosporu zonēšanas shēmas, tādējādi paverot jaunas iespējas nogulumu korelēšanai Galvenā un Centrālā devona lauka teritorijā.

Brigita Šēnemane (Bonna) un Juāns Klarksons (Edinburga) ir iesnieguši divus rakstus. Vienā autori pievēršas kembrija izplatītāko posmkāju — trilobītu redzes sistēmas smalkajai uzbūvei. Pateicoties jaunas pētījumu metodes izmantošanai, labi saglabājušos trilobītu acu tomogrāfija ļāvusi pirmo reizi saskatīt ne tikai acs ārējo, bet arī iekšējo uzbūvi, tādējādi noskaidrojot, ka dažu Phacopidae dzimtas trilobītu acis ir bijušas tikpat komplicētas kā vairākiem mūsdienu posmkājiem ar mozaīkveida redzi. Otrā rakstā šie autori apskata Ķīnas unikālās Čengjangas biotas pārstāvju — dažādu senāko posmkāju vizuālās sistēmas un sniedz to īpašnieku paleoekoloģiskās interpretācijas.

Pateicības. Esam pateicīgi Latvijas Universitātes vadībai par konferences finansiālo atbalstu un iespēju publicēt konferences dalībnieku sagatavotus darbus kā Latvijas Universitātes Rakstu speciālo sējumu. Konference nevarēja notikt bez organizācijas komitejas locekļu L. Kalniņas (LU), E. Lukševiča (LU, priekšsēdētājs), D. Ozola (Ziemeļvidzemes ģeoparks), Ģ. Stinkuļa (LU), I. Upenieces (LU), J. Vasiļkovas (LU), A. Zabeles (LU), V. Zelča (LU), I. Zupiņa (Latvijas Dabas muzejs) aktīvas darbības. Lauka ekskursijas organizēšanā un vadīšanā Ģ. Stinkulim un V. Zelčam palīdzējuši O. Āboltiņš, M. Nartišs, I. Upeniece un I. Zupiņš. Lielu ieguldījumu rokrakstu vērtēšanā snieguši Dimitri Kaljo, Laimdota Kalniņa, Ervīns Lukševičs, Valentīna Mancurova, Tinu Meidla (*Tõnu Meidla*), Helje Pērnaste (*Helje Pärnaste*), Anto Raukas, Jonas Satkūnas, Valdis Segliņš, Ģirts Stinkulis, Ilze Vircava, Vitālijs Zelčs un Ivars Zupiņš.

The Eighth Baltic Stratigraphical Conference

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The current special volume of the *Acta Universitatis Latviensis* comprises the papers submitted by participants of the Eighth Baltic Stratigraphical Conference (8th BSC) held in Riga, Latvia, on 28 August – 2 September 2011. We hope that the reader will find the papers interesting and important, as they include results of continuous studies carried out in the Baltic States and their neighbouring countries.

Baltic Stratigraphical conferences became traditional meetings of researchers of the Baltic States and neighbouring countries since the first one in Vilnius, 1976. Various problems of stratigraphy, palaeontology and fields related to these branches are discussed during these conferences (Grigelis this volume; Kaljo and Hints 2009). Collaboration of stratigraphers of the East Baltics became very close since establishment of the Baltic Regional Stratigraphic Commission (BRSC; known also as abbreviation BRMSK in Russian) in 1969. The First Baltic Stratigraphical Conference was organised in 1976 in Vilnius and its results found practical application in geological survey and stratigraphical studies in all the Baltic republics. Successful collaboration of Baltic stratigraphers continued in 1980ies (Grigelis this volume), but only after long time the second conference took place.

The BRSC was reformed to less formal organisation in 1990 as the Baltic States regained their independence. Stratigraphical commissions of all three Baltic republics reached an agreement to collaborate within the Baltic Stratigraphical Association, and its statutes had been ratified by each national stratigraphical commission in 1991. The major aim of the BSA is promotion of collaboration among researchers in the field of stratigraphy and organisation of regular conferences.

Since the Second Conference in Vilnius, 1993, the BSCs have become true international meetings. The guests come not only from the Baltic States and closely neighbouring countries, but also other European countries and even wider areas overseas. The Third BSC in Tallinn, 1996 was focused on the high-resolution biostratigraphy and Baltic regional stratigraphy, the Fourth BSC in Jūrmala, 1999, was called "Problems and methods of modern regional stratigraphy", and the Fifth BSC in Vilnius, 2002, was devoted to the basin stratigraphy, modern methods and problems in its study.

Researchers of the north-eastern part of Russia have maintained good contacts with the colleagues from the East Baltic and in 2003 under leadership of T. Koren' decided to join the BSA activities by organizing the Sixth BSC in St Petersburg in 2005. This conference not only focused on the themes related to stratigraphy but also to wider problems, and this new tradition got a support also in the next conferences



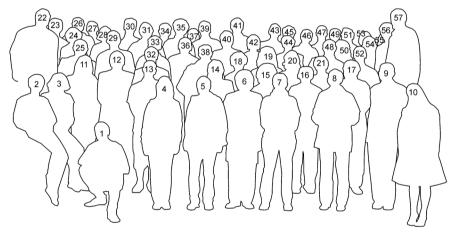


Figure. Participants of the meeting. 1, Vadim Glinsky; 2, Olga Afanassieva; 3, Marina Raskatova; 4, Karin Truuver; 5, Oive Tinn; 6, Valentina Mantsurova; 7, Anna Žylińska; 8, Elga Kurik; 9, Stanislaw Skompski; 10, Daiga Pipira; 11, Ieva Upeniece; 12, Algimantas Grigelis; 13, Vincent Perrier; 14, Laimdota Kalniņa; 15, Maria Tsinkoburova; 16, Elena Mikhailova; 17, Anto Raukas; 18, Larisa Norova; 19, Daria Bezgodova; 20, Anna Tarasenko; 21, Aleftina Jurina; 22, Vitālijs Zelčs; 23, Aivars Markots; 24, Linda Hints; 25, Tõnu Meidla; 26, Alexander Ivanov; 27, Albertas Bitinas; 28, Helje Pärnaste; 29, Pavel Beznosov; 30, Siim Veski; 31, Tõnu Martma; 32, Ģirts Stinkulis; 33, Juri Vassiljev; 34, Valdis Segliņš; 35, Philip Gibbard; 36, Madis Rubel; 37, Sigitas Radzevičius; 38, Vladimir Smirnov; 39, Piotr Luczyński; 40, Leho Ainsaar; 41, Alexey Zaitsev; 42, Tiiu Märss; 43, Peter Königshof; 44, Dimitri Kaljo; 45, Atis Mūrnieks; 46, Ursula Toom; 47, Olle Hints; 48, Atko Heinsalu; 49, Jānis Karušs; 50, Daiga Blāķe; 51, Jaak Nõlvak; 52, Normunds Stivriņš; 53, Enli Kiipli; 54, Aija Ceriņa; 55, Elīza Kušķe; 56, Marina Kharkina; 57, Volodymyr Gritsenko. Photo by E. Lukševičs.

The Seventh BSC was held in Tallinn in 2008 and the Eighth BSC welcome the guests in Riga in 2011. Representatives of BSA, Faculty of Geography and Earth Sciences of the University of Latvia, Natural History Museum of Latvia and North Vidzeme Geopark participated in organization of this conference. The Eighth BSC continued the tradition which started in the Fourth BCS to support the aims of IUGS IGCP projects: special sessions devoted to the IGCP Project 591 "The Early to Middle Palaeozoic Revolution" and IGCP Project 596 "Climate Change and Biodiversity Patterns in the Mid-Palaeozoic (Early Devonian to Late Carboniferous)" have been organized. The conference was aimed also to introducing its participants to the most interesting Devonian and Quaternary sections, deposits and fossils in the Vidzeme, as well as the activities of the first geopark in Latvia, during the post-conference geological excursion (Stinkulis and Zelčs 2011).

The abstract volume of this conference contains 64 papers (Lukševičs *et al.* 2011). More than a third part of all papers were devoted to palaeontological topics, a fourth to stratigraphy, and a bit less to sedimentology. The remaining ones were dealing with other topics like Quaternary geology, chemostratigraphy, biodiversity and biogeography, as well as the applied studies in geology and geological data bases. Some 27% of contributions concerned the Devonian Period, 24% the Quaternary, 20% the Ordovician and the same per cent the Silurian, 5% (3 presentations) the Cambrian and one presentation to each period like Jurassic, Cretaceous and Palaeogene. The above brief statistics seem to be in good harmony with the current research trends and specific geological structure of the East Baltic area and neighbouring regions.

Workshop devoted to the geological data bases took place during the conference. Discussions related to deepening the collaboration, development or improvement of home pages of the national commissions, as well as the organisation of the next BCS took place during the Plenary Session. The Lithuanian Stratigraphical Commission expressed the willingness to organize the next BSC in 2014 in Vilnius.

This special issue of the Acta Universitatis Latviensis comprises the papers based on some contributions to the Eight BSC, which are focused mostly on the themes of palaeontology and stratigraphy, as well as the aspects of applied geology. Some presentations are published already or planned to publish in other scientific journals.

Algimantas Grigelis (Vilnius) as one of the leaders of the Baltic Regional Stratigraphic Commission (BRSC) provides the analysis of activities of the Commission during the period from 1970 to 1990 and the main results of these activities. The most remarkable achievements of the leading stratigraphers collaborating within the frames of the BRSC were elaboration of unified stratigraphic classification with correlation stratigraphic charts of the Baltic region and elaboration of wider correlation charts of the Baltic region with extension to the whole European Russia in the frame of the East-European Platform.

Aleftina Jurina (Moscow) and Marina Raskatova (Voronezh) describe macroscopic remains of the most ancient progymnosperm *Swalbardia bankssi* from the Devonian deposits in the Lode clay pit and discuss palaeobiogeographic and biostratigraphic significance of these findings. Miospore assemblage discovered in the same deposits allows aging of the taphocoenosis A from the Lode Formation and correlation of the section with the uppermost Givetian of the Middle Devonian.

Larisa Norova (St-Petersburg) discusses recent advances in the studies of palaeovalleys as complicated geological objects with unstable engineering-geological

properties in the largest city of the north-western part of Russia, paying particular attention to the till deposits of various ages. The author shows the great practical importance of palaeovalleys containing such common building materials as sand and gravel, as well as drinking water. Land subsidence in valleys may reach several metres, impeding town construction, transport infrastructure and normal exploitation of water and sewage communications.

Marina Raskatova (Voronezh) and Aleftina Jurina (Moscow) review the distribution of miospore assemblages in the Frasnian sequence of the central and eastern part of Latvia and Pskov Region of Russia, and analyse biostratigraphic significance of these assemblages. Five miospore assemblages have been established. The comparison of taxonomic composition of the spore assemblages from the Main Devonian Field with the assemblages from the Central Devonian Field and Belarus and discoveries of zonal miospore taxa allowed trace some zones of the East European Platform miospore zonation thus providing new possibilities to correlate Frasnian sections of the Main and Central Devonian fields.

Brigitte Schoenemann (Bonn) and Euan N. K. Clarkson (Edinburgh) have submitted two articles. The fine structure of the compound eyes of trilobites, dominating form of arthropods from Cambrian, has been discussed. Using modern techniques, the computer tomography of the well preserved eyes of phacopid trilobites revealed not only the outer, but also the internal sensory structures. The analysis shows that these structures worked as apposition eyes and demonstrates that the trilobites had a mosaic-like vision, as today living organisms with compound eyes. The second article is devoted to the vision system of arthropods from the Chengjiang Lagerstätte, Lower Cambrian of China. The structure of compound eyes has been analysed. The light habitat of arthropods with various visual systems has been reconstructed using modern physiological methods.

Acknowledgements. We are very grateful to the University of Latvia for financial support and opportunity to publish these papers as a special volume of Acta Universitatis Latviensis. The meeting was made possible through organizational support from members of the Organization Committee L. Kalniņa, E. Lukševičs, G. Stinkulis, I. Upeniece, J. Vasiļkova, A. Zabele, V. Zelčs, I. Zupiņš. The assembly of a volume takes a large amount of work and the Guest Editor of the volume (E. L.) would like to thank the following individuals for reviewing the papers that are published here: Dimitri Kaljo, Laimdota Kalniņa, Ervīns Lukševičs, Valentīna Mantsurova, Tõnu Meidla, Helje Pärnaste, Anto Raukas, Jonas Satkūnas, Valdis Segliņš, Ģirts Stinkulis, Ilze Vircava, Vitālijs Zelčs and Ivars Zupiņš.

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Twenty Years of the Baltic Regional Stratigraphic Commission (1970–1990)¹

Algimantas Grigelis

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Activities of the Baltic Regional Stratigraphic Commission (BRSC; previously known in Russian as BRMSK) during 1970–1990 are analysed. The main tasks of the Baltic RSC were to develop stratigraphy of the whole Baltic Region from a theoretical time-rock classification to practical use of the stratigraphic subdivision in geological cartography and compilation of geological maps. The common problems of the regional stratigraphy of the Baltic region are discussed. The most remarkable achievements of the Baltic RSC are elaboration of unified stratigraphic classification with correlation stratigraphic charts of the Baltic region, that were examined and confirmed in 1976. This achievement got next step in 1980-ies when BRSC plays an important role in elaboration of wider correlation charts of the Baltic region with extension to the whole European Russia in the frame of the East-European Craton.

Keywords: Stratigraphy • Geology • Stratigraphic charts • Lithuania • Latvia • Estonia • Baltic region

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Introduction

Stratigraphy – the study of strata, or layers – applies the Law of Superposition to every stratified system: geological stratum, composition of soil, archaeological materials in order to determine the relative ages of rocks. The complex goals of this wide branch of geological sciences need use conventional international rules and, in particular, have a system of international and regional tools for scientific cooperation. Such a system works under aegis of the IUGS International Commission on Stratigraphy (ICS) and it numerous bodies (see www.stratigraphy.org).

The Baltic Regional Stratigraphic Commission (BRSC; previously known in Russian as BRMSK) was established in 1969 as a regional body of the All-Union Interdepartmental Stratigraphic Committee (MSK), located at the VSEGEI, St. Petersburg (Leningrad). This Committee, established in 1955, reached excellent results during 55 years under leadership of the outstanding Russian stratigraphers, academicians Dmitriy Vasilyevich Nalivkin (led from 1955 to 1975), Boris Sergeyevich Sokolov (from 1976 to 1988) and Aleksandr Ivanovich Zhamoida

Based on report made at the 8th Baltic Stratigraphical Conference, 29 August 2011, Riga, Latvia.

(since 1988), in different issues of the stratigraphic classification, nomenclature and terminology (Zhamoida 2004; Zhamoida and Prozorovskaya 2005).

The goals of the Baltic Stratigraphic Commission were stated as follows: application of uniform methodology it the stratigraphy studies, introduction of the internationally accepted rules, unification of stratigraphic classification at the local and regional levels, adaptation to the constantly renewing International Stratigraphic Chart (Grigelis 1971).

Remarkable steps towards a common policy in geology studies of the Baltic (Soviet) Republics became obvious in the mid of 1970-ies thanks to several circumstances:

- strengthening of the national geological surveys;
- rise of well-educated scientists in the basic fields of geosciences;
- research of the Baltic Region as a specific unit of geological evolution.

These ambitious points enhanced, in particular, development of a well-grounded stratigraphic basis. In this progress fundamental documents of the field of that time like "A Stratigraphic Code of the USSR" (Zhamoida *et al.* 1977; 2nd edition 1988), and "International Stratigraphic Guide" (Hedberg 1976; 2nd ed.: Salvador 1994) played essential role. As well as important conditions supporting successful activities of the Baltic RSC, as a structurized body in the world stratigraphy system, were formed through relationships with the All-Union MSK and, via institutional and individual channels, with the International Commission on Stratigraphy (ISC) of the IUGS.

Noteworthy to mention about the goals of the ISC that during decades have been changing, but quoted below as it is written in 2011:

ICS: Its primary objective is to precisely define global units (systems, series, and stages) of the International Chronostratigraphic Chart that, in turn, are the basis for the units (periods, epochs, and age) of the International Geologic Time Scale; thus setting global standards for the fundamental scale for expressing the history of the Earth [http://www.stratigraphy.org/; interactive, 2011-09-10].

According to James G. Ogg, into the approaching of these goals was added the ICS Task Force for Stratigraphic Information [formerly called "Stratigraphic Information System (SIS) Subcommission"] established in 2000. This commission is aiming [...] to enable the world geoscience community to have quick and free access to a vast amount of stratigraphic information, thus helping to spread the knowledge of Earth's history and foster the advancement of stratigraphic sciences. The Task Force priority is to gather selected stratigraphic information (such as stratigraphic databases and links, compilation of biozonal schemes, regional time scales, stratigraphic standards and GSSP information, geohistory teaching modules), to logically organize the databases and related links, and make easy search and use of the contents through its website [James G. Ogg, Chair; https://engineering.purdue.edu/Stratigraphy/index.html [interactive, 2011-09-09].

Historical setting

Background agreements for formation of the Baltic Regional Stratigraphic Commission (BRSC) were elaborated under guidance of the Lithuanian Geological Prospecting Institute (LitNIGRI) in 1968, in co-operation with geological institutes and geological surveys of Estonia, Latvia, and Lithuania. A foundation meeting of the Baltic RSC was held on 19th

January 1969. Structure and management of the Commission were formed and approved in the same year, and it went into power.

Acad. Juozas Dalinkevičius was appointed a first chair of the Commission but in 1970 he was substituted by Algimantas Grigelis (Vilnius). Acad. Karl Orviku (from 1969) and Dimitri Kaljo (from 1981, both Tallinn), Rita Ulste (Riga) and Juozas Paškevičius (Vilnius) were appointed the chairs of the Estonian, Latvian and Lithuanian stratigraphic commissions, respectively. Researcher working groups for every geological period/system were established as a main tool of collaborative work.

The well-known professional Baltic stratigraphers (Figure) as follows below played leading role in these groups:

Vendian–Cambrian Arnis Brangulis, Ārija Fridrihsone, Tadas Jankauskas,

Kaisa Mens, Lidija Paškevičienė, Enn Pirrus,

Angelina Zabele

Ordovician Lilita Gailīte, Evlampijus Lashkovas, Ralf Männil,

Juozas Paškevičius, Arvo Rõõmusoks, Rita Ulste

Silurian Lilita Gailīte, Dimitri Kaljo, Petras Lapinskas, Heldur

Nestor, Juozas Paškevičius, Nijolė Sidaravičienė, Rita

Ulste

Devonian, Carboniferous Valentina Karatajūtė-Talimaa, Visvaldis Kuršs,

Lyubov Lyarskaya, Elga Mark-Kurik, Atis

Mūrnieks, Vytautas Narbutas, Lyudmila Savvaitova, Vitalijs Sorokins, Herbert Viiding, Stasys Žeiba

Permian-Triassic Valentinas Kadūnas, Jurgis Kisnėrius, Visvaldis Kuršs,

Lyudmila Savvaitova, Povilas Suveizdis

Jurassic-Cretaceous Algimantas Grigelis, Romualda Mertinienė,

Lilijana Rotkytė, Petras Šimkevičius

Paleogene–Neogene Vytautas Baltakis, Algimantas

Grigelis, Vladas Katinas

Quaternary Igors Danilāns, Algirdas Gaigalas, Kalju Kajak,

Ona Kondratienė, Elsbet Liivrand, Anto Raukas, Vilnis Stelle, Jānis Straume, Petras Vaitiekūnas,

Vytautas Vonsavičius



Karl Orviku (1903-1981)**



Tadas Jankauskas (1938-2005)*



Ralf Männil (1924-1990)**



Nijolė Sidaravičienė (1936–2001)*



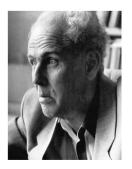
Juozas Dalinkevičius (1893–1980)*



Rita Ulste (1931-1991)***



Arvo Rõõmusoks (1928-2010)**



Vitālijs Sorokins (1936-2008)***

Note: Photos are published by courtesy of the * Institute of Geology and Geography, Vilnius; ** Institute of Geology at Tallinn University of Technologies; Tallinn; *** Department of Geology, University of Latvia, Rīga.



Visvaldis Kuršs (1928–2000)***



Kalju Kajak (1929-2011)**



Stasys Žeiba (1916–1999)*



Vytautas Vonsavičius (1929–1991)*



Algirdas Gaigalas (1933–2009)*



Elsbet Liivrand (1932–2011)**



Jurgis Kisnėrius (1922–1986)*



Igors Danilāns (1928–2007)***

A successive form of cooperation was the annual meetings (assembly) of the Commission, and thematic stratigraphical conferences held every two–three years followed by geological field excursions (Table 1). This tradition is kept till now, in particular when BRSC in 1990 was reorganized into three republican commissions of the independent Baltic States and their umbrella – organisation the Baltic Stratigraphic Association (BSA) was founded.

Table 1
The selected annual meetings of the Baltic RSC

Event	Year	City	Country
The First Baltic Stratigraphic Conference "Approval of the unified stratigraphic charts of the East Baltic region"	1976	Vilnius	Lithuania
XII Assembly of the Baltic RSC "Regional correlation of the biostratigraphic zones"	1981	Rīga–Jūrmala	Latvia
XIII Assembly of the Baltic RSCK "Problems of Phanerozoic stratigraphy"	1982	Tallinn– Lohusalu	Estonia
Joint Assembly of the Baltic and Belarus Regional Stratigraphic Commissions "Problems of stratigraphy and correlation".	1982	Vilnius	Lithuania

Results

The Baltic RSC worked actively during twenty years having main task to develop stratigraphy of the whole Baltic Region from a theoretical time-rock classification to practical use of the stratigraphic subdivision in geological cartography and compilation of geological maps. The common problems of the regional stratigraphy of the Baltic region first were discussed (Grigelis 1972).

The most remarkable achievements of the Baltic RSC could be mentioned below:

- Elaboration of unified stratigraphic classification with correlation charts of the whole Baltic region, that were examined and confirmed at the Baltic Stratigraphic Conference held in Vilnius, 11–12 May 1976.
- Evaluation and approval of detailed stratigraphic schemes and correlation charts by the All-Union Interdepartmental Stratigraphic Committee (MSK) and its publication (Grigelis ed. 1978).
- Application of the palaeontological method became widely used in geological mapping and compilation of detailed stratigraphic schemes and correlation charts of the Phanerozoic sedimentary rocks.
- Elaboration of principles of detailed stratigraphic legends and the user guide on methods of compilation of geological maps of the Baltic region (Grigelis 1979; Grigelis ed. 1981).
- Compilation and publication of the set of regional geological maps at a scale of 1:500 000 of the Baltic Republics based on the detailed stratigraphic correlation charts (Grigelis ed. 1982).

- Regular labour of regional and thematic working groups on improvement of the detailed stratigraphic schemes.
- Later work with the Baltic regional stratigraphic schemes of 1976 (1978) including their data to the whole East-European platform for Cambrian system in 1983 (Vilnius; published 1986 by VSEGEI); for Ordovician and Silurian systems in 1984 (Tallinn; published 1987 by VSEGEI); for Devonian system (Rzhonsnitskaya and Kulikova 1990) that had a much wider sense than only Baltic region.
- Persistent relations with the International Commission on Stratigraphy (ICS), the International Subcommission on Stratigraphic Classification (ISSC), and the Subcommissions on stratigraphy of geological systems where the Baltic stratigraphers have had the officers and membership positions providing sufficient contribution to its activity.

Future trends

The Baltic RSC properly transferred its power after restoration of the independence of the Baltic Republics to the national commissions on stratigraphy, which were set up in Estonia, Latvia, and Lithuania in September–October, 1990. Thus, instead of the Baltic RSC the Baltic Stratigraphic Association (BSA) was established on 16th October 1990 in Vilnius at the meeting by the delegates of these commissions (Grigelis 1991). Later, in 2003 the NW Russian national commission on stratigraphy joined the Baltic Stratigraphic Association (BSA).

The main goal of the BSA was declared to unite activities of the Estonian, Latvian and Lithuanian researchers to determine and solve the problems of the stratigraphy of the entire Baltic Region (Kaljo and Hints 2009). A new BSA statute was approved by the first Baltic Stratigraphic assembly meeting in 1991. The fruitful cooperation has a good continuation, and the BSA regularly calls open international conferences devoted to various aspects of regional geology and stratigraphy.

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Frasnian Miospore Assemblages and Zones of Southern Latvia and North-Western Russia (Pskov Region)

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The present work is a result of studies of Frasnian miospores found in various stratigraphic units of Latvia and NW Russia. These units are characterized by zonal miospore assemblages which comprise a stratigraphical interval from the Pļaviņas to the Stipinai regional stages. The taxonomic composition of spore assemblages of the Main Devonian Field has been compared with the miospore assemblages of the Central Devonian Field. Some units were characterized with miospore zones.

Keywords: Biostrarigraphy • Main Devonian Field • miospore zonation • systematics • Upper Devonian

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Introduction

The purpose of the article is to re-describe and illustrate the Frasnian miospores from Latvia and Western Russia on the basis of some previously published and unpublished materials; to give detailed elaboration of existing biostratigraphic scheme of the Frasnian Stage for the studied area; to allocate zones and subzones based on the changes of miospore assemblages; to review some previous definitions of miospores and transfer taxa from the old system into the new one.

Regular studies of miospore assemblages from the Upper Devonian deposits of Latvia were started by V.R. Ozoliņa (1963). She published a monographic report on the studies of miospores from the three outcrops located in the basins of the rivers Gauja and Daugava and from 12 boreholes in the vicinities of Rembate, Pļaviņas, Branti close to Tirza, Ālande, etc. Ozoliņa (1963) described and illustrated in detail five miospore assemblages for the Frasnian deposits from Latvia: assemblage I, common for the Amula and Bauska formations, assemblage III typical for the Ogre Formation (Fm), assemblage III from the Daugava Fm, assemblage IV, common for

the Salaspils and Pļaviņas fms, and assemblage V, common for the Amata and Gauja fms. The work of Ozoliņa has the great importance as it showed for the first time the possibility of stratigraphic subdivision of the Frasnian deposits in Latvia, using miospores. Besides, miospore assemblages allocated by Ozoliņa are important for the comparative analysis.

Later, palynological data obtained by S.N. Starikova, G.I. Kedo and L.G. Raskatova for the Snezha, Ogre and Amula regional stages (RS) of Latvia were used within the biostratigraphic research. These miospore assemblages were compared with their counterparts from the coeval deposits of Belarus and the Central regions of Russia (Central Devonian Field, or CDF) (Sorokin 1981). Thus, by the time of the beginning of our studies many of the Frasnian stratigraphic units have been briefly characterized by miospores.

The position of the Givetian-Frasnian boundary in the Baltic area is debatable, but the authors agree with the opinion that the boundary is traceable below the Plaviņas Fm (e.g., Stinkulis and Zelčs 2011). According to this point of view, the Frasnian Stage in the studied area corresponds to the Pļaviņas RS, Dubnik RS (Salaspils Fm in Latvia), Daugava RS (Daugava Fm in Latvia; Porkhov, Svinord, Il'men', Buregi, Altovo beds in Russia), Stipinai RS and Amula RS in Latvia (for the detailed correlation of stratigraphic units of Latvia and NW Russia see, e.g. Rzhonsnitskaya and Kulikova 1999; Lukševičs 2001). According to the position of the Middle/Upper Devonian boundary accepted here, the assemblage V described by Ozoliņa corresponds to the Givetian Stage.

In the beginning of 1980-ies the authors began the studies of taxonomic composition of spore assemblages from various stratigraphic units of Latvia and NW Russia and compare these assemblages with the miospore assemblages of the Central Devonian Field (CDF). The first attempt to allocate miospore zones and subzones was made and the obtained material was partially published (Raskatova M. 1977, 1999; Raskatova L. *et al.* 1988). These studies analysing the available palynological material for detailed biostratigraphy of the Frasnian deposits of Latvia and NW Russia were continued during 2010-2011.

Material and methods

The study is based on the materials collected during the fieldwork of 1975 to 1976 in the south, south-eastern Latvia and the Pskov region of Russia. All samples were selected from the boreholes located near the following towns: Bauska (boreholes no. 5, 13), Daugavpils (borehole no. 1-T), Ilūkste (borehole no. 6) in Latvia; Velikie Luki (borehole no. 9) and Ostrov district of the Pskov Region (borehole no. 38) of Russia (Fig. 1). The samples were technically processed using alkali-free maceration of rocks (Teterjuk and Philippov 1989). More than 100 preparations, including 35 constant ones, were prepared: 21 from Latvian sections and 14 from NW Russia (Pskov region sections).



Figure 1. Map of Latvia and NW Russia showing the location of studied boreholes.

Results and interpretation

Miospore assemblage of the **Pļaviņas RS** is characterized on the basis of 36 samples selected from three boreholes no. 5, 9, and 38. The largest part (80%) of samples was empty, and 20% contained miospores and acritarchs. Miospores from the Pļaviņas deposits of Latvia have the subordinated value and are characterized by the following composition: *Leiotriletes perpusillus* Naum., *Calamospora minutissima* (Naum.) Lub., *Calamospora atava* (Naum.) McGregor, *P. solidus* (Naum.) Byvsch., *Lophotriletes minutissimus* Naum., *Apiculatisporis eximius* (Naum.) Oshurk., *A. dentatus* (Naum.) Obukh., *Geminospora rugosa* (Naum.) Obukh., *G. notata* (Naum.) Obukh., *Archaeozonotriletes variabilis* Naum. var. *insignis* Sen., *Stenozonotriletes definitus* Naum., *Densosporites* sp. (Fig.2, A-F).

Miospore assemblage from the sections of two boreholes in the Pskov region is more representative than in Latvia, which results in a greater species diversity within the genus *Geminospora*, occurrence of large miospores with long processes within the genus *Ancyrospora* and presence of a large miospore *Biharisporites*. Ozoliņa allocated the united miospore assemblage IV from the Pļaviņas and the Salaspils fms of Latvia, indicating, in her opinion, the absence of distinctions in flora from these formations. Probably, it was also associated with little palynological material. Assemblage IV was characterized by the presence of large miospores with processes

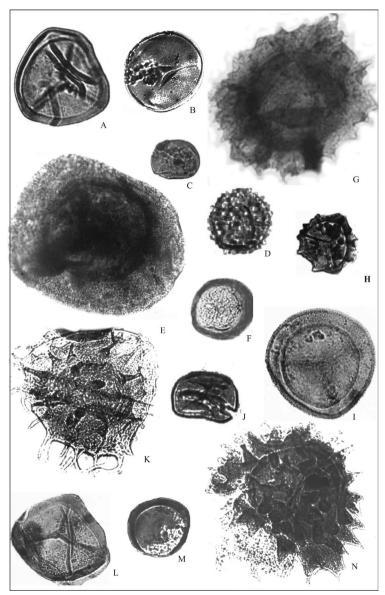


Figure 2. Frasnian miospore assemblages from Latvia. A-F, miospores from the Pļaviņas RS: A, Geminospora notata (Naum.) Obukh.; B, Punctatisporites atavus (Naum.) Andr.; C, Calamospora minutissima (Naum.) Lub.; D, Apiculatisporis eximius (Naum.) Oshurk.; E, Biharisporites sp.; F, Archaeozonotriletes variabilis (Naum.) var. insignis Sen. VSU, no L2011/24-25. G-N, miospores from the Dubnik RS: G, Densosporites cf. sorokinii Obukh.; H, Convertucosisporites curvatus (Naum.) Turnau; I, Geminospora micromanifesta (Naum.) Arch.; J, Retusotriletes simplex Naum.; K, Ancyrospora melvillensis Owens; L, Geminospora rugosa (Naum.) Obukh.; M, Archaeozonotriletes variabilis Naum.; N, Ancyrospora pulchra Owens. VSU, no L2911/27. Magnification x 500.

and by the first occurrence of the genus *Archaeoperisaccus* (Ozoliņa 1963). However, no species of the genus *Archaeoperisaccus* have been found in the sections of the Pļaviņas RS during our studies.

The Pļaviņas RS yields rather poor miospore assemblage, aging as the Frasnian because the index species of the subzone IB *Archaeozonotriletes variabilis insignis* and species of the genera *Apiculatisporis* and *Densosporites* appear in its composition. These genera are typical for this subzone, which corresponds to the Sargaevo RS of the CDF (Avkhimovitch *et al.* 1993), and are absent in the miospore assemblage from the Gauja RS (Jurina and Raskatova 2011).

Miospores from the Dubnik RS were studied from the section of borehole no. 5 in Latvia, and from two boreholes, no. 9, and 38, in Russia (Pskov region), where 14 samples were selected. 25% of the studied samples contained from 180 to 200 miospores. The most complete palynological characteristic of the Dubnik deposits was obtained from the borehole no. 5. The diversity of the Dubnik miospores is wider than in the Plavinas assemblage. The Dubnik assemblage which was established during this study contains Leiotriletes laevis Naum., Calamospora minutissima (Naum.) Lub., C. simplicissima (Naum.) Oshurk., Cyclogranisporites rugosus (Naum.) Oshurk. var. minor Naum., Geminospora rugosa (Naum.) Obukh., G. micromanifesta (Naum.) Arkh., G. semilucensa (Naum.) Obukh. et M. Rask., and Reticulatisporites retiformis (Naum.) Obukh. Some species were found in a small number of spores: Retusotriletes simplex Naum., R. communis Naum., Stenozonotriletes definitus Naum., S. pumilus (Waltz) Naum., S. recognitus Naum., Kedoesporis angulosus (Naum.) Obukh., Ancyrospora pulchra Owens A. melvillensis Owens, Densosporites cf. sorokinii Obukh., Verrucosisporites grumosus (Naum.) Obukh., Converrucosisporites curvatus (Naum.) Turnau (Fig.2, G-N). In general the miospore assemblage from the Dubnik RS has common features with the Plaviņas assemblage. Some differences between these two assemblages consist in the almost total absence of miospores with conate sculpture of the exine (1%), in the presence of miospores with verrucate ornamentation and considerable diversity of species within the genera Stenozonotriletes and Ancyrospora typical to the Dubnik RS.

The general structure of the Dubnik miospore assemblage from Latvia and NW Russia indicates the Frasnian age of deposits and shows some similarity with the XI miospore assemblage from the Rudkino RS of the CDF (Raskatova L. 1969). The miospore assemblage from the Rudkino RS is characterized by wider diversity of species within the genera *Geminospora*, *Acanthotriletes*, *Apiculatisporis*, *Stenozonotriletes*, by presence of patinate miospores *Archaeozonotriletes* (*A. variabilis* Naum.) up to 20%, constituting 3% in the Dubnik assemblage. A common feature for the two assemblages is the presence of large numbers of acritarchs (up to 45% in the borehole no. 5, depth 116.5 m). The structure of the Dubnik miospore assemblage enables to allocate the analogue of the zone Acanthotriletes bucerus – Archaeozonotriletes variabilis insignis (BI) (Frasnian) (Avkhimovitch *et al.* 1993) for the deposits studied by the authors in Latvia and the Pskov area.

First results of studies of the miospore assemblage from the **Daugava RS** were gained from the Il'men' Fm in the Pskov area (borehole no. 9), where a rich miospore assemblage has been found (Raskatova M. 1977). Later miospores from

the Daugava deposits in boreholes no. 9 and no. 5 were studied and compared with miospore assemblage from the Semiluki RS of the CDF (Raskatova L. *et al.* 1988). Later two miospore assemblages were established for the Daugava RS: the first one is similar in the composition to that of the SD (Geminospora semilucensa – Perotriletes donensis) miospore zone and the second one resembles in composition that of the SB (Spelaeotriletes bellus) miospore subzone, entering into the OG (Archaeoperisaccus ovalis - Verrucosisporites grumosus) zone characteristic for the Buregi and Altovo fms (Raskatova M. 1999).

In this paper the results of studies of the miospore assemblage from the **Daugava** deposits in Latvia (boreholes no. 5 and 1-T; 15 samples from two sections) and in Pskov region (borehole no. 9; 4 samples) are presented. 35% of samples from the sections of the Daugava deposits in Latvia contained a significant amount of miospores (180-200). In the section of borehole no. 9 the content of miospores is higher than in other boreholes (up to 250). Distinctive features of the assemblage are the first appearance of the genus Archaeoperisaccus (A. ovalis Naum.) (Fig. 3 C) in the lower part of the section, increased diversity of species in the upper part of the RS (A. concinnus Naum., A. mirus Naum.) (Fig. 3 E, M), and domination of genera Geminospora and Stenozonotriletes. However, there are some differences between the dominant miospore genera in the assemblages from the sections of boreholes no. 5 and 1-T as they include Geminospora rugosa (Naum.) Obukh., G. semilucensa (Naum.) Obukh. et M. Rask., Stenozonotriletes laevigatus Naum., S. definitus Naum., Converrucosisporites curvatus (Naum.) Turnau. The diversity in the genera Geminospora (13%) and Stenozonotriletes (10%) is much less than in the assemblage from the borehole no. 9 (45.5%). Miospores belonging to the genus Converrucosisporites make 13% of all spores, but consist mainly of the remains of one species, namely C. curvatus (Naum.) Turnau. The miospore assemblage from the borehole no. 1-T is characterized by abundant large miospores with bifurcate processes Archaeotriletes conspicuous Naum. and Ancyrospora fidus (Naum.) Obukh. (Fig. 3 G,N). The assemblage from the borehole no. 9 contains the following species: Geminospora rugosa (Naum.) Obukh., G. compacta (Naum.) Obukh., G. plicata Owens, G. opipara Owens, G. semilucensa (Naum.) Obukh. et M.Rask., G. micromanifesta (Naum.) Arkh., G. nalivkinii (Naum.) Obukh. (Fig. 3 K, L), Apiculiretusispora verrucosa (Caro-Moniez) Streel (Fig. 3 F), Archaeozonotriletes variabilis Naum (Fig. 3 B), Hymenozonotrilete argutus Naum. (Fig. 3 O), Calyptosporites krestovnikovii (Naum.) Oshurk. (Fig. 3 J), Ancyrospora laciniosa (Naum.) Mants. (Fig. 3 H), Convolutispora subtilis Owens (Fig. 3 I), Kedoesporis livnensis (Naum.) Obukh. (3.1%), K. angulosus (Naum.) Obukh., Stenozonotriletes conformis Naum., S. simplex Naum., S. definitus Naum., S. conspersus Naum., S. extensus Naum. var. major Naum., S. pumilus (Waltz) Naum., S. simplicissimus Naum., S. calamites Naum., and S. formosus Naum. The species of the genus Kedoesporis dominates this assemblages reaching up to 6% in some samples. Small and medium-sized miospores with simple sculpture are also present including Leiotriletes microrugosus (Ibr.) Naum., Calamospora minutissima (Naum.) Lub. and Punctatisporites solidus (Naum.) Byvsch. Miospores with the contact area Retusotriletes communis Naum., R. simplex Naum., R. pychovii Naum., and

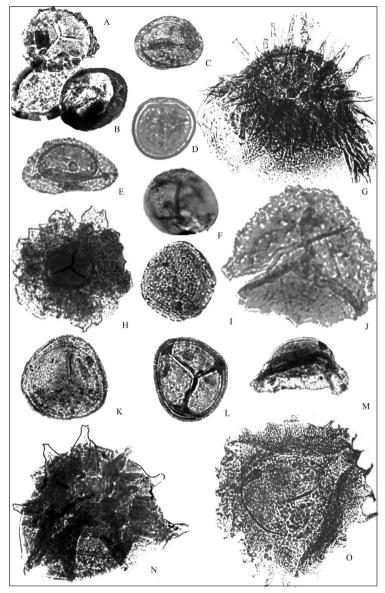


Figure 3. Frasnian miospore assemblages from Latvia. A-O, miospores from the Daugava RS: A, Verrucosisporites scurrus (Naum.) McGreg. et Camf.; B, Archaeozonotriletes variabilis Naum.; C, Archaeoperisaccus ovalis Naum.; D, Stenozonotriletes formosus Naum.; E, Archaeoperisaccus concinnus Naum.; F, Apiculiretusispora verrucosa (Caro-Moniez) Streel; G, Archaeotriletes comspicuus Naum.; H, Ancyrospora laciniosa (Naum.) Mants.; I, Convolutispora subtilis Owens; J, Calyptosporites krestovnikovii (Naum.) Oshurk.; K, Geminospora micromanifesta (Naum.) Arkh.; L, G. nalivkinii (Naum.) Obukh.; M, Archaeoperisaccus mirus Naum.; N, Ancyrospora fidus (Naum.) Obukh.; O, Hymenozonotriletes argutus Naum. VSU, no. L2011/29-31.

Verruciretusispora semilucensa (Naum.) Oshurk. are more abundant in the deposits from the Pskov region than in the samples from Latvia.

Ozolina (1963) described the miospore assemblage III from the deposits of the Daugava Fm, which was characterized by the reduced regular structure with prevalence of such genera as Stenozonotriletes, Verrucosisporites and Lophozonotriletes. This assemblage differs from the miospore assemblage established by the authors of this work. The comparison of the Daugava miospore assemblage with that from the Semiluki RS of the CDF (Raskatova L. 1969) demonstrates that most of the species are common and Geminospora and Stenozonotriletes dominate the miospore assemblages of both units. However, there are less miospores belonging to Stenozonotriletes and zonal index Perotrilites donensis (10.4%) dominates in the Semiluki miospore assemblage, whereas this zonal index is absent in the Daugava assemblage. Miospores with contact area are widely represented in both units by such species as Retusotriletes communis Naum., R. pychovii Naum. and Verruciretusispora semilucensa (Naum.) Oshurk. Miospores with verrucate ornamentation are more diverse on a species level in the Semiluki RS than in the Daugava RS, but the dominant species for both units is Converrucosisporites curvatus (Naum.) Turnau (1.9%). Thus the miospore assemblage from the Daugava RS shows the change in species composition in time, corresponding to the two Frasnian zones: Geminospora semilucensa – Perotriletes donensis (SD) and lower portion of the Archaeoperisaccus ovalis – Verrucosisporites grumosus (OG) zone (Avkhimovitch et al. 1993).

The detailed palynological study of deposits of the **Katleši RS** from two boreholes no. 5 and 6 in Latvia and borehole no. 9 in Russia shows total absence of miospores in all samples. Some samples contained fragments of the changed dark matter.

The Pamūšis RS (Ogre Fm) is characterized by miospores showing considerable variety and good preservation. Miospores of the Pamūšis RS were studied from two boreholes no. 5 and 13 in Latvia. The miospore assemblage from the Pamūšis RS is characterized by abundant species of the genus Geminospora: G. rugosa (Naum.) Obukh. (12%), G. compacta (Naum.) Obukh. (4%), G. semilucensa (Naum.) Obukh. et M.Rask. (4%), G. notata (Naum.) Obukh. (4%), as well as by a significant presence of the genus Archaeoperisaccus: A. mirus Naum. (6%), A. echynatus Rask. (3%), A. ovalis Naum. (2%), A. menneri Naum. (2%), and A. mirandus Naum. (1%). Spores of Cyclogranisporites rugosus (Naum.) Oshurk. (6%), Tuberculispora perspicua (Naum.) Oshurk. (5%), Retusotriletes communis Naum. (4%), Stenozonotriletes definitus Naum. (4%), S. simplicissimus Naum. (3%), S. pumilus (Waltz.) Naum. (3%), S. conformis Naum. (2%), Hymenozonotriletes argutus Naum. (1%), Kedoesporis evlanensis (Naum.) Obukh. (2%), Lophozonotriletes torosus Naum. (3%), Verrucosisporites grumosus (Naum.) Obukh. (2%) (Fig.4 A-G, L) are also present. Simple miospores without sculpture and ornamentation of exine are also present in significant amounts: Calamospora microrugosa (Ibr.) Schopf, Wilson et Bentall (6%), Calamospora atava (Naum.) McGregor (2%), Leiotriletes laevis Naum. (5%), L. simplex Naum. (4%). At the same time there are a lot of acritarchs (36%) in the samples from this interval. Their maximum corresponds to the depth of 38.5 m in borehole no. 5, where the forms of small size with a smooth, scabrate, or spiny exine sculpture belonging to the genera Leiosphaeridia, Lophosphaeridium,

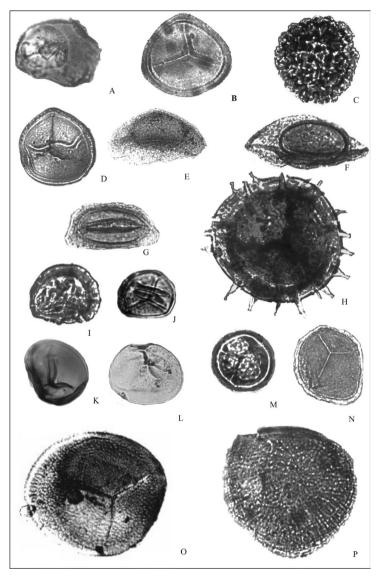


Figure 4. Frasnian miospore assemblages from Latvia. A-G, K-L, O, miospores from the Pamūšis RS: A, Cyrtospora expleta Arkh.; B, Geminospora semilucensa (Naum.) Obukh. et M.Rask.; C, Convolutispora crassitunicata (Obukh.) Obukh.; D, Geminospora notata (Naum.) Obukh.; E, Archaeoperisaccus mirandus Naum.; F, A. menneri Naum.; G, A. concinna Naum.; L, Calamospora ef. atava (Naum.) McGregor; O, Geminospora macromanifesta (Naum.) Owens. VSU, no L2011/32-33. K, microspore from uncoordinated sporangium: Stenozonotriletes laevigatus Naum. VSU, L2011/32mc. H-J, M-N, P, miospores from the Stipinai RS: H, Hystricosporites cf. grandiusculus (Kedo); I, Tholisporites densus McGreg.; J, Kedoesporis evlanensis (Naum.) Obukh.; M, Retusotriletes pychovii Naum.; N, Diaphanospora rugosa (Naum.) Byvsch.; P, Membrabaculisporis radiatus (Naum.) Arkh. VSU, no L2011/35.

Micrhystridium predominate. The remains of uncoordinated sporangium were found in the borehole no. 13. This sporangium contains acavate zonate microspores (Fig. 4 K) of small size (35-40 μ m), without sculpture. These microspores are similar to the dispersed taxon *Stenozonotriletes laevigatus* Naum.

The comparison of the Pamūšis miospore assemblage from Latvia and miospore assemblage XV from the Lower Voronezh RS of CDF (Raskatova L. 1975) shows that the content of the species in the dominant genus *Geminospora* in both assemblages is nearly the same: *G. rugosa* (12%), *G. compacta* (4%) and *G. semilucensa* (1.5-2%). In general proportions of species belonging to the genus *Archaeoperisaccus* are similar: *A. mirus* Naum. (6% and 2.1% respectively), *A. ovalis* Naum. (2 % and 2.1%), *A. menneri* Naum. (2% and 1.4%). A typical feature of these two assemblages is the presence of the index species of the genus *Archaeoperisaccus* representing the OG zone of the Middle Frasnian. The miospore assemblage from the Pamūšis RS corresponds to the middle portion of the Archaeoperisaccus ovalis – Verrucosisporites grumosus (OG) zone.

S.N. Starikova (Sorokin 1978) has allocated the miospore assemblage for the lower part of the Pamūšis RS (Lielvārde Member; Mb) near Lielvārde, Latvia. This assemblage is characterized by the abundant species of the genus *Archaeoperisaccus*, that allowed compare this member with the Petino Fm of the CDF. During this study this assemblage was not found in the sections of boreholes no. 5 and no. 13. Basing on the lithology and miospore assemblage documented in the two boreholes (8 samples were taken in the interval from 83.7 to 37.1 m, borehole no. 5; 7 samples were taken in the interval from 91.2 to 56.3 m, borehole no. 13), it can be assumed that the Lielvārde Mb is absent in the studied sections.

Ozoliņa (1963) provided a uniform miospore assemblage for the whole Ogre Fm which is characterized by the great diversity of species in the genera *Calamospora*, *Retusotriletes*, *Geminospora*, *Stenozonotriletes*, *Archaeoperisaccus*, and *Verrucosisporites*. This assemblage corresponds to the Pamūšis miospore assemblage established by the authors of this paper, which demonstrate a considerable diversity in the genera *Geminospora*, *Stenozonotriletes* and *Archaeoperisaccus*.

The miospore assemblage of the Pamūšis RS is compared with the miospore assemblages XIV of Belarus (Golubtsov *et al.* 1975) and miospore assemblages XIV – XV of the CDF (Smirnova 1974; Raskatova L. 1975). It is necessary to note that the miospore assemblage from the Pamūšis RS can be attributed to the Archaeoperisaccus mirus – Diducites radiatus (MR) regional zone which has been established for the Voronezh RS in Belarus (Obukhovskaja *et al.* 2005).

Miospores of the **Stipinai RS** were studied from borehole no. 5 in Latvia. This miospore assemblage is characterized by the dominance of species of the genus *Geminospora*: *G. rugosa* (Naum.) Obukh. (7%), *G. compacta* (Naum.) Obukh. (6%), *G. micromanifesta* (Naum.) Arkh. (4%), and *G. semilucensa* (Naum.) Obukh. et M. Rask. (2%). Other genera are represented by approximately the same percentage of the species: *Membrabaculisporis radiatus* (Naum.) Arkh. (2%), *Diaphanospora rugosa* (Naum.) Byvsch. (3%), *Stenozonotriletes conformis* Nuam. (4%), *S. definitus* Naum. (3%), *Tholisporites densus* McGreg (2%), *Verrucosisporites grumosus* (Naum.) Obuch. (2%), *Converrucosisporites curvatus* (Naum.) Turnau (3%),

L. grumosus (Naum.) Sull. (2%), Retusotriletes communis Naum. (4%), R. pychovii Naum. (4%), Cyclogranisporites rugosus (Naum.) Oshurk. (5%), C. rotundus (Naum.) Oshurk. (2%), Kedoesporis evlanensis (Naum.) Obukh. (7%), and Hystricosporites cf. grandiusculus (Kedo) (3%) (Fig.4 H-J, M-N, P,). Simple miospores without sculpture and ornamentation of exine are also present in the miospore assemblage: Calamospora minutissima (Naum.) Lub. (7%), C. atava (Naum.) McGregor (3%) and Punctatisporites solidus (Naum.) Byvsch. (3%). Small acritarchs (30%) with a smooth exine belonging to the genera Leiosphaeridia, Trachysphaeridium, Baltisphaeridium, and Yranomarginata have been found within the assemblage from the depth 34.7 m. Archaeoperisaccus is not presented in the material of this study from the Stipinai RS, what can be explained by a small number of the studied samples, although the corresponding stratigraphic level in other regions is characterized by a steady enough presence of the species of this genus.

The first (I) miospore assemblage allocated for the Bauska Beds and the Amula RS in western Latvia by Ozoliņa (1963) contains small quantity of miospores thus differing from the miospore assemblages from the Upper Frasnian deposits of the CDF.

The Stipinai miospore assemblage has been compared with the miospore assemblage XVI of the CDF (Raskatova 1975), which was established for the Upper Voronezh RS of the Upper Frasnian of the East European Platform. The miospore assemblage from the Stipinai RS is characterized by the appearance of *Membrabaculisporis radiates* (index species of the MR subzone) and species such as *Diaphanospora rugosa* (Naum.) Byvsch., *Kedoesporis livnensis* (Naum.) Obukh., and *Verrucosisporites grumosus* (Naum.) Obuch., which are typical for the Auroraspora speciosa (AS) subzone. This subzone characterizes the Evlanovo RS. As it was already noted for the Pamūšis RS the miospore assemblage from the Stipinai RS can be referred to the MR regional zone which was allocated in Belarus (Obukhovskaja *et al.* 2005).

Conclusions

Miospore assemblages, zones and subzones are of a great importance in modern international and regional scales. There is not enough material to trace all miospores zones and subzones in the Upper Devonian deposits of Latvia, but the first steps have been already made. In this study five miospore assemblages characteristic for the Pļaviņas, Dubnik, Daugava, Pamūšis and Stipinai RS, Frasnian deposits of Latvia has been allocated, and the attempt to identify miospore zones and subzones for the deposits of the Pļaviņas, Dubnik, Daugava, Pamūšis and Stipinai RS has been made.

Previous researchers have described only miospore assemblages, based on the studies carried out in the middle and second half of the 20th century when the zonal miospore biostratigraphy of the Devonian has only started to develop. Compared with the studies of Ozoliņa (1963), in this study each regional stage for the first time is characterized by a separate miospore assemblage.

One subzone BI (Acanthotriletes bucerus – Archaeozonotriletes variabilis insignis) and two miospore zones, SD (Geminospora semilucensis – Perotriletes

donensis) and OG (Archaeoperisaccus ovalis – Verrucosisporites grumosus), have been identified according to the miospore zonation of the Frasnian Stage of the East European Platform. Regional zone MR (Archaeoperisaccus mirus – Diducites radiatus), first described from the Voronezh RS of Belarus (Obukhovskaja *et al.* 2005), has been traced within the Pamūšis and Stipinai regional stages. The miospore assemblage of the Pamūšis RS is compared to the miospore assemblage XIV of Belarus (Golubtsov *et al.* 1975) and miospore assemblages XIV–XV of the CDF (Smirnova 1974; Raskatova L. 1975).

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Different Tills in Palaeovalleys of Saint-Petersburg

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Studied palaeovalleys are complicated geological objects with unstable engineering-geological properties being analyzed. Palaeovalleys are mainly filled with Upper Valdaian (Weichselian) glacial (tills), glaciofluvial (sand, gravel and pebbles), limnoglacial (varved clay) and Holocene marine sandy-gravelly deposits. The deposits of the Middle Pleistocene of varying composition, structure, physical and mechanical properties are also present. This paper deals with the main results of geotechnical and geo-environmental studies of the tills helping the rational use of areas with palaeovalleys. The palaeovalleys have great practical importance as they contain common building materials (sand and gravel) and drinking water. Land subsidence in valleys may reach several metres, impeding town construction and normal exploitation of water and sewage communications.

Keywords: Quaternary deposits • incised valleys • tills • geotechnical properties • geoecology

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Introduction

The Quaternary history in Saint-Petersburg area can be divided into three main stages.

Stage 1, Middle Pleistocene (390 000-140 000 years ago) is marked by two glaciations, Vologda (Dnieper) and Moscow, which are separated by interglacials. Glacial deposits of the mentioned glaciations form "lower" and "middle" till beds in the buried valleys in the most part of the city's territory.

Stage 2, Late Pleistocene (140 000-10 000 years ago) marked by Mikulino (Eemian) interglacial and Valdaian (Weichselian) glaciation. The climate of the Mikulian time was warm and humid. The uppermost part of the glacial deposits belongs to the Ostashkovo Regional Stage or the Luga stage of the Valdaian glaciation. Within the limits of Saint-Petersburg the Luga till is spread everywhere and has uneven thickness and topography. The thickness of the till bed changes from some to dozens of meters and locally it crops out to the surface. This till bed has great practical importance in the city building.

Stage 3, Late- and post-glacial period linked to the evolution of the Baltic Sea with 6 cycles: local proglacial lakes, the Baltic Ice Lake, the Yoldia Sea, the Ancylus Lake, the Littorina Sea, and the Limnea Sea.

Among the Quaternary deposits different genetic types such as glacial, glacio-fluvial, limnoglacial, marine and limnic are distinguished. Quaternary deposits in Saint-Petersburg area cover the uneven surface of the pre-Quaternary rocks, varying from the Upper Vendian Kotlin and Redkino Regional Stages (RS; Fig. 1) to the Lower Cambrian Lontova RS, Lomonosov and Siverskaya formations (Fm) almost everywhere; Middle Cambrian Sablino Fm, Upper Cambrian Ladoga Fm, Lower and Middle Ordovician and Middle Devonian deposits are distributed only in the southern part of the city (Spiridonov 2009).

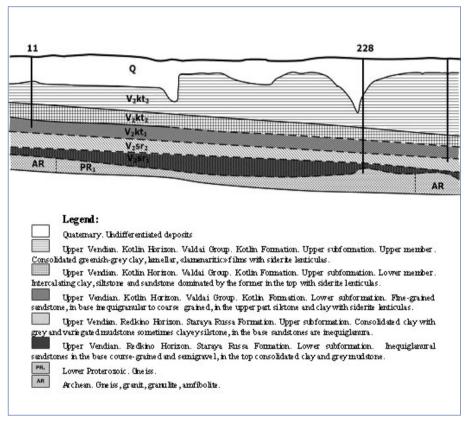


Figure 1. Geological section of the northern part of St. Petersburg (according to data of GGUP SF Mineral).

Pre-Quaternary (buried or partly buried) relief is cuesta like, corresponding to the denudation plain gently dipping south-eastwards. The bedrock is dissected by a network of up to 130-140 meters deep incisions (paleovalleys) (Fig. 2). They form the well-developed Pre-Pleistocene river system which was controlled by a network of tectonic dislocations.

Two paleovalleys which cross the northern and central parts of St.-Petersburg are the largest (Fig. 3), the third one is located at the right bank of the Neva River.

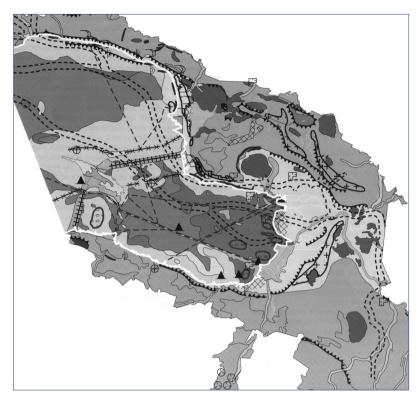


Figure 2. Geomorfological map of St. Petersburg (from: Geological atlas of Saint-Peterburg, 2009). Palaeovalleys are designated by dotted line.

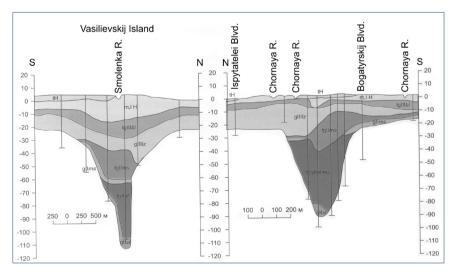


Figure 3. Distribution of buried valleys in the northern part of Saint Petersburg near the square of Muzhestva and on the Vasilievskij Island along the Smolenka River.

Buried paleovalleys are extremely complicated geological objects with heterogeneous engineering, geological and hydrogeological conditions regarding thickness, composition and geotechnical properties of Quaternary deposits, which are highly influencing to the stability of the territory. Land subsidence in valleys may reach several metres, impeding town construction and normal exploitation of water and sewage communications. Especially complicated are the processes on the slopes of the valleys (Dashko and Norova 2001; Dashko *et al.* 2011, Kiryukhin and Norova 2009). The depth of incisions into the bedrock varies considerably (Table 1). Steepness of slopes is relatively small (12-18°). The width of the buried valleys can reach several kilometers. In the valleys detailed engineering-geological, hydrodynamic and hydrochemical studies are needed. Special attention should be paid to the technogenic pollution of the groundwater.

Table 1 Systematization of the buried valleys by the depth of incision

Type of valley	Depth of incision in the basement clay, m	Thickness of the Quaternary deposits, measured from the surface, m		
Deep	60-90	up to 120		
Medium deep	30-60	up to 90		
With a small erosional incision	less then 30	up to 40		

When solving engineering-geological problems in this area special attention should be paid to the glacial deposits. Tills of three stages of glaciations are recognized in the Quaternary succession of paleovalleys: the upper, Ostashkovo till (gIIIos), the middle, Moscow till (gIIms) and the lower, Vologda till (gIIvl).

Materials and methods

Till in general and in paleovalleys are characterized by their textures and structures, composition, and physical and mechanical properties. Often they are changed by hypergenetic (soil-formation) processes. Magmatic and metamorphic rocks from Finland and their fragments form a large part of tills. The mudstone-like tills can reach extremely high density and strength as a result of self-compression.

Mineral and grain-size composition of glacial deposits is closely related to the composition of bedrock where the glaciers moved. The main rock-forming mineral in silty and sandy fractions of tills is quartz and in the heavy subfraction there are a lot of amphiboles, garnets and iron minerals (magnetite and hematite). Feldspars, micas and other minerals are of secondary importance (Table 2).

Clay fractions consist mainly of illite with low exchange capacity; absorption capacity does not exceed 5-8 mg/equiv to 100 g of rock; Ca²⁺ and Mg²⁺ prevail in the composition of the absorbed cations. Chaotic, nest and rarely porphyritic textures are typical of glacial deposits.

Table 2
Mineral composition of the fractions of tills

		Content					
Fraction	Minerals	According to G.P. Mazurova	According to E.V. Ruhinoy (1960)	According to M.E. Vigdorchik (1962)			
		(1964)		Moscow till	Ostashkovo till		
Light	Quartz	70-80	79,4	63,4	60,2		
	Feldspars	10-20	15,5	15,7	11,3		
	Mica	1-5	2,4	0,7	0,3		
	Carbonates	-	-	12,7	13,2		
Heavy	Hornblende	35-50	32,1	10,5	8,6		
	Pomegranate	-	10,3	2,0	24		
	Epidote	5	8,6	3,0	1,9		
	Zircon	-	3,6	6,2	3,9		
	Rutile	-	-	1,3	2,0		
	Siderite	-	-	0,6	3,9		
	Barite	-	-	15,6	0,4		
	Ore minerals	10-25	34,6	52,6	62,1		

Tills are characterized by the high variability in grain-size distribution (Kagan and Solodukhin 1971, Fursa 1975, Norova 2000, Dashko and Norova 2001). Silt dominates (56% on an average) in the till composition, the content of sand and clay fractions is relatively small: 22 and 18% respectively. However, the content of different fractions in the tills within paleovalleys varies widely. Archive materials testify that about 60% of the tested deposit specimens belong to loam, somewhat more than 33% constitute sandy loam, less than 10% clay. The comparison of Ostashkovo and Moscow tills shows their similarity.

General heterogeneity increases when tills contain lenses and interbeds of coarse sand, (more rarely silty and fine sand) with pressure water. Such lenses may play a negative role when constructing the deep foundation pits and underground structures.

Tills often contain boulders of different sizes. Sometimes gravel-boulder-pebble inclusions in tills significantly complicate underground building.

Comparison of the mean values of the physical properties of different aged tills shows that from the lower to upper strata the moisture content and porosity increase, and density decrease (Table 3).

Different aged tills sometimes contact each other, but more often they are separated by glaciofluvial or limnoglacial deposits, which consist mainly of sand fractions, loam (from a very stiff to very soft consistency), more rarely of sandy loam, clay or gravel.

		(Fursa,	1975)					
The soils	Plasticity index, %	Soil density, g/sm ³	Dry soil density, g/sm ³	Void ratio	Water content, %			
Vologda Regional Stage (gIIvl)								
Loam and clay	9	2,26	2,05	0,33	10,0			
Moscow Regional Stage (gIIms)								
Loam	10	2,14 1,87		0,43	13,5			
Sandy loam	5	2,27	2,08	0,29	9,7			
	Ostas	hkovo Regioi	nal Stage (gIIIos)					
Silty clay 20		2,02	1,69	0,67	25,3			
Silty loam	Silty loam 10-11		1,70-1,82	0,60-0,71	17,2-22,0			
Sandy loam	3	2,21	1,96	0,36	13,0			

Table 3
Main indicators of physical properties of tills of different age from St. Petersburg
(Fursa, 1975)

Intertill sandy deposits in paleovalleys contain ground water with low protective characteristics, especially in the upper intertill aquifer close to the surface. Changing lithological composition of the upper aquitard and existence of "hydrogeological windows" influences the quality of the groundwater. Evaluating the hydrogeological conditions in the paleovalleys it is important to solve the problems of protection of the fresh ground water deposits which are linked to the intertill aquifers. During the research work drilling stations should be safely protected and later eliminated to prevent the flowing of the ground water into other aquifers.

It is also important to consider the changing of piezometric level in the lower Kotlin aquifer which affects the deformation properties of the rocks and diminishes the stability of the utilities themselves.

Results and interpretation

A large amount of experimental studies carried out by the Department of Hydrogeology and Engineering Geology under the supervision of prof. R.E. Dashko showed that it is important to use differentiated approach to deposits in palaeovalleys, depending on the lithotype, the depth of rocks and pollution probability.

Studies on various sites showed that differences of the engineering-geological features of tills depend on the spatial position of the till horizon (Dashko *et al.* 2000, 2001, 2011). Several types of tills can be established:

Type I: till is spread in conditions of surface bedding and sufficient aeration (oxidizing conditions).

Type II: till under limnoglacial deposits without the organic matter (microaerophilic or reducing conditions).

Type III: till under the Litorina Sea deposits with the organic matter and deposits of the Baltic Ice Lake (reducing conditions).

Type IV: till under buried peat bogs (reducing conditions).

The indicators of durability, deformational capability and physical condition of these genetically solid formations are greatly variable. In most cases they cannot serve the bearing horizon for rammed in and bored piles at constructing and reconstructing of ground structures (Table 4).

 $\label{eq:Table 4} Water content (W), liquidity index (I_L), strength parameters (cohesion C, angle of internal friction <math display="inline">\phi$) and the modulus of total deformation (Eo) of till sandy loam and loam in standard sections

The section	W. %	T	Strength p	Fo MDo		
The section	VV, 70	I _L	C, MPa	φ,°	Eo, MPa	
I	8-14	<0,25	>0,15-0,32	>15-25	≥40-50	
II	14-17	0,25-0,45	0,04-0,07	6-10	2,4-4,3	
III, IV	16-19	0,25-0,50	0,03-0,05	0-7	2,1-3,6	

Pollution greatly affects the status and parameters of physical and mechanical properties of the till in the palaeovalleys. Studying the properties of glacial deposits near the square of Muzhestva and on the Vasilievskij Island allowed estimate some regularities of their condition and properties transformation. Contamination of groundwater leads to the development of complex physical, chemical and biochemical interactions between the liquid and solid phases of dispersed soil.

Special attention must be paid to the nature of deformation and strength of loam and sandy loam tills. For all samples the nature of plastic deformation without breaking the continuity of the sample is indicated.

Modulus of deformation of the upper tills has anomalously low values of 1.1 MPa on the average. The modulus of total deformation of the Moscow till is higher reaching up to 4 MPa on the average and up to 7.5 MPa in some cases.

Ostashkovo and Moscow tills preserve high density and have a wide variation of strength parameters (cohesion-C = 0.03-0.05 MPa and 0.10-0.14 MPa, respectively, ϕ = 0-14 °). Moscow till is a little stronger, as it is less affected by anthropogenic factors.

Table 5
Some indicators of the grain-size composition, physical and mechanical properties of the tills, depending on their position in the section (slope of paleovalley on Vasilievskij Island)

	Grain-size composition,			e, %		Strength parameters		,	
Depth, m	gravel	gravel sand silty fraction clay Moisture,	Consistence	Cohe- sion, MPa	Angle of internal friction, deg	Comment			
26,5 - 33,6	traces	11	66	23	22 24	firm – stiff soft – firm	0,043 0,024	10 4	Number of determinations
33,7 - 35,0	-	1	69	30	26	firm – stiff	0,040	3	more then 25

In the palaeovalley slope under the Smolenka River the content of clay and silt fractions, the values of moisture content, plasticity limits are shown in the table 5. The mechanical properties of till formations are characterized according to data of triaxial compression tests. The results show that glacial deposits in the zone of intense pollution here are highly deformable and weak. The destruction of samples in triaxial compression apparatus mostly occurs without the formation of the glide plane. Modulus of deformation of till loam varies in a rather wide range from 0.6 to 3.3 MPa.

Thus our studies of the till properties show that strength and deformation capacity parameters differ in accordance with natural and technogenic factors and the level of contamination. The development of natural and natural-technogenic processes in the palaeovalleys has great influence on the conditions of structure's construction and exploitation. For tills it is a non-uniform compressibility, frost heave and others.

Conclusions

The geological structure of Quaternary strata within the palaeovalleys is changeable. This changeability has been formed due to the effect of river erosion and appears in sharp power fluctuations and variety of different genetic types of deposits. In the longitudinal profile of the erosion incision both clayey and sandy areas, which serve as repositories of pressure, intertill aquifers are observed. The most important features of glacial deposits in the palaeovalleys from the engineering-geological point of view are:

- 1) The presence of the three horizons of tills of different age and peculiar conditions of their occurrence;
- 2) Greater variability in the grain-size composition;
- 3) The presence of intertill sand, weak soft clay and loamy interlayers which create difficulties during construction;
- 4) Significant variation in mechanical properties in accordance with the spatial position of the tills, pollution and other factors;
- 5) The risk of natural and natural-technogenic processes going on.

Thus engineering-geological conditions in the palaeovalley zones are on the whole characterized as unfavourable for all kinds of building processes. While the process of integrated development of this territory is necessary to provide identification of: the depth of the roof of the bedrock, the position and parameters of till formations, spread of intertill artesian waters and areas of "hydro-windows". The study of engineering-geological features should be complex and detailed.

Engineering-geological zonation is important already at the pre-project stage of a research. Working out of the structure of the local complex monitoring is recommended at building of complicated objects and solving problems of protecting ground waters. Geophysical methods are required in addition to the drilling and sampling.

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New Data on the Devonian Plant and Miospores from the Lode Formation, Latvia

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The higher plant of Progymnospermopsida *Svalbardia bankssi* Matten is described from taphocoenosis A of the Devonian Lode Formation in Lode clay pit. This locality is the second in the world besides the type locality from North America where this plant has been found. Miospores taken from the same deposits containing impressions of *S. banksii* demonstrate the Givetian age of the taphocoenosis A.

Key words: Frasnian • Givetian • Lode clay pit • miospores • progymnosperm. *Manuscript submitted 5 October 2011; accepted 12 December 2011.*

Introduction

Devonian period is characterized by rapid development of higher plants from the first primitive land plants to the first representatives of gymnosperms. Flora is represented by hundreds of plant genera and species in many parts of the world. Information about the Devonian plants from Latvia is scarce. In the early 80-ies of the last century mass graves of fishes, as well as plant remains were discovered at the base of the supposedly Upper Devonian deposits cropping out in the Liepa (Lode) clay pit in the north-eastern part of Latvia (Kuršs and Lyarskaya 1973). In 1971-1972 one of us (A.L. Jurina) had opportunity to collect fossil plants in the Lode quarry by the invitation of L.A. Lyarskaya. Plants are represented by imprints, preserved in clay. According to the method used in storing and transporting of fossil remains, the clay gypsum-plaster capsules with the rock and the fossils inside them were prepared. During transportation from Riga to Moscow samples were lost in the Moscow State University and seemed impossible to find. Fortunately, as a result of enhanced searching most of the capsules with the plant remains were found.

The purpose of this article is to describe these plants, discuss the status of the genus *Svalbardia* and evaluate the age of the deposits based on the described plants and miospores extracted from the clay, containing imprints of plants.

Stratigraphy

Typical deposits of the Lode Formation (Fm) are present in the Lode clay pit. This formation has been established for the north-eastern Latvia by V. Kuršs (1975) and corresponds to the upper part of the Gauja Regional Stage (RS). Many researchers (Kuršs and Lyarskaya 1973; Kuršs 1975; Kuršs et al. 1998; Upeniece 2001, 2011) placed this formation within the Upper Devonian (Frasnian). Now the most of scientists attribute this formation to the Late Givetian age and suggest drawing the Givetian-Frasnian boundary between the Amata and the Plavinas RS (Lukševičs 2001; Stinkulis et al. 2011; and others). In Lode clay pit the Lode Fm contains mainly fish and plant remains, forming several taphocoenoses designated by capital Latin letters (Kuršs et al. 1998). Plant and miospore assemblages described in this paper have been collected in the taphocoenosis A (Kuršs and Lyarskaya 1973). Fishes Asterolepis ornata Eichw., Laccognathus panderi Gross, Panderichthys rhombolepis Gross in this taphocoenosis are found at three levels. Plants lie below the levels with fishes. Taphocoenosis A was situated probably in the upper part of the Lode Fm in accordance with verbal supposition of E. Lukševičs. His opinion is that the taphocoenosis A approximately is slightly older than the taphocoenosis F and situated below (Kuršs et al. 1998). Now this part of geological section with taphocoenosis A is deeply buried under the scree.

It was originally mentioned (Kuršs and Lyarskaya 1973; Kuršs *et al.* 1998) that flora in the taphocoenosis A is represented by *Rhacophyton* sp. and *Archaeopteris* sp. (preliminary determination of A.L. Jurina). Later it was considered that the collection is lost. A.L. Jurina (1988) has made specification in flora definition based on the field sketches as *Archaeopteris fissilis* Schmalh., which appeared incorrect as the preliminary determinations. A new study of collection material shows that there is the higher plant *Svalbardia banksii* Matten in the taphocoenosis A.

Systematic palaeontology

Class Progymnospermopsida Beck Order Pityales Family Svalbardiaceae Nemejc Genus *Svalbardia* Høeg, 1942 *Svalbardia banksii* Matten, 1981 Figs 1-2 *Svalbardia banksii*: Matten, 1981, p. 1383, fig. 1-7.

Holotype. Southern Illinois University, Paleobotanical Collection, No 685; Sullivan County, New York State; Delaware River Flags, Oneonta Formation, lower Upper Devonian (Frasnian).

Description. The larger axis is about 12 mm wide at its base and up to 5 mm wide in upper part and is 51 cm long. This main axis (or the axis of first order?) bears spirally arranged up to 5 cm long and from 5 to 7 mm wide subordinate axes. The angle between the main and subsidiary axes is 30°-35°. All the axes are



Figure 1. Svalbardia banksii Matten, 1981, from Liepa (Lode) clay pit; Devonian, Lode Fm, taphocoenosis A. A, general view of the imprint of the main (first order?) and lateral axes, MSU, No 330/11. B, attachment of leaf to the axis, MSU, No 330/2. C, irregularly striated axes, MSU, No 330/10. D, axis of first order with three lateral axes (the "ribs" reflected of vascular strands), MSU, No 330/1. E, irregularly striated axes, MSU, No 330/15. Scale bars 1 cm.

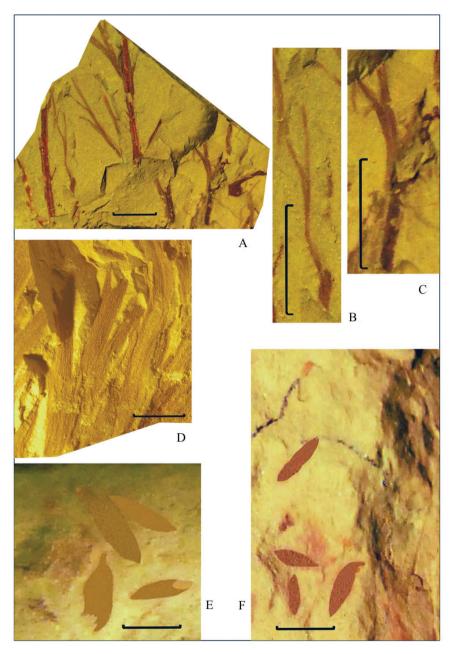


Figure 2. Svalbardia banksii Matten, 1981, from Liepa (Lode) clay pit; Devonian, Lode Fm, taphocoenosis A. A, isolated leaves, MSU, No 330/3. Scale bar 1 cm. B-C, the same specimen as in A, leaf dichotomized two times. Scale bar 3 cm. D, dichotomized striated leaves, MSU, No 330/8. Scale bar 3.5 cm. E, uncoordinated sporangia, MSU, No 330/7. Scale bar 2 mm. F, uncoordinated sporangia, MSU, No 330/6. Scale bar 2 mm.

somewhat irregularly striated, perhaps reflecting remains of vascular strands passing towards the leaves. The subordinate axes bear what are interpreted as leaves. Leaves unwebbed dichotomizing from 2 to 4 (in the main 3) times are deeply divided into identically long (from 7 mm to 1-2 mm) and wide (0.5-0.6 mm) four, sometimes eight, lobes. The angle between lobes is 8°-10°. The leaves are cuneiform (overall outline is fan-shaped), about 3 cm long and up to 4 mm at the base. In the matrix the leaves are found in the main separately from axes.

We have seen no evidence of sporangia being preserved in organic connection with axes. There are four impressions of uncoordinated sporangia of poor preservation disposed in the matrix nearby the described axes. The sporangia are cylindrical, 1.5-2 mm long and 0.5-0.7 mm thick. These sporangia possibly belong to *Svalbardia banksii*.

Locality. Liepa (Lode) clay pit is located in the Liepa municipality, north-east of Riga, 15 km to the south from Valmiera, at the left bank of the river Gauja.

Horizon. Gauja RS, Lode Formation, taphocoenosis A, Devonian.

Material. The described plant remains occur in the clay. When clay dries up, the imprints break up to numerous fragments which are difficult to combine. About 30 fragments of impressions (parts and counterparts) with axes of different orders and leaves are preserved. This complicates the description and photography of specimens. Studied material belongs to the collection No 330, Department of Palaeontology, Faculty of Geology, Moscow State University, Moscow, Russia.

Miospores

Miospores are taken from the same clay containing *Svalbardia banksii* and have been studied by M.G. Raskatova. Miospores were studied with light microscope POLAM-312 and photographed by NIKON camera in the Laboratory of Historical Geology and Palaeontology, Faculty of Geology, Voronezh State University (VSU), Voronezh, Russia. Collection of preparations No L2011 is housed in VSU.

Composition of the assemblage from taphocoenosis A is reduced. Miospores have satisfactory and seldom good preservation. In total there are about 20 species of miospores in the assemblage including Leiotriletes perpusillus Naum., L. laevis Naum., L. simplex Naum., Calamospora minutissima (Naum.) Lub., Punctatisporites solidus (Naum.) Byvsch., Lophotriletes minutissimus Naum., Retusotriletes radiosus Rask., R. simplex Naum., Dictyotriletes sp., Apiculatisporis uncatus (Naum.) Oshurk., A. eximius (Naum.) Oshurk., Iugisporis impolitus (Naum.) Oshurk., Geminospora rugosa (Naum.) Obukh., G. notata (Naum.) Obukh., G. micromanifesta (Naum.) Arkh., G. micromanifesta (Naum.) Arkh. var. crispus Tschibr., G. cf. nalivkinii (Naum.) Obukh., Ancyrospora incisa (Naum.) M.Rask. et Obukh., A. fidus (Naum.) Obukh., A. furcula Owens, Chelinospora concinna Allen, C. cf. timanica (Naum.) Loboz. et Streel, Stenozonotriletes simplex Naum., Biharisporites sp., Hystricosporites sp. Miospore assemblage is characterized by the dominance of genus Geminospora: G. micromanifesta – 8.5%, G. rugosa – 7.5 %, G. nalivkinii – 5.5%, G. notata – 4.5% and also contains large miospores (<300 μm) with processes: Ancyrospora incisa – 3%, A. fidus – 3.5%, A. furcula – 1.2%, Hystricosporites sp., some of them with lost

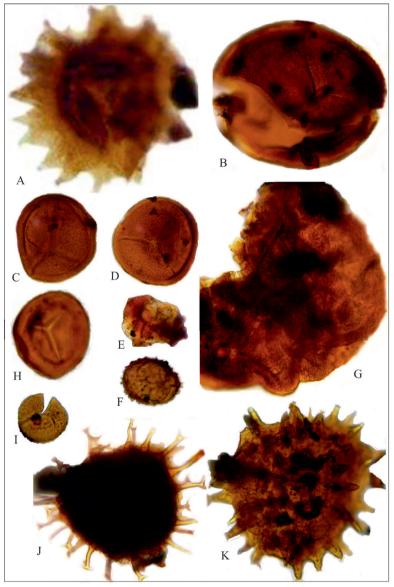


Figure 3. A-C, E-F, H-K: Miospore assemblage belonging to the Ancyrospora incise Geminospora micromanifesta (IM) subzone. A, Ancyrospora incisa (Naum.)
M.Rask. et Obukh.; B, Biharisporites sp.; C, Geminospora micromanifesta
(Naum.) Arkh. var. crispus Tschibr.; E, Chelinospora cf. timanica (Naum.)
Loboz. et Streel; F, Chelinospora concinna Allen; H, Retusotriletes radiosus
Rask.; I, Apiculatisporis eximius (Naum.) Oshurk.; J, Hystricosporites sp.;
K, Ancyrospora fidus (Naum.) Obukh., VSU, No L2011/4d; magnification x
500. D, microspore from dispersed microsporangium Geminospora cf.
nalivkinii (Naum.) Obukh., VSU, L2011/5ms, x 500. G, fragment of dispersed
microsporangium with microspores, VSU, L2011/5sp, x 450. All specimens
from the Liepa (Lode) clay pit; Devonian, Lode Fm, taphocoenosis A.

processes and dark in colour. Other large miospores ($<200 \,\mu\text{m}$) from this assemblage belong to *Biharisporites* sp. -3.5%, some of them were destroyed. Miospores with conate ornamentation: *Apiculatisporis uncatus*, *A. eximius*, *Iugisporis impolitus* and with reticulate patina: *Chelinospora concinna*, *C.* cf. *timanica* are present in equal amounts (2-3%). Species of *Leiotriletes* (10-15 $\,\mu\text{m}$) with a smooth exine partially covered with sporangial tissue have also been found in preparation. From the same clay we have taken one destroyed sporangium in which microspores are preserved, most likely, connected in tetrads. These microspores are very similar to the dispersed taxon *Geminospora* cf. *nalivkinii*.

Discussion

I. Genus *Svalbardia* was introduced by Høeg (1942) with one species of *S. polymorpha* based on a large amount of factual material. According to Høeg *Svalbardia* is a plant with spirally arranged branches and forked unwebbed leaves. Høeg (1942) recognized also the striking resemblance between his new genus and *Archaeopteris fissilis* (Schmalhausen 1894). The last is species with unwebbed pinnules. The separation between *Svalbardia* and *Archaeopteris* (especially *A. fissilis*) had gradually been eroded. There is considerable discussion in the literature concerning status of *Svalbardia* as a valid genus. Most of researchers (Høeg 1942; Petrosjan and Radczenko 1960; Stockmans 1968; Chaloner 1972; Matten 1981; Schweitzer 2006, as well as one of the authors of this paper, Jurina) accept *Svalbardia* as valid genus while minority (Beck 1971) can't agree with this opinion. Beck proposes to include it into the genus *Archaeopteris*, considering it a synonym of the latter. Gensel and Andrews (1984) incline toward the latter opinion but left themselves the possibility to solve this problem in the future when more information will come.

Carluccio et al. (1966) examined similarities and differences of Svalbardia from Archaeopteris and proposed the following conception: genus Archaeopteris possessing varying degrees of webbed pinnules; a species of Svalbardia are with unwebbed pinnules. The authors of this paper accept the proposal of Matten (1981) and use the genus Svalbardia in this sense as the form-genus. In conclusion according to Carluccio et al. (1966), Matten (1981) and our opinion Archaeopteris fissilis should be placed in genus Svalbardia. Chaloner (1972) also noted the difference between the two genera: species of Archaeopteris have laminate leaves, but species of Svalbardia have leaves dissected into narrow lobes. However, the reproductive structures of the two genera are of basically rather similar organization.

II. Seven species have been mentioned in literature belonging to the genus *Svalbardia*: the type species *S. polymorpha* Høeg, 1942 (Givetian or Frasnian, Spitsbergen); *S. osmanica* Petrosjan et Racdczenko, 1960 (Frasnian, Russia); *S. boyi* Kräusel et Weyland, 1960 (Givetian, Germany); *S. fissilis* (Schmalhausen) Carluccio *et al.*, 1966 (Upper Devonian, Ukraine, Canada); *S. avelinesiana* Stockmans, 1968 (Givetian, Belgium); *S. scotica* Chaloner, 1972 (Givetian, Scotland); *S. banksii* Matten, 1981 (Frasnian, New York, USA). Lode in Latvia is now the second locality of *S. banksii* in the world. Today the third and fifth of seven species just cited are not belonging to the genus *Svalbardia*. *S. boyi* is considered to be a species of

Archaeopteris (Carluccio et al. 1966). We agree with the opinion of Beck (1971) that Svalbardia avelinesiana might be assigned to several different genera including Archaeopteris, Pseudosporochnus and others. It is necessary to study the original material. According to our concept of the genus Svalbardia and following Carluccio et al. (1966) and Matten (1981) we include the species Archaeopteris fissilis into the genus Svalbardia. The species of Svalbardia are characterized by variability in leaf form, between several deeply divided lobes of various length and width with filiform segments. The filiform segments of leaves are typical only to S. polymorpha. S. banksii is characterized by long and narrow leaf segments which are divided dichotomously more than twice into four or eight lobes. S. banksii more closely resembles S. osmanica from the Frasnian of Russia but differs from it by lack of decurrent petioles.

III. C.B. Beck (1960) proposed the class of higher plants Progymnospermopsida. It is characterized by free spore-bearing plants with a pteridophyte standard of reproduction and foliage combined with gymnospermous anatomy. Beck demonstrated that certain fossils of fern-like foliage (genus *Archaeopteris*) were borne on petrified stems of gymnospermous anatomy (genus *Callixylon*). Later several orders have been allocated into this class. *Archaeopteris* is placed in the Pityales of this class. The researchers previously described *Svalbardia* noted the similarity with genus *Archaeopteris*. We accept the views of Carluccio *et al.* (1966) and Chaloner (1972) that similarity between these two genera should be acknowledged grouping in the same order Pityales. Gensel and Andrews (1984) and Taylor *et al.* (2009) include tentatively genus *Svalbardia* in the order Archaeopteridales because all distinctive features of the progymnosperms are not present.

IV. Devonian miospores of Latvia for the first time have been studied by Ozoliņa (1963). She distinguished miospore assemblages on the basis of study of large material from the boreholes and outcrops in Latvia. Gauja Fm and Amata Fm were characterized by a uniform assemblage V. Ozoliņa compared the V assemblage to the XVI assemblage of the Central Devonian Field (CDF). She didn't propose zones and subzones. We compared miospore assemblage from the Lode Fm with the miospore assemblage V of Ozoliņa. Miospore assemblage V is characterized by a larger number of genera and species (about 30) in comparison with the assemblage from taphocoenosis A because the former corresponds to a wider stratigraphical interval and studied in a wide area (Plaviņas, Ālanda, Līvāni, Katlakalns, Ķemeri). The common forms for the assemblage from the taphocoenosis A and assemblage V are species of genera: *Geminospora, Apiculatisporis, Lugisporis* and *Retusotriletes*. Difference between them consists in the absence of *Ancyrospora incisa* in the assemblage V.

Miospores have been examined in details from the Lode Member (Gauja Fm) in the locality Küllatova (Estonia). Following assemblage of miospores has been established there and was compared to the IM Subzone (Mark-Kurik et al. 1999): Geminospora micromanifesta (Naum.) Arkh., G. lemurata Balme, emend. Playford, Retusotriletes regulatus Riegel, Cristatisporites triangulatus (Allen) McGreg. et Camf., Samarisporites eximius (Allen) Loboz. et Streel, Ancyrospora sp. cf. A. incisa (Naum.) M.Rask. et Obukh., Dictyotriletes sp. cf. Reticulatisporites perlotus (Naum.) Obukh., Perotriletes sp. cf. Rugospora? impolita (Naum.) Tchibr.

Systematic composition of the miospore assemblage from Küllatova is close to the assemblage from taphocoenosis A. Species in common are: *Geminospora micromanifesta*, *G. lemurata*, *Ancyrospora incisa*. Difference consists in the absence of *Cristatisporites triangulatus*, *Samarisporites eximius*, *Reticulatisporites perlotus*, *Rugospore*? *impolita* in the assemblage from taphocoenosis A. Miospore assemblage described from the Lode Fm by us is richer in systematic composition (20 species compared with 8), miospores demonstrate a better preservation in the whole, and the index of Subzone has better preservation. Distinctive feature of the assemblage from taphocoenosis A is the presence of megaspores *Biharisporites* differing it from the assemblage V (Ozolina 1963) and from the Küllatova assemblage.

According to our research the general structure of miospore assemblage from the taphocoenosis A corresponds to the *Ancyrospora incisa - Geminospora micromanifesta* (IM) Subzone, which previously was located at the base of the Frasnian stage (Avkhimovitch *et al.* 1993). At the present time Stratigraphical Committee of Russia offers to trace the boundary of the Givetian and Frasnian stages at the base of the Upper Timan Substage of the East European Platform (Sobolev and Evdokimova 2008). According to this decision IM Subzone is moved to the Givetian stage and characterizes its upper part. We have made a conclusion that the age of the taphocoenosis A in the Liepa clay pit, according to miospores, is Late Givetian.

V. Svalbardia banksii was established in the taphocoenosis A. Holotype of Svalbardia banksii has been found from the Upper Devonian (Frasnian) of New York State (Delaware River Flags, Oneonta Fm). From the same locality of Oneonta Fm other plants have been also described. The palaeobotanists consider their age as Frasnian. The age of the host rocks of the Lode Fm by the presence of only one plant Svalbardia banksii could be defined as the Frasnian. Miospores are characteristic for the upper part of the Givetian (subzone IM). Therefore it is possible that in Latvia representatives of Svalbardia banksii appeared earlier than the type area, in Late Givetian. This doesn't contradict the stratigraphical interval of genus Svalbardia from Givetian to Frasnian, which may be sporadically found even in the Famennian (Ukraine, Donbass). We can't discuss the age of all the Lode Fm because we have material (imprints of higher plants and miospores) only from the taphocoenosis A.

VI. Presence of the higher plants and algae in the Liepa (Lode) clay pit in the Lode Fm was mentioned by I. Upeniece (2001, 2011). She provided photos of some plant remains, which were defined by N.M. Petrosjan (Russia, St. Petersburg), without the descriptions. Identification of genera and species causes some doubt. Short comments: on the photo of *Archaeopteris fissilis* Schmalh. (correct name of this plant in modern representations should be *Svalbardia fissilis* (Schmalh.) (Carluccio *et al.*, 1966) attributes of this specimen are not shown (Upeniece 2001, pl. 4, fig. 1). *S. polymorpha* Høeg (ibid., pl. 4, figs 2, 3, 5) most likely concerns *S. banksii*. The fragment of plant *Platyphyllum* sp., which belongs to the higher plants instead of algae (ibid., pl. 4, fig. 4), doesn't reflect the features of this genus. For the final conclusion about regular structure of the plants determined by N.M. Petrosjan from the Lode Fm of Latvia, it is necessary to work with originals of plants and redefine them.

Acknowledgements

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Compound Eyes in the Chengjiang Biota

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The oldest metazoan record is that from the Chengjiang Biota, of the lower Cambrian of China (~525 to 520 Ma). This fauna is dominated by arthropods, even here the structures of compound eyes can be well observed and analysed. By modern physiological methods it is possible to assign the ancient owners of these compound eyes to their light ecological habitats. The structures of the found compound eyes are different – there are the more basal, grapelike arranged facets in stem-line close arthropods, but also advanced systems, comparable to modern compound eyes with densely packed hexagonal facets are represented. Because compound eye designs adapt to the light ecological demands these designs are highly variable and hardly of use for systematic analyses. A second visual system besides the compound eyes, median eyes, has been discovered in some of the arthropods. These are autapomorphic for euarthropods, and may be of great use for cladistic analyses.

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Introduction

Fossilised compound eyes are known from a wide range of stratigraphic levels. They appear in the Tertiary Baltic amber with incomparable beauty, revealing even internal structures (Tanaka et al. 2009), they can be observed in Jurassic crustaceans and have been recorded even in Cambrian fossils from Emu Bay shale recently (Lee et al. 2011). Emu Bay, however, is slightly younger than the Chengjiang Lagerstätte, which reveals the oldest metazoan fossil record known so far, and here compound eyes of different morphological and functional complexity can be described.

Compound eyes, recent and fossilised, are adapted to the light conditions of the environments their owners inhabit, and thus, the other way round, they mirror the life style of their ancient owners. Modern physiology has elaborated good theoretical methods to interpret recent compound eye designs in their ecological contexts, and here it will be shown, that it is possible to apply these methods to fossilised systems, too. By this, it becomes possible to assign compound eyes, which are more than half billion of years old, to the light habitats they once inhabited. This reveals great insights to early life, and a wider understanding of Cambrian ecological systems.

Theoretical Background of the Physiological Analysis of the Cambrian Compound Eyes of the Chengjiang Biota

The optical system of eyes of all kinds obeys physical rules. This means that the morphological structure, for fossilized as for recent systems, mirrors the adaptation to the light conditions of the environment. Because the taxa regarded here are arthropods, the following considerations refer to compound eyes, and if not indicated otherwise, to apposition eyes. Higher differentiated forms of compound eyes such as all forms of superposition eyes are very much younger than the organisms investigated here (Gaten 1998).

Apposition eyes (Fig. 1) are a common design of compound eyes among recent diurnal crustaceans and insects. Those compound eyes may contain up to 20.000 visual units per eye as represented in the dragonfly *Aeschna*, and their visual impression is like a mosaic (Exner 1829), while each facet contributes an image point like a pixel contributes to a computer graphic. The light captured inside the opening angle of each facet is focused by a small lens system onto a central light-guiding structure, the so called rhabdom, which is part of the sensory cells and contains the visual pigments. The energy of the incident light changes the sterical configuration of the pigment, causing an electrical signal, which can be processed by the nervous system of the organism.

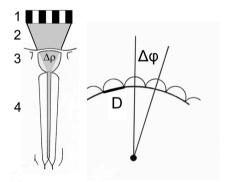


Figure 1. Functional principle of an apposition eye: contrast distribution of the environment (1) inside the visual field of the ommatidium (2) is focused by the dioptric apparatus (3) onto the central rhabdom, which is part of the sensory cells (4). Explanation of the parameters: $\Delta \rho$ opening angle of the visual unit (rhabdom), $\Delta \phi$ opening angle of the entire ommatidium, D lens diameter, aperture.

In the seventies of the 20^{th} century a set of extraordinary theoretical developments was published, which made it possible to describe the relation between morphology of the optic apparatus and ecological conditions of light, which define them, for recent arthropods. Because in good preservation these structures are perceived in fossil organisms too, methods of modern physiology can be applied for the analysis of fossilized eye systems too, or methods must be adapted if certain structures, such as the rhabdom, are missing in the record.

The initial concept is comparatively simple. Each individual facet of a compound eye needs a certain amount of light to work efficiently. Constant light conditions in a habitat the species has to adapt to, low light conditions lead to a wide aperture during evolution, and consequently wide lenses. Because in an apposition eyes each facet contributes one pixel of the entire image in a mosaic-like vision of the compound eye, it needs as many facets per each angle of space [sr] to achieve an image as acute as possible. In the limited space of a compound eye, however, this leads to a 'conflict of interests' between the acuity of vision and the ability of light perception, which, under natural conditions ends up in a kind of compromise. This compromise is characterised by the so-called Eye Parameter p, which was defined by Horridge (1977), Snyder (1977, 1979) and Snyder $et\ al.\ (1977)$. The Eye Parameter is expressed by the product of the opening angle of a facet $\Delta\varphi$ and the aperture D (diameter of the lens).

Snyder (1977) explains, that to be able to discriminate two point objects, which seen from the eye have a distance of $\Delta \gamma$, three facets are needed, one each to detect the object points, and one in between. He shows that a compound eye can discriminate these two points if with squared pattern of facets $\Delta \varphi = \Delta \gamma/2$, if hexagonally arranged $\Delta \varphi = \Delta \gamma/\sqrt{3}$. This expression was called the Sampling Frequency. Snyder (1977, eq. 18) describes for compound eyes, that lenses which in a space-limited compound eye should be as small as possible for the best possible acuity, thus work at the diffraction limit. The equation for threshold discrimination of diffraction-limited lenses of a sinusoidal distribution of contrast with a spacing equal to the Sampling Frequency by following equation below, while $m^2 \hat{I}$ is the contrast intensity parameter; it describes the signal/noise ratio under given light intensity, while e is the base of the natural logarithm, λ wavelength of light in vacuum (e.g., 550nm), ω angular velocity of the eye in relation to the object, Δt effective time-interval of integration of the eye, and p is the eye parameter.

$$1 = 0.455 \cdot p \cdot (m^2 \hat{I})^{\frac{1}{2}} \cdot e^{-0.89[(\lambda/p)^2 + (\omega \Delta t/\Delta \varphi)^2]}$$

Thus the Eye Parameter p results to $p_{\text{hex}} = \frac{1}{2} \cdot D \cdot \Delta \varphi \cdot \sqrt{3}$, for a hexagonal pattern of visual units, and to $p_{\text{quadr}} = \frac{1}{2} \cdot D \cdot \Delta \varphi$, the unit is [μ m rad].

The Eye Parameter stays for at threshold perception in a curvilinear relation with the parameter of contrast $m^2\hat{I}$. This characteristic gives optimal values of p in threshold perception of the sinusoidal pattern mentioned above under various light conditions. Horridge (1977) and Fordyce and Cronin (1989, 1993) investigated different insects and crustaceans which all fit perfectly into and match this theoretical concept.

Horridge showed in his paper of 1977, which became classic, that diurnal insects have an eye Parameter between 0.5 and 1 [μ m rad], crepuscular insects ~2 [μ m rad], diurnal marine crustaceans show an Eye Parameter between 2 and 4 [μ m rad], deep sea amphipodes between 0.6 and 20 [μ m rad]. During the following decades numerous investigations were undertaken with recent organisms, which proved this method; an overview can be found in Land (1981). Because morphological structures in fossilised eyes can be well preserved, the Eye Parameter may become a relevant

tool, and makes it possible to assign organisms to their ecological habitat, even several hundred million of years after they lived and died. For fossilised arthropods, namely trilobites, the Eye Parameter has been applied twice (Fordyce and Cronin 1989, 1993, McCormick and Fortey 1998). Because due to absorption in light flooded oceans in recent like in those of the Palaeozoic locations investigated here (Hou *et al.* 2004), the light intensity decreases every 70 meters one decimal power (Land 1989). The limitations and different ways of interpretation, possibility of application and necessity to change, adapt and modify them due to different demands of fossilised visual systems rather than in those of recent times will be discussed later on.

Besides the Eye Parameter there exists a direct method to describe how many photons are captured by an individual visual system. This characteristic is named Absolute Sensitivity S. Introduced by Land (1981) still it is a relevant tool for characterizing visual systems of organisms living today (Frederiksen and Warrant 2008). It is defined by the number of photons emitted by a plane with a standardized radiation R=1. ((Luminance:) 1 cd·m⁻² = 1 lm·m⁻²·sr⁻¹ = 0.314 millilambert = 1.46 · 10⁻³ watt·m⁻²· sr⁻¹ correlate to 4.09·19¹⁵ photons· sr⁻¹ m⁻² sr⁻¹ (Radiance), Land 1981 p. 480, Land and Nilsson 2002, p. 22ff). The Absolute Sensitivity depends on the aperture of the system, normally the lens diameter D, the term P_{abs} which is added to take into account the amount of absorbed photons by the photoreceptor and depends on the characteristic of the receptor. The term $P_{abs} = (1 - e^{-kl})$ expresses that light absorbed by a light perceiving structure with the length 1, usually the rhabdom, absorbs the light with an exponential characteristic with the coefficient k (peak absorption coefficient of the visual pigment (Kirschfeld 1969, Land 1981, Warrant and Nilsson 2006). P_{abs} normally is not available for fossils, but because of mathematical contexts it lies between 0.1 and 1. The greatest possible error which can be made thus lies lower than 10, which can be considered as low in comparison with values S usually can reach, while additionally just ranges have to be estimated. So calculated S ranges from 0.01 [µm² sr] in human beings up to 4200 [µm² sr] at Cirolana, a marine deep-sea isopod (comp. Land 1981, Land and Nilsson 2002). For P_{abs} here a mean value (0.5) will be used which lies rather close to an actual value, such as in Cirolana with 0.51 (Land 1981). A factor 0.62 (= $(\pi/4)^2$) results from a circular aperture of the visual unit and the comprehension of several parts of the term in the deduction of the expression (for details see Land 1981 p. 480ff). So far the Absolute Sensitivity S was used just to characterize recent compound eye systems. The reason was that S depends from the opening angle $\Delta \rho$ of the light perceiving structure which is the rhabdom inside the ommatidium. In fossils, however, these sensory structures have been not available so far, and thus the absolute sensitivity could not be determined. Within the theoretical deduction of the eye parameter p Snyder gives in 1979 a characteristic curve (Snyder 1979, p. 249), from which an optimal relation between $\Delta \rho$ and $\Delta \varphi$, $(\Delta \rho/\Delta \varphi)$, can be estimated for each given p. Assumed that these systems establish themselves close to this relation, as can be observed at the housefly Musca domestica (Stavenga 1975), it is possible after having provided the eye parameter p to estimate $\Delta \rho$, because of course $\Delta \rho = p \cdot \Delta \varphi$. Furthermore this characteristic indicated that $\Delta \rho/\Delta \varphi \leq 2$, and thus any error made is not greater than a factor 2, which again is not relevant in the range of values for S. Thus it reveals that the Absolute Sensitivity can be estimated to a reliable amount, and thus is an applicable parameter to describe the mode of adaptation to existing light conditions, not just for recent systems, but for fossilized as well, and it becomes possible to compare both with each other.

There is another parameter which should be introduced finally, which describes the fineness of resolution of a visual system. It is the Anatomical Acuity, developed by Snyder also in 1977. It is characterized by the so-called Spatial Frequency v_s . In an idealised visual field the distribution of the patterns of the environment is represented by a sinusoidal distribution of contrasts with a length of period of $\lambda = 2S$, the distance of the receptor centres is rs. The finest resolvable grating is of a period length of 2rs.

Because smaller period lengths mean a better resolving, the inverted expression is used, the frequency ($v_s = 1/\lambda$). This resolving power depends on the divergence angle $\Delta \varphi$ and the geometrical situation inside the compound eye, whether the facets are hexagonally or squared packed. Following the ideas mentioned before, there results a highest possible spatial frequency v_s in a hexagonally packed facet eye to $v_s = (1/\sqrt{3})$ and for a compound eye with squared packing $v_s = \frac{1}{2} \cdot \Delta \varphi$ (for deduction see Snyder 1977, Snyder *et al.* 1979). Because in many fossilised eyes the pattern of the facets is well sustained, here another possibility to compare the performances of fossilised and recent systems is opened. Some of the here presented works use these instruments to characterise and compare fossilised visual systems with those of today.

The limitations of these theoretical tools, possibility of application and necessity to change, adapt and modify them due to different demands of fossilized visual systems rather than in those of recent times will be discussed later on.

Morphometrical analysis of compound eyes of the Chengjiang fauna

The oldest record of a metazoan life community is the so-called Chengjiang Fauna, which is dominated by arthropods. It was discovered in Chengjiang, Yunnan Province of China, at Mount Maotianshan in 1984. The Lagerstätten preservation brings out finest details for analysis, for appendages, gut contents, but especially for eye structures also. Most of these arthropods appear strange and dissimilar to modern ones, many of them are the so called stem-line representatives, and thus it is not possible to assign them to any particular systematic group, because they stay at the beginning of this diversification. The facetted eyes of these early arthropods are characterised by globular units covering the visual surfaces, not as densely packed as in modern arthropods such as flies or most crustaceans. These structures rather probably formed a spherical dioptric apparatus, functioning as lenses. Whether the visual units below were ocelli, small cups with a small retina below the lenses, or whether they already were proper ommatidia, however, must remain open. There are, however, also highly advanced and well developed compound eye systems such as those of Cindarella, with a hexagonal, dense pattern of facets giving a high acuity, and for these the development of true ommatidial structures may already be assumed. Most eyes are stalked, just some are sessile.

The work presented here was undertaken during two research visits to the Key Laboratory for Palaeobiology (YKLP), Kunming, Yunnan Province China, and is an analysis of well preserved visual systems from Chengjiang fossils housed in this institute. The analysis uses all parameters explained above: Eye Parameter, Absolute Sensitivity and Spatial Frequency in order to discover an appropriate assignment of these organisms to their light-determined life habitats and life-styles.

Some examples are here chosen and their characters presented briefly below.

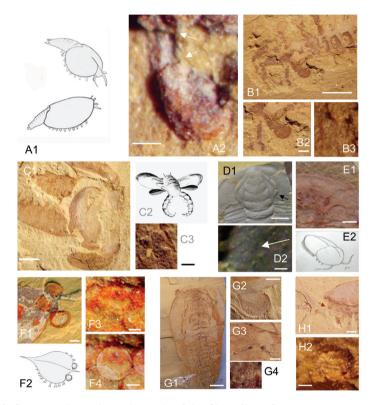


Figure 2. Compound eyes in Arthropods of the Chengjiang fauna.

A1: Waptia (Chuandianella) ovata (Lee, 1975). A2: compound eye of A1. Notice the socles of the former lenses bar 100 μm. B1: Head of unspecified arthropod, bar 2 mm. B2: Eye systems: large globular is more sensitive (dim light adapted) than the flat less sensitive one (bright light adapted), bar ~500 μm. B3: relicts of lenses. Lens diameters ~ 200 mm (less sensitive eye). C1: Anomalocaris sp. ventral aspect, bar ~1 cm. C2: Reconstruction. C3: lenses of the Anomalocaris eye, bar ~ 200 μm. D1: Head of Eoredlichia intermedia (Lu, 1940), trilobite, bar ~ 5 mm. D2: Facets, bar ~ 250 μm. E1: Naraoia (Misszhouia) longicaudata (Zhang and Hou, 1985), ventral aspect, notice the eye at the margin of a suture, bar ~ 1 mm. E2: reconstruction (courtesy J. Adamek). F1: Head of Isoxys auritus Jiang, 1982 (Isoxys 1), bar ~ 500 μm. F2: Reconstruction. F3: relicts of lenses, bar ~ 50 μm. F4: F3 with lenses indicated by pale circles. Scale ~ 50 μm. G1: Cindarella eucalla Chen, Ramsköld, Edgecombe et Zhou 1996, bar ~ 1 cm. G2: eye of another specimen, notice the palpebral lobe, bar ~ 2 mm. G3: Median eyes, ocelli, bar ~ 2.5 mm. G4: facets, diameter ~ 80 μm. F1: Head of Leanchoilia illecebrosa (Hou, 1987), arrow indicating pedunculate eyes, bar ~ 2 mm. F2: Compound eye of another specimen, bar ~ 100 μm.

A. Waptia ovata (Lee, 1975) (Fig. 2 A) is a solid arthropod of some few centimetres length, but with remarkably small facetted eyes of just some hundred microns. Their resolution with ~ 2.3 [cycles/rad] is comparatively low, and almost equal to Nautilus (3.6 [cycles/rad]) or Cirolana, a deep-sea isopod (1.9 [cycles/rad] (Land and Nilsson 2002)). The Absolute Sensitivity of ~ 0.88 (between ~ 0.2 and ~ 1.56 [µm² sr]) characterises it as a diurnal arthropod (Horridge 1977). Waptia is known to be a benthic organism, feeding on a sedimented organic material (Hou et al. 2004, Briggs et al. 1994). This eye system would allow Waptia to gain a rough orientation in its environment at the sea floor. Probably it was able to recognise rough patterns as shelters, it could have noticed external movements, for example of social partners and predators. The comparatively low sensitivity indicates a life style close to the water surface. Thus in all probability Waptia may have been a peaceful, diurnally active inhabitant of areas close to the shore.

B. The next organism analysed here, equipped with two different stalked compound eye systems, is a very rare, until now undescribed arthropod (Fig. 2B). The one of these eye systems shows the characteristic of a crepuscular organism, or of an animal living at greater depth (p=17.5 [µm rad], $S=\sim132$ [µm² sr] while the other is characterised by a higher acuity and is less light sensitive ($p=\sim2$ [µm rad], $S=\sim2$ [µm² sr], their resolution: $v_s=\sim3$ vs. 14 [cycles/rad]. This is difficult to interpret, because under bright light conditions the more sensitive system would become bleached if such adaptive mechanisms as pigment sheeting did not already exist. This may have been possible, however, as melanin, as shown before, already formed part of some sensory systems. Because this fossil is so extremely rare, even if compared to other soft bodied fossils of Chengjiang, it could well be, that it was a vagrant wanderer through the ancient seas, and thus as an immigrant it is not very typical for the Chengjiang Biota. Assuming that both structures really were eye systems, such a mechanism, possessing two different systems for different tasks would not be represented in recent arthropods.

C. Anomalocaris (Fig. 2 C) has been interpreted as the most ferocious predator of its time. Actually some species of this group can reach a size of several meters, and their life style can be well imagined by their enormous armed tentacles and the huge size of its solid body. More recently, however, another, different life-style has been assumed, for at least certain species of Anomalocaris floating over algal lawns of the Palaeozoic seafloors, which was indicated by their mouth parts, probably more able to graze.

The reconstruction of the *Anomalocaris* in the National History Museum of London, following a drawing of Conway-Morris (1998), shows short stalked eyes, attached dorsally to the head. The fossil investigated here, however, is different. The eyes arise ventrally, as in recent crustaceans, and show a mace-like shape. Probably they were stretched out laterally, which is highly probable, because, as in other arthropod eyes of Chengjiang, these eyes are covered by a palpebral lobe, a kind of cuticularian top. If the eyes had been carried pendulous downwards, the visual surface would have been positioned to the internal side, which would not allow any view to the environment. Held up laterally, however, it would have enabled the animal to scan the ground below while floating over it. With an acuity of ~ 11 [cycles/rad] which is significantly higher than that of *Limulus* (4.8 [cycles/rad], Land

and Nilsson 2002), and even almost reaches the acuity of the wolfspider (16 [cycles/rad], Land and Nilsson 2002), a visual system of a terrestrial organism equipped with a retina rather than a compound eye. The Eye Parameter of $\sim 9~\mu m$ rad and an Absolute Sensitivity of $\sim 27~[\mu m^2~sr]$ indicates a crepuscular life style, or a presence at a depth up to 200 m (after Land 1989). It has been shown, however, that the depth of the sea in the Chengjiang biota's area was not deeper than 70-120 m, and that there were clear water conditions (Chen and Zhou 1997, Chen 2004), thus the species of *Anomalocaris* investigated here rather probably was a crepuscular if not night active form, well equipped for hunting in the dark.

- D. *Eoredlichia intermedia* (Lu, 1940) is a trilobite (Fig. 2 D). All oculate trilobites have a facial suture part which runs above the eye (palpebral suture). Until the later Cambrian trilobites possess subocular suture below the visual surface, so that the lens bearing areas of the eyes were lost after moulting or death of the organism. Thus any knowledge about the visual characteristics of these trilobites is lost. In later forms this suture becomes fused to the librigena, and thus the lentiferous surfaces are retained in the fossil record. Thus the eyes of these early trilobites are known just as small slits and not much is known so far about their visual structures until the late Cambrian (Clarkson 1959, 1997). The rare specimen described here shows a fortunate case where the eye of a Cambrian trilobite appears as a compound facetted eye for the very first time. An acuity of ~ 12.5 [cycles/radian] in a more squared rather than hexagonal packing of the facets is comparatively high, the absolute sensitivity (~ 7.3 [µm² sr] indicates a diurnally active (Land 1981) trilobite. Thus this is the first time, when the eyes of an early Cambrian trilobite could be described and characterised in this way.
- E. Naraoia (Fig. 2 E) is one of the most important and most abundant arthropods of the Chengjiang Fauna, and has generally been regarded as blind (Hou et al. 2004, p. 150). Størmer (1959, p. 030) described in the first edition of the Treatise of Invertebrate Palaeontology small 'sessile eyes', for Naraoia compacta of the Burgess Shale. In the new edition, however, a systematic discussion of Naraoia is not included any longer and the term 'Trilobitomorpha', Naraoia is taken as a sistergroup to the trilobites, because among other items, a lack of facial sutures (Fortey 1997, p. 293). In the example of Naraoia (Misszhouia) longicaudata (Zhang and Hou, 1985) (ventral aspect) here being presented, very clearly a facial suture can be seen, very similar in shape to those of trilobites. Together with it, there is reniform structure, which lies, especially in relation to this suture in the relative position of an eye if compared to trilobites, furthermore showing the characteristic shape of trilobitomorph eyes. Thus this structure, which can be observed also in other specimens more or less clearly, should likely be interpreted as the relict of a small eye.
- F. *Isoxys auritus* (Jiang 1982) (Fig. 2 F) is an arthropod, which occurs for example among the Chengjiang fauna, at Sirius Passet and in the Burgess Shale. It is usually about 2 cm in size but can also reach dimensions of four centimetres and more. It is assumed to have lived in the pelagic realm, and several morphological features characterise it to have been a vagrant predator (Walcott 1890, Garcia-Bellido *et al.* 2009 a,b, Stein *et al.* 2010, Vannier *et al.* 2009). *Isoxys* is equipped with large, well developed eyes, but hitherto no further analysis of these has been undertaken,

other than but the report that they existed. *Isoxys auritus* is quite abundant among the Chengjiang fauna, the quality of preservation, however, was good enough for further investigations in only two specimens.

The hemispherical eyes of *Isoxys* (*Isoxys* 1 YKLP 11043) are positioned on ~ 1.5 mm long stalks, though in these no clear articulation can be observed. In many arthropods of the Chengjiang fauna the shells of these so-called 'soft-shelled' fossils living at that time were remarkably thin, but even delicate structures like movable eye-stalks can sometimes be preserved. The eyes are covered by a circular top ('palpebral lobe') and due to the excellent preservation it could be shown, that this palpebral lobe consists of the same material as the shell of the organism, in other words of cuticular material. This palpebral lobe held and stabilised the huge spherical eye, while concentrating the view downwards, but it also shielded the visual surface from the bright light from the water surface above, with its constantly changing contrasts.

The visual surface itself consists of globular units (mostly ~ 100 -150 µm in diameter). Those directed towards the body of the organism are slightly smaller, as some even smaller units can be observed among the larger, which may be new ones inserted into the eye during growth. Due to the hemispherical character of the eye and the mobile stalks a wide field of view must have resulted. The Eye Parameter ($p = \sim 9.91~\mu m$ rad]) indicates, if it was not a crepuscular organism, a life habitat of up to 140m depth (for a diurnal arthropod) (Land 1981), while the latter is in accordance to conclusions of Vannier and Chen which they had drawn by other characteristics of the animal (Vannier and Chen 2000, p. 308). The values of the Absolute Sensitivity ($S = \sim 42~[\mu m^2~sr]$) indicate the same. They are in the range of those of *Limulus* (83-317 $[\mu m^2~sr]$), which is a crepuscular shore inhabitant. The results are also similar to *Phronima* (38-120 $[\mu m^2~sr]$), which is a hyperiid amphipod, living in a depth up to 200m (Land 1989, Land and Nilsson 2002).

There exists, however, another form of *Isoxys*, (*Isoxys* 2 (RCCBYU 10261)), which originates from a different location, Mafang, whose eyes differ conspicuously from those of *Isoxys* 1. Short eye stalkes probably existed, but cannot be seen in the specimen. The diameter of the visual units is remarkably smaller (~58 μ m). The Eye Parameter results to ~ 3.2 [μ m² sr], the absolute sensitivity to ~3 [μ m² sr]. This low sensitivity indicates an arthropod which lived close to the water surface and was diurnally active (Land 1989, Land and Nilsson 2002). Indeed a comparison of both locations, where the fossils have been found (Hou *et al.* 2004, p. 22) yields that the habitat of *Isoxys* 1 (Chengjiang) lay further off shore than that of *Isoxys* 2 (Mafang), which lived close to the ancient coast.

Considering the acuity of vision in both forms, *Isoxys* 1 (YKLP 11043) with a resolvable spatial frequency of $v_s = 6,3-63$ [cycles/rad] again is comparable to that of *Limulus* (4.8 [cycles/rad]), or to that of the shore crab *Leptograpsus* (~ 19 [cycles/rad]). All is similar to the second form of *Isoxys*, *Isoxys* 2, where the resolution is slightly better than in *Isoxys* 1 ($v_s = \sim 9.3-93$ [cycles/rad]). A detailed description may be found in Schoenemann and Clarkson (2010).

G. Probably amongst the most highly developed compound eyes in the Chengjiang arthropod fauna is the eye of *Cindarella eucalla* Chen, Ramsköld,

Edgecombe et Zhou 1996 (Fig. 2 G). Cindarella is a relatively large arthropod up to 15 cm in size. The stalked eyes insert ventrally, and in contrast to the compound eyes described so far, those of Cindarella are characterised by a dense packing of small strictly hexagonal facets, while most other compound eyes of representatives of this early fauna are composed of spherical, more haphazardly arranged units. A hexagonal arrangement results from packing globular structures most densely, because this is the most optimal strategy for saving space, as we find it realised in honeycombs and compound eyes of modern arthropods with advanced visual systems, such as those of many crustaceans, bees and numerous other insects. Thus it seems to be not improbable that the eyes of Cindarella represent an advanced stage of evolution within this fauna. It seems possible that during evolution a set of loosely packed visual units, frequently arranged in a mulberry shape, became transformed into a hexagonally arranged dense system enabling a higher acuity of vision. This system is that of modern designs in insects or many crustaceans. The Eye Parameter found in the eyes of C. eucalla $(p = \sim 1.9 \mu \text{m rad})$ and the Absolute Sensitivity ($\sim 1 [\mu \text{m sr}]$ indicate a diurnal organism, the acuity of ~ 24 [cycles/rad] is among the highest observed in this fauna. Surely this heavy and solid arthropod can be interpreted as a benthic inhabitant of the sea floor rather than an active predator – a result which may contribute an important aspect to the discussion, about who should be equipped with eyes of a better performance – prey or predator in the competition for life. This was, as mentioned, a crucial element of the light switch hypothesis of evolution, formulated by Andrew Parker (1998, 2003). This theory enlightens that quality of vision is a motor for the dynamics of evolution in the race to survive between prey and predator.

In *Cindarella* four dark structures set medially in the dorsal head region are of special importance. At higher magnification it becomes evident that they are relicts of pigmented cups, which, always found in a characteristic position in the arthropod's head, indicate four median eyes. These ocellar cups, the median eyes, are autapomorphies of Euarthropods (Ax 1999), and are not present in most of the other arthropods in the Chengjiang fauna. So far they have only been found in *Leanchoilia*. Thus the presence of these median eyes, where they exist, may be an important instrument for cladistic analyses in distinguishing arthropods close to the stem-line from advanced euarthropods.

The importance of this new biological method, introduced here, for analysing fossil eye-structures becomes evident also by the analysis of the morphometry of two further species of the Chengjiang fauna: *Cindarella eucalla* Chen, Ramsköld, Edgecombe et Zhou 1996 and *Leanchoilia illecebrosa* (Hou, 1987).

H. Leanchoilia (Fig. 2 H) is one of the commonest non-trilobite arthropods of the early Cambrian. It has recently been regarded as part of the 'short great appendage arthropods' clade, and is normally considered as a predator, both on account of its raptorial appendages (Hou and Bergström 1997) and serial midgut digestive glands (Butterfield 2002). The presence or absence of eyes has been one of the most controversial aspects of its morphology, despite pedunculate eyes having been described in the original descriptions of L. superlata Walcott 1912, and L. illecebrosa (Hou, 1987), as was suggested for L. illecebrosa as well by Chen et

al. (1996), Chen and Zhou (1997), and Chen (2004) in his reconstruction (fig. 460). These pedunculate ventral eyes, however, were first demonstrated by Schoenemann (2006). The restorations made between 1935 (Raymond 1935) and 1983 (Bruton and Whittington 1983) did not show any eyes, and so most of the reconstructions of Leanchoilia lack eyes, as the genus was considered to contain blind species by Bruton and Whittington (1983, p. 574). In the here presented paper pedunculate eyes have been demonstrated in four out of about fifty specimens of L. illecebrosa from the Chengjiang and Haikou areas. They are delicate and slender which explains their rare preservation. Distally they are structured like a bunch of grapes, with about 100 spherical units, presumably lenses, each with a diameter of about 60 µm. of $v_{\rm s} = \sim 1.2$ cycles per rad. In terms of the effective light collecting arrangement – wide opening angle, and not particularly small lenses – the sensitivity, is comparatively high, and ranges between 109 and 426 µm² sr. This indicates a life style under dim light conditions, repuscularly or compared to amphipodes investigated by Land (1979) in waters deeper than 200 m. Because water absorbs light, with increasing depth, light is reduced by a factor of ten for each 70 m, even under clear water conditions (Land and Nilsson 2002, p. 51). Thus, the calculated results indicate (comp. Tables Land 1981, p. 556, Snyder 1977, p.174, Horridge 1977, p. 8) that it was adapted to dim light conditions. Because the sea floor upon which the Chengjiang biota lived is estimated to be at a depth of 70-120 m (Chen and Zhou 1997, p. 15), this crepuscular life style seems realistic, as in many crustaceans among the living shrimps, which in many ways resemble Leanchoilia morphologically.

The Eye Parameter lies between ~ 20 and 37 µm rad, likewise indicating, by calculation, adaptation to dim light (Horridge 1997). Probably *Leanchoilia* could detect movement, but could not form images. Furthermore *Leanchoilia* possesses two pairs of median eyes, as mentioned before, autapomorphies of euarthropods. Thus, like many modern euarthropods, *L. illecebrosa* has two kinds of eyes – two stalked ventral eyes, and two probably ventrally inserted (ocellar) median eyes (Garcia-Bellido and Collins 2007), which would be different from recent insects for example, where these ocelli sit dorsally (Laughlin 1981), while in crustaceans they may be dorsal and ventral structures as well (Fahrenbach 1964). Its short stalked eyes, orientated downwards and covered by the headshield, suggest that *Leanchoilia* was a benthic animal, feeding on benthic or infaunal animals.

Discussion

Many of these early compound eyes have a slightly different construction than modern ones. The compound eyes of *Isoxys*, *Leanchoilia*, *Waptia*, *Anomalocaris* and others show loosely packed visual units, which have the character of a mulberry rather than they show a densely packed hexagonal arrangement. This type of compound eye may be a more basal one in comparison to most recent. If globular systems, however, are packed as economical as thus densely as possible, they are packed in a hexagonal arrangement, as we know not just from honeycombs. Such advanced compound eyes, optimised towards acuity with as many facets as possible, can be found, however, already in the Chengjiang fauna also – for example in *Cindarella eucalla* (Chen *et al.* 1996). This shows that even higher advanced compound eye systems were already present during these times.

This article shows that it is possible to assign fossilised compound eyes, even the oldest known so far from the Chengjiang Biota, to their light habitats. Half a billion years after these organisms died, by their eyes it is possible to say for some of them, that they lived a crepuscular life style, that they were bottom dwellers or lived close to the light flooded surfaces of the oceans. Because the pattern of compound eyes facets, are variable with respect to their light adaptations, they are not of use for cladistic analyses. The median eyes, however, as found in *Leanchoilia* and *Cindarella* may be of great use here, because they reveal a contact to euarthropods being autapomotphic for those.

Finally an overview of all available Chengjiang arthropods in their palaeo-ecological contexts has been established, assigning them to their light ecological habitats, and consequently their life style. This is shown in figure 3.

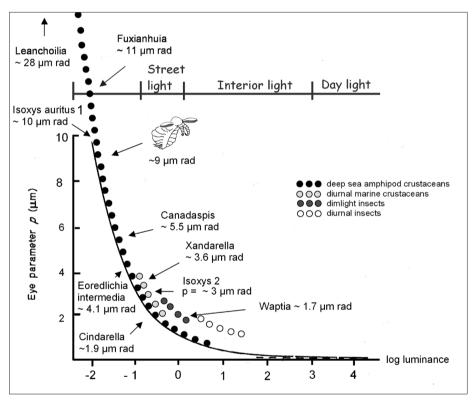


Figure 3. Eye Parameter versus light conditions of the environment and the assignment of the investigated arthropods to these consditions by means of the Eye Parameter.

(The log luminance is the light condition, which is morphologically "interpreted" as expressed by the Eye Parameter of the different eye systems. Thus the morphological adaptation (Eye Parameter) to certain light conditions (log luminance) is shown in the graphic.)

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Insights to Eyes of Phacopid Trilobites

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Trilobites are the dominating form of arthropods during the Palaeozoic. They appear in the Cambrian with well developed compound eyes in many different well adapted forms. By the fossil record three main types were evolved: the holochroal, the schizochroal and the abathochroal type. The latter derived from the basal holochroal eyes by paedomorphosis. While as normal in fossils, just the outer structure is preserved in these compound eyes, nothing is known about the internal sensory systems so far. However, by computer tomography it was possible to show, that these sensory structures left traces during the fossilisation process in certain schizochroal eyes of phacopid trilobites. The analysis reveals that these eye systems worked as apposition eyes, a common system in recent diurnal arthropods. This implicates that the trilobites had a mosaic-like vision, as today living organisms, which still possess such compound eyes.

Keywords: compound eye • vision • trilobite • ommatidium • Palaeozoic *Manuscript submitted 28 September 2011; accepted 20 December 2011.*

Introduction

The dominating arthropods of the Palaeozoic were trilobites, which appeared with well equipped compound eyes in the early Cambrian. When the trilobites became extinct in the late Permian, in the meanwhile the types of compound eyes had been developed: the holochroal eye, which was the most common and most basal, the schizochroal eye, which occurs just in the suborder Phacopina, and the abathochroal eye, which is restricted only to the small group of eodiscid trilobites (Jell 1975, Zhang & Clarkson 1990). Holochroal eyes may consist of several thousand facets, covered by a pellucid membrane all in common, the cornea. The abathochroal eye consists of less numerous, irregularly packed facets, and each of them has an own cornea by itself. The schizochroal eye, as the abathochroal eye, developed from the holochroal eye by paedomorphosis (Clarkson & Zhang 1991). These are equipped typically with much larger lenses, up to millimetres in size, staying separated from each other, and as in the abathochroal eyes, each of the units possess an own cornea, covering the lens. In opposite to the abathochroal eyes, however, this thin membrane is prolonged into the interior of the eye, forming a small capsule, usually of about

the 1.5-fold of the lens diameter. All trilobite lenses consist of primary calcite (Towe 1973, Lee *et al.* 2007), which is highly useful under aqueous conditions because of the high refractive index of calcite, but it is unique in the arthropod realm so far. Clarkson & Levi-Setti (1975) could show that the lens in at least some phacopids is not a simple homogenous structure, but consists of a lens doublet, which due to a sophisticated interface between the both parts ensures a sharp image. This is remarkable, because all thick lenses suffer by spherical aberration, a lens aberration, which arises by the fact that rays, entering at the periphery of the lens are focused closer to the lens than the more centrally incident. (For an overview about the compound eyes of trilobites, their development and functional analyses compare Clarkson *et al.* 2006, Schoenemann 2007).

Nothing however could be said so far about the internal structures of trilobite eyes, because during fossilisation usually just shells or bones, calcified or silicified structures are preserved. In this analysis, however, it was possible, to show by computer tomographic techniques that the sensory structures left traces inside the fossilised eyes, and a functional interpretation is possible.

Material and Methods

The eyes of several specimens of the phacopid trilobite *Geesops schlotheimi* (Bronn, 1825) (Fig. 1A), Middle Devonian, Ahrdorf Formation, Flesten Member, Gees, Gerolstein, Germany, were investigated by thin sections light-microscopically, and with computer-tomographical techniques at the Steinmann-Institut, Universität Bonn, Fraunhofer-Institut für Zerstörungsfreie Prüfverfahren, Dresden and Phoenix/x-ray, Munich.

Results

Broken visual units of *Geesops schlotheimi* (Bronn, 1825) (Fig. 1B) show an internal structure consisting of an outer coating of a central unit under the lens. The thin sections of these compound eyes clearly show a structured small capsule (Fig. 1C), as has been demonstrated for other phacopid species earlier (Clarkson 1967, 1969, Bruton & Haas 2003). The computer tomography of a compound eye (Fig. 1D) in an oblique section (Fig. 1E) shows these sublensar capsules regularly arranged in a wide hexagonal pattern. A higher magnification at a resolution of \sim 2 μ m reveals a rosette-like arrangement (Fig. 1F) of ovaloid structures arranged around a central star-shaped centre. Darker circular elements can be observed at the periphery alternating to the ovaloids.

Discussion

This documentation shows clearly that the sensory structures left tracings at least during this special process of fossilisation in the middle Devonian of Gees. It is rather extraordinary to have such delicate structures sustained on cellular level. By comparison with recent compound eyes it becomes obvious, that this structure is in principle identical to that of an apposition eye, which was considered to be the

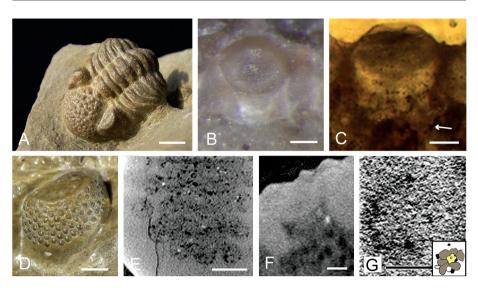


Figure. A, Geesops schlotheimi (Bronn, 1825), Middle Devonian, Ahrdorf Fm., Flesten Mb., Gees, Gerolstein, Germany; bar ~5 mm. B, broken ommatidium of G. schlotheimi; bar ~100 μm. C, thin section of an ommatidium, showing the capsule, arrow indicating the membrane of the capsule. D, compound eye of G. schlotheimi. E, oblique section through compound eye of G. schlotheimi using computer tomographical techniques (CT). F, CT of an ommatidium of G. schlotheimi showing a capsule beyond the lens (upper half of the lens is eroded). G, CT-cross section through an ommatidium showing the apposition eye character. Inset: half schematic drawing of G; yellow: rhabdom, grey: sensory cells, black: pigment cells.

oldest form of compound eyes by systematic comparisons of compound eye bearers (Gaten 1998). Apposition eyes are composed of units, so called ommatidia, which are represented by the lenses, forming the facets of the outer aspect. Below these lenses, and sometimes an additional dioptrical apparatus like the crystalline cone, which focus the incident light, usually lie about eight light sensitive sensory cells, which are arranged radially around a central light guiding structure, the so called rhabdom. This rhabdom is part of the sensory cells, and contains the visual pigments. The sterical structure of the pigments is changed by the energy of the incident light, which causes a small electrical signal to be processed by the nervous system of the organism. This sensory unit is isolated from its neighbours by pigment cells.

Thus, the structures found in the computer tomography can be interpreted very clearly. The ovaloids are traces of the sensory cells, with a diameter of about 80 μm ; they are rather large, but not of untypical size. The star-shaped centre is formed by the rhabdom, and each of the former sensory cells contributed a part of it. The pigment cells formed the periphery, which are represented by the dark structures distally of the sensory cells. The visual impression the phacopid trilobites had thus a mosaic-like vision, as in modern arthropods with compound eyes. So we find in the phacopid eye all elements to be represented in the classic apposition eye, which turns out to be an efficient system since at least almost half a billion of years.

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