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Ordovician Proetid Trilobites in Baltoscandia and Germany

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Declaration: Hereby I declare that this doctoral thesis, my original investigation and achievement, submitted for the doctoral degree at Tallinn University of Technology has not been submitted for any degree or examination.

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Baltoscandia ja Saksamaa Ordoviitsiumi proetiidsed trilobiidid

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CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, referred to in the text with Roman numerals as listed below:

I **Popp, A**. and Pärnaste, H. 2008a. Morphometric study of the Ordovician proetid trilobite *Cyamella stensioei* Owens, 1978. *In* I. Rabano, R. Gozalo & D. Garcia-Bellido (eds.): *Advances in Trilobite Research. Publicaciones del Instituto Geológico y Minero de España, Serie: Cuadernosdes Museo Geominero 9*, 327–332.

II Pärnaste, H., **Popp, A**. & Owens, R.M., 2009. Distribution of the order Proetida (Trilobita) in Baltoscandian Ordovician strata. *Estonian Journal of Earth Sciences 58(1)*, 10–23.

III Pärnaste, H. and **Popp, A**. 2011. First record of Telephina (Trilobita) from the Ordovician of northeastern Estonia and its stratigraphical implications. *Estonian Journal of Earth Sciences 60(2)*, 83–90.

IV **Popp, A**. and Pärnaste, H. 2011. Biometry and lifestyle of the Ordovician proetid trilobite *Cyamella stensioei* Owens, 1979. GFF [accepted].

1 INTRODUCTION

For the class Trilobita Walch, 1771, today there are more than 5000 generic names available (Jell & Adrain 2003). Representatives of the order Proetida Fortey & Owens, 1975 are known from the early Ordovician to the late Permian with at least 470 genera worldwide (Jell & Adrain 2003).

As it is understood today, proetid trilobites are highly diversified and adapted to differing parts of the shelf regions as benthic faunal elements (e.g. Proetoidae, Tropidocoryphidae, Aulacopleuridae, etc.), of which some were adapted to reefs or mud mounds (Mikulic 1981). In having a morphology enabling to drift or actively swim some proetids (e.g. Telephinidae) were part of the pelagic realm (McCormick & Fortey 1999).

On the basis of phylogenetic studies and studies on early ontogenetic (e.g. larval) stages, which are 'adult-like', discussions on higher-level systematics on the Proetida are ongoing. Possible ancestors of this group are seen in representatives of the late Cambrian Ptychopariida (Fortey 2000a). Different evolutionary patterns and processes could recently be demonstrated on proetid trilobites (McNamara 2009). It is therefore important to investigate the ontogeny of proetid species in order to see possible systematic linkages to other taxa. Since the erection of the order by Fortey & Owens in 1975 there is an ongoing discussion on the specific characters of the Proetida and its internal systematic structure (e.g. Ahlberg 1995a, b, Adrain & Chatterton 1993, 1994, 1996, Adrain et al. 2001, Bergström 1977, Bergström & Suzuki 2005, Chatterton 1994, Chatterton et al. 1998, 1999, Edgecombe et al. 1997, Fortey 2006, Gröning 1986, Hahn & Hahn 1996, Holloway 1994, Jell & Adrain 2003, Lieberman 1994, Lütke 1980, 1990, Owens 1981, 2004, Owens & Hammann 1990, Owens & Fortey 2009, Přibyl & Vaněk 1981, Tomczykowa 1991, Yuan et al. 2006).

Being the last trilobites, which vanished in the end Permian mass extinction, the Proetida are known in Europe from Ordovician to Carboniferous strata. In Baltoscandia their occurrence is limited to Ordovician and Silurian strata. On the basis of confacies belts identified for the Ordovician strata (Jaanusson 1982, 1995) proetid material from Estonia, Sweden and from geschiebes of northern Germany and Denmark were investigated during my studies.

This thesis aimed to revise the systematics of proetid taxa in the Lower Palaeozoic strata of Baltoscandia, but it appeared that the current status of both systematics and regional stratigraphy did not allow such a revision. Therefore an overview on existing Ordovician taxa was created (II). The well preserved *Cyamella stensioei* samples were investigated biometrically (I, IV) in order to identify important characters, which change during ontogeny. Conclusions from these ontogenetic changes were used to identify possible relationships to taxa elsewhere in the world (IV). Future studies should evaluate the validity and the use of these charcters in tracing the phylogeny of Baltoscandian proetids.

2 HISTORY OF RESEARCH ON BALTOSCANDIAN PROETIDA

In Baltoscandia the research on trilobites (syn. “Entomolithus” (partim), “Palæaden”, “Trilobiterna”, “Trilobiten”, “Trilobitis”) can be traced back to the times of Linné (*23.05.1707-+10.01.1778). The trilobite research had its rise during the late 18th to early 19th century with authors like Walch, 1771, Boeck 1828, Dalman 1827, Eichwald 1825, Emmrich 1839, Pander 1830 and Sars 1835 (see Burmeister 1843 and Bruton et al. 1997 for more references).

The history of research on Proetida in Baltoscandia runs parallel to the rise of general research on trilobites, but for the proetids often only names in mostly general geological and palaeontological works and under differing genus names can be found. For example, for the genus *Proetus* (syn. “Proëtus”) commonly genus names like *Calymene* or *Aeonia* were used (see Beyrich 1846) of which only the former is of zoological relevance today, but within the Order of Phacopida. Dalman 1827 and Lovén 1845 speak of *Calymene concinna* from the Silurian of Gotland, Sweden, which later became the species *Proeuts concinnus*. This example shows one of the difficulties in tracing back the Proetida in the history of research. But without doubt the works of Angelin (1851, 1854) for the Scandinavian part and of Nieszkowsky (1857, 1859) for the Baltic part can be regarded as major milestones in this respect.

Thereafter, the work of Schmidt (1894, 1907; see also Bruton et al. 1997) was a major milestone. Descriptions of individual genera and species are scattered through monographic works from the late 19th and early 20th centuries, including works of Olin 1906, Hadding 1913, Warburg 1925, Öpik 1925, 1927, 1928, 1937 and Thorslund 1940 (see II for further references).

Another important aspect is the history of research on glacial erratic boulders (geschiebes). Long before the occurrence of the geschiebes was made plausible by Torrell in 1875 (Kahlke 1994) trilobites from geschiebes were described and figured (e.g. Klöden 1834, Roemer 1861, 1885, Steinhardt 1874, Wigand 1888, Pompeckj 1890). Also the Proetida were treated or figured by several authors, most recently by authors like Neben & Krueger 1971, 1973, 1979, Schrank 1972, Schöning 1982, 1995, 2010, Rudolph 1992, 1997, Hansch 1994, Schimmelpfennig & Schneider 1997, Rhebergen 2001, Bilz 2001, 2010, Popp & Schöning 2006, Rudolph et al. 2010.

Proceeding a first study (Popp & Pärnaste 2008b) for the Ordovician Proetida of Baltoscandia a historical and systematic review on the genus level is given (II), including representatives of at least seven families from the lower Palaeozoic strata (Fig. 1): Telephinidae Marek, 1952; Dimeropygidae Hupé, 1953; Proetidae Salter, 1864; Tropidocoryphidae Přibyl, 1946; Aulacopleuridae Angelin, 1854; Rorringtoniidae Owens in Owens and Hammann, 1990; Scharyiidae Osmólska, 1957.

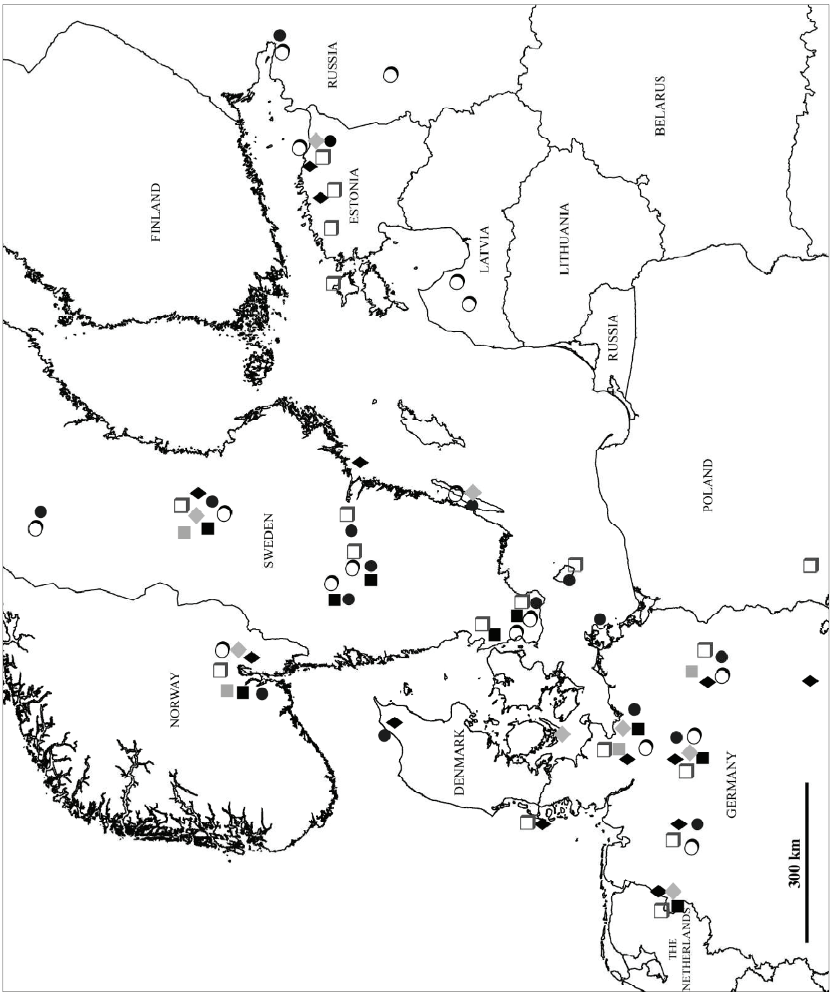


Figure 1. *Map showing the distribution of Baltoscandian proetid families during the Ordovician based on published (paper II and additional literature on geschiebes) and unpublished data (of Rhebergen; Schöning; Popp). Besides the localities with outcropping strata also data from cores and from geschiebes (Germany, Poland, Denmark and Sweden) or erratics (The Netherlands and Germany) was included. The symbols represent the following families: circle, dark grey – Dimeropygidiae; circle, empty (white) – Telephinidae; rhomb, grey – Scharyiidae; diamond, black – Aulacopleuridae; quadrangle, black – Rorringtoniidae; quadrangle, grey – Proetidae; quadrangle, empty (white) – Tropidocoryphidae.*

3 MATERIAL AND METHODS

This chapter comprehends information on the objects of investigation and the techniques used for their analysis.

3.1 SOURCE AND REPOSITORY

The material for this thesis is housed in the following institution's collections, which are abbreviated as: GIT - the Institute of Geology at Tallinn University of Technology; RM - Swedish Museum of Natural History in Stockholm; D - Museum of Evolution, Uppsala University, Sweden.

Six rock samples from three localities in the Siljan District were investigated (I, IV), namely the quarries of Kallholn (samples K1: RM Ar45665, see also Popp & Pärnaste 2008; K2: GIT 436-66; K3: D 2171), Unskarsheden (U1: priv. coll. W. Drichelt; U2: GIT 436-67) and Solberga (Sol1: GIT 436-68).

Additional material was used from several private collections (see Acknowledgements), but only material of priv. coll. F. Rhebergen (erratics from the border area of Germany and The Netherlands; see Fig. 1), which will be deposited in the collection of the National Museum of Natural History in Leiden (The Netherlands), and material of Andrea Rohde (*Telephina* from the kukersite) could be incorporated. Further Ordovician proetid material was collected by me from the following localities (Tab. 1):

Country	Locality	Stratgraphy	Year
Estonia	Kohtla-Nömme (kukersite heaps)	Kukruse stage	2008, 2010
	Sompa (kukersite heaps)	Kukruse stage	2008, 2010
	Porkuni area	Porkuni stage	2008, 2010
	island of Hiiumaa	Nabala - Pirgu stages	2009
	island of Vormsi	Vormsi - Pirgu stages	2009
Sweden	Siljan area	Boda Limestone (Pirgu - Porkuni stage)	2007, 2008, 2010
	Kinnekulle area	Mudstone (Pirgu - ?Porkuni stage)	2008
Germany	Schönhagen (geschiebes)	Boda Limestone (Pirgu - Porkuni stage)	2010, 2011
	Steinbeck (geschiebes)	Boda Limestone (Pirgu - Porkuni stage)	2011
	WWW area (erratics)	silicified limestones (Idavere - Jöhvi substages)	2008, 2010
Denmark	island of Langeland (geschiebes)	Boda Limestone (Pirgu - Porkuni stage)	2010

Table 1. *Overview of localities for Ordovician proetid material, which were visited during this thesis.*

The material from Estonia (Tab. 1) was mainly collected during joint field trips (with Dr. Helje Pärnaste, Tallinn) and was integrated into the collection of the Institute of Geology at Tallinn University of Technology (GIT).

The huge material from the Siljan area in Sweden still needs further investigation. There was one juvenile proetid cranidium collected at the slope of Mount Kinnekulle from a loose boulder, probably representing a mudstone of the Jonstorp Formation. This cranidium needs further investigation.

The collecting of geschiebes in the northern part of Germany and in Denmark is an ongoing process with the main interest on geschiebes of the Backsteinkalk ("brick limestone"; see Popp 2007 and Fig. 3) and the Boda Limestone. But also erratic boulders ('erratics') were collected in the westernmost part of Germany (see Rhebergen 2009 and chapters 3.2.2 and 4.3), yielding also Ordovician proetid fragments.

3.2 METHODS

A variety of techniques and methods was used within the scope of this thesis. Standard methods were not described to a deeper detail in the published papers, where only the main information is given. For example this accounts to the preparation of the hand samples, which was done under stereo microscopes mechanically by using a pneumatic preparation tool and needles.

3.2.1 Literature

In order to understand the history of research and also the palaeogeographic and systematic interrelations published material and data, especially from other regions of the world, was included. For example for the study of the palaeogeographic distribution of Ordovician Proetida in Baltoscandia more than 65 references were used for data compilation, resulting in a data base entry of 28 genera, that was published (II).

Besides proetid literature on Baltica also literature on four other palaeogeographic regions (Laurentia, Avalonia, South China and Sibumasu terranes) was used for the review of rorringtoniid trilobites similar to *Cyamella*. This compilation gathered references from the Darriwilian to the Hirnantian (IV).

3.2.2 Terminology

The following terms are used in this paper and defined herein to avoid any misunderstanding or confusion. If not differently stated the terminology for exoskeletal features of trilobites follows the standard terminology given in the revised version of the Treatise (Whittington 1997). All measurements in saggital direction are termed 'length' and abbreviated with L, transversal measurements are termed 'width' and abbreviated with W. For the biometrical investigation the following abbreviations were used (Fig. 2).

From originally 15 cranidial sections only eleven were used, of which the latter were termed ‘key measurements’.

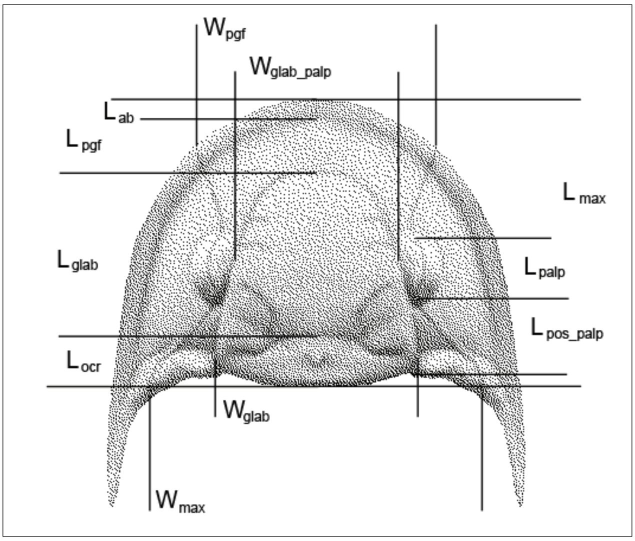


Figure 2. *Key measurements on cranidia of Cyamella stensioei Owens, 1979 used for the biometric analysis (IV) are abbreviated as follows: L – length measurements, W – width measurements, ab – anterior border, glab – glabella, glab_palp – glabella at palpebral lobes, max – maximum, ocr – occipital ring, palp – palpebral lobe, pgf – preglabellar field, pos_palp – position of palpebral lobe.*

The term “geschiebes” (pl.) has a long tradition of use and is used herein for rock samples, which have undergone a glacial transport and might have been relocated several times from the point of their provenance to their final location. The term “geschiebes” is synonymous to the longer term “glacial erratic boulders” (see Schallreuter 1994). In this work only the geschiebes of sedimentary rocks are treated.

The term “erratics” (pl.) is used here for rock samples, which have been transported by any other natural force and might have been relocated several times until their sedimentation at the place of finding. This term is used here for material, which is of unknown origin but might have been transported by the Eridanos river system (Miocene to early Pliocene) in a relative east to west direction (Overeem et al. 2001, Rhebergen 2001, 2007, 2009). The term erratics is mainly related to transported silicified material (former limestones, calcitic exoskeletons, sponges) which are also termed ‘silifications’.

3.2.3 Measuring techniques

Only cranidia were investigated, as these are the most diagnostic part of *C. stensioei* as well as of the genus compared with other aulacopleuroidean trilobites such as *Panarchaeogonus* or *Isbergia* (Owens 1979).

Two different methods were used for measuring cranidia of *Cyamella stensioei*. The first was direct measurement using a microscope and a graticule (I). The second way of gathering data on predefined measurements was using a pixel/scale ratio from digital photographs of whitened (magnesium oxide) specimens oriented in a planar position (IV). Photographs of specimens were taken by using a Nikon AZ100 Microscope with a Nikon Digital Microscope Camera. By using the image-processing program ImageJ (version 1.43; see Abramoff et al. 2004) a scaled section was converted into a certain amount of pixels, which gave the defined ratio for continued measuring. The advantages and disadvantages of both measuring techniques were treated (IV), but the measuring of digital images is preferred.

In order to reduce the measuring errors more iteration could be realised more comfortably and within a shorter time compared to the direct measuring method. All measurements were given as maximum values in millimetres and were calculated (mean value) after repeated measuring of every measurement. For the morphometric analysis especially the sub-millimetre area was of high importance, but less prone to rounding errors. If a tolerance limit of 0.04 mm between the highest and lowest measured values was exceeded, additional readings were made. Assuming symmetry of some cranidial features, some sections were measured in half distance and doubled afterwards. This enabled gathering more data per cranidium and gave a basis for comparison of most published data, but the danger of doubling errors is given.

The morphometric analysis is based on trilobite specimens showing a nearly complete set of characters. This enables a better comparison between the specimens and gives an idea of variation and change during growth. For 17 cranidia 15 sections were measured, but only eleven measurements (see Fig. 2) were included in a detailed investigation (IV).

3.2.4 Statistical methods

Statistical and multivariable analyses were carried out using the statistical package PAST (version 2.00; Hammer et al. 2001), the Student's t-test and the Shapiro-Wilk test.

The Student's t-test is a statistical procedure to test if samples were taken from statistical populations with the same mean (Hammer & Harper 2006). The Student's t-test was carried out in order to test whether the data on *Cyamella* available for the two localities (Kallholn and Unskarsheden) are likely to show the same size range (null hypothesis H0). Therefore it was performed as a two-sample test (permutation rate N= 10000) for selected sections (IV).

The Shapiro-Wilk test, invented in 1965, is a robust procedure to test for normal distribution, especially for small sample sizes (n <20) (Wetherill 1981).

A normal distribution is the basis for several further tests and assumptions, but it is not per se proven, if the null hypothesis (H_0: the sample has been taken from a sample with normal distribution) could not be rejected (Hammer & Harper 2006). In the case of the *Cyamella* samples this test seemed crucial, wether the size ranges of specimens were normally distributed or were skewed due to possible taphonomical fractionation and sorting of exoskeletal parts.

3.2.5 Isotope measurements

$\delta^{13}C$ bulk-rock analysis was undertaken (IV) to view possible variations between all samples. Measuring points of the matrix were chosen from top and bottom of three samples, about 1 cm apart from each other. The data on carbon isotopes of the *Cyamella* samples were obtained by whole rock analyses of four samples. For K3 only one value from the top surface was available.

The measured values were positive values over 2, ranging between 2.08 to 2.42 $\delta^{13}C$ (parts per mil), and do not show strongly differing results, which underlines the possible similarity of the samples, which could be compared with published isotope data.

3.2.6 Taphonomic analysis

All *Cyamella* samples show no preferred orientation of trilobite remains on their surfaces (IV). The trilobites' orientations were measured by using the ImageJ software with an angle-measuring tool on the surface of sample K1. Directions were read according to the orientation of cephala along their long axes. The same process was also done for thoracic elements and pygidia by using the suggested orientation of cephala. A set of eight directional classes for the measured directions spanning in steps of 45 degrees was identified, but without any preferred orientation.

3.2.7 Lithologic analysis

The samples with *Cyamella* from the two localities of the Siljan area showed differing lithologies (IV). At least two lithotypes could be described. One additional sample from the quarry of Solberga (GIT 436-68) was sawn vertical to its suggested bedding plane and polished, resulting in a slab of 6.3 cm maximum height and 12 cm maximum width. The polished surface was used for the description of lithology and taphonomy within the pockets. This sample showed a possible event-like sedimentation within one pocket, underlining not only the different possible processes within one pocket but also the possible differing sedimentary, taphonomic and diagenetic histories between the pockets.

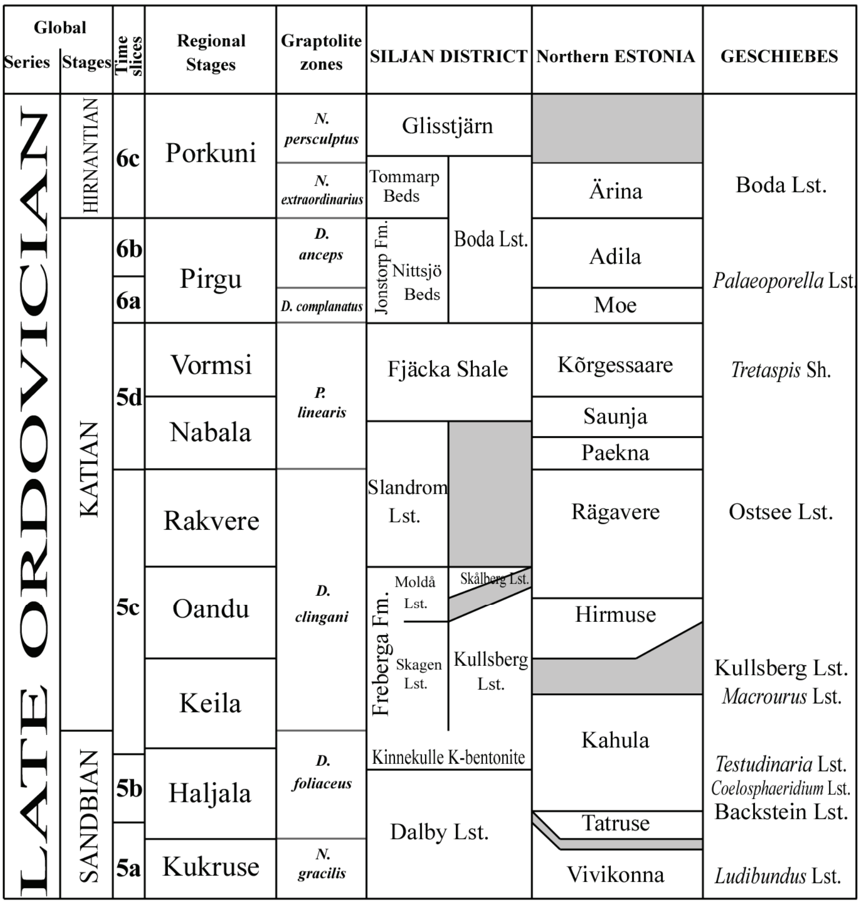
4 GEOLOGICAL SETTING AND STRATIGRAPHY

As introduced in chapters 2 and 3, the Ordovician Proetida of Baltoscandia treated in this paper derive from several geologic units. This chapter aims to comprehend the most important and most recent stratigraphical knowledge on the different rock units and their age determination (Fig. 3).

The Upper Ordovician of Estonia belongs to the North Estonian Confacies Belt (Jaanusson 1982, 1995). Due to the low-angle (2-5 m/km) dipping of nearly horizontal strata to the south, the layers of the Upper Ordovician are accessible in the northern part of Estonia (Schmidt 1858, see Meidla et al. 2008). Here, mostly small outcrops (e.g. quarries, road cuts, temporary excavations, mines) or natural exposures like rivulets, meteorite craters or the coastal areas in NW-Estonia (islands of Hiiuma and Vormsi) give access to differing carbonate facies types (mostly pure limestone or limestone-marl successions, but also dolomites). Knowledge on the Upper Ordovician strata and its distribution (e.g. in the central and southern parts) was mostly gathered by the study of drill cores. The recent stratigraphy for the Upper Ordovician of Estonia is based on biostratigraphic zonation and chemostratigraphic zonation. The latter method enables a correlation of different sedimentary units between Estonia and Sweden. A stratigraphic chart compiled from the recent works of (Meidla et al. 2008) is given in Fig. 3.

The Siljan area, situated in Dalarne, Sweden, is part of the Central Baltoscandian Confacies Belt (Jaanusson 1982, 1995). Its geologic structure is much more complex and has been strongly influenced by if not been a consequence of a meteorite impact. The Upper Ordovician is represented mainly by carbonates, marls and shales. Characteristic sediments of this area are the mud mound sediments of the Boda Limestone (‘Upper *Leptaena* Limestone’ of Warburg 1925). A stratigraphic chart compiled from the recent works of Ebbestad et al. 2007 is given in Fig. 3.

Geschiebes and erratics both represent allochtonous rocks, which contain various important information like faunal (or floral) and facial composition on their former area and time of origin. Their age determination can be made by using biostratigraphical, lithological or petrographical analysis. As pointed out earlier, there still is a high potential on geschiebes for trilobite research (Popp 2007). Additional material from geschiebes containing new information on proetid taxa will follow in the next chapter. The geschiebes treated in this thesis represent rock units, which dominantly derive from the the Central Baltoscandian Confacies Belt sensu Jaanusson (1982, 1995). A stratigraphic chart for the most important geschiebes (in northern Germany) is given in Fig. 3. The terms used are more or less traditional terms, which might be outdated (for the rest of Baltoscandia). Except for the ‘*Palaeoporella* Limestone’, which rarely contains other macrofossils than algae, nearly all listed geschiebes can contain proetid trilobites. The highest chances to find such remains in there are from the 'Backstein Limestone', which can contain *Harpidella*-type trilobites. But also the 'Ostsee Limestone' and geschiebes of the 'Boda Limestone' can yield trilobites, which most probably will belong to the Tropidocoryphidae, Proetidae or Aulacopleuridae. Representatives of the other families are more common in the geschiebes of earlier strata. Brief description on erratics is given by Rhebergen (2009), who also gives determinations for the silicified material of being either of mid to late Sandbian (Haljala stage: Idavere to Jõhvi substages) or late Katian (Pirgu stage) age. Erratics of the first age resemble the 'Backstein Limestone' in its porous structure and brownish to light yellowish colours.



Global Series	Global Stages	Time slices	Regional Stages	Graptolite zones	SILJAN DISTRICT	Northern ESTONIA	GESCHIEBES
LATE ORDOVICIAN	HIRNANTIAN	6c	Porkuni	*N. persculptus*	Glisstjärn	▨	Boda Lst.
				N. extraordinarius	Tommarp Beds Boda Lst.	Ärina	
	KATIAN	6b	Pirgu	*D. anceps*	Jonstorp Fm.: Nittsjö Beds	Adila	*Palaeoporella* Lst.
		6a		*D. complanatus*		Moe	
		5d	Vormsi	*P. linearis*	Fjäcka Shale	Kõrgessaare	*Tretaspis* Sh.
			Nabala		Slandrom Lst. ▨	Saunja Paekna	
		5c	Rakvere	*D. clingani*		Rägavere	Ostsee Lst.
			Oandu		Freberga Fm.: Moldå Lst. Skålberg Lst.	Hirmuse	
			Keila		Skagen Lst. Kullsberg Lst.	▨ Kahula	Kullsberg Lst. *Macrourus* Lst.
	SANDBIAN	5b	Haljala	*D. foliaceus*	Kinnekulle K-bentonite Dalby Lst.	Tatruse	*Testudinaria* Lst. *Coelosphaeridium* Lst. Backstein Lst.
		5a	Kukruse	*N. gracilis*		Vivikonna	*Ludibundus* Lst.

Figure 3. *Stratigraphic chart for the Late Ordovician units for Sweden (Siljan), northern Estonia and geschiebes from northern Germany. If not stated differrntly the units for the Siljan District and northern Estonia represent local formations. Abbreviations are: Fm – formation, Lst – limestone ('Kalk'), Sh – shale ('Schiefer'). Chart was compiled and simplified from Ebbestad et al. 2007, Meidla et al. 2008, Rudolph 1997 and Rudolph et al. 2010.*

5 RESULTS AND DISCUSSION

The following chapter comprises several results (I-IV), mainly based on the biometric studies (I and IV) on *Cyamella stensioei*, but also gives additional results and discussions on other aulacopleuroideans (*Panarchaeogonus*, *Niuchangella*, and a new taxon) and a bathyuroidean taxon (*Telephina*).

5.1 ONTOGENETIC AND PHYLOGENETIC TRENDS

Trends during ontogeny were identified on cranidia of *Cyamella stensioei* (IV). Cranidial features like the position and size of the eye, form of the facial suture in front of the eye and behind of it, the preglabellar area and the axial furrows showed the ontogenetic changes in *Cyamella stensioei*. The ontogenetic observations also enabled the separation of *Paracyamella* from *Cyamella*, in which different modifications and trends were recognized (IV). On the basis of these observations other possible relationships to closely related rorringtoniid taxa could be investigated leading to a history of character changes during the Ordovician (IV). The biometric study on the cranidia of *Cyamella stensioei* showed several groupings in measurements, when plotted in a binary diagram (IV). These groupings were interpreted as instars sensu Chatterton & Speyer 1997.

5.1.1 Ontogeny of Panarchaeogonus

Another aulacopleuroidean trilobite, a member of the family Scharyiidae Osmólska, 1957, is the genus *Panarchaeogonus* Öpik, 1937. This genus was described with the two species *P. atavus* Öpik, 1937 and *P. parvus* Öpik, 1937 both from the early Sandbian Kukersite sediments of Estonia. Owens (1979) regarded *P. atavus* as a junior subjective synonym of *P. parvus*, because both species only differ in their size, glabellar outline and the incision of S1. *Panarchaeogonus* was suggested as a possible ancestor of *Cyamella* (see Owens 1979) linking both families of Sharyiidae and Rorringtonidae.

Apart from *P. parvus* further species of *Panarchaeogonus* are known from Baltoscandia (Owens 1979), namely the mid Sandbian to Katian *P. phlyzacius* Owens, 1979, occurring in the Arnestadt (4bα) and Frognerkilen (4bβ) Formations of the Oslo Region, Norway. *P. holmi* (Warburg, 1925) and *P. trigodus* (Warburg, 1925) are present in the late Katian and early Hirnantian Boda Limestone Formation of the Siljan Area, Sweden. The latter is also known from the Chair of Kildare Limestone, Ireland (see Thomas et al. 1984). Owens (1979, p. 208) regarded the pygidia of *P. whittardi* Dean, 1974 from the Chair of Kildare Limestone (Ireland) as belonging to the species *P. trigodus*.

In their cladistic revision of proetid families the concept of *Panarchaeogonus* was revised by Adrain & Chatterton (1993). The two species *P. phlyzacius* and *P. holmi* from Baltoscandia were attributed to the genus

Niuchangella, known by the species *N. meitanensis* Chang, 1974 from the Silurian of China (Chang 1974). The species *N. holmi* (Warburg, 1925) from the late Katian and early Hirnantian Boda Limestone Formation of the Siljan Area, Sweden, is also known from the Chair of Kildare Limestone, Ireland (see Thomas et al. 1984).

Accepting *P. atavus* being a junior subjective synonym of *P. parvus*, some features and their change during ontogeny become visible on the type material of Öpik 1937, which is refigured in Owens 1979 (Fig. 4), and additional material collected from the Estonian oil shale. This includes also a cranidium of *Otarion* sp., which was described by Öpik in 1937 and is regarded here as belonging to *Panarchaeogonus parvus* (Fig. 4N,O). Besides the overall gain of size, the following morphological trends during the ontogeny of *Panarchaeogonus parvus* become visible (Fig. 4):

(**1**) The preglabellar field is spanning (tr.) between the two anterior branches of the facial suture. A stronger divergence of the facial suture and thus a relatively wider preglabellar field (Wpgf) is detectible in smaller cranidia. Wpgf shows a relative narrowing during growth, which is also related to a relative lowered divergence of the anterior branches of the facial suture. (**2**) The preglabellar field is relatively smaller (sag.) in younger growth stages than in older ones, in which a relative size gain (Lpgf) compared to the cranidal length (Lmax) and glabellar length (Lglab) becomes visible. Also the relative size change compared to the length of the anterior border (Lab) becomes visible, where smaller stages show a relative equality of both lengths. During growth the preglabellar field (Lpgf) shows a stronger gain in size (sag.) than the anterior border (Lab). (**3**) The preglabellar field shows a significant median depression in smaller growth stages, disappearing in larger stages during growth. (**4**) Eye ridges are visible in smaller growth stages (see Öpik 1937 for the description of *P. atavus*), forming two small, adaxially diverging incisions in front of the glabellar at the anterior axial furrow. These two incisions become less prominent in larger specimens and resemble the ones visible in toernquistiids (Fig. 4A,D,G,K). (**5**) The glabellar outline changes during growth from an elongate oval pre-occipital glabella, with minute oval lobes laterally attached to a more subtriangular glabella with stronger lobes, which tend to be shifted from their position in the axial furrow into the sides of the glabella. From the subtriangular outline, the glabellar outline changes to a more rounded, trapezoidal, nearly subrectangular shape in dorsal view. During this change L1, which is separated from the glabella by a narrow, deeply incised S1, gets more and more integrated in larger specimens, ending in a lateral glabellar position bordered by a less incised and more widened S1. (**6**) The glabellar inflation is decreasing during growth, starting with a highly inflated glabella, resembling some otarionid forms (Fig. 4N,O), in smaller growth stages it finally reaches a low-relief cranidium which still keeps its overall vaulting.

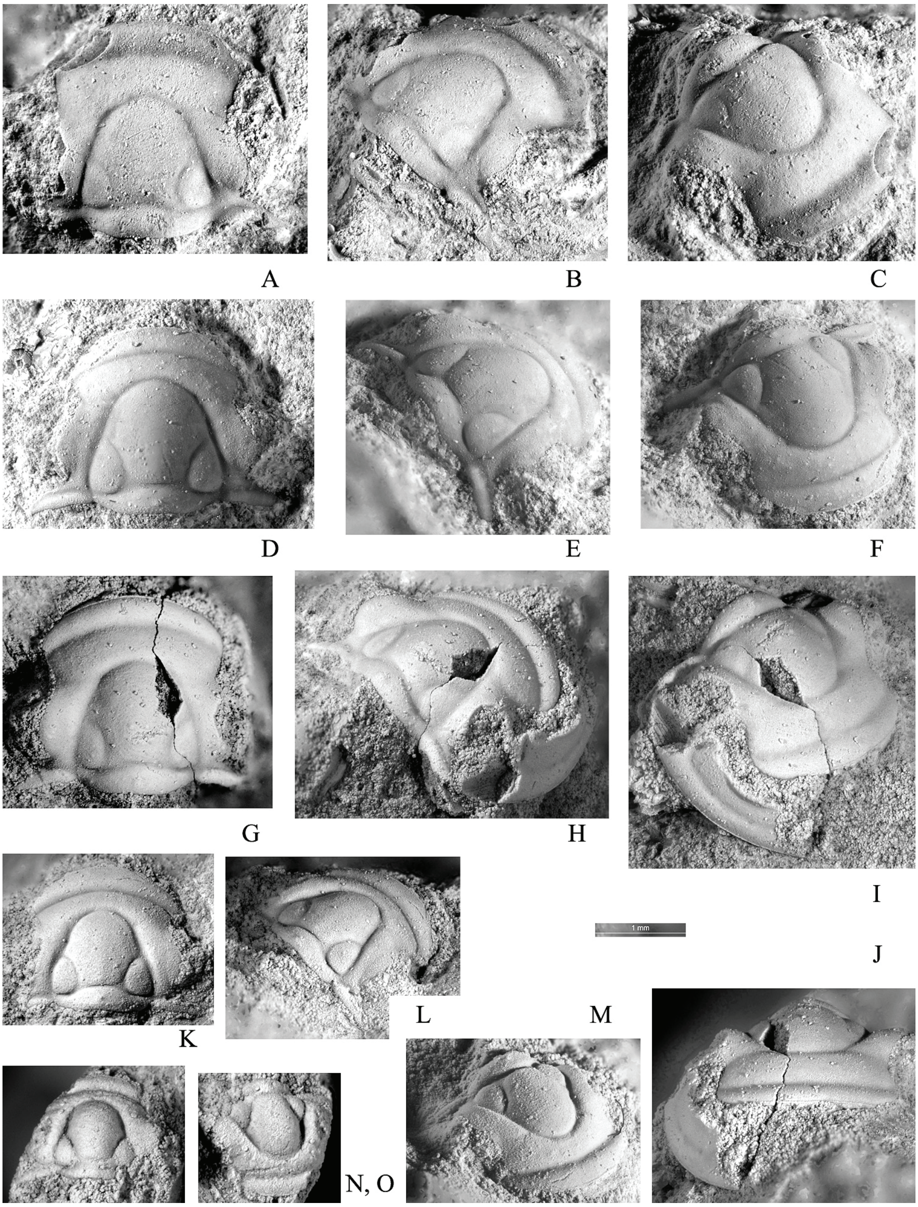


Figure 4. *Type material of A. Öpik from Kukruse Stage, all probably belonging to Panarchaeogonus parvus Öpik, 1937, showing differences during growth: P. parvus Öpik, 1937 (G-J: holotype), P. atavus Öpik, 1937 (K-M: holotype) and Otarion sp. of Öpik, 1937 (N-O). All specimens are housed in the collection of the Tartu University. All specimens were whitened with Ammoniumchloride. Scale bar equals 1 mm.*

(**7**) During growth also the shape of L1 shows a change from an oval shape in very small specimens to a rounded drop- or tear-shaped appearance to a relatively narrow, elongated, subtriangular and more edged form in bigger specimens. (**8**) The axial and cranidial furrows in smaller specimens are narrower and more deeply incised compared to larger specimens, in which a tendency of widening and effacement of these furrows becomes recognisable. There seems a general loss of the cranidial morphology in larger specimens, additionally cranidia of later growth stages show a tendency to lose the overall vaulting and tend to flatten. (**9**) The exoskeletal surface of the cranidia strongly resembles otarionid trilobites in being covered with relative large spine-like tubercles. These tubercles decrease in size during cranidial growth and are transformed into large granules, which remain in the central part of the glabella (forming two anteriorly diverging rows of paired granules) and as a rim around the glabella on the higher elevated parts on the pregalbellar field and the fixigena. These granules disappear during growth, leaving the larger specimens with a smooth surface. (**10**) Although only visible in some specimens, the lateral extension of the posterior fixigenal part seems to relatively shorten during growth. Smaller specimens have much narrower (sag.) but much stronger extended (tr.) posterior parts of the fixigena. This seems to be reversed during growth by ending in a much larger (sag.) but laterally shortened posterior fixigenae in large specimens.

5.1.2 Variability in Panarchaeogonus

There are deviations in the observed ontogenetic trends described above, which are a possible sign of intraspecific variability. The following observations can be made: (**A**) Besides the general trend of a relative narrowing of Wpgf during growth as described under (1), the area of maximum width of the preglabellar field seems to lie either nearly at the same height (sag.) of the front of the glabellar or significantly away from this anterior part of the glabella. This also correlates with a stronger rounded cranidial front, which seems to shift backwards the line of maximum width of the preglabellar field, and with a more elongated glabellar outline. (**B**) There seems to be a variation of the size ratio between the length of the preglabellar field (Lpgf) and the length of the anterior border (Lab) as described under (2). Some specimens seem to have a relative shorter (sag.) anterior border, compared to the length of the pregalbellar field. It needs to be investigated, if this is a result of differing orientation of specimens during photographing.

5.1.3 Phylogenetic comparisons for Panarchaeogonus

The ontogenetic trends which are observable for the Kukersite material are in a way comparable to cranidia of *Panarchaeogonus trigodus*, which derive from a geschiebe of probable Boda limestone (late Katian and early Hirnantian), which was found in Denmark (Fig. 5).

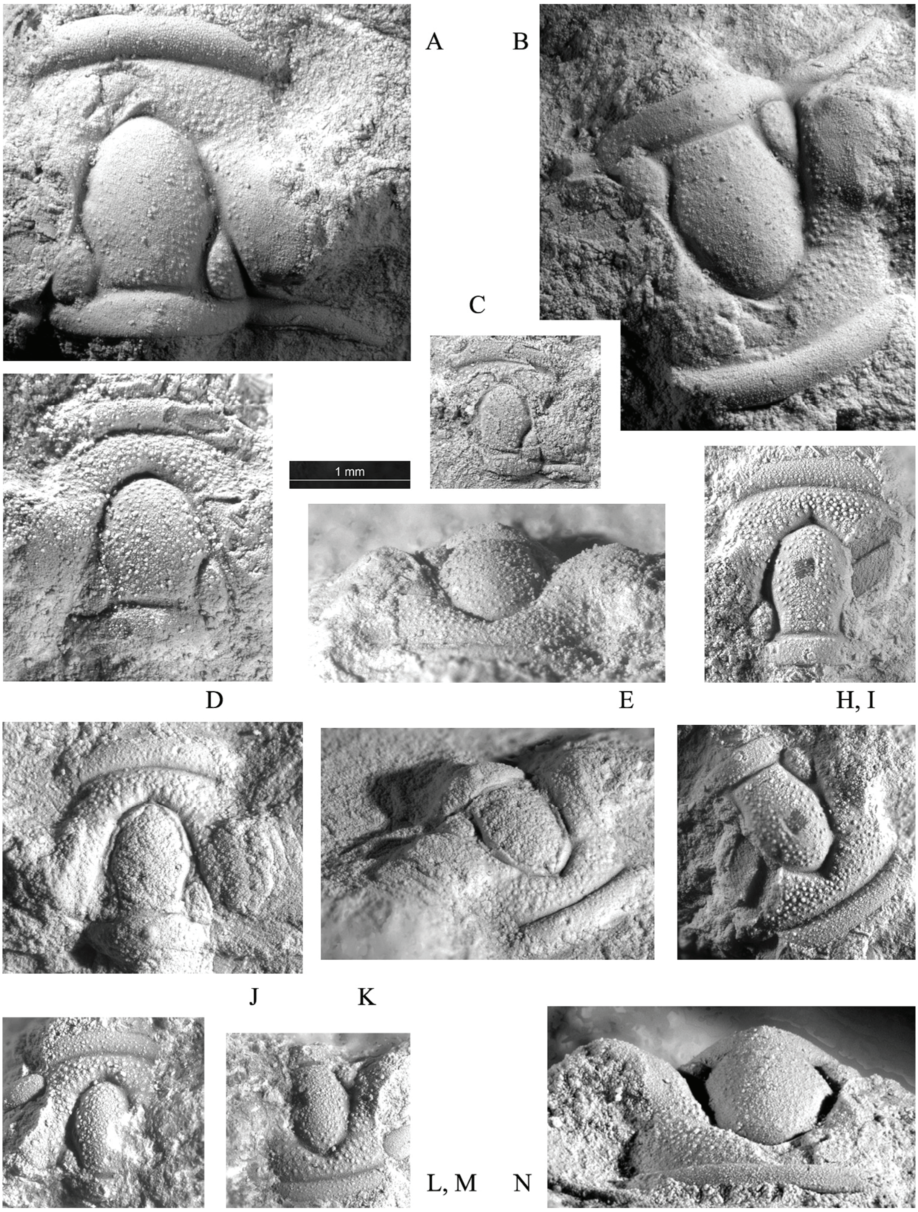


Figure 5. *Specimens of Panarchaeogonus trigodus (Warburg, 1925) from a geschiebe of Boda Limestone from the isle of Langeland (Denmark)showing ontogenetic changes. All specimens were whitened with Ammoniumchloride. Scale bar equals 1 mm.*

These stratigraphically younger specimens are similar to the specimen of *Panarchaeogonus parvus* in the general shape of the glabella being subtriangular, having an anterior border, which is shorter (sag.) than the preglabellar field (Lpgf), elongated (tr.) posterior parts of the fixigena, showing the toernquistiid-like incisions in front of the glabella (Fig. 5) and their loss of overall morphology by effacement of axial furrows.

The specimens of *P. trigodus* from the Boda limestone differ from the ones of the Kukersite in their more parallel sided anterior branches of the cranidial suture, which narrows the overall width of the preglabellar field (Wpgf), in having a more elongated shape of the glabella and much smaller and much stronger isolated basal glabellar lobes, a granulouse exoskeletal surface of the cranidia, which only decreases in intensity during growth, a more clearly pronounced anterior border, which is nearly straight or less curved abaxially than in comparable specimens of *P. parvus*.

The ontogenetic trends detected in *Cyamella* (IV), resemble the ones described here for *Panarchaeogonus*, likely linking the two genera.

5.1.4 A new taxon

Based on additional formerly unknown exoskeletal parts from erratics and geschiebes helped to identify a new taxon, which was only known from cranidia and termed *Cyamella* sp.1 by Owens 1979 (p. 212). It was hithero assigned to the genus and regarded as a possible ancestor of the form in the Boda Limestone. The assignment of new exoskeletal to the cranidia of *Cyamella* sp. 1 shows differences to *Cyamella stensioei* or other closely related aulacoleuroid taxa like *Panarchaeogonus*. *Cyamella* sp.1 probably represents a new genus and will be treated in a forthcoming paper.

5.2 SUGGESTED LIFESTYLE OF *CYAMELLA STENSIOEI*

The Ordovician proetid trilobite *Cyamella stensioei* has so far only been found in local aggregations ('clusters' or 'lenses') inside former horizontal cavities (Owens 1979, Suzuki & Bergström 1999). No reports of findings of this species from outside these pockets (e.g. from the Boda Limestone 'core facies' or from the marly 'flank facies') are known to me. This might be a possible artefact of its size, and therefore of sampling, but it might also be a primary signal of behaviour or adaptation.

The biometric, taphonomic and lithologic investigations (IV) show a variety of features, which lead to the conclusion that the different samples might represent different conditions of deposition. If this conclusion proves to be right, the reason(s) for the mass accumulation still seem to be cryptic. The rock sample from Solberga shows a section through a layer of possible transport of exoskeletons of *Cyamella stensioei*. Such transport-influenced or current-induced layers would not comprehend complete specimens on a rock surface without signs of (current-induced) orientation or tilting. But the rock surfaces showing complete specimens of different size classes (together with larvae and hypostomata) but without any additional fauna leave the question, what caused this accumulation. The search for shelter for or during moulting or mating was discussed for this cryptic behaviour (Owens 1979, Chatterton et al. 2003, Chatterton & Fortey 2008).

Another aspect was introduced by Suzuki & Bergström (1999) for smaller mostly isolated exoskeletal parts being current-tansported and trapped by (or 'glued to') microbial mats. This could account for small disarticulated sklerites but does not explain the gathering of articulated specimens in mass accumulations.

Cyamella stensioei was found from pockets at different locations of the Boda Limestone, being distributed over the whole Siljan area. This raises the questions, how it could spread in between the Boda mounds without being found outside the pockets (in the surrounding sediments) and why it is then only found in monospecific mass accumulations. It can be a possible artefact of preservation and be related to its minute body size, that a single specimen of *Cyamella stensioei* has not been found elsewhere in the different facies of the Boda Limestone. One other alternative is a possible planktonic larval stage, which could drift and in doing so enable the wide spread of this taxon in the Siljan area.

Findings of possible instars, representing different size classes found beneath each other indicate the in situ-state of these mass accumulations. The latter are a hint for a special environment and a special adaptation of *Cyamella stensioei*, since there are no ostracods and no microgastropods present as in other pockets for example with *Isocolus sjoegreni* Angelin, 1854 (Popp & Rohde 2010, IV). The missing accompanying fauna hints to a restricted environment, which might be only accessible for specialised taxa. Physico-chemical factors like low oxygen levels (dysoxic) or even 'poisonous' (sulphur?) bottom waters within the cavities are possibilities for limiting or restricting access to the open space structures for other faunal elements. Chemosymbiosis or a chemosymbiotic metabolism is not unusual in modern vent and seep populations. Also fossil examples of vent and seep biota exist (Bełka & Berkowsky 2005, Kiel 2010, Sandy 2010). And even in trilobites it was suggested by Fortey (2000b) for olenids and trilobites with an olenid-like morphology (bauplan). In this respect a chemotrophic lifestyle was found probable for *Aulacopleura konincki* (Barrande, 1846) by Fortey (2000b). On the basis of its bauplan, its environment and analogies to modern arthopods it was concluded, that also *Cyamella stensioei* was a highly adapted cave-dweller (IV).

5.3 POSSIBLE MODELS OF POCKET FORMATION

The climate during the deposition of the Boda Limestone has been controversially discussed in the past (Fortey & Cocks 2005, Cherns & Wheeley 2007). However, one of the most interesting features of the Boda Limestone is the presence of so-called pockets within its 'core facies' (Suzuki & Bergström 1999). In their revision of the upper part of the Boda Limestone Suzuki et al. (2009) mentioned the presence of pockets only from their units A and D of the

Upper Boda member (Hirnantian). Different modes for the formation of these pockets were discussed.

1.) Carstification as a result of sea-level fall (see Cherns & Wheeley 2007) can be one possible reason for the pocket formation. This process would be linked to a subaerial exposure. As recently shown by Calner et al. (2009) for the Slandrom Limestone (middle Katian) such an exposure has happened once in stratigraphic levels below the Boda Limestone, reaching down to the Kullsberg Limestone (latest Sandbian to early Katian). A subaerial exposure which led to the formation of pockets would result in the consequence that *Cyamella stensioei* could not be longer regarded as contemporaneous with the fauna of the Boda Limestone.

2.) A tectonic or gravitational way of pocket formation is also possible. Here the mound structure would have grown beyond stability and would have broken off. The resulting cracks and hollows could at least have formed some of the (more) vertical pockets (e.g. 'neptunian dykes'). Brecciated sediments occur in the Siljan area for example in the Boda Limestone at Kallholn, but without any traceable macrofauna. The horizontal pockets from which *Cyamella stensioei* is more likely derived could hardly be explained by this tectonic pocket formation.

3.) A synsedimentary processes could be related to the washing out of less stable and less lithified inhomogenous parts of the mound sediment (M. Zwanzig 2011, unpubl.). Such a process would demand either a strong current in order to increase the chemo-mechanic washing out or would demand longer periods of time.

4.) Another synsedimentary process of the formation of pockets could be related to former seepage conduits of fluids or gases. Krause (2001, Krause et al 2004) related the stromatactis structures to the degassing of methane (clathrate hydrate). Hydrothermal vents, seepage of methane hydrate or cold seep sites are recently investigated and their complex faunal and environmental links not yet fully understood. Such sites on the seafloor might have functioned as an initial to mud mound evolution (Naeth et al. 2005, Krause 2001). Thus the pockets could represent pathways or conduits of fluids or gases veining through the body of the growing mound. Like in modern vent sites such environments could be populated by highly specialised organisms. It is assumed here, that the monospecific accumulations of Cyamella stensioei could represent an adaptation to an extreme (dysoxic?) environment. One possible adaptation could be linked to a chemosymbiotic lifestyle as discussed above (5.3).

5.4 PALAEOGEOGRAPHY OF ORDOVICIAN PROETIDS

The value of trilobites and their use for palaeogeography and palaeobiogeography has long been recognised (Whittington & Hughes 1972). With their different adaptations also proetids were treated in this respect (McCormick & Fortey 1999, Lieberman 1994).

As could be demonstrated in chapter 2, the aulacopleuroidean trilobites are widely distributed within the Upper Ordovician strata of Baltoscandia. Compared with the other proetid groups, the bathyuroidea and the proetoidea, for Baltoscandia they mostly occur in the stratigraphical higher units, but there their representatives are the most abundant. If this is a possible artefact of the data or true primary signal needs to be proven in the future.

The finding of *Telephina* in the kerogenous sediments of the Viivikonna Formation (Kukruse regional stage) is interpreted as a possible signal related to sea-level fluctuations (III). A changing sea-level can enable fauna from different regions or continents to cross or bypass former natural barriers. In this case a correlation between the Estonian strata with strata in Sweden and the Oslo region was made (III). The pelagic lifestyle of *Telephina* enabled its wide distribution. Another related form *Carolinites* has a global appearance (McCormick & Fortey 1999).

6 CONCLUSIONS

Within this thesis and the included papers (I-IV) several aspects of the world of Upper Ordovician proetids have been investigated.

1.) Compilation of scattered literature on the Ordovician proetids led to a first overview for Baltoscandia (II). The distribution of Ordovician Baltoscandian Proetida is an important step towards a unified scope on palaeoecology, systematics, palaeo(bio)geography and also biostratigraphy of this area. Correlations between Estonia, Sweden and also material (geschiebes and erratics) from northern Germany and neighbouring countries show promising potential in this respect.

2.) *Cyamella stensioei* showed several groupings of data plots for measured cranidial sections, which possibly represent instars. Such instars are the expression of growth stages and are also related to the exuviations process in trilobites. The co-occurence of different growth stages led to the conclusion that the *Cyamella* pockets represent in situ accumulations.

3.) *Cyamella stensioei* possibly had a chemosymbiotic lifestyle (IV) as a consequent adaptation to an otherwise restricted environment within the cavities in the mounds of the Boda Limestone.

4.) On the basis of faunistic, taphonomic and lithologic observation a possible process for the pocket formation within the mounds of the Boda Limestone was identified. In this new model the seepage of fluids or gases from below the sea-surface not only initiated the mound growth, but also was responsible for the build-up of a complex system within the mound body. These conduits were later infilled (e.g. shells of nautiloids and remains of larger trilobites) or inhabited by the highly specialised trilobite *Cyamella stensioei*.

5.) The morphological differences between the Scandinavian genus *Cyamella* and the Asian genus *Paracyamella* Zhou & Xiang, 1993 led to the re-assessment of the latter genus (IV).

6.) A taxon formerly termed *Cyamalla* sp. 1 by Owens, 1979 was regarded as a possible ancestor of *Cyamella stensioei*. Additional new material from erratics and geschiebes showed differences to the type species from the Boda Limestone and identified *Cyamalla* sp. 1 as a new genus, which will be treated in a forthcoming paper. Thus *Cyamella stensioei* Owens, 1979 as the type species of the genus exclusively occurs in the Boda Limestone.

7.) Ontogenetic character changes and character changes through time could be recognised in *Panarchaeogonus*. The similarity of trends during growth in the cranidia of *Cyamella* (IV) and *Panarchaeogonus* could link these genera.

8.) The finding of *Telephina biseriata* (Asklund, 1936) in the kukersite beds of the Viivikonna Formation of northern Estonia not only hints to possible sea-level changes (III) but shows the importance of active collecting and its contribution to science.

9.) About 30 genera with more than 70 species of Baltoscandian proetide trilobites have been studied over 150 years. Out of the 21 genera of Proetida of which nine occur in the Pirgu, all belonging to the Proetoidea and Aulacoplauroidea survived the end Ordovician extinction event. As elsewhere all Bathyuroidea do not cross the Ordovician-Silurian border and became extinct. The influx of pelagic genera into Baltoscandia was possibly related to eustatic events.

10.) The use of proetid trilobites for biostratigraphy and correlation, palaeo-environmental assumptions and palaeogeography is considered here as an important contribution to understand the processes of the earth's history.

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9 ENGLISH SUMMARY

This thesis on Ordovician proetid trilobites in Baltoscandia shows the importance of palaeontology and its relationship to the neighbouring disciplines of geology. Starting from a purely systematic overview and ranging from biometrics over statistics and analytical methods to palaeobiology this studies soon faced also the questions on facies distribution and sedimentation, but also stratigraphy and correlation. Today, almost 30 proetide genera with more than 70 species are known from the Ordovician successions of Baltoscandia, including geschiebes from Northern Europe (**paper II**). Because of their relatively small size proetide trilobites can be found in small rock samples (borehole cores, geschiebes), offering the possibility of a high biostratigraphical potential. Proetida are relatively minor components of most Ordovician trilobite faunas, but representatives of all three superfamilies occur across all confacies belts (sensu Jaanusson 1982). The study of literature for the overview paper of proetid distribution in Baltoscandia revealed the conjunction between recent and past systematics and recent and past stratigraphy.

Biometric analyses of the trilobite *Cyamella stensioei* Owens, 1979 from the Upper Ordovician Boda Limestone of Sweden (**papers I and IV**) helped to identify important cranidial characters and their change during ontogeny for this species. These characters were used for a comparison to closely allied rorringtoniid taxa from outside Baltoscandia and revealed possible systematic as well as palaeoecological connections. Analysis of key measurements of cephala of *C. stensioei* show a number of instars and for the first time a meraspis stage of *C. stensioei* is published. Also for the first time a thorough lithological and taphonomical investigation of a sample from a *Cyamella* pocket is presented, with additional isotope data (**paper IV**).

A cranidium of *Telephina biseriata* (Asklund, 1936) was collected from the kerogenous Kiviõli Member of the Viivikonna Formation, Kukruse Stage in the vicinity of the oil-shale mining area of northeast Estonia (**paper III**). The occurrence in the North Estonian Confacies Belt of *Telephina*, known as a deep-water inhabitant, probably reflects the peak of a transgression event at that time.

As a genus uniting features of both families Rorringtoniidae and Scharyiidae in this thesis a first discussion on the character changes and cranidial development during growth for Panarchaeogonus Öpik, 1937 is given, which will be treated in more detail in a forthcoming publication.

10 ESTONIAN SUMMARY

Antud doktoritöö Baltoskandia Ordoviitsiumi proetiidsetest trilobiitidest näitab paleontoloogia tähtsust integreeritult teiste lähedaste geoloogia distsipliinidega. Alustades puhtalt süstemaatilisest ülevaatest jõuti peagi läbi statistiliste analüüsimeetodite, biomeetria ja paleobioloogia silmitsi fatsiaalse leviku, settimise ja stratigraafilise korrelatsiooni probleemidega. Tänaseks on Baltoskandia Ordoviitsiumi läbilõikest koos Põhja-Euroopas levinud glatsiaalsete rändkivide materjaliga ühtekokku teada seltsist Proetida ligi 30 perekonda oma rohkem kui 70 liigiga (**Artikkel II**). Tänu nende miniatuursetele mõõtmetele võib neid leida väikesemõõdulistest kivimpaladest nii nagu ka puuraukudest ja glatsiaalsetest veeristest omades seetõttu kõrget biostratigraafilist potensiaali. Kuigi proetiidid on Ordoviitsiumi trilobiidifauna suhteliselt väike komponent, on nende esindajad levinud kõigis fatsiaalvööndites (*sensu* Jaanusson 1982). Kirjandusepõhine ülevaade proetiidide levikust Baltoskandias tõi esile võrdluse nii varasemate ja hilisemate autorite süstemaatika erinevustes kui ka varasema ja praeguse stratigraafia erinevustes.

Ülem-Ordoviitsiumi Boda lubjakivi trilobiidi *Cyamella stensioei* (sugukond Rorringtoniidae) biomeetriline analüüs (**Artiklid I ja IV**) aitas leida sellele liigile iseloomulikult ontogeneesi käigus muutuvad tunnused. Neid tunnuseid kasutati võrdlemaks väljaspool Baltoskandia piire leiduvate teiste lähedaste trilobiitidega ehk rorringtoniididega ning leiti võimalikke süstemaatika ja paleoökoloogia seoseid. *Cyamella stensioei* peakilpide peamised mõõtmed näitasid erinevate larvistaadiumite esinemist ja esmakordselt kirjeldati selle liigi meraspiidi staadium. Samuti on esmakordselt esitatud “*Cyamella*-taskute” litoloogiline ja tafonoomiline kirjeldus koos isotoop-analüüsi andmetega (**Artikkel IV**).

Kirde-Eesti põlevkivi kaevandamise piirkonnast leiti Kukruse lademe Viivikonna kihistust *Telephina biseriata* peakilp (**Artikkel III**). Üldiselt süvaveelise faatsiese perekonnana teatud *Telephina* leid Põhja-Eesti fatsiaalvööndist viitab tõenäoliselt transgressiooni sündmusele sel ajal.

Viimasena on diskuteeritud Panarchaeogonus’e kui perekonna, mis ühendab endas nii Rorringtoniidae kui ka Scharyiidae sugukonna tunnuseid, peakilbi tunnuste muutused ja areng ontogeneesi jooksul.

11 GERMAN SUMMARY

Diese Doktorarbeit über proetide Trilobiten in Baltoskandien und Deutschland zeigt die Wichtigkeit der Paläontologie und ihre Beziehung zu den Nachbardisziplinen innerhalb der Geologie auf. Ausgehend von einer rein systematischen Übersicht später die Biometrie einbeziehend, über Statistik und analytische Methoden bis hin zur Paläobiologie erreichten diese Untersucungen auch die bestehenden Fragen der Faziesverteilung und Sedimentation, aber auch der Stratigraphie und Korrelation. Es sind heute nahezu 30 proetide Trilobitengattungen mit mehr als 70 Arten aus den ordovizischen Ablagerungen Baltoskandiens, die Geschiebe aus Nordeuropa mit einbezogen, bekannt (**Artikel II**). Durch ihre verhältnismäßig geringe Größe können proetide Trilobiten auch in kleinen Gesteinsproben (Bohrkernen, Geschieben) gefunden werden, was ein großes biostratigraphisches Potential birgt. Zwar stellen die Proetida nur einen geringen Anteil der übrigen ordovizischen Trilobitenfaunen dar, aber die Vertreter aller drei Überfamilien sind in allen Konfaziesgürteln (sensu Jaanusson 1982) vorhanden. Die Literaturrecherche für die Übersichtspublikation über die Verteilung der Proetiden in Baltoskandien verdeutlichte die Verknüpfung zwischen aktueller und überholter Systematik und aktueller und überholter Stratigraphie.

Anhand biometrischer Analysen des Trilobiten *Cyamella stensioei* Owens, 1979 aus dem oberordovizischen Bodakalk Schwedens (**Artikel I und IV**) konnten wichtige Craniduim-Merkmale und ihr Wandel während der Ontogenie für diese Art identifiziert werden. Diese Cranidium-Merkmale wurden für einen Vergleich mit nahe verwandten rorringtoniiden Taxa von außerhalb Baltoskandiens herangezogen und ließen so auf mögliche systematische und paläoökologische Verbindungen schließen. Bei der Analyse bedeutender Messstrecken an Cephala von *C.stensioei* ergab sich eine Anzahl von Wachstumsstadien und erstmals wird ein Meraspis-Stadium von *C. stensioei* veröffentlicht. Ebenfalls erstmalig wird eine gründliche lithologische und taphonomische Untersuchung einer *Cyamella*-Tasche präsentiert, die zusätzlich Isotopenmessungen enthält (**Artikel IV**).

In der Umgebung der Ölschieferabbaue in Nordestland wurde ein Cranidium von *Telephina biseriata* (Asklund, 1936) aus dem kerogenhaltigen Kiviõli Members der Viivikonna Formation, Kukruse Stufe, gefunden (**Artikel III**). Dieses Auftauchen von *Telephina*, die als Tiefseebewohner gilt, im Nordestnischen Konfaziesgürtel spiegelt möglicherweise die Hochphase einer Transgression zu dieser Zeit wider.

Da die Gattung sowohl Eigenschaften der Familien Rorringtoniidae als auch Scharyiidae vereint, werden in dieser Doktorarbeit vorab der Merkmalswandel und die Cranidium-Entwicklung während des Wachstums an *Panarchaeogonus* Öpik, 1937 diskutiert, um in einer zukünftigen Veröffentlichung ausführlicher diskutiert zu werden.

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List of Publications:

Popp, Adrian; Pärnaste, Helje (2011). Biometry and life style of the Ordovician proetid trilobite Cyamella stensioei Owens, 1979. *GFF*, [accepted].

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ORIGINAL PUBLICATIONS

PAPER I

Popp, A. and Pärnaste, H. 2008a. Morphometric study of the Ordovician proetid trilobite *Cyamella stensioei* Owens, 1978. *In* I. Rabano, R. Gozalo & D. Garcia-Bellido (eds.): *Advances in Trilobite Research. Publicaciones del Instituto Geológico y Minero de España, Serie: Cuadernosdes Museo Geominero 9*, 327-332.

I.Rábano, R. Gozalo and D. García-Bellido (Eds.), *Advances in trilobite research.*
Cuadernos del Museo Geominero, nº 9. Instituto Geológico y Minero de España, Madrid, 2008. ISBN 978-84-7840-759-0

MORPHOMETRIC STUDY OF THE ORDOVICIAN PROETID TRILOBITE *CYAMELLA STENSIOEI* OWENS, 1978

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Keywords: Trilobita, statistical analysis, size range, carbonate mud mound, Boda Limestone, Siljan District, Sweden.

INTRODUCTION

The genus *Cyamella* was first described by Owens in 1978 as *Cyamops*, but was renamed (Owens in Owens and Hammann, 1990, p. 240) as the original genus name was preoccupied. *Cyamella stensioei* Owens is a small proetide trilobite from the Boda Limestone of the Siljan District in Dalarna (Sweden). The Boda Limestone (Upper Ordovician) is regarded as a carbonate mud mound showing core and flank facies (Jaanusson, 1982). Mass accumulations of trilobites within the Boda Limestone are regarded as a result of sedimentary infill and are termed pockets or cavities (Suzuki and Bergström, 1999). To our knowledge *C. stensioei* has not yet been described from outside these limited areas within the mounds. One rock specimen from the Boda Limestone in the quarry at Kallholn (NW part of the Siljan Ring between Orsa and Skattungsbyn) is investigated here. The aim of this study is to trace any morphometric variation of the proetid exoskeletons in one of such pockets, assuming this being a case of one particular accumulation and therefore representing variation in morphology within a species during as short a time period as possible.

MATERIAL AND METHOD

The limestone quarry at Kallholn is the type locality for *C. stensioei* (see Owens, 1978) and has yielded several slabs with mass accumulations of the species. One slab derived from Kallholn is investigated (Fig. 1) without any information given about the exact locality or orientation. Referring to Suzuki and Bergström (1999, p. 168; see also Owens 1978, p.202), it can be regarded as an *in situ* type of internal cavity filling.

Most trilobite specimens on the rock sample do not show all of the features regarded as important for the analysis. Twenty-four suitable cranidia were chosen for the final comparison. Specimens are named by using the following code: CTP stands for a complete specimen with cephalon/cranidium, thorax and pygidium, CTH stands for cephalothorax and CR stands for cranidium. The measurements were taken with a stereoscopic microscope using a measuring ocular. Longitudinal sections are termed lengths, all transverse sections are termed widths. All values are regarded as being absolute and measurements were taken in units, where forty units represent one millimetre. Later translation into millimetres does not affect the size ratios investigated. The trilobite specimens were oriented in a planar position (perpendicular to the optical path).

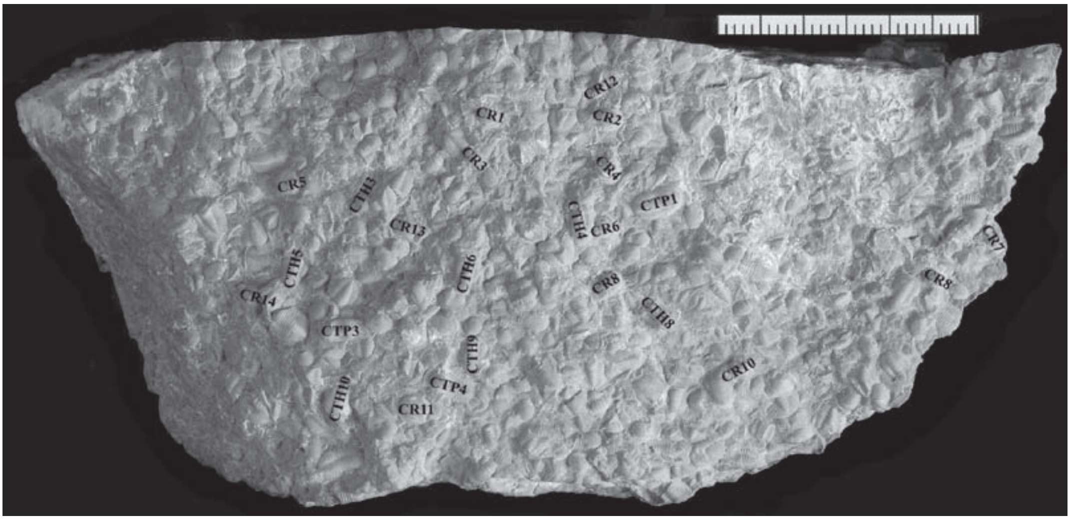

Figure 1. Rock specimen from Boda Limestone of Kallholn quarry, Sweden, showing a mass accumulation of the minute proetide *Cyamella stensioei*. Investigated remains are indicated using CTP for specimens with cranidium, thorax and pygidium, CTH for cephalothorax and CR for cranidium (Natural History Museum, Stockolm; Ar 45665). Scale graduated in mm.

A multiple orientation method was used for measuring the thirteen different sections of the cranidia (Fig. 2). By measuring from the centre of the graticule to the outer limit of the field of view, errors arising from the convexity of the exoskeleton were reduced. Measuring tracks were repeated three to five times to minimize measuring error. If a tolerance limit of six units between the highest and lowest values was exceeded, additional readings were made. An average value was calculated and chosen as the final measuring result. Where incomplete, some sections were measured in half length/width and doubled - assuming the measured specimens as being symmetrical in its feature.

The thirteen measurements used in the analysis are shown on Fig. 2. Their abbreviations stand for total cranidial length (Lmax), total cranidial width (Wmax), glabellar length (LGLABmax), glabellar width (WGLABmax), glabellar width at the middle of palpebral lobes (WGLAB_PALP), distance or position of palpebral lobes measured from posterior cranidial border (e.g. occipital ring) (LposPALP), length of preglabellar field (LPGFmax), width of preglabellar field (WPGFmax), length of palpebral lobes (LPALPmax), width of palpebral lobes (WPALPmax), length of occipital ring (LOCRmax), distance or position of median tubercle on occipital ring measured from posterior cranidial border (LposMTB), length of anterior cranidial border (LACBmax). In order to compare our values to those given by Owens (1978, p. 212), including those of the holotype, the palpebral width of the cranidium (σ–σ, sensu Owens) was calculated via WGLAB_PALP and WPALPmax. The dimensions of the cranidium of the holotype of *C. stensioei* (RM Ar47556) and an additional specimen (RM Ar47518) given by Owens (1978, p. 212) were compared with our measurements.

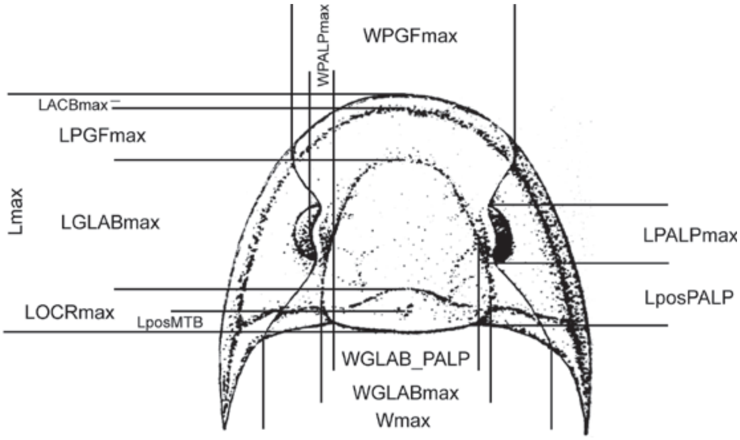

Figure 2. Measured sections on the cranidium of *C. stensioei*. L indicates length, W stands for width.
(Figure modified after Owens, 1978).

RESULTS

As they are the most distinctive for identification and comparison, only cranidia were included in the investigation. The longest cranidium (CR13) shows a maximum length of 3.59 mm, whereas the shortest cranidium (CR12) measures 2.32 mm. The size difference is about 35 per cent and is a continuum, not showing grouping into separate instars (Fig. 3). The average is 3.007 mm, and calculated without the maximum and minimum values 3.011 mm. The median value is 2.955 mm. Cranidial widths could be measured on sixteen of the specimens. CR11 is the widest at 4.48 mm, the narrowest (CR12) measures 2.51 mm. The average is 3.43 mm, and calculated without the maximum and minimum values, 2.993 mm. The median value is 3.495 mm. The cranidial width-length ratio (Fig. 4A) changes from 78 to 97 per cent (average 87%, variability 19%), and that of the glabella (Fig. 4B) from 76–98 per cent (average 86%, variability 22%). Similar ratios (3/4–9/10) were described from the other slab (Owens, 1978, p. 211 here, and for following comparison). Sagittally the length of the preglabellar field occupies 34–52 per cent (average 42%, variability 18%) of the cranidial length, and is about 19–27 per cent (average 23%, variability 8%) of the length of the glabella. The ratio of the lengths of the palpebral lobe/glabella varies from 26 to 45 per cent (average 35%, variability 19%). For last two ratios 1/3 was described as diagnostic by Owens (1978). The width of the preglabellar field is equivalent to 63–89 percent of the maximum width of the cranidium, and 76–97 per cent of the length (variability 26% and 21% respectively). The occipital ring comprises from 21 to 36 per cent (average 29%, variability 15%) of the sagittal length of the glabella, which is more than was shown by Owens (1/4). The occipital tubercle is not positioned exactly to the middle length of the occipital ring, but slightly rearwards or forwards reaching to 5 per cent or 15 per cent respectively in comparison of LposMTB to LOCRmax (average 54%, variability 20%). The palpebral width of the cranidium (σ–σ) comprises 80% of the length of cranidium of holotype, but ranges from 57 to 74 per cent on this slab (Fig. 4C).

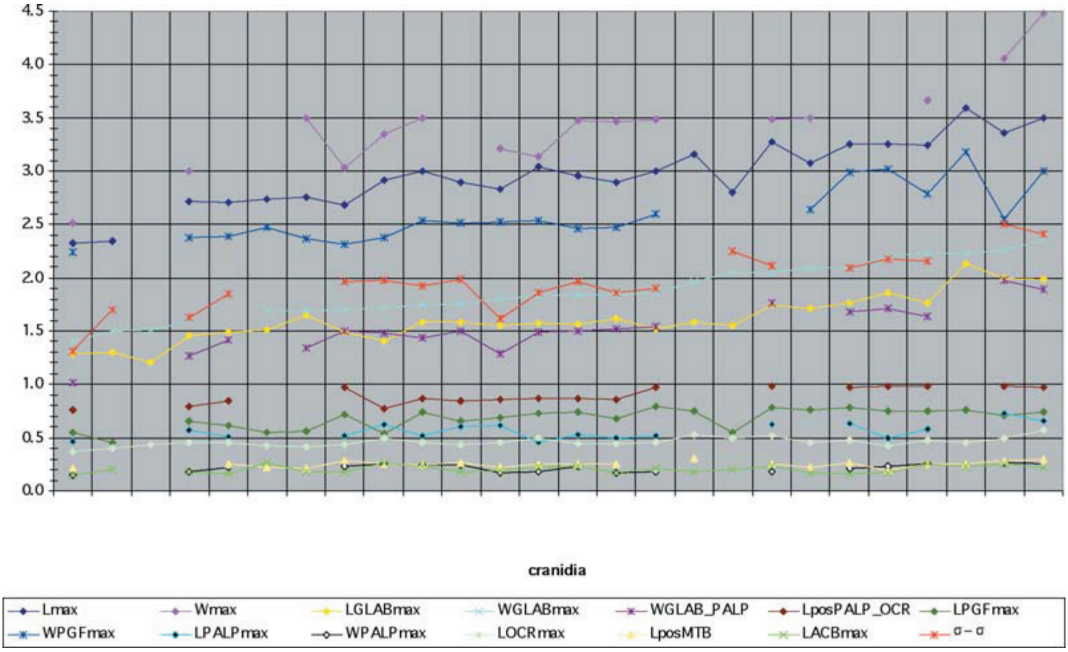

Figure 3. Measurements (in mm) for different trilobite sclerites. Sigma-to-sigma-values are calculated for our measurements. Additionally Owens' data (1978, p. 212) are used for comparison.

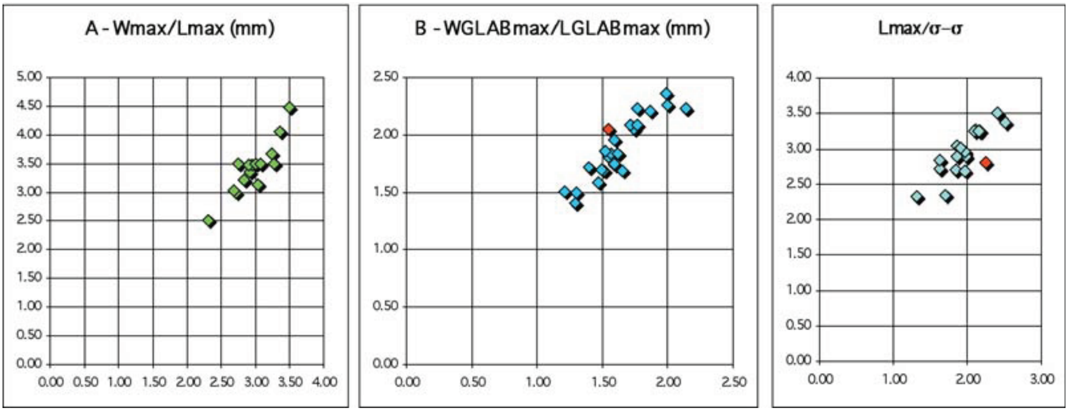

Figure 4. A–C, graphs plotting one character against another (see also Fig. 3). The holotype is shown by red.

While the maximum total length for the holotype (see Ar47556, Fig. 3) is situated in the lower part of the size distribution for all cranidia and differs by more than 1.2 mm from the longest cranidium measured, the maximum width is not given by Owens and therefore this ratio cannot be compared here. However, when sorted by the maximum width of the glabella the maximum cranidial length, glabellar length and the length of the preglabellar field show relatively lower values. The paratype cranidium (Ar47518) shows average cranidial length - glabellar width ratio, but again, somewhat lower value of the length of the preglabellar field. The differences described above in the data of the type specimens may be due to differences in measuring methods. The other possible reasons could be that these samples are from different pockets of the same or of possibly different age, or from different taphonomic situations.

The cranidial length and width only show a slight correlation, which could be a result of measuring errors (e.g. doubling the measured half-sections) superimposed on a small size variance signal. Another reason could be the small number of specimens used here. A better correlation is seen in the comparison of glabellar width and length, which show a proportional growth. More data are needed to clarify this in a more sophisticated way. The length of the occipital ring seems to change to a smaller degree compared to the increase of the cranidium. When plotted as graphs, most values of the thirteen measured sections show some peaks but these do not appear systematically. This can be seen, when sorting after one value first, than doing another plot with a different sorting of values. The sorting effect can be interpreted as a primary signal, showing variance on the species level. Also statistical explanations are possible.

CONCLUSIONS

Suzuki and Bergström (1999, p. 171) considered preservational reasons to be responsible for the relatively narrow size range for the minute trilobites *Ityophorus* and *Isocolus* also appearing within pockets and cavities of the Boda Limestone mounds. Maybe this is also the case for *Cyamella stensioei*.

Measurements of twenty-four cranidia of *C. stensioei* for one particular slab show 35 per cent of size difference, and no evidence for moulting instars or dimorphism. Maybe all individuals preserved belong to one generation, showing the natural size-variation. Further studies are needed to explain the differences between the type specimens and the specimens of this study. This also includes borrowing and re-measuring the type specimen and additional material stored in Stockholm. Besides statistical and morphometric analysis, further studies should also include sedimentological obeservations for supporting the theory of Suzuki and Bergström (1999) on life of *C. stensioei*.

Winnowing effects and trapping of hard-parts by algae were discussed by Suzuki and Bergström (1999) and further sedimentological analysis could help identifying the reason for the *Cyamella*-accumulations including whether or not they represent living communities within the cavities (or pockets). Smaller individuals including larvae can be expected if *C. stensioei* was fully adapted to this environment. Statistical analysis could also help to show morphometric differences within different *Cyamella*-accumulations, which could prove their separation from each other, being limited to one specific carbonate mud mound within the Boda Limestone facies.

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PAPER II

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Distribution of the order Proetida (Trilobita) in Baltoscandian Ordovician strata

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Abstract. The trilobite order Proetida forms a minor but important faunal element within the Ordovician strata of Baltoscandia. This review follows the current systematic, taxonomic, and stratigraphical usage and discusses the distribution of these trilobites within the context of the Confacies Belt model. A database of species-level information was derived from numerous publications relating to the Scandinavian and Baltic states and relevant neighbouring regions. Important additional information on stratigraphical occurrences of genera has been derived from glacial erratic boulders (geschiebe) from northern Germany and adjacent areas. The representatives from Baltoscandia of three superfamilies, Bathyuroidea, Aulacopleuroidea, and Proetoidea, are listed. The genus level was chosen as the most practicable to plot on the maps, one showing the time interval for the Kukruse Regional Stage (or Global Stage Slice Sa1), the other that for the Pirgu and Porkuni stages (or stage slices Ka4 and Hi1–Hi2). These intervals each show a diversity peak within the ranges of about 30 genera of Proetida and over 70 species from the Ordovician successions of Baltoscandia. Out of these a total of nine genera cross the Ordovician–Silurian boundary.

The regional comparisons from within Baltoscandia show differences in facies dependency of certain genera, with possibly also a latitudinal component. During the late Ordovician the faunal resemblance appears to be closest to the neighbouring palaeocontinent Avalonia, suggesting a faunal exchange between or pathways to both continents from elsewhere. Besides climatic and geographical proximity of palaeocontinents, sea-level changes also have to be considered in explaining the distribution of Proetida in Baltoscandia.

Key words: Ordovician, Baltoscandia, geschiebe, Trilobita, Proetida, distribution, biodiversity.

INTRODUCTION

The trilobite order Proetida Fortey & Owens, 1975, comprises at least 470 Early Ordovician to Permian genera worldwide. In its original definition it included the families Aulacopleuridae Angelin, Bathyuridae Walcott, Brachymetopidae Prantl & Přibyl, Celmidae Jaanusson, Dimeropygidae Hupé, Glaphuridae Hupé, Otarionidae Richter & Richter, and Proetidae Salter. New data, especially on the ontogeny and morphology of early representatives of the group, have generated considerable discussion on the concept and composition of its component families and on the classification of the order (e.g. Bergström 1977; Lütke 1980, 1990; Owens & Hammann 1990; Adrain & Chatterton 1994, 1996; Chatterton 1994; Ahlberg 1995a, b; Edgecombe et al. 1997; Chatterton et al. 1998, 1999; Adrain et al. 2001; Jell & Adrain 2003; Owens 2004; Bergström & Suzuki 2005; Fortey 2006; Yuan et al. 2006). This has been taken into account in our review on the Baltoscandian Proetida. We here follow the revised edition of *Treatise on Invertebrate Paleontology* (Fortey 1997, p. 300), with modifications by Jell & Adrain (2003), and include three superfamilies – Proetoidea Salter, Aulacopleuroidea Angelin, and Bathyuroidea Walcott in the order.

There is a long history of research into the Proetida of the Baltic area, dating from Angelin (1851, 1854) for Scandinavia and Nieszkowski (1857, 1859) for the Baltic states. Thereafter, the work of Schmidt (1894, 1907; see also Bruton et al. 1997) was a major milestone. Descriptions of individual genera and species are scattered through monographic works from the late 19th and early 20th centuries (e.g. Eichwald 1861; Linnarsson 1869; Törnquist 1884; Olin 1906; Warburg 1925; Öpik 1925, 1927, 1928, 1937). A large number of later publications include or deal specifically with Ordovician Proetida: Hadding (1913), Asklund (1936), Thorslund (1940), Jaanusson (1956), Balashova (1961), Männil (1963), Nikolaisen (1963), Owens (1970, 1973, 1974, 1979, 1981, 2004), Rõõmusoks (1970, 1997), Bruton & Owen (1979), Owen & Bruton (1980), Owen (1981, and in Owen & Harper 1982; Harper & Owen 1984; Harper et al. 1984), Bruton (1983), Wandås (1984), Ahlberg (1995a, b), Suzuki & Bergström (1999), Bergström &

Suzuki (2005), Bruton & Høyberget (2006), Pärnaste (2006), Popp & Pärnaste (2008a, b), Hansen (2008, in press). Important monographic works on faunas (which include Proetida) from glacial erratic boulders (geschiebe) were published by Roemer (1861, 1885), Steinhardt (1874), and Pompeckj (1890). More recent contributions on geschiebe faunas are those by Neben & Krueger (1971, 1973, 1979), Schöning (1982), Rudolph (1997), Schimmelpfennig & Schneider (1997), Bilz (2001), Popp & Schöning (2001, 2006), Rhebergen (2001), Krueger (2004), and Popp (2007). Data derived from these sources were used to compile Table 1.

Initially, a simple database was established for entering species-level information, but due to different levels of data quality and confidence it was decided that it would be more appropriate to use genus level. Today, almost 30 genera of Proetida with more than 70 species are known from the Ordovician successions of Baltoscandia, including glacial erratic boulders (geschiebe) from Northern Europe (Table 1). The locality data are organized according to the Confacies Belt structure of the basin (Männil 1966; Jaanusson 1982a), to demonstrate the facies distribution of different genera. It is obvious that the pattern is rather uneven, biased towards areas of outcrop (e.g. Oslo Region, Siljan District) compared to those where material has been collected only from borehole cores (e.g. Latvia, Lithuania). Because of their relatively small size these trilobites can be found in small rock samples (borehole cores, geschiebe), offering the possibility of a high biostratigraphical potential. Although data from geschiebe cannot be plotted on palaeogeographical maps, they reveal important information for genus level presence in various stratigraphical levels within the Ordovician of Baltoscandia. Proetida are relatively minor components of most Ordovician trilobite faunas, but representatives of all three superfamilies occur across all confacies belts (here modified after Jaanusson 1982a, 1995).

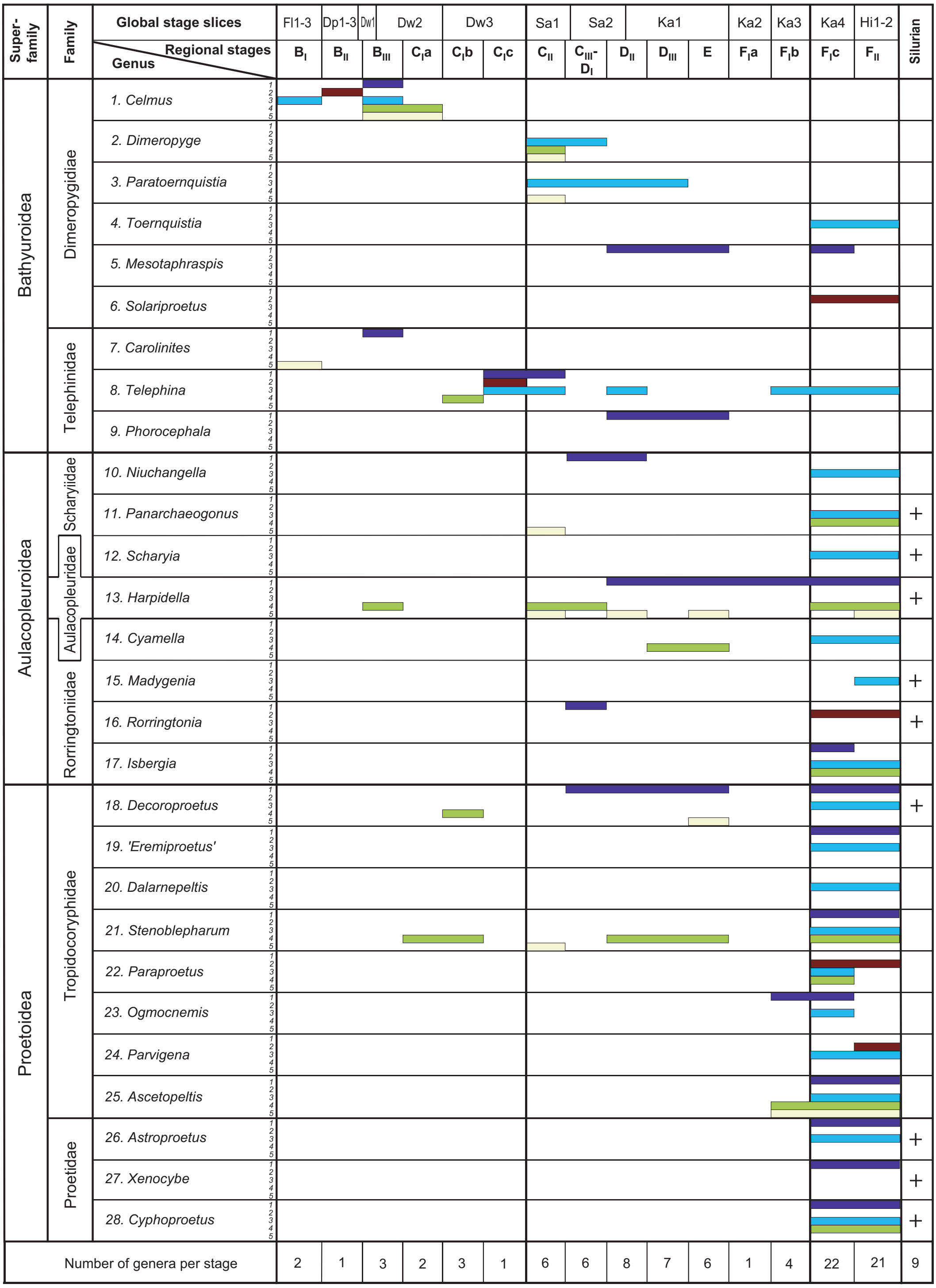
BATHYUROIDEA

Two families, Telephinidae Marek and Dimeropygidae Hupé, are represented in the Ordovician of Baltoscandia. These families include the earliest Proetida known from this region.

Telephinidae

The family Telephinidae is represented in the Lower Ordovician by *Carolinites* Kobayashi, the type species of which, *C. genacinaca* Ross, is the most widely distributed trilobite species known, according to McCormick & Fortey (1999). The broad palaeogeographical distribution of this genus is explained by its pelagic life style. Balashova (1961) described *C. popovkiensis* from calcareous glauconite sandstones belonging to the Mäeküla Member (Leetse Formation) of the St Petersburg region, which she believed to be of Tremadoc age. This unit is now correlated with the lower part of the Billingen Stage ($B_{I}\beta$) (Pärnaste 2006) and time slice 2b (Nõlvak et al. 2007) or stage slices Fl1–Fl2 (Bergström et al. in press). Another closely related taxon determined as komaspidid (Nikolaisen 1962; Hansen 2008) or aff. *Carolinites* (Wandås 1984) is known from the uppermost Stein Formation of the Kunda Stage on Helgøya, Oslo Region (Hansen in press). In general, *Carolinites* is more common outside Baltica, for example in Laurentia (Adrain et al. 2004, fig. 24. 4) and in South China Plate (Turvey & Zhou 2004), and is also known from Siberia, Australia, France (Montagne Noire), Turkey (see references in McCormick & Fortey 1999), and Iran (Bruton et al. 2004).

Telephina Marek is another genus adapted to pelagic habits. It was reviewed by Ahlberg (1995a, b), who documented its occurrence in the Oslo Region, Norway (see also Nikolaisen 1963; Bruton & Høyberget 2006; Hansen in press), Jämtland (see also Thorslund & Asklund 1935), Dalarna, Västergötland, Öland, and Scania in Sweden (see also Angelin 1854; Månsson 1995), in Bornholm, and in Latvia (Blidene Marls) (Ahlberg 1995b). Whilst most species occur in shales and/or intercalated dark grey limestones, two are known from pure limestone facies. *Telephina bicuspis* occurs in the Folkeslunda Formation of Öland, the Uhaku Stage ($C_{I}c$) of western Latvia, the Elnes Formation in the Oslo Region (Bruton & Høyberget 2006), and in the Andersö Shale in Jämtland (Ahlberg 1995a, b). *Telephina bicuspis* is the most common species of *Telephina* from geschiebe of the Upper Grey *Orthoceratite* Limestone, which belong to the Lasnamägi Stage ($C_{I}b$) (*Schroeteri*-Kalk, Rudolph 1997, p. 34). *Telephina wegelini*, as interpreted by Ahlberg (1995a, pp. 272–273), occurs in the Fjäcka Shale Formation and is represented by a single specimen in the Boda Limestone Formation (Warburg 1925, p. 90), thus being the youngest known *Telephina* in Baltoscandia. This occurrence of *Telephina* is unusual, because it is neither a typical inhabitant of carbonate mound environments, nor has it been recognized elsewhere in Baltica during this time interval, although another single specimen that may be conspecific has been recorded from the Kildare Limestone Formation, eastern Ireland (Dean 1971, p. 46). Outside Baltoscandia it is known from approximately coeval deposits in Bohemia and Kazakhstan (Dean 1978, p. 112). Before they arrived in Baltica, *Telephina* species inhabited a range of environments in the Precordillera from the Arenig *evae* Biozone (Fl2) to the Caradoc, and in Laurentia from the Llanvirn to the


Super-family
Family
Global stage slices
Regional stages
Genus
Fl1-3
Dp1-3
Dw1
Dw2
Dw3
Sa1
Sa2
Ka1
Ka2
Ka3
Ka4
Hi1-2
Silurian
B$_I$
B$_{II}$
B$_{III}$
C$_I$a
C$_I$b
C$_I$c
C$_{II}$
C$_{III}$-D$_I$
D$_{II}$
D$_{III}$
E
F$_I$a
F$_I$b
F$_I$c
F$_{II}$
Bathyuroidea
Dimeropygidae
Telephinidae
Aulacopleuroidea
Scharyiidae
Aulacopleuridae
Rorringtoniidae
Proetoidea
Tropidocoryphidae
Proetidae
1. Celmus
2. Dimeropyge
3. Paratoernquistia
4. Toernquistia
5. Mesotaphraspis
6. Solariproetus
7. Carolinites
8. Telephina
9. Phorocephala
10. Niuchangella
11. Panarchaeogonus
12. Scharyia
13. Harpidella
14. Cyamella
15. Madygenia
16. Rorringtonia
17. Isbergia
18. Decoroproetus
19. 'Eremiproetus'
20. Dalarnepeltis
21. Stenoblepharum
22. Paraproetus
23. Ogmocnemis
24. Parvigena
25. Ascetopeltis
26. Astroproetus
27. Xenocybe
28. Cyphoproetus
1 2 3 4 5
+
Number of genera per stage
2
1
3
2
3
1
6
6
8
7
6
1
4
22
21
9

Caradoc. Chatterton et al. (1999) described a surprising radical metamorphosis that occurs late in the meraspid period in *Telephina* and suggests that they changed their lifestyle from benthic to pelagic mode (usually the change is in the opposite order). This might explain why *Telephina* had a preference for particular areas or benthic conditions, or facies, and was restricted to one confacies belt in Baltoscandia.

Dimeropygidae

The earliest confirmed dimeropygid, which appears in the Kunda Stage (B_{III}), is *Celmus* Angelin (Jaanusson 1956; Bruton 1983), but two possible representatives, *Celmus*? *insolita* (Tjernvik) from Sweden and *C.*? *longifrons* Poulsen from Bornholm, Denmark, appeared even earlier, respectively in the Hunneberg ($B_I\alpha$; Fl1) and Volkhov (B_{II}; Dp1) stages (Pärnaste 2006). Adrain et al. (2004, p. 235) note that *Celmus* is a member of those Baltic Arenig–Llanvirn trilobite faunas that are common to Laurentia. It is one of the few trilobite genera that cross the Kunda–Aseri (B_{III}–C_Ia) boundary, and has been found in limestones in Östergötland, Öland, St Petersburg region, and in geschiebe in Germany. Bergström & Suzuki (2005) concluded that *Celmus* was a cheirurid, but we do not accept this view.

Dimeropyge Öpik appears in oil shale (Öpik 1937) belonging to the Kukruse (C_{II}) Stage of Estonia and at an equivalent horizon of the lower *Chasmops* Limestone in Jämtland (Thorslund 1940). Whittington & Evitt (1954) revised *Dimeropyge minuta* Öpik, which was established on a pygidium, and associated it with the cranidium attributed by Öpik (1937) to *Toernquistia*? *minuta* (Nieszkowski).

Mesotaphraspis Whittington & Evitt and *Toernquistia* Reed are both known from the Upper Ordovician, the former from the Oslo district, Norway (Owen & Bruton 1980; Owen 1981), and the latter from Sweden (Jämtland and the Siljan District). *Toernquistia* occurs mainly in carbonate mudmounds, and the type species, *T. nicholsoni* (Reed), is known from the Boda Limestone Formation, the Keisley Limestone Formation, northern England (type stratum), and from the Kildare Limestone Formation, eastern Ireland (Dean 1974, p. 65). *Solariproetus* Qu occurs in the Lindegård Mudstone Formation in Scania, and in the '*Dalmanitina* Beds' of Bornholm. *Mesotaphraspis* and *Toernquistia* were placed in a revived Toernquistiidae Hupé by Chatterton et al. (1998) and *Solariproetus* was added by Owens (2004), but Dr J. M. Adrain (pers. comm. to RMO, September, 2005) has prepared a revised phylogenetic analysis of the Dimeropygidae which places toernquistiids in synonymy with them. We follow this classification here.

AULACOPLEUROIDEA

Three family-level taxa are present in Baltoscandia, viz. Aulacopleuridae Angelin, Rorringtoniidae Owens, and Scharyiidae Osmólska. The last-named has been regarded by some authors as a subfamily, by others as a family (see Owens & Fortey in press). Herein, it is treated as a family.

Aulacopleuridae

Aulacopleurid trilobites from Baltoscandia and from geschiebe have been assigned variously to *Harpidella* M'Coy, *Otarion* Zenker, and *Cyphaspis* Burmeister. Following their revision by Adrain & Chatterton (1994, 1996), the latter two are restricted to Silurian and Devonian strata, with only *Harpidella* being represented in the Ordovician. Until these Ordovician species are fully revised, they are placed in *Harpidella* (*s.l.*), following Owen (1981) and Owen & Bruton (1980). This genus occurs in small numbers throughout much of the Upper Ordovician succession.

Rorringtoniidae

Four genera are present in the Ordovician of Baltoscandia: *Rorringtonia* Whittard, *Cyamella* Owens, *Isbergia* Warburg, and *Madygenia* Petrunina. The first-named occurs at two horizons: in the lower *Chasmops* Shale (Owens 1970, p. 329), now termed as the Arnestad Formation in the Oslo district (Owen et al. 1990), and in the Lindegård Formation in Scania (Owens 2004). *Cyamella* is confined almost exclusively to the Boda

Table 1. Stratigraphical distribution of genera of Proetida, for which the locality data are divided into five Baltoscandian Confacies Belts (Jaanusson 1982a, 1995), from top to bottom, for each genus: 1, Oslo Confacies Belt; 2, Scanian Confacies Belt; 3, Central Baltoscandian Confacies Belt; 4, geschiebe (most material probably originating from the previous belt); 5, North Estonian Confacies Belt. Continuation into the Silurian, marked with the plus sign, relates to genera worldwide. Correlation within Baltoscandia is based on Nõlvak et al. (2007), Ebbestad & Högström (2007), and Owen et al. (1990), and with global stage slices on Bergström et al. (in press). Note that the range bars show the presence on unit level and are not limited to show on a more precise level. Abbreviations for regional stages: B_I, Hunneberg–Billingen; B_{II}, Volkhov; B_{III}, Kunda; C_Ia, Aseri; C_Ib, Lasnamägi; C_Ic, Uhaku; C_{II}, Kukruse; C_{III}-D_I, Haljala; D_{II}, Keila; D_{III}, Oandu; F_Ia, Nabala; F_Ib, Vormsi; F_Ic, Pirgu; F_{II}, Porkuni; and for global stage slices: Fl, Floian; Dp, Dapingian; Dw, Darriwilian; Sa, Sandbian; Ka, Katian; Hi, Hirnantian

Limestone Formation, where it has been found in vast numbers in cavities (Owens 1979; Suzuki & Bergström 1999; Popp & Pärnaste 2008a), with a single earlier record from a limestone erratic of the Moldå Formation from Öland. *Isbergia* occurs in the Boda Limestone Formation (Warburg 1925; Owens 1979) and in the Bønsnes Formation in Ringerike, Oslo district, Norway (Owens 1979; Owen 1981). *Madygenia* is restricted to one cranidium from the Hirnantian Loka Formation, Ålleberg, Västergötland (Owens 2004).

Scharyiidae

The earliest confirmed species of *Scharyia* Přibyl, *S. heothina* Owens, occurs in the Boda Limestone Formation (see Owens 1974). *Panarchaeogonus parvus* Öpik and *P. atavus* Öpik from the Kukruse Stage, Estonia, were synonymized by Owens (1979), who also included Öpik's *Otarion* sp. a (Öpik 1937, p. 29, pl. 3, fig. 7). This synonymy is followed here. The pygidium figured by Öpik (1937, pl. 4, figs 1, 2, 6) as *Toernquistia*? *minuta* (Nieszkowski), which occurs together with cephala of *P. parvus*, may prove to belong to this species. *Panarchaeogonus phylzacius* Owens from the lower *Chasmops* Shale and Limestone (Owens 1979), or from the Arnestad and Frognerkilen formations, respectively, in the Oslo district (Owen et al. 1990) and *P. holmi* (Warburg) from the Boda Limestone Formation were transferred to the closely related scharyiid *Niuchangella* W Chang by Adrain & Chatterton (1993, p. 1636). *Panarchaeogonus* Öpik and *Niuchangella* both have been recorded from outcrops of the Boda Limestone Formation and also from Upper Ordovician geschiebe at Hulterstad on Öland (Owens 1979, p. 206). One cranidium of *Panarchaeogonus* has been collected by the second author of this paper in a geschiebe of the so-called 'brick-limestone' (Backsteinkalk), Darriwilian (Popp 2007). It is the oldest representative of the family known from Baltoscandia.

PROETOIDEA

This superfamily includes the 'typical proetids', which morphologically have a rather conservative style. Owens (1973) listed 29 species, of which 17 are known from the carbonate mound facies (Kullsberg Limestone, Boda Limestone) and 12 from other facies. All were included in the Proetidae Salter, mostly in the subfamilies Proetinae Salter and Tropidocoryphinae Přibyl. It is now apparent that the latter should be accorded family-level status. Thus restricted, the Proetidae are represented by a comparatively small number of taxa, whilst Tropidocoryphidae are more widespread, and with a far greater number of species. Many of the latter have been attributed to *Decoroproetus* Přibyl, but this genus has been used in a very broad sense, and certainly includes a number of different taxa (Owens 2004). Some of these are placed in the Cornuproetinae Richter, Richter & Struve. We here follow Jell & Adrain (2003) in placing this subfamily in the Tropidocoryphidae Přibyl.

Proetidae

Three genera of Proetidae occur in the Upper Ordovician (Ka4): *Astroproetus* Begg in the Boda Limestone Formation, *Xenocybe* Owens in late Upper Ordovician strata in the Oslo district, Norway, and *Cyphoproetus* Kegel in both (Owens 1973).

Tropidocoryphidae

Decoroproetus (*s.l.*) is widespread, being present in small numbers throughout much of the Upper Ordovician, and is common in the Fjäcka Shale Formation and in pockets in the Boda Limestone Formation (Owens 1973; Suzuki & Bergström 1999). It is included in the Tropidocoryphinae. *Stenoblepharum* Owens, *Ogmocnemis* Kielan, *Ascetopeltis* Owens, *Paraproetus* Přibyl, and *Parvigena* Owens are all attributed to the Cornuproetinae. *Stenoblepharum* includes the earliest tropidocoryphids (and Proetoidea) from Baltoscandia, being present in geschiebe of Red *Orthoceratite* Limestone, of late Darriwilian age, from northern Germany (Popp & Schöning 2006). It is represented in the Viivikonna Formation (Sa1), Kullsberg Limestone Formation (Ka1), Langåra Formation (Ka4–Hi1), and is especially abundant in the Boda Limestone Formation (Ka4–Hi1). The earliest *Ogmocnemis* occur in the Nakkholmen and Furuberget formations (Ka1) in the Oslo district and range up to Ka4 in Baltoscandia. '*Proetus*' *kertelensis* from the Vormsi Stage (F_Ib; Ka3), Hiiumaa, belongs to an undescribed cornuproetine genus. *Ascetopeltis* and *Paraproetus* are mostly restricted to the late Upper Ordovician, stage slice Ka4, although the former is also present in the Porkuni Stage (F_{II}), Hi1–Hi2. '*Proetus*' *ramisulcatus* Nieszkowski, which belongs to a second undescribed cornuproetine genus, is restricted to this stage.

DISTRIBUTION AND DIVERSITY PATTERNS

The first summary of trilobite distribution in Baltoscandia was that of Schmidt (1907). Ralf Männil (1962) published a table showing the distribution of 13 genera that occur in the Upper Ordovician and Lower Silurian succession of northern Estonia, with gradual increase from 7 genera in the Oandu Stage (D_{III}) to 13 in the Porkuni Stage (F_{II}) (only 2 of them are Proetida); there is a sudden decrease to 3 genera at the Silurian boundary. Later, Reet Männil (1992) published a revised version which also included genera from other facies belts. She showed that the terminal Ordovician extinction was stepwise, starting from the late Caradoc through the Ashgill, and that it was different in two adjacent facies belts in the East Baltic. In the northern Estonian near-shore facies, the diversity decrease was insignificant, with two out of three genera crossing the Pirgu–Porkuni boundary, but in the Latvian Depression most genera disappeared and were replaced by the low-diversity, cosmopolitan *Mucronaspis* [*Dalmanitina*] fauna. Species-level trilobite diversity through the Ordovician shows two major increases, one in the Aseri Stage (C_Ia) and the other in the Kukruse Stage (C_{II}) (Männil 1966; Männil et al. 1966). The same peaks are traced when including data from Sweden and Norway (Hammer 2003; Hammer in Adrain et al. 2004). Similar trends can be followed in the genus level compilation of Rõõmusoks (1997).

These diversity changes are reflected in the Proetida from the point at which they appeared, when one to two (possibly 3) genera per stage occurred in the basin. Then from the Kukruse (C_{II}) to Rakvere (E) stages (or Sa1–Ka1, or Caradoc), 6 to 8 genera occurred and after a short reduction to one and four genera from the Nabala (F_Ia; Ka2) and Vormsi (F_Ib; Ka3) stages there was a sudden increase to 22 genera in the Pirgu–Porkuni (F_Ic–F_{II}; Ka4–Hi2) interval (Table 1). Interestingly, the brief reduction in the number of genera in the Nabala Stage involves only the Proetida; the total number of trilobite genera (including Proetida) is 20 for the Rakvere Stage, 18 for the Nabala Stage, and 19 for the Vormsi Stage (see Rõõmusoks 1997, pp. 236–237, table 38). Against a background of an essentially stable level of diversity of Proetida, with two stepwise rises (at Sa1 and Ka4), a few new genera appeared, whilst some became extinct. Of the 22 genera present in the late Pirgu–late Rawtheyan, excluding those in the Boda Limestone, five (two bathyuroids, three cornuproetines) do not occur in later Ashgill strata. Assuming that the ranges of all 14 genera recorded from the Boda Limestone extend into the uppermost, Hirnantian part of the formation, nine disappear at the HA regression (for Lowstand HA see Bergström et al. 2006). Nine genera of Proetida that occur in Baltoscandia survive into the Silurian. The end Ordovician mass extinction resulted in the trilobites losing about half their global taxonomic diversity (Adrain et al. 2004); this is reflected broadly in the case of Baltoscandian Proetida. Of these, the Bathyuroidea became extinct, whilst Aulacopleuroidea lost three out of eight genera, and the Proetoidea seven out of eleven. This general pattern is repeated in other areas.

In conjunction with Avalonia

Owen (2007) analysed changes in trilobite diversity through the Ordovician of Avalonia and showed that in contrast to elsewhere, it reached a peak immediately prior to the Hirnantian extinction event, rather than in the Caradoc or earlier. His data (Owen 2007, fig. 1A) record five genera of Proetida in the Cautleyan–Rawtheyan stages (Ka4) that have an earlier history in Avalonia. Of these, *Dimeropyge*?, *Toernquistia*, and *Panarchaeogonus* occur in the lower Caradoc (first in Sa1, two others in Sa2), but are absent from the intervening upper Caradoc and lower Ashgill. Other genera in this category, *Ogmocnemis* (included in the range of *Decoroproetus* by Owen 2007) and *Harpidella* (*s.l.*), occur sporadically throughout the succession. Other genera of Proetida, for example *Ascetopeltis*, *Paraproetus*, and *Stenoblepharum*, in Avalonia do not have a pre-mid Ashgill history in the region.

In Baltoscandia Proetida show an increase in diversity similar to that in Avalonia. There are similar gaps in the records of, for example, *Toernquistia* (assuming that the closely related *Paratoernquistia* is synonymous), which occurs in the Lower *Chasmops* Limestone (Sa1–Sa2) of Jämtland and the Kullsberg Limestone Formation (Ka1) of Dalarna and recurs in the Boda Limestone Formation (Ka4–Hi2). The scharyiids *Panarchaeogonus* and *Niuchangella* show a similar pattern, but are more widespread geographically. The latter occurs in the Arnestad and Frognerkilen formations of the Oslo Region and the former in the Estonian oil shale (Viivikonna Formation, Sa1). Both disappear from the record until the Rawtheyan and lower Hirnantian stages (the upper part of Ka4 and Hi1), but do not range up to the Ordovician–Silurian boundary.

Ascetopeltis occurs in the mid-Ashgill (Cautleyan Stage, the lower part of Ka4) of Avalonia. If '*Proetus*' *kertelensis* from the Vormsi Stage (F_Ib; Ka3) belongs to its ancestral stock, this genus might have immigrated into Avalonia from Baltica. Owen (2007, p. 267), however, referred to a Laurentian origin for *Ascetopeltis*. His suggestion that *Ascetopeltis* may have had a Laurentian ancestry arose from the comment by Owens (1973) that its origins may lie in *Cyphoproetus*. That genus had an earlier history in the Girvan district, which was located on a terrane that lay on or close to the Laurentian margin during the Ordovician (Dr A. W. Owen pers. comm., November, 2008). A Laurentian source is thought to be most likely for *Dimeropyge*, made possible by a narrowing Iapetus during the Ordovician (Chatterton 1994, p. 545; Yuan et al. 2006, p. 541). The earliest *Dimeropyge* from Baltoscandia (from the Kukruse and Haljala stages, C_{II}–C_{III}-D_I; Sa1–Sa2) are of about the same age as those from Avalonia, and the presence of *Dimeropyge*?

ericina Adrain & Fortey in the Arenig Tourmakeady Limestone of western Ireland indicates a Laurentian origin for the genus. The same applies to *Celmus*, which appears in the Kunda (B_{III}) and Aseri (C_I) stages of the Middle Ordovician in Baltoscandia and is also present in the Tourmakeady Limestone (Adrain & Fortey 1997).

DISTRIBUTION WITHIN THE CONFACIES BELTS

When genera are plotted according to their stratigraphical occurrence (Table 1), two time intervals show levels of stepwise rise to a higher diversity of Proetida. In Fig. 1A, B these were plotted on distribution maps in order to illustrate facies dependence and areas of preference.

Six genera are recorded in the early Upper Ordovician (Kukruse Stage, C_{II}, *gracilis* Biozone, Sa1) (Fig. 1A). *Telephina*, a genus adopted to an epipelagic lifestyle (Fortey 1975), is common in the deeper-water areas of the Oslo and Central Baltoscandian confacies belts (abbreviated CB hereafter). Ahlberg (1995a) concluded that in Baltica and Laurentia at least, *Telephina* is restricted to the periphery of the continental plates, and so far, there are no known occurrences from nearshore sequences. *Dimeropyge* is known from the offshore Central Baltoscandian CB and nearshore North Estonian CB. If the pygidium figured by Öpik (1937, pl. 4. figs 1, 2, 6) as *Toernquistia*? *minuta* (Nieszkowski) belongs to *Paratoernquistia* Chatterton et al., then this genus is also known from both areas. *Harpidella* (*s.l.*) and *Stenoblepharum* are recorded only from the Northern Estonian CB during the Kukruse Stage. However, the latter is known from both older and younger beds from geschiebe, suggesting that it was present in a range of environments. The most favourable area for Proetida during the Kukruse Age was in algal-rich shallow-water carbonates in the Northern Estonian CB.

The second time interval (Fig. 1B) comprises the Pirgu Stage (F_Ic; equivalent to the Cautleyan–Rawtheyan stages and Ka4) and the Porkuni Stage (F_{II}; equivalent to the Hirnantian and Hi1–Hi2). Note that here the Boda Limestone Formation includes strata of Pirgu and Porkuni age following e.g. Jaanusson (1982b), Ebbestad & Högström (2007), and Schmitz & Bergström (2007). However, there are ongoing discussions on the upper limit of this formation. Suzuki & Bergström (1999) suggest it possibly reaches into the Silurian. Other authors argue that findings of the brachipod *Holorhynchus* Kiaer in the flank deposits of the upper part of the Boda Limestone in Osmundsberget (Jaanusson 1982b) with low carbon isotope values prove it is pre-Hirnantian (Brenchley et al. 1997). In contrast to the previous interval, it shows different centres of diverse trilobite occurrences: the Lake Siljan area and the Oslo Region. Of the 28 Ordovician genera of Proetida identified in Baltoscandia, 14 (*Astroproetus*, *Cyamella*, *Dalarnepeltis* Přibyl & Vaněk, *Decoroproetus*, *Isbergia*, *Niuchangella*, *Panarchaeogonus*, *Parvigena*, *Scharyia*, *Stenoblepharum*, *Toernquistia*, *Cyphoproetus*, ‘*Eremiproetus*’, and *Telephina*) have been recorded from the Boda Limestone Formation in Siljan. These carbonate mudmounds can be subdivided into a so-called core facies (see Suzuki & Bergström 1999; Ebbestad & Högström 2007), containing different types of ‘pockets’, and a ‘flank facies’ (here taken as synonymous to ‘off reef’ of Owens 1973; see Suzuki & Bergström 1999; Ebbestad & Högström 2007) characterized by marly limestones. Of the genera listed above, *Decoroproetus* and *Stenoblepharum* are abundant in the ‘core facies’ (see Owens 1979, table 2) and *Cyamella* occurs very abundantly in so-called pockets (see Suzuki & Bergström 1999) within the ‘core facies’. Only *Stenoblepharum warburgae* Přibyl is reported from both facies types from the Boda Limestone. Elsewhere *Ascetopeltis bockeliei* Owens is found within the ‘flank facies’ of the Boda Limestone in Dalarna and also in Östergötland (Jonstorp Formation) and the Oslo district (Langåra Formation), with a similar, unnamed species (Owens 1973, pp. 129–130) in the Ärina Formation, Porkuni Stage, Estonia.

The algal-rich carbonates of the Langåra and Bønsnes formations in the Oslo district share several taxa with the Boda Limestone Formation, for example *Stenoblepharum*, *Cyphoproetus*, ‘*Eremiproetus*’, and *Isbergia*. In the two last-named genera the same species is represented. A number of taxa are also shared with the Keisley Limestone Formation of northern England and the Kildare Limestone Formation of eastern Ireland, both carbonate mudmound deposits (see Dean 1978). This facies has yielded the most diverse faunas of Proetida from the Ordovician anywhere. *Paraproetus*, *Ogmocnemis*, and *Harpidella* (*s.l.*) occur more sporadically in the Central Baltoscandian and Oslo confacies belts, but are absent from carbonate mudmounds.

Representatives of the Proetoidea are the dominant element on this map. Of these *Ascetopeltis* is present in all three major confacies belts (Oslo, Central Baltoscandian, and North Estonian CBs), indicating perhaps a latitudinal rather than a facies-bound distribution. *Ascetopeltis* appears to be the most widely distributed genus of the Proetoidea during that time in Baltoscandia. Records of the genus from geschiebe (Neben & Krueger 1979, pl. 139) and erratic boulders (Rhebergen 2001, p. 41) point to a probable wider distribution than indicated by data from existing outcrops. *Ascetopeltis* also occurs in Avalonia (see above).

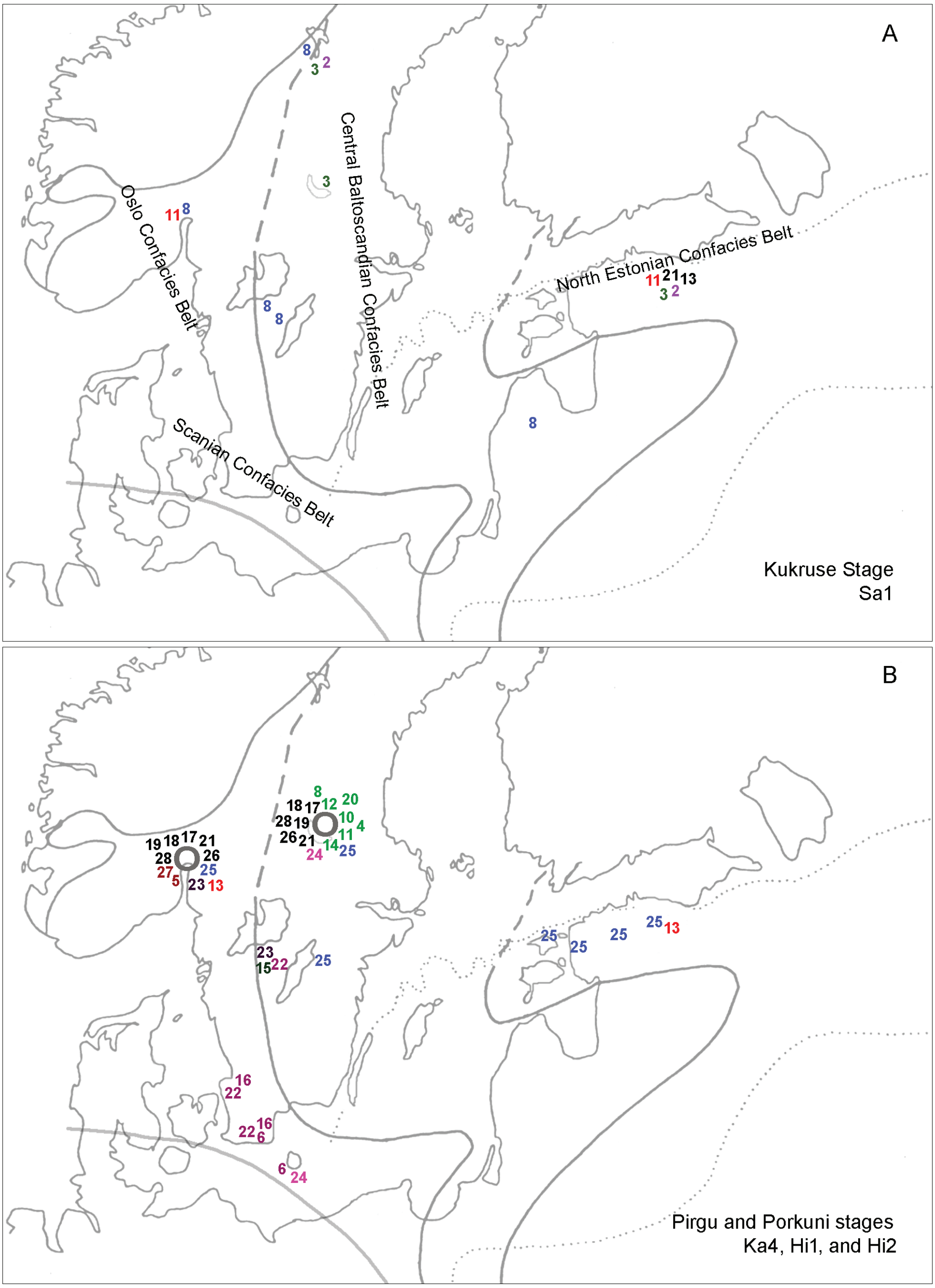


Fig. 1. Distribution maps of genera (numbering follows that in Table 1) on the Baltoscandian Confacies Belt map (modified after Jaanusson 1982a, 1995), showing facies preferences of different genera. (A) Kukruse Stage (C_{II}; or Global Stage Slice Sa1); (B) Pirgu and Porkuni stages (F_{I}c and F_{II}; or stage slices Ka4 and Hi1–Hi2) (see Bergström et al. in press). The Pirgu and Porkuni stages are taken together, considering that the Boda carbonate mounds accumulated throughout most of that period (Jaanusson 1982a, b; Suzuki & Bergström 1999) and the precise interval of occurrences is often unknown.

Stenoblepharum seemingly made a shift from its former more restricted occurrence within the North Estonian CB (Fig. 1A) to a wider distribution within the Central Baltoscandian CB and the Oslo CB. But its occurrence in mid-Darriwilian geschiebe of Red *Orthoceratite* Limestone (Popp & Schöning 2006) indicates its presence at that time within the Central Baltoscandian CB. As in the case of *Ascetopeltis*, there may be a latitudinal trend (Fig. 2B), but this might also be related to the presence of *Stenoblepharum* in (different) carbonate facies (Owens 1979, table 2). This idea is supported by observations by Owen (2007, fig. 1), who included *Stenoblepharum* in immigrant taxa restricted to pure carbonates in Avalonia.

Rorringtonia and *Solariproetus* seem to be restricted to the Scanian CB, being collected from the deeper-water Lindegård Mudstone Formation. The first appears in the Shelve Inlier, Shropshire, in the lower Caradoc (Sa1), with younger Ordovician species from the *Staurocephalus* Beds in Scania; the second occurs in the late Ashgill of the Holy Cross Mountains, Poland, and the English Lake District (Owens 2004). A third genus, *Paraproetus*, is recorded from the same areas in the late Ashgill, as well as in Västergötland in the Central Baltoscandian CB. These genera occur in the most offshore environment.

Madygenia is interesting in its palaeogeographical occurrence. Its origin appears to be in the late Caradoc–early Ashgill of the northern Alai Ridges, Uzbekistan–Kyrgyzstan borders. In the early Ashgill *Madygenia* occurred in South China. Thereafter it reached Sardinia by the late Ashgill (Rawtheyan) and soon afterwards Baltoscandia, together with other globally dispersed Hirnantian fauna. One specimen has been recorded from the *Dalmanitina* Beds (Loka Formation, Porkuni Stage, Hirnantian). *Madygenia* survived the end-Ordovician extinction event and is known from the Silurian of northern England (Owens 2004).

CONCLUSIONS

Diversity patterns of about 30 genera with more than 70 species of Proetida in Baltoscandia studied over 150 years have been analysed. The first representatives of this trilobite order in the region appeared in the Billingen Stage ($B_I\beta$–$B_I\gamma$), or possibly earlier in the Arenig. In the background of stepwise increase in genera, two diversity peaks occurred in the Ordovician, the first in the Kukruse Stage (C_{II}), and the second in the Pirgu–Porkuni stages (F_Ic–F_{II}). Nine proetide genera out of 21 occurring in the Pirgu Stage (F_Ic) survived the end-Ordovician extinction event. In the background of the global extinction of Bathyuroidea, the survivors included Proetoidea and Aulacoplauroidea.

The influx of pelagic genera into Baltoscandia was possibly related to eustatic events. The common palaeogeographical occurrence of *Carolinites* in the Ordovician tropical regions is explained by their epipelagic and active surface swimming lifestyle (Fortey 1975). Rare occurrences of this genus in higher latitudes, like in Baltica, and even farther towards the South Pole, in the Montagne Noire, France, and in Turkey, have been explained by gyres originating from the equatorial current that moved southwards (McCormick & Fortey 1999). An additional factor could be the Evae Drowning Event (see Nielsen 2004) (Fl2), supporting the widespread migration and arrival of new faunal elements. The second arrival of pelagic Proetida (*Telephina*) came with the Furudal Highstand during the Uhaku Age (C_Ic). The largest Phanerozoic eustatic highstand, in Caradoc times (Hallam 1992) (starting from the Kukruse Age; C_{II}), introduced a new wave of benthic immigrants.

The most diverse fauna of trilobites and other organisms occurs in the Boda mudmounds. This environment provided a wide range of habitats, coupled presumably with a rich food supply, and supported 14 genera of Proetida, some of which are restricted to it. Opinions on the climatic conditions under which the Boda Limestone Formation was deposited vary from global warming (the ‘Boda Event’; see Fortey & Cocks 2005) to a general cooling (Cherns & Wheeley 2007). The top of the formation is of early Hirnantian age, following Jaanusson (1982a, b) and Schmitz & Bergström (2007, p. 135), when carbonate deposition continued at the latitudes (30° S and less) of Baltica, Avalonia, and eastern Laurentia. Although general cooling is indicated by the Hirnantian isotopic carbon excursion (HICE; see Schmitz & Bergström 2007), this environment continued to support diverse faunas. The Ärina Formation in northern Estonia, although contemporaneous with the upper part (Hirnantian) of the Boda Limestone Formation, yields a different fauna of Proetida, dominated by ‘*Proetus*’ *ramisulcatus* and *Ascetopeltis* sp. Neither of these species is represented in the Boda Limestone, although the latter occurs in the flank facies. No Proetida have been recorded in the Saldus and Kuldiga formations of southern Estonia, which have yielded a typical *Hirnantia* association (Kaljo et al. 2008), with *Mucronaspis* Destombes and *Brongniartella* Reed. Only one genus of Proetida, *Madygenia*, is recorded from later Hirnantian strata in Baltoscandia (Owens 2004). With the termination of carbonate mound deposition by the HA regression that resulted from the first of the Hirnantian glacial episodes (Schmitz & Bergström 2007), the rich fauna of Proetida disappeared from the region, and many genera became extinct.

During the Ordovician Baltica moved progressively closer to the tropics, and lay about 30° S by the end of the period (Cocks & Torsvik 2002). Its anticlockwise rotation led to approximate latitudinal alignment of the points corresponding to the present-day sampling sites in the Oslo, Central Baltoscandian, and N Estonian confacies belts, all of which were located in a 'belt' about 300 km wide, oriented in a north–south direction, corresponding to 2°–3°. The distribution of genera of Proetida shows a pattern of occurrences seemingly limited by latitude. Some genera pass through (W–E) all confacies belts and some only adjacent ones, but do not occur in much higher or lower latitudes. This may show a possible adaptation to very restricted, temperature-related environmental conditions, which might have been prevalent in the area due to global cooling. However, because of the very sparse coverage of data over the sample area, this assumption must remain provisional.

In general, understanding of the global palaeogeographical distribution and migrations of Proetida during the Ordovician needs further study, with careful checks of systematic identifications and stratigraphical information, although it is well known that the Boda Limestone Formation, the Keisley Limestone Formation, northern England, and the Kildare Limestone Formation, eastern Ireland, share common faunas (e.g. Dean 1978) including Proetida, and all three were deposited at a similar latitude (e.g. Fortey & Cocks 2005). In addition, this study confirms that there was some influx of pelagic proetide taxa that are common in the Laurentian Bathyurid Province during the Floian. At this time connection with Laurentian faunas is also apparent in some trilobites belonging to other orders (Hoel 1999; Pärnaste 2006), planktic acritarch assemblages (Servais et al. 2005), and epipelagic graptolites (Cooper et al. 1991). During the later Ordovician ever increasing numbers of faunal exchanges between Baltica and Avalonia occurred, due to the progressive narrowing of the Tornquist Sea, leading up to its ultimate closure and the soft docking of the two.

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Trilobiidiseltsi Proetida levik Baltoskandia Ordoviitsiumi läbilõikes

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Trilobiidiselts Proetida moodustab väikese, kuid mitte vähetähtsa faunaelemendi Baltoskandia Ordoviitsiumi läbilõikes. Suure hulga antud regiooni trilobiite käsitleva publikatsiooni põhjal on kogutud liigi tasemel andmebaas. Lisaks Skandinaavia ja Baltimaade andmetele on liidetud ka andmed Põhja-Saksamaal ning selle ümbruskonnas levivatest glatsiaalsetest rändpangastest ehk nn *geschiebe*'dest. Järgides tänapäevast süstemaatikat, taksonoomiat ja stratigraafilist baasi, on antud ülevaade nende trilobiitide eri perekondade levikust erinevas settekeskkonnas läbi Ordoviitsiumi.

Nimetatud piirkonnas on esindatud Proetida kõigi kolme ülemsugukonna esindajad (Bathyuroidea, Aulacopleuroidea ja Proetoidea) kokku üle 70 liigiga umbes 30 perekonnast. Nad ilmusid Billingeni eal (või isegi veidi varem) ja enamasti mõne perekonna kaupa lademe kohta, vahetades välja mõne varasema, nii et mitmekesisus püsis enam-vähem stabiilne. Erandiks olid kaks taset, Kukruse ja Pirgu iga, kus toimus hüppeline mitmekesisuse suurenemine. Kõige rikkalikuma proetiidifaunaga Pirgu ja Porkuni eal elanud 21 perekonnast vaid 9 elasid üle Ordoviitsiumi lõpu jäätumise ning on esindatud Siluri läbilõikes. Samas suri ülemsugukond Bathyuroidea välja. Selles levikupildis on sarnasusi proetiidide levikupildiga Avalonias, mis näitab kas otsest või kaudset ühendust selle piirkonnaga.

Neid kaht ülalmainitud taset settekeskkonda iseloomustava fatsiaalvööndite mudeli taustal võrreldes selgub, et proetiidide levikupildid on neis erinevad. Kui esimesed proetiidid, mis Balti paleobasseini jõudsid, olid globaalse levikuga pelaagilise elustiiliga ja nende ilmumine langes kokku globaalse meretaseme tõusuga – *evae*-sündmusega, siis bentiliste proetiidide esimene hüppeline mitmekesistumine langeb kokku Fanerosoikumi suurima eustaatilise kõrgtasemega Kukruse eal. Seejuures esineb suurim mitmekesisus eelkõige Põhja-Eesti fatsiaalses vööndis, kus põlevkivide settealal oli tõenäoliselt rikkalik toiduallikas vetikate ja muu elustiku näol selle üheks faktoriks. Suurim Ordoviitsiumi ajastu proetiidide mitmekesisus on aga teada Oslo ja Kesk-Baltoskandia (Siljani piirkond) fatsiaalvööndeist Pirgu eal, kui regioon paiknes paleoekvaatori lähedal ning kus globaalsele jahenemisele vaatamata kihas äärmiselt rikkalik elustik, mis kajastub praegu Boda litohermis.

PAPER III

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First record of *Telephina* (Trilobita) from the Ordovician of northeastern Estonia and its stratigraphical implications

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Abstract. For the first time a telephinid trilobite was recorded from the shallow-water rocks of the North Estonian Confacies Belt in the oil-shale mining area of northeast Estonia. A cranidium of *Telephina* (*Telephops*) *biseriata* (Asklund) was collected from a loose boulder of the kerogenous limestone of the Viivikonna Formation, Kukruse Stage, together with a rich assemblage of other trilobites, bryozoans, ostracods and rare graptolites. In its type area Jämtland, Sweden, *T. biseriata* occurs together with *Pygodus anserinus* and *Hustedograptus teretiusculus* in the Ståltorp Limestone Member of the Andersö Shale Formation, marking the latest Darriwilian. The occurrence in the North Estonian Confacies Belt of *Telephina*, known as a pelagic trilobite inhabiting deeper-water areas, probably reflects a transgression event at this time. Together with *T. biseriata*, other trilobite taxa such as *Remopleurides* and *Lonchodomas*, common in the *Hustedograptus teretiusculus* Biozone in deeper-water areas, arrive in the North Estonian Confacies Belt. Graptolites from the other loose boulders at the same locality have been identified as *Hustedograptus* cf. *uplandicus*, which occur together with a few dendroids.

Key words: Ordovician, Baltoscandia, Viivikonna Formation, Kukruse Stage, trilobites, *Telephina*.

INTRODUCTION

A relatively large cranidium of *Telephina* (*Telephops*) *biseriata* (Asklund, 1936) with a partly preserved test was found when collecting small proetid trilobites during fieldwork in the summer of 2010. It comes from a loose boulder on the tip-heap of the Sompa mine, Kohtla-Järve, where kerogen-rich limestone is mined for oil production. This oil shale is well known from its very abundant faunal assemblage, which includes about fifty trilobite species that have been studied since the beginning of the 19th century. This is the first record of *Telephina* Marek, 1952 from this area, and from Estonia in general.

In Baltoscandia *Telephina* first appears in marls of the lower Darriwilian Helskjer Member (Kunda Regional Stage) in the Mjøsa area of Norway (Nikolaisen 1963; Hansen 2009), and is widely distributed within the late Darriwilian fine-grained rocks. A few records are known from the lower Sandbian, and the latest from the Boda Limestone of latest Katian or possibly Hirnantian age (e.g. Nikolaisen 1963; Ahlberg 1995a, 1995b; Hansen 2009; Pärnaste et al. 2009). Nikolaisen (1963) described a case of explosive evolution of *Telephina* in the dark shales of the Elnes Formation (formerly *Ogygiocaris* Series) of Norway and coeval strata in Scandinavia, and concluded that they were adapted to waters low in oxygen. Altogether at least 15 species have been identified from the Ordovician of Norway (Nikolaisen 1963; Wandås 1984; Bruton & Høyberget 2006; for synonymy see Ahlberg 1995a; Hansen 2009), many of which occur in contemporaneous beds in different areas of Sweden (Hadding 1913a, 1913b; Thorslund & Asklund 1935; Asklund 1936; Ahlberg 1995a; Månsson 1995). In addition, some rare occurrences are known from drill cores of Latvia and of the Pskov district of western Russia (Männil 1963; Ahlberg 1995b). Following Nikolaisen, Ahlberg (1995a) noted that in Baltica and Laurentia *Telephina* was restricted to the periphery of the continental plates, and so far, there are no known occurrences from nearshore sequences. A new find of this genus in the North Estonian Confacies Belt may reflect a sea-level highstand. However, most of the specimens are preserved in calcareous lenses and interlayers or concretions within the shales (e.g. Bruton & Høyberget 2006), as well as in some thicker carbonate beds such as the Ståltorp Limestone Member of the Andersö Shale in Jämtland (Månsson in Pålsson et al. 2002). Occurrences are also known from limestones of the Killeröd Formation in Scania, southern Sweden (Månsson 1995), and in the Vollen Formation (formerly *Ampyx* Limestone) in Norway (Nikolaisen 1963). Therefore the appearance of *Telephina* in the North Estonian Confacies Belt is not totally unexpected (Fig. 1).

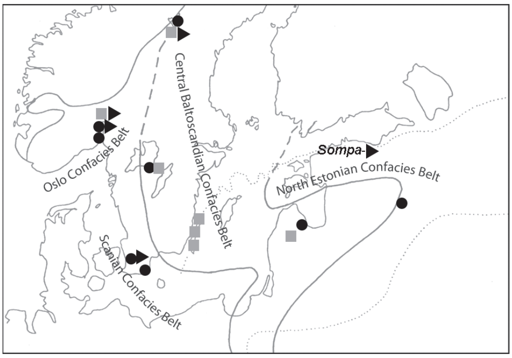


Fig. 1. Map of Baltoscandian confacies belts showing occurrences of *Telephina*. Grey squares indicate occurrences of *Telephina* (*Telephina*); black triangles show species of *Telephina* (*Telephops*) with the anterior glabellar spines situated close to each other, and black circles mark those with the wider space between the anterior glabellar spines.

Material used in this study (trilobites and graptolites) is deposited in the collections of the Institute of Geology at Tallinn University of Technology (repository acronym GIT). The trilobite specimen (not the graptolites) was whitened with magnesium oxide before photographing. The terminology used herein follows that of Whittington & Kelly (1997).

SYSTEMATIC PALAEONTOLOGY

Order PROETIDA Fortey & Owens, 1975
Family TELEPHINIDAE Marek, 1952
Genus *Telephina* Marek, 1952

Type species. *Telephus fractus* Barrande, 1852 from the Katian–Hirnantian (Ashgill) Králův Dvůr Formation, Bohemia, Czech Republic.

Diagnosis. See Nikolaisen (1963), Ahlberg (1995a) and Hansen (2009).

Remarks. A short-lived group of Baltoscandian *Telephina* species characterized by a pair of spines on the frontal part of the glabella was assigned by Nikolaisen (1963) to his subgenus *Telephina* (*Telephops*). Other workers considered that this character is only of specific significance (Tripp 1976; Ahlberg 1995a; Hansen 2009), but we agree with Chatterton et al. (1999), who argued on the basis of ontogenetic studies that this feature may have a higher value in the taxonomy of these trilobites. The paired glabellar tubercles appear in their early life stages, and these are reduced during the ontogeny (Chatterton et al. 1999). A different case is with the paired spines, developed in the most frontal part of the glabella on *Telephina* (*Telephops*). The possible meraspid stage of one of the Scandinavian telephinids, designated as *Fialoides antiquatus* Hadding, 1913b, shows no tubercles and most probably represents *Telephina* (*Telephina*). The anterior glabellar spines likely are derived from the glabellar tubercles, which are known in the other meraspid telephinids. This group occurs together with spineless forms (Fig. 1). Thus it shows no geographic or lithostratigraphic variety, and we consider *Telephina* (*Telephops*) as a valid taxon.

Subgenus *Telephina* (*Telephops*) Nikolaisen, 1963

Type species. *Telephus granulatus* Angelin, 1854 from Norway (for comments, see Ahlberg 1995a, p. 274).

Diagnosis. See Nikolaisen (1963).

Telephina (*Telephops*) *biseriata* (Asklund, 1936)
Figure 2

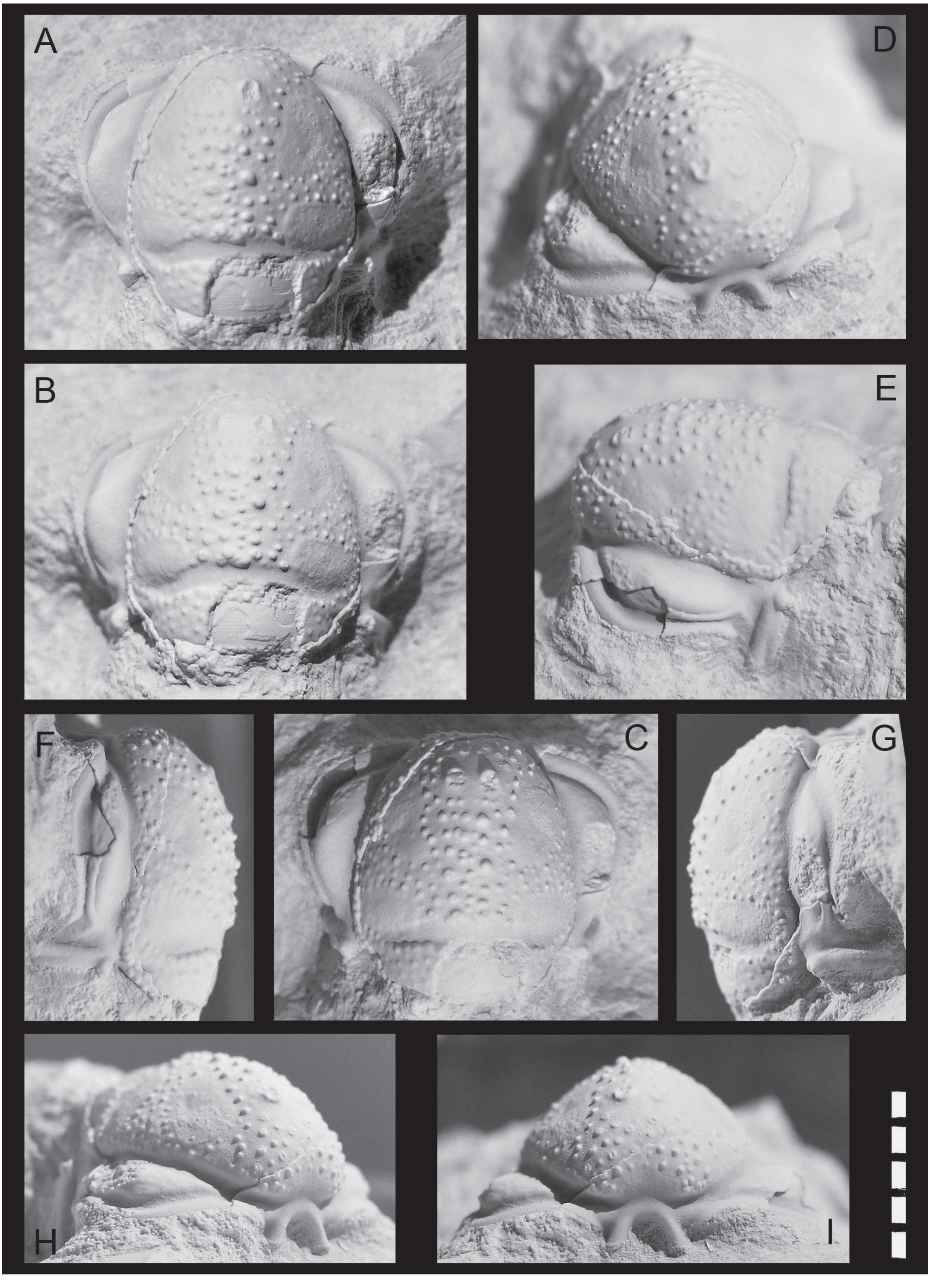
Synonymy. See Ahlberg (1995a, p. 277).

Material. A partly exfoliated cranidium (GIT 360-335). It is preserved in light terracotta-brown kerogenous limestone of the Kukruse Stage from the tip-heap of the Sompa mine, near Kohtla-Järve, northeastern Estonia.

Diagnosis. See Ahlberg (1995a).

Description. Length of cranidium (sag.) about 0.85 times its width, and fixigena narrow (tr.), occupying 18 per cent of the cranidium at its maximum width; anterior border convex in profile, also curving antero-ventrally; glabella highly convex, medially 1.15 times longer than its maximum width at the occipital furrow, and truncate in front. The surface sculpture of glabella including the occipital ring consists of relatively large tubercles, except for three pairs of smooth muscle attachment areas; the posterior one is transversely elongated and situated just in front of S0, occupying about a third of the glabellar width; the middle is kidney-shaped and surrounds a shallow bifurcated lateral glabellar furrow situated mid way from the sagittal line towards the axial furrow; the anterior one is nearly circular, rather small

Fig. 2. *Telephina* (*Telephops*) *biseriata* (Asklund, 1936) in the Kiviõli Member of the Viivikonna Formation, Kukruse Regional Stage. **A–I**, GIT 360-335. A–C, dorsal views; D, oblique anterior view; E, oblique dorso-lateral view; F, G, lateral views; H, anterolateral view; I, anterior view. All ×6. Scale bar 5 mm.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and positioned close to the axial furrow just in front of the second one; the largest tubercles occur sagittally, and a pair of glabellar spines occurs on the far anterior, close to the mid-line. The lateral glabellar furrow S1 is shallow, diverging symmetrically into short branches at the mid point of palpebral fixigena; S0 prominent, slightly parabolic anteriorly, widest medially, narrowing shortly behind the muscle area, dying out without reaching the axial furrow; L0 relatively long, extending over 27 per cent of the glabellar length, its median part is broken off and the presence or absence of an occipital spine cannot be confirmed. The palpebral fixigena is narrow (tr.), evenly rounded and slightly concave; palpebral furrow rather deep, widest anteriorly; palpebral rim widens slightly anteriorly; a specific pattern of lirae (see Bruton & Høyberget 2006) covers the anterior part of the palpebral fixigena, and the posterior part with the muscular pattern is bounded adaxially by a narrow ridge. The ridge and the palpebral rim run parallel to each other and both slope downwards at the posterior suture of the fixigena, narrowing shortly thereafter. Triangular postocular fixigena very short (exsag.) behind the palpebral area, ending posteriorly in a ridge-like posterior border, which is also narrow transversely, together with the articulating area which is distinctly pointed up to the prominent fulcrum on the posterior border, from where it curves steeply down abaxially at nearly 90 degrees. Posterior border convex dorsally in profile, like the anterior border, but has additional shallow border furrow close to the posterior edge dying out adaxially before reaching the fulcrum.

DISCUSSION

On the basis of the distance between the anterior glabellar spines *Telephina* (*Telephops*) can be subdivided into two groups, one with a narrow space and the other with a wider space. In stratigraphical succession, the former occurs first, in the *Hustedograptus teretiusculus* Biozone or below, and includes *T. biseriata* from the middle Andersö Shale of Jämtland, *Telephina* sp. A *sensu* Ahlberg (1995a) from the Almelund Shale (formerly lower *Dicellograptus* Shale) at Röstånga, Scania in Sweden, and *T. invisitata* Nikolaisen, 1963 and *T.* aff. *granulata* (Angelin, 1854) *sensu* Hansen (2009) from the Elnes Formation (formerly *Ogygiocaris* Shale) in the Oslo, Hadeland and Mjøsa regions, Norway. Of these, the last species incorporates two juvenile cranidia more closely resembling *T. invisitata* than *T. granulata*.

The second group appears in the *Nemagraptus gracilis* Biozone and is represented by *T. granulata* (Angelin, 1854) from the Vollen Formation (formerly *Ampyx* Limestone) in the Oslo Region, Norway, the upper Dalby Limestone in Västergötland, Sweden, and the upper Andersö Shale in Jämtland, Sweden. It also includes *T. armata* Nikolaisen, 1963 from the Vollen Formation in Asker, Norway. The geographical range of *T. granulata* extends farther east to the Livonian Tongue area, where it appears in the Blidene drill core, western Latvia, and the Lopatovo well in western Russia (Männil 1963; Ahlberg 1995b). The wide space between the anterior glabellar tubercles is also common in post-Darriwilian *Telephina* outside Baltica, for example in *T. bicornis* (Ulrich, 1930) from the Whitesburg Limestone of Virginia and *T.* cf. *bicornis* from the Brickwork's Quarry Shales Member of the Knockerk Formation in the Grangegeeth area, eastern Ireland (see Romano & Owen 1993). This feature might prove to be a good marker for biostratigraphical correlation, and in recognizing the Darriwilian–Sandbian boundary.

In our specimen the anterior glabellar spines are situated close to each other, as in a specimen of *T. biseriata* from the middle Andersö Shale (middle–upper *H. teretiusculus* Biozone) on Andersön, central Storsjön area, Jämtland, Sweden (see Ahlberg 1995a, pl. 6: 11, 12). However, the glabellar furrows are less pronounced in the Estonian specimen, but this is similar to other Swedish specimens of *T. biseriata*, including the holotype (Ahlberg 1995a, pl. 6: 9, 13). The glabellar tubercles are coarser in the Estonian specimen and in this respect, it resembles *T.* aff. *biseriata* (Ahlberg 1995a, pl. 6: 14) from a dark grey limestone in the middle Andersö Shale (probably the upper *H. teretiusculus* Biozone) on the northwestern shore of Andersön. Unfortunately, the latter is too fragmentary for detailed comparison. *Telephina* aff. *biseriata* also resembles our specimen in its proportionally wider glabella, but differs in the width of the palpebral lobes. In the shape of the glabella, its anterior truncation and in the size of tubercles our specimen also resembles *T.* aff. *granulata* from the Killeröd Formation (upper *H. teretiusculus* Biozone) at Rödmölla and Killeröd, southeast Scania. This is the only representative of the 'wide' group determined from the beds equivalent to part of the upper *H. teretiusculus* Biozone (Bergström 1973; Ahlberg 1995a). Of the three known specimens, the two smaller have the prominent glabellar spines rather close adaxially, resembling the older species (e.g. *T. biseriata*), but in the largest specimen these spines are farther apart. Perhaps this combination of the anterior spines moving apart during the late holaspid period also shows the phylogenetic sequence in the *biseriata*–*granulata* lineage. These three specimens differ from our specimen in having very shallow glabellar furrows located closer to the sagittal line.

In their biostratigraphical and palaeoecological study on graptolites, trilobites and conodonts of the Andersö

Shale in Jämtland, Pålsson et al. (2002) showed parallel the ranges of these groups. They also established a new lithostratigraphical unit, the Ståltorp Limestone Member. This is a dark-coloured, rather pure, and richly fossiliferous bedded limestone, overlying the Lower Andersö Shale Member. Previously this unit was informally called the '*Telephina biseriata* beds' (Thorslund 1960), or simply '*biseriata* limestone' (Karis 1982). *Telephina biseriata* and *T.* aff. *biseriata* co-occur in the Ståltorp Limestone (Månsson in Pålsson et al. 2002, p. 45, fig. 10), which is assigned to the lower part of the *Pygodus anserinus* Biozone (Bergström in Pålsson et al. 2002, p. 47, fig. 12), and tentatively to the upper part of the *H. teretiusculus* Biozone (Pålsson in Pålsson et al. 2002, p. 41, fig. 7). *Pygodus anserinus* has not been recorded from the oil-shale mining area in northeastern Estonia but it occurs rarely to the south in drill cores from the upper part of the Uhaku Stage (Viira et al. 2006; Hints et al. 2007; Viira 2008). Representatives of the younger *Amorphognathus tvaerensis* Biozone are numerous in northern and southern Estonia, except in Kohtla, which is close to Sompa. In Kohtla this conodont species appears in the first limestone interbed A/B at about 30 cm from the base of the Kukruse Stage, and is very rare until bed G in the upper part of the stage (Viira et al. 2006). Elsewhere, Viira (2008, p. 33) points out an interval without any of these index species at the boundary of the Uhaku and Kukruse stages. The age of this 'barren' interval is obscure. It seems that there is a potential for correlation within Baltoscandia based on the distribution of trilobite genera *Telephina*, *Remopleurides* Portlock, 1843 and *Lonchodomas* Angelin, 1854, represented in both areas and stages.

Graptolites are scarce in the North Estonian carbonate succession. Some fragmentary graptolites (Fig. 3P, Q), which derive from the same piece of rock as the telephinid trilobite described above, resemble *Dicranograptus irregularis* Hadding (in Pålsson et al. 2002, p. 40, fig. 6), but are too poorly preserved for precise identification. An assemblage of graptolites (Fig. 3A–F) from other loose boulders at the same locality includes more complete material identified probably as *Hustedograptus* cf. *uplandicus* (Wiman, 1895). This species co-occurs with *Laufeldochitina stentor* (Eisenack, 1937) in the Dreimani Formation in the Aizpute core, western Latvia, i.e. the Livonian Basin (Männil 1976, fig. 2). The others (Fig. 3G–O) resemble *Dendrograptus rigidus* Bulman, 1936, which is known from somewhat older beds of the Engervik Member of the Elnes Formation in the Oslo Region (Maletz & Egenhoff 2004), and also *Dendrograptus*? *balticus* Wiman, 1895. The latter was collected from the South Bothnian district together with *H. uplandicus* (Wiman 1895). However, these are not recorded from the '*biseriata* limestone' in Jämtland (Pålsson et al. 2002) or from the Almelund Shale in Scania, and so direct correlation with the Viivikonna Formation on the basis of these graptolites is not possible. In Jämtland *Nemagraptus gracilis* (Hall, 1847), the index graptolite for the lower boundary of the Sandbian, appears above the Ståltorp Limestone Member. Some recent finds of *N. gracilis* from Estonian and Latvian sections are summarized by Nõlvak and Goldman (2004, 2007). They show that all these specimens of *N. gracilis* come from the upper part of the Viivikonna Formation of the Kukruse Regional Stage, dating it as Sandbian. In general, the Kukruse Stage has been considered to be roughly coeval with the *gracilis* Biozone, and consequently the boundary between the Middle and Upper Ordovician has been drawn mainly at the boundary between the Uhaku and Kukruse regional stages. Recently, *N. gracilis* has been found in the upper part of the Kõrgekallas Formation of the Uhaku Stage in the Männamaa drill core, Hiiumaa, western Estonia (Nõlvak 2008), bringing the lower boundary of the Sandbian downwards in Estonia. The exact level of the base of the Upper Ordovician in Estonia is nevertheless debatable (see discussions in Nõlvak & Goldman 2004; Viira et al. 2006; Hints et al. 2007).

CONCLUSIONS

Telephina (*Telephops*) *biseriata* is common in the Ståltorp Limestone Member of the Andersö Shale Formation in Jämtland, where it co-occurs with conodonts of the lower part of the *P. anserinus* Biozone as well as with graptolites of the upper part of the *H. teretiusculus* Biozone. The record of *T. biseriata* in the kerogenous limestone of the Viivikonna Formation, Kukruse Regional Stage, in the vicinity of Kohtla-Järve suggests that the lower part of this formation may be contemporaneous with the '*biseriata* limestone' of the *H. teretiusculus* Biozone in Jämtland. The presence of *Hustedograptus* cf. *uplandicus* at the same locality as *T. biseriata* at Sompa, however, is insufficient to prove or disprove this suggestion. Thus, the lowermost part of the Viivikonna Formation in north-eastern Estonia may possibly belong to the uppermost Darriwilian, or also to the Sandbian, if there is a shift in time in occurrences of *T. biseriata* in Estonia compared to the Jämtland area.

The appearance of a pelagic trilobite *Telephina biseriata* (Asklund), previously known as a deep-water inhabitant (Fortey 1975), in the North Estonian Confacies Belt, may reflect the peak of a major sea-level highstand event embracing the late Darriwilian–early Sandbian (Haq & Schutter 2008).

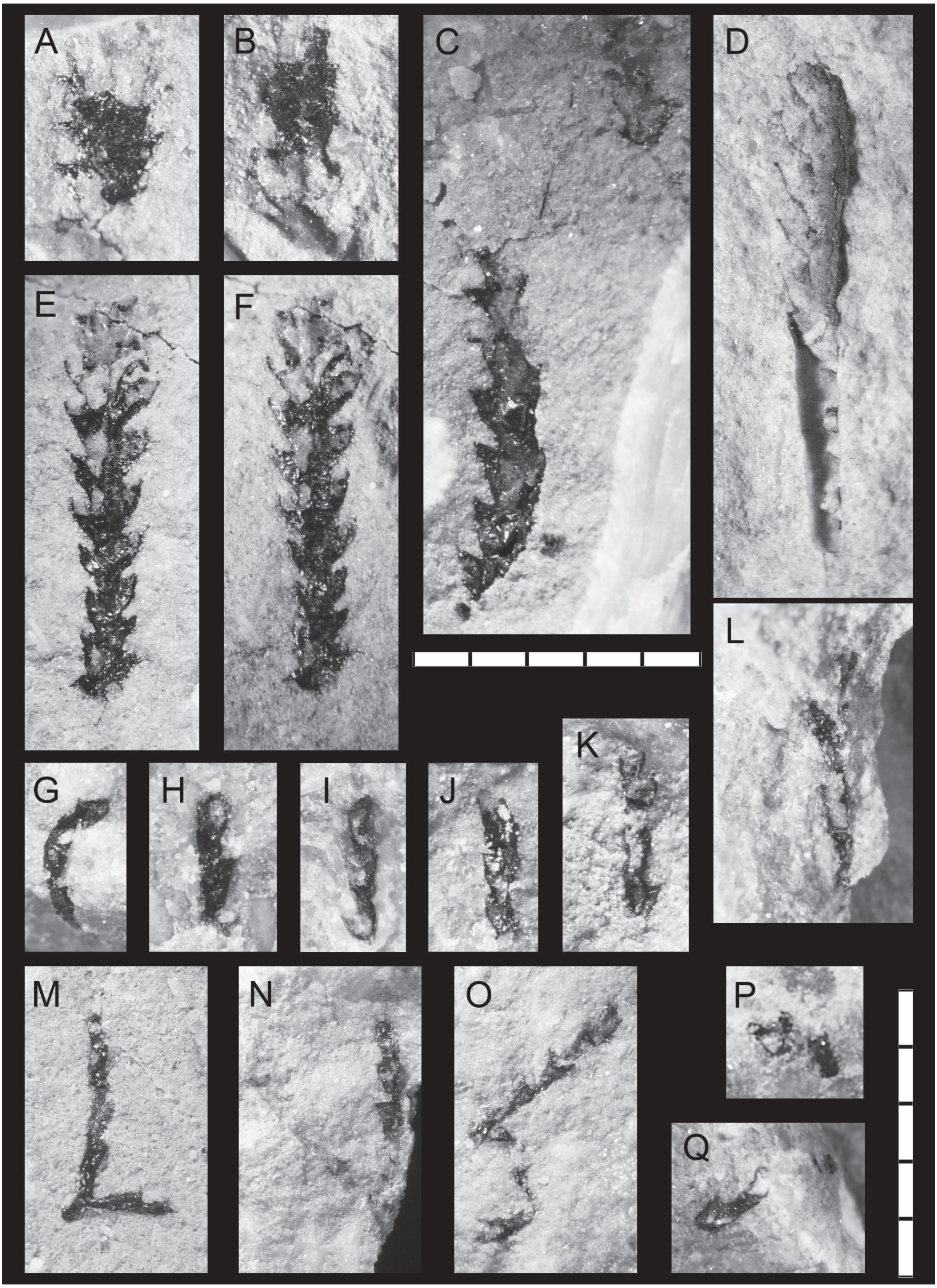
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Fig. 3. Graptolites from the Viivikonna Formation, Kukruse Regional Stage of the Sompa mine, Kohtla-Järve, northeastern Estonia. **A–F**, *Hustedograptus* cf. *uplandicus* (Wiman). A, GIT 360-345-1; B, GIT 360-345-2; C, GIT 360-346-1, -2; D, GIT 360-347; E, F, GIT 360-345-3. **G–Q**, *Dendrograptus*? sp. G, GIT 360-338; H, GIT 360-339; I, GIT 360-340; J, GIT 360-341; K, GIT 360-342; L, GIT 360-343; M–O, GIT 360-344-1, -2, -3; P, GIT 360-336; Q, GIT 360-337 (P, Q, from the same piece of rock as the trilobite *Telephina* (*Telephops*) *biseriata*). All ×10. Scale bars 5 mm.

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Telephina (Trilobita) leid Kirde-Eesti Ordoviitsiumist ja selle stratigraafiline tähendus

Helje Pärnaste ja Adrian Popp

Kukruse lademe seni teadaolevale viiekümnele trilobiidi liigile lisandus *Telephina* (*Telephops*) *biseriata* (Asklund). Selle perekonna esindajad on senini teada olnud vaid sügavamaveelistest faatsiestest Norra, Rootsi ja Läti vastavates piirkondades. Uus leid Kohtla-Järvelt Sompast on esimene kaldalähedasest Põhja-Eesti fatsiaalvööndist. Rootsis Jämtlandi regioonis esineb see liik Ståltorpi lubjakivi kihistikus Andersö kiltade vahel koos *Pygodus anserinus*'e konodonditsoonile ja *Hustedograptus teretiusculus*'e graptoliiditsoonile iseloomuliku fossiilikooslusega. Viimased markeerivad Darriwili globaalse lademe ülemist osa. Kirde-Eesti *T. biseriata* peakilp esineb lahtisel kivimpalal koos mittemääratava dendroidi fragmendiga ja ei võimalda täpsemat biotsonaalset määrangut. Samast leiukohast, kuid samuti määramata tasemest on pärit graptoliit *Hustedograptus* cf. *uplandicus*, mida on korreleeritud Sandbi lademe *Nemagraptus gracilis*'e tsooniga. *N. gracilis* leiti hiljuti Hiiumaa puuraugust Kõrgessaare kihistust, mida on peetud Viivikonna kihistust vanemaks, ja seega joonistub piir globaalsete lademete Darriwili ning Sandbi vahel Uhaku regionaalse lademe sisse. Uus *T. biseriata* leid põlevkivi levilas viitab võimalusele, et see liik esineb Kirde-Eestis hiljem kui Kesk-Rootsis Jämtlandi piirkonnas, või ka võimalusele, et Viivikonna kihistu alumine osa Kirde-Eestis võib lokaalselt olla Hilis-Darriwili vanusega.

PAPER IV

Popp, A. and Pärnaste, H. 2011. Biometry and lifestyle of the Ordovician proetid trilobite *Cyamella stensioei* Owens, 1979.

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Biometry and lifestyle of the Ordovician proetide trilobite *Cyamella stensioei* Owens, 1979

A. Popp and H. Pärnaste

Abstract: Biometric analyses of the trilobite *Cyamella stensioei* Owens, 1979 from cavities in the Upper Ordovician Boda Limestone of central Sweden, along with a comparison to closely allied rorringtoniid taxa from outside Baltoscandia, reveal important systematic and ecological information on this proetide taxon. Biometric analysis of cephala of *C. stensioei* shows a number of instars, reflecting several ontogenetic stages, and a meraspis stage of this taxon is figured for the first time. The lifestyle of *C. stensioei* as being a cavity-dweller, possibly adapted to the cavities in the Boda Limestone by chemosymbiosis, is presented. Some of these cavities are interpreted as former seepage conduits. Comparison of *C. stensioei* with other rorringtoniid trilobites suggests possible ancestors occurring in South China and Sibumasu terranes, determined earlier as *Decoroproetus* sp. and *Cyamella* sp., all differing from the genus *Paracyamella*, which is here reassessed. In wider terms of ancestry they originate from Baltica or Laurentia, where the first rorringtoniids are known from the middle Darriwilian.

Keywords: Trilobita, Proetida, morphometry, biometric analysis, variability, ontogeny, instars, Boda Limestone, Hirnantian.

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Introduction

The small proetide trilobite *Cyamella stensioei* Owens, 1979 from the Boda Limestone of the Siljan District in Dalarna, Sweden (Fig. 1) has hitherto only been found in mass accumulations. Typically these mono-specific mass accumulations consist of well-preserved and commonly completely articulated trilobite specimens and are regarded as *in situ* fillings of former fissures and cavities (termed 'pockets' by Suzuki & Bergström 1999). These pockets show different geometry, orientation and complexity, and are common in the carbonate mud mounds of the late Katian and early Hirnantian Boda Limestone Formation (Suzuki et al. 2009). Before introducing the biometric part of this study it is necessary to explain the geological background, separately.

Geology and stratigraphy

The upper part of the Boda Limestone has recently been investigated by Suzuki et al. (2009) who defined a new formal Upper Boda Member on the basis of lithologic, faunistic and chemostratigraphic aspects. This member encompasses the four different sub-units A-D, all assigned to the Hirnantian Stage. The entire Boda Limestone extends from the Katian to the Hirnantian, but the pocket-type accumulations are known from units A and D of the Upper Boda Member only. The exact stratigraphic position of those pockets containing *C. stensioei* is unknown. Although the type locality for *C. stensioei*, the limestone quarry at Kallholn (Owens 1979), has yielded several slabs with mass accumulations of the species, additional material derived from other localities in the Siljan District seems scarce, and is so far only known from Kallholn, Osmundsberget, Unskarsheden and Solberga. As *C. stensioei* has not yet been described from outside the pockets, it is treated as an *in situ* type of internal cavity filling (Suzuki & Bergström 1999, p. 168; see also Owens 1979, p. 202). This assumption is crucial for the recent study, so the samples were investigated and treated separately in order to identify possible differences in trilobite morphology between the localities.

To our knowledge *C. stensioei* has not yet been discovered in a still accessible pocket, therefore assumptions on its lifestyle, taphonomy and stratigraphic position given herein are drawn from samples housed in collections. During the process of revision of this paper one additional sample from another locality (Solberga) was collected by the first author (AP). This single rock sample was not used for biometric investigation but for taphonomic interpretation and environmental discussion. In this study detailed lithologic and taphonomic descriptions of a *Cyamella* pocket are published for the first time.

Biometric investigations

A previous morphometric study on cranidia of *C. stensioei* by Popp & Pärnaste (2008) of only one sample surface (about 50 cm^2) assumed that this surface represents the shortest time span possible to be resolved in this Ordovician cavity environment. Within

24 cranidia, a size variation of 35% occurred and trends in changes of morphology during the ontogeny of the late holaspid stage were recognised. There was no indication of instars or dimorphism. Few differences were detected between the data of the sample compared to data published by Owens (1979).

In this study all available samples represent up to six different pockets yielding detailed information on specific environmental and taphonomic conditions at a specific time for the three localities (Kallholn, Unskarsheden and Solberga). In order to detect possible differences in the morphology of the proetide exoskeleton, in this case the cranidia of *C. stensioei*, by comparing key measurements from four different samples derived from pockets at two different localities (Kallholn and Unskarsheden). The measured data were compared according to their origin (outcrop), in order to detect any possible local variance of *C. stensioei*. The ontogenetic trends described in this study can help to clarify the placement of *C. stensioei* within higher level systematics and its relation to other taxa.

Systematic aspects

The genus name *Cyamops* applied to a proetide trilobite by Owens (1979) proved to be preoccupied and was changed to *Cyamella* by Owens in Owens & Hammann (1990). Within the Aulacopleuridae Angelin, 1854, *Cyamella* was originally placed into Scharyiinae Osmólska, 1957, together with *Panarchaeogonus* Öpik, 1937 and *Isbergia* Warburg, 1925 (Owens 1979). After establishing the family Rorringtoniidae Owens in Owens & Hammann, 1990 *Cyamella* and *Isbergia* were incorporated into that new family, whereas *Panarchaeogonus* remained in the Sharyiidae. Discussion of the systematic positions of these three taxa continues (e.g. Adrain & Chatterton 1993; Hammann & Leone 1997; Owens & Fortey 2009) mainly because of the lack of data on their ontogeny.

The genus *Paracyamella* Zhou & Xiang, 1993, with the type species *Paracyamella huijabaensis* Zhou & Xiang, 1993, was erected for material from the Pagoda Limestone Formation in South China. *Paracyamella* is closely allied to the genus *Cyamella* and was regarded as its junior synonym by Fortey (1997). We here consider *Paracyamella* to be a valid genus, the reasons for which are discussed below. The occurrence of this Chinese material is restricted to units deposited in an outer shelf-slope setting during the latest Darriwilian and the earliest Sandbian (Zhou Z.-Q. et al. 2000; Zhou Z.-Y. et al. 2000; Zhou & Zhen 2008a, b). In Thailand, it occurs in presumably contemporaneous beds of the Pa Kae Formation, as *Cyamella* sp. 1 of

Fortey (1997), within an association of genera similar to that in South China (Fortey 1997). For *Cyamella* sp. 1 Fortey (1997, p. 425) stressed the resemblance in glabellar outline to 'some *Rorringtonia* species, e.g. *R. lenis* Owens and Hammann, 1990'. The present biometric study of *Cyamella stensioei* includes discussion of other representatives of the Rorringtoniidae as well as their palaeogeographic distribution (Fig. 1).

The aim of this study is a review the species *Cyamella stensioei*, Owens 1979 based on the biometric investigation. This review includes ontogenetic, systematic, palaeoecologic, taphonomic and stratigraphic information.

Material and methods

Material

The specimens used for this paper are housed in three institutions abbreviated as follows: GIT – the Institute of Geology at Tallinn University of Technology; RM – Swedish Museum of Natural History in Stockholm; D – Museum of Evolution, Uppsala University, Sweden.

Six rock samples from three localities in the Siljan District were investigated, namely the quarries of Kallholn (samples K_1: RM Ar45665, see also Popp & Pärnaste 2008; K_2: GIT 436-66; K_3: D 2171), Unskarsheden (U_1: priv. coll. W. Drichelt; U_2: GIT 436-67) and Solberga (Sol_1: GIT 436-68). Additional measurements of *Cyamella stensioei* from Owens (1979, p. 212) for the dimensions of the cranidia of the holotype (RM Ar47556) and the paratype (RM Ar47518), both termed as sample K_4, were used for comparison. Data published by Zhou & Xiang (1993) for the Chinese species *Paracyamella hujiabaensis* Zhou & Xiang, 1993 and *Paracyamella subacuta* Zhou & Xiang, 1993 from the Pagoda Limestone of the northern Upper Yangtze Platform, China were compared with the Swedish specimens.

Because no additional macrofaunal element could be detected, all samples are treated as mono-specific accumulations. Smaller parts of trilobite exoskeletons such as hypostomata and larvae were found in samples K_1 and U_2, indicating an environment favourable for preserving small and fragile parts of the exoskeleton.

Sample Sol_1 was sawn vertical to its suggested bedding plane and polished, resulting in a slab of 6.3 cm maximum height and 12 cm maximum width. The polished surface was used for the description of lithology and taphonomy within the pockets.

Methods

Only cranidia were investigated, as these are the most diagnostic part of *C. stensioei* as well as of the genus compared with other aulacopleuroidean trilobites such as *Panarchaeogonus* or *Isbergia* (Owens 1979).

Two different methods were used for measuring cranidia of *Cyamella stensioei*. The first was direct measurement using a microscope and a graticule (see Popp & Pärnaste 2008). The second way of gathering data on predefined measurements was using a pixel/scale ratio from digital photographs of specimens oriented in a planar position. By using the image-processing program ImageJ (version 1.43; see Abramoff et al. 2004) a scaled section was converted into a certain amount of pixels, which gave the defined ratio for continued measuring. Although, orientation of specimens is crucial for both methods, measuring from digital photographs is preferred, because the position of the measured object does not change during repeated measuring of the sections. Direct measuring under the microscope has the higher potential of measurement error due to a slightly changed orientation. The process of digital measuring is less time consuming and results are reproducible. In addition, the results are comparable with those made from published photographs of other researchers. In order to reduce the measuring errors more iteration could be realised more comfortably and within a shorter time compared to the direct measuring method. If a tolerance limit of 0.04 mm between the highest and lowest values was exceeded, additional readings were made. Some sections were measured in half distance and doubled afterwards, assuming the measured specimens as being symmetrical in their feature. In doing so, measurements become comparable to most published data, but the danger of doubling errors is recognised. Due to scaling pixels directly against distances in millimetres, for the small distances on the cranidia, the sub-millimetre area is less prone to rounding errors. The small distances can be read directly. After repeatedly measuring for every measurement, the mean value was calculated and chosen as the final result. If not stated explicitly, all values represent maximum values. The morphometric analysis is based on trilobite specimens showing a nearly complete set of characters. For 17 cranidia 15 sections were measured, but only eleven measurements (see Fig. 2) were included in a detailed investigation. Statistical and multivariable analyses were carried out using the statistical package PAST (version 2.00; Hammer et al. 2001), the Student's t-test and the Shapiro-Wilk test.

$\delta^{13}C$ bulk-rock analysis of four samples (K_1, K_2, K_3, U_1) was undertaken to view possible variations between all samples. Measuring points of the matrix were chosen from top and bottom of three samples, about 1 cm apart from each other. For K_3 only one value from the top surface was available.

Photographs of whitened (magnesium oxide) specimens were taken by using a Nikon AZ100 Microscope with a Nikon Digital Microscope Camera.

The pockets

Lithology

The five slabs containing the trilobites that were studied biometrically comprise at least two lithotypes (Fig. 3).

Lithotype 1 (samples K_1, K_2, K_3, U_2): This is a loosely to densely packed biomicrite. The trilobites are arranged horizontally in mm-scale layers and are mostly sorted with the dorsal side up (convex-up). The specimens display different degree of articulation, but are mostly complete or only with missing or displaced free cheeks. The orientation on the horizontal plane varies (Fig. 3A–C, F). Small exoskeletal parts like hypostomata and larvae are preserved. The colour of horizontal layers varies from yellowish or brownish light grey to (secondarily?) rose-coloured (Fig. 3D, E, G–I). Very small pyrite crystals are common (Fig. 3G, H, J). Apart from its faunal composition, lithotype 1 seems similar to the samples containing *Ityophorus undulatus* Warburg, 1925 described by Suzuki (2002). Lithotype 1 is interpreted here as an autochthonous low-energy sediment possibly deposited under low-oxygen conditions at the bottom of a horizontally-shaped cavity in the mound structure.

Lithotype 2 (sample U_1): This is a loosely packed biosparite without internal layering, which is white to (secondarily?) brownish light grey in colour. Trilobites are the only macrofossil element and occur in horizontal to sub-horizontal groupings, differing from each other in: a) surface orientation, b) having the dorsal or ventral side upwards, and c) degree of articulation. Lithotype 2 is interpreted as a higher energy (e.g. current-induced?) sediment. This is supported by the presence of sparite cement in lithotype 2.

Sample Sol_1 from Solberga (Fig. 3I–L) seems to be a possible combination of the two mentioned lithotypes of Kallholn and Unskarsheden. The orientation of the slab was established by the presence of geopetal structures. Two units are visible in this slab (described from the bottom of the slab to the top):

Unit 1 (Fig. 3J): This unit is about 17 to 19 mm thick and is light grey at the base and rose or flesh-coloured at the top. It cosists of sets of micrite and possible microsparite, at its base with an obscurely mottled texture, followed by very thin-laminated (sub-millimetre scale), slightly irregular spaced stratification. The lower laminae show darker crumbled elements of uneven, slightly wavy appearance that are possibly microstromatolites. Some upper laminae consist of light grey ovoid granules (peloids?) and the topmost laminae are more horizontal and appear as dark crumbled (slightly wavy) elements. The angle of laminae suggest that this facies is cross-laminated. Rare trilobite fragments (mostly cranidia in convex-up orientation) become more frequent towards the top of this unit, with one vertical section of a cranidium in normal position (convex-up) covering a cluster of sparite (calcite cement). Pyrite crystals are present throughout the whole unit, but are enriched in some laminae as larger cubicles (of up to 1 mm side length) (Fig. 3J).

Unit 2: This unit is about 46 mm thick and overlies unit 1 with a diffuse contact (Fig. 3J). The lithotype is transitional from a poorly washed biosparite at the base to a packed biomicrite at the top. It is rose to brownish grey or light grey in colour. In its lower part there are common geopetal structures below convex-up trilobite fragments (Fig. 3J–K), neighbouring each other in some areas. In some parts a weakly defined layering is indicated by a colour contrast (Fig. 3L).

At the base of unit 2 the trilobite fragments are generally stacked and in a chaotic orientation (mixed convex-up and convex-down, partly vertical position), becoming more layered and more horizontal towards the top with increasing degree of articulation (common cranidia with thoracic segments) (Fig. 3L). Pyrite crystals are randomly distributed. One large object at the right side is seamed with white calcitic cement (sparite) and a dark line (shell?), its inner core consists of a greyish dark brown infill (Fig. 3I). One small stylolite is present at the top of the unit (Fig. 3L).

Here, unit 1 is regarded as an internal sediment from the bottom of a former cavity similar to the ones described and figured by Suzuki and Bergström (1999, fig. 2 and 6) and Suzuki (2002, fig. 2). The cross-stratification and the different angles of the laminae are regarded as the result of changing directions of sedimentary input. Crumbled surfaces (laminae) in unit 1 could indicate the presence of microbial mats (see Suzuki & Bergström 1999). The fine lamination (stratification) and the pyrite crystals could indicate low energy sedimentation under lowered oxygen (dysoxic?) conditions. It is therefore remarkable, that trilobite remains are present.

Unit 2 is comparable to the *Stenoparia* pocket figured and described by Suzuki and Bergström (1999, fig. 4), for which transport was suggested. Unit 2 might represent at least one sedimentary event, with stronger current-conditions compared to unit 1 and a possible re-location of trilobite exoskeletons, which possibly originally accumulated elsewhere under more quiet conditions. In its sparitic matrix the base of unit 2 most closely resembles lithotype 2 (sample U_1), but differs from it in the stacking and chaotic ordering of mostly disarticulated trilobite remains. The biometrically investigated samples K_1, K_2, K_3 and U_2 differ from the top of unit 2 (sample Sol_1) in their much higher degree of articulation of trilobite exoskeletons, whiche are dominantly in convex-up position. The samples K_1, K_2, K_3 and U_2 are therefore regarded as in situ accumulations of *Cyamella stensioei* (see Suzuki & Bergström 1999), in contrast to sample Sol_1.

No contacts to the former walls (i.e. boundaries) of the cavities (i.e. pockets) are detectable in any of the investigated samples. Discovery of a pocket in the field containing accumulations of *Cyamella stensioei* would enable further interpretation on its geometry and depositional history.

The data on carbon isotopes of the *Cyamella* samples were obtained by whole rock analyses of four samples, taken from their upper and lower surface about one centimetre apart from each other. All samples for $\delta^{13}C$ bulk-rock analysis (Tab. 1) show values over 2 with always a slightly higher value from the bottom point than from the top surface. The values for all samples range between 2.08 to 2.42 $\delta^{13}C$ (parts per mil). The measured values are positive values and do not show strongly differing results, underlining the possible similarity of the samples. The comparison of our isotope values with published data (Schmitz & Bergström 2007; see Kaljo et al. 2007, 2008) and the descriptions of Suzuki et al. (2009) for the pocket containing units (A and D) suggest a late Hirnantian age for the *Cyamella* pockets.

Taphonomy

The biometrically investigated samples represent two lithotypes. The sample U_1, being the only representative of lithotype 2, shows a grouping of trilobite exoskeletons, which might be the result of a disturbed sedimentation or relocation also visible in sample Sol_1. All samples show no preferred orientation of trilobite remains.

A taphonomic study was carried out by measuring the trilobites' orientations in the ImageJ software with an angle-measuring tool on the surface of sample K_1 (Fig. 3C). Directions were read according to the orientation of cephala along their long axes. The same process was also done for thoracic elements and pygidia by using the suggested orientation of cephala. A set of eight directional classes for the measured directions spanning in steps of 45 degrees was identified, but without any preferred orientation.

Based on this result, a current induced orientation for the morphometrically investigated sample K_1 seems unlikely. The other samples (K_2, U_1, U_2), although not investigated to closer taphonomic detail due to scarcity of measurable cranidia, show a similar disorder of articulated specimens on their surfaces.

Isocolus sjoegreni Angelin, 1854 and *Ityophorus undulatus* are considered to represent typical cavity-dwelling trilobites of the Boda mound (Suzuki & Bergström 1999; Suzuki 2002). In their miniaturised body and their reduced (*Ityophorus*) or absent (*Isocolus*) visual surfaces they seem well adapted to the cavities. These minute and blind trilobites are associated – in differing proportions – with other faunal elements such as gastropods, ostracods, sponge spicules, crinoid ossicles, cephalopods, brachiopods, bryozoans, bivalves and machaeridians (Högström et al. 2009). Most of these faunal elements probably lived outside the cavities. In particular the presence of cephalopods and crinoid ossicles indicates possible transport into the cavities by currents. Because of their dominance an adaptation to the cave environment is suggested for the ostracods (see Aubrecht & Kozur 1995) and gastropods.

I. sjoegreni and *I. undulatus* have been observed together in samples from Kallholn (Popp & Rohde 2010), indicating coexistence rather than separation of niches as suggested by Suzuki & Bergström (1999). These samples show similar taphonomic features (different sizes, orientations, degree of articulation) as described here for the lithotype 1, but differ in lithological, faunal and taphonomic aspects. Both *I. sjoegreni* and *I. undulatus* occur in accumulations mostly arranged in sheet-like surfaces in between limestone layers and are covered with a clayey-marly residue (Popp & Rohde 2010), differing from the ones with *C. stensioei* in reaching only some mm-thickness, but not the cm-scale of the latter (see Fig. 3I–L).

Biometry

The key measurements on the cranidia of *Cyamella stensioei* were plotted for selected combinations. In order to separate the two localities Kallholn (K_1, K_2) and Unskarsheden (U_1, U_2) data from them were plotted using different symbols. Data for the holotype and paratype (K_4) are given as reference (Fig. 4).

The four combinations for length and width generally plot in the same way along the respective regression lines. Observed differences between reference sample K_4 and our data seem relatively small. The data do not show any significant difference for the two localities.

Where the sample size (>3) allows, the Shapiro-Wilk test was performed on selected measurements in order to determine whether the samples of K and U were taken from populations with statistically normal distribution. The Shapiro-Wilk test is regarded as a very robust method for small sample sizes above three and below 50. Its significance level is expressed by the value p, which is generally taken as 0.05. If the outcome is below 0.05, the null hypothesis is rejected. The null hypothesis H_0 of the test is: the sample has been taken from a statistical population with normal distribution. An alternative hypothesis H_1 is: the sample has been taken from a statistical population with non-normal distribution. The results of five measurements of nine samples for Kallholn and Unskarsheden specimens are mostly above the $p=0.05$ significance value (Fig. 5). For these values there is no need to reject the null hypothesis. The Shapiro-Wilk test shows that it is possible that the values for the two localities are normally distributed. A normal distribution suggests that these samples are not current-sorted it should therefore be possible to identify instars if they are present.

The Student's t-test was carried out in order to test whether the investigated samples represent mathematical populations with the same mean; in other words, whether the data available for Kallholn and Unskarsheden are likely to show the same size range (null hypothesis H_0). Therefore it was performed as a two-sample test (permutation rate $N=10000$) for selected sections (Tab. 2). The p-values of all selected measurements lie clearly above the significance level of $p=0.05$, therefore the null hypothesis is accepted. The measurements represent populations with the same mean. Similar means are visible in other measurements, with no hint of a local signal. For this reason the data were treated as one set in the following discussion.

As already visible in Fig. 4, the measured values of *C. stensioei* show a tendency to plot in more or less diffuse accumulations (clouds) along the regression line (trend line). In order to highlight these accumulations the data were plotted in addition of a third or a fourth component (Fig. 6). This method was used for morphometric analysis of trilobites before (e.g. Temple 1957). A matrix of three values shows accumulated data points, indicating a proportional growth. In the first step (Fig. 6A) the values of glabellar width (W_{glab}) and glabellar width at palpebral lobes (W_{glab_palp}) were plotted against the glabellar length (L_{glab}; x-axis). A comparison between both plotted combinations shows a slight division towards the end of the accumulations, suggesting a slower general growth in width in the middle of the glabella compared to the maximum glabellar width.

The lowermost data point in both plots represents a meraspis stage (K_1_meraspis). Between this first end point and the last end point perhaps four clouds are present along the regression lines (x-values for L_{glab}; 1: between 1.05 to 1.30 mm; 2: between 1.30 to 1.50 mm; 3: between 1.50 and 1.70 mm; 4: between 1.70 to 1.90 mm).

In order to test the reproducibility of the point accumulations the cranidial length (x-axis) is plotted against the cranidial width and in addition to the glabellar length (Fig. 6B). The last plot shows again L_{max} (x-axis) being plotted against W_{max} and in addition to the length of the occipital ring (Fig. 6C). Again perhaps four accumulations between the end points of each regression line are visible in both plots.

We regard these point groupings as probable instars (sensu Chatterton & Speyer 1997). Several are observable in the plotted data for *C. stensioei*. The similar pattern is also a manifestation of the primary proportional growth signal (see Temple 1957).

Morphologic trends during ontogeny and phylogeny

Ontogeny of *Cyamella*

The investigation of the monospecific accumulations is based on the reasonable assumption that the smaller specimens are taken as younger individuals than the larger ones. Besides the figured relation between cranidial sizes (L_{max}, W_{max}) and glabellar length (L_{glab}) (Fig. 6B), other morphological trends during the ontogeny of *Cyamella stensioei* are visible (Fig. 7A, D, E). (**1**) The width of the preglabellar field (W_{pgf}, Fig. 2) is defined by the anterior branches of the facial sutures which show a stronger divergence anteriorly in smaller cranidia than in larger ones. A relative narrowing of W_{pgf} in relation to the width of glabella is observable during growth. The ratio of the preglabellar field to the width of glabella is around 1.5:1 in smaller growth stages and about 1.3:1 in larger specimens. (**2**) In younger growth stages (Fig. 7A, D), the triangular post-ocular portion of the fixed cheek (L_{pos_palp}) is much shorter, the posterior branch of the facial suture has a stronger divergence compared to cranidia of older specimens. (**3**) A relative change of eye size is visible when comparing growth of palpebral lobes (L_{palp}) to an increase in cranidial size (L_{max}). Smaller specimens show relatively larger eyes, with a ratio of 1:4 compared to L_{max}. In larger specimens the eye size is about 1:5. (**4**) A change in the glabellar shape is present: small cranidia (Fig. 7A) have a relatively narrow (W_{glab_max}), conical pre-occipital glabella with basal lobes swollen at a distinct forwards arching S0; medium sized cranidia (Fig. 7D) have a less conical, more trapezoidal glabellar outline, with the occipital furrow slightly bowed forwards medially; the larger cranidia (Fig. 7J) have a trapezoidal, anteriorly rounded glabella which narrows slightly anterior from the palpebral lobes and the occipital furrow is shallower medially and nearly straight (tr.) along its entire length. (**5**) In small specimens, the occipital ring is lenticular in outline, tapering strongly abaxially and clearly separated laterally from the basal lobes. The median tubercle, which is situated on the anterior half of the occipital ring has a wide, slightly triangular base extended into a rearward curving spine-like point. In medium sized specimens, the occipital ring becomes more parallel-sided and less declined abaxially and the median tubercle is less spinose. In the larger specimens, the occipital ring is transversally nearly parallel-sided. The sides seem to be integrated in the postero-lateral parts of the pre-occipital glabella, where the occipital furrow is only weakly impressed and does not reach to the axial furrow. (**6**) The glabellar furrows are nearly effaced if present at all in the larger specimens whereas they are well seen in younger specimens.

Changes in morphology during the late holaspid period of *Cyamella* differ partially or are even opposite to those in *Paracyamella*. The late ontogeny is discernible in a set of specimens of *Paracyamella subacuta* from layer 25 in the Hujiaba section of the Pagoda Limestone in South China (see Zhou & Xiang 1993, pl. 4) and illustrated here in Figure 8. Comparing smaller specimens (Fig. 8F) with the larger ones (Fig. 8G) indicates that the eyes become larger and closer (tr.) to the glabella and the posterior fixigena becomes shorter during the ontogeny of the holaspid period. The same trends which are seen in the late ontogeny of *P. subacuta*, continue in the development of characters within the evolutionary line of the species *P. subacuta.* (Fig. 8G) and *P. hujiabaensis* (Fig. 8H). The species appear sequentially in the early Sandbian off-shore limestone succession in South China.

Character changes in different palaeogeographical regions

As the ontogenies of *Cyamella* and *Paracyamella* have a different pattern, it is instructive to assess other closely related taxa for comparison (Fig. 8). The genus *Rorringtonia* is very similar to *Cyamella* except in its better-pronounced glabellar furrows and the type species has the anterior sutures running parallel to each other (Fig. 8E). *Rorringtonia* is more widely distributed (Fig. 1) than *Cyamella*, though still rare (Owens 1981). *Phaseolops*? sp. Whittington, 1963 (Fig. 8A) from the middle Darriwilian Middle Table Head Formation of western Newfoundland (Whittington 1965, p. 337, pl. 19, figs 1–5) is possibly the oldest known representative of *Rorringtonia* (Owens 1981). Another possible *Rorringtonia* (Fig. 8B; *Cyamella* sp. of Popp 2007) was found from a broadly contemporaneous geschiebe of the Red

Orthoceratite Limestone (Beinhorn near Hannover, Germany) from Baltoscandia. The Laurentian species has an anteriorly expanding preglabellar field similar to that of *Cyamella* (Fig. 8K, M, N), but in the Baltic species it is nearly parallel-sided, similar to those of *Paracyamella* from South China (Fig. 8F, G, H) and *Rorringtonia* in Avalonia (Fig. 8C, D, E), i.e. taxa from late Darriwilian and early Sandbian.

By the late Darriwilian – early Sandbian, the range of *Rorringtonia* expanded to Avalonia (e.g. Wales: Owens 1981; Fortey 2006) with the three species in order of appearance, *Rorringtonia kennedyi* Owens, 1981 (Fig. 8C, D) from Builth, Wales; *R. flabelliformis* Whittard, 1966 (Fig. 8E) from the Shelve Inlier, Shropshire, England and *R. multisegmentata* Fortey, 2006 from Pembrokeshire, Wales. The representatives of this lineage change in the following features: the eyes become smaller and placed more anteriorly and closer (tr.) to the glabella, while the post-ocular fixigena elongates exsagittally. In addition, the number of segments increases from nine to twelve in the thorax and from seven to probably nine in the pygidium. The features of the earliest Avalonian species, *R. kennedyi*, are shared by other rorringtoniids from approximately contemporaneous sediments in Baltica, in South China and in Thailand (Sibumasu).

By the early Katian the number of segments decreases back to nine and six in the thorax and the pygidium respectively, as seen in *Rorringtonia ursina* (Owens, 1970) from the Oslo Region of Baltica (Fig. 8J). The eyes on *R. ursina* (Fig. 8J) are small and close to the glabella, but the posterior fixigena is shorter than in the Sandbian *Rorringtonia* (Fig. 8E) from Avalonia. The entire cephalon is proportionally shorter, as in the Laurentian *R. vetula* (Reed, 1935) (Fig. 8I). The border area is much wider, while the preglabellar and fixigenal fields become much narrower (Fig. 8J). The shortening of the cephalon accompanied by an enlarging glabella and shallower lateral glabellar furrows is also typical of the late Katian species *Rorringtonia scanica* (Olin, 1906) from Scania (Fig. 8L) and Bohemia (see Owens 2004). The Hirnantian *Cyamella stensioei* differs from all these late Sandbian and Katian taxa by having a large anteriorly widening preglabellar field with a concave border area. A juvenile stage of *C. stensioei* (Fig. 8M) most strongly resembles the Darriwilian *Rorringtonia*? sp. (Fig. 8A) from western Newfoundland, known only from a tiny, probably juvenile cranidium, suggesting a close phylogenetic relationship. The late meraspid and early holaspid stages of *C. stensioei* strongly resemble *Rorringtonia* in the appearance of the glabellar furrows, which are effaced in the later stages of *C. stensioei*, and suggest the possibility of being derived from *Rorringtonia*.

The earliest rorringtoniid species with the ill-defined glabellar furrows characteristic for *Cyamella*, come from the latest Darriwilian to the earliest Sandbian in South China (Zhou Z.-Y. et al. 2003), and possibly equivalent beds in Thailand (Fortey 1997). Of these trilobites, *C. stensioei* most closely resembles *Cyamella* sp.1 of Fortey (1997, p. 425, pl. 5: 6, 9) from the Pa Kae Formation in Southern Thailand (Fig. 8K) and a specimen first identified as *Decoroproetus* sp. by Zhou et al. (2005, pl. 5: 13) from the Puxihe Member of the Pagoda Formation in Yichang, Hubei Province and which probably belongs to *Rorringtonia*. Most notably they share anteriorly diverging facial sutures, a concave anterior border, and eyes positioned opposite L2. The *Rorringtonia*? from the Puxihe Member is of the same size as the meraspis of *C. stensioei*. It has similar glabellar furrows and is very similar to the Swedish taxon in its overall morphology, suggesting a close relationship. However, the two mentioned Asian taxa are also close to *Rorringtonia lepida* (Zhou & Xiang, 1993) and were probably being derived from the same stock. As noted above, *Paracyamella* Zhou & Xiang, 1993 (comprising *P. subacuta and P. hujiabaensis*) from the Pagoda Limestone Formation of South China was synonymized with *Cyamella* by Fortey (1997). It differs from *C. stensioei* in its elongated anteriorly pointed glabella, nearly parallel anterior branched of the facial suture, narrow and straight occipital furrow, the anterior border is not concave in lateral view the horizontal plane and in the presence of terrace ridges on the external surface of the exoskeleton. In addition, the Pagoda Formation species show a different pattern in their ontogeny (see above) than that of the type species of *Cyamella*. For these reasons we retain *Paracyamella* as a separate genus.

Further interpretation of the rorringtoniids is limited by the lack of significant modern systematic treatment and illustration of taxa. The surface sculpture, the lateral parts of the cranidia (e.g. posterior fixigena) and the connection of the posterior border furrow with the occipital furrow are regarded here as being crucial for degtermining relationships within the rorringtoniids.

Discussion of the lifestyle of *Cyamella*

Unlike the blind *Isocolus* and *Ityophorus*, *Cyamella stensioei* possesses well-developed eyes, which would be untypical for a cavity dweller. However, it is assumed, that the interval represented by the pockets was possibly too short for evolutionary adaptations to the cavity environment to develop (e.g. eye reduction). A cave-dwelling lifestyle has been suggested for some recent and fossil arthropods including examples in the ostracods (Aubrecht & Kozur 1995) and amphipods (Stock & Iliffe 1990).

Cyamella stensioei could have been a visitor to the cavities, possibly for moulting (Suzuki & Bergström 1999; see Chatterton et al. 2003). However, if there was ready access to the cavities, why are there no other macrofaunal elements such as ostracods or (micro-)gastropods – as was the case for the pockets containing *Isocolus sjoegreni* and *Ityophorus undulatus*? Given their smaller size, ostracods and gastropods would have had easy access to these shelters. It is more likely that *C. stensioei* inhabited a specific palaeoecological niche (see Owens in Owens & Hammann 1990) with restricted access (size) or other limiting environmental conditions (food, oxygen supply). The presence of pyrite in differing concentration in some samples indicates the possibility of lowered oxygen (dysoxic) conditions. A chemosymbiotic lifestyle, analogous to olenid trilobites and possibly for *Aulacopleura konincki* (Barrande, 1846) as discussed by Fortey (2000), could have been a possible adaptation for the aulacopleuroidean trilobite *C. stensioei*. Although differing from olenid morphology, this possible adaptation could be supported by the relatively thin exoskeleton of *C. stensioei*, its enlarged pleural field (see criteria of Fortey 2000), the monospecific (but in situ) accumulation and the presence of pyrite in the surrounding fine grained sediments. Chemosymbiosis with sulphur-metabolizing bacteria is common in low-oxygen, hydrogen-sulphide-rich environments (see Joye et al. 2004; Levin 2005; Van Dover & Fry 1994; Van Dover 2002; Zbinden et al. 2008). However, chemosymbiosis in soft tissues is unlikely to be reflected in the exoskeleton. Unlike the morphologically similar off-reef taxon *Rorringtonia*, for which the particle feeding was suggested by Fortey (2006), *C. stensioei* possibly could have fed on microbial mats like the recent vent shrimp *Rimicaris exoculata* Williams & Rona, 1986 (see Van Dover et al. 1988). The presence of such biofilms inside the cavities of the Boda mounds has been shown by Suzuki & Bergström (1999). For *C. stensioei,* a cavity-dwelling lifestyle analogous to that of *I. sjoegreni* and *I. undulatus* on the bottom of former cavities (Suzuki 2002) is therefore advocated.

The pockets in the Boda Limestone are of unknown origin. Based on the differing lithologies from the pockets, it seems likely that various depositional processes were involved. It is possible that some pockets formed as former seepage conduits, which might have initialised the mound formation (see Naeth et al. 2005). A mixture of partly stabilised hollows within the microbial framework of the limestone and conduits could possibly enable the well-adapted *C. stensioei* to colonise this restricted environment. Collapsing open spaces could have trapped the trilobites, leading to starvation or direct burial in life position (see Popp & Rohde 2010). Although there seem to be possible connections between fault structures and fluid pathways and the genesis of mounds, the whole concept is not yet fully understood (Huvenne et al. 2007; Naeth et al. 2005; see Hovland & Svensen 2006) and is beyond the scope of this paper.

Conclusions

Judging from the taphonomic and lithologic characteristics of the monospecific accumulations investigated, the results are taken as a primary signal of variability in *Cyamella stensioei*. Our study shows:

1.) Based on morphometric investigations it is concluded that not all individuals of *C. stensioei* belong to one generation. Meraspis stages and smaller exoskeletal parts were recognised. Several instars of the early holaspid stage are probably present within the data set.

2.) The biometrically investigated samples from the two localities, Kallholn and Unskarsheden, do not show morphologic differences, indicating broadly coeval populations and a short time span for the occurrence of the *Cyamella*-bearing pockets. The comparison between the different samples of *Cyamella* pockets on the one hand and other pockets containing trilobites such as *Ityophorus* or *Isocolus* on the other hand reveals the complexity of, and differences in, sedimentation within these former open space structures.

3.) Pockets containing *C. stensioei* are regarded as being *in situ* sediments in open space structures of late Hirnantian age. *C. stensioei* is regarded here as a cavity-dwelling organism, being extremely tolerant to restricting environmental factors and possibly adapted to an extreme environment by chemosymbiosis.

4.) Some of the pockets in the mounds of the Boda Limestone are interpreted as possible former seepage conduits.

5.) The comparison of cranidial characters of *Cyamella stensioei* enables a reassessment of the genus *Paracyamella* Zhou & Xiang, 1993.

6.) Relationship to other rorringtoniid trilobites can be shown on the basis of specific characters as the surface structure, the lateral parts of the cranidia (e.g. posterior fixigena), the position of eyes and the connection of the posterior border furrow with the occipital furrow. These characters are of high systematic significance. Further investigations on the phylogeny of rorringtoniid trilobites are needed to make sophisticated statements.

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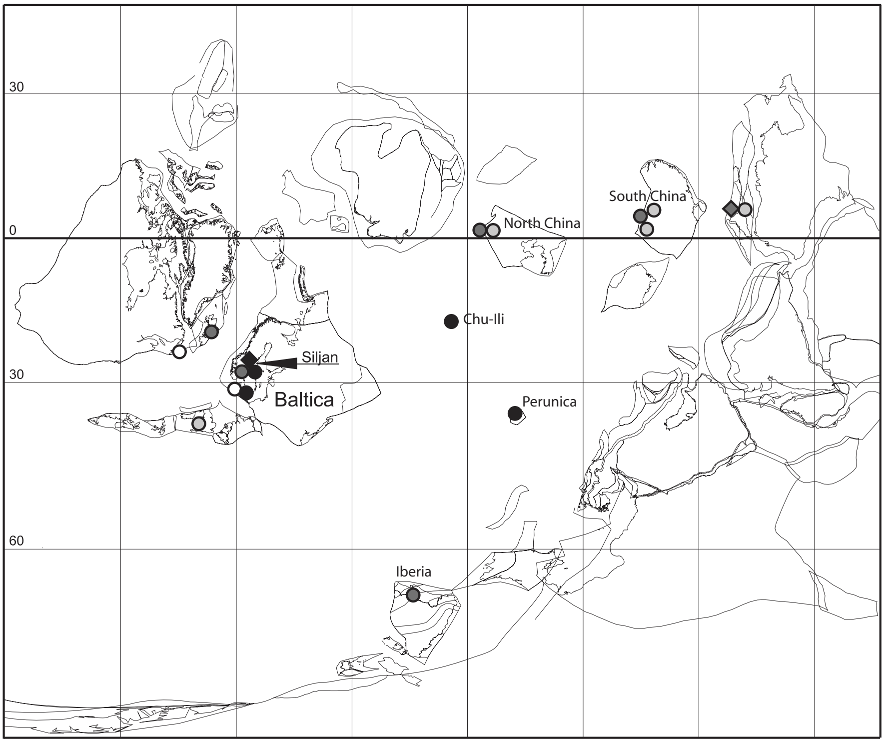


Fig. 1. Palaeogeographic distribution of *Cyamella* (rhombs), and *Rorringtonia* and *Paracyamella* (solid circles) during the Late Ordovician. Different time slices are represented as follows: white infill for Darriwilian; light grey infill for the latest Darriwilian to the early Sandbian; dark grey for the late Sandbian to the early Katian; black for the late Katian to Hirnantian. Map generated using the T.H. Torsvik's GIS-oriented software from 2009, BugPlates: Linking Biogeography and Palaeography.

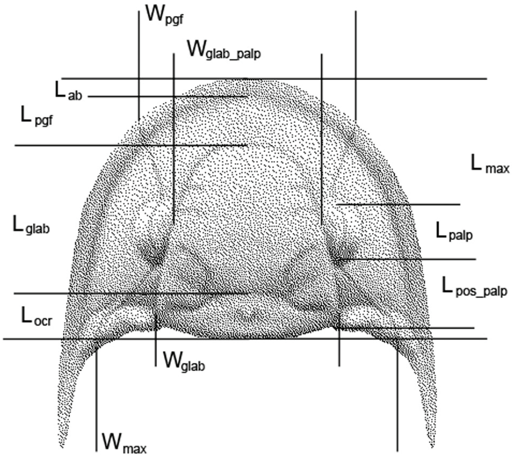


Fig. 2. Key measurements on the cranidium of Cyamella stensioei. L indicates length and W stands for width. Abbreviations are: ab, anterior border; glab, glabella; glab_palp, glabella at palpebral lobes; max, maximum; ocr, occipital ring; palp, palpebral lobes; pgf, preglabellar field; pos_palp, position of palpebral lobes.

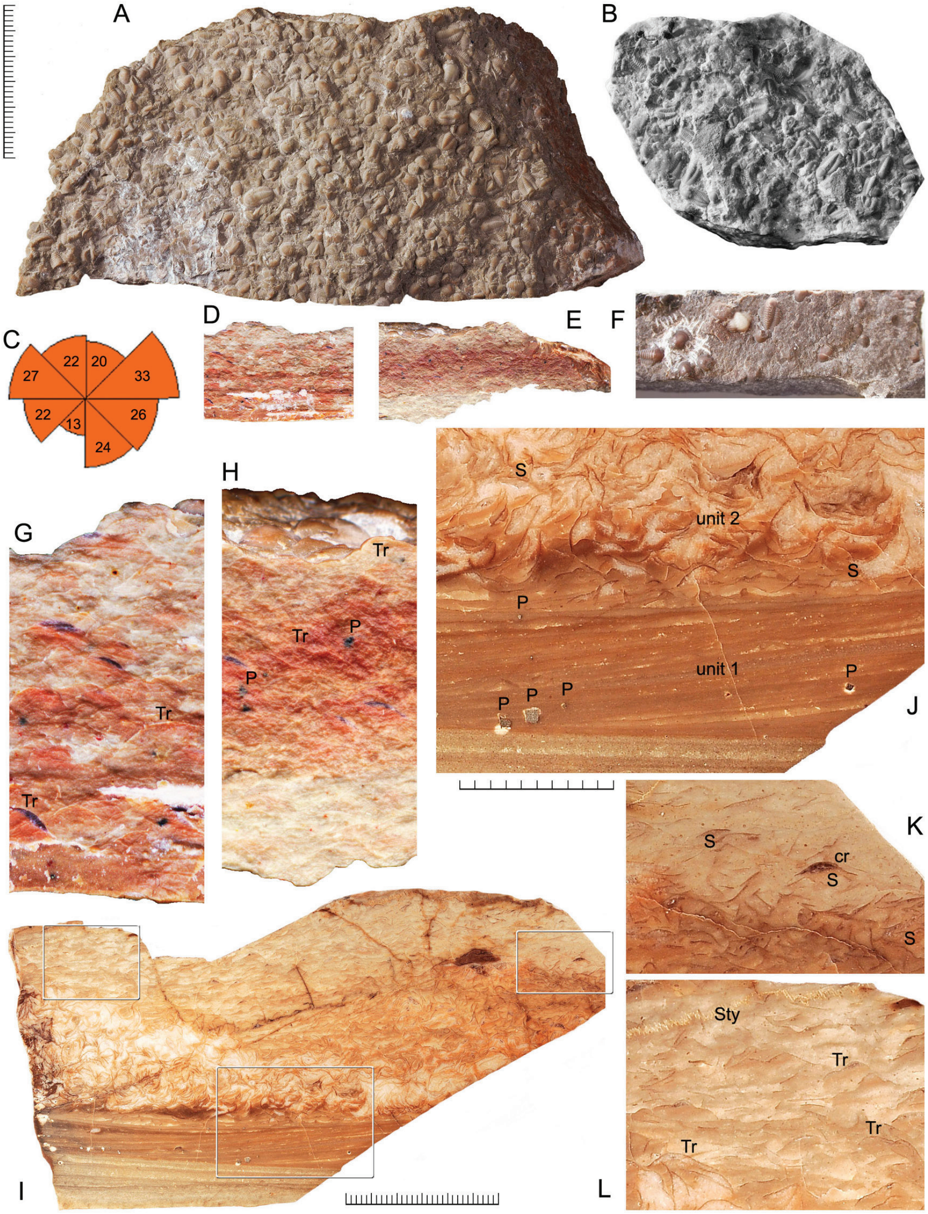


Fig. 3. Studied rock samples showing accumulations of Cyamella stensioei. A, top surface view of K1, Kallholn; B, top surface view of U2, Unskarsheden showing a dense spacing of completely preserved trilobite exoskeletons; C, taphonomic information from the surface of K1 as a rose plot (total: n= 187; cranidia: n= 52, pygidia: n= 75, thoracic elements: n= 60); plot is oriented according to the surface of K1 as figured in A.; D, G, side views of K2, Kallholn ; G, showing convex-up orientation of trilobites (Tr) in enlarged detail; E, H, side views of K1 Kallholn, showing closely spaced trilobite exoskeletons; H, note the convex-up orientation of trilobites (Tr) and the pyrite crystals (P). F, top surface view of K3, Kallholn; note the wider spaced trilobite exoskeletal parts; I–L, vertical section of sample Sol1, Solberga; I, differing lithologies of unit 1 (bottom) and unit 2 (top) are recognisable; J, detail of I, showing the boundary between the two units, note the abundant large pyrite crystals (P) in unit 1and the geopetally arranged sparite (S) below trilobite remains in unit 2; K, detail of I with increasing degree of orientation in trilobite remains from bottom to top, note sparite cement (S) below trilobite cranidium (cr); L, detail of I, showing the horizontal arrangement of trilobite remains, note the high degree of articulation in trilobites (Tr) and the stylolithic suture (Sty). Scale bar is 30 mm long and relates to all samples except for G, H and J–L, which are enlarged three times compared with others (see smaller mm scale bar below J).

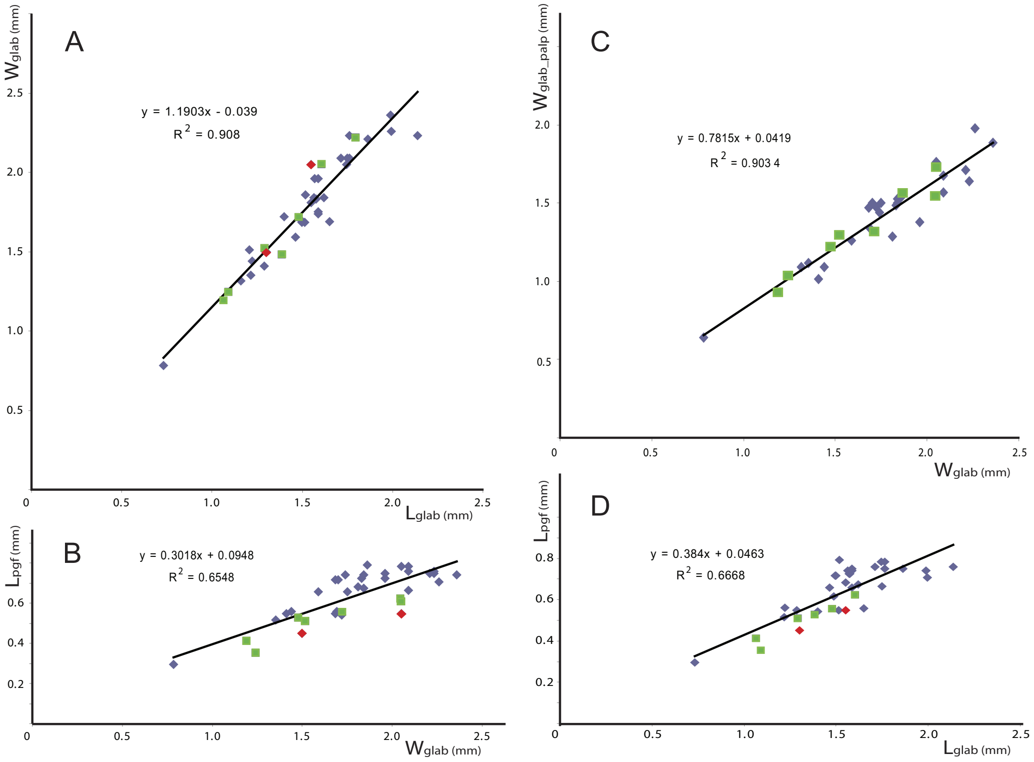


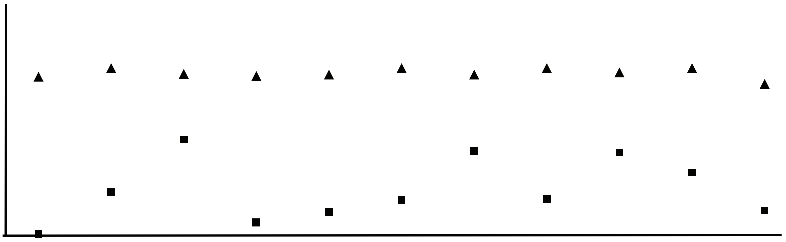
Fig. 4. Measured values for selected cranidial sections of Cyamella stensioei plotted for the localities Kallholn (blue rhombs) and Unskarsheden (green quadrangles) and a reference for holotype and paratype (red rhombs) from Kallholn. Note the spaced accumulation of points. A, Plot for glabellar length (Lglab) against glabellar width (Wglab). The plots for both localities are arranged along the regression line. B, Plot for glabellar width (Wglab) against length of preglabellar field (Lpgf). The data for Unskarsheden plots below the regression line, maybe caused by the low number of available points. C, Plot for glabellar width (Wglab) against glabellar width at palpebral lobes (Wglab_palp). D, Plot for glabellar length (Lglab) against length of preglabellar field (Lpgf). All abbreviations as Fig. 2.

samples	K1	K2	K3	U1
top surface	2.08	2.25		2.11
lower surface	2.42	2.26		2.16
2 cm below the surface with *Cyamella*			2.42	

Table 1. δ13C isotope values for Cyamella-pockets of Kallholn (K) and Unskarsheden (U) localities in the Siljan area, Sweden. Note that the values are positive and given in parts per mil (‰).

	Lmax_K	Lmax_U	Lglab_K	Lglab_U	Wmax_K	Wmax_U	Wglab_K	Wglab_U
N:	32	5	33	7	19	2	32	10
Mean:	2.87	2.59	1.55	1.39	3.31	2.83	1.8	1.78
Var.:	0.19272	0.25305	0.074153	0.071167	0.31717	0.5408	0.11399	0.17912
p(same):	0.1985		0.1639		0.267		0.8713	

Table 2. Student's t-test (two samples), separated by localities K and U, for selected cranidial measurements (Lmax, Lglab, Wmax, Wglab). A local signal can be excluded by the presence of same means in the different samples.



	Lmax_K	Lmax_K*	Lmax_U	Wmax_K	Wmax_K*	Lglab_K	Lglab_U	Wglab_K	Wglab_U	Wglab_palp_K	Wglab_palp_U
▲Shapiro-Wilk W	0.9083	0.9574	0.9231	0.9104	0.9211	0.96	0.92	0.9558	0.9327	0.9585	0.8683
■ p(normal)	0.0102	0.2492	0.5499	0.0754	0.1352	0.21	0.49	0.2107	0.4754	0.3628	0.1451

Fig. 5. Shapiro-Wilk test for normal distributions. All sample sizes are above N= 3. Note the change of Lmax_K, if the meraspid value is excluded. Asterisk * marks data excluding the meraspis. This analysis gives no reason to assume a non-normality of the samples. All abbreviations as Fig. 2.

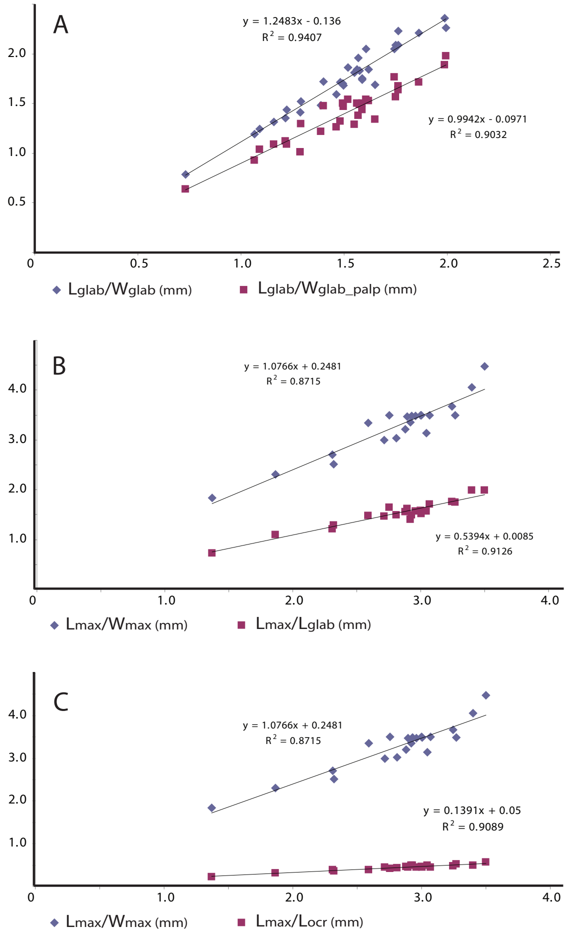


Fig. 6. Plots for different samples for length and width measurements of C. stensioei cranidia. One value at the x-axis is plotted against two values at the y-axis. Note the gathering of data points along the regression lines, possibly representing instars; lowermost data point for K1_meraspis. A, Lglab (n= 31) against Wglab and Wglab_palp; B, Lmax (n= 21) against Wmax and Lglab; C, Lmax (n= 21) against Wmax and Locr. All abbreviations as Fig. 2.

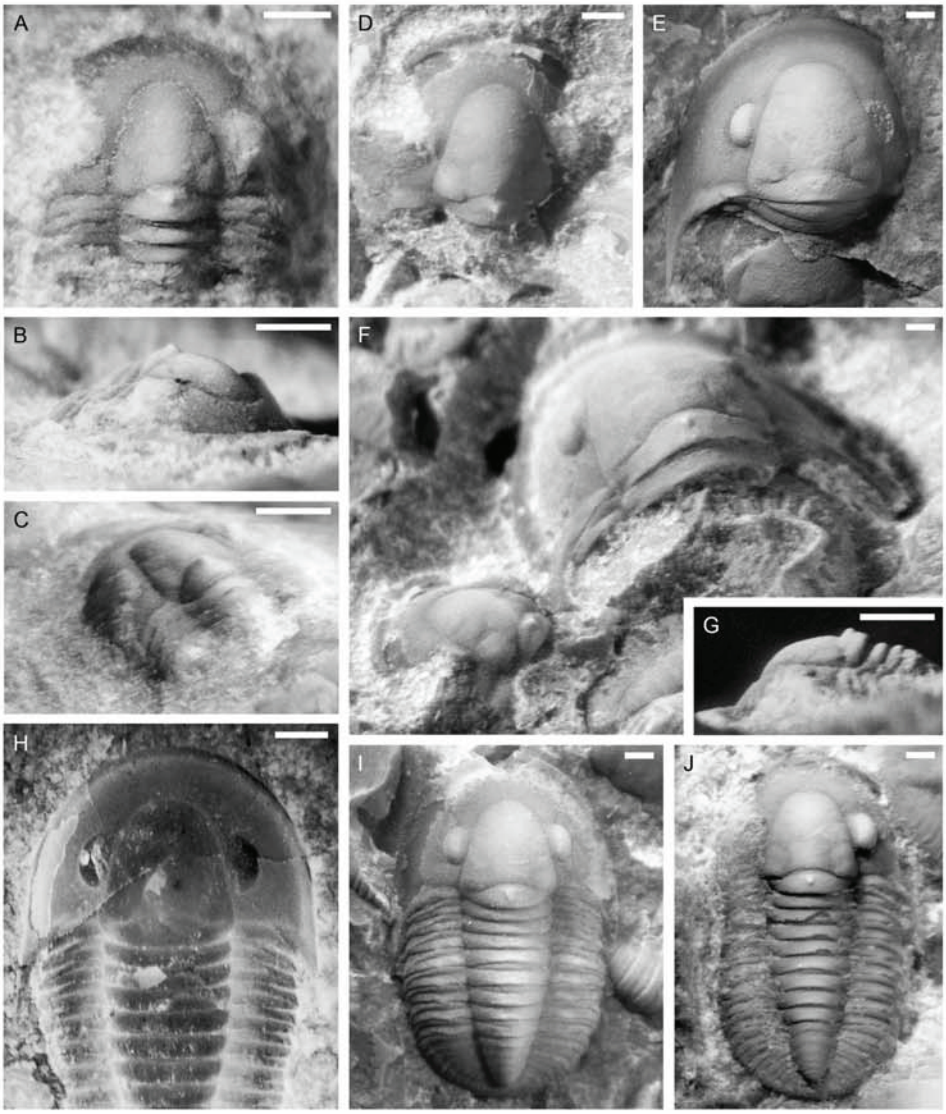


Fig. 7. *Cyamella stensioei* (Owens, 1979) from Boda Limestone Formation, Siljan district, Sweden. **A–C, G**, RM Ar45665: K1_meraspis, the meraspid cephalothorax with free cheeks slightly preserved, photographed in dorsal, antero-lateral, postero-lateral, and lateral views. **D**, RM Ar45665: K1_cr12, dorsal view of a juvenile holaspid cranidium. **E**, RM Ar45665: K1_cp11, dorsal view of holaspid cephalon. **F,** RM Ar45665: K1_cr12, and _cp2, postero-lateral view showing the changes in basal part of the glabella, and the development of occipital ring and furrow in younger and older individuals. **H**, GIT 436-67-5: U2_ctp5, ventral view of a nearly complete specimen, showing the smoothened inner morphology of the glabella. **I**, RM Ar45665: K1_ctp1, dorsal view of complete specimen. **J**, GIT 436-67-1: U2_ctp1, dorsal view of complete specimen. **A-G, I,** Kallholn; **H, J**, Unskarsheden. Scale equals to 1 mm.

Fig. 8. Sketch of discussed rorringtoniid trilobites listed according to their palaeogeographic and stratigraphic position. Capital letters in the sketch indicate adult stages whereas lower case letters indicate juvenile specimen. A, Phaseolops? sp. of Whittington 1965 from the middle Darriwilian of western Newfoundland. B, Rorringtonia sp. from a geschiebe of Red Orthoceratite Limestone indicating the presence of this taxon during the Darriwilian in Baltica; see Popp 2007, figured here. C, Rorringtonia kennedyi Owens, 1981 from Wales. D, Rorringtonia kennedyi Owens, 1981 from Wales. E, Rorringtonia flabelliformis Whittard, 1966 from the Rorrington Shale Formation, Wales. F, Paracyamella subacuta Zhou & Xiang, 1993 from the Pagoda Limestone in South China. G, Paracyamella subacuta Zhou & Xiang, 1993 from the Pagoda Limestone in South China. H, Paracyamella hujiabaensis Zhou & Xiang, 1993 from the Pagoda Limestone of South China. I, Rorringtonia vetula (Reed, 1935) from the Balclatchie Group of Girvan, Scotland. J, Rorringtonia ursina (Owens, 1970) from the Frognerkilen Formation, Oslo region, Norway. K, Cyamella sp. 1 of Fortey, 1997 from the Pa Kae Formation, Southern Thailand. L, Rorringtonia scanica (Olin, 1906) from the Lindegård Mudstone Formation in Scania, Sweden. M, meraspis stage of Cyamella stensioei Owens, 1979 from the Boda Limestone, Sweden; figured herein (Fig. 7 A–C, G). N, C. stensioei holaspis stage.

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