

**THE GENUS *PRISTIOGRAPTUS*
IN WENLOCK OF EAST BALTIC AND
THE HOLY CROSS MOUNTAINS**

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TARTU UNIVERSITY
PRESS

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This dissertation is accepted for the commencement of the degree of Doctor of Philosophy (in Geology) at the University of Tartu on 21.12.2006 by the Council of Faculty of Biology and Geography of the University of Tartu.

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The thesis will be defended at the University of Tartu, Vanemuise 46, room 246, on 2.03.2007.

Publication of this thesis is granted by the Institute of Geology, University of Tartu.

Taxonomic disclaimer: This doctoral thesis and included reprints are not considered a publication in sense of International Code of Zoological Nomenclature.

ISSN 1024-2658

ISBN 978-9949-11-532-7 (trükis)

ISBN 978-9949-11-533-4 (PDF)

Autoriõigus Sigitas Radzevičius, 2007

Tartu Ülikooli Kirjastus

www.tyk.ee

Tellimus nr 4

CONTENTS

LIST OF ORIGINAL PUBLICATIONS.....	6
AUTHOR'S CONTRIBUTION	6
ABSTRACT.....	7
1. INTRODUCTION	8
2. PALAEOGEOGRAPHY	11
2.1. Palaeogeography of Baltica in Wenlock	11
2.2. Palaeogeography of the Holy Cross Mountains in Wenlock.....	12
2.3. Global sea level changes in Wenlock.....	12
2.4. Palaeoclimate of Wenlock.....	13
2.5. Bioevents in Wenlock	13
3. SRATIGRAPHY AND GEOLOGICAL SETTING	14
3.1. Stratigraphy of Wenlock in the East Baltic	14
3.2. Stratigraphy of the upper Wenlock and lower Ludlow in the Holy Cross Mountains.....	17
4. MATERIAL	20
5. SYSTEMATICS	23
5.1. Terminology and morphology.....	23
5.2. The genus <i>Pristiograptus</i>	24
6. MORPHOTYPES OF <i>PRISTIOGRAPTUS</i> IN WENLOCK	35
7. DISTRIBUTION OF <i>PRISTIOGRAPTUS</i> IN WENLOCK	38
8. EVOLUTION AND PHYLOGENY OF <i>PRISTIOGRAPTUS</i> IN WENLOCK	41
9. HOMERIAN BIOSTRATIGRAPHY	44
9.1. Homeric biostratigraphy of the East Baltic	44
9.2. Homeric biostratigraphy of the Holy Cross Mountains	47
CONCLUSIONS	49
ACKNOWLEDGEMENTS	51
REFERENCES	52
SUMMARY IN ESTONIAN.....	57
PUBLICATIONS.....	59

LIST OF ORIGINAL PUBLICATIONS

- I. **Radzevičius S.** & Paškevičius J. 2000. Pristiograptids (Graptolites) and their adaptive types of the Wenlock (Silurian) in Lithuania. *Geologija*, **32**, 88–109.
- II. **Radzevičius S.** 2003. Pristiograptids (Graptoloidea) from the *perneri-lundgreni* biozones (Silurian) of Lithuania. *Carnets de Geologie / Notebooks on Geology*, Article 2003/07 (CG2003_A07_SR), 1–14.
- III. **Radzevičius S.** & Paškevičius J. 2005. *Pristiograptus* (Graptoloidea) from the Upper Wenlock of the Baltic Countries. *Stratigraphy and Geological Correlation*, **13**(2), 159–169.
- IV. **Radzevičius S.** 2006. Late Wenlock biostratigraphy and the *Pristiograptus virbalensis* group (Graptolithina) in Lithuania and the Holy Cross Mountains. *Geological Quarterly*, **50**(3), 333–444.

AUTHOR'S CONTRIBUTION

- Paper I: The author is responsible for data analysis and for writing the manuscript.
- Paper II: The author is responsible for collecting the material and for writing the manuscript.
- Paper III: The author is responsible for data analysis and for writing the manuscript.
- Paper IV: The author is responsible for collecting the material and for writing the manuscript.

ABSTRACT

The Wenlock *Pristiograptus* in the East Baltic (west part of the East European Platform or Baltica) were studied in the sections of nine boreholes in the Lithuanian–West Latvian carbonaceous–clayey facies, in the intermediate zone between clayey and carbonaceous facies of the Baltic Palaeobasin and in the Pragowiec ravine, the Holy Cross Mountains (Małopolska Block, Kielce Unit). In the East Baltic area the genus *Pristiograptus* is recognised throughout the *cyphus* to *parultimus*–*ultimus* biozones. The greatest diversity of *Pristiograptus* is observed in the Late Wenlockian *parvus*–*ludensis* biozone. Only *Pristiograptus* and Retiolitidae are recorded throughout the interval whilst other characteristic Wenlockian graptolite species become extinct within this interval. Accordingly, only the members of the genus *Pristiograptus* can be used effectively in detailed graptolite biostratigraphy of the *parvus*–*ludensis* interval. At the end of *lundgreni* time, species of such important genera, such as *Cyrtograptus*, *Monoclimacis* and *Monograptus* become extinct. This is related to one of the greatest crises in the evolution of Silurian graptolites (the Mulde Event).

New morphological features analysed in the species from Wenlock of the eastern Baltic area and the Holy Cross Mountains allow easier identification of the species of the genus *Pristiograptus*. These features are: (1) the angle between the thecal apertural lip and the succeeding metathecal wall and (2) the end of the thecal apertural lip at the disto-lateral margin of the thecal aperture. The first feature allows the genus *Pristiograptus* to be divided into groups, the second is important to distinguish the taxa within the *dubius* group. Four morphotypes of *Pristiograptus* are distinguished in Wenlock: *dubius*, *lodenicensis*, *virbalensis* and *deubeli*. *Pristiograptus dubius dubius* (Suess), *P. pseudodubius* (Bouček), *P. d. ludlowensis* (Bouček), *P. parvus* Ulst, *P. meneghini* (Gorthani) and their subspecies are described and three new forms of *P. dubius* designated as varieties: *P. dubius* var. A, *P. dubius* var. B and *Pristiograptus* sp. These species, subspecies and variations belong to the *dubius* morphotype. The second morphotype, the *lodenicensis* type is represented in the material by one species only – *P. lodenicensis* Přibyl. The *virbalensis* morphotype was distinguished and discussed, and *P. virbalensis* Paškevičius was newly described. The fourth morphotype of *Pristiograptus* in Wenlock is the *deubeli* type. Three species of this group are described: *P. praedeubeli* (Jaeger), *P. deubeli* (Jaeger) and *P. ludensis* (Murchison). An overview is given of the distribution, morphological evolution and phylogeny of *Pristiograptus* in Wenlock.

Graptolites from Lithuania and The Holy Cross Mountains comprise a succession of the *lundgreni*, *parvus* (except for the Holy Cross Mountains), *nassa*, *praedeubeli*, *deubeli* and *ludensis* biozones of the upper Wenlock, the *parvus*, *praedeubeli*, *deubeli* biozones being recognised for the first time in Lithuania.

1. INTRODUCTION

Graptolites (Phylum Hemichordata) are extinct, colonial marine invertebrates now believed to bear a distant affinity to chordates. Abundant stick-like fossils found in lower Palaeozoic rocks are generally fragments of larger colonies. The exoskeleton of graptolites consists of organic matter.

The term “graptolite” means “written marks on the stone” (Greek: *graptos* – to write; *litos* – stone). Their colonies (or rhabdosomes) are straight, spiral, involute in general form and consist of thecae, which contained zooids of unknown morphology.

The first graptolites appeared in the Middle Cambrian and this group disappeared in the early Carboniferous. Graptolites are among the most abundant fossils in the Ordovician and Silurian. A total of about 300 graptolites species are recognized in the East Baltic (Paškevičius, 1994).

Graptolites are useful for stratigraphic correlation for several reasons. Graptolite fossils are found both in shales formed in deeper marine environments and in limestones formed in the shelf zone. They evolved very rapidly and most species were very widespread; new species proliferated very fast in the seas and oceans. A great deal of data has been assembled from many regions and well-elaborated taxonomy allows for proper identification.

Stratigraphy of the Ordovician and Silurian is based on graptolites. Graptolite zonation forms an important part of standard global correlation charts. Many important stratigraphic boundaries are defined according to graptolite distribution, for example, the Ordovician – Silurian boundary is drawn at the appearance level of *Parakidograptus acuminatus* and the Silurian – Devonian boundary is marked by the disappearance of *Monograptus transgrediens* (Koren' *et al.*, 1996). In addition, all boundaries of the Silurian stages are defined in terms of graptolite zonation.

The Silurian period extended from 443.7 ± 1.5 Ma (million years ago) to 416.0 ± 2.8 Ma (for a total duration of about 28 Ma). The system is subdivided into 27 graptolite biozones (Koren' *et al.*, 1996), meaning that each biozone is equivalent to roughly 1 Ma. Other groups of Silurian fauna did not evolve so quickly.

The genus *Pristiograptus* (see reconstruction in Fig. 1) belongs to the order Monograptidae. The generic name, *Pristiograptus*, was introduced in 1889 by Jaekel (Latin: *pristis* – sea monster; Greek: *graptos* – to write), who distinguished *Pristiograptus* from *Monograptus* according to specific thecal morphology. The rhabdosomes of *Pristiograptus* are straight, sometimes curved ventrally or dorsally. Thecae are simple, cylindrical, with straight or only slightly curved free ventral wall and without any distinctive apertural processes. They are distinctive from *Monograptus*, which has thecae with hooks, shoot and possess an apertural processes.

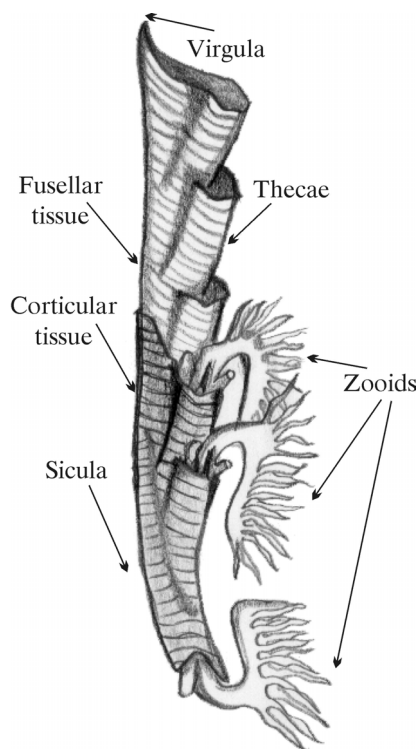


Fig. 1. Reconstruction of *Pristiograptus* sp. (after Münch, 1952; Urbanek, 1966) and principal morphologic features.

The graptolite genus *Pristiograptus* is found throughout the *cyphus* to *parul-timus-ultimus* biozones, from Llandovery to Přidoli. The highest diversity of *Pristiograptus* is associated with the late Wenlock (*parvus-ludensis* biozones). The specific importance of this genus stems from the fact that this time interval is known as a deep crisis in the development of graptolite fauna. Most graptolite species characteristic of the Wenlock became extinct within a short period, by the end of the *lundgreni* age. The only exceptions are some species of *Pristiograptus* and some representatives of Retiolitidae. The species of *Pristiograptus* have been recorded throughout this interval and, consequently, only *Pristiograptus* and Retiolitidae can be used effectively in the detailed graptolite biostratigraphy of the *parvus* – *ludensis* interval. However, Retiolitidae are found more rarely than the species of *Pristiograptus*. The morphology of Retiolitidae can be determined only by means of chemical preparation; this process is time consuming and inapplicable for some rock types (for example, shales).

The genus *Pristiograptus* is also important to biostratigraphy of the Ludlow, where the *Pristiograptus tumescens* biozone was established, but its biostrati-

graphic value to Wenlock, and the Homerian in particular, cannot be overestimated.

This genus has been studied previously, only briefly in the interval comprising the upper Sheinwoodian-lower Homerian (*perneri* through *lundgreni* biozones). This was probably because the biozonation of this interval is based on the species of genus *Cyrtograptus* and not on the species of *Pristiograptus*, which lie on the basis of biozonation of the upper Homerian. However, working in a subsurface area, it is almost impossible to find samples of *Cyrtograptus*, because their colonies are big and particularly rare in borehole material. This makes the species of *Pristiograptus*, which are smaller and more abundant (and therefore more likely to be found), particularly valuable.

These aspects are covered in the present thesis, which addresses the systematics, distribution and evolution of *Pristiograptus* in Wenlock, in the critical interval in which new data and improvements to taxonomy have potentially high biostratigraphic significance. For this purpose, new collections were obtained from Lithuania and from the Holy Cross Mountains. All existing Lithuanian collections and also collections in Latvia, Estonia, Poland and Gotland were investigated. As a result of detailed morphological measurements of *Pristiograptus*, SEM studies and analysis of morphological changes in the stratigraphic succession, the stratigraphically valuable taxa were revised, their diagnoses justified, the distribution of the species documented and improvements to biostratigraphy proposed in four papers and in the present summary.

Aims of the thesis:

1. to elaborate improved diagnoses and better understanding on general morphology that collectively could lead to improved identification of the species of this genus;
2. to document stratigraphic distribution of the species of *Pristiograptus* in Wenlock;
3. to document morphological changes in *Pristiograptus* through Wenlock and to propose reconstruction of phylogeny in the species of *Pristiograptus* in Wenlock;
4. to propose improvements to the graptolite biostratigraphy of Wenlock.

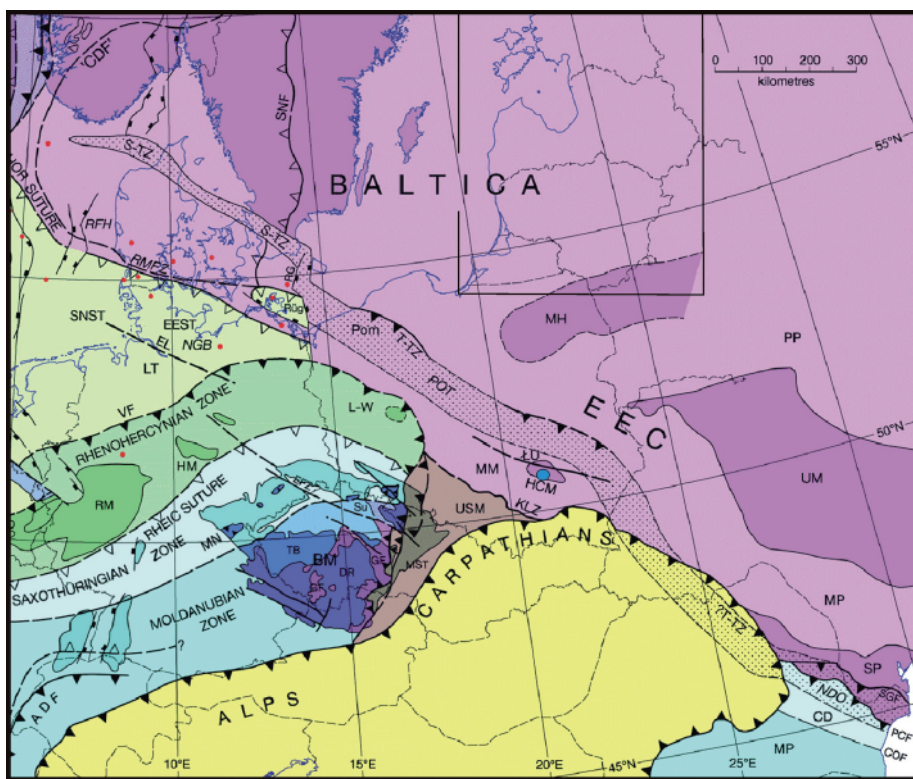


Fig. 2. Basement tectonics of the *TESZ* and adjacent areas (T.C. Pharaoh and TESZ Project Core Group, 2000). Key: Post-Palaeozoic basins and platforms: ADF, Alpine Deformation Front; CD, Central Dobrogea; MP, Moesian Platform; NDO, North Dobrogea Orogen; NGB, North German Basin; POT, Polish Trough; RFH, Rynkobing-Fyn High; RMFZ, Romo-Mon Fracture Zone; SP, Scythian Platform. Postulated Palaeozoic terranes and possible terrane/sub-terrane boundaries: EEST, East Elbian Suspect Terranes; EL, Elbe Lineament; KLZ, Kraków-Lubliniec Zone; LT, Lüneburg Terrane; LU, Lysogory Unit (?Terrane); MM, Malopolska Massif (?Terrane); MST, Moravo-Silesian Terrane; PCF, Peceneaga-Camena Fault; SNST, Southern North Sea Terrane; SGF, Sfântu Gheorghe Fault. Proterozoic-Palaeozoic tectonic elements: BM, Bohemian Massif; CDF, front of Caledonian deformation; COF, Capidava-Ovidiu Fault; DR, Drosendorf Unit (of BM); EEC, East European Craton; EFZ, Elbe Fault Zone; GF, Gföhl Unit (of BM); HM, Harz Mountains; HCM, Holy Cross Mountains; L-W, Leszno-Wolsztyn Basement High; MH, Mazurska High; MN, Münchberg Nappe (of BM); PP, Pripyat Trough; RM, Rhenish Massif; USM, Upper Silesian Massif (=MST); SNF, Sveconorwegian Front; S-TZ, Sorgenfrei-Tornquist Zone; Su, Sudetes Mountains; TB, Tepla-Barrandian Basin (of BM); T-TZ, Teisseyre-Tornquist Zone; UM, Ukrainian Massif; VF, Variscan Front.

2. PALAEOGEOGRAPHY

The species of *Pristiograptus* in Wenlock of Lithuania, Latvia and the Holy Cross Mountains, Bardo ravine, are investigated in this thesis. These territories belong to different regions in terms of tectonic structure. Lithuania and Latvia are situated in the western part of the East European Platform, whereas the Holy Cross Mountains are located to the southwest. (Fig. 2).

2.1. Palaeogeography of Baltica in Wenlock

According to palaeogeographic reconstructions based on palaeomagnetic data and palaeontological evidence, the Baltica palaeocontinent was located at the equator during Wenlock time (Torsvik *et al.*, 1996; Golonka, 2000; Cocks & Torsvik, 2002, 2005) (Fig. 3). The Avalonia palaeocontinent collided with Baltica from the southwest about 440 Ma (in the early Llandovery). These two accreted palaeocontinents collided with Laurentia in the west about 425 to 420 Ma (Wenlock–Ludlow) and formed the Laurussia palaeocontinent (Fig. 4). The Scandian Orogeny developed along the contact of Avalonia and Baltica with Laurentia (Cocks, Torsvik, 2002) during which the Iapetus Ocean gradually closed (Torsvik & Cocks, 2005).

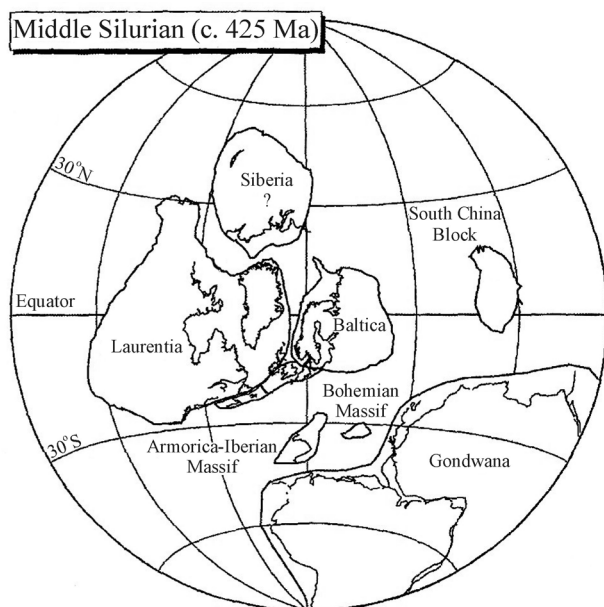


Fig. 3. Palaeogeographic map of Wenlock (Silurian) (Torsvik *et al.*, 1996; Lenz, Kozłowska-Dawidziuk, 2002).

After the collision, the Baltica, Avalonia and Laurentia (Laurussia) palaeocontinents drifted rapidly southward and underwent a counter-clockwise rotation (Cocks & Torsvik, 2005) with the Kara terrain near Baltica to the northwest. The Aegirian Ocean (Torsvik & Cocks, 2005) or Uralian Ocean (Golonka, 2000) met the north bank of Baltica, whereas the Rheic Ocean embraced Baltica from the south (Fig. 4). During Wenlock the Rheic Ocean started to close and brought the Perunica (or Bohemia) Palaeocontinent closer to Baltica.

2.2. Palaeogeography of the Holy Cross Mountains in Wenlock

The region of the Holy Cross Mountains consists of two distinct units: the Łysogóry Unit in the north and the Kielce Unit in the south. These units are separated by the east-west oriented Holy Cross fault running through the Holy Cross Mountains. The Łysogóry Unit is a part of the Łysogóry Block and the Kielce Unit forms the northern, exposed part of the Małopolska Block.

The Bardo ravine in the southern part of the Holy Cross Mountains belongs to the Kielce Unit, Małopolska Block. There are two opinions regarding the geotectonic provenance of the Małopolska Block: the first considers it a Gondwana-derived terrain (Belka *et al.*, 2000), whereas the second treats it as a proximal terrain detached from Baltica before the Ordovician (Narkiewicz, 2002). The Małopolska Block was adjacent to Baltica during the middle Cambrian (Winchester *et al.*, 2002). In early Ordovician, the Małopolska Block was closer to Baltica at about 60° latitude and moved gradually to north, reaching the middle latitudes of the Southern Hemisphere in the late Ordovician (Trela, 2004). Until the late Silurian, the Małopolska Block was located in the same position at the southwestern margin of Baltica (Nawrocki, 2000).

2.3. Global Sea Level Changes in Wenlock

Two large declines in global sea level in Wenlock have been recognized (Johnson *et al.*, 1991): the first in early Wenlock (*murchisoni*, *centrifugus* biozones) and the second at the end of *lundgreni* age. The latter is accepted by many authors (Loydell, 1998; Calner and Jeppsson, 2003; Lazauskienė *et al.*, 2003; Martma *et al.*, 2005; Kaminskis *et al.*, 2006), but the decline in the *murchisoni-centrifugus* biozones is more controversial. For example, Loydell (1998) suggested a sea level rise in this interval, followed by a minor sea level fall in the late *spiralis* Biozone and reaching the end of *murchisoni* Biozone. According to Loydell's interpretation, a minor sea level drop occurred during the *firmus* and the early part of the *riccartonensis* biozones (Loydell, 1998). In

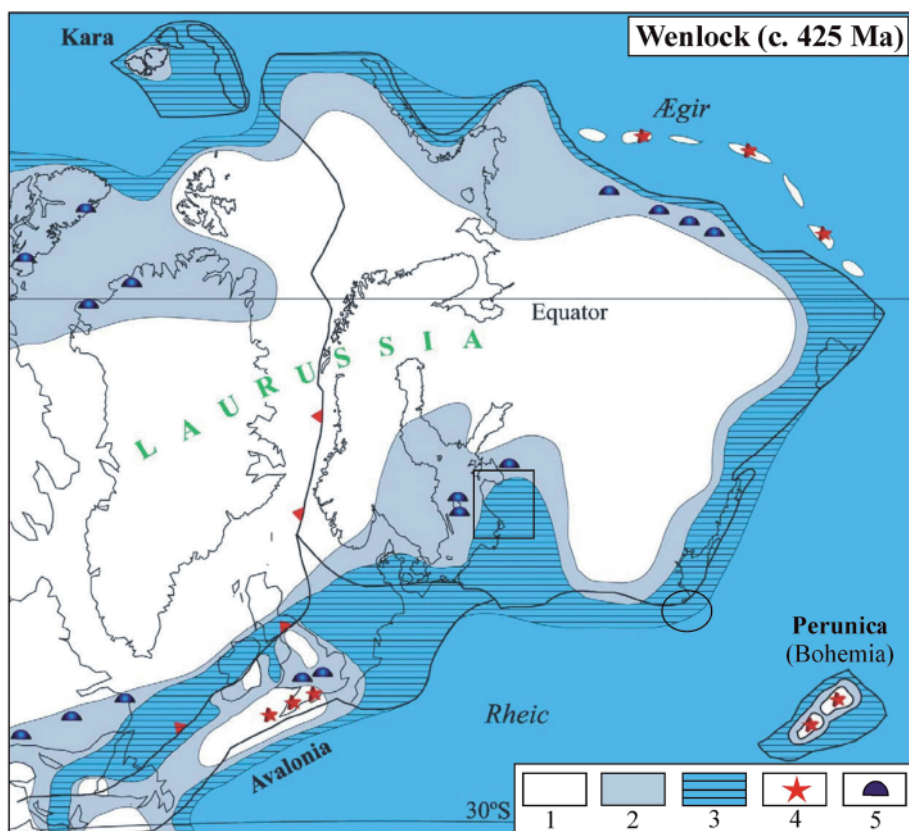


Fig. 4. Palaeogeography of eastern Laurussia in Wenlock (425 Ma) including the Baltica, Avalonia and eastern Laurentia sectors (Cocks & Torsvik, 2005). East Baltic region is marked by rectangle and approximate location of the Holy Cross Mountains by circle. Legend: 1 – land; 2 – shallow shelf; 3 – deep water; 4 – volcanoes; 5 – bioherms.

contrast, Johnson and co-authors (1991) proposed a sea level rise in *riccarto-nensis* Biozone. As a result, Loydell's and Johnson's sea level changed of early Wenlock are totally different.

Climate changes influence the global sea level changes and may be related to bioevents. These could be related to the appearances and extinctions of graptolites and also be responsible for evolutionary changes in *Pristiograptus*. Therefore, palaeoclimate and the bioevents of Wenlock are addressed in the following subchapters.

2.4. Palaeoclimate of Wenlock

The climate was variable in Wenlock. There were two glaciations in the Southern Hemisphere in Wenlock (Kaljo *et al.*, 1997): the evidence for the first one is recorded at the Llandovery – Wenlock boundary and for the second in the upper Wenlock *nassa* biozone in Gondwana. Baltica and the Holy Cross Mountains were located in a warm climatic zone at the equator in Wenlock time, as evident by the occurrence of corals, which formed coral reefs in Gotland (Mötus & Klamann, 1999).

2.5. Bioevents in Wenlock

Based on diversity changes of the fauna in Wenlock, Jeppsson (Jeppsson, 1993; 1998; Jeppsson *et al.*, 1995) distinguished the Ireviken (Llandovery-Wenlock boundary), Boge (*rigidus* biozone), Valleviken (lower part of *lundgreni* biozone) and Mulde (*parus* – *praedeubeli* biozones) bioevents in Wenlock. The Ireviken and Mulde bioevents can also be evident in the East Baltic area (Kaljo *et al.*, 1997, 1998; Martma *et al.*, 2005). The Ireviken bioevent is marked by a mass extinction of conodonts and acritarchs and by a considerable decline in chitinozoans. The Mulde Bioevent caused a mass extinction of graptolites and a considerable decline in the chitinozoan diversity. New data has shown that changes in the distribution of the species of *Pristiograptus* can be ascribed to the bioevents mentioned above. A great proliferation of *Pristiograptus* occurs in the *praedeubeli* Biozone, or post Mulde event.

3. STRATIGRAPHY AND GEOLOGICAL SETTING

Wenlock is the second epoch of the Silurian, which began at about 428.2 ± 2.3 Ma and ended 422.9 ± 2.5 Ma. Two stages are distinguished in Wenlock: the Sheinwoodian and the Homerian. The first stage encompasses the *centrifugus*, *murchisoni*, *riccartonensis*, *belophorus*, *rigidus*, *perneri* generalized graptolite biozones, whereas the Homerian consists of the *lundgreni*, *parvus*, *nassa*, *praedeubeli*, *deubeli*, *ludensis* biozones (Koren' *et al.*, 1996) (Fig. 5).

System	Series	Stages	Generalized graptolite biozones	Graptolite biozones of east Baltic	Regional stages	Correlation of Lithuanian sequences		
						West Lithuania	Central Lithuania	East Lithuania
SILURIAN	Wenlock	Homerian	<i>ludensis</i>	<i>ludensis</i>	Gėluva	Siesartis	Gėluva	Nevėžis
			<i>deubeli</i>	<i>deubeli</i>				Lower Member
			<i>praedeubeli</i>	<i>praedeubeli</i>				Dotnuva Beds
			<i>nassa</i>	<i>nassa</i>				Birštonas
			<i>parvus</i>	<i>parvus</i>				Jonava Beds
			<i>lundgreni</i>	<i>lundgreni</i>				Vilkiškės Beds
	Sheinwoodian	Homerian	<i>perneri</i>	<i>perneri</i>	Jaagarahu	Ančia Mb.	Riga	Verknė
			<i>rigidus</i>	<i>rigidus</i>				Jočiūnys
			<i>belophorus</i>	<i>flexilis</i>				Sutkai Beds
			<i>riccartonensis</i>	<i>riccartonensis</i>				
			<i>murchisoni</i>	<i>murchisoni</i>				
			<i>centrifugus</i>	<i>centrifugus</i>				

Fig. 5. Correlation of the generalized Wenlock graptolite biozonation (Koren' *et al.*, 1996) with graptolite biozones of East Baltic and regional stages and formations.

3.1. Stratigraphy of Wenlock in the East Baltic

Three regional stages distinguish the Wenlock of the East Baltic: the Jaani (*centrifugus* – *flexilis* biozones), Jaagarahu (*perneri* – *lundgreni* biozones) and Gėluva (*parvus* – *ludensis* biozones) stages. These stages are composed of clayey and carbonate rocks. Facies vary from deep-water to shallow-water and even lagoonal environments (Fig. 6).

Four major tectonic structures can be distinguished in the East Baltic: the Baltic syncline, Latvian Saddle, West slope of Belarus – Mazurian Anticline and the Southern slope of the Baltic Shield. All these areas are characterized by varying thickness, stratigraphic completeness, facies and faunal composition of the Wenlock succession (Paškevičius, 1965, 1997). The Rootsikūla Regional Stage in Estonia is distinguished in the upper Wenlock (Nestor, 1997, Kaljo *et al.*, 1977). The Rootsikūla and Gėluva regional stages are largely equivalent but use of the Rootsikūla Regional Stage is preferred in the shallow water facies of the Baltic basin.

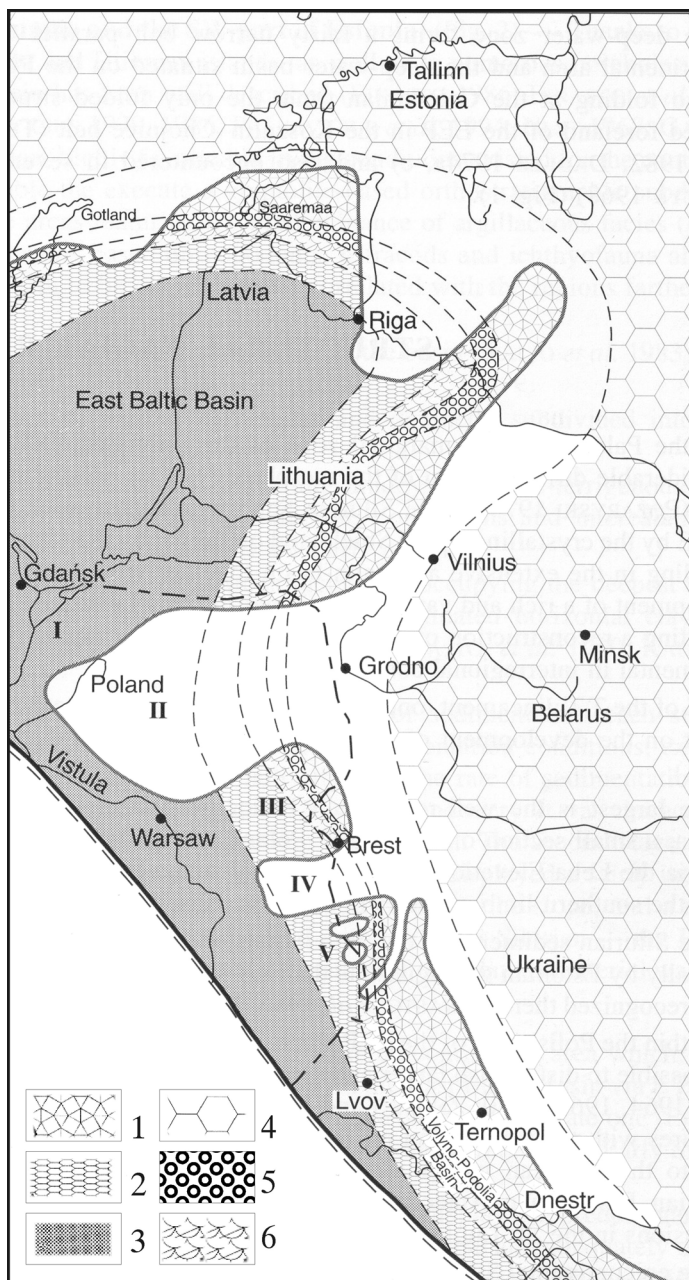


Fig. 6. Facies map of the western margin of the East Europe Platform in late Wenlock (Einasto *et al.*, 1986; Teller, 1997). I – Baltic Syncline; II – Belorussian–Mazurian anticline; III – Podlasie depression; IV – the Holy Cross Mountains. 1 – lagoonal zone; 2 – slope zone; 3 – deep water zone; 4 – land; 5 – lagoon barrier; 6 – open shelf zone.

The Ragainė and Siesartis formations and the Ančia Member express the Wenlock of the Baltic syncline (West Lithuania, West Latvia, Kaliningrad) (Figs 5, 6). The Ragainė Formation, named after the town of Ragainė (now – Neman) in the Kaliningrad Enclave (Paškevičius, 1994), has its stratotype in the Stoniškiai–1 borehole (1792–1875 m interval) (Paškevičius, 1994). The formation is composed of dark, grey argillite and carbonaceous clay with an overall thickness of about 90 m. It contains graptolites of the *centrifugus* – *lundgreni* biozones.

The Ančia Member overlies the Ragainė Formation with conformity. The member was named after the Ančia River in Lithuania (Paškevičius, Lapinskas, 1978) and its stratotype is in the Viduklė–61 borehole (1308 – 1310 m interval). It is composed of micro-laminated argillite and marl and its overall thickness varies from 0.5 to 4 m. This unit contains graptolites of the *lundgreni* (upper part) to *parvus* biozones but a graptolite-free interval occurs in the middle part of Ančia Member.

The Siesartis Formation overlies the Ančia Member with conformity. It is named after the Siesartis River in Lithuania (Paškevičius, Lapinskas, 1978). The stratotype of this unit is the Viduklė–61 borehole (1282–1308 m interval) (Lapinskas, 2000). The formation is composed of dark grey and black massive argillite and marl. Its overall thickness varies from 17.7 to 47.4 m. This formation contains graptolites of the *nassa* – *ludensis* biozones.

There is an intermediate zone between the clay-rich facies in the Baltic Syncline and the carbonate dominated facies in the west slope of the Belarus-Mazurian Anticline, extending from Central Lithuania into Central Latvia. The Riga and Gėluva formations distinguish the Wenlock of this zone.

The stratotype of the Riga Formation in Latvia is the Škirotava–2 borehole (561–585 m interval) (Ulst, 1976). This formation is composed of dark grey and black horizontally thin-laminated argillite and clayey marl in the lower part and of dark grey argillite and carbonaceous clay with clayey limestone layers in the upper part. The thickness of this formation varies from 26 to 121 m. The formation contains graptolites of the *centrifugus* – *lundgreni* biozones. The Riga Formation is overlain by the Gėluva Formation, which is named after Gėluva village in Lithuania (Lapinskas *et al.*, 1985). The stratotype of this formation is the Viduklė – 61 borehole (773.9 – 813 m interval). The Gėluva Formation overlies the Riga Formation with conformity and is subdivided into three members: the lower is composed of grey marl with nodules of microcrystalline limestone, the middle of light grey nodular, microcrystalline, occasionally detritic limestone, and the upper of greenish-grey marl that is dolomitic in its upper part. The total thickness of the formation attains about 34 m (Figs 5, 6). Graptolites are recorded in the formation in western and central Lithuania.

The Paprieniai, Birštonas, Nevėžis, Jočionys and Verknė formations distinguish the Wenlock on the west slope of the Belarus–Mazurian Anticline (East Lithuania, East Latvia) (Fig. 5). These formations are composed of clayey limestone, limestone, clayey dolomite and dolomite. The Paprieniai Formation

is named after the village of Paprieniai, Lithuania. The stratotype of the formation is in the Prienai-3 borehole (58.3–543.5 m interval). This formation is equivalent to the Jaani Regional Stage. The Paprieniai Formation consists of the Sutkai and Vilkija beds (Paškevičius, Lapinskas, 1978). The Sutkai Beds are composed of greenish–grey massive marl, with concretions of microcrystalline limestones with a thickness of about 18 m. The Vilkija Beds are composed of grey marls with limestone interlayers with a thickness of up to 51 m.

The Birštonas Formation is named after the town of Birštonas, Lithuania. The stratotype of the formation is in the Prienai-3 borehole (543.5–471 m interval). The formation comprises the Jonava and Dotnuva beds (Paškevičius, 1958). The Jonava Beds is composed of grey marl with limestone interlayers with a thickness of about 27 m. The Dotnuva Beds is composed of grey nodular microcrystalline and organodetrital limestones up to 37.6 m thick.

The Nevėžis Formation is named after the Nevėžis River in Lithuania (Lapinskas, Paškevičius, 1976). The stratotype of the formation is in the Ledai–179 borehole (646.4–628.1 m interval). The Nevėžis formation is subdivided into two members, the lower being composed of grey marl with nodular limestone and lenses of gypsum, overlain by the grey dolomitic limestone, marl and dolomite of the upper member. The maximum thickness of the Nevėžis formation attains 36 m.

The Jočionys Formation is named after Jočionys village in Lithuania (Paškevičius & Lapinskas, 1978). The stratotype of the formation is in Jočionys – 299 borehole (189.4–173.6 m interval). The Jočionys formation is composed of microcrystalline and organodetrital dolomite with a thickness of 15–26 m.

The Verknė Formation is named after the Verknė River in Lithuania (Paškevičius, 1958). The stratotype of the formation is in the Prienai–3 borehole (464.8–422.8 m interval). The formation is composed of red dolomitic marl with gypsum and layers of red dolomite (Lapinskas, 2000).

Graptolites are generally rare in eastern Lithuania and completely absent in the Verknė and Jočionys formations.

3.2. Stratigraphy of Upper Wenlock and Lower Ludlow of the Holy Cross Mountains

The upper Wenlock sequence is well exposed in the Holy Cross Mountains in the Kielce area (Fig. 7), about 2 km north of Bardo village on the northern side of the Bardo Syncline, especially along the Prągowiec Ravine (Fig. 7). The upper Wenlock and the lower Ludlow in this area are about 600 m thick (Tomczyk, 1962). In this ravine the upper Wenlock deposits are represented by dark yellow and brown clayey shale in the *lundgreni* Biozone (upper part of the Bardo beds). The *nassa* – *Pristiograptus tumescens* – *Saetograptus leintwardinensis* biozones

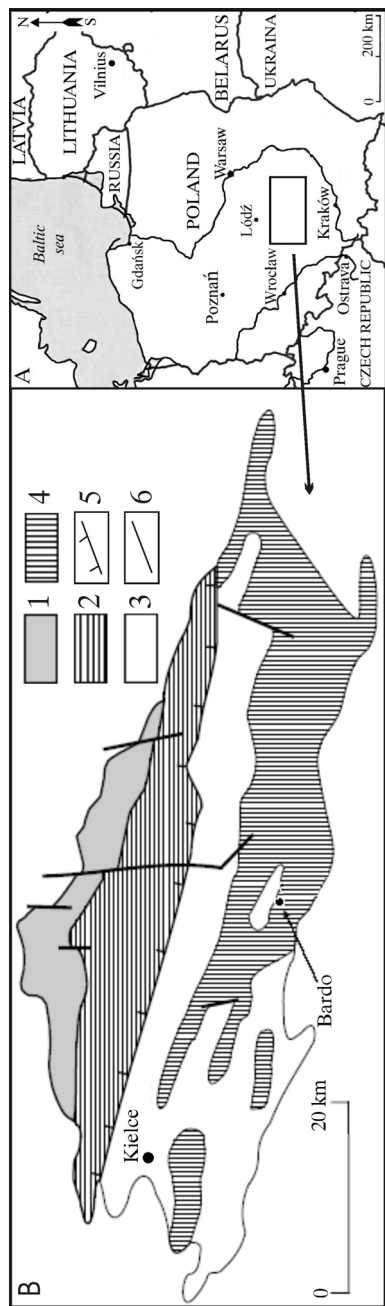


Fig. 7. (A) General map of Lithuania and Poland with the Holy Cross Mountains location (delineated area). (B) Location of the Bardo Ravine in the Holy Cross Mountains (Masiak *et al.*, 2003). 1 – Lysogóry Unit, younger Palaeozoic rocks; 2 – Łysogóry Unit, older Palaeozoic rocks 3 – Kielce Unit, younger Palaeozoic rocks, 4 – Kielce Unit, older Palaeozoic rocks, 5 – Holy Cross fault, 6 – other faults.

are represented by dark grey silty shale, with some limestone concretions (the Prągowiec Beds). Graptolites are common in Bardo in the Prągowiec beds. *Bohemograptus bohemicus* Biozone (Fig. 8) is represented by greywacke (the Niewachlów greywacke) (Tomczyk, 1962). There are only rare graptolites in the Niewachlów Beds.

Series	Stages	Beds	Holy Cross Mountains (Tomczyk, 1962)
Wenlock	Ludlow	Gorstian	
	Homerian	Prągowiec	<i>nilssoni</i>
			<i>gotlandicus</i> <i>dubius</i> <i>vulgaris</i>
			<i>nassa</i>
	Bardo		<i>lundgreni</i> <i>testis</i>

Fig. 8. Upper Wenlock stratigraphic scheme of the Holy Cross Mountains (Tomczyk, 1962).

4. MATERIAL

This research is based on both the museum collections and the newly collected material.

New palaeontological material of late Wenlock has been recovered from Lithuania, Latvia and from the late Homerian (*lundgreni-ludensis* Biozones) of the Holy Cross Mountains.

The new Lithuanian material originates from nine boreholes (Table 1). The rhabdosomes were extracted from 150 rock samples by HCl or HF. About 500 isolated fragments of semi-flattened and 3-dimensionally preserved rhabdosomes were collected, including early astogenetic stages.

Table 1.

Boreholes	Interval	Regional stages	Biozones
Kunkojai-12	1227.75–1202.6 m	Gėluva	<i>parvus – deubeli</i>
Kurtuvėnai-161	1430–1274 m	Jaani, Jaagarahu, Gėluva	<i>centrifugus – ludensis</i>
Likėnai-396	736–690.6 m	Jaagarahu, Gėluva	<i>lundgreni – nassa</i>
Paežeriai-222	736–690.6 m	Jaagarahu	<i>perneri – lundgreni</i>
Parovėja-9	663–528	Jaani, Jaagarahu, Gėluva	<i>centrifugus – ludensis</i>
Pilviškės-143	779.5–764.3 m	Gėluva	<i>praedeubeli – deubeli</i>
Šiupyliai-69	1123.5–969 m	Jaani, Jaagarahu, Gėluva	<i>centrifugus – ludensis</i>
Sutkai-87	899–768.5 m	Jaani, Jaagarahu, Gėluva	<i>centrifugus – deubeli</i>
Vilkaviškis-131	1100–1052 m	Jaagarahu, Gėluva	<i>lundgreni – deubeli</i>

The material of *Pristiograptus* from the Talsi-55 borehole (603–640 m interval) (Latvia) were examined in the R. Ulst's collection in Riga, Nature Museum. D. Kaljo lent material for examination from the borehole Priekulė-20 (depths of 1156.6, 1046.4, and 1145.6 m) (Latvia). This material is derived from the interval of the *lundgreni–ludensis* biozones. All these cores are taken from the western part of Latvia and in the western and central parts of Lithuania (Fig. 9).

One hundred samples were collected from nine outcrops and 15 samples from the scree in the Pragowiec Ravine (the Holy Cross Mountains) (Fig. 10). There are no isolated rhabdosomes in the collection from the Holy Cross Mountains, because it was impossible to extract them with HCl or HF. Therefore, it was also impossible obtain SEM photos of graptolites from the Holy Cross Mountains. The samples from *nassa* (upper part) and *nilssoni* (upper part) – *bohemicus* interval, which had been sampled previously, were no longer accessible because the ravine is overgrown by trees and bushes.

L. Jeppsson's graptolite collection from Gotland (Lund University, Sweden) and A. Urbanek's, A. Kozłowska-Dawidziuk's and L. Teller's graptolite collections from boreholes in Poland (Warsaw Institute of Palaeobiology, Poland) were also examined.

Images of the material were taken with scanning electronic microscope (SEM) in the Laboratory of Materials Research at Tallinn Technical University (Estonia), at the Institute of Geology, Lund University (Sweden) and at the Institute of Palaeobiology in Warsaw (Poland).

The material from Lithuania and a part of the material from the Holy Cross Mountains are stored at the Department of Geology and Mineralogy, Vilnius University. The material from the Holy Cross Mountains (*lundgreni* Biozone) is stored at the Institute of Geological Sciences, Wrocław University (Poland).

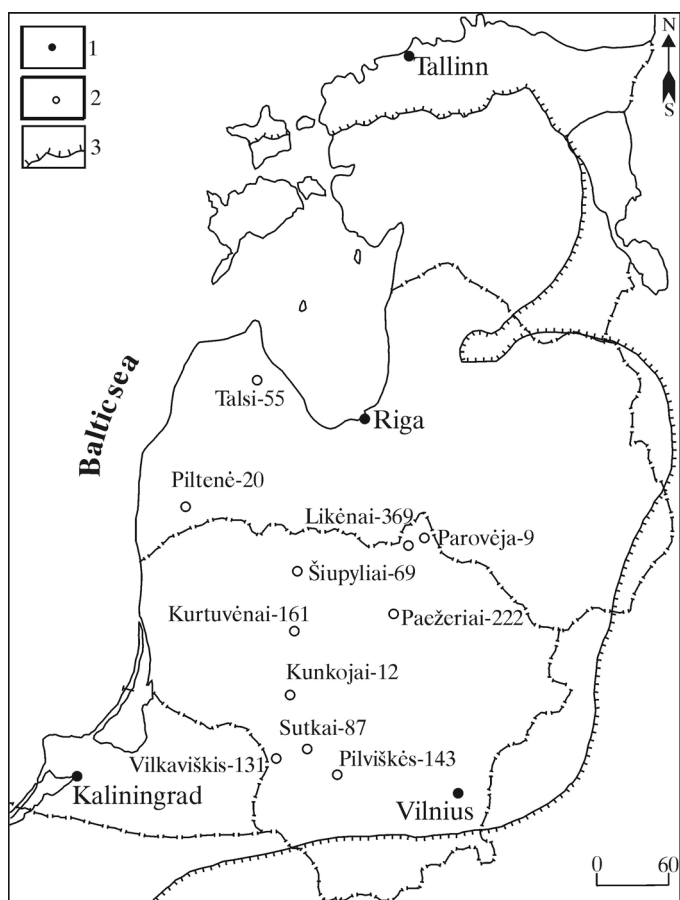


Fig. 9. Localities of boreholes and distribution of Silurian rocks in the Baltic region: 1 – major cities; 2 – boreholes, 3 – boundary of Silurian rocks distribution area.

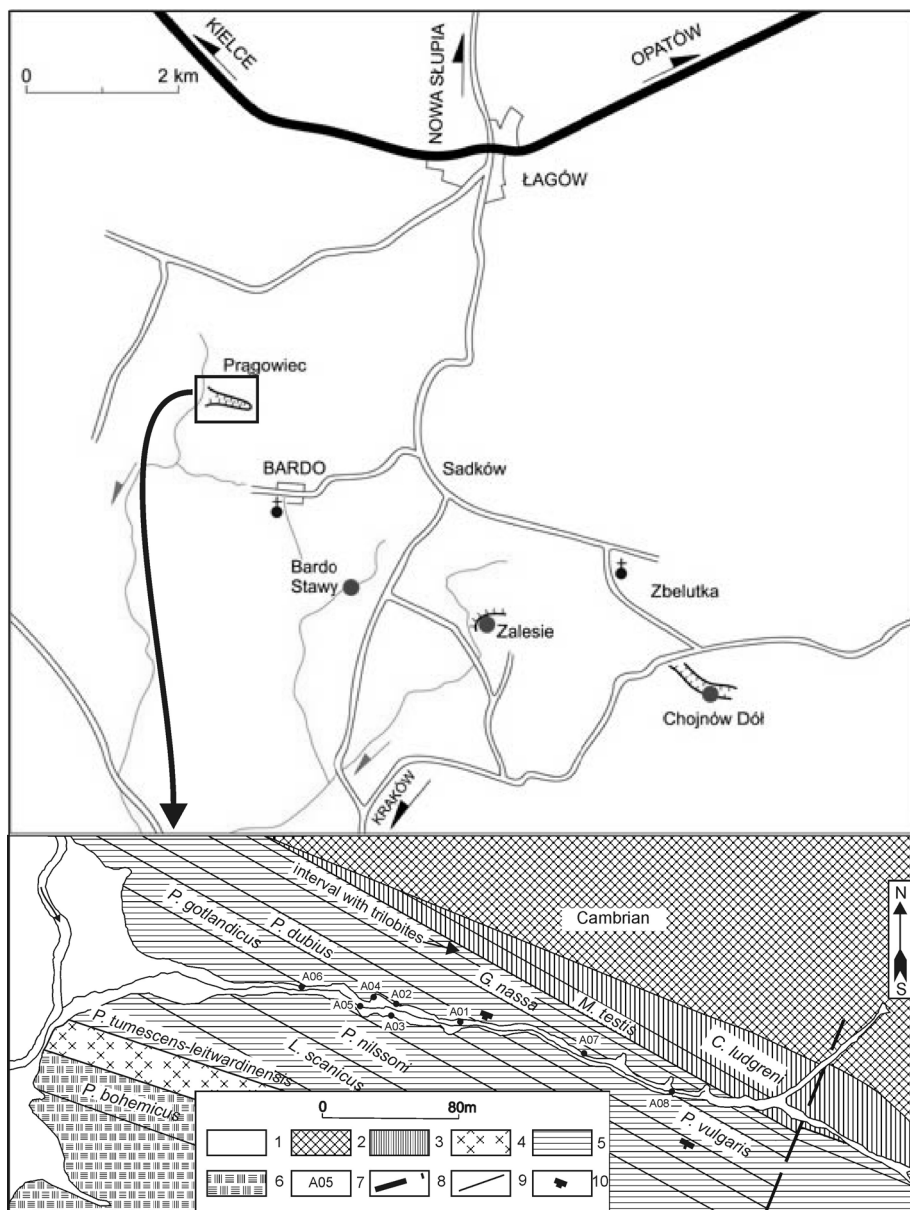


Fig. 10. (A) Position of Pragowies ravine and (B) lithostratigraphic interpretation of the Silurian deposits in the Bardo Syncline (Tomczyk, 1962) and sampling sites. 1 – Quarternary alluvium deposits, 2 – Cambrian sandstones, 3 – dark yellow and brown clayey shale (upper part of the Bardo beds), 4 – diabase, 5 – dark grey silty shale sometimes with concretion of limestone (Pragowiec Beds), 6 – greywacke (Niewachłów greywacke), 7 – sampling sites, 8 – fault, 9 – boundary between graptolite biozones, 10 – direction of dip.

5. SYSTEMATICS

5.1. Terminology and Morphology

This thesis employs largely the terminology developed by Teller (1964), Urbanek (1997) and Radzevičius & Paškevičius (PAPERS I, II). A number of morphological features were introduced by the author of this thesis, such as **angle β** – the angle between the thecal apertural lip and the succeeding metathecal wall, and the **end of the thecal apertural lip** at the disto-lateral margin of the thecal aperture. Variation of angle β allows the distinction of the genus *Pristiograptus* into groups. The location of the end of the thecal apertural lip is an important taxonomic feature in distinguishing forms of the *dubius* group (Fig. 11).

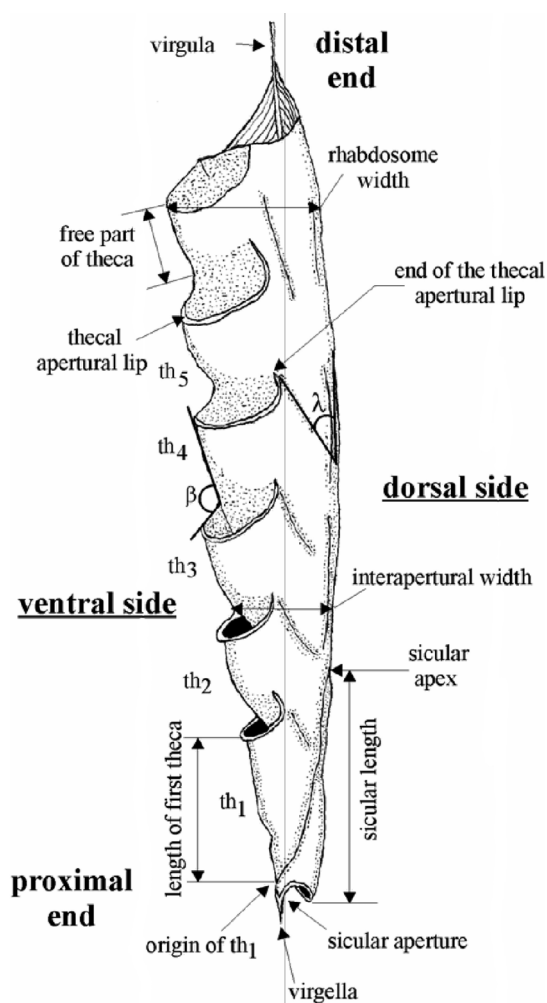


Fig. 11. Morphological elements of a *Pristiograptus* rhabdosome: th1 – the first theca, β – angle between thecal aperture and succeeding theca; λ – angle between thecal axis and virgula.

Descriptions of *P. praedeubeli* and *P. deubeli* from the East Baltic are given for the first time in PAPER I and PAPER III.

5.2. Description of the Genus *Pristiograptus*

The taxonomical position of the genus *Pristiograptus* is described as follows (Příbyl, 1948; Bulman 1970, Ulst, 1974):

CLASS Graptolithina Bronn, 1843
Order Graptoloidea Lapworth, 1875
Suborder Axanopora Frech, 1875
Family Monograptidae Lapworth, 1873
Subfamily Pristiograptinae Gürich, 1908
Genus *Pristiograptus* Jaekel, 1889

Type species. *Pristiograptus frequens* Jaekel, 1889

Diagnosis. Thecae are simple, cylindrical, with straight or only slightly curved free ventral wall and without any distinctive apertural processes. Rhabdosome is straight or slightly curved ventrally.

Pristiograptus dubius dubius (Suess, 1851), (PAPER I)

1913 *Monograptus dubius* (Suess) – Elles & Wood, 1913, p. 376–378, text-fig. 247a–b.

1943 *Pristiograptus dubius dubius* (Suess) – Příbyl, 1943, p. 3–4, pl. I, figs 4–6.

1952 *Pristiograptus dubius dubius* (Suess) – Münch, 1952, p. 85, pl. XVIII, fig 1.

1958 *Pristiograptus dubius dubius* (Suess) – Příbyl, 1958, p. 117.

1994 *Pristiograptus dubius dubius* (Suess) – Lenz, 1994, p. 1420, pl. II, figs A–D.

1997 *Pristiograptus dubius dubius* (Suess) – Urbanek, 1997, p. 157–159, pl. XV, figs 1–4, 7, text-fig. 43.

2000 *Pristiograptus dubius dubius* (Suess) – Radzevičius & Paškevičius, 2000, p. 91–92, pl. I, fig. 2, pl. VI, fig. A (PAPER I).

Holotype. *Graptolitus dubius* Suess, 1851. Plate IX. Fig. 5. Lower Wenlock, *Monograptus riccantonensis* Biozone, black metamorphosed clay shale.

Diagnosis. Rhabdosome long, massive. $L > 26$ mm. Rhabdosome slightly curved to ventral side. Bend begins against fifth–sixth thecae. W with aperture edge against $th_1 - 0,8$ mm. W without aperture edge: $th_1 - 0.7$ mm. W_{max} is against $th_{15} - 1.95 - 2$ mm. 11 thecae in 10 mm interval in proximal part and 8 thecae in medial and distal parts, all of form of a simple cylinder. Overlapping

part of a theca comprises half of its length. In proximal part, the thecal average inclination to rhabdosome axis is 28° and 35° in medial and distal parts. Length of first theca is 1.1 mm; its width against the apertural lip is 0.3 mm. The apertural lip is oblique to thecal axis. Sicular is slightly bent to ventral side, narrow, conical, 1.7–2 mm long and 0.45 mm wide. Apex of sicular is positioned against the place where nose of aperture edge of the first theca grows together with the second theca. A length of non-covered part of a sicular is 0.3 mm. Edge of sicular mouth is curved, has a form of arch. Virgella is fine and short, to 0.6 mm long.

Description. See PAPER I, p. 91–92.

Age and geographical distribution. In Lithuania *P. d. dubius* is found in the Lower Wenlock in the upper part of the *riccartonensis* Biozone and throughout the *anntenularius* Biozone.

Pristiograptus pseudodubius (Bouček, 1932), (**PAPER I**)

- 1943 *Pristiograptus pseudodubius* (Bouček) – Přibyl, 1943, p. 8–9, pl. 1, text-fig 1,3;
1952 *Pristiograptus pseudodubius* (Bouček) – Münch, 1952, p. 86, pl. 18, fig. 7;
1965 *Pristiograptus pseudodubius* (Bouček) – Obut *et al.*, 1965, p. 72, pl. XIII, fig. 2;
1965 *Pristiograptus pseudodubius* (Bouček) – Rickards, 1965, p. 260, pl. 29, fig. 10, text-fig. 2, I;
1967 *Pristiograptus pseudodubius* (Bouček) – Koren' et Ulst, 1967, p. 243–244, pl. XXVIII, figs 8–9, text-fig. 57;
1974 *Pristiograptus pseudodubius* (Bouček) – Ulst, 1974, p. 108–109, pl. XII, figs 1–2; pl. XI, fig. 1.
2000 *Pristiograptus pseudodubius* (Bouček) – Radzevičius & Paškevičius, 2000, p. 92–94, pl. II, fig. 1; pl. VI, fig. H. (**PAPER I**)

Lectotype. *Monograptus pseudodubius* Bouček, 1932, p. 152. figs 2e and f in text. Upper Wenlock in Czechia.

Diagnosis. Rhabdosome narrow, its proximal end is curved to ventral side. This bend begins at th_5 . $L > 20$ mm. W with theca aperture edge against th_1 theca is 0.7 mm. W without aperture edge of theca against th_1 is 0.6 mm. W_{max} is at th_{10} and it is 1.4 mm. Eleven thecae in 10mm in proximal part, 10 in medial and 11 in dorsal part. Thecae have a form of a simple cylinder. The length of the first theca is 1mm, width 0.35 mm. The thecal apertural lip reaches the neighbouring theca. Thecae are bent towards virgula at 30° angle. Sicular is narrow and short, 1.7 mm long and 0.34 mm wide. The apex of sicular is against an aperture edge of the second theca. Virgella is thin, short (0.4 mm).

Description. See PAPER I, p. 92–94.

Age and geographical distribution. *P. pseudodubius* is found in Lithuania in the Upper Wenlock, from the middle of *flexilis* Biozone to the top of *lundgreni* Biozone.

Pristiograptus dubius var. “A” Radzevičius, 2003, (PAPER II)

2003 *Pristiograptus dubius* var. “A” – Radzevičius, 2003, p. 6–7; figs. 5–7.

Type. No S.P9–220, Fig. 5 A, Parovėja-9 borehole, depth 605.25 m, *Cyrtograptus perneri* Biozone.

Diagnosis. The rhabdosome is robust and straight, although some specimens show ventral curvature proximally. L is >11.5mm. The rhabdosome widens gradually from 0.8mm at th_1 , to 0.9mm at th_2 , 1mm at th_3 , and 1.2mm at th_4 . W_{max} is 1.7mm. There are 5–5.5 thecae in 5mm. Thecae are cylindrical. Th_1 is 1mm long. The free part of each theca comprises a half of its length. The thecal apertural lip is distinct and connected to that of the succeeding theca (apparently except for th_1 and th_2 , although it may have been obscured in these thecae by overgrowth of cortical tissue). The connection of apertural lip is particularly obvious in the medial and distal parts of the rhabdosome. The thecae are inclined at 30° to the virgula. L is 1.8 mm and apertural W is 0.4mm. The apex of the sicula reaches the base of th_3 . Th_1 rises 0.1 mm above the aperture. The virgella is short, up to 0.6 mm long. In one specimen there is a thickened protrusion.

Description. See PAPER II, p. 6–7.

Age and geographical distribution. *P. dubius* var. “A” is widespread throughout northern Lithuania in the upper part of the Riga Formation, in the *perneri* Biozone of the Sheinwoodian Stage, comprising the lower part of the Jaagarahu Regional Stage.

Pristiograptus dubius var. “B” Radzevičius, 2003 (PAPER II)

2003 *Pristiograptus dubius* var. “A” – Radzevičius, 2003, p. 7–8; figs 8–9.

Type. No. S.P 222–229, fig. 8 A, Paežeriai-222 borehole, depth 730 m, *Cyrtograptus lundgreni* Biozone.

Diagnosis. The rhabdosome is straight and narrow. L is >12.5 mm. W is 0.7mm at th_1 . W_{max} is 1.1 mm. The minimum, inter-apertural width is 0.5 mm at th_1 and 0.9 mm at th_5 . There are 5–5.5 thecae in 5 mm. The free part of each theca comprises a half of its length. The thecal apertural lip is distinct, extending onto the ventral wall of the succeeding theca, but does not reach its apertural lip, ending at midway up along the ventral wall. Thecae are inclined at 30° to the virgula. The sicula is 2 mm long and its apertural width is 0.35 mm.

The apex of sicula is approximately at the level of the apertural lip of th_2 . Th_1 arises 0.2 mm above the sicular aperture. The virgella is long (1.35 mm) and narrow.

Description. See PAPER II, p. 7–8.

Age and geographic distribution. *Pristiograptus dubius* var. “B” is widespread throughout central and western Lithuania. It is found in the *lundgreni* Biozone of the Lower Homerian Stage within the Jaagarahu regional Stage, which spans the upper part of the Riga Formation and the overlying Birštonas Formation.

Pristiograptus sp. Radzevičius, 2003, (PAPER II)

2003 *Pristiograptus* sp. – Radzevičius, 2003, p. 8–9, fig. 10.

Material. Specimen no S.P9–219, from the Parovėja-9 borehole, depth 595.4m; rhabdosome with th_{1-8} .

Diagnosis. The rhabdosome is straight, massive. L is >11.1 mm. The rhabdosome widens gradually. W is 0.8 mm at th_1 . W_{max} is 1.6mm. The interapertural width is 0.57 mm at th_1 and 0.91 mm at th_5 . There are 5–5.5 cylindrical thecae in 5 mm. Th_1 is 1.6 mm long. The free part of each theca is equal to half of its length. The thecal apertural lip is distinct, extending over the free part of the succeeding theca and being connected with its apertural lip. This connection is easily discernible in the medial and distal parts of the rhabdosome. Th_1 and th_2 either do not have such thecal apertural lip connections or are covered by cortical tissue. The thecal apertural lip bifurcates – a feature well developed in the distal part of the rhabdosome. An intergrowth arch is well developed especially in the proximal part of the rhabdosome. The distance between the thecal apertural lip connection to the succeeding theca and the origin of its bifurcation is 0.25 mm for th_1 and th_2 , and 0.35 mm for th_{3-5} . Thecae are inclined at 30° to the virgula. The sicula is short and narrow, 2mm long with an apertural width of 0.4 mm. The apex of the sicula reaches the base of the th_2/th_3 intertheal septum. Th_1 arises 0.15mm above the sicular aperture. The sicular aperture is strongly concave in profile view. The virgella is thick and short, 0.74 mm long.

Description. See PAPER II, p. 8–9.

Age and geographic distribution. *Pristiograptus* sp. is recorded only from the Parovėja-9 borehole, northern Lithuania, in the *perneri* Biozone of the Sheinwoodian Stage.

Pristiograptus parvus Ulst, 1974, (**PAPER I**)

- 1974 *Pristiograptus parvus* Ulst, 1974 – p. 111–113, pl. XII, fig. 43; pl. XI, fig. 5;
1991 *Pristiograptus dubius parvus* Ulst – Jaeger, 1991, p. 316–318, pl. 25, figs 2–6, 8;
1996 *Pristiograptus dubius* “*parvus*” Ulst – Gutierrez–Marco *et al.*, 1996, p. 660, pl. 1, figs 1–3;
1999 *Pristiograptus dubius parvus* Ulst – Kozłowska–Dawidziuk, 1999, p. 356, fig. 3a.
2000 *Pristiograptus parvus* Ulst – Radzevičius & Paškevičius, 2000, p. 95–96, pl. II, figs 2, 3; pl. VI, fig. F. (**PAPER I**)

Holotype. Western Latvia, Bernatai borehole, depth 823,4 m, stored in the Natural Museum in Latvia (Riga), collection No 32/03, 1 specimen. Upper Wenlock, *Gothograptus nassa* Biozone, Ulst, 1974, p. 111–113, Pl. XII. Fig. 5.

Diagnosis. Rhabdosome is straight, sometimes very slightly curved to ventral side. It is fine, studied specimens are > 0.7 mm long, but can be longer. W with edge of theca aperture at th_1 is 0.6 mm. W_{max} is 1 mm. W without edge of theca aperture at th_1 is 0.5 mm. Virgula is thin short – 1.2–1.5 mm. Thecae are cylindrical. Length of first theca is 0.9–1 mm, width 0.3 mm. It begins against the sicula mouth. Thecae become slightly broader towards the mouth. The thecae mouth is oblique to theca axis. A free part of theca comprises half of its length. Thecae have an average inclination to rhabdosome axis at an angle 30°. Eleven to twelve thecae in 10 mm. Sicula is fine, 1.3 – 1.5 mm long and 0.2–0.3 mm wide. An apex of sicula reaches the beginning of the second theca. Virgella is 0.3 mm long.

Description. See PAPER I, p. 95–96.

Age and geographic distribution. *P. parvus* is widespread in the Upper Wenlock of the Baltic Syncline, in the lower part of the *nassa* Biozone and very often it is associated with microlaminated and clayey limestones of the Ančia Member. The interval of its vertical distribution ranges only some meters (1–3 m).

Pristiograptus dubius ludlowensis (Bouček, 1932), (**PAPER I**)

- 1943 *Pristiograptus dubius ludlowensis* (Bouček) – Přibyl, 1943, p. 5–6;
1952 *Pristiograptus dubius ludlowensis* (Bouček) – Münch, 1952, p. 85, pl. XVIII, fig. 3;
1967 *Pristiograptus ludlowensis* (Bouček) – Koren' & Ulst, 1967, p. 245–246, pl. XXVIII, figs 10–11, text-fig. 60;
1974 *Pristiograptus ludlowensis* (Bouček) – Ulst, 1974, p. 110–111, pl. XIII, Figs 3–4ab, pl. XI, fig. 3.

2000 *Pristiograptus ludlowensis* (Bouček) – Radzevičius & Paškevičius, 2000, p. 94–95, pl. VI, fig. B. (**PAPER I**)

Lectotype. *Monograptus dubius ludlowensis* Bouček, 1936. Plate I. Fig. 8. Lower Ludlow. *Monograptus nilssoni*–*Monograptus scanicus* biozone (now *Neodiversograptus nilssoni*–*Lobograptus scanicus* biozone).

Diagnosis. L mostly up to 30 mm but may be longer. The proximal end of rhabdosome is slightly curved towards ventral side. This bend begins from fifth–sixth theca. W with theca aperture edge at th_1 is 0.75 mm. W_{max} is 2 mm. Rhabdosome is sharp and gradually becomes broader, and W_{max} is reached at th_{10-15} . W without thecal aperture edge at th_1 is 0.7 mm and th_{10} – 1.5 mm. Thecae are cylindrical. The length of first thecae is 1.1 mm, its width – 0.4 mm. The overlapping part of a theca makes half to two-thirds of its length. The thecal apertural lip is distinct and approaches the middle part of neighbouring theca. Thecal mouth is oblique to the thecal axis. Thecae are inclined to virgula at an average angle of 30°. In the proximal part of rhabdosome 11 thecae in 10mm interval, in medial and distal parts – 9–10 thecae. Sricula is conical. Its length is 2 mm, width 0.38 mm. Apex of sricula reaches a middle part of aperture edge of second theca. Virgella is 0.75 mm long.

Description. See PAPER I, 94–95.

Age and geographic distribution. *P. d. ludlowensis* is distributed throughout the Baltic syncline in a wide stratigraphic interval. This species is found from the middle part of the *nassa* Biozone, Upper Wenlock to the top of *scanicus* Biozone, Lower Ludlow. Most often *P. d. ludlowensis* is found in clay rocks, clayey limestones, calcareous clays, marls. *P. d. ludlowensis* described by B. Bouček in Czechia is found in the *nilssoni* – *scanicus* biozone.

Pristiograptus meneghini (Gorthani, 1922), (**PAPER I**)

1948 *Pristiograptus meneghini meneghini* (Gorthani) – 1948, p. 10–11, pl. I, figs 1–2, text-plate II, figs E1, 2, 3.

1952 *Pristiograptus meneghini meneghini* (Gorthani) – Münch, 1952, p. 86, pl. 18, fig. 9.

1965 *Pristiograptus meneghini meneghini* (Gorthani) – Rickards, 1965, p. 258–259, pl. 29, fig. 7, text-plate, fig. 2j.

1989 *Pristiograptus meneghini* (Gortani) – Lenz & Melchin, 1989, p. 7, pl. 3, fig. M.

1991 *Pristiograptus meneghini* (Gorthani) – Lenz & Melchin, 1991, p. 228, pl. 16, figs B, C.

2000 *Pristiograptus meneghini* (Gorthani) – Radzevičius & Paškevičius, 2000, p. 96, pl. I, fig. 1, pl. VI, fig. C.

Lectotype. Specimen selected by Přibyl from the Gorthani work (1922), Plate VIII, Fig. 4, from Goni Sardinia, *Monograptus flexilis* Biozone.

Diagnosis. Rhabdosome is straight and narrow. Proximal end of a colony is slightly curved to ventral side. L – 20 mm. W against th_1 is 0.75 mm, W_{max} – 1.7 mm at th_{15} . W without aperture edge of theca against th_1 is 0.5 mm, and th_5 – 1 mm. Nine to ten thecae in 10 mm. Length of the first theca is 1.26 mm, its width – 0.4 mm. A theca mouth is oblique to theca axis. A non-covered theca part comprises half the length of theca. Theca is average inclination 25–30°. Sacula in conical. Its length is 1.7–1.9 mm and width at mouth is 0.35 mm. Sacula apex reaches aperture edge nose of the second theca. Virgella is acute and thin. Its length is 0.7 mm.

Description. See PAPER I, p. 96.

Age and geographic distribution. The *P. meneghini* is very rare in the East Baltic and its distribution interval is uncertain. The species seems to occur in the upper part of *antennularius* Biozone. This taxon needs to be re-investigated, especially the lectotype.

Pristiograptus lodenicensis Přibyl (1943), (PAPER I, II)

1943 *Pristiograptus lodenicensis* – Přibyl, 1943: pp. 23–24, text-figs C, D, J, K; pl. III, figs 8–11.

1952 *Pristiograptus lodenicensis* Přibyl – Münch, 1952, p. 91, pl. 20, fig. 7;

1967 *Pristiograptus lodenicensis* Přibyl – Koren' & Ulst, 1967, p. 224, text-fig 58; pl. XXIX, figs 4–5;

1974 *Pristiograptus lodenicensis* Přibyl – Ulst, 1974, p. 115, pl. XIII, figs 1–2 a, b; pl. XI, fig. 7.

2000 *Pristiograptus lodenicensis* Přibyl – Radzevičius & Paškevičius, 2000, p. 97–98, pl. IV, figs 1a, b, c, 2a, b, c, pl. VI, fig. D. (PAPER I)

2003 *Pristiograptus lodenicensis* Přibyl – Radzevičius, 2003, p. 10–11, figs 10–11. (PAPER II)

Holotype. *Pristiograptus lodenicensis* Přibyl, 1943. Plate I, fig. 2. Upper Wenlock (Homeric stage), *Cyrtograptus lundgreni* Biozone.

Diagnosis. The rhabdosome is straight and massive; the proximal end of some specimens is slightly curved ventrally as far as up to th_4 or th_5 . L is at least 30 mm. W is 0.7 mm at th_1 and W_{max} is normally 1.5 mm but may reach 2 mm by th_{16-18} . The inter-apertural width is 0.55mm at th_1 and 0.9mm at th_5 . Thecae are uniform, slightly curved, and widen towards the aperture. The apertural lips of symmetrically flattened thecae form an acute angle (β) with the succeeding thecae. Thecae are slightly curved, widening towards the aperture, which shows a small ventral depression and curvature at the connection with the succeeding theca. Overall, thecal apertures are perpendicular to the rhabdosomal axis. Th_1 is 0.9–1 mm long and overlaps for 1/3–1/2 of its length. Thecae are inclined to

the rhabdosomal axis at an angle 29–32°. The sicula is small, 1.2–1.5 mm long, and 0.25–0.3 mm wide aperturally. It is slightly curved ventrally. The sicular apex attains a level between the middle and the top of th_2 .

Description. See PAPER I, p. 97–98; PAPER II, 10–12.

Age and geographic distribution. *P. lodenicensis* is widespread in the East Baltic area (Lithuania, Latvia). It is found in the upper part of the Riga Formation and in the Birštonas Formation, in the *lundgreni* Biozone of the Homerian Stage, Jaagarahu Regional Stage. *P. lodenicensis* is also found in the Czech Republic and Poland.

Pristiograptus virbalensis Paškevičius, 1974, (PAPER I, III)

1974 *Pristiograptus virbalensis* sp. nov. – Paškevičius, 1974, p. 128, figs 3–6, text-fig 2;

1979 *Pristiograptus virbalensis* Paškevičius – Paškevičius, 1979, p. 155–157, pl. IX, figs 1–2, pl. XXIV, figs 3–6.

2000 *Pristiograptus virbalensis* Paškevičius – Radzevičius & Paškevičius, 2000, p. 96–97, pl. III, figs 1–2, pl. VI, fig. G. (PAPER I)

2005 *Pristiograptus virbalensis* Paškevičius – Radzevičius & Paškevičius, 2005, p. 163–166, pl. II, fig. E. (PAPER III)

Holotype. *Pristiograptus virbalensis* Paškevičius, 1974, p. 128, pl. 17, Figs 3ab; text-fig. 2a. Lithuania, Virbalis-5 core, depth 1026.75 m, specimen 920, Upper Wenlock, *virbalensis* Biozone. Holotype is stored in the Geological Museum of the Department of Geology and Mineralogy of the Vilnius University.

Diagnosis. Rhabdosome is large; its proximal end is curved to ventral side against 5–8 thecae. L is equal to 30–40 mm. W against th_1 is 0.8 mm and W_{max} is against 10–15 thecae where it reaches 2–2.5 mm. W with out aperture edge of theca against th_1 is 0.7 mm and th_5 – 1.2 mm. Length of the first theca is 1.2 mm, its width is 0.4–0.5 mm. The apertural lip of first thecae resembles the thecae of the *dubius* type but the medium and distal parts of the thecae have not such a distinctly curved apertural lip. In the proximal part of the rhabdosome the apertural lipe forms an acute angle (63–68°) to the thecal axis, whereas in the medial and distal parts the edge of thecal aperture is perpendicular to the thecal axis. The overlapping part of the theca equals two-thirds of the whole thecal length. Thecae are inclined to virgula at angle of 30–40°. In the interval of 10 mm 10–11 thecae are counted. Sicula is narrow, it is conical. Its length is 2.25–2.5 mm, width against the mouth is 0.4 mm. Mouth of a sicula is slightly concave. The apex of sicula is positioned near the nose edge of the second thecae. Virgella is large, obtuse, 0.7–0.8 mm long and 0.1 mm wide. Virgula terminates with a small drop-like structure.

Description. See PAPER I, p. 96–97; PAPER III, p. 163–166.

Age and geographic distribution. *P. virbalensis* is widespread throughout the East Baltic and Holy Cross Mountains. It is found in the *virbalensis* Biozone (equivalent to *praedeubeli*–*deubeli* biozone in Arctic Canada, Gotland, Central Asia, Poland), Homerian Stage, (Gèluva Formation), Upper Wenlock.

Pristiograptus praedeubeli (Jaeger, 1991), (**PAPER III**)

- 1969 *Monograptus ludensis* (Murchison) – Holland *et al.*, 1969, p. 670, fig. a;
1969 *Pristiograptus jaegeri* – Holland *et al.*, 1969, p. 670, text-plate 120, fig. m (*partim*);
1991 *Pristiograptus praedeubeli* (Jaeger) – Jaeger, 1991, pp. 318–326, pl. 26, figs 1–8; pl. 27, figs 1–11, 14, pl. 29, fig. 11, text-figs 4–18;
1992 *Pristiograptus praedeubeli* (Jaeger) – Koren' & Suyarkova, 1992, pp. 95–97, pl. 8, figs B–E, pl. 9, figs A, B, D, E;
1994 “*Pristiograptus*” *praedeubeli* (Jaeger) – Lenz, 1994, p. 1420, pl. 2, figs 2E–G, pl. 3, figs 3A–E;
1994 “*Pristiograptus*” *ludensis* (Murchison) – Lenz, 1994, p. 1422, pl. 3, fig. G (*partim*);
1996 *Colonograptus* ? *praedeubeli* (Jaeger) – Gutierrez–Marco *et al.*, 1996, p. 660, pl. 1, figs 4–6;
1997 *Colonograptus* ? *praedeubeli* (Jaeger) – Kozłowska–Dawidziuk, 1997, p. 394, text-fig. 2;
1997 *Colonograptus praedeubeli* (Jaeger) – Zhang & Lenz, 1997, p. 1227, pl. 4, figs 4A–D; pl. 5, figs 5T–W.
2005 *Pristiograptus praedeubeli* (Jaeger) – Radzevičius & Paškevičius 2005, p. 166–167; pl. I, figs C, F, G, I, pl. II, figs C, D. (**PAPER III**)

Holotype. Refigured *Monograptus praedeubeli* Jaeger presented by Jaeger (1991), Plate 27, Fig. 2 (proximal part) and Plate 30, Fig. 3 (whole rhabdosome of the holotype); g697.1.12 erratic boulders, near Rügen Island, Baltic Sea, the *praedeubeli* biozone.

Diagnosis. Rhabdosome is massive and long; it is slightly curved to dorsal side in proximal part. L reaches 25mm, but longer rhabdosomes are also found. W against th_1 is 0.76–0.8 mm and at th_{10} – 1.25 mm. The rhabdosome widens rapidly between the first theca and fourth-fifth thecae, further on its width remains nearly constant. W_{max} is against the th_{18-19} and reaches 1.8–2 mm. W without aperture edge of thecae against th_1 is 0.55–0.6 mm and against th_{10} – 1–1.15 mm. Thecae are cylindrical. Length of the first theca is 1.1 mm, its width 0.35 mm. First four thecae differ of the thecae located in the medial and distal parts of the rhabdosome, by original zigzag-form of thecal apertural lip. In the middle part of thecae it descends. The apertural lip of thecae in the medial and distal parts of the rhabdosome lack such hollows like it is characteristic of *Pristiograptus* type. The thecal apertural lip is straight. Thecae in the distal part

are larger, 1.7–2 mm long and 0.6–0.8 mm wide. In the proximal end of rhabdosome, the length of the free part of the theca equals 0.4 of its length, and in distal part it reaches one third of the whole theca length. Thecae are inclined to the rhabdosome axis at a 30–35° angle. In the proximal part of the rhabdosome 12–13 thecae are counted in 10 mm interval, in the distal part the same value is 10–11.5. Sicular is massive, 1.9–2 mm long and 0.25–0.3 mm wide. It is leaned to the dorsal side of rhabdosome. Against the mouth the sicular is curved to the ventral side. Due to this bend the sicular is horn shaped. The curvature begins in the non-covered free part of the sicular, which is 0.4–0.45 mm long. Sicular bears a massive, acute virgella, 0.8–1 mm long. Apex of the sicular ends against the aperture edge of the second theca.

Description. See PAPER III, p. 166–167.

Age and geographic distribution. *P. praedeubeli* is widespread in the East Baltic area, in the lower part of the *virbalensis* Biozone. *P. praedeubeli* is known also from Arctic Canada, Gotland (Sweden), Ireland, Russia (southern Urals, northern Nuratau Range and the Alai Range), East Poland.

Pristiograptus deubeli (Jaeger, 1959), (PAPER III)

1959 *Monograptus deubeli* – Jaeger, 1959, pp. 126–127, pl. 10, figs 4–8;

1969 *Monograptus deubeli* Jaeger – Holland *et al.*, 1969, p. 672–673, pl. 130, fig. 3;

1969 *Pristiograptus jaegeri* – Holland *et al.*, 1969, p. 670, text-fig. 2, fig. k (*partim*);

1994 *Monograptus deubeli* Jaeger – Koren' & Suyarkova, 1994, p. 93–95, plates 6–7; pl. 8, figs F–G, pl. 9, figs C, F–K, pl. 10, figs D–M;

1994 “*Pristiograptus*” *ludensis* (Murchison) – Lenz, 1994, p. 1422, pl. 3, fig. F (*partim*).

2000 *Pristiograptus deubeli* (Jaeger) – Radzevičius & Paškevičius, 2000, p. 99–100, pl. V, figs 1a–c. (PAPER I)

2005 *Pristiograptus deubeli* (Jaeger) – Radzevičius & Paškevičius 2005, p. 167–168; pl I, figs. A, B, H, pl. II, fig G. (PAPER III)

Holotype. *Monograptus deubeli* Jaeger, 1959, Table 10, Fig. 5. Upper Wenlock, previous *Gothograptus nassa*–*Pristiograptus vulgaris* zone in Germany, at present considered the *Pristiograptus deubeli* Biozone.

Diagnosis. Rhabdosome is massive, its proximal end slightly curved to dorsal side. $L > 30$ mm. W with edge of thecal aperture against th_1 is 0.8–1 mm and th_5 – 1.15–1.3 mm. W without edge of theca aperture against th_1 is 0.7–0.8 mm and th_5 – 1.0–1.2 mm. Rhabdosome W near th_{10} is 1.4 mm. W_{max} is against the th_{15-17} and equals 2 mm. Thecae cylindrical and can be divided between two types. First three–four thecae are of the *Colonograptus* type, whilst the thecae in the medial and distal parts of the rhabdosome are of the *Pristiograptus* type.

Length of the first theca is 1–1.15 mm, its width – 0.35–0.38 mm. First three-four thecae have a specific lip of thecal aperture edge: it is curved, and thecae have a distinct bend in ventral side. The bend in the first theca is most distinct. Upon the fifth theca this excavation disappears, and the apertural lip becomes smooth. The thecae in distal part are larger, length is 1.7–1.75 mm, width – 0.55–0.6 mm. The overlapping part of the theca comprises half its length. Theca is inclined to rhabdosome axis at an angle of 30–35°. In the proximal part of the rhabdosome, 13 thecae are counted in a 10 mm interval, in medial and distal parts the corresponding number is 11–12 thecae. Sicula is long, massive. Its length mostly attains 2 mm but longer ones (up to 2.4 mm) are also found. Its width against the mouth is 0.15–0.2 mm. Sicula broadens downwards, is conical and protrudes into the dorsal side of the rhabdosome. The projection of the sicula is curved to dorsal side of the rhabdosome. The sicula apex reaches the end of aperture edge of the second theca. Sicula has a large, massive virgella which protrudes towards ventral side of the rhabdosome. Length of the virgella reaches 1 mm.

Description. See PAPER III, p. 167–168.

Age and geographic distribution. *P. deubeli* is widespread in Lithuania, however in a very narrow vertical interval. It is found in the Upper Wenlock, in the upper part of the *virbalensis* Biozone. *P. deubeli* is known in many localities of the Europe, but also in northern Africa, Australia, Arctic Russia and the southern Urals.

Pristiograptus ludensis (Murchison, 1839)

1969 *Monograptus ludensis* (Murchison 1839), sensu Wood 1900 – Holland *et al.*, 1969, p. 673–676, pl. 130, fig. 2, text-figs 2a–j, 3a–e.

1991 *Pristiograptus ludensis* (Murchison) – Lenz et Melchin, 1991, p. 219, 228, figs 3 A–D, figs 16 D, E.

2003 *Pristiograptus ludensis* (Murchison) – Radzevičius, 2003, p. 49–50; pl. I, figs L, M.

Lectotype. *Monograptus ludensis* (Murchison 1839); Holland, Rickards and Warren, text-figs Af and 3b, *ludensis* biozone, upper Wenlock.

Diagnosis. Rhabdosome is massive and straight; occasionally proximal end is curved ventrally. $L > 35$ mm. The W_{max} is 2.3 mm. W_{th1} is 0.9 mm. There are 10–11 thecae in 10 mm. Thecae have cylindrical form and are dimorphic. Thecae in medial and distal part without apertural processes and thecae in proximal part have small bilateral apertural lobes. L of sicula is 2 mm and W – 0.25 mm. Sicula is curved to ventral side of rhabdosome.

Age and geographical distribution. *P. ludensis* is known from upper Wenlock, in *ludensis* Biozone of East Baltic, Poland, Wales, Arctic Canada, Czech Republic, Germany, Sweden, Central Asia.

6. MORPHOTYPES OF *PRISTIOGRAPTUS* IN WENLOCK

A. Přibyl was the first (1943) to distinguish the *dubius* type of species within *Pristiograptus*. Since then, the numerous species of *Pristiograptus* have been associated according to general morphology. Four morphological groups of *Pristiograptus* were recognised by the author in the Wenlock: *dubius*, *lodenicensis*, *deubeli* (also called the *ludensis* or the *ludensograptus* type) and *virbalensis* (Radzevičius & Paškevičius, 2000),

The *dubius* type is the first, the oldest and the most abundant type of *Pristiograptus*. The rhabdosome of a *dubius* type species is robust, the proximal end generally has a slight ventral curvature up to th^4 – th^6 , although sometimes it is straight. Thecae are uniform, cylindrical, and inclined to the rhabdosomal axis at 25–35°. There is a distinct thickening of the thecal apertural margin, the thecal apertural lip (a term introduced in the PAPER II), which extends onto the lateroventral wall of a succeeding theca. The angle between the apertural margin of the thecae and the succeeding thecal wall (β) is always obtuse, especially in the more proximal thecae. The sicula is conical with short, thin, slightly curved virgella. These features are characteristic of *P. praedubius* (Bouček, 1931); *P. dubius dubius* (Suess, 1851); *P. dubius latus* (Bouček, 1932); *P. pseudodubius* (Bouček, 1932); *P. meneghini* (Gortani, 1922); *P. dubius* var. A Radzevičius, 2003; *P. sp.* Radzevičius, 2003; *P. dubius* var. B Radzevičius, 2003; *P. parvus* Ulst, 1974; *P. piltenensis* Koren et Ulst, 1967; *P. dubius ludlowensis* (Bouček, 1936) and, therefore, all these species are considered to be *dubius* type.

Pristiograptus of *dubius* type is widespread, having been reported in Lithuania, Latvia, Poland, Russia, the Czech Republic, Sweden, Germany, Bulgaria, Arctic Canada, Australia, British Isles, France, Italy, Tunisia, Algeria, Morocco, etc. This thesis concentrates on the Wenlock material but the group ranges from the Upper Llandovery up to the Pridoli.

The *virbalensis* is the second adaptive type comprising *P. jaegeri* Holland, Rickards et Warren, 1969; *P. virbalensis* Paškevičius, 1974 and *P. auctus* Rickards. The rhabdosome is massive. The proximal end is ventrally curved up to th_5 – th_8 . Thecae are biform, inclined to the rhabdosomal axis at 20° (proximal end) – 45° (distal end). The angle (β) between the apertural margin of the theca and the succeeding thecal wall is always obtuse in the proximal end but is 90° in medial and distal parts, thus the thecae are biform. The sicula is conical, with a thick and comparatively straight long obtuse virgella. The species of the *virbalensis* group are very similar. The main characteristic of *P. auctus*, is “the presence of a short virgella (0.6 mm), which swells into a bulb-like shape, and has the appearance of a droplet hanging from the proximal end of the rhabdosome. Its swelling is 0.4–0.5 mm in diameter” (Rickards, 1965, p. 260). A rhabdosome of *P. virbalensis* appears similar to that of *P. auctus*; it is straight

with a hanging droplet on the end of virgella. In some cases the virgella has no droplet, but is simply obtuse, but it differs from that in the *Pristiograptus* of *dubius* type, which has sharply ending virgella. The droplet reaches 0.1 mm in diameter and is a little bit thicker than the virgella itself. The virgella of *P. virbalensis* is twice as long as that in *P. auctus*.

Pristiograptus of *virbalensis* type have been reported in Lithuania, Latvia, Poland, Sweden and the group ranges from the *praedeubeli* into the *nilssoni* Biozone.

The *lodenicensis* type includes *P. lodenicensis* Přibyl, 1943; *P. lodenicensis peribalticus* Jaworowski, 1965 and probably *Monograptus* ? *massai* Jaeger, 1991. These species are distinct from the *dubius* group, and *P. lodenicensis* was assigned previously to the *vulgaris* group (Přibyl, 1943). Subsequently, *P. vulgaris* (Wood) was synonymised with *P. ludensis* (Murchison). Therefore, *P. vulgaris* is no longer a valid name so the group must be renamed. A rhabdosome of the *lodenicensis* type is massive. The proximal end is straight or ventrally curved up to th^4 or th^5 . Thecae are uniform and widen towards their apertures, which show small depressions centrally. Thecal apertures are perpendicular to rhabdosomal axis and the angle (β) between the apertural margin of the thecae and the succeeding thecal wall is always acute. Sricula is small and conical, with a slender, short virgella.

The taxonomic position of the *lodenicensis* group is unclear, because *P. lodenicensis* is not a typical *Pristiograptus*. Its thecae are similar to those of *Colonograptus* (e.g. *Colonograptus gerhardi* (Kühne)), differing only in a smaller curvature of the lip of the thecal aperture, as is also the case with *Pseudomonoclimacis* (e.g. *Pseudomonoclimacis latilobus* (Tsegelniuk)) and *Monograptus massai* Jaegeri (the latter species has been reported in the Ludlow of NW Libya). However, the Libyan species *M. massai* could be assigned to the *lodenicensis* group of *Pristiograptus*, because it possesses a typical *Pristiograptus*-like sricula. It is even possible that this group could be distinguished as a separate genus.

The *lodenicensis* group is known from the *lundgreni* Biozone of Lithuania, Latvia, the Czech Republic and Poland.

The *deubeli* type of *Pristiograptus* is characterized by a massive rhabdosome, which is straight or bent to dorsal side. Thecae are biform, they are of *Colonograptus* type in the proximal part and of *Pristiograptus* type in medial and distal parts of the rhabdosome. Mouth of all thecae is perpendicular to thecae axis (β). A sricula of *deubeli* type is bent to ventral side and is horn or cone (or funnel) shaped, with a clear dorsal process. *Pristiograptus praedeubeli* (Jaeger, 1991); *Pristiograptus deubeli* (Jaeger, 1959); *Pristiograptus ludensis* (Murchison, 1839) and *Pristiograptus sigmoidalis* (Bouček, 1936) are attributed to this type.

All “non-*dubius*” species, including *P. lodenicensis*, were formerly assigned to *vulgaris* group (Přibyl, 1943). However, *P. vulgaris* (Wood) was synonymised with *P. ludensis* (Murchison) and this name is no longer valid.

Therefore, this group needs to be renamed. The first attempt was made by Tsegelniuk (1988), who established the *ludensi* group, comprising *Graptolithus ludensis* Murchison 1839, *Monograptus gerhardi* Kühne 1955; *Monograptus deubeli* Jaeger 1959, *Monograptus parultimus* Jaeger 1975, *Colonograptus latilobus* Tsegelniuk, 1976 and *Pseudomonoklimacis podolicus* Tsegelniuk 1976. Currently, *M. gerhardi* is assigned to *Colonograptus*, *M. parultimus* is attributed to the new genus *Neocolonograptus* (Urbanek, 1997), and *C. latilobus* to the genus *Pseudomonoclimacis* (Urbanek, 1997). The corrupted name was changed to *deubeli*.

Several authors attribute *P. deubeli* to the genus *Colonograptus* (Zhang & Lenz, 1997; Lenz, Kozłowska-Dawidziuk, 2002), but others to *Pristiograptus* genus (Lenz & Melchin, 1989; Lenz & Melchin, 1991; Lenz, 1994; Maletz *et al.* 2002) or to *Monograptus* (Koren' & Suyarkova, 1992). *P. deubeli* is very similar to *P. sigmoidalis* (Bouček, 1936). A rhabdosome of *P. sigmoidalis* is curved to the dorsal side. Mouths of all thecae are perpendicular to thecal axis (β) and only the form of thecae and the maximum width enable the distinction between *P. sigmoidalis* and *P. deubeli*. In the former, the maximal length is 2 mm while 2.2 mm in the latter. In *P. deubeli* thecae broaden upwards, whereas in *P. sigmoidalis* they become narrower. Moreover, there is a distinct age difference; *P. sigmoidalis* is attributed to the *nilssoni* Biozone, and is, therefore, younger. The form of rhabdosome in this species resembles the general morphological pattern of the *deubeli* group and the angle between the thecal apertural lip and the succeeding metathecal wall (β) is 90°. Based on this evidence the species is attributed to the *deubeli* group. However, we cannot affirm that *P. deubeli* is equivalent to *P. sigmoidalis*, due in part to the low quality images of *P. sigmoidalis* (Bouček, 1936), particularly of the medial part of the rhabdosome. This problem can be remedied by re-examination of the holotype of *P. sigmoidalis*.

The species of the *deubeli* group are known from *praedeubeli* – *ludensis* biozones of Lithuania, Latvia, the Czech Republic, Poland, Wales, Arctic Canada, Czech Republic, Germany, Sweden and Central Asia.

7. DISTRIBUTION OF *PRISTIOGRAPTUS* IN WENLOCK

A total of 17 species, subspecies and varieties of the genus *Pristiograptus* were identified in Wenlock in the Baltic States and the Holy Cross Mountains in Poland: *P. deubeli*, *P. dubius dubius*, *P. dubius* var. A, *P. dubius* var. B, *P. dubius latus*, *P. jaegeri*, *P. lodenicensis*, *P. ludensis*, *P. ludlowensis*, *P. meneghini*, *P. parvus*, *P. piltenensis*, *P. praedeubeli*, *P. praedubius*, *P. pseudodubius*, *P. virbalensis* and *P. sp.* These species represent all four morphotypes of *Pristiograptus* (Fig. 12).

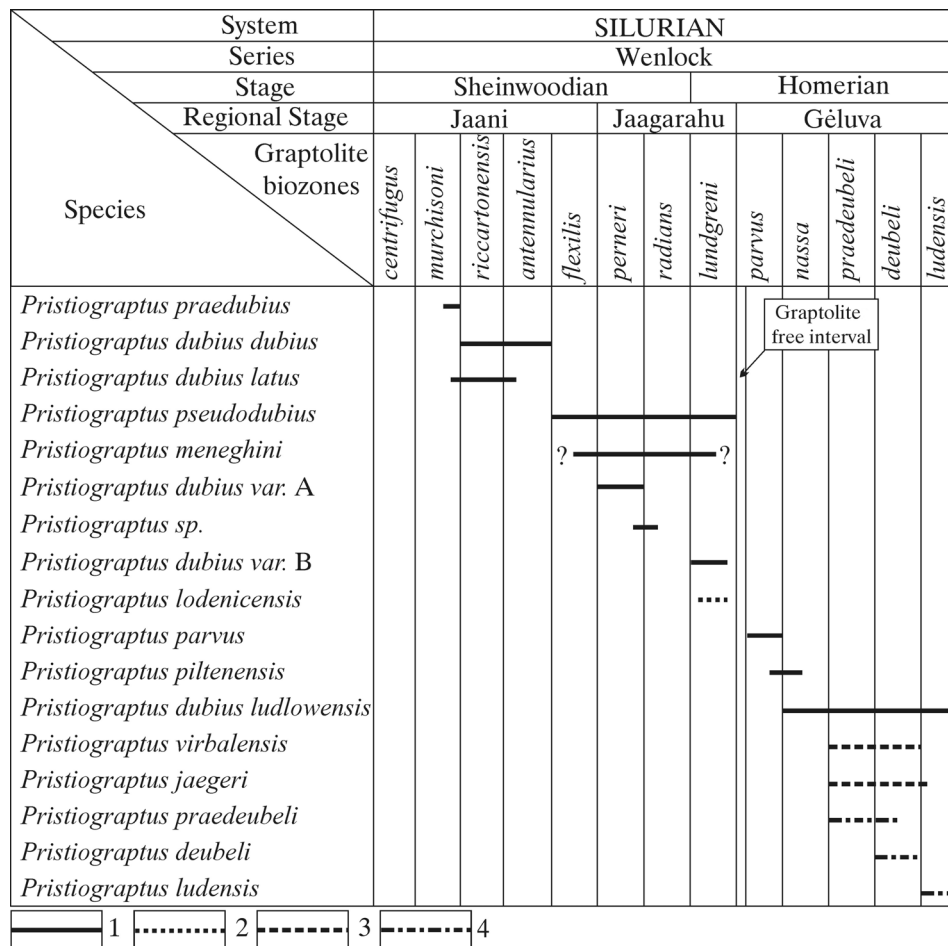


Fig. 12. Distribution of Wenlock *Pristiograptus*, 1 – *dubius* type; 2 – *lodenicensis* type; 3 – *virbalensis* type; 4 – *deubeli* type.

The lineage of *dubius* type of the genus *Pristiograptus* originated in late Llandovery of Bohemia (Příbyl, 1943). Rickards & Wright (2003) claim that first *Pristiograptus* of *dubius* type appears in Llandovery *griestonensis* Biozone, but in the eastern Baltic area, the genus *Pristiograptus* is represented by the species of proposed *nudus* type and the first lineage reaching Wenlock is represented by *P. praedubius* which appears in the *centrifugus* Biozone (Fig. 12). Further on, two new species of this group appear in the *riccartonensis* Biozone: *P. dubius dubius* and *P. dubius latus*. In the *flexilis* Biozone, these two species are replaced by the new species, *P. pseudodubius* and *P. meneghini*. There is *P. meneghini* recorded in the local *instrenus* – *kolobus* Biozones (= *riccartonensis*–*rigidus* biozones) in the Canadian Arctic islands (Lenz, Melchin, 1991). However, the distribution of *P. meneghini* is unclear; it seems to appear higher in the *antennularius* Biozone and disappearing earlier than *P. pseudodubius*. The latter species became extinct at the time of the *lundgreni* crisis.

The greatest diversity of the *dubius* type is found in the *perneri* Biozone (Jaagarahu Stage), in which the total number of the species of *Pristiograptus* is four, though some are of uncertain nomenclature. Together with *P. meneghini* and *P. pseudodubius*, *P. dubius* var. A. and *P. sp.* have been recorded. *P. dubius* var. A. is restricted to *perneri* Biozone, *P. sp.* occurs through the *perneri* – *radians* interval. The appearance of *P. lodenicensis* and *P. dubius* var. B. in the *lundgreni* Biozone marks the appearance of the second, the *lodenicensis* type of *Pristiograptus*. However, the *lodenicensis* type existed in only a very short interval, while *P. lodenicensis* disappeared at the end of *lundgreni* Biozone, before *M. testis testis* and *Cyrtograptus lundgreni*. All graptolite species considered characteristic of Wenlock, except for *Pristiograptus* and Retiolitidae, became extinct by the end of *lundgreni* Biozone.

Only *P. parvus* occurs in the lower part of Gêluva Stage. This species belongs to the *dubius* type and occurs only in the lower part of the *parvus* Biozone. The vertical distribution interval of this species is very narrow – max 5 m, but the quantity of rhabdosomes is great. The upper part of *parvus* Biozone is characterized by *P. piltenensis*, which ranges into the lower part of the *nassa* Biozone. The *nassa* Biozone marks the appearance of *P. dubius ludlowensis*, which is a long ranging species disappearing only in the *invertus* Biozone of Ludlow (Rickards & Wright, 2003).

A new diversification of the genus *Pristiograptus* is recorded in the Upper part of the Gêluva Stage, in the *praedeubeli* Biozone. There are 6 species of *Pristiograptus* recorded in the upper part of Gêluva Formation and the appearance of the *virbalensis* and *deubeli* types is reported also in the upper part of the Gêluva Stage.

The *virbalensis* type consists of *P. jaegeri*, *P. virbalensis* and *P. auctus*. In the eastern Baltic area, *P. jaegeri* appears in the lower part of *praedeubeli* Biozone, but in Arctic Canada this species appears a somewhat earlier, in the *nassa* Biozone (Lenz & Kozłowska-Dawidziuk, 2002). This species ranges up

to the *ludensis* Biozone in the eastern Baltic area. *P. virbalensis* is widespread in the *praedeubeli* – *deubeli* interval in the East Baltic, but in the Holy Cross Mountains it ranges up to the lower part of the *ludensis* Biozone. Typical *P. auctus*, which is known from the sections in *nilssoni* Biozone (Ludlow) in Northern England (Rickards, 1965), is not found in the Baltic States nor in the Holy Cross Mountains. In the Sutkai–87 borehole, *P. cf. auctus* was identified in *deubeli* Biozone but seems to represent only a transitional form between *P. virbalensis* and *P. auctus*.

In the Gėluva Stage, *P. virbalensis* is accompanied by species of the *deubeli* type: *P. praedeubeli*, *P. deubeli* and *P. ludensis*. These species are found in the *praedeubeli* – *ludensis* interval, but the ranges differ in the East Baltic and other areas. *P. praedeubeli* occurs in the *praedeubeli* – *deubeli* interval in the East Baltic, but in the Holy Cross Mountains it is found in *praedeubeli* – *ludensis* interval. In Central Asia (Koren; 1991) and in Arctic Canada (Lenz & Kozłowska–Dawidziuk, 2002) *P. deubeli* (the *deubeli* Biozone) and *P. ludensis* have the same ranges in the eastern Baltic area and in the Holy Cross Mountains, Poland.

The lower part of Ludlow is characterized by species of *Pristiograptus* belonging to the *dubius* type.

8. EVOLUTION AND PHYLOGENY OF *PRISTIOGRAPTUS* IN WENLOCK

The oldest and the most widespread morphotype of *Pristiograptus* in Wenlock is the *dubius* type. The origin of the *dubius* type of *Pristiograptus* was not analysed specifically, but data on the distribution of the particular species shows that the appearance and wider speciation of this type in the eastern Baltic area coincides with the Ireveken event.

The first species of the *dubius* type, *P. praedubius*, appears in the *centrifugus* biozone in the East Baltic. A rhabdosome of this species is straight and the thecal apertural lip ends at a succeeding theca.

A new generation of *Pristiograptus* appears in the *riccartonensis* Biozone and is represented by *P. dubius dubius* and *P. dubius latus*. Both species lack sicula rings and the thecal apertural lip ends at a succeeding theca (Fig. 13A), but the rhabdosome is inclined to the ventral side. The difference between these species is the width of their rhabdosome: in *P. d. dubius* maximal width is 2.5 mm, in *P. d. latus* it is 2 mm. *P. d. dubius* also has more thecae (8 – 11) in the 10 mm rhabdosome interval than *P. d. latus* (8 thecae), but in other features a relationship to *P. praedubius* is obvious suggesting that *P. d. latus* and *P. d. dubius* evolved from *P. praedubius*.

It is likely that *P. pseudodubius* originated from *P. d. dubius*, like *P. meneghini*, at the end of *riccartonensis* Chron. Thecal apertural lip in both these species reaches the middle of succeeding thecae (Fig. 13B) and these species have no sicula rings as well. Further changes of the thecal apertural lip led to the appearance of seemingly two new variations of *P. pseudodubius*: *P. dubius* var. A and *P. sp.* In both these species the thecal apertural lip merges into the thecae apertural lips of neighbouring theca, which is typically seen in *P. dubius* var. A (Fig. 13C), but in *P. sp.* it also forms an intergrowth arch (Fig. 13D). The appearance of these two variations in the *perneri* Biozone seems to coincide with the Boge event (Fig. 14). Noting the changes throughout the Sheinwoodian, it is obvious that the evolution of the genus *Pristiograptus* led towards more massive and stronger rhabdosomes, the thecal apertural lip grow longer and finally coalesced with the thecal apertural lip of a neighbouring theca and formed and intergrowth arch. It is noticeable that siculae had no rings throughout early Wenlock.

The new, *lodenicensis* type was derived from *P. pseudodubius* in the early Homerian (Fig. 14). In this species the angle between the thecal apertural lip and the neighbourhood theca is acute (Fig. 13E). The sicula in *P. lodenicensis* fits the general pattern of the *dubius* type but the apertural lip in *P. lodenicensis* has a depression in ventral part of thecae that is atypical of the genus *Pristiograptus*. However, it is easy to propose that the species is related to *P. pseudodubius* or other member of *dubius* type, being formed as a result of gradually changing angle between thecal apertural lip and the neighbourhood

theca. This suggestion gains additional support from the fact that L. Teller's graptolite collection from NE Poland includes intermediate variations between *P. pseudodubius* and *P. lodenicensis*. Phylogenetic branch of *P. lodenicensis* was blind and this species disappeared during the *lundgreni* crisis (PAPER IV).

A further variation the *dubius* type, *P. dubius* var B. appears also in the *lundgreni* Biozone. Thecal apertural lip of *P. dubius* var. B again no longer reaches the middle of the succeeding theca, like *P. d. dubius*. The rhabdosome is thin, sicula has a free part and a long virgella. On the background of changes throughout Sheinwoodian, this variation is like a step backwards. The end of thecal apertural lip is positioned in the same part of the second theca like in *P. d. dubius*. This variety occurs together with *P. pseudodubius* in the *lundgreni* Biozone.

During the *parvus* time, the appearance of small rhabdosomes that otherwise are rather similar to *P. pseudodubius* is recognised. In some cases, *P. pseudodubius* and *P. parvus* are even assigned to a single species (Rickards, 2005). However, not only the size difference but also some differences in morphology allow distinction of these taxa. The thecal apertural lip in *P. parvus* terminates in the lower part of the neighbouring theca and the rhabdosome is straight, similar to *P. praedubius* (Fig. 13F). Like the older species of *Pristiograptus*, the sicula in *P. parvus* still has no rings. Appearance of this species with small rhabdosomes coincides with the extinction of *lundgreni* at the beginning of Mulde event.

The Mulde event was associated with the glaciation near the South Pole, which caused global regression of sea level (Loydell, 1998). Roundly graptolites *P. parvus*, *Gothograptus nassa* with small colonies are typical of *parvus* time and is often a mass occurrence. The core of a diameter of 5 cm could occasionally show 30 or more rhabdosomes on a surface. We can infer that these features (reduced size of the specimens and high population density) could be indicative of great ecologic stress related to changes in ocean circulation patterns.

A new radiation of the genus *Pristiograptus* took place in *nassa* time (Fig. 14), when more massive *P. piltenensis* and *P. dubius ludlowensis* originated from *P. parvus*. The thecal apertural lip of these species reaches the middle of neighbouring theca but some representatives of *P. d. ludlowensis* have sicula rings. Clearly, *P. d. ludlowensis* gave rise to other species of the *dubius* group characteristic of Ludlow. The species of the *dubius* type in Ludlow have one, two or even more sicula rings.

The new *virbalensis* type that appeared in *nassa* was very likely derived from the *dubius* type. This type is characterized by the proximal end of the rhabdosome being ventrally curved up to $th_5 - th_8$. Thecae are inclined to rhabdosomal axis at 20° (proximal end) to 45° (distal end). The angle (β) between the apertural margin of theca and the succeeding theca wall is always obtuse in proximal end and it is 90° in medial and distal parts. This shows that the thecae are biform in the species of *virbalensis* type. The sicula is conical

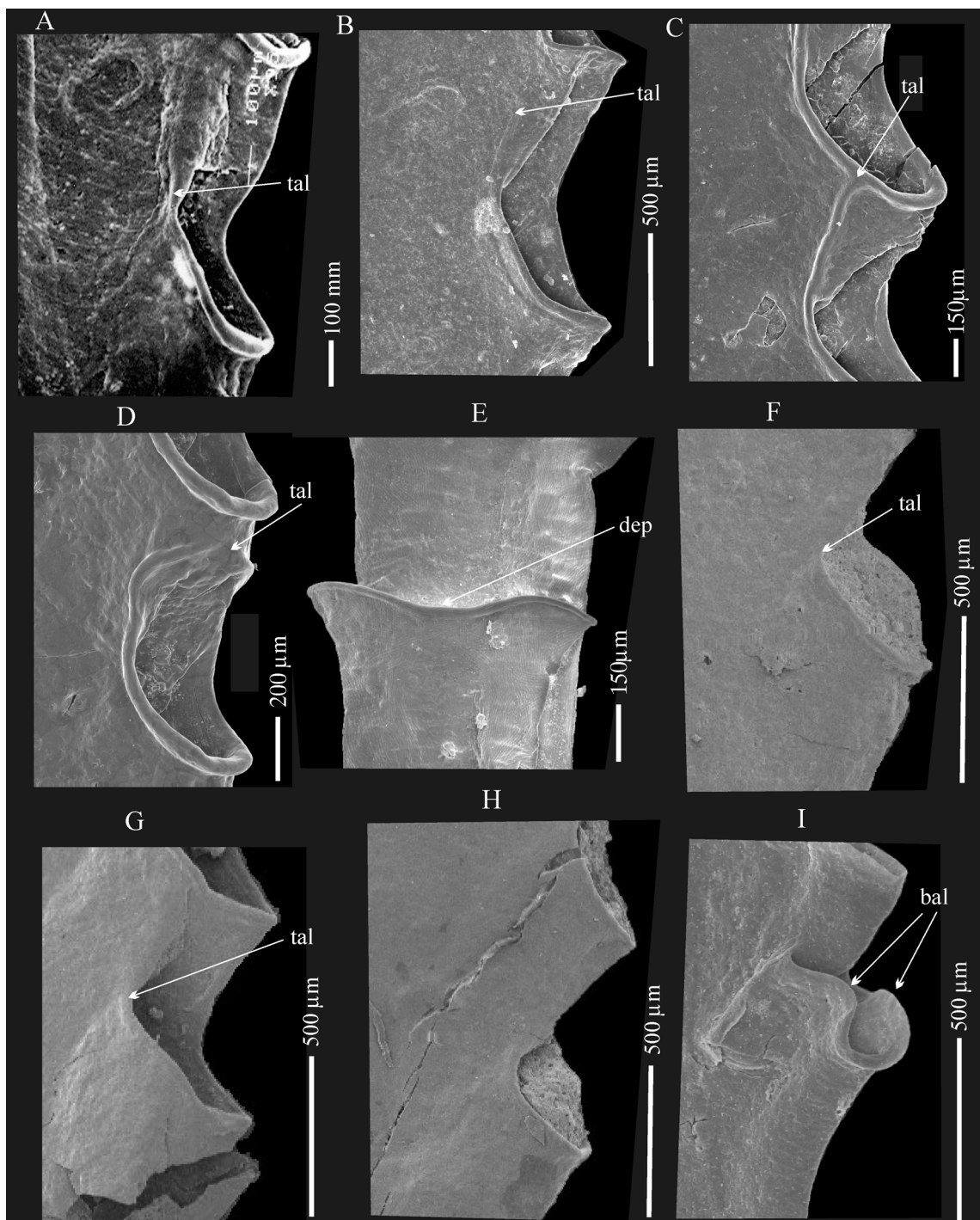


Fig. 13. Shape of thecal apertural lip in the *Pristiograptus* species in Wenlock. A – *Pristiograptus dubius dubius* (Suess), Parovėja-9 borehole, depth 644.8 m, *riccartonensis* Biozone, no S.P9–31, the end of thecal apertural lip (tal); B – *Pristiograptus pseudodubius* (Bouček), Kurtuvėnai – 161 borehole, depth 1374.1 m, *perneri* Biozone, no S.K161–305a; the end of thecal apertural lip (tal); C – *Pristiograptus dubius* var. A. Radzevičius; Parovėja-9 borehole, depth 605.25 m, *perneri* Biozone, no. S.P9–214; thecal apertural lip joining that of succeeding thecae (tal). D – *Pristiograptus* sp. Parovėja-9 borehole, depth 595.4 m, *perneri* Biozone, no. S.P9–219; intergrowth arch (tal) and unclear thecal apertural lip on succeeding thecal. E – *Pristiograptus lodenicensis* Přibyl; Parovėja-9 borehole, depth 558.3 m, no. S.P9–211, *lundgreni* Biozone; depression of thecal apertural lip (dep). F – *Pristiograptus parvus* Ulst; Kybartai–14 borehole, depth 1071.7 m, *parvus* Biozone, P.K14–108; the end of thecal apertural lip (tal). G – *Pristiograptus virbalensis* Paškevičius; Sutkai–87 borehole, depth 768.9 m, *praedeubeli* Biozone, no. P.S87–71; the end of thecal apertural lip (tal). H – *Pristiograptus praedeubeli* (Jaeger); Sutkai–87 borehole, depth 776 m, *praedeubeli* Biozone, no. P.S87–134. I – *Pristiograptus ludensis* (Murchison); Šiupyliai–69 borehole, depth 981 m, *ludensis* Biozone, no. 63a; bilateral apertural lobes (bal).

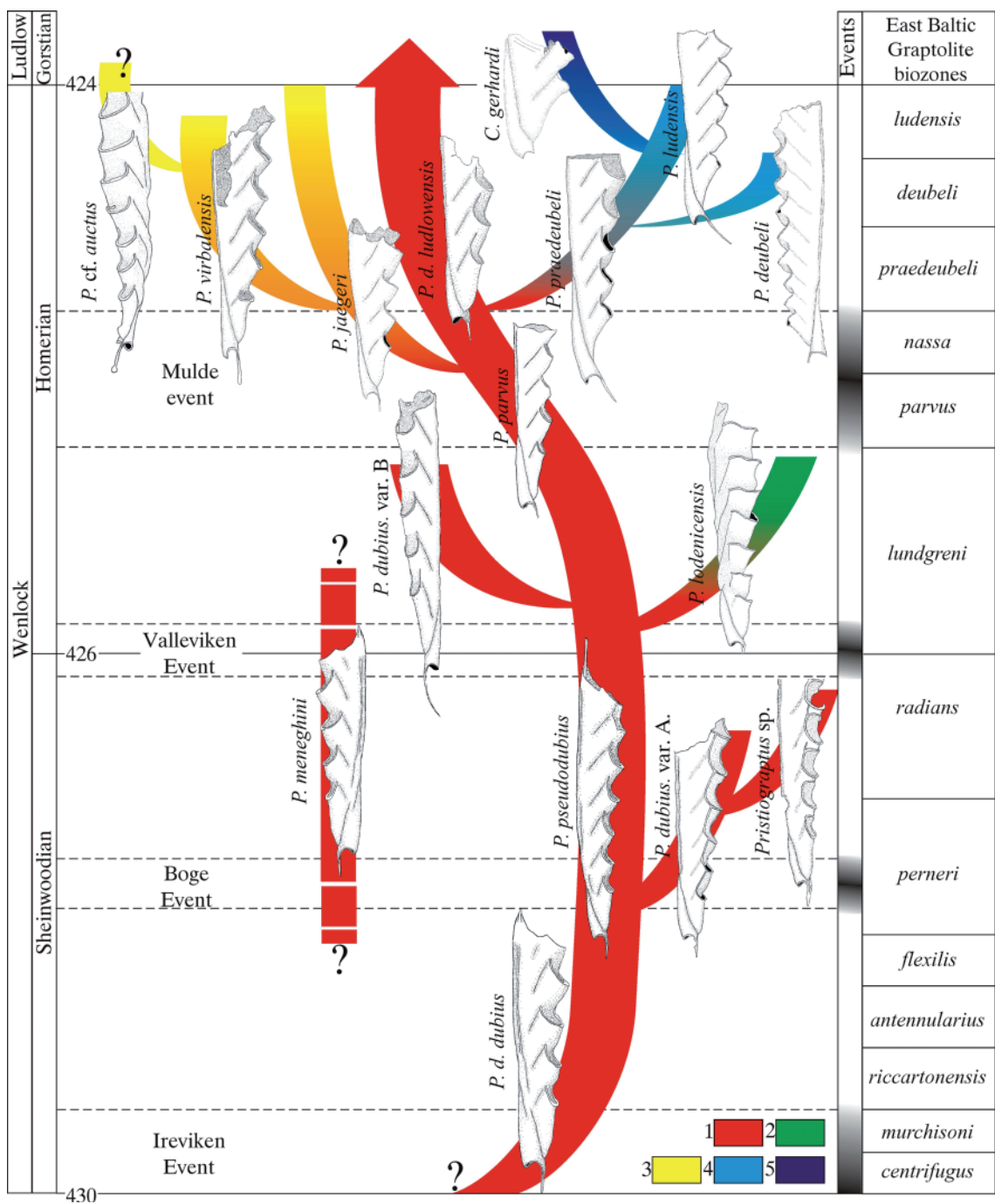


Fig. 14. Proposed phylogenetical relationships among Wenlock *Pristiograptus*. 1 – *dubius* type lineage; 2 – *lodenicensis* type lineage; 3 – *virbalensis* type lineage; 4 – *deubeli* tupe lineage; 5 – *Colonograptus* lineage. Events according to L. Jeppsson (Jeppsson et al., 1995).

with a thick and comparatively straight, long and obtuse virgella. Species of this type are characterized by a notable thickness of interthecal septae and by a massive thecal apertural lip (Fig. 13G). The first representative of this type is *P. jaegeri* (Lenz, Kozłowska-Dawidziuk, 2002), which has a massive rhabdosome, a strong, massive and sharp virgella and massive thecae apertural lip. *P. virbalensis* most likely originated from the previous species, being generally similar but having massive and obtuse virgella with a droplet-like termination. The morphological similarity suggests that *P. auctus*, which has a short and strong virgella with distinct thickening at its end, may have originated from *P. virbalensis* or related species, but *P. auctus* was not recorded in the eastern Baltic area. Graptolites of this group disappeared in the early Ludlow to form a blind branch.

The greatest morphological diversity of the genus *Pristiograptus* occurs in the *praedeubeli* – *ludensis* interval. In addition to the *virbalensis* and *deubeli* types already discussed, one more distinct morphotype occurs from *praedeubeli* time onward. Lenz, Koren' and others analysed their phylogeny (Lenz, 1993; Koren', 1994) and state that the members of the *deubeli* group are not typical *Pristiograptus* species in every respect and could represent a transitional branch between *Pristiograptus* and *Colonograptus*. The angle between thecal aperture and succeeding theca (angle β) of *deubeli* type is 90° (Fig. 13H). All species of the *deubeli* type have biform thecae; the thecae in the proximal part of the rhabdosome differ in having bilateral apertural lobes (Fig. 13I). The first representative of *deubeli* type in the East Baltic is *P. praedeubeli*, which has a massive rhabdosome and a cone-shaped sicula that is bent to ventral side. The very similar and probably closely related *P. deubeli* has a clear dorsal process. This was a short-ranged species that went extinct in early *ludensis* time. *P. ludensis* evolved from *P. praedeubeli* in *ludensis* time and the first thecae of this species have distinctly bilateral apertural lobes.

At the very end of Wenlock a new graptolite genus – *Colonograptus* – originated from *P. ludensis*.

Three radiations of *Pristiograptus* can be distinguished in Wenlock. The first is related to the Boge Event in *perneri* Biozone. The Boge Event initiated the appearance of varieties of *dubius* type. The second radiation co-occurs with the Valleviken Event in the *lundgreni* Biozone and is responsible for the appearance of the new *lodenicensis* type. In general, an extensive radiation of graptolite fauna is recorded after the Valleviken Event (Paškevičius, 1997): 21 species and subspecies recorded in Lithuania compared to just 11 species and subspecies of graptolites before the Valleviken Event (Paškevičius, 1994). The third radiation of *Pristiograptus* was influenced by the Mulde Event in the *parvus*–*nassa* biozones. Before the Mulde Event, all graptolites typical of the Wenlock in Lithuania became extinct. The Mulde Event was followed by the appearance of new types of *Pristiograptus* (*virbalensis* and *deubeli* types). A new genus typical of Ludlow, *Colonograptus*, evolved from the *deubeli* type at the end of Wenlock.

9. HOMERIAN BIOSTRATIGRAPHY

The recent detailed information allows distinction of the *lundgreni*, *parvus*, *nassa*, *praedeubeli*, *deubeli* and *ludensis* graptolite biozones in the Homeric in Lithuania (Fig. 15) (Radzevičius & Paškevičius, 2005; Radzevičius 2006). The *lundgreni*, *nassa*, *praedeubeli*, *deubeli* and *ludensis* Biozones can be recognized in the Holy Cross Mountains (Radzevičius, 2003a; PAPER IV).

Series	Ludlow	Gorstian	Beds	Holy Cross Mountains (Tomczyk, 1962)	Holy Cross Mountains (this paper)	Lithuania (this paper)
	Wenlock			Homeric	Pragowiec	
Wenlock	Homeric	Pragowiec		<i>nilssoni</i>	<i>nilssoni</i>	<i>nilssoni</i>
			<i>gotlandicus</i>	?	<i>ludensis</i>	<i>ludensis</i>
			<i>dubius</i>	?	<i>deubeli</i>	<i>deubeli</i>
			<i>vulgaris</i>		<i>praedeubeli</i>	<i>praedeubeli</i>
			<i>nassa</i>		<i>nassa</i>	<i>nassa</i> <i>parvus</i>
	Bardo		<i>lundgreni</i> <i>testis</i>	<i>lundgreni</i>	<i>lundgreni</i>	

Fig. 15. Correlation of the Holy Cross Mountains (Tomczyk, 1962) Upper Wenlock graptolite biozonation with those of revised Holy Cross Mountains and Lithuanian.

9.1. Homeric biostratigraphy of the East Baltic

The *lundgreni* Biozone (range zone of the nominate species) was adapted by Paškevičius (1997) in Lithuania. This interval was formerly included in the *testis* Biozone (Paškevičius, 1979, 1991; Brazauskas & Paškevičius, 1981). In Lithuania this biozone contains *Cyrtograptus lundgreni* Tullberg, *Monograptus testis testis* (Barrande), *M. t. inornatus* Elles, *M. flemingi flemingi* (Salter), *Monoclimacis flumendosae* (Gorthani), *P. lodenicensis* Přibyl, *P. pseudodubius* (Bouček) and *Gothograptus* cf. *kozłowski* Kozłowska-Dawidziuk. The lower boundary of the overlying biozone, the *parvus* Biozone, is drawn at the disappearance level of *Cyrtograptus*, *Monograptus* and *Monoclimacis*. However, these species do not disappear simultaneously, as *P. lodenicensis* disappears distinctly earlier than *M. testis testis*, *M. t. inornatus* and *M. flumendosae*. All these species disappear in the topmost *radians* Biozone in the boreholes of Lithuania. However, it has also been documented that *C. lundgreni* disappeared earlier than *M. t. testis* in the Bartoszyce borehole in Poland (Porębska *et al.*,

2004). *C. lundgreni* becomes extinct, together with *M. f. flemingi*, *P. pseudodubius* and *Gothograptus* cf. *kozłowski*, in the lower part of Ančia Member.

The *parvus* Biozone (a concurrent range zone) begins with a graptolite-free interval. This is because the lower boundary of this biozone is drawn according to the disappearance of *C. lundgreni*, *M. testis testis*, *M. t. inornatus*, *M. flemingi flemingi*, *M. flumendosae*, *P. lodenicensis*, *P. pseudodubius* and *G. cf. kozłowski*. Ulst (1974) distinguished in Latvia the *P. parvus* – *P. piltenensis* local Biozone, which included the entire interval of *nassa* Biozone The *parvus* Biozone is recognized for the first time in PAPER IV and previously these strata were attributed to the lower part of *nassa* Biozone. Both *P. parvus* Ulst and *G. nassa* (Holm) appear in the upper part of Ančia Member in Lithuania and only these two species occur in this biozone.

The complete absence of graptolites is characteristic of the interval between the last occurrence of *C. lundgreni* and *P. pseudodubius* and the first occurrence of *P. parvus* and *G. nassa* (middle part of the Ančia Member). The thickness of this graptolite-free interval ranges from 0.7 m (Šiupyliai-69) to 2 m (Vilkaviškis-131). The thickness of the range of *P. parvus* varies between 5 m in Kurtuvėnai-161 borehole and 2.4 m in Vilkaviškis-131 borehole. A similar graptolite-free interval is recognized in Gotland between the *lundgreni* and *parvus* biozones (Calner & Jeppsson, 2003). This interval is represented by the Bara Oolite and the lower part of the Mulde Brick-clay (Fig. 16) (both attributed to the Halla Formation: Calner & Säll, 1999).

Series	Stages	Graptolite zonation	Formations and Members			
			West Lithuania	Central Lithuania	Gotland	Holy Cross Mountains
Ludlow	Gorstian	<i>nilssoni</i>	Rusnė	Dubysa	Hemse	Pragowiec
		<i>ludensis</i>	Siesartis	Gėluva	-----	
	Homerian	<i>deubeli</i>			Klinteberg	
		<i>praedeubeli</i>			Djupvik Mb.	
		<i>nassa</i>			Mulde Mb.	
		<i>parvus</i>			Halla Mb.	
		<i>lundgreni</i>	Ančia Mb.		Bara Oolite	Bardo
			Ragainė	Upper Riga	Fröjel	

Fig. 16. Correlation of the Wenlock graptolite biozones with formations of the East Baltic, Gotland (Calner, 2003) and the Holy Cross Mountains.

The *nassa* Biozone in Lithuania was recognized by Paškevičius (1965) and included the interval with *P. parvus*. This biozone was divided later into two intervals: the lower *nassa* Biozone with *P. parvus* and the upper *nassa* Zone characterized by *P. dubius ludlowensis* (Bouček) (Radzevičius, 2004). Both these parts are elevated to the rank of biozones by Radzevičius (2006). The lower boundary of *nassa* Biozone, a concurrent range zone, is drawn according to the disappearance of *P. parvus*. The *nassa* Biozone, like the *parvus* Biozone, reveals just a few species: *G. nassa* and *P. dubius ludlowensis*. The thickness of the *nassa* Biozone is 6.5 m in the Vilkaviškis-131 borehole.

The *praedeubeli* range Biozone was recognised for the first time in Lithuania in PAPER IV. Because of a lack of data, this interval was previously called *virbalensis-deubeli* Biozone (Paškevičius, 1997; Radzevičius & Paškevičius, 2000). Later it was considered the lower part of *virbalensis* Biozone with *P. praedeubeli* (Radzevičius & Paškevičius 2005). The lower boundary is marked by the appearance of *P. praedeubeli*, and *P. G. nassa* and *P. dubius ludlowensis* are also recorded from this biozone, together with *P. idoneus* ? (Koren'), recorded from the lower part of biozone for the first time. *P. jaegeri* (Holland, Rickards et Warren) is present in the upper part of the biozone. The thickness of *praedeubeli* Biozone attains 5.8 m in Vilkaviškis-131 borehole and 8 m in Šiupyliai-69 borehole.

The *deubeli* range Biozone was recognised also for the first time in Lithuania here in PAPER IV as a result of changes described above. This interval was previously called the *virbalensis-deubeli* Biozone (Paškevičius, 1997; Radzevičius & Paškevičius, 2000). The lower boundary is drawn at the first appearance of *P. deubeli*. The assemblage comprises *P. jaegeri* (in the lower part), *P. deubeli*, *P. praedeubeli*, *P. virbalensis* and *P. d. ludlowensis*. Because the lack of graptolites in the upper part of Wenlock in Vilkaviškis-131 borehole, the thickness of this biozone could not be estimated in this section, but in Šiupyliai-69 borehole it is 5 m.

The definition of the *ludensis* Biozone (range zone) was justified by Paškevičius (1979). Previously this biozone encompassed the interval from *nassa* to *nilssoni* Biozones (Paškevičius, 1979), while Paškevičius (1997) defined it in its present meaning. The lower boundary of the biozone at the appearance level of *P. ludensis* (Murchison), and the zone extends to the appearance level of *Neodiversograptus nilssoni* (Barrande), *Colonograptus colonus* (Barrande) and *Bohemograptus bohemicus bohemicus* (Barrande). Graptolite assemblages of this biozone include *P. ludensis*, *P. praedeubeli* and *P. dubius ludlowensis*. *Colonograptus gerhardi* (Kühne) appears in the upper part of the *ludensis* zone and this taxon is also found in the upper *nilssoni* Biozone.

9.2. Homeric Biostratigraphy of the Holy Cross Mountains

Homeric graptolite biostratigraphy was investigated by H. Tomczyk (1962), who recognised *lundgreni*, *testis*, *nassa*, *Pristiograptus vulgaris*, *Pristiograptus dubius*, *Spinograptus spinosus* – *Pristiograptus gotlandicus*, *nilssoni*, *Lobograptus scanicus*, *tumescens* – *leintwardinensis* and *bohemicus* biozones in the Bardo syncline (the Holy Cross Mountains) in the Wenlock – Ludlow boundary interval. Tomczyk (1962) also recognized intervals with trilobites in the lower part of *nassa* Biozone.

In more recent stratigraphic schemes, the *testis*, *vulgaris*, *dubius* and *spinosus* – *gotlandicus* biozones are not in use and graptolite biostratigraphy could be justified. The samples collected from Prągowiec ravine revealed a graptolite succession in which the *lundgreni*, *nassa*, *praedeubeli*, *deubeli*, *ludensis* and *nilssoni* biozones could be distinguished. However, the boundaries of graptolite biozones in this locality were not always distinguishable, because of lack of material. It is difficult, for the time being, to correlate the interval of the *praedeubeli*, *deubeli* and *ludensis* biozones with the units distinguished by Tomczyk (1962) in Prągowiec near Bardo (Fig. 5), because several species were poorly defined and are not valid today (*P. gotlandicus* and *P. vulgaris*). A proper comparison would require a revision of Tomczyk's collection from the Prągowiec ravine.

The oldest graptolite biozone identified in Prągowiec ravine was the *lundgreni* Biozone in the upper part of upper Bardo Beds. Graptolite assemblage of *lundgreni* biozone comes from the A09 outcrop and includes *M. t. testis*, *M. f. flemingi*, *C. lundgreni* and *G. cf. kozłowski*.

The *parvus* Biozone was not identified in the Prągowiec ravine, as *P. parvus* was not discovered. Vertical distribution of this species is very narrow in Lithuania and it is likely that the interval with this species was just overlooked because of wide sampling interval. More likely the *parvus* Biozone is represented with a layer with trilobites recorded above the *lundgreni* Biozone (a possible equivalent to the graptolite-free strata in the Wenlock of Lithuania).

Upwards in the section of the Prągowiec ravine, the *nassa*, *praedeubeli*, *deubeli*, *ludensis* and *nilssoni* biozones were identified in the Prągowiec layers. The graptolite assemblage of the *praedeubeli* Biozone was found in the outcrops A07, A01 and A02 and it is very similar to that in Lithuania, comprising *G. nassa*, *P. d. ludlowensis*, *P. virbalensis*, *P. praedeubeli* and *P. cf. ? idoneus*.

The graptolite assemblage of the *nassa* Biozone was found in the A08 outcrop and consists of *G. nassa* and *P. d. ludlowensis*. It is overlain by the *deubeli* Biozone, which was identified in the outcrops in A01 (in its lower part), A02 and A04. The graptolite assemblage from this interval includes *G. nassa* ?, *P. d. ludlowensis*, *P. praedeubeli* and *P. virbalensis*. *P. praedeubeli* is rare in

the *deubeli* Biozone in Lithuania, but occurs in the *deubeli* and *ludensis* biozones in Central Asia (in northern Naratau and the Alai Ridge – Koren' & Suyarkova, 1994b) and in Arctic Canada (Lenz & Kozłowska-Dawidziuk, 2002).

The *ludensis* Biozone was recognized in A03, A04 and A05 outcrops and the graptolite assemblage in this interval featured *P. d. ludlowensis*, *P. praedeubeli*, *P. deubeli*, *P. virbalensis* and *C. gerhardi*. This composition is generally similar to that in Lithuania, where only *P. virbalensis* is absent in *ludensis* Biozone.

The *nilssoni* Biozone in the A05 (in its lower part) and A06 outcrops is distinguished based on the appearance of *C. gerhardi*, *N. nilssoni* and *Saetograptus* sp.

CONCLUSIONS

Pristiograptus is a genus of Monograptidae characterized by high number of species. New morphological features analysed in the species from Wenlock of the eastern Baltic area allow easier identification of the species of the genus *Pristiograptus*. There features are (1) the angle between the thecal apertural lip and the succeeding metathecal wall and (2) the end of the thecal apertural lip at the disto-lateral margin of the thecal aperture. The first feature allows the genus *Pristiograptus* to be divided into groups, the second is important to distinguish the taxa within the *dubius* group (**PAPER I, PAPER II**).

The papers provide the amended descriptions and discussions on stratigraphically valuable species, subspecies and variations of *P. deubeli* (first time from the East Baltic) *Pristiograptus* (*P. dubius dubius*, *P. dubius ludlowensis*, *P. dubius* var. A. (new), *P. dubius* var. B (new), *P. lodenicensis*, *P. ludensis*, *P. meneghini*, *P. parvus*, *P. praedeubeli* (first time from the East Baltic), *P. pseudodubius*, *P. virbalensis*, *P. sp.* (new). *P. dubius* var. A. and var. B (new) are new varieties, which can be used for improved correlation of the Wenlock sections in the Eastern Baltic area. *P. deubeli* and *P. praedeubeli* were discovered for the first time in the Eastern Baltic area and this information allows a better correlation of the eastern Baltic sequence to the global graptolite zonation (**PAPER I, PAPER II, PAPER III**).

Morphological analysis identifies four morphotypes of *Pristiograptus* in Wenlock (*centrifugus* – *ludensis* biozones): in addition to the *dubius* type, the *virbalensis* (*nassa* – *ludensis* biozones), *lodenicensis* (*lundgreni* Biozone), *deubeli* (*praedeubeli* – *ludensis* biozones) types are distinguished for the first time and their distribution discussed. (**PAPER I, PAPER II** and **PAPER IV**).

The first diversity peak of *Pristiograptus* in Wenlock of the eastern Baltic area occurs in the Jaagarahu Stage (*perneri* Biozone), six species, subspecies and varieties of *dubius* type were recorded. The greatest diversity of *Pristiograptus* is related to the Gêluva Stage (*parvus* – *ludensis* biozones). There are eight species and subspecies of *dubius*, *virbalensis* and *deubeli* type are common to the East Baltic and the Holy Cross Mountains. (**PAPER II, PAPER III** and **PAPER IV**).

Investigation of morphological changes allows reconstruction of the evolutionary history of the genus *Pristiograptus* in Wenlock of the East Baltic area. An obvious phyogenetic succession of the species of *dubius* type (*P. d. praedubius*, *P. d. dubius*, *P. pseudodubius*, *P. parvus*, *P. d. ludlowensis*) was revealed. The timing of the appearance of new species and other morphotypes reveals obvious relationships of graptolite diversification and the Silurian oceanic events, whereas the morphological variation increased progressively. The Boge event is marked by the appearance *P. dubius* var. A and *P. sp.*, developed from *P. pseudodubius*. The appearance of *P. dubius* var. B and *P. lodenicensis* (the *lodenicensis* type) in *lundgreni* Biozone is related to the

Valleviken Event. The appearance of a new line of *virbalensis* type, derived from *P. parvus* or *P. dubius ludlowensis* (both *dubius* type), is related to the Mulde event dated as the *praedeubeli* Biozone (Mulde Event). Since the Mulde Event, a gradual diversification of *Priostiograptus* is recognized, leading to the appearance of a new genus *Colonograptus* at the end of Wenlock. These data suggest strong environmental control on the evolution of the genus *Pristiograptus* in the *lundgreni-nassa* stratigraphic interval (**PAPER I, PAPER IV**).

The Homeric succession in Lithuania comprises the following graptolite biozones: *lundgreni*, *parvus*, *nassa*, *praedeubeli*, *deubeli* and *ludensis*. *Parvus*, *praedeubeli*, *deubeli* biozones are described for the first time in the East Baltic. The Homeric section of the Holy Cross Mountains in Poland shows a largely similar succession, only the *parvus* Biozone cannot be distinguished. There is a distinct graptolite-free interval about 2 m thick in the Silurian of the eastern Baltic area, between the last *C. lundgreni* and the first *P. parvus*. This interval is tentatively attributed to the *parvus* Biozone and seems to be related to the Mulde event. We may correlate this graptolite-free interval with the “interval with trilobites” in the Holy Cross Mountains and with the Bara Oolite in Gotland. This correlation suggests possible the sea level control on the graptolite abundance (**PAPER III, PAPER IV** and chapter **Homeric biostratigraphy**).

ACKNOWLEDGEMENTS

First of all, I am thankful to my supervisor, Prof. Tõnu Meidla (University of Tartu, Estonia), for offering support and constructive criticism during all stages of the work. I am also grateful to my second supervisor, Prof. Juozas Paškevičius (Vilnius University, Lithuania). Prof. P. Musteikis and Prof. G. Motuza (Vilnius University) are thanked for access to the laboratory of the Department of Geology and Mineralogy, Vilnius University, and for enthusiastic discussions and support. Dr. P. Raczyński (Wrocław University) helped to collect graptolites in the Holy Cross Mountains and Sudet Mountains. I would also like to thank Prof. A. Urbanek, Dr. A. Kozłowska, Prof. L. Teller (Institute of Palaeobiology, Warsaw), Prof. D. Kaljo (Tallinn Technical University) and Prof. L. Jeppsson (Lund University) for permission to make acquaintance with their graptolite collections. In addition, Dr. V. Mikli (Tallinn Technical University), Dr. A. Čečys (Vilnius University) and T. Miyazu (Lund University) helped in photographing graptolites by SEM. I am obliged to J. Stasevičiūtė-Radzevičienė, Prof. D. Loydell (University of Portsmouth), Prof. J. Zalasiewicz (University of Leicester) and Dr. R. Szava-Kovac (University of Tartu) for improvements in the English of the presentation.

The research was supported by the Estonian Ministry of Education and Research (No. 0182531s03), the Estonian Science Foundation (grant No. 6460), Ministry of Education and Science of the Republic of Lithuania (SUT-729) and the Swedish Institute.

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SUMMARY IN ESTONIAN

Käesolev uurimus käsitleb Wenlocki graptoliitide perekonda *Pristiograptus* Baltikumis (Ida-Euroopa platvormi e. Baltica paleokontinendi lääneosas). Töö materjal pärineb üheksast Leedu ja Lääne-Läti puuraugust, mis esindavad Balti paleobasseini savikas-karbonaatset ja karbonaatset faatsiest koos nendevahelise üleminekuvööndiga, ning Prągowieci läbilõikest Püha Risti mägedes (Malo-polska blokk, Kielce piirkond, Poola). Balti riikide territooriumil esinevad perekonna *Pristiograptus* liigid kogu *cyphus*'e kuni *parultimus-ultimus*'e tsonaalse intervalli ulatuses, kuid perekonna kõrgeim liigiline mitmekesisus on seotud Hilis-Wenlocki *parvus-ludensis*'e biotsooniga. Selles intervallis on graptoliidid esindatud vaid perekonna *Pristiograptus* ja sugukonna Retiolitidae esindajatega, teised Wenlocki graptoliidid puuduvad. Seetõttu on *parvus*'e-*ludensis*'e intervalli biostratigraafiline liigestamine graptoliitide leviku alusel võimalik vaid *Pristiograptus*'e leidude põhjal. *Lundgreni* ea lõpp tähistab selliste oluliste perekondade nagu *Cyrtograptus*, *Monoclimacis* ja *Monograptus* väljasuremist ning see on seotud ühe suurima kriisiga Siluri graptoliitide arengus, nn Mulde sündmusega.

Uute morfoloogiliste tunnuste rakendamine Baltikumi ja Püha Risti mägede Wenlocki graptoliidimaterjali kirjeldamisel võimaldab perekonna *Pristiograptus* liikide senisest paremat identifitseerimist ja eristamist. Selliste tunnustena on kasutusele võetud (1) nurk teeka apertuuri välisserva ja järgneva teeka välisseina vahel ning (2) teeka apertuuri välisserva distolateraalse osa morfoloogia. Esimesena nimetatud tunnuse alusel liigendub perekond *Pristiograptus* gruppideks, teine tunnus on oluline *dubius*'e gruppi kuuluvate taksonite eristamisel. Wenlockis eristub perekonnas *Pristiograptus* neli morfotüüpi: *dubius*'e tüüp, *lodenicensis*'e tüüp, *virbalensis*'e tüüp ja *deubeli* tüüp. Töös on kirjeldatud *Pristiograptus dubius dubius* (Suess), *P. pseudodubius* (Bouček), *P. d. ludlowensis* (Bouček) *P. parvus* Ulst, *P. meneghini* (Gorthani) ja nende alamliigid ning kolm uut varieteeti (*P. dubius* var. A, *P. dubius* var. B ja *Pristiograptus* sp.), mis kõik esindavad *dubius*'e morfotüüpi. Teine, *lodenicensis*'e morfotüüp on kogutud materjalis esindatud vaid ühe liigiga – *P. lodenicensis* Přibyl. Töös on kirjeldatud ning diskuteeritud *virbalensis*'e morfotüüpi ning esitatud liigi *P. virbalensis* Paškevičius uus kirjeldus. Neljas Wenlocki *Pristiograptus*'e morfotüüp on *deubeli* tüüp, mida esindavad kolm töös kirjeldatud liiki – *P. praedeubeli* (Jaeger), *P. deubeli* (Jaeger) ja *P. ludensis* (Murchison). Loetletud liikide põhjal on väitekirja kokkuvõttes osas ning avaldatud artiklites käsitletud perekonna *Pristiograptus* levikut, morfoloogilist evolutsiooni ning fülogeneesi Wenlocki ajastikul.

Leedu ja Püha Risti mägede noorema Wenlocki biotsonaalne liigestus koosneb *lundgreni*, *parvus*'e (see tsoon eristub ainult Leedus), *nassa*, *praedeubeli*, *deubeli* ja *ludensis*'e biotsoonist, kusjuures *parvus*'e, *praedeubeli* ja *deubeli* biotsoonid on Leedu Siluri liigestamisel esmakordselt kasutusele toodud käesolevas töös.

PUBLICATIONS

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Radzevičius S. & Paškevičius J. 2000. Pristiograptids (Graptolites) and their adaptive types of the Wenlock (Silurian) in Lithuania. *Geologija*, **32**, 88–109.

PAPER II

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PAPER III

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1993 – graduated from Secondary school Nr. 6, Vilnius
1994–1998 Vilnius University, Geology
1998–2000 Vilnius University, Geology (Master's degree)
2000– PhD student of Tartu University, (Estonia), Geology (Palaeontology and Stratigraphy)

WORK EXPERIENCE

1993–1994 Hydrogeology company AB Artva,
1996 summer Lithuanian Geological Survey,
1997 summer Lithuanian Institute of Geology,
1997–2001 Vilnius University, Department of Geology and Mineralogy, Laboratorian,
2001– to date Vilnius University, Lecturer.

RESEARCH TRAINING

2001 May Wrocław University, Institute of Geology, Poland;
2002 May University of Latvia, Department of Geology, Latvia;
2002 May Institute of Palaeobiology, Warsaw, Poland;
2003 Feb. Lund University, Department of Geology, Sweden;
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COURSES

1999 Modelling and geoinformatics for geoscientists, Vilnius University;
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TÖÖKOGE MUS

1993–1994 hüdroteoloogiafirma AB “Artva”,
1996 summer Leedu Geoloogiateenistus,
1997 summer Leedu Geoloogia Instituut,
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Alates 2001 Vilniuse Ülikool, lektor.

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2001 May	Wroclawi Ülikool, Geoloogia Instituut, Poola;
2002 May	Läti Ülikool, geoloogia osakond;
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1999 Modelling and geoinformatics for geoscientists, Vilniuse Ülikool;
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