

**EARLY ORDOVICIAN TRILOBITES
OF SUBORDER CHEIRURINA
IN ESTONIA AND NW RUSSIA:
SYSTEMATICS, EVOLUTION AND
DISTRIBUTION**

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This dissertation is accepted for the commencement of degree of Doctor of Philosophy (in Geology) at the University of Tartu on October, 21, 2004 by the Council of the Faculty of Biology and Geography of the University of Tartu.

Opponent: Prof Per Ahlberg

The thesis will be defended at the University of Tartu, Vanemuise 46, room 246, on December, 17, 2004.

Publication of this thesis is granted by the Faculty of Biology and Geography, University of Tartu.

Taxonomic disclaimer: This doctoral thesis and included unpublished article are not a publication in sense of International Code of Zoological Nomenclature.

Autoriõigus Helje Pärnaste, 2004

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Dedicated to Armin Aleksander Öpik
and *Krattaspis viridatus*
for teaching me
the trickiness of the Trilobite World

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LIST OF ORIGINAL PUBLICATIONS

- I. **Pärnaste, H.** 2003. The Lower Ordovician trilobite *Krattaspis*: the earliest cyrtometopinid (Cheiruridae) from the Arenig of the east Baltic. *Special Papers in Palaeontology*, 70, 241–257.
- II. **Pärnaste, H.** (accepted) The earliest encrinurid trilobites from the East Baltic and their taxonomic interest. *Palaeontology*.
- III. **Pärnaste, H.** 2004a. Revision of the Ordovician cheirurid trilobite genus *Reraspis* with description of the earliest representative. *Proceedings of the Estonian Academy of Sciences, Geology*, 53, 2, 125–138.
- IV. **Pärnaste, H.** 2002. The Lower Ordovician Pilekiidae and Pliomeridae (Trilobita) of Baltoscandia. In: Satkunas, J. and Lazauskiene J. (eds). *The Fifth Baltic Stratigraphical Conference. “Basin Stratigraphy — Modern Methods and Problems”, Extended Abstracts*. Geological Survey of Lithuania, Vilnius, 151–153.
- V. **Pärnaste, H.** 2004b. The trilobite zonation of the Billingen Stage in the East Baltic. In: Hints, O. and Ainsaar, L. (eds). *WOGOGOB-2004 Conference Materials*. Tartu University Press, Tartu, 81–82.

ABSTRACT

This study is focusing on taxonomy, ontogeny and phylogeny of the Lower Ordovician trilobites of suborder Cheirurina (Papers I–IV), with the implications to trilobite distribution and zonation in Baltoscandia (Papers I and V). As the studied trilobites include the earliest representatives of several phylogenetic lineages, one of the aims of this study was to contribute to better understanding of systematics and phylogeny of different cheirurin families.

Paper I deals with the first representatives of the family Cheiruridae, clearing up concept of genus *Krattaspis*, whose holotype is affected by some distortions, consequently carrying several characters misleading earlier researchers. Some trends in ontogeny and phylogeny of *Krattaspis* are first described. The concept of subfamily Cyrtometopinae established by Öpik is restricted to include more homologous group. Paper III includes the revision of another cyrtometopine genus *Reraspis* and the description of its first representative. Papers I and III discuss also the relationships of the described genera with other cyrtometopine genera.

The earliest representative of subfamily Encrinurinae is described in Paper II, where taxonomy of other Ordovician encrinurids, and especially that of the *Encrinuroides sensu lato* is discussed. In addition, two new characters distinguishing Encrinurinae and Cybelinae from each other are introduced to support the monophyly of these subfamilies. Paper IV shows the distribution of pliomerid and pilekiid trilobites in the Baltoscandian palaeobasin and reveals trilobite characters specific to the near-shore facies (in the northern East Baltic). This short paper is the first step on handling of this group. Paper V gives a preliminary account on the trilobite zonation of the Billingen and Hunneberg stages in the Estonia and northwestern Russia.

INTRODUCTION

Trilobites are extinct marine arthropods with calcified exoskeleton (Fig. 1). Their body is divided by furrows longitudinally into medial and lateral regions and transversely into cephalon, thorax and pygidium. Mostly, only the mineralised portion of the cuticle, the exoskeleton is preserved, usually partially or wholly disarticulated, or even in a fragmentary state. Growth of the exoskeleton proceeded by moulting and therefore the fossil-remains of these animals are relatively common. With more than 5000 genera (Jell and Adrain 2003) trilobites are among the most abundant fossils in the Palaeozoic. They appeared quite suddenly early in Cambrian, evolved rapidly during the Cambrian and Ordovician, dominating among the Ordovician faunas. The composition of trilobite fauna changed repeatedly being controlled by major events in the Earth history. The extinction periods were usually followed by recovering and a new evolution, however, they did not survive the major extinction in late Permian.



Figure 1. Reconstruction of the earliest cheirurin trilobite of the Baltoscandia, the pilekiid *Parapilekia speciosa* (Dalman, 1827) (Paper IV), and one of the earliest cheirurins found from Estonia, cheirurid *Krattaspis viridatus* Öpik, 1937 (Paper I).

The suborder Cheirurina Harrington and Leanza, 1957 appeared in early Tremadoc and became extinct in the Middle Devonian Taghanic — *Pharciceras* “Extinction Event” (Feist 1991). The earliest cheirurins were Pliomeridae Raymond, 1913 and Pilekiidae Sdzuy, 1955, followed by Encrinuridae Angelin, 1854 and Cheiruridae Hawle and Corda, 1847. The exact ancestral relationships of these families and their subfamilies remain unclear due to the sparse fossil record of this group, especially at the beginning of its radiation. The studies by Öpik (1937), Whittington (1961), Lane (1971), Demeter (1973), Evitt and Tripp (1977), Přibyl *et al.* (1985), Edgecombe *et al.* (1988), and Lee and Chatterton (1997) have contributed to the understanding of Cheirurina. This thesis and related articles present a new data and discuss the phylogeny of this suborder.

In the Baltoscandian Ordovician palaeobasin the earliest representatives of suborder Cheirurina appear simultaneously with the beginning of the carbonate sedimentation, i.e. in Varangu time (late Tremadoc) in its western part, and in Billingen time (or late Hunneberg ?) (middle Arenig) in the eastern part of the basin. The last records of cheirurins are from the very sparsely preserved

Ludlow, Silurian. Likewise, the Silurian was the time of the global extinction of several cheirurina lineages. The East Baltic Cheirurina have been studied previously by Nieszkowski (1857, 1859), Schmidt (1881, 1907), Öpik (1937), Jaanusson (1940), Rosenstein (1941), Ralf Männil (1958), Reet Männil (1968, 1977), Edgecombe and Ramsköld (1996), and Lane (2002).

The aim of this work was to study the earliest representatives of different trilobite families of suborder Cheirurina focusing on taxonomy, ontogeny and phylogenetic relationships of cyrtometopines, encrinurines and related (sub)families. The results of these studies were used in the context of revealing the trilobite distribution and zonation in the East Baltic. The framework of the revised zonation, based on many trilobite groups, allowed more precise estimation of the stratigraphic level of studied specimens, that is crucial for phylogenetic discussions.

1. GEOLOGICAL SETTING AND PALAEOGEOGRAPHY

According to the palaeogeographic reconstructions based on palaeomagnetic data, the Baltica palaeocontinent was located at temperate southern latitudes in the Early Ordovician, bordered from the East by the Iapetus Ocean. The north-eastern part of Baltica was influenced by the Palaeotethys Ocean and the southern part by the Tornquist Sea (Fig. 2). (Scotese and McKerrow 1990, Torsvik 1998). The Baltoscandian Palaeobasin was a cold epicontinental sea at the margin of the Iapetus Ocean. Like most Early Ordovician shelf fauna of the Baltoscandia, the trilobites are fairly unique, showing relative isolation of this basin. The olenid trilobites were prevailing in the early Tremadoc and the asaphids in the Arenig. However, some faunal exchange of benthic shelf trilobites of Baltoscandia with the other provinces took place occasionally, in addition to the global dispersal of several pelagic trilobites.

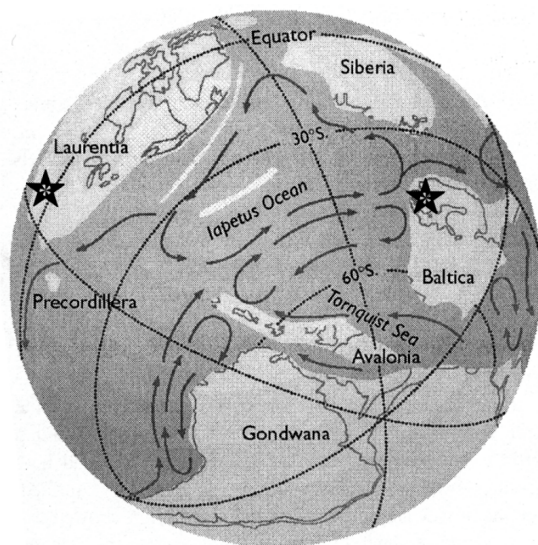


Figure 2. Early Ordovician (Arenig) palaeogeography of the Iapetus Ocean and the Baltica Continent and the ocean circulation (cyclonic and anticyclonic gyres — see arrows) after Christiansen and Stouge (1999), who roughly followed Torsvik *et al.* (1992) positioning the Baltica. Stars mark distribution of the benthic shelf cheirurid trilobite genus *Hintzeia* Harrington, 1957 (see data Hoel, 1999) across the Iapetus Ocean.

Sediments of the Baltoscandian epicontinental sea show rather low rate of deposition, namely 1–3 mm /1000 years (Lindström 1971, Jaanusson 1976, 1982). Usually, the Ordovician succession is less than 200 m thick, and is

nearly horizontally bedded. The deposits are rhythmically bedded, with regionally numerous breaks caused by repeated fluctuation of depth of the sea or by appearance of submarine non-deposition or denudation, although, they are continuous basin-wide (Jaanusson 1982). Beds are undisturbed tectonically except those in the Oslo Region, where they are folded, cleaved and thrust, reaching 500 m in thickness (Owen *et al.* 1990). In addition, sparsely distributed allochthonous deposits follow the 1800 km long Caledonian front (Bruton *et al.* 1985). The studied area, northern Estonia and Ingria (the old province of St. Petersburg region between the rivers Narva and Syas) constituted the shallowest part of the basin. During the Hunneberg and early Billingen time the terrigenous sediments were settling in the east (Estonia and Ingria), whereas the limestones and shales were deposited westwards (Sweden and Oslo Region) (Fig. 3).

In Estonia, the Lower Ordovician succession is represented by quartzose sandstones of Kallavere Formation, dark laminated graptolite shales of Türisalu Formation and light claystone of Varangu Formation of Tremadoc age, followed by glauconitiferous silts, sands and calcareous sandstones of Leetse Formation, and glauconitic limestones of Toila Formation (Männil and Meidla 1994). First trilobites occur in the upper part of the Leetse Formation, the Mäeküla Member (Papers I, II; text-figs. 2).

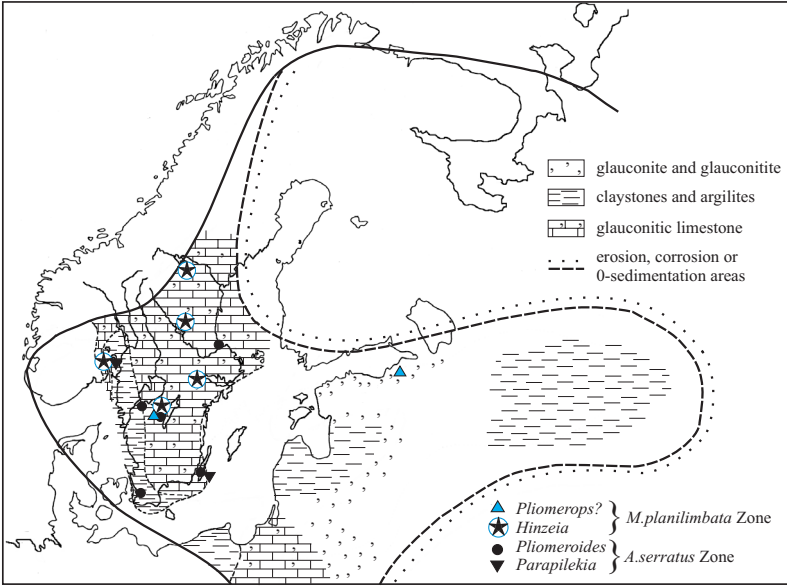


Figure 3. Facies distribution of Baltoscandian palaeobasin during Hunneberg (modified after Erdtmann 1965, Erdtmann and Paalits 1994), showing the chelurur data, and for comparison the Tremadocian chelururins from the *A. serratus* Zone.

The Mäeküla Member consists of alternating variously dolomitized glauconitic sandstone, calcareous sandstone and glauconitic sandy limestone, with clay films or layers often covering discontinuity surfaces. Disarticulated skeletal parts of the trilobites are often preserved on the upper or lower surface of sandstone layers (Fig. 4A) or on nodules covered by clay (at Jägala, Nõmmeveski, Saka). The clay probably protected the fossils from dolomitization and dissolution observed in sandy beds, where rare poorly preserved molds of asaphid fragments turn up. Most of the testiferous cranidia of cheirurid *Krattaspis* Öpik, 1937 discovered from the surfaces occur upside down and are tilted forwards to lie on the anterior glabellar lobes, or backwards on the posterior glabellar lobes (Fig. 4A). Often they are also tilted sideways on the fixed cheek. Probably this was the most stable attitude, although it is the reverse to the results of the experiment described for *Flexicalymene* Shirley, 1936 (Lask 1993, p. 222), which were preserved mainly upside upwards (concave-down). The cephalon of *Krattaspis* are also flattened and glabella and furrows are deformed or even distorted (see Paper I, text-fig. 6). Deformation was probably the result of compression by relatively large sand bodies deposited during bigger storms. The clay films and layers were settling during the quiet periods at a very low rate of deposition, when the sediment was reworked by soft-bodied fauna leaving horizontal and flattened burrows filled with clay. Some thin soft clay layers contain three-dimensional well-preserved trilobites, when usually they are much deformed in claystone.

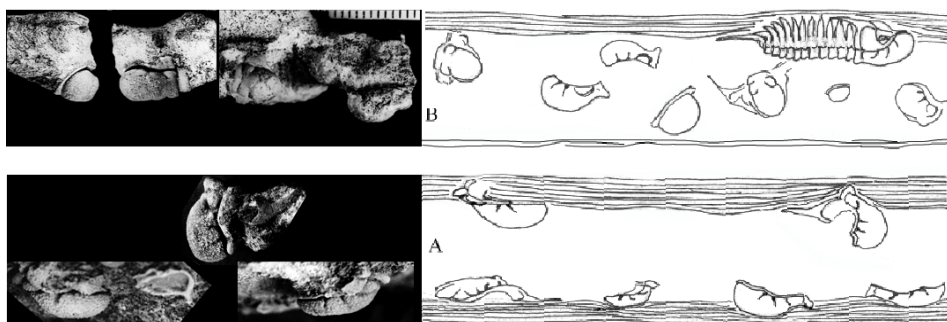


Figure 4. Orientation of trilobites: **A**, in the Mäeküla Member skeletal parts are mostly oriented upside down and lay on their anteriormost lobes (LA and L3), or on their posteriormost lobes (L2, L1 and L0) on the clayey surface; **B**, in the Vassilkovo Beds the skeletal parts are non-oriented and occur throughout the entire layer.

The trilobite sclerites are non-orientated and occur throughout the entire unit (Fig. 4B), in the Vassilkovo Beds (e.g. in Lava section), indicating rapid burial conditions or bioturbation (cf. Speyer 1987). The skeletal remains, varying in size, are better preserved probably due to the lower degree of dissolution within

this somewhat finer-grained sediment with higher content of the clay. Exceptionally, the preservational conditions of the Mäeküla Member in Harku trench resemble with that of Vassilkovo Beds containing trilobites throughout the beds.

The dolomitized limestone unit of the Päite Member is mostly 0.3–0.4 m thick in Estonia (Orviku 1960) but increases to 0.7 m in the St. Petersburg Region (Popov *et al.* 1997; Dronov *et al.* 1997a; Pushkin and Popov 1999), and is thickest (1.13 m) at the Tõrvajõe locality (Orviku 1960) in north-eastern Estonia. So far, *Krattaspis* has been found only from the lowest layer of the Päite Member at the Popovka locality. All specimens found from the lower surface of layer 9 (Paper I, text-fig. 3) were oriented upside down and deformed, similar to that in the Mäeküla Beds. Disarticulated sclerites of *Megistaspis* Jaanusson, 1956 are very abundant throughout the Päite Member, producing so called ‘trilobite cemeteries’ by several layers, similar to the lowest beds of the overlying Saka Member. Most commonly, the pygidia are preserved, being oriented upside down or opposite, arranged horizontally, showing some degree of sorting processes.

2. MATERIAL AND METHODS

2.1. The studied collections

In the lowermost Ordovician carbonate rocks of the East Baltic, trilobites are very rare. Only 55 specimens assigned to 18 species were previously recorded from the calcareous glauconitic sandstone of the Mäeküla Member (Schmidt 1904, 1907; Lamansky 1905; Öpik 1937; Balashova 1961, 1966). Most of that material was revised by Balashova (1966). Subsequent revision showed that only 15 species of the above 18 are valid (Papers I, V). The majority of specimens came from the Popovka River district close to Pavlovsk, the remainder from localities along the banks of the rivers Tosna, Izhora, Lava, and Volkhov in Ingria (the old province of St. Petersburg Region between the rivers Narva and Syas) (Fig. 5). Seven specimens have been found from Estonia, including the holotype of the type species of cheirurid *Krattaspis*, established by Öpik (1937), based on one incomplete cranidium with displaced hypostome (Paper I).

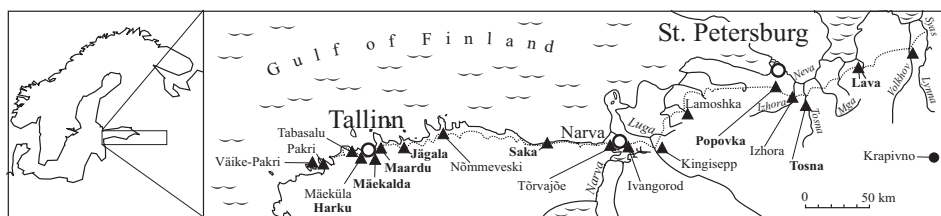


Figure 5. Locality map of sections in North Estonian and St. Petersburg regions showing sampled localities. The names of the sections studied bed-by-bed are written in bold. Dotted line shows the Baltic-Ladoga Clint (escarpment).

This study was initiated by Dr Leonid Popov who kindly gave me his trilobite collection from Ingria collected in 1960s and 1970s. The additional material is collected by the author during two expeditions to Ingria in 1986 and 1987, and during the fieldwork in Estonia. The new collections contain more than 50 specimens of *Krattaspis* (Cheiruridae) (Paper I); 26 specimens of *Encrinuroides* Reed, 1931, two specimens of *Cybele* Loven, 1845 (Encrinuridae) (Paper II), more than a hundred specimens of *Evropeites* Balashova, 1966 and two specimens of *Pliomerops* ? Raymond, 1905 (Pilekiidae, Pliomeridae) (Paper IV), as well as several hundreds of non-cheirurin trilobites (Paper V). Comparative cheirurin material was collected from analogous sandy deposits of somewhat younger beds (Paper III). This quantity of specimens has allowed to carry out morphometric studies for revealing the ontogenetic and phylogenetic aspects of the generic variability (Papers I and III).

Relevant cheirurid trilobites from Baltoscandia have been studied at the geological institutes of Tallinn and Tartu, and during several visits to different museums. A respectable set of bed-by-bed collected cheirurids (nearly 200 specimens) were studied at the Geological Museum of the Copenhagen University. The morphometric study of this Scandinavian material with comparison of asaphid data is in progress in cooperation with Dr Arne T. Nielsen. Some statistics is used for comparison of the facies and phylogenetic variability within the closely related *Krattaspis* (Paper I) (see below). The originals of Brögger, Skjeseth, Owen, Wandås, Ebbestad and Hoel were studied at the Paleontological Museum of the Oslo University (Papers I–IV). Another large collection of cheirurids was studied at the Swedish Museum of Natural History, where Professor Jan Bergström kindly showed me over 100 specimens from Östergötland, including *Cyrtometopus* Angelin, 1854, *Ceraurina* Cooper, 1953, *Paraceraurus* Männil, 1958, *Nieszkowskia* Schmidt, 1881, and *Pseudosphaerexochus* Schmidt, 1881 (Papers I, III). The earliest Baltoscandian cheirurids *Pliomeroides primigenus* (Angelin, 1854) and *Parapilekia speciosa* (Dalman, 1827) (the originals of Moberg and Segerberg 1906) were studied at the Department of Geology, Lund University (Paper IV). In addition, different collections are loaned from following institutions: Museum of Evolution at the Uppsala University, Geological Museum of the Copenhagen University, Department of Geology at the Lund University, and Paleontological Museum of the Oslo University (Papers I, IV, V). Professor Philip Lane from Keele University kindly sent me a latex copy of the type specimen of *Cyrtometopus clavifrons* (Dalman, 1827) (Paper I).

2.2. Sampling and preparation

The trilobite material was collected by different methods. First, trilobites were sampled bed by bed from the strata *in situ* in all the studied localities. Thickness of the sampled beds varied from 1 to 10 (rarely 15) cm. Slabs of sandstone covered by clay film were brushed clean in the river- or seawater to recover the fauna on the topside. Then the slabs were crashed down to the small pieces to detect fauna inside. Thin soft clay layers were washed through a 1-mm sieve to remove the clay, and observed under the microscope in the laboratory. Some layers were empty, but some were rich in different fauna (trilobites, brachiopods, ostracodes, bryozoans, echinoderms, and conodonts). Secondly, trilobites were traced on the loose boulders in localities where trilobites of the Mäeküla Member were preserved only on the outer surface of the particular beds. Some extent of weathering had revealed the fauna on top. As the lithology of different beds of these thin members is easily recognisable, it was possible to estimate roughly the stratigraphic level of these slabs.

Later, during the laboratory period, trilobites were prepared by removing the matrix under the microscope, using either needle or the pneumatic tool, when sandstone was enough compact. In cases of softer matrix, some soaking with water made the preparation with the needle much easier.

2.3. Measuring

Standardisation of orientations of measurements and illustrations was discussed during the First Trilobite meeting in Oslo in 1973. The results were summarised by Temple (1975), and three possibilities were suggested for a single-orientation method. However, these rules have not been always followed by different further authors. An image on a photo can vary remarkably on highly convex cheirurina taxa, depending on which plane has been taken as horizontal. It concerns, for example, the projection of length of the glabella, or its basal lobes (L0), which are the diagnostic characters for cheirurina. Therefore, this aspect is pointed out once more (Paper I), showing the effect related to chosen 'horizontal' planes (compare the posterior fixigena horizontal *versus* the palpebral lobe horizontal in Paper I, text-figs 6D, E *versus* H, I; and L *versus* M, N). Often, choosing any of these suggested planes (Temple 1975, p. 463) is complicated with such a fragmentary material as the studied one. Therefore dorsal and lateral views are organised sideways on the photo-figures for easier reading.

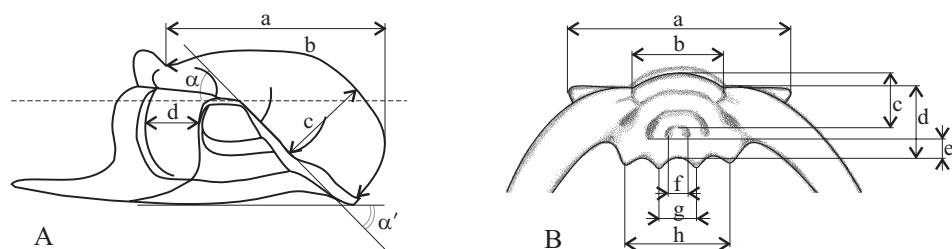


Figure 6. Diagram showing some measurements taken on specimens; **A**, cephalon; **B**, pygidium. Range of glabella excludes occipital ring. Pygidial axis is measured without terminal piece and anterior articulated half-ring.

There are two approaches for linear measurements: (1) taking them along the surface of the exoskeleton (Fig. 6A, b, from Paper I), or (2) as the projections in plan (Fig. 6A, a), when all specimens are oriented in the same 'horizontal' plane. Despite the single orientation method (2) had become prevalent in measurements in the part of systematic description, the conquering method (1) was used for this study after comparison of some results (see below). However,

where it was impossible, the first method (2) was used. Then the abbreviation ‘(proj.)’ is mentioned. All specimens were measured under the stereo-microscope, using a mm-paper (with very thin lines). Measurements were repeated 10 times, and the mean value was given with an accuracy of 0.1 mm. The accuracy higher than that was not reasonable as far most of the measurements were made from one furrow to the other, and defining their midpoint was too vague.

Comparative measurements of cephalon of *Krattaspis* (Fig. 7) and *Cyrtometopus* as well as *Nieszkowskia* showed that the length — width ratios of the glabella could vary a lot depending on the orientation of the specimen in the sediment (cf. Fig. 4). Here it is illustrated by the *Krattaspis*-evidence (Fig. 7B). The compression factor was considered in detecting the variation of characters when describing the type species *Krattaspis viridatus* Öpik, 1937 and three new taxa; *K. popovi*, *K. vitalis* and *K. sp. A* (see below, Fig. 15) (Paper I). Most effectively, this factor is reflected in features like the curvature down anteriorly or laterally of cephalon, course of genal spine; shape of glabella: length relations of its lateral lobes, course of the lateral furrows.

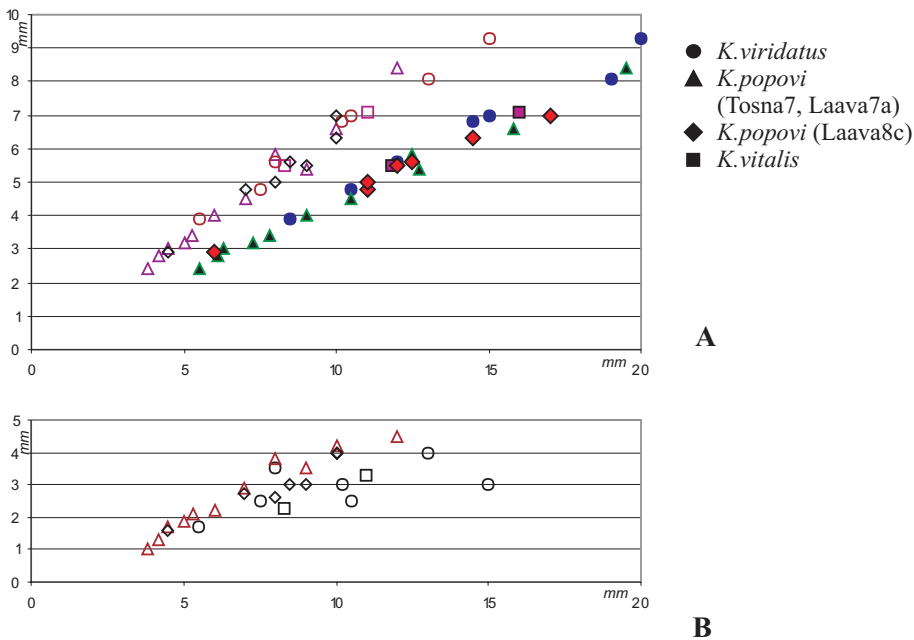


Figure 7. Scatter plots of length-width relations of different dimensions of *Krattaspis* cranidia. Empty markers show measurements as projections in plan (Fig. 6A, a) and shadowed markers as those measured along the surface of the exoskeleton (Fig. 6A, b). **A**, width of the glabella at basal lobes plotted against length of the glabella (without L0). **B**, high of the glabella anteriorly at the S3 furrow (Fig. 6A, c) plotted against the length of the glabella.

Measurements related to coaptation

The coaptation of an enrolled specimen of the *Cyrtometopus* (Paper I, text-fig. 5R–T) was studied to reveal the characters related to each other (Fig. 8). Simultaneous study was made by Lane (2002), when redescribing the type material of *Cyrtometopus*. In general, his results are improved by my statistics: e.g. the spines of rostral plate are fitting into the angle between the innermost and middle pairs of the pygidial spines. In contrast to Lane's interpretation, I think that the outermost pair of spines also took part in coaptation, and that spines of the specimen figured herein (Fig. 8; Paper I, text-fig. 5R–T), fit to the abaxial part of the embayment in anterior librigena just at the eyes, leaving some space for probably prominent antennula, giving some protection to both, the antennula and the eyes. As is seen in Figure 8, the spacing of the pygidial spines is concordant to the construction of the anterior border (the width of rostral plate, position of the rostral spines, the embayment of the anterior margin of cephalon (antennal notch) at the eyes, etc.). Hence the spacing of the pygidial spines serves the diagnostic interest, and is considered on describing the new taxa of *Krattaspis* (Paper I).

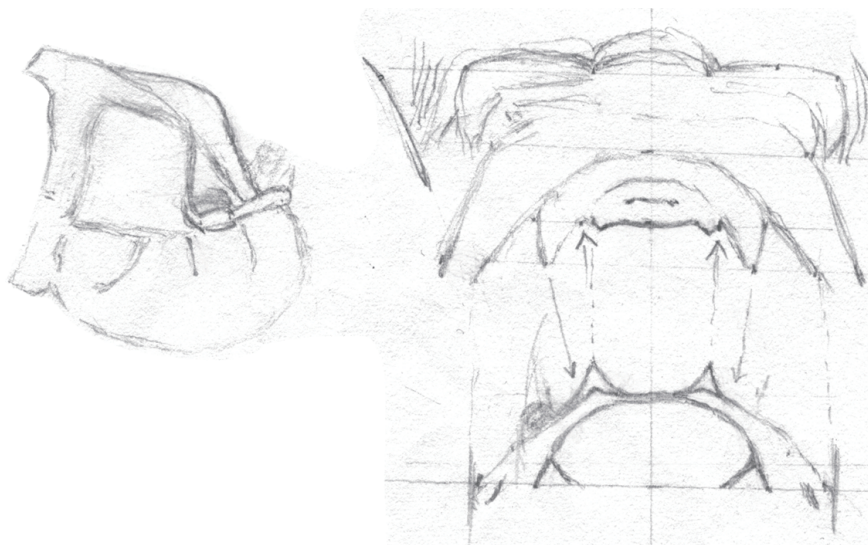


Figure 8. The sketch of coaptation of the enrolled *Cyrtometopus*.

3. SYSTEMATICS

3.1. Terminology and morphology

The descriptive terminology (Fig. 9) used throughout all papers mainly follows the revised Treatise on Invertebrate Paleontology, Part O (Whittington *et al.* 1997). Apart from where stated, all dimensions in sagittal or exsagittal directions are discussed in terms of length, and all dimensions in transverse direction in terms of width. Nevertheless, all cheirurin families have several specific characters and certain problems with defining some. That part of terminology is treated additionally below.

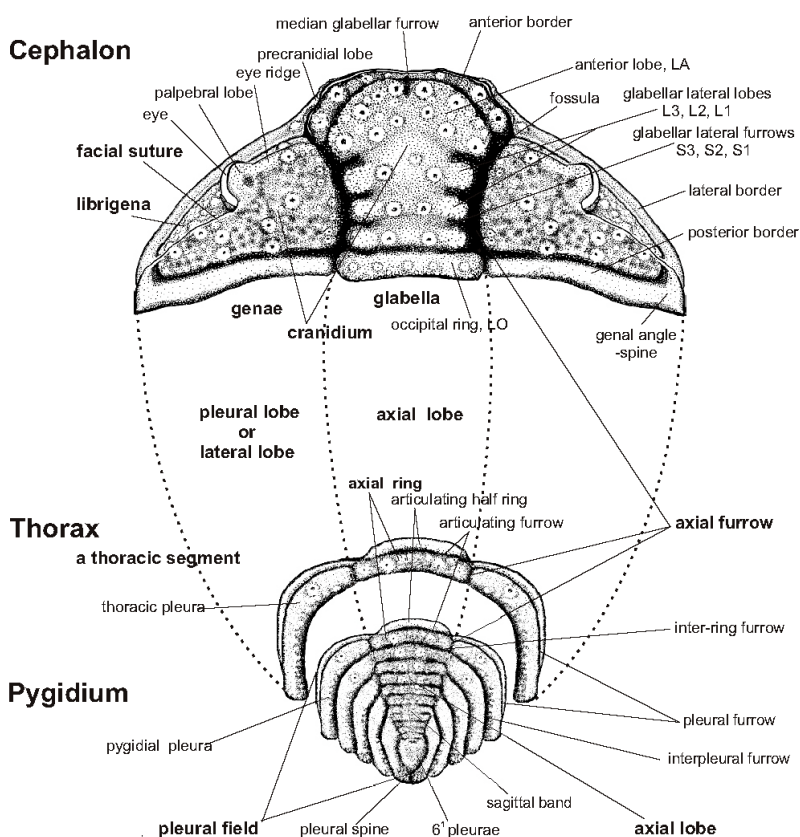


Figure 9. Schematic figure of the cheirurin trilobite, showing morphology of the exoskeleton (a reconstruction of the *Encrinuroides regularis* sp. nov. (Paper II)).

Notes on terminology specific to Cheiruridae (Papers I, III)

Three new terms are introduced, two of those (LM, LA) are for the glabellar lobes in addition to the traditional ones: L0, L1, L2, and L3 well employed within Cheirurina.

LM, used for the middle portion of the glabella between the frontal lobe and the occipital furrow and bounded laterally by the adaxial ends of lateral glabellar furrows.

LA, for the frontal lobe of the glabella situated between the preglabellar furrow and LM, and abaxially between S3 furrows.

Pre-eye-ridge fixigena, for the anterolateral triangular pitted area of the anterior fixigena ahead of the eye-ridge (synonym of 'triangular pitted area ahead of the eye-ridge') (Fig. 10A, B).

The characteristics of the pre-eye-ridge fixigena have been highly weighted in classification of the cheirurids, pliomerids and pilekiids (e.g. at the subfamilial level). Still, several miss-interpretations occur in recognition and delimiting it. One example is that with cheirurids with very narrow anterior fixigena, being nearly entirely covered by the eye-ridge. Latter is delimited from the pitted fixigenal field by the furrows, which are distinct in cheirurines and very shallow and ill-defined on cyrtometopines. The last group was characterized by Öpik (1937) as possessing the reduced eye-ridge, running from the palpebral lobe along the anterior suture at the edge of the anterior fixigena to the anterior border and not crossing the anterior fixigena. As the studied material shows, the eye-ridge still crosses the fixigena, ending at the fossula opposite of the anteriormost glabellar furrow S3 (Fig. 10A). Thus, the eyes are connected with the axial part of the cephalon (the glabella and hypostome) via the eye-ridge (Papers I, III), and is better seen on taxa with somewhat wider anterior fixigena like for example on the newly described *Krattaspis vitalis* (Paper I, text-fig. 9).

Investigation of the array of anterior furrow of the cephalon, meeting the axial furrow and S3 in relation the position of the fossula (Fig. 10), shows clear distinction in between these subfamilies (Cheirurinae vs Cyrtometopinae). Hence, the position of the fossula has been considered diagnostic at subfamilial level already within Encrinuridae it is reasonable to use that as well within Cheiruridae. The fossula of the cyrtometopines slopes deeply down rearwards into the axial furrow joining the S3 apodeme. That of the cheirurines curves down forward from the S3 furrow to meet the prefixigenal and the preglabellar furrows somewhat ahead (Fig. 10A vs B) (Paper III).

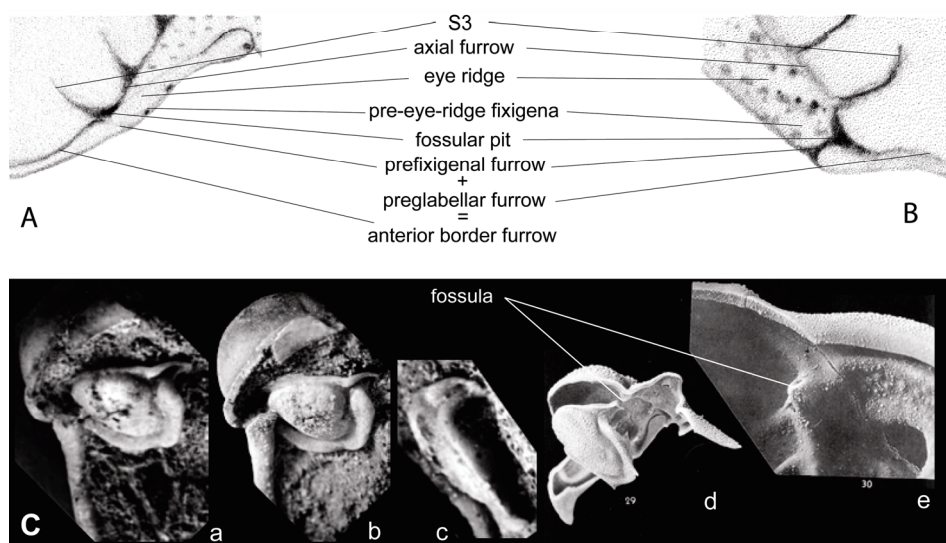


Figure 10. Position of the fossula in **A**, Cyrtometopinae (*Cyrtometopus*) and **B**, Cheirurinae (*Paraceraurus*). **C**, a–e, hypostomal attachment; a–c, *Krattaspis popovi* (from text-fig. 7, Paper I) (Cyrtometopinae), d–e, *Ceraurinella typa* Cooper, 1953 (from Whittington and Evitt, 1954, pl. 63) (Cheirurinae).

Notes on terminology specific to Encrinuridae (Paper II)

Terminology specific to the encrinurine exoskeletal morphology mainly follows Evitt and Tripp (1977). The terms ‘major row’ and ‘inter-row’ glabellar tubercles are adopted from Edgecombe and Chatterton (1987), and a ‘row of circumocular tubercles’ from Ramsköld (1986) with some addition (Fig. 11, from Paper II). Some characters, treated contradictory by different authors, follow (for detailed discussion see Paper II):

The lateral extent of the glabella is taken to be delimited by the fixigenal lobe distinguished by the pitted surface sculpture, when the abaxial ends of the lateral glabellar furrows and the axial furrow are effaced.

The tubercular notation is based on Strusz (1980) and Owen and Heath (1989), but with two exceptions (Fig. 11A). First, the major rows on the frontal lobe are marked by subscription as $4L_1$ and $4L_2$, corresponding to F4 and F6 of Strusz (1980). As the inter row tubercles represents the lobe area rather than furrows, the second exception presents an intermediate system for the inter-row notation using l (lower case) instead of S (Owen 1981) or i (a small roman numeral of Tripp 1957), though the number in lowered position counts the inter-rows at the particular lobe.

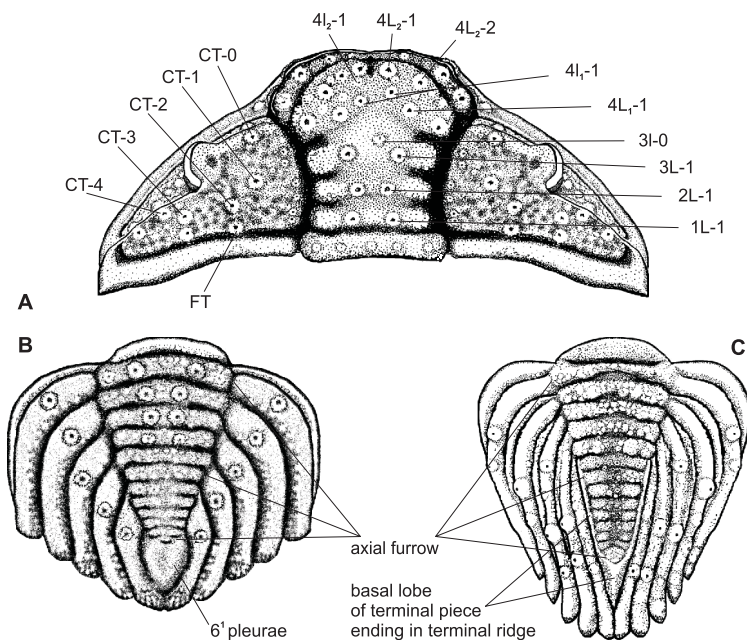


Figure 11. A, notation of the glabellar and fixigenal tubercles of encrinurine cephalon. B–C, differentiation of the axial part of pygidial terminal portion among the Encrinurinae (B) and Cybelinae (C).

FT, the **fulcral tubercle** is another prominent fixigenal tubercle, situating near the posterior edge of the fixed cheek on the connecting line between the eye and the outset of the posterior border doublure of cephalon. It marks the beginning of doublure with a slight curvature on the ventral side not clearly discernible in dorsal view. It is probably equivalent to the postocular tubercle (pt) of Evitt and Tripp (1977), which has been considered homologous to CT2 (Ramsköld 1986, Edgecombe and Chatterton 1987, Edgecombe *et al.* 1988). The appearance of the additional tubercle behind the ‘main ring’ of circumocular tubercles (e.g. CT2) in the newly described encrinurine throws doubt on that presumed homology.

CT0, the circumocular tubercle that is possessed on the eye-ridge is introduced in addition to those described by Ramsköld (1986).

The axial furrow of pygidium is recognised as delimiting the axial rings abaxially (see discussion by Temple and Tripp 1979, p. 228), leaving an intermediate area between the rings and the hindmost interpleural furrows. The area terminates sagittally in a variably developed post-axial termination, and is interpreted as a homology of the pleural rib(s) on encrinurines (Temple and Tripp 1979, Ramsköld 1986, p. 530) (Fig. 11B), and non-homology of that of cybelines (Owen and Tripp 1988, p. 280). The intermediate area with anterior bands of the pleurae of cybelines is called **a basal lobe of the terminal piece** herein (Fig. 11C).

The description of **continuity of pygidial pleurae and axial rings** is preferred to the number of congruent pygidial segments (see for discussion Temple and Tripp 1979). The first is often difficult to assess. However, the last is also depending on width-length-high relations to the number of pleurae and the angle between the pleural and axial furrows, and is therefore rather a graphical by-product, than the appearance of homology. Unfortunately, the system describing the pleural and axial ring relations, as used herein, is often impossible to use due to the insufficient preservation.

Pygidial doublure. The area underlying the tips of pleural ribs of pygidium is here following Whittington and Campbell (1967), Tripp, Temple and Gass (1977), referred to as the border, not as the doublure. The pygidial doublure is reflected ventrally and is not seen in dorsal or side-views. The pygidial border of encrinurids usually bears a variably developed groove, the vincular furrow reflected between the outer side of the border and ventral side of the spines. Analogous coaptative structure appears on some pliomerid and phacopid pygidia as well as on encrinurine cephalae.

* **The predominant evolving area** during the ontogeny and phylogeny. The area on the exoskeleton where it evolves on ontogeny and phylogeny, in the process of broadening — elongating and narrowing — shortening during the sea-level fluctuations and (or) migrations into the new facial conditions over the time.

- * **The preference area of developing spines.** The development of spines is limited to the particular areas, which differ between subfamilies.

* — see for discussion below (p. 26)

3.2. Taxonomy

The last taxonomic classification proposed for suborder Cheirurina in the new Treatise (Whittington *et al.* 1997) is as follows:

Order Phacopida Salter, 1864

Suborder Cheirurina Harrington and Leanza, 1957

Superfamily Cheiruroidea

Family Cheiruridae Hawle and Corda, 1847

Family Pliomeridae Raymond, 1913

Family Pilekiidae Sdzuy, 1955

Family Encrinuridae Angelin, 1854

Family Staurocephalidae Prantl and Přibyl, 1947

Family Hammatocnemidae Kielan, 1959

Discussion on Pliomeridae and Pilekiidae (Paper IV)

The number of thoracic and pygidial segments are relatively constant in cheirurin (sub)families and has been highly weighted in classification of these taxa seen in the old Treatise (cf. Harrington *et al.* 1959, pp O430–O449). Accordingly, the cheirurines have in general 11 thoracic and 3 pygidial segments. The cybelines possess respectively 11 (or 12) and 5 (or 4), but the encrinurines 11 (12) and 5 to multiple. Pilekiids have usually 11 to 12 segments on thorax and 4, rarely 5 or 3 segments on the pygidium. Only pliomerids are varying greatly in number of thoracic segments (11–19), but that of the pygidium is nearly constantly 5 (or exceptionally 4). The immature pliomerid pygidia may have seven spinous segments, being reduced to five with the growth (Ross 1951). Analogous trend is observed on cheirurid *Krattaspis* (Paper I).

The Tremadocian pliomerids and pilekiids of the Baltoscandia (Paper IV) resemble with typical representatives of the group, but some of those developed in early Arenig bear the reduced number of pygidial segments on holaspides. For example, *Pliomerops ? linnarssoni* (Wiman, 1906) from greenish grey compact limestone of *M. planilimbata* Zone in Västergötland and probably conspecific material from the glauconite sandstone of Lamoshka locality, St. Petersburg region (Figs 3, 5, 12) have 14 thoracic and only 4 pygidial segments on the mature specimen. They differ from *Hintzeia actinura* (Dalman, 1827), which has 14 thoracic and 5 pygidial pleural segments, but otherwise seem

closely related taxa. Also *Evropeites toernquisti* (Holm, 1882) from gray limestone of *M. dalecarlicus* Zone in Dalarne (Tjernvik and Johansson 1980) and *E. lamanskii* (Fig. 13) from glauconite sandstone of various localities in the East Baltic (Fig. 17, below) have the reduced number of segments (11/2) compared with the other pilekiids. *Evropeites* is the only pilekiid bearing only two pairs of pygidial pleurae, resembling in this the cheirurid acanthoparyphines. Thus, the Baltic material reveals, that the number of pygidial segments should be taken with some reservation on the (sub)familial classification (Paper IV).

Discussion on Encrinuridae (Paper II)

The characters considered as diagnostic for subfamilies Encrinurinae Angelin, 1854 and Cybelinae Holliday, 1942 were listed by Evitt and Tripp (1977) and Strusz (1980). Many of those are plesiomorphic within the family Encrinuridae (see for discussion Edgecombe *et al.* 1988, p. 796), and several other apomorphic characters have exceptions within the subfamily. Two new characters are described below to prove the homology of these subfamilies. Moreover, I suggest they help to find the probable ancestors among the Tremadocian paraphyletic Pilekiidae and Pliomeridae of which some genera share characters with encrinurines and some with cybelines (and some with cheirurids).

- * **The predominant evolving area** during the ontogeny and phylogeny. The area on the exoskeleton where it evolves on the process of broadening — elongating and narrowing — shortening during the sea-level fluctuations and (or) migrations into the new facial conditions over the time.

The encrinurine pygidia commonly change in a number of pleurae and axial rings and in conjunction of those with each other. As the ontogeny shows, the appearance of additional rings can arise all over the breadth (sag.) of axis, not only at the posterior portion of it (Paper III). In contrast, the cybeline pygidia generally possess a constant number of pleurae continuous with axial rings, and the new rings on holaspides appear only on the terminal piece, or a new segment embodies conjoined pleural and axial part when appearing. The development of the cybelines mostly includes changes on the size of the anterior pleural bands (plus on size of axis and number of axial rings on terminal piece). Still, decrease in the number of continuous pygidial segments (from five to two) of the latter subfamily is a phylogenetic trend towards the end of Ordovician. However, the number of pleurae and axial rings on adults is quite constant within the individual genera of both subfamilies.

In other Cheirurina an analogous pattern of reduction of the pygidial axial rings in certain evolutionary circumstances is observed, like in an evolutionary

Pliomerops ? linnarssoni (Wiman, 1906)

Megistaspis planilimbata Zone ?

Glaucconitic sandstone at Lamoshka River, Ingria

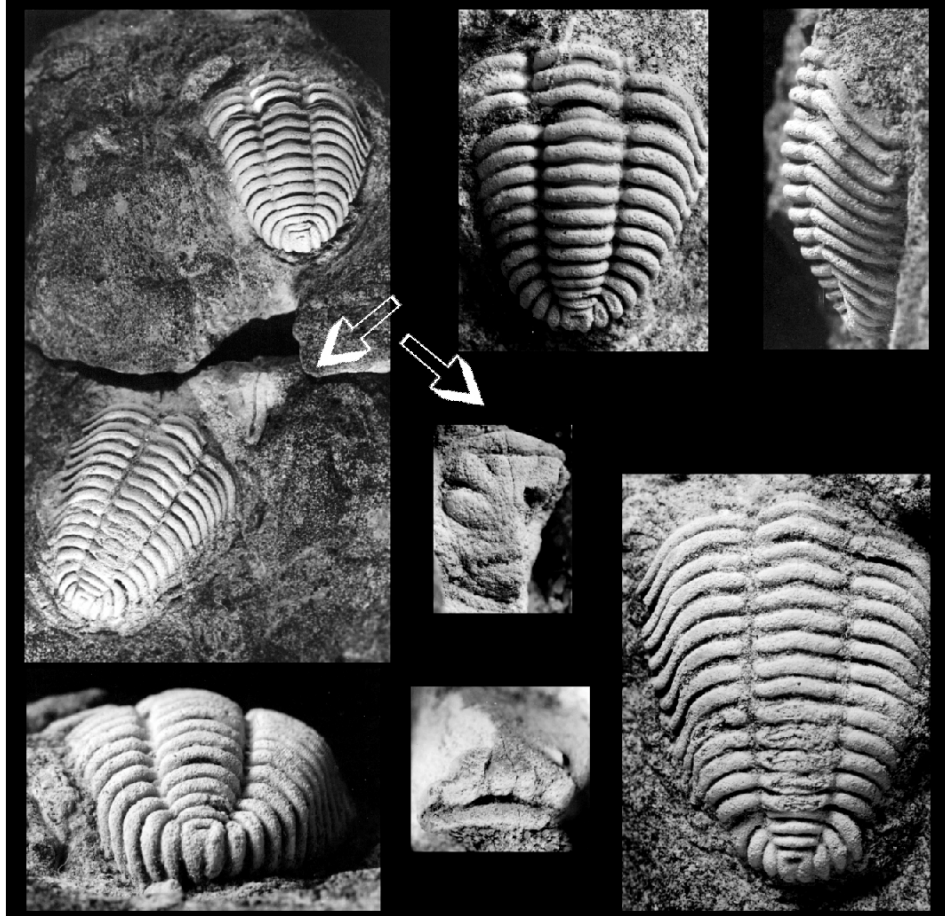


Figure 12. A slab of glauconite sandstone with two exoskeleton of *Pliomerops ? linnarssoni* *in situ* (?) deposited, showing the moulting style of this group (a head, pointed by arrow, and a free cheek are upside down slightly ahead of the thoracopygon, which is somewhat disarticulated to the segments that are not shifted away, also the pygidium is disarticulated but still in place. This evidence provokes to the periods of quiet settling in this area.

Europeites lamanskii Schmidt, 1907

Megalaspides dalecarlicus Zone ?

Glauconitic sandstone of Estonia and Ingria

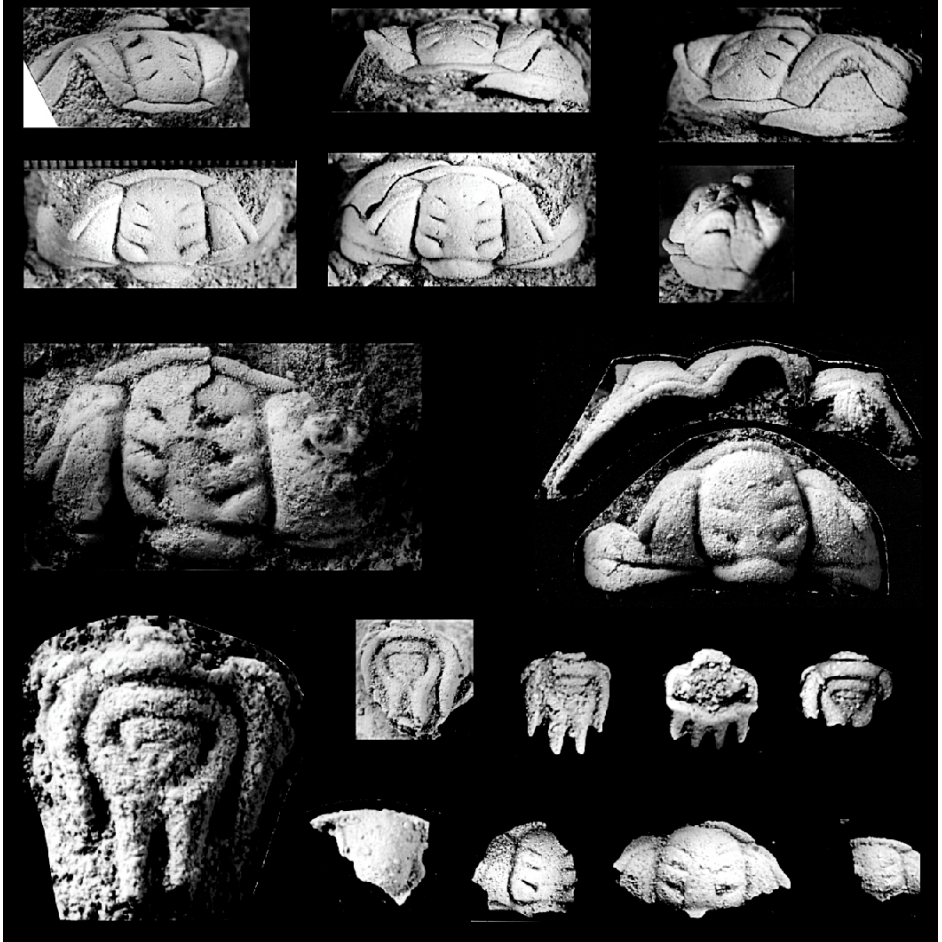


Figure 13. *Europeites lamanskii* a close relative of *Europeites toernquisti* and probably descendant from *Anacheirurus* Reed, 1890.

lineage *Sphaerocoryphe* Angelin, 1854 — *Deiphon* Barrande, 1850 during the late Ordovician. The reappearance of additional pygidial axial rings has been documented in the lineage *Sphaerocoryphe* Angelin, 1854 — *Onycopyge* Woodward, 1880 (see Holloway and Campbell 1974, p. 412) distributed across the Ordovician-Silurian border.

- * **The preference area of developing spines.** The development of spines is limited to the particular areas, which differ between sub-families.

The spines on encrinurines are developed on the axial area: on some thoracic rings, pygidial axis (considering mucro as such), or on the glabella. In contrast, the cybelines obtain spines on the periphery of the exoskeleton. The spines are developed on pleural tips of the posterior half of the thorax, and commonly with an appearance of the macropleura on the anteriormost of those. They also may arise on the border areas all over the cephalon: on the anterior cranidial border, librigenal border, on the rostral plate, also on the occipital ring. In some instances, long spines appear on tips of pygidial pleurae. Differentiation of arrangement of spines indicates to the different type of enrolment, moulting and mode of life of these two groups.

Interesting is that the representatives of Dindymeninae Henningsmoen, 1959 and Eodindymeninae Kielan, 1960 could be splitted between Cybelinae and Encrinurinae by the above-mentioned characters. Considering the blindness as homoplastic, the dindymenines together with the *Eodindymene* strikingly are dividable between Cybelinae and Encrinurinae. Similarly, considering the extreme elongation and bulbousity of the anteriormost lobe of the glabella as homoplastic, the Staurocephalidae Prantl and Přibyl, 1948 are also resolved within the Encrinuridae.

Discussion on Cheiruridae (Papers I, III)

The history of subdivision family Cheiruridae is reviewed by Lane in 1971. Among the rest he concluded that subfamily Cyrtometopinae Öpik, 1937, based on possession of a transverse furrow or line of pits on the thoracic pleurae falls into junior synonymy of the Cheirurinae (Lane, 1971, 2002) (Table 1; 2, A). The significance of that character has been emphasised by Schmidt (1881) and Barton (1916) earlier before Öpik. Restudy of genera involved shows that this group still exhibits a natural group in *sensu stricto* (Table 1), considering some additional diagnostic characters (Papers I, III).

Table 1. Composition of subfamily Cyrtometopinae *sensu* Öpik, 1937 and *sensu stricto* (Papers I, III), and systematic position of same genera by Lane (1971).

Cyrtometopinae		subfamilian assessment
<i>sensu</i> Öpik 1937	<i>sensu stricto</i> Pärnaste 2003	<i>sensu</i> Lane 1971
* <i>Cyrtometopus</i> Angelin, 1854	<i>Cyrtometopus</i>	Cheirurinae
* <i>Eccoptochile</i> Hawle & Corda, 1847		Eccoptochilinae
* <i>Pseudosphaerexochus</i> Schmidt, 1881	<i>Actinopeltis</i> (partim.)	Eccoptochilinae
* <i>Actinopeltis</i> Hawle & Corda, 1847		Cheirurinae
<i>Nieszkowskia</i> Schmidt, 1881	<i>Hemisphaerocoryphe</i>	Acanthoparyphinae
<i>Hemisphaerocoryphe</i> Reed, 1896		Deiphoninae
<i>Pilekia</i> Barton, 1916	<i>Reraspis</i>	Pilekiinae
<i>Youngia</i> Lindström, 1885		Acanthoparyphinae
<i>Anacheirus</i> Reed, 1896	<i>Krattaspis</i> Öpik, 1937	Pilekiinae
* <i>Kawina</i> Barton, 1916		Acanthoparyphinae
<i>Parapilekia</i> Kobayashi, 1934	<i>Cyrtometopella</i> Nikolaisen, 1961	Pilekiinae
<i>Seisonia</i> Kobayashi, 1934		Pilekiinae
* <i>Reraspis</i> Öpik, 1937	<i>Sphaerocoryphe</i> Angelin, 1854	Cheirurinae
? <i>Protopliomerops</i> Kobayashi, 1934		Cheirurinae
* accepted as Cyrtometopinae in Henningsmoen and Harrington 1959		Deiphoninae

Table 2. Subdivision of the family Cheiruridae; **A**, Lane (1971); **B–D**, three possibilities brought forth by Pärnaste (2001a, Paper I).

<i>sensu</i> Lane 1971	<i>sensu</i> Pärnaste 2001		
A	B	C	D
Cheirurinae Hawle and Corda, 1847	Cheirurinae	Cheirurinae	Cheirurinae
Deiphoninae Raymond, 1913	Cyrtometopinae including <i>Sphaerocoryphe</i>	Deiphoninae	Cyrtometopinae
	Deiphoninae without <i>Sphaerocoryphe</i>		-----?----- Deiphoninae
Acanthoparyphinae Whittington and Evitt, 1954	Acanthoparyphinae	Acanthoparyphinae	Acanthoparyphinae
Areiinae Prantl and Pribyl, 1948	Areiinae	Areiinae	Areiinae
Eccoptochilinae Lane, 1971	Eccoptochilinae		-----?----- Eccoptochilinae
Sphaerexochinae Öpik, 1937	Sphaerexochinae	Sphaerexochinae	Sphaerexochinae

Genera listed in Cyrtometopinae *sensu stricto* (Pärnaste 2001a, 2003) (Fig. 14) share several apomorphies in different combinations, showing various processes of heterochrony and consequently shared ancestry (see below). The transitional

forms with cheirurines, acanthoparyphines or sphaerexochines are not recorded. Therefore, cyrtometopines are suggested to present a natural group (Table 2, B). Although, Deiphoninae Raymond, 1913 was established to incorporate cheirurid taxa with bubble-like glabella; such as *Deiphon*, *Staurocephalus*, *Sphaerocoryphe* (Raymond 1913), it is obvious that *Deiphon* is descendant from Cyrtometopinae *s. str.* Then, analogous to the Staurocephalidae-example (see above), considering that particular character homoplastic, Cyrtometopinae *s. str.* falls into junior synonymy of Deiphoninae (Table 2, C). However, when considering the other character, the reduction of the lateral lobes (fixigenal field, pleural area adaxial from fulcral line, pygidial field) to the obliteration, of higher weight, Deiphoninae could be kept separate, but with exclusion of *Sphaerocoryphe* (Cyrtometopinae). Another extremity seems to be the blindness, and considering that homoplastic, Eccoptochilinae Lane, 1971 can be considered as a junior synonym of Areiinae Prantl and Přibyl, 1948. After all, there are some apomorphies that may serve subdivision in family level, dividing all these ‘subfamilies’ into two major groups as presented in Table 2, D. Consequently, the validity of Cyrtometopinae and other taxa should be tested, when undertaken entire suborder Cheirurina together.

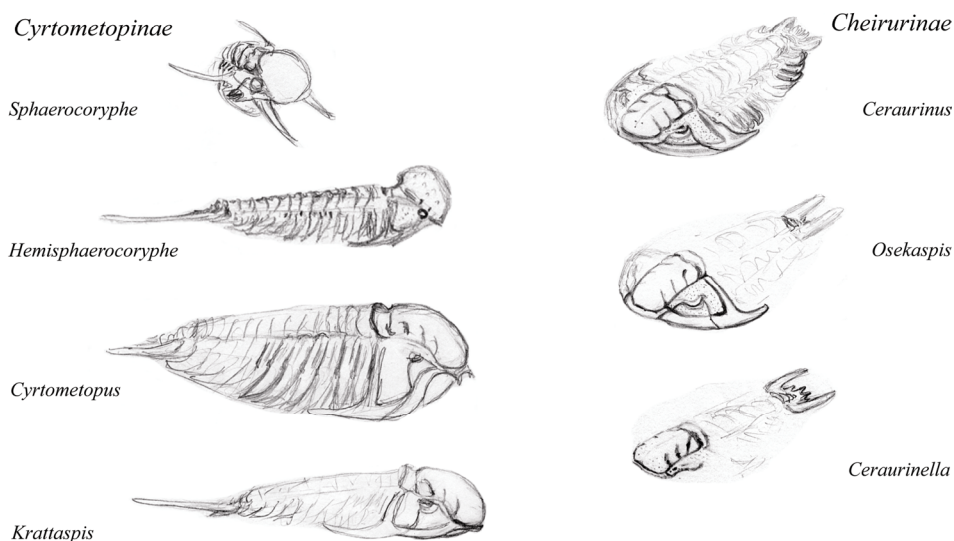


Figure 14. Subdivision into Cheirurinae and Cyrtometopinae coincides with the designs of their exoskeleton. Fortey and Owens (1990) described eight morphotypes of trilobite exoskeleton. Both these groups fall into that with marginal cephalic spines. However, these cheirurids are in addition dividable: Cyrtometopinae (+Deiphoninae), those with anteriorly declined cephalon with glabella overhanging the anterior border, and Cheirurinae, those with generally flat image, possessing the anterior portion of the cephalon and spines in nearly horizontal plane. They also have different type of the pleural furrows, reflecting to the different attachment of muscular system, i.e. mode or activity of movements (Figure from my talk in the Third International Conference on Trilobites and their Relatives, Oxford, April 2001).

Cyrtometopinae sensu stricto (Papers I, III)

Diagnosis (Paper I). Cheirurids with transverse thoracic pleural furrows. The axial lobe of the entire exoskeleton is relatively convex with wide and deep axial furrows. Glabella overhanging the anterior border, relatively wide glabellar furrows expanding towards the axial furrow, S2 and S3 can be reduced to obliteration, but still leave impressions of muscle pits as wide shallow grooves on the internal mould. Faintly distinguishable, slightly elevated eye-ridge runs from palpebral lobe adaxially across the anterior fixigena, covering most of it, into the deep axial furrow opposite the anteriormost glabellar furrow (S3), which curves backwards ending in a deep exsagittally elongated apodemal pit. Smaller muscle pit is developed in preglabellar furrow ahead of S3. The anterior fixigena is separated from the anterior border by faint, usually hardly discernable furrow. The anterior wing of cyrtometopine hypostome slopes ventrally inwards more sharply compared to that of cheirurines (cf. Ludvigsen 1977, text-fig. 3), leaving a larger space between ventral and dorsal exoskeletons. Also the wing protrusion on the hypostomal anterior border of these genera is more prominent. Thorax has axial rings with wide and deep rounded articulating furrow. The axial rings as well as the occipital ring and the first axial ring of pygidium are inflated evenly and without diagonal furrow or shallow depression running anteriorly from the posteriormost corner as in Cheirurinae *sensu stricto*. Pygidium with three (or four in neotenic forms) segments, more or less radial abaxially; pleurae ending on free points of different size and direction, although the innermost two pairs of spines can be reduced to obliteration. Only the first axial ring (when it has three segments) is separated from the pleural field by the axial furrow, and the anterior pair of pleurae shows the pleural furrow. The interpleural muscle scars run radially.

Genera included (*type species):

***Actinopeltis* Hawle and Corda, 1847**

Diagnosis. (from Treatise, 1956, p. O434). Bulbous glabella protruding over anterior margin, with preoccipital lateral furrows curved to meet occipital furrow; eyes opposite L2 lobes; posterior sections of facial sutures almost transverse. Thorax with 11 segments, pointed pleurae with transverse row of minute pits. Pygidium with four pairs of pleural spines.

Some additional diagnostic characters (Papers I, III). Thorax with 10 segments (but 11 on immature skeleton, e.g. holotype of the type species), pointed pleurae with transverse furrow or row of densely spaced minute pits. Pygidium with four pairs of radial pleural spines of equal size. The anteriormost is a preanterior segment, neotenic from thorax.

Species list. **Actinopeltis carolialexandri* Hawle and Corda, 1847; *A. barrandei* Kielan, 1959; *A. completa* (Barrande, 1872); *A. gryphos* (Barrande, 1872); *A. insocialis* (Barrande, 1852); *A. spjeldnaesi* Hammann, 1972.

Distribution. Upper Ordovician, Gondwana.

***Cyrtometopus* Angelin, 1854**

Diagnosis (from Lane 2002). Anterior cranial border angulate in outline anterolaterally, connected to palpebral lobe by sutural ridge. Glabella moderately inflated, L1 ovate, its long axis directed at about 45 degrees anteriorly diverging from sagittal line, distinctly isolated S2 and S3 very short. Genae with deep antennal notch anteriorly. Eye anteriorly placed, extending from opposite S3 almost to S2. Rostral plate with pair of short anteriorly-directed spines which, in enrollment, fit between middle and posterior pairs of pygidial spines. Hypostome with anterior wings placed far forward; border furrows wide and borders narrow. Three pairs of pygidial spines, anterior very long, middle short and posterior very short; terminal piece of axis forms a slight median posterior projection.

Additional diagnostic characters (Papers I, III). LA meets the anterior border at sharp angle in lateral view, as well it can be rather elongated (being reflected in length of hypostome). The S3 furrow in *Cyrtometopus* diverges from the preglabellar furrow at an obtuse angle (in side-view). Eye of juveniles placed somewhat rearwards extending to S1. Eyes relatively small. Elongated hypostome has conically vaulted middle body with comparatively short posterior lobe and the anterolateral corners stretched laterally. Thorax has eleven and pygidium three segments.

Species list. **Cyrtometopus clavifrons* (Dalman, 1827); *C. affinis* Angelin, 1854; *C. priscus* Tjernvik, 1956; *C. ? aries* (Eichwald, 1843).

Distribution. Early and Middle Ordovician, Baltica.

***Sphaerocoryphe* Angelin, 1854**

Diagnosis. (from Treatise, 1956, p. O438). Like *Hemisphaerocoryphe* but bulbous part of glabella more dominating.

Additional diagnostic characters (Papers I, III). Cranidium with sphaeric glabella rising up ahead of L1 lobes. Width of the glabella is comparatively smaller at the occipital lobe and L1 than at the sphaeric frontal lobe, integrating L2 and L3. The glabellar S3 and S2 apodemes are reduced to a low knob in the axial furrow (seen ventrally) with no furrows continuing adaxially onto the glabella on dorsal side. Lateral border has one or two spines (profixigenal spine *sensu* Tripp *et al.* 1997) close to the suture. Thorax with nine pygidium with four segments. The pre-anterior segment (axial ring and pleura) has short spines, the anterior pair has stout prominent spines, and following two has no spines. The additional tiny spines can be observed on the ventral side of the pygidium.

Species list. **Sphaerocoryphe dentata* Angelin, 1854; *S. akimbo* Tripp, 1967; *S. arachniformis* Bradley, 1930; *S. atlandiades* Öpik, 1937; *S. cranium* (Kutorga, 1854); *S. erratica* Männil, 1958; *S. exserta* Webby, 1974; *S. gemina* Tripp et al., 1997; *S. globiceps* (Portlock, 1843); *S. goodnovi* Raymond, 1913; *S. hastata* Begg, 1940; *S. kingi* Ingham, 1974; *S. longispina* Tripp et al., 1997; *S. ludvigseni* Chatterton, 1980; *S. maquoketensis* Slocum, 1913; *S. major* Ruedemann, 1901; *S. murphyi* Owen et al., 1986; *S. pemphis* Lane, 1971; *S. psiles* Tripp, 1954; *S. punctata* (Angelin, 1854); *S. robusta* Walcott, 1875; *S. saba* Tripp, 1962; *S. salteri* Billings, 1866; *S. schmidtii* Männil, 1958.

Distribution. Middle and Upper Ordovician, Laurentia, Baltica, Avalonia.

***Hemisphaerocoryphe* Reed, 1896**

Diagnosis. (from Treatise, 1956, p. O438). Well-developed fixigenae with genal spine; bulbous part of glabella only slightly wider than remainder.

Remark. *Sphaerocoryphe* and *Hemisphaerocoryphe* probably represent only one genus according to some authors (Lane 1971, Holloway and Campbell 1974, Tripp et al. 1997). Considering differences listed below, I think that these should not be amalgamated, also even on subgeneric level suggested by Zhou et al. (1998), and followed by Chen and Zhou (2002) (Paper III).

Additional diagnostic characters (Papers I, III). Cranidium with elliptic glabella (in side-view) arching up from the occipital furrow and sloping sharply down together with the anterior genae. S2, S3 furrows weak and short on dorsal side of exoskeleton, but wide on ventral. Posterior fixigena wide but short laterally, sloping down. Lateral border without spine. Thorax with 10 and pygidium with three segments. The spines of the pygidium diverge rearwards, the anteriormost prominent, second shorter and flatter, but the third reduced.

Species list. **Hemisphaerocoryphe pseudohemicranium* (Nieszkowski, 1859); *H. dolichocephalus* (Schmidt, 1881); *H. granulata* (Angelin, 1854); *H. huebneri* (Schmidt, 1881); *H. inflatus* Nikolaisen, 1961; *H. sphaericus* (Esmark, 1883); *H.? elliptica* (Lu, 1975); *H.? rosenthali* (Schmidt, 1881); *H.? sulcata* Thorslund, 1940; *H.? verrucosus* (Brögger, 1882).

Distribution. Middle (?) and Upper Ordovician, Baltica, Gondwana (?).

***Krattaspis* Öpik, 1937**

Emended diagnosis (Paper I). Cyrtometopine with parallel-sided to slightly expanding glabella bending downwards together with palpebral and anterior fixigena, as much as its inflated glabella is over-lapping the anterior border. Convexity of the glabella starts slowly from the middle of L1 lobes, where sometimes a shallow groove is developed over LM uniting S1 furrows. Glabellar furrows directed from the axial furrow in radial directions, thus S3 trends anteriorly, forming a sharp (or acute) angle with the preglabellar furrow. LA meets the anterior border at an acute angle. Eyes situated moderately close to the glabella opposite L2 lobes based on relatively high eye-socket. Hypostome is subquadrate with gently vaulted ventrally trapezoidal middle body evenly

tapering and rounded rearward with rounded anterolateral corners. Glabella and genal area are densely tuberculated, and deep, comparatively rare muscle pits are developed on fixigenal area. Thorax has eleven segments. Pygidium has three pairs of pleurae the anteriormost of which has long, stout pleural spine running laterally and curving rearwards distally as well as two flat inner pairs which have short knob-like spines. Only the first pair of pleurae has a pleural furrow and is separated from axis by distinct axial furrow, the other pleurae conjoin the axial rings evenly.

Species list. **Krattaspis viridatus* Öpik, 1937; *K. popovi* Pärnaste, 2003; *K. vitalis* Pärnaste, 2003; *K. sp. A* (see Pärnaste 2003).

Distribution. Lower Ordovician, Baltica.

***Reraspis* Öpik, 1937**

Emended diagnosis (Paper III). Cyrtometopines with subrectangular slightly expanding glabella, possessing broad, relatively low trapezoidal anterior lobe (LA); medially it slopes (curves) down together with the anterior border. The preglabellar furrow is relatively shallow and narrow, becoming weaker medially. The lateral glabellar furrows are well impressed, S1 joins the occipital furrow bounding relatively large elongated (exsag.) subquadrate L1 lobe. The long relatively large eyes are positioned close to the lateral border. The palpebral furrow is prominent and delimits the eye-ridge posteriorly, dying out shortly adaxially, also joining a shallow posterior sutural furrow (indicated by row of pits). Librigenal field is reduced, eye-socket reaches the lateral border. The genal angle ends in a pointed tip or in a very short spine. The parallel-sided (tr.) occipital ring carries a small occipital tubercle. Subtriangular hypostome has triangular median body with an ill-defined posterior lobe, effaced maculae and middle furrow. The posterior notch of the posterior border is absent, the wing protrusion on the anterior border is well developed. Thorax has ten segments and pygidium three, ending in short spines, also the fulcrum is pointed in a short spine.

Species list. **Reraspis plautini* (Schmidt, 1881); *R. latifrons* (Warburg, 1925), *R. orvikui* Pärnaste, 2004, *R. ? kaljoi* Männil, 1958.

Distribution. Middle and Upper Ordovician, Baltica.

***Cyrtometopella* Nikolaisen, 1961**

Diagnosis (from Nikolaisen, 1961). Cranidium subsemicircular in outline, glabella oval in outline, with three pairs of lateral glabellar furrows, reaching or nearly reaching the occipital furrow. Eyes located opposite or slightly behind S2. Eye ridges present or not (if present partly coalesced with sutural ridges). Pygidium with two pairs of pleural spines, posterior pair reduced.

Some additional diagnostic characters (Paper III). Cyrtometopines with strongly convex (tr.) glabella of conical shape, the lens-shaped relatively high occipital ring elongated oval in dorsal view. Sagittal convexity of the glabella starts evenly behind the occipital ring then showing higher convexity at the

middle and thereafter slopes down so LA meets the preglabellar furrow at a sharp angle. Glabellar furrows deep but relatively short. Axial and border furrows are deep as well. Genae strongly convex. Eye-ridge marked by distinct wide palpebral furrow, running to the axial furrow at S3.

Remarks (Paper III). Nikolaisen (1961, p. 288) established *Cyrtometopella* and proposed to include *C. rosenthali*, a suggestion later followed by Bruton *et al.* (1997, p. 102). I agree that *Cyrtometopella? askerensis* Nikolaisen, 1961 indeed is rather similar to *rosenthali*, sharing the deep and short S2, S3 of an elongate glabella that is flattening and narrowing anteriorly and overhanging the anterior border. In that respect both are resembling *Hemisphaerocoryphe? sulcata* Thorslund, 1940 and *Cyrtometopus? aries* (Eichwald, 1843). The pygidia identified with *C. ? askerensis* much resemble those of *Hemisphaerocoryphe*, possessing only one pair of pleural spines between the stout anterior pair. However, several apomorphies of the type species, *Cyrtometopella tumula*, are not shared with the above-mentioned group, such as the conical shape of the glabella, the lens-shaped relatively high occipital ring, etc. It is not clear whether these differences warrant a differentiation at generic or species level. Since no pygidia of the preceeding species have been found (together with cephalo) the generic position and status of the genus *Cyrtometopella* stays unclear. Alternatively *rosenthali* and *aries* may also represent *Cyrtometopus* (Schmidt 1881, Lane 2002, p. 164).

Species list. **Cyrtometopella tumula* Nikolaisen, 1961; *C.? askerensis* Nikolaisen, 1961.

Distribution. Upper Ordovician, Baltica.

***Krattaspis* as a stem-group for *Cyrtometopinae* s. str.**

Krattaspis viridatus is the earliest representative of *Cyrtometopinae* in accordance of the conodont and trilobite evidence (Papers I, V). *K. popovi* and *K. vitalis* continue this phylogenetic lineage ancestral to the *Cyrtometopus* turning up in late Billingen *Megistaspis* (*P.*) *estonica* Zone (Tjernvik 1956) and somewhat younger beds of Volhkov age (Lamansky, 1905). *K. viridatus* resembles much with *Reraspis orvikui*, which appears in similar conditions of settling the sandy deposits (Paper III). However, the cranidium of *K. sp. A* (Fig. 15) and that of the biggest *K. popovi* are rather similar to (the last is less so) that of *Hemisphaerocoryphe* by its higher glabella, widely spaced and upraised eyes, and the course of genal spines. This indicates to the probable ancestry for that genus as well. Moreover, *Reraspis? kaljoi* (Männil 1958, pl. III, figs 6–7), which is very similar to *Cyrtometopella* (Paper III), also resembles *Krattaspis*, especially *K. popovi* (Paper I, Text-fig. 8). The most similar is the shape of the glabella and its lateral furrows. However, they differ mainly in characters of the anterior border area of the cephalon, plotted against the pygidial characters (number and shape of the pygidial spines) (cf. Fig. 8), and the shape and course of the genal spines. The latter had probably the balancing role facing variously inflated glabella (cf. Fig. 14). The balancing role is also confirmed by appearance of the additional spine(s)

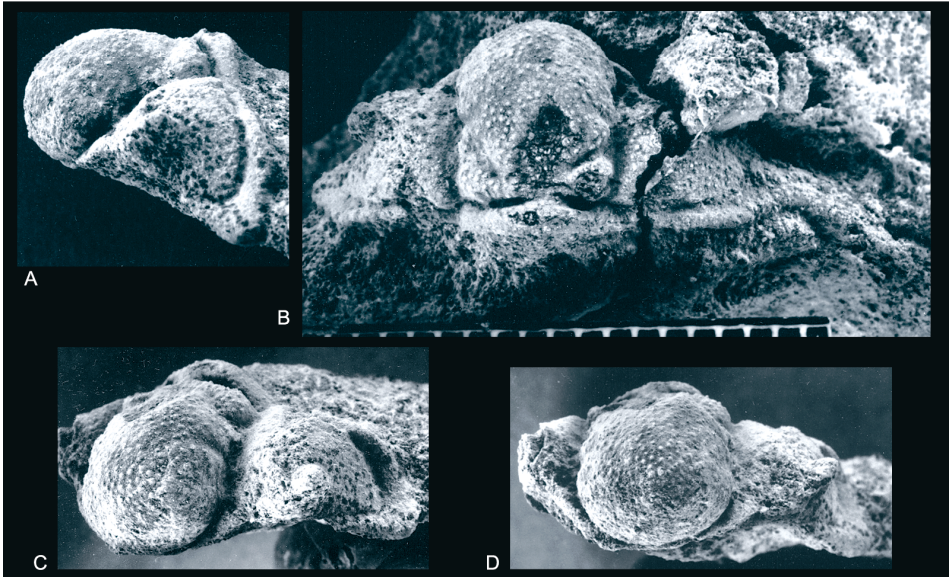


Figure 15. A–D, *Krattaspis* sp. A (Pärnaste 2003); lateral, dorsal, anterolateral and anterior views of the cranidium with weathered and broken test (318-1); Mäeküla Member, Maardu, vicinities of eastern Tallinn; $\times 4$.

on the lateral border of *Sphaerocoryphe*, *Deiphon*, and *Onycopyge*, all having the bubble-shape glabella that is overhanging the anterior border. Consequently, *Krattaspis* is apparently a stem-group for the entire subfamily Cyrtometopinae, serving mixture of several succeeding genera, resulting from different patterns of heterochrony, which are reflected by the certain environmental conditions during its evolution.

Encrinuroides and related genera (Paper II)

The concept of genus *Encrinuroides* and its paraphyly is discussed in detail by Edgecombe and Chatterton (1990), Lespérance and Desbiens (1995) and Edgecombe *et al.* (1998). They used cladistic parsimony analysis and the characters chosen for the investigation by numerical taxonomic methods by Temple and Tripp (1979) (Edgecombe and Chatterton 1990), or somewhat different attributes (Lespérance and Desbiens 1995, Edgecombe *et al.* 1998). They revealed several ambiguous aspects of the phylogeny of *Encrinuroides* and the encrinurids generally. The new material from the Mäeküla Member of the East Baltic is the earliest record of this subfamily, and gives a new aspect for clarifying the systematics of that. However, the cladistic parsimony analyse is not used in this study, because of lack of some character data of other relevant taxa.

The encrinurid genera related to this study areas follows:

Encrinuroides Reed, 1931

Encrinuroides s. str.

Physemataspis Evitt and Tripp, 1977

Physemataspis (Physemataspis)

Physemataspis (Prophysemataspis) Lespérance and Desbiens, 1995

Frencrinuroides Lespérance and Desbiens, 1995

Walencrinuroides Lespérance and Desbiens, 1995

Erratencrinurus Erratencrinurus Krueger, 1971

Celtencrinurus Erratencrinurus Krueger, 1971

Lasaguaditas Edgecombe *et al.*, 1998

Two genera *Frencrinuroides* and *Walencrinuroides* were restricted from *Encrinuroides* by Lespérance and Desbiens (1995). Each genus was based on a single autapomorphy uniting its contained species. An autapomorphy, supposedly diagnostic of *Walencrinuroides*, the shape of the pygidium (as wide as long) can be facies- dependent as shown by a study of Männil (1977), as can be the shape of the cranidium claimed to be diagnostic to *Frencrinuroides*. Moreover, the last and other supposedly diagnostic characters of *Frencrinuroides* are shared with representatives of *Walencrinuroides* and *Encrinuroides s. s.* (see Edgecombe and Chatterton, 1990). Edgecombe *et al.* 1998, claimed, that mono-

phyly of the two genera requires additional character support. They included three new characters to the original Lespérance and Desbiens' matrix, which still failed to confirm the monophyly and composition of *Frencrinuroides* and *Walencrinuroides*, but assisted in delimiting *Erratencrinurus*. However, their character no. 19 (sculpture of the lateral border) in combination with some additional synapomorphies suggested here and in related papers clusters the Ordovician encrinurines into several groups, and supports restriction of *Encrinuroides* s. s. (Paper II). Yet, the new features described do not support the recognition of *Walencrinuroides* and *Frencrinuroides*, but sustain the usefulness of an *Encrinuroides sensu lato* grouping.

Physemataspis was erected as a monotypic genus based on *P. coopi* Evitt and Tripp, 1977. Lespérance and Desbiens (1995) erected a new subgenus *P. (Prophysemataspis)* basing on semicircular glabella, and included *E. neuter* Evitt and Tripp, 1977 and *E. uncatus* Evitt and Tripp, 1977 in it. Comparison of other characters suggests these two species are better assigned to *Erratencrinurus*, as probably should be the poorly preserved *E. lapworthi*, and thus the subgenus *P. (Prophysemataspis)* falls into its junior synonymy.

Specific characters of the Argentinian encrinurine *Lasaguaditas oweni* Edgecombe *et al.*, 1998 comprise the shortness of the cephalon (especially of LA) and the pygidium, which is also relatively less segmented; and the tuberculation is diminutive and sparse in both areas. The first character is homoplastic with Laurentian Middle and Upper Ordovician cheirurids (cf. Laurentian acanthoparyphines versus Baltic *Nieszkowskia* Schmidt, 1881, and *Holia* Bradley, 1930 versus *Ainoia* Männil, 1958 in Adrain 1998). The appearance of the same neotenic pattern in different families probably refers to its environmental or climatic implication. The unpaired sagittal tubercles shared with *Erratencrinurus* are also known on the pygidium of an undetermined Upper Ordovician encrinurid from Tasmania (Edgecombe *et al.* 1999, p. 246, text-fig. 7F). The latter shows the ancestral condition of continuity of segmentation between the axial and lateral lobes (more pleurae are continuous with corresponding axial ring). Thus, the *Lasaguaditas* Edgecombe *et al.*, 1998 may be the ancestor of the *Erratencrinurus*.

3.3. Ontogeny

Trilobites molted their exoskeleton at regular intervals in ontogeny and also underwent the metamorphosis. The postembryonic part of the trilobite life cycle is divided into three main intervals, protaspid, meraspid and holaspid periods (Fig. 16). Data on early periods is an important source of information critical to our understanding of taxa. Therefore, investigation of ontogeny helps to solve taxonomic problems and has implications to phylogenetic interpretations (e.g. McNamara, 1986).

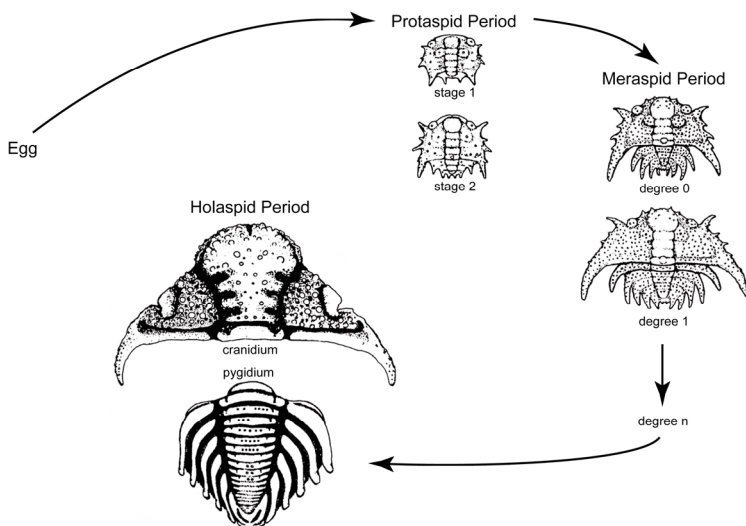


Figure 16. Growth stages of the life history of the encrinurine trilobite (Speyer and Chatterton 1989).

The life cycles of trilobites included a radical metamorphosis early in ontogeny, usually accompanied by a change from a planktic to a benthic mode of life. Several distinctive characters of overall morphology describe these certain modes of life. The first calcified protaspis stage of cheirurines is considered planktic and the later stages benthic (Speyer and Chatterton 1990).

The meraspis period of Krattaspis (Paper I)

Data on the early stages of cyrtometopine trilobites are very rare. The only other records of some close relatives are that of *Sphaerocoryphe* (Shaw 1968, Tripp *et al.* 1997) and *Deiphon* (Chatterton and Perry 1984). Any detail is of great importance on clearing up the phylogenetic relationships between the cheirurine taxa. Two delicate specimens of *Krattaspis vitalis* Pärnaste, 2003 were found from Popovka (layer 9, Fig. 17, p. 40) preserved in calcite: a cephalothorax and a thoracopygon together with the adult holaspides (Paper I, text-fig. 9). Several cyrtometopine characters were recognized, some (1, 2, see below) maintain to holaspis stage:

- 1) strongly inflated axial lobe distinguished by deep furrows from the lateral lobes;
- 2) cephalon sloping steeply anteriorly having bulbous glabella and long relatively stout genal spine based from posterolateral corner and directed evenly rearwards;
- 3) occipital ring long, bearing a large occipital tubercle;
- 4) thoracic pleurae divided by a strong pleural furrow into equal parts;

- 5) pygidium with five (up to seven?) flat pleurae with no visible pleural furrow (possibly due to the poor preservation) and ending in short spines curving backwards close to one another;
- 6) pygidial axis wide and strongly arched, ending in elongated terminal piece.

Comparison with meraspides of cheirurines *Ceraurinella* Cooper, 1953 (see Shaw 1968, Chatterton 1980, Edgecombe *et al.* 1999) and *Hadromeros* Lane, 1971 (see Chatterton and Perry 1984) shows following differences diagnostic to those:

- 1) axial lobe low;
- 2) cephalon almost flat, both transversely and sagittally with nearly horizontal genal spines (calling to the benthic life-style).

Growth of Krattaspis during the holaspid period (Paper I)

Several trends of ontogeny based on *Krattaspis popovi* Pärnaste, 2003 were observed in Lava section. Nine cranidia (width of glabella 2.3–8.0 mm) were found in a layer 0.1 m thick (layer 7a, Fig. 17), and eight cranidia (width of glabella 2.8–6.8 mm) in a somewhat higher layer (0.04 m thick) (layer 8c, Fig. 17).

- 1) The anterior lobe of glabella is relatively longer in larger cranidia similar to those of representatives of *Cyrtometopus* and *Nieszkowskia*.
- 2) L1 lobes are slightly longer in larger specimens in relation to the length of the axial furrow, or length of glabella, or width of glabella at L1.
- 3) The palpebral lobes of small specimens are more upright than those of larger specimens.
- 4) The genal angle (measured as a posterolateral corner of the fixigenal field) varies from 90 degrees in juvenile to 60 degrees in adult specimens.
- 5) The angle between the posterior border and genal spine varies from 90 to 130 degrees (both angles measured in dorsolateral view perpendicular to the posterolateral fixigena).
- 6) The middle body of hypostome is slightly longer in longer specimens.

Early stages of trilobites and notes on migration (Papers I–IV)

Chatterton *et al.* (1990) pointed out that despite the protaspid larvae were much simpler in form, they carried the morphological information of the adult stage (holaspid) of the taxa. However, as far the morphology of the exoskeleton was influenced by the environmental conditions, they were easily evolving group often resulted by different heterochronic patterns. Edgecombe and Chatterton (1988) demonstrate the mosaic evolution on two encrinurine lineages *punctatus* and *variolaris*, diverging from a common ancestor by different changes in

developmental timing. Recognition of different heterochronic (paedomorphic or peramorphic) patterns would give some extra information about the migration of fauna and palaeogeographic situation. One of such examples, showing some faunal change between Baltica and Avalonia in Arenig, is evidenced by the early representatives of *Encrinuroides*. *E. hornei* Dean, 1974 from late Arenig or early Llanvirn of north-eastern Newfoundland (Avalonia) is quite different from early Arenigian *E. regularis* (Baltica), but is most probably descendant from latter, showing its immature or progenetic character compared to *E. regularis* (Paper II).

Most of the cheirurins obtained the benthic life-style already in late protaspides stage and inhabited the near-shore shelf environments (Fortey 1975, Ludvigsen 1978). By being restricted to such specific environmental conditions, they were inconsiderably involved in global migration. However, the local migration into somewhat shallower or deeper conditions (biofacies shift) occurred, causing several changes in their morphology well observed on cyrtometopines (Papers I, III).

The Early Ordovician Laurentian cheirurin genus *Hintzeia* Harrington, 1957 has been recognised far outside of the Laurentia in Hunnebergian of the Baltoscandia by Hoel (1999; Paper IV) (Fig. 2, p. 10). One explanation for that phenomenon is the pelagic lifestyle of trilobite larvae, while protaspides (Fig. 16) were planktic and could cross the oceanic 'barriers' with current circulation, gyres.

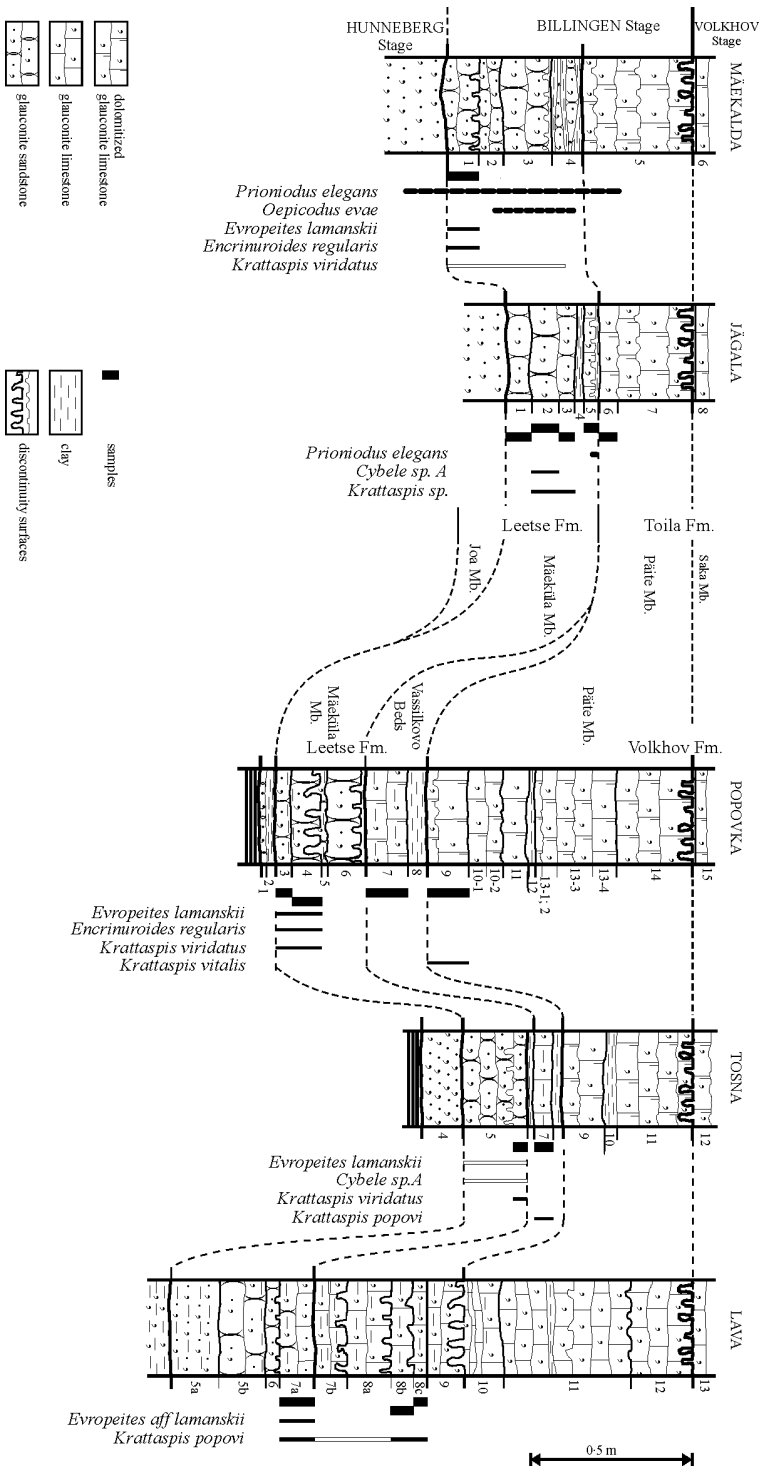


Figure 17. Lithological columns of sections studied bed by bed, showing distribution of the accumulated cheirurium trilobites (Papers I, II, V), and the conodonts *P. elegans* and *O. evae* (Viira et al. 2001).

4. DISTRIBUTION

Krattaspis viridatus Öpik, 1937 together with *Krattaspis* sp. A (Paper I) are the earliest representatives of the genus in accordance of the conodont and trilobite evidence (Papers I, V). *K. popovi* Pärnaste, 2003 and *K. vitalis* Pärnaste, 2003 appear slightly later (Fig. 17). The species distribution is usually following lithology, but not always. *K. vitalis* has been recorded only from the glauconitic limestone of the Päite Member, where all the seven specimens were found together in one slab. *K. viridatus* occurs usually in the lowest beds of the Mäeküla Member, but *K. popovi* appears in a slightly finer-grained sediment above it (cf. Tosna, Text-fig. 3, Paper I). The latter species occurs in both Mäeküla and Vassilkovo beds in Lava section, where the grain size of the Mäeküla beds is somewhat finer, as compared to that in Popovka or Mäekalda sections.

The encrinurids, *Encrinuroides regularis* Pärnaste, sp. nov. and *Cybele* sp. A (Paper II) appear in the lowermost beds of the Mäeküla Member. The encrinurines are known only from that particular level, then they disappear from Baltoscandia to reappear again in Oandu age (late Ordovician). Different from encrinurines, the cybelines are distributed in Baltica throughout the entire Ordovician, inhabiting different facies, usually preferring more clayey beds.

A pilekiid *Europeites lamanskii* is quite common in the lowest beds of the Mäeküla Member (Fig. 17) (Papers IV, V). A slightly different form of *Europeites* is found from same member of the Lava section. *Europeites* is very rare elsewhere in Baltoscandia, only one specimen of *E. toernquisti* is found from Sweden.

5. TRILOBITE ZONATION

5.1. Trilobite zonation of the Early Ordovician in the East Baltic

Lamansky (1905) made the first attempt to use trilobites for correlation of the Lower Ordovician rocks of East Baltic and Scandinavia. He recognized the Scandinavian *Megalaspis limbata* and *M. planilimbata* zones in the lowest limestone unit (B_{II}α), and established the *Megalaspides* Zone in the topmost Glauconite Sandstone (B_Iβ) (Fig. 18, from Paper V). Balashova (1966) described five local trilobite zones within the current Billingen Stage and provided correlation with the trilobite zonation of Sweden, which was worked out by Tjernvik (1956). Later, Tjernvik (Tjernvik and Johansson 1980) restricted a new zone in the uppermost strata of previous *M. planilimbata* Zone, drawing the boundary between the Hunneberg and the Billingen (sub)stages to the base of the new trilobite zone, the *M. (P.)* aff. *estonica* Zone. The last version has been followed by the author in earlier works (Pärnaste 2001*b*, Papers I, II, IV) and herein.

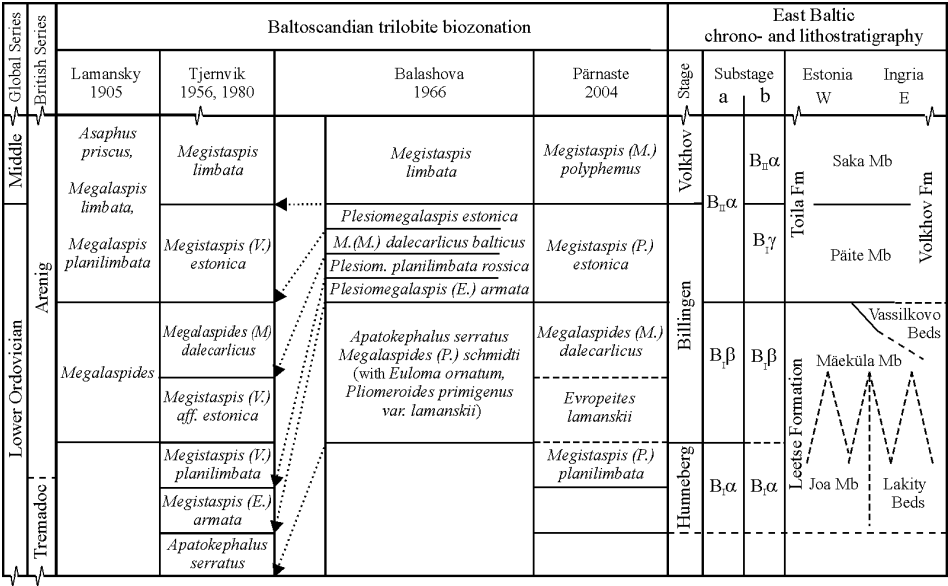


Figure 18. The Baltoscandian trilobite zonation in correlation with chrono- and lithostratigraphy of the East Baltic. Dotted lines show the correlation of Balashova (1966), including the Mäeküla Member to the Tremadocian.

Balashova (1966) recognized five local trilobite zones within the interval now interpreted as the Billingen Stage. Her lowest zone was correlated with upper Tremadocian and the following zones with the lower Arenigian. Unfortunately, her correlation (dotted lines in Fig. 18) of the Mäeküla Sandstones with the *Apatokephalus serratus* Zone was based on several erroneous identifications. First, the fragment of her *A. serratus* (Boeck, 1838) rather belongs to *Remopleurides*? Portlock, 1843 than to *Apatokephalus* Brøgger, 1896. Secondly, a very tiny and poorly preserved fragmentary cranidium of *Euloma ornatum* Angelin, 1854 (Balashova, 1966, pl. 1, fig. 1) most probably belongs to *Ptychometopus schmidtii* Balashova, 1966. The third evidence, indicating the *A. serratus* Zone was the recorded new subspecies of *Pliomeroides primigenus* (Angelin, 1854) (Paper IV, Tab.). However, the *Pliomeroides* (*Evropeites*) *primigenus lamanskii* (Schmidt, 1907) is rather different and has been further considered as an independent genus (Fortey 1980, p. 86), as well as a species *Evropeites lamanskii* (see Aru 1990, p. 72, Ebbestad 1999, p. 107). Lamansky (1905, p. 6, pl. 1, fig. 1) mistakenly identified a fragment of the latter species as the Tremadocian *Triarthrus angelini* Linnarsson, 1869. Also, a fragmentary pygidium attributed to the index species of the succeeding *Megistaspis* (*Ekeraspis*) *armata* trilobite Zone (Balashova 1966, p. 16, pl. 2, fig. 12) is too poorly preserved to allow a confident identification. Besides, judging by the original it appears that the retouch and cutting the figure is rather subjective. This leaves no evidence confirming that any of these Scandinavian trilobite zones can be recognized in the East Baltic.

Recognition of the next Swedish zones in the East Baltic is somewhat complicated. In particular, during the holaspide period, the isotelines (the group of index trilobites) vary considerably in their diagnostic characters (e.g. the number of pleural segments and length/width ratios of the axis or cephalon and pygidia in general; see Nielsen 1995). The width of the pygidia and number of the pleurae increases on *Megistaspis* (*Paramegistaspis*) Balashova, 1976, during the holaspide period. The same tendency is observed as well as on the phylogenetic lineage *M. (P.) planilimbata* — aff. *estonica* — *estonica*. The relatively narrow pygidium of *M. (P.) planilimbata* (Angelin, 1854) has six pleural ribs, and that of the stratigraphically younger *M. (P.) estonica* (Tjernvik, 1956) eight ribs, being also slightly wider. Unfortunately, the hitherto published material on *Megistaspis* (*Paramegistaspis*) does not allow adequate comparison of species, and a special study of growth variation is needed. However, some dubiously identified pygidia of *M. (P.) planilimbata* from the Tosna River locality indicate probable occurrence of that zone in the eastern Baltic. *Pliomerops*? *linnarssoni* (Wiman, 1906) known from the *M. planilimbata* Zone in Skultrop, Västergötland (Fig. 3; Paper IV, tab.), has also been identified from Lamoshka, which further supports that possibility.

The trilobites, indicative of the *Megistaspis (P.) aff. estonica* Zone in Sweden, like *Pricyclopyge gallica* (Tjernvik, 1956) and *Raymondaspis brevicauda* Tjernvik, 1956 are not recorded eastwards. However, there is a potential

to use some undescribed taxa mentioned by Tjernvik, belonging to the genera like *Geragnostus* Howell, 1935, *Symphysurus* Goldfuss, 1843 and *Megalaspides* Brøgger, 1886.

In most of the studied localities the trilobite assemblage of the lowest part of the Mäeküla Member contains fragmentary *Rhinoferus* (*Popovkiaspis*) *leuchtenbergi* (Lamansky, 1905) [synonymous with *Rhinoferus* (*Popovkiaspis*) *pogrebowi* (Lamansky, 1905)], accompanied by *Evropeites lamanskii*, *Encrinuroides regularis* Pärnaste, sp. nov. and *Ptychometopus schmidtii*. In addition, *Proasaphus primus* Balashova, 1966 *sensu lato* turns up, showing clear change in morphology throughout the Billingen Stage. The agnostids *Geragnostus* and *Arthrorhachis* Hawle and Corda, 1847 and raphiophorids *Globampyx* Fortey, 1975 and *Ampyx* Dalman, 1827, whose close relatives are also common in the Swedish succession, appear in the overlying beds. Until further study proves the applicability of Scandinavian isoteline zonation in the East Baltic, the earlier established ***Evropeites lamanskii* Zone** (see Popov *et al.* 1997, fig. 2, after Balashova 1966) is temporarily accepted for that assemblage, because this taxa has been recorded from most localities. Yet, the last species is closely related to *E. toernquisti* (Holm, 1882) (Paper IV, tab.), known only by the type specimen from the *M. dalecarlicus* Zone in Dalarna. If the appearance of this particular genus in the Baltoscandian palaeobasin was synchronous basin-wards, this assemblage could be correlated with the ***Megalaspides* (*M.*) *dalecarlicus* Zone**. However, *Evropeites* itself is apparently a descendant of the Tremadocian *Anacheirurus* Reed, 1890 from Avalonia, showing its earlier appearance. Consequently, the study of trilobites shows that the faunal association of different beds of the Mäeküla Member is varying by localities, indicating diachrony of the lowest calcareous beds of the Estonia and Ingria as mentioned already by Pärnaste (Paper I).

Agnostids, pliomerids and encrinurids are lacking in the trilobite association of the more clayey Vassilkovo Beds, where both *M. (M.) dalecarlicus* (Holm, 1882) and *M. (M.) paliformis* Tjernvik, 1956 are common. The last is the index species for the **upper part of the *M. dalecarlicus* Zone** in Sweden. In addition, *Krattaspis* Öpik, 1937, *Proasaphus* Balashova, 1966 and *Ottenbyaspis* Bruton, 1968 are rather common, but *Rhinoferus* Balashova, 1976 is rare.

A new, almost monospecific association comprising ***Megistaspis* (*P.*) *estonica*** appears in the Päite Member, marking the corresponding zone, which can be well correlated across the Baltoscandia. Yet, some other poorly preserved and obscure isotelines were newly described by Balashova in 1966 as *M. (P.) planilimbata rossica*, *M. (P.) putilovensis*, *M. (P.) popovkiensis* and *Megalaspides* (*Lannacus*) *popovkiensis*. *M. (P.) popovkiensis* and *M. (P.?) scutata* Tjernvik, 1956 show several similarities with *Megistaspis* (*M.*) Jaanusson, 1956, being likely ancestors of the latter. Similarly, *M. (L.) popovkiensis* is the ancestor of *Rhinoferus* (*Lawiaspis*) Balashova, 1976. *M. (M.) dalecarlicus balticus* Balashova, 1956 apparently belongs to *Protoptychopyge* Balashova, 1959, bringing down the first appearance of that group. A few rare raphiophorids,

niobinids, cheirurids and cybelines are also recorded from the Päite Member. The appearance of *Megistaspis* (*Megistaspis*) just above the discontinuity surface of the “Püstak-kiht” marks the Billingen–Volkhov boundary. Both, the index trilobite *M. (M.) polyphemus* (= *M. lata* synonymized by Nielsen in 1995) and *M. (M.) limbata baltica* Balashova, 1976 are very abundant in the overlying Saka Member of the Volkhov Stage.

5.2. Correlation of trilobite zones with the graptolite and conodont zones

The Early Ordovician Baltoscandian trilobites are highly provincial. Therefore, the correlation between trilobite zonation and the graptolite and conodont zonation was made in the first step (Fig. 19, from Paper I), to reveal the ancestral-descendant relationship of studied cheirurins in global respect. The records of conodonts *Priniodus elegans* Pander, 1856 or *Oepikodus evae* Lindström, 1955 were especially good markers in the worldwide comparison of contemporaneous trilobite faunas. In contrast with strata from the earlier parts of the post-Tremadoc, the transgressive *O. evae* Zone beds are traceable all over the world (Löfgren 1994).

All conodont data of studied area available for the author (Mägi and Viira 1976; Mägi 1984; Bergström 1988; Mägi *et al.* 1989; Dronov *et al.* 1995; Einasto *et al.* 1996; Dronov *et al.* 1997a, p. 15; Dronov *et al.* 1997b, p. 22; Viira *et al.* 2001; Viira pers. comm. 2001) were considered in correlation of conodont zones within the local lithological units (Paper I, text-fig. 2). Correlation of Baltoscandian conodont zones with those of trilobites (Tjernvik 1956; Tjernvik and Johansson 1980) and graptolites (Cooper and Lindholm 1990; Lindholm 1991a) was mainly agreeing that of Löfgren (1996), but with two exceptions. First, the lower boundary of the *Priniodus elegans* Zone is slightly shifted upwards relative to that of *M. (P.)* aff. *estonica* Zone and that of the upper subzone of the *Tetragraptus phyllograptoides* Zone, following Löfgren (1993, 1994, 1997). This interpretation is based on the evidence of the first appearance of *P. elegans* somewhat higher in sections (cf. figs 4, 5 in Maletz *et al.* 1996). The second exception concerns somewhat lowered position of the *Baltoniodus navis*/*B. triangularis* Zone in respect of the Billingen/Volkhov boundary. It is based on the evidence from the Ontika (Mägi, 1990, fig. 38) and Aseri (Mägi 1984, fig. 1) sections in northeastern Estonia, where *B. triangularis* (Lindström, 1955) has been identified below the ‘Püstak-kiht’ together with the *Stolodus stola* (Lindström, 1955) above the last appearance of *O. evae* and below the first appearance of *B. navis* (Lindström, 1955), and co-occurs with the zonal trilobite *M. (P.) estonica* (Tjernvik, 1956). However, the conodonts may have been redeposited, so this assumption should be taken with some caution.

Global Series	British Series	Baltoscandian biozones			East Baltic chrono- & lithostratigraphy								
		Graptolite zones	Conodont zones	Trilobite zones	Stage	Substage a b		Estonia W E		Ingria			
Lower Ordovician	Arenig	<i>Didymograptus hirundo</i>	<i>Baltoniodus navis</i> <i>Baltoniodus triangularis</i>	<i>Megistaspis (M.) polyphemus</i>	Volkhov	B _{II} α	B _{II} α	Toila Fm.	Saka Member	Volkhov Fm.			
		<i>Phyllograptus ang. elongatus</i>		<i>Megistaspis (P.) estonica</i>							B _I γ	Päite Member	
		<i>Phyllograptus densus</i>	<i>Oepikodus evae</i>	<i>Megalaspides (M.) dalecarlicus</i>	Billingen	B _I β	B _I β						Leetse Formation
		<i>Didymograptus balticus</i>	<i>Prioniodus elegans</i>	<i>Megistaspis (P.) aff. estonica</i>									
		<i>Tetragraptus phyllograptoides</i> <small>upper</small>	<i>Paroistodus proteus</i>	<i>Megistaspis (P.) planilimbata</i>				Hunneberg	B _I α	B _I α	Joa Mb.	Lakity Beds	
	<i>Hunnegraptus copiosus</i> <small>lower</small>	<i>Megistaspis (E.) armata</i>											
	Tremadoc												

Figure 19. East Baltic upper Tremadoc and Arenig chrono- and lithostratigraphy correlated with Baltoscandian Biozones (Paper I).

The boundary between the Hunneberg and Billingen groups (later stages or substages) was placed between the *Megistaspis (P.) planilimbata* and *Megalaspides dalecarlicus* trilobite zones when established, coinciding with the lower boundary of graptolite *Phyllograptus densus* Zone (Tjernvik 1956). Later, Tjernvik (Tjernvik and Johansson 1980) agreed with Lindström (1957) that the uppermost strata of *M. planilimbata* Zone with divergent fauna (so called Transitional Bed) should be correlated with *Didymograptus balticus* Zone. In several sections this Transitional Bed still contains some survivors from the lower succession but also the first representatives of an ‘*estonica* sequence’. Thus the boundary between the Hunneberg and the Billingen was brought down to the base of the new trilobite zone, the *M. (P.) aff. estonica* Zone (Tjernvik and Johansson 1980). However, Lindholm (1991b, p. 287) recommended that it is better to use the Hunneberg (Series) in its original extent suggested by Tjernvik in 1956 as the unit filling a hiatus between Tremadoc and Arenig in their type area Wales. Since then, both versions have been in use or the conquering Latorp Stage (established by Jaanusson 1960), amalgamating those (sub)stages.

CONCLUSIONS

- (1) The subfamily Cyrtometopinae is re-established and revised as Cyrtometopinae *sensu stricto* within the family Cheiruridae. However, it may prove to be a junior synonym of Deiphoninae, or even Cheirurinae. This question about the validity of Cyrtometopinae can likely be solved by analysing all genera and families of the entire suborder together.
- (2) The extreme rarity, the meraspid *Krattaspis* exhibits several cyrtometopine characters already in that early stage. Comparison with cheirurines shows a few differences, which might be explained by different life-styles. The flatter image and well-developed thoracic muscular pattern of cheirurines suggest that this group was probably adapted to active life in the sea bottom.
- (3) Comparison of *Krattaspis* with other cheirurid genera suggests that it apparently is a stem-group for the entire subfamily Cyrtometopinae *s. str.* The morphological variation range of that genus displays features of several succeeding genera. Although the trilobites are extinct and the genetic basis of their body plan evolution is unknown, the comparison of *Krattaspis* and related genera appears to suggest that the morphology of its descendants in many lineages can be explained by changes in developmental timing (heterochrony).
- (4) The measurements, made over the surface of exoskeleton, revealed certain growth trends of the ontogeny of *Krattaspis*. During the holaspid period the following skeletal parts enlarged the most: the anterior lobe (LA), basal lobe (L1), the angle between genal spine and posterior border; but the postero-lateral angle of the fixigena decreased, and the eyes were less upright.
- (5) The regions of skeletal parts, most affected by changes during the late ontogeny (holaspid stage), were also changing most during the phylogeny observed in subfamily Cyrtometopinae *s. str.* In addition to the above-mentioned characters, the pygidial segmentation together with character of spinosity was changing most. The latter is well reflected in construction of the anterior part of the cephalon being ruled by exact coaptation during the enrolment of trilobite.
- (6) As the studied new material verifies, the assessment of the monotypic *Krattaspis* was based on confusing characters caused by distortion of the exoskeleton. (Due to compression the type specimen's glabella is actually more expanded forwardly and deformed posteriorly, the S1 furrows are joined over the glabella, and the conjoined S1-S1 and the occipital furrow are more distinct, and the occipital ring is more parallel-sided (tr.) than on the other specimens.) These characters led Öpik to the imprecise subfamilial assessment. Now, *Krattaspis* is redescribed, based on sufficient material, including *K. viridatus*, *K. popovi*, *K. vitalis*, and *K. sp. A*, and assigned to Cyrtometopinae.

- (7) Many characters traditionally considered as diagnostic for subfamilies Encrinurinae or Cybelinae are plesiomorphic within the family Encrinuridae, and most of the other apomorphic characters have exceptions within each subfamily. Two newly described characters (the predominant developing area of the pygidial axis and the general array of spines on exoskeleton) help to distinguish the Encrinurinae and Cybelinae. However, these resolve Staurocephalidae and Dindymeninae within Encrinuridae.
- (8) The earliest record of subfamily Encrinurinae from the Mäeküla Member, Billingen Stage of Estonia and NW Russia provides a new root for the phylogenetic tree that helps to clarify its branching and palaeogeographic origin. The analysis of the data matrix used in previous studies shows that features basic for restricting some new genera (e.g. *Walencrinuroides*, *Frencrinuroides*) within *Encrinuroides* s. l. are highly facies dependent and serve no importance in cladistic analysis as being plesiomorphic. In conclusion, *Encrinuroides* s. str. is reassessed, and it is suggested that *Physemataspis* (*Prophysemataspis*) is a junior synonym of *Erratencrinurus*.
- (9) The Baltoscandian Plimeridae and Pilekiidae possess an exceptional state of character diagnostic to these families. The studied new material shows slightly higher variation in number of pygidial segments than known before. In comparison with related taxa, the Baltoscandian taxa possess pygidia with reduced number of segments. *Evropeites* is the only pilekiid bearing only two pairs of pygidial pleurae, resembling in this the cheirurid acanthoparyphines.
- (10) The study of the collection of the Lower Ordovician trilobites from Estonia and NW Russia Mäeküla and Päite members revealed that most previous correlations with Scandinavian trilobite zones have been in error because of misidentification of stratigraphically significant species. In contrast to the conclusions of Balashova (1966), there is no sound evidence of the occurrence of the trilobites of the *Apatokephalus serratus* and *Megistaspis* (*Ekeraspis*) *armata* zones in Estonia and NW Russia whilst several data indicate to the appearance of the next *Megistaspis* (*Paramegistaspis*) *planilimbata* and *Megistaspis* (*P.*) aff. *estonica* zones in some localities. The *Megalaspides dalecarlicus* Zone is quite well represented in Estonia and Ingria, and its upper part indicated by the appearance of *Megalaspides paliformis* is observed in the Vassilkovo Beds in Ingria just below the *Megistaspis* (*P.*) *estonica* Zone. The latter is the homogeneous interval traced on the glauconite limestone succession throughout the entire area containing skeletons of the index trilobite settled as the 'trilobite cemeteries'.

ACKNOWLEDGEMENTS

This work has been carried out with sincere help and useful advice from many colleagues and friends from different institutions in Estonia and abroad.

First relevant persons, Dr Silvi Mägi and Dr Leonid Popov (Cardiff) are thanked for leading me to this work, by accompanying me in the first field-works and supplying with the first collection from St. Petersburg Region.

I cannot overestimate the role of my supervisor Prof Tõnu Meidla (University of Tartu) who offered support and constructive criticism during all my PhD studies. He is greatly thanked for that and for his patience. Also I am grateful to my colleagues Dr Linda Hints, Prof Dimitri Kaljo, Dr Jaak Nõlvak, and Dr Olle Hints for general discussions on Ordovician geology and palaeontology, giving advise whenever it was needed.

This trilobite work gained greatly from backing of my trilobite-colleagues, my dear friends Prof David L. Bruton (Paleontological Museum, University of Oslo), Dr Arne T. Nielsen (Geological Museum, University of Copenhagen), Dr Alan W. Owen (University of Glasgow), and Dr Kristina Månsson (Department of Geology, Lund University), whose valuable discussions and kind help is greatly appreciated. In addition to them, I want to thank my other colleagues, Prof Jan Bergström, for kindly showing me the cheirurid collection at the Swedish Museum of Natural History, Dr Philip D. Lane from Keele University for sending me the mould of the type specimen of the *Cyrtometopus* and photos of the other originals. Dr Arne T. Nielsen shared his respectable collection of cheirurine trilobites from Komstad Limestone and experience on trilobites during my visit to the Geological Museum in Copenhagen. I am also grateful to Prof Richard A. Fortey (London, Natural History Museum), Dr Alan W. Owen, Prof Brian Chatterton (University of Alberta), Dr Greg Edgecombe (Australian Museum, Sidney), Dr Philip D. Lane, Prof Euan N. K. Clarkson (School of Geosciences, University of Edinburgh), Prof Madis Rubel (Tartu University) and an anonymous referee for their helpful reviews and detailed corrections, on trilobites and linguistics, which greatly improved my papers.

Linguistic help has been offered also by Anne Noor regarding papers included to the this work, and Dr Ivar Puura made his intensive effort on final linguistic revision of the doctoral thesis. Technical assistance in photography has been provided by Gennadi Baranov. My sincere thanks are addressed to them.

Curators of the Paleontological Museum, University of Oslo; Geological Museum, University of Copenhagen; Department of Geology, Lund University, Swedish Museum of Natural History, and especially Vivianne Berg-Madsen from the Museum of Evolution, Uppsala University, are thanked for loans of the material, and being very kind in handling repeated requests of prolongation of the loans.

Finally, I want to express my gratitude to my parents for continuous encouragement and support, and my family, all my four kids and my husband, for replacing me by turns at home on my mother's duties, when I was lost in Trilobite World.

The articles included and this doctoral thesis were financially supported by grants of the Estonian Science Foundation (Nos 3516, 4674, 5922), and by Danish Natural Science Foundation in the framework of the project 'Faunal events and geological development of the North European Platform (Precambrian-Devonian)'. This investigation is a contribution to the International Geological Correlation Program projects nos 410 'The Great Ordovician Biodiversification Event', and 503 'Ordovician Palaeogeography and Palaeoclimate'.

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SUMMARY IN ESTONIAN:

VARA-ORDOVIITSIUMI TRILOBIIDID ALAMSELTSIST CHEIRURINA EESTIS JA LOODE-VENEMAAL: SÜSTEMAATIKA, EVOLUTSIOON JA LEVIK

Käesolev doktoritöö käsitleb Eesti ja Loode-Venemaa Alam-Ordoviitsiumi kihtidest pärit alamseltsi *Cheirurina* kuuluvate trilobiitide taksonoomiat, ontogeneesi ja fülogeneesi (artiklid I–III). Näidatakse nende esinemist kihiti ja geograafiliselt ning võrreldakse seda üldises trilobiitide levikupildis ja -tsonaalsuses (atriklid I, IV–V). Ilmnes, et mitmed uuritud trilobiitidest on vastavate fülogeneetiliste ridade vanimad esindajad. Sellest tulenevalt võimaldas antud materjal täpsustada sugukondade *Cheiruridae* ja *Encrinuridae* arengulugu ja süstemaatikat.

Esimeses artiklis uuritakse ühte sugukonna *Cheiruridae* varajaseimat esindajat *Krattaspis* 't täpsustades selle perekonna konseptsiooni. Nimelt selgus uue materjali põhjal, et selle perekonna tüüpliigi *Krattaspis viridatus* 'e tüüp-eksemplar on tegelikult settes defromeerunud ja kannab endas tunnuseid, mis tulenevad hoopis muljutusest. Need “valed” tunnused on olnud eksitavaks faktoriks selle rühma taksonoomilises käsitluses. Mõõtmistulemused annavad ettekujutuse *Krattaspis* 'te tunnuste muutumisest ontogeneesi käigus ja aitavad leida seaduspärasusi selle grupi fülogeneesis. Nii artiklis I, kui ka III on kaalutud Öpiku poolt püstitatud alamsugukonna *Cyrtometopinae* valiidsust, ning analüüsi tulemusena on selle kontseпти kitsendatud, et see oleks oma tunnustelt homogeensem. Sugukonna revisjoni käigus uuendatakse ka sama alamsugukonna teise perekonna, *Reraspis* 'e diagnoosi, revideeritakse selle koosseisu ja kirjeldatakse selle vanim esindaja.

Artiklis II käsitletakse varajaseimat alamsugukonna *Encrinurinae* esindajat ja ühes sellega diskuteeritakse kogu Ordoviitsiumi encrinuriinseid trilobiite, ning eriti perekonda *Encrinuroides sensu lato*. *Encrinuridae* sugukonna kahe alamsugukonna esindajate võrdlemise käigus on leitud kaks uut tunnust, mis aitavad neid eristada toetades nende mõlema monofüülsust.

Artiklis IV, mis on sissejuhatuseks järgmiste cheiruriinsete sugukondade *Pliomeridae* ja *Pilekiidae* põhjalikumale käsitlusele, näidatakse nende trilobiitide levikut Baltoskandias. Selgub, et kaldalähedasemates fatsiaalsetes tingimustes levinud taksonitel on vähem sabakilbi lülisid, kui vastavatele sugukondadele tavapäraselt iseloomulik.

Artikkel V annab esialgse ülevaate trilobiitide tsonaalsusest Billingeni ja Hunnebergi lademetes Eesti ja Loode-Venemaa aladel, aidates ühtlasi määratleda uuritud materjali suhtelist vanust kõrvutamaks neid ülejäänud sugulastega globaalses skaalas.

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Peamine uurimisteema

Ordoviitsiumi trilobiitide süstemaatika ja evolutsioon, nende seos funktsionaal-
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Teaduspublikatsioonid

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