Cyrtometopinid trilobites from the upper Volkhov and lower Lynna formations (lower Darriwilian) of NW Russia

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Two cyrtometopinid trilobite taxa from the lower Darriwilian of NW Russia are examined. A new species of the genus *Krattaspis* is described, extending the stratigraphical range of the genus into the lower Darriwilian (Middle Ordovician). *K. paraspinosis* n.sp. is the youngest representative of the genus, but is closest to forms assigned to *Cyrtometopus* and confirms the derivation of *Cyrtometopus* from *Krattaspis*. Ontogenetic studies of *K. paraspinosis* n.sp. and *Cyrtometopus clavifrons* Angelin, 1854, from the same beds indicates a forward displacement of the eyes with increasing size, which may be contrary to all other known members of the family Cheiruridae.

Keywords: *Cyrtometopus clavifrons*, *Krattaspis paraspinosus* n.sp., Cyrtometopinae, NW Russia, lower Darriwilian.

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The lower Darriwilian trilobites from Baltoscandia are described in several monographs (e.g., Dalman 1827; Angelin 1854; Linnarsson 1869; Schmidt 1881-1907; Brøgger 1882; Törnquist 1884; Lamansky 1905; Balashova 1953, 1976; Männil 1958; Přibyl, Vanek & Pek 1985; Nielsen 1995). These papers have resulted in an extensive knowledge of the geographical distribution of species, whereas the stratigraphical occurrences in most cases are known only at zonal or formational level. The biostratigraphy is thus from a modern point of view relatively coarse. Some initial steps have been taken in filling those gaps (e.g., Wandås 1984; Nielsen 1995; Hansen & Nielsen 2003; Ivantsov 2003), but much work remains to be done.

In the spring of 2000, intensive sampling was carried out at the Lynna River east of St. Petersburg, Russia (Fig. 1). The field work formed part of a larger project between St. Petersburg State University, the University of Copenhagen and the Geological Survey of Denmark and Greenland, with the main purpose to study the biostratigraphy of the Volkhov and Kunda stages (upper Dapingian to middle Darriwilian). The present study deals with the uppermost part of the $B_{II}\beta$, the entire $B_{II}\gamma$ and the lower part of the $B_{III}\alpha$ zones sensu Lamansky (1905), representing the upper part of the Volkhov Stage (B_{II}) and the lower part of the Kunda Stage (B_{III}). The studied section was divided into 11 beds and 50 sub-beds and sampled for fossils. This yielded 3920 mostly disarticulated trilobite specimens of which 151 or nearly four percent represented the subfamily Cyrtometopinae Öpik, 1937. The general biostratigraphic results for the trilobites have been treated elsewhere by Hansen & Nielsen (2003). The cyrtometopinid material contains three species, *Cyrtometopus clavifrons* Angelin, 1854, *Krattaspis paraspinosis* n.sp. and *Hemisphaerocoryphe platinflata* Hansen, 2005. *Hemisphaerocoryphe* Reed, 1896 has been treated elsewhere (Hansen 2005) and its taxonomical belonging to the cyrtometopinids is also not accepted by all (e.g. Congreve & Lieberman 2010). *C. clavifrons* was redescribed by Lane (2002) who observed some variation in morphology between various geographical areas, but did not find any systematic differences. This may, however, be because of coarse biostratigraphic resolution.

The aim of the present work is to present a description of the new species *Krattaspis paraspinosis* n.sp and how it supports the proposed relationship between *Krattaspis* and *Cyrtometopus*. Furthermore new data on ontogenesis and stratigraphically related changes in morphology of *Cyrtometopus clavifrons* are discussed.
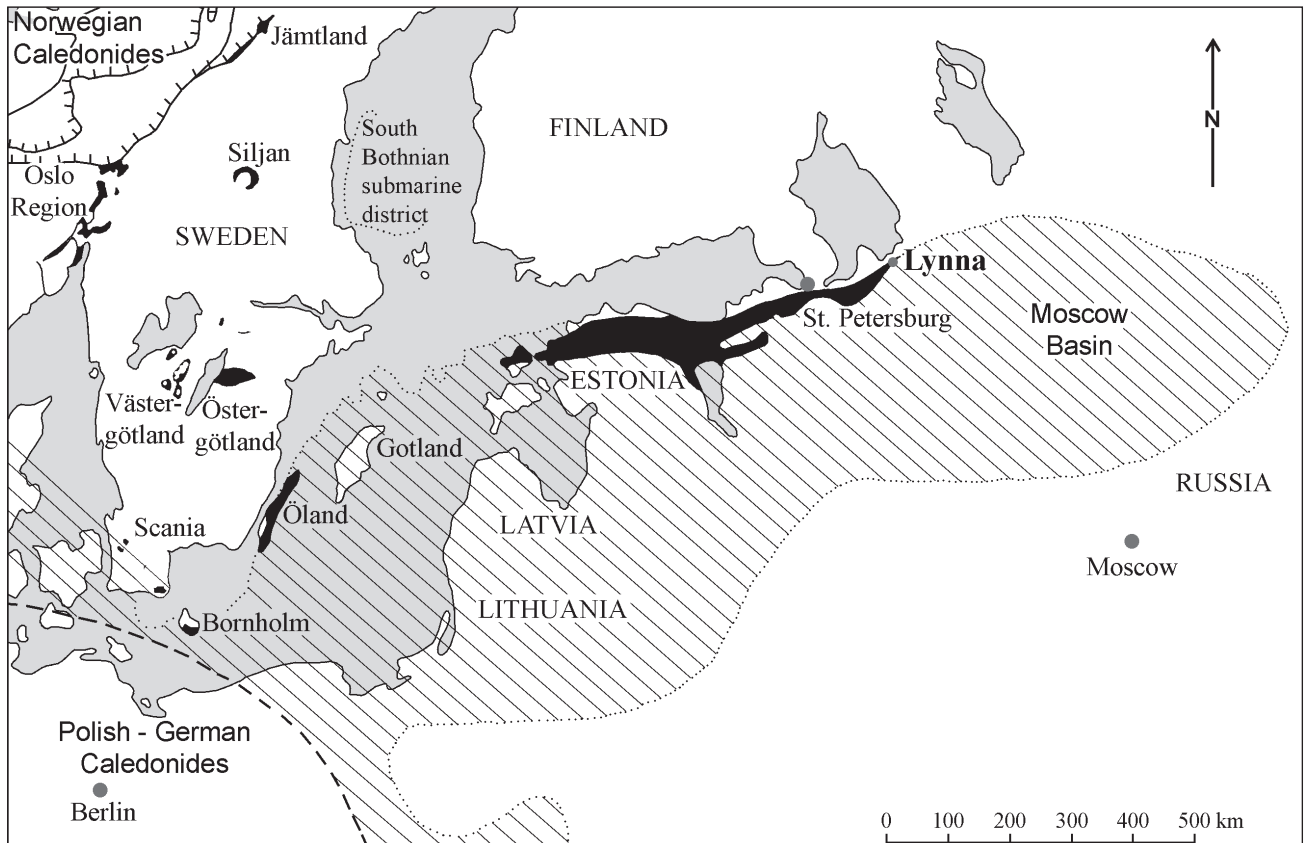
Fig. 1. Map showing distribution of Ordovician deposits in Baltoscandia. Outcrops are shown in black, while submarine and sub-surface deposits are marked with diagonal stripes. The map is modified after Jaanusson (1982) and Nielsen (1995).

Geological setting

The studied exposure is located near the outlet of the Lynna River, about 150 km east of St. Petersburg, Russia (Fig. 1). The outcrop, which is more than 10 metres high, exposes Middle Ordovician rocks including the upper part of Volkhov Stage and the entire Kunda Stage. The section comprises yellowish to grey calcareous packstone and wackestone beds with numerous marl intercalations and high glauconite content in the lower half. This paper only deals with the lower 4.2 metres, which extend from the middle part of the Volkhov Formation (top of $B_{II}\beta$) to the basal part of the Lynna Formation (basis of $B_{III}\alpha$) (Fig. 2).

At the time of deposition the Baltic continent was situated in a temperate belt at about 50° S (Christiansen & Stouge 1999). The continent was largely covered by an epicontinental sea with only a few smaller land areas. Because of the low topography and extensive flooding the supply of terrigeneous sediments was extremely low. This together with a low cool-water carbonate production resulted in a very small net rate of sedimentation approximating 1 to 3 mm/1000 years (Jaanusson 1982). The low supply of terrigene-

ous sediments together with higher energy, reworking and removal of the clay particles resulted in extensive cool-water carbonate ramps in the shallow-watered Baltic area (Tolmacheva *et al.* 1999), whereas the outer shelf in south-western Scandinavia was characterized by siliclastic, muddy deposits (Jaanusson 1982, Nielsen 1995).

The sediments at Lynna were deposited below fair-weather wave base in a middle carbonate ramp environment containing a rich benthic fauna. Except for the constant alternation between marl and more coarse-grained limestone the succession is very uniform, indicating a largely stable environment. Even the sea level changes occurring throughout the period only resulted in slight changes such as a generally coarsening of the sediments and a variable glauconite and clastic content.

The area around Oslo, southern Norway, was characterized by deposition of impure carbonates through most of the Volkhov and Kunda stages and probably represents a mid shelf environment much like that found in the East-Baltic area, although influenced by a slightly higher terrigeneous input.
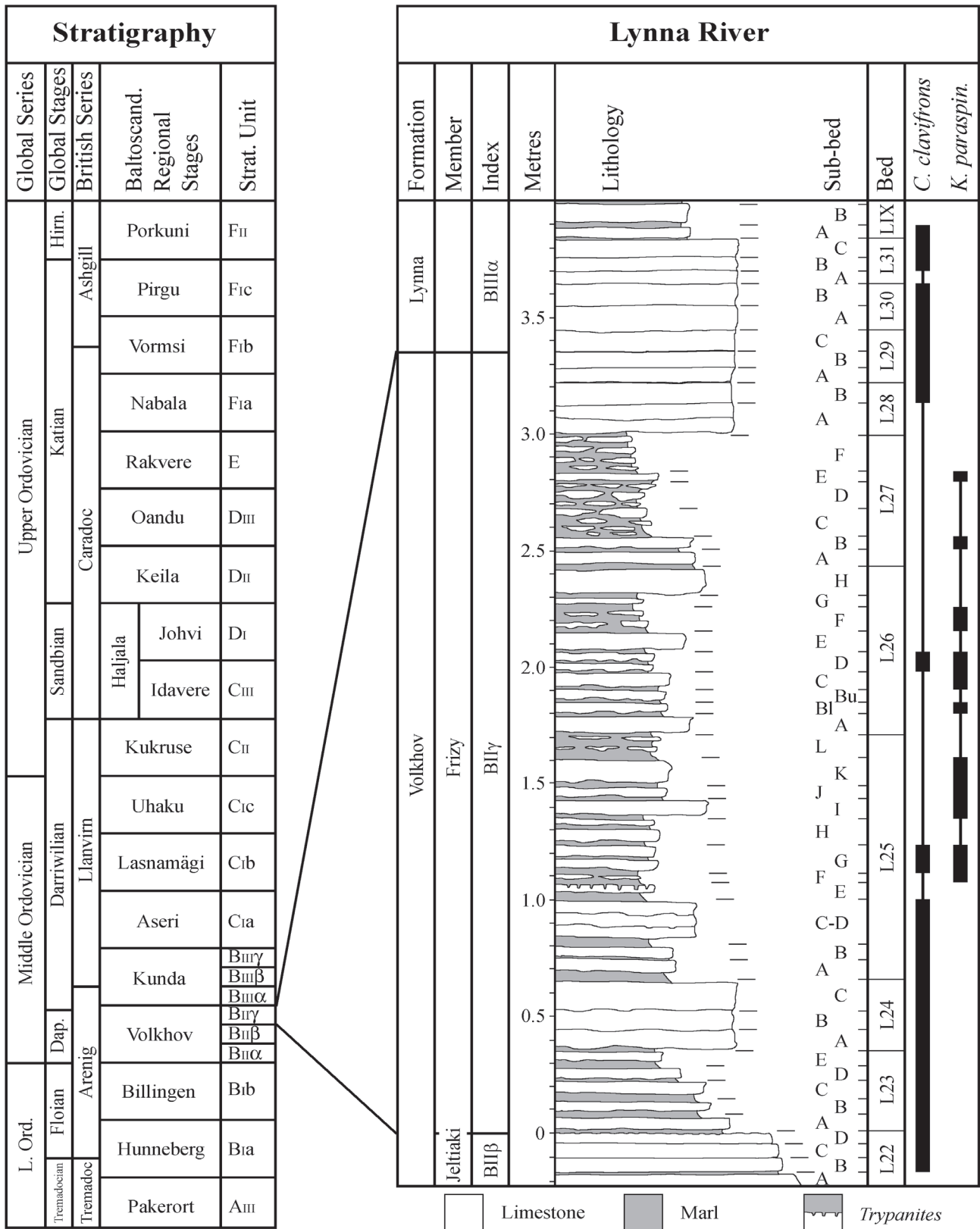
Fig. 2. Lithological log for the Lynna section. The log is based on data made available by Andrei Dronov. The formal lithological units on the right side column follow Dronov (1997). The stratigraphical units used for the Volkhov and Kunda Regional Stages on the left side column follow the subdivision proposed by Lamansky (1905). The rest follow the coarser system proposed by Männil (1966). The stratigraphical occurrences of the two species are shown on the right.

Measurements

All measurements were made using goniometric and measuring ocular, and are given to nearest half millimetre or, for the smallest specimens, with an accuracy of 0.1 mm. Cranidial measurements are shown on Fig. 3 and summarized in Tables 1 and 3 and the appendix. Glabella is defined as the area outlined by the occipital, axial and preglabellar furrows. The specimens were examined in random order in order to avoid measuring bias. A number of specimens selected at random were re-measured in order to estimate the measuring error. The error in general appears to be less than 5 % for the distance measurements and a couple of degrees for the angles. Increased variability of measurements related to systematic changes in preservation or deformation up through the studied interval are regarded as negligible.
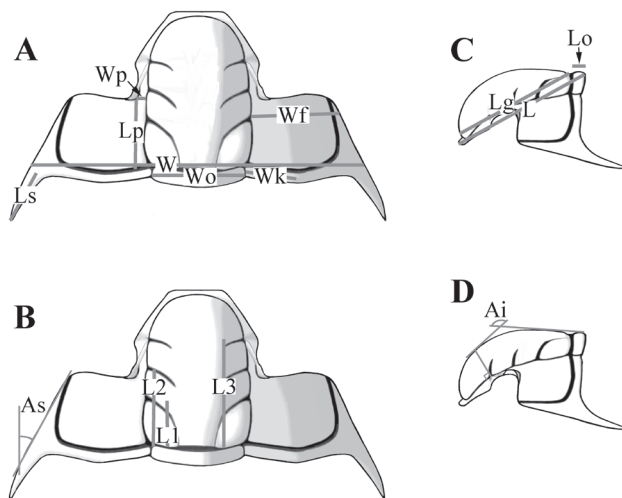
Ontogenetic examinations were based on the cranidial length as size-indicator. The analysis was done with Reduced Major Axis on a double-logarithmic scale. The possibility of no correlation between size and morphometric ratio is given by p(uncorr.) together with the number of specimens measured, N, and Pearson´s product correlation-coefficient, r, which is negative when the line of best fit is negative and vice versa. In cases where two populations were compared statistically each population was initially tested with Shapiro-Wilks test for a normal distribution. If both populations were accepted ($p \geq 5$ %), the similarity was tested using the F- and t-test. In cases where the test for normal distribution was rejected for one or both populations, the similarity was tested with two distribution independent tests named Mann-Whitney U-test and Kolmogorov-Smirnov test. All tests were made with the statistical program Past (cf. Hammer, Harper & Ryan 2001).

Fig. 3. Cranidial measurements. The bend on the posterior fixigenal border commented in the text is illustrated on Fig. 3B. The anterolateral border furrow is located at the fixigenal expansion opposite S3 (sub-fig. B). Abbreviations: **Ai** = angle of inflation, an angle formed between the sagittal line touching the occipital ring and posterior part of the glabella proper and the sagittal tangent to the glabella at the point, where a line perpendicular to the fixigena may be extended up from the lateral opening of S3 (high angles denotes cranidia with a small sagittal curvature) (Fig. 3D); **As** = angle between longitudinal axis of cranidium and anterior half of abaxial spine margin; **L** = cranidial length; **L2** = distance from occipital furrow to the opening of lateral glabellar furrow S2; **Lg** = glabellar length (excluding occipital ring); **Lo** = length of occipital ring; **Lp** = length between the pleuroccipital furrow and the posterior edge on the palpebral lobe; **Ls** = length of genal spine; **W** = cranidial width; **Wf** = width of fixigena; **Wk** = distance from axial furrow to the downwards bend on the posterior border; **Wo** = width of occipital ring; **Wp** = distance from the posterior edge on the palpebral lobe to the axial furrow.

Systematic palaeontology

Suborder Cheirurina Harrington & Leanza, 1957
Family Cheiruridae Hawle & Corda, 1847
Subfamily Cyrtometopinae Öpik, 1937

Cyrtometopinae was separated from the Cheiruridae by Öpik (1937). The subfamily is characterized by possessing a transverse furrow or line of pits across the thoracic pleurae. Lane (1971, 2002) considered the morphological variation within the group too large for a separation from the Cheirurinae Hawle & Corda, 1847 and Cyrtometopinae was therefore regarded as a junior synonym of this subfamily. The group was re-examined by Pärnaste (2003), who proposed a resurrection of the Cyrtometopinae but with fewer genera. These were *Actinopeltis* Hawle & Corda, 1847; *Cyrtometopella* Nikolaisen, 1961; *Cyrtometopus* Angelin, 1854; *Krattaspis* Öpik, 1937; *Reraspis* Öpik, 1937; *Sphaerocoryphe* (*Sphaerocoryphe*) Angelin, 1854 and *Sphaerocoryphe* (*Hemisphaerocoryphe*) (Reed, 1896). The emended diagnosis of Pärnaste (2003, p. 245) is followed here.

Genus *Cyrtometopus* Angelin, 1854
Type species.- *Calymene? clavifrons* Dalman, 1827 (designated by Schmidt 1881)

Cyrtometopus clavifrons Angelin, 1854
Fig. 3, 7A-E, Table 1, 2
1827   *Calymene? clavifrons* – Dalman, p. 260.

1854	*Cyrtometopus clavifrons*. Dalm. [partim] – Angelin, p. 32-33, pl. XXI: 4; pl. XXXIX: 9, a (non pl. XXI: 4a).			

1854   *Cyrtometopus clavifrons*. Dalm. [partim] – Angelin, p. 32-33, pl. XXI: 4; pl. XXXIX: 9, a (non pl. XXI: 4a).

1869   *Ch. (Cyrtometopus) clavifrons* Dalm. – Linnarsson, p. 60, 86.

1881   *Cheirurus (Cyrtometopus) clavifrons* Dalm. – Schmidt, p. 152-157, pl. VIII: 4-6; XVI: 7-12.

1882   *Cheirurus clavifrons*, Dalm. [partim] – Brøgger, p. 131-134, pl. V: 1-4, 6-9 (fig. 5 belongs to *Nieszkowskia tumida gibba*).

1884   *Cyrtometopus clavifrons* Dalm. – Törnquist, p. 16.

1907   *Cyrtometopus clavifrons* Dalm. – Schmidt, p. 9, 91.

1936   *Cyrtometopus clavifrons* (Dalm.) – Poulsen, p. 48.

non 1952   *Cyrtometopus* cf. *clavifrons* (Dalman, 1826) – Skjeseth, p. 173-174, pl. IV: 3, 4, 6 (Assigned to *Cyrtometopus priscus* by Tjernvik (1956)).

1970   *Cyrtometopus clavifrons* (Dalman) – Tomczykowa & Tomczyk, p. 184, 190, tab. 9.

1984   *Cyrtometopus clavifrons* (Dalman, 1827) – Wandås, p. 235-236, pl. 13B, C, E.

1995   *Cyrtometopus* sp. – Nielsen, p. 71, fig. 33, 34, 36, 48, 49.

2002   *Cyrtometopus clavifrons* (Dalman, 1827) – Lane, p. 155-164, fig. 1, pls. 1-3.

2003   *Cyrtometopus clavifrons* – Hansen & Nielsen, p. 108, 110, fig. 3.

2009   *Cyrtometopus clavifrons* (Dalman, 1827) – Hansen, p. 142, pl. 27: 5-9.

A more complete synonymy list is presented by Lane (2002).

Emended diagnosis: The cranidium is defined by the central location of the maximal width and height of glabella and by the genal spines, directed approximately 30° outwards relative to the symmetric axis (modified from Angelin (1854) and Schmidt (1881)).

Type material: The type material is in the Swedish Museum of Natural History, Stockholm, Sweden. The lectotype cranidium RM Ar.17907 selected by Lane (2002) is from the Expansus or lower Raniceps Limestone of the Swedish Holen Limestone at Skarpåsen, Östergötland.

Material: The material from Lynna consists of 123 cranidia of which the 54 most well-preserved have been measured. The Russian material has been supplemented by 16 cranidia from Scandinavia, six of which are kept at the Natural History Museum, University of Oslo, Norway. The rest together with the material from Lynna are deposited at the Geological Museum, Natural History Museum of Denmark, University of Copenhagen.

Description: Modified from Schmidt (1881, p. 152-157) and Lane (2002, p. 158-164).

Examined cranidia between 3.8 and 20.0 mm long, averaging 13 mm. Cranidium trapezoidal in outline, width corresponding to nearly twice the length. Glabella subrectangular in outline with slightly convex flanks and evenly rounded front; highest point at L2. Glabella widest at anterior end of L2, width corresponding to approximately 75 % of glabellar length (occipital ring excluded). Anterior margin nearly straight with two sharp anterolateral edges. Posterior edge of palpebral lobe positioned between 79 % and 102 % of the distance between S2 and occipital furrow from pleuroccipital furrow. Distance from posterior edge to the axial furrow corresponding to between 30 % and 52 % of the distance between posterior edge and pleuroccipital furrow. Genal spine diverging posteriorly with an angle of about 30° to sagittal line.

The rest of the exoskeleton is described in full by Schmidt (1881) and Lane (2002).

Table 1. Table for the number of specimens (N), extremities (Min., Max.), average (μ) and scatter (σ) on *Cyrtometopus clavifrons*. Abbreviations are explained on Fig. 3.

	Cyrtometopus clavifrons (Dalman, 1826)				
	N	Min.	Max.	μ	σ
L (mm)	41	3,8	20	13,3	4,14
L/W	17	0,47	0,63	0,54	0,045
Wo/W	19	0,25	0,35	0,29	0,025
Lp/L2	35	0,79	1,02	0,9	0,056
Lp/Lg	30	0,41	0,48	0,45	0,021
Wp/Lp	38	0,3	0,52	0,41	0,061
As	9	27	34	30	2,8

Table 2. Ontogenetic investigations of selected morphometric ratios and angles. p(a = 1) is used to distinguish between allometric (p < 5 %) and isometric (p ≥ 5 %) distributions. p(uncorr.) is a test for non correlation between ratio and size indicator (usually L). r (Pearson´s product correlation index) is negative for decreasing distributions and visa versa.

	Ratio	Size indicator	Transf.	N	p(a = 1)	p(uncorr.)	r
C.cl.	Lp/Lg	L	Loglog	28	0	0,001	0,578
	Wk/Wf	L	Loglog	16	5,22E-22	0,003	0,699
K. pa.	Lp/Lg	L	Loglog	14	7,93E-3	0,008	0,676
	Lp/L2	L	Loglog	14	0	0,007	0,684
	Wk/Wf	L	Loglog	8	8,69E-9	0,062	0,683

Remarks: The specimen figured by Angelin (1854, Pl. XXI: 4a) does not belong to *C. clavifrons* because the eyes are located posterolaterally.

Ontogeny: The material represents only holaspids, but even so a clear forward movement of the eye is observed from small to large specimens (Tab. 2). Chatterton (1980) examined the ontogenetic variation within a large number of cheirurid species. A comparison with the material at hand reveals differences between *Cyrtometopus* and most other genera of Cheiruridae. The most pronounced difference concerns the location of the palpebral lobe. Chatterton (1980) found that nearly all the genera examined showed a retreating trend for the eyes during growth, whereas a few showed stasis. The eye on *Cyrtometopus* is in contrast located more anteriorly on the larger individuals. It may prove interesting to undertake similar examinations on the closely related *Cyrtometopella*, which may exhibit the same trend. At the moment the knowledge is too limited to make assumptions, but the observation may well prove valid for phylogenetic analysis. Unlike most genera examined by Chatterton (1980) no ontogenetic variations in the lateral placement of the eye or in the relative distance between the lateral glabellar furrows have been observed in the available material, but this may be due the small size of the material or that it contains only holaspids.

Morphostratigraphy: An examination of the stratigraphical variations in the cranidial length was negative and size-changes should thus not influence the stratigraphic variations in morphometry.

The cranidium of *C. clavifrons* is overall characterised by morphological stasis through time. Exceptions are found in the relative width of the occipital ring, which increases through time in the East Baltic area as shown by the two morphometric ratios Wo/W (Fig. 4) and Wp/Lp. The differences between the oldest and youngest population of both ratios were tested with an F- and t-test. The F- and t-test for Wo/W gave: F = 1.8103, p(same σ) = 0.395, t = -3.0893, p(same μ) = 0.00666. The t-test was rejected. The F- and t-test for Wp/Lp gave: F = 1.763, p(same σ) = 0.448, t = -3.3564, p(same μ) = 0.00187. The hypothesis that the difference in average was zero was rejected. The stratigraphic differences are thus significant. The same is the case for the angle of inflation, Ai, which is decreasing from basis to top of the Lynna section (Fig. 5), reflecting an increase in the sagittal curvature of the glabella. A mean change of more than 5 degrees from the lower to the upper population is too large to be explained by measuring errors, especially because the measurements were made in random order, and the observed changes are regarded as genuine morphological changes in the population through time. Because of the absence of the species in the central part of the Lynna section, it is impossible to tell whether the stratigraphic development is gradualistic or punctualistic, but a gradual change is hinted at in Fig. 5. Examinations of Norwegian material from the Dapingian to middle Darriwilian Huk Formation and basal Elnes Formation indicate that the stratigraphic changes of the Ai angle and Wo/W-value are very poorly expressed or missing in this region. The Norwegian material was measured on internal moulds in contrast to the better preserved Russian material, adding a possible source of error, but even so the observed changes appear to represent a local phenomenon, and are likely ecophenotypic in origin.

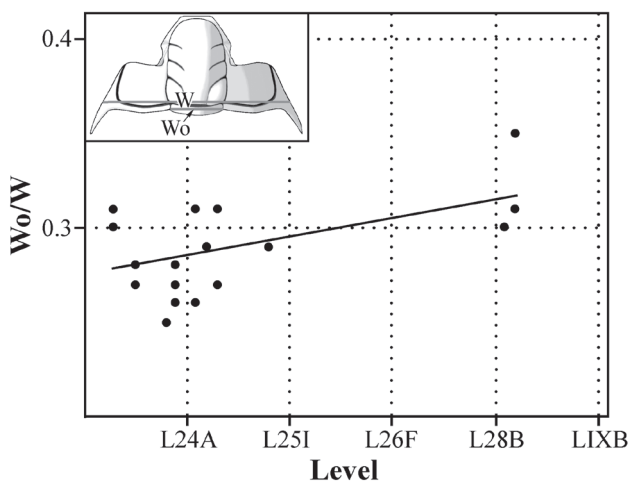Fig. 4. Stratigraphical variations in the cranidial Wo/W-ratio on *Cyrtometopus clavifrons*. Only the numbers of every tenth sub-bed are shown.
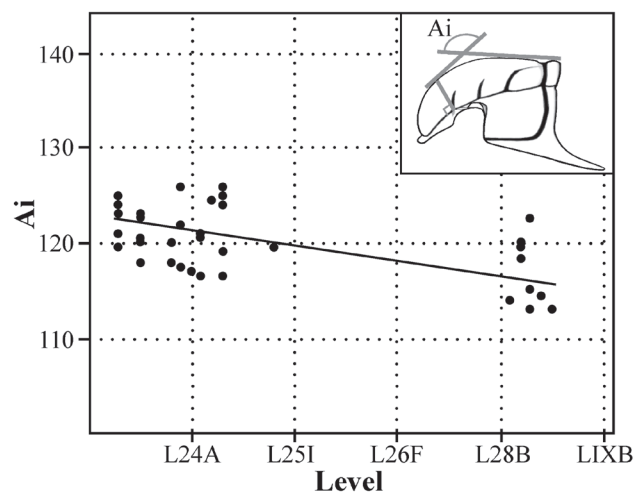

Fig. 5. Stratigraphical variations in the cranidial angle of inflation on *Cyrtometopus clavifrons*.

Occurrence: *Cyrtometopus clavifrons* is relatively common at the boundary between B$_{II}$β and B$_{II}$γ (sub-bed L22B to L25B) and again in the Volkhov-Kunda boundary interval at the top of the studied section (sub-bed L29A and upwards). In between it is nearly absent from sub-bed L25C-D to L28B (Fig. 2). The species is known from the Volkhov and Lynna formations (Glauconite limestone) and up into the Sillaoru and Obukhovo formations (Vaginaten limestone) in the East-Baltic (Schmidt 1881, 1907; Brøgger 1882), i.e. Volhkov-Kunda and maybe also top of the Billingen Stage. Lamansky (1905, p. 169) indicates an occurrence throughout B$_{II}$. However, this may well be too broad a stratigraphic interval and most probably includes the closely related but stratigraphically older *Cyrtometopus prisca* Tjernvik, 1956. Outside the East-Baltic area *C. clavifrons* is known from the Huk and lower Elnes Formation in the Oslo Region, Norway, where it ranges from the Dapingian *Megistaspis* (*Megistaspis*) *simon* Zone (B$_{II}$β) and up into the middle Darriwilian Aseri Stage (Brøgger 1882; Wandås 1984; Nielsen 1995; Hansen 2009; this study).

It is also found in the Komstad Limstone and Holen Formation in most of southern and central Sweden (Linnarsson 1869; Brøgger 1882; Törnquist 1884; Bohlin 1949; Nielsen 1995); in the Komstad Limestone at Vasagaard, Bornholm (Poulsen 1936; Nielsen 1995), and in the Polish Miedzygórz bed (Tomczykowa & Tomczyk 1970). In summary it ranges from the upper Dapingian to the middle Darriwilian.

Genus *Krattaspis* Öpik, 1937

Type species.- *Krattaspis viridatus* Öpik, 1937

The genus was redescribed and revised by Pärnaste (2003) and now includes the following species:

K. paraspinosis n.sp.
K. popovi Pärnaste, 2003
K. viridatus Öpik, 1937
K. vitalis Pärnaste, 2003

The inclusion of the new species allows the diagnosis of of the genus given by Öpik (1937) and Pärnaste (2003) to be emended thus: Glabella parallel-sided to slightly expanding, somewhat inflated; S3 furrows generally forward directed, describing an obtuse to weakly sharp angle to the preglabellar furrow. Eyes large; situated moderately close to glabella opposite L2 lobes and based on fairly high eye socle. Glabella and genal areas densely tuberculated.

The genus ranges from the Billingen Stage to the top of the Volkhov Stage (Floian to lower Darriwilian) and is geographically restricted to Baltoscandia (Pärnaste 2003; this study).
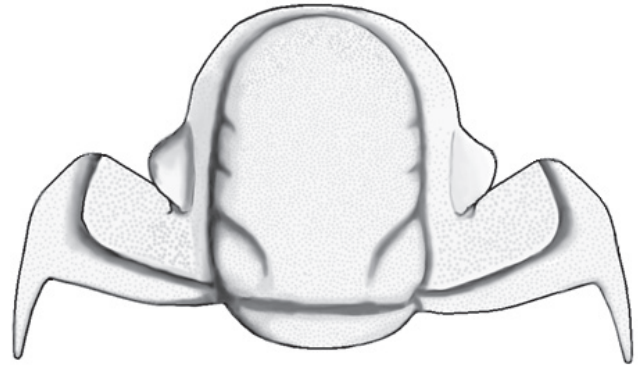

Fig. 6. Reconstruction of the cranidium of *Krattaspis paraspinosis* n.sp..

Krattaspis paraspinosis n.sp.
Fig. 6, 7F-L, Table 2, 3

Derivation of name: With reference to the genal spines, which diverge only slightly backward.

Diagnosis: Cranidium with slightly forward diverging axial sutures and short (sag.) occipital ring. Glabella low, S3 furrows directed slightly posteriorly. Genal spines short, diverging at about 15° from exsagittal line. Surface of cranidium with comparatively fine and dense granulation.

Material: The material at hand consists of 26 cranidia of which 18 well-preserved specimens have been selected for measurements. The description is largely based on these specimens. The holotype, MGUH 29201 (sample

Table 3. Morphometric ratios and angles for *Krattaspis paraspinosis* n.sp..

		Krattaspis paraspinosis n.sp.			
	N	Min.	Max.	μ	σ
L (mm)	16	3,3	9,7	6,6	1,8
L/W	9	0,56	0,76	0,64	0,06
Lo/Wo	14	0,21	0,29	0,24	0,024
Wo/W	10	0,33	0,38	0,36	0,015
Lp/L2	15	0,58	0,75	0,67	0,049
Lp/Lg	14	0,25	0,36	0,31	0,033
Wp/Lp	16	0,36	0,59	0,46	0,074
Wk/Wf	9	0,4	0,53	0,45	0,043
Ls/L	2	0,23	0,37	?	?
Ai	16	116	131	123	4,02
As	3	11,5	15	13	1,9

RL 2859) (Fig. 7G, H), is from sub-bed L26D in $B_{II}\gamma$. Paratype MGUH 29202 (sample RL 3784) was found in sub-bed L27E ($B_{II}\gamma$), whereas paratypes MGUH 29205, MGUH 29204 and MGUH 29203 (sample RL 2682, 3620 and 4315) were collected from sub-bed L26C, L27B and L29C ($B_{II}\gamma$) respectively. Two specimens, PMO 89691 and PMO 67269, from the Norwegian Huk Formation are housed at the Natural History Museum, University of Oslo. The rest of the material including all measured specimens, are deposited at the Geological Museum, University of Copenhagen, Denmark.

Description: Examined cranidia 3.3 to 9.4 mm long, averaging 6.4 mm. Length between 56 and 76 % of the width. Outline crescentic to rounded trapezoid; sagittal angle of inflation, Ai, around 123°; transverse inflation moderate to strong. Occipital ring relatively short (sag.), length between 21 and 29 % of the width; occipital ring occupies from 33 to 38 % of cranidial width. Glabella moderately inflated sagittally as well as transversely, but less so than in the other species within the genus. Glabella oblong rectangular in outline with frontal lobe describing neatly rounded dome; widest opposite S2, width corresponding to 75 % of glabellar length. Glabella highest at L2. Two anterior pairs of glabellar furrows shallow, posterior pair deeper. Posterior lobe, L1, bloated egg-shaped; L2 and L3 not inflated. Frontal glabellar lobe semi-elliptical in outline, width approximately twice the length. Axial furrow deep, describing, except for a slight curve around L1, a nearly straight line from posterior border to preglabellar furrow.

Fixigena with narrow palpebral area and broad posterior fixigenal field corresponding to approximately 40 % of cranidial length. Border short (sag.) with no or only indistinct frontal edges. Palpebral area very narrow, anteriorly bordered by normally indistinct eye-ridges running obliquely forwards to S3. Eye-ridge posteriorly transforming into relatively long and well developed palpebral lobe. Anterior part of lobe situated opposite S2 or posterior part of L3, posterior edge reaching back to a point between 58 and 75 % of length between S2 and occipital furrow from pleuroccipital furrow. Distance between posterior edge and axial furrow approximating 46 % of distance to pleuroccipital furrow. Posterior border on fixigena short (exsag.) bending sharply downwards about halfway to genal spine. Lateral border posteriorly continuing out into short genal spine with a length corresponding to between 23 and 37 % of cranidial length for the two measured specimen. Genal spine diverging from symmetric axis with about 13°. Facial sutures nearly parallel frontally, bending sharply outward and slightly forward immediately anteriorly of S1. Posterior branch sigmoidal, curving sharply backwards at

lateral furrow, continuing in a nearly straight line to cranidial margin shortly anterior of genal spine.

Cranidial surface with relative fine and dense homogenous granulation; fixigena furthermore characterized by pits arranged in more or less distinct rows.

Thorax known only from specimen MGUH 29202 (Fig. 7F), showing the two anterior segments. Axial ring moderately inflated and relatively broad (tr.), length corresponding to approximately 20 % of axial width. Width (tr.) of pleurae corresponding to axial ring width. Inner half of pleurae divided into an equal anterior and posterior part by deep pleural furrow. Pleural furrow starting from axial furrow centrally (exsag.) on segment, continuing in a straight line abaxially, terminating nearly 40 % of axial ring width from axial furrow. Pleura distally narrowing into a sharply pointed spine.

Ontogeny: The morphometric examination showed that the eye move forward through ontogeny as seen on *C. clavifrons* (Table 2).

Discussion: *Krattaspis paraspinosis* n.sp. differs from the other assigned species by having less forward directed S3 furrows, a slightly narrower glabella, more backwardly directed genal spines and by having a generally more uniform and dense distribution of fine glabellar granules (see Pärnaste 2003). It is morphologically closest to *K. vitalis* Pärnaste, 2003, but differs in having a wider palpebral lobe and narrower (tr.) palpebral area.

The outline of the glabella together with the nearly perpendicular S3 furrow and the fine and uniform glabellar granulation places this species morphologically closer to *Cyrtometopus* than any of the earlier forms, but is still clearly separated by the larger and more posteriorly placed eyes; lack of anterolateral edges on the anterior cranidial border and by the arched and not conical glabellar cross-section. The large morphological and ontogenetic resemblance between species of *Cyrtometopus* and *Krattaspis paraspinosis* n.sp, the youngest species known, supports the idea proposed by Pärnaste (2003, p. 245) that *Krattaspis* gave rise to *Cyrtometopus*.

Occurrence: From sub-bed L25F to L27E in $B_{II}\gamma$ at Lynna (Fig. 2). It is relatively common and uniformly distributed throughout the interval. Additional material has been exmined from the contemporaneous Huk Formation in southern Norway.
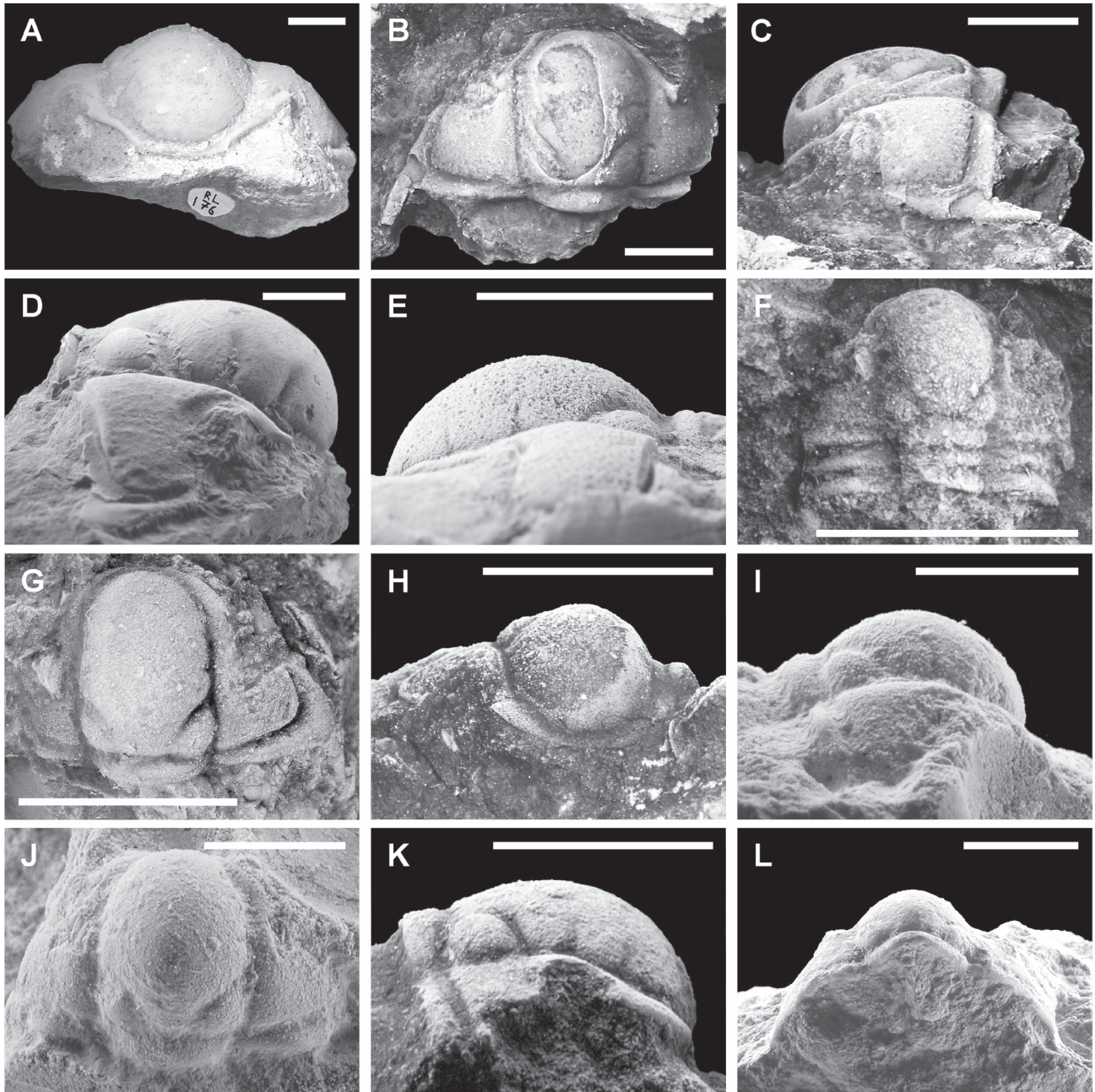
Fig. 7. ■ A-C. *Cyrtometopus clavifrons* Angelin. ■ A. Frontal view of cranidium. MGUH 29199 (sample RL176). Sub-bed L22C. B$_{II}$β. ■ B, C. Dorsal and lateral view of cranidium. MGUH 29200 (sample RL318). Sub-bed L23A. B$_{II}$γ. ■ D Lateral view of cranidium PMO 1994. Collected from the upper part of the Huk Formation at Huk, Bygdøy, Norway. ■ E. Lateral view of cast of cranidium PMO 102.474. Collected four to five metres above base of Elnes Fm. at Vikersund skijump, Modum, Norway. ■ F-L. *Krattaspis paraspinosis* n.sp.. ■ F. Cranidium and thoracic segments of early holaspid. Paratype MGUH 29202 (sample RL3784). Sub-bed L27E. B$_{II}$γ. ■ G, H. Dorsal and frontal view of cranidium. Holotype MGUH 29201 (sample RL2859). Sub-bed L26D. B$_{II}$γ. Note the nearly parallel genal spines; the lacking frontal edges and the posteriorly placed palpebral lobes. ■ I, J. Lateral and dorsal view of cranidium. Paratype MGUH 29203 (sample RL 4315). Sub-bed L29C. B$_{II}$γ. ■ K. Lateral view of cranidium. Paratype MGUH 29204 (RL 3620). Sub-bed L27B. B$_{II}$γ. ■ L. Posterior view of cranidium. Paratype MGUH 29205 (RL 2682). Sub-bed L26C. B$_{II}$γ. Scale bars represent five millimetres.

Appendix 1
Morphometric measurements on the cranidium of *Cyrtometopus clavifrons* and *Krattaspis paraspinosis* n.sp. from the locality at Lynna, Russia.

Sample	Taxon	Sub-bed	L	W	Lg	Wo	Lo	Lp	Wp	Wf	Ls	L2	Wk	Ai	As
RL4120	C. clavifrons	L29A	15,5	29,5	13,5	9	2	6,5	2,5	10	?	7	5	114	?
RL4157	C. clavifrons	L29B	8	?	7	4,5	1	?	?	?	?	3,5	?	119,5	?
RL4166	C. clavifrons	L29B	12,5	24	10,5	7,5	1,5	4,5	2	8	?	5,5	4	120	?
RL4173	C. clavifrons	L29B	13	21	11	7,5	1,5	4,5	2,5	7,5	?	5,5	?	118,5	?
RL1130	C. clavifrons	L24B	6,5	10,5	5,5	3	1	2,5	1	4	?	2,5	1,5	120,5	?
RL1759	C. clavifrons	L25G	6	11,5	5,5	3	1	2,5	1	4,5	?	2,5	?	119,5	?
RL992	C. clavifrons	L23E	?	?	?	?	?	4	1,5	7	4,5	?	?	?	?
RL4312	C. clavifrons	L29C	16	?	13,5	?	2,5	?	?	?	?	7	?	122,5	?
RL1267	C. clavifrons	L25A	12,5	22,5	9,5	6	2	4,5	1,5	7,5	6,5	5,5	3,5	124	27
RL282	C. clavifrons	L23A	?	28,5	?	8	2	6	2	9	?	6,5	4,5	?	?
RL4275	C. clavifrons	L29C	20	?	17	11	2,5	7,5	3	?	?	9	7	113	?
RL272	C. clavifrons	L23A	15,5	?	13	8,5	2	6	2	8,5	?	6,5	4,5	120,5	?
RL999	C. clavifrons	L23E	15	30	13	8	1,5	?	?	10	?	6,5	4	126	30
RL306	C. clavifrons	L23A	15,5	?	13	8	2	5,5	2	?	?	6,5	4	123	?
RL4458	C. clavifrons	L30B	4	?	3,5	2	?	1,5	0,5	?	?	16,5	?	?	?
RL132	C. clavifrons	L22C	18,5	?	17,5	11	2,5	?	?	?	?	8,5	6	125	?
RL896	C. clavifrons	L23E	9,5	19	8	5,5	1,5	3,5	1,5	6	?	4	2,5	117,5	33,5
RL1251	C. clavifrons	L24C	18,5	36	15,5	10,5	2,5	7,5	3,5	?	?	8	6,5	124,5	27
RL1601	C. clavifrons	L23C	?	?	?	?	?	6,5	3	?	?	6,5	4,5	?	?
RL1287	C. clavifrons	L25A	13,5	27,5	11,5	7,5	2	5	2	9	?	6	4	119	?
RL4464	C. clavifrons	L30B	10	?	8,5	5	1,5	?	?	?	?	4,5	?	113	?
RL4210	C. clavifrons	L29B	8,5	?	7,5	?	1	3,5	1,5	?	?	3,5	?	118,5	?
RL864	C. clavifrons	L23D	?	?	?	?	?	7	2,5	12,5	?	?	5	?	33
RL1062	C. clavifrons	L24A	18	?	17	?	?	?	?	?	?	8	?	117	?
RL291	C. clavifrons	L23A	16	?	13,5	8,5	2	?	?	?	?	6,5	?	118	?
RL871	C. clavifrons	L23D	15	32	13	8	2,5	6	2,5	11	?	6,5	5,5	118	30
RL1465	C. clavifrons	L25B	?	?	6	?	?	2,5	1	?	?	3	?	?	?
RL1137	C. clavifrons	L24B	20	?	17,5	9,5	2,5	8	2,5	?	?	8,5	?	116,5	?
RL318	C. clavifrons	L23A	11	20	10	5,5	1,5	4	1,5	6,5	?	4,5	3,5	122,5	27,5
RL4282	C. clavifrons	L29C	9	16,5	8	?	1	3,5	1,5	5,5	?	3,5	2,5	115	?
RL922	C. clavifrons	L23E	?	26,5	11,5	?	?	5,5	1,5	8	?	5,5	4	?	?
RL936	C. clavifrons	L23E	?	17	?	4,5	1	3,5	1	5,5	?	4	3	?	?
RL4526	C. clavifrons	L31B	?	?	11	?	?	?	?	?	?	5,5	?	?	?
RL182	C. clavifrons	L22C	11,5	?	10	5,5	1,5	4,5	2	7	?	5	3,5	123	?
RL1325	C. clavifrons	L25A	?	22	?	7	1,5	4,5	2	7	5,5	4,5	3	126	?
RL1123	C. clavifrons	L24B	14	24,5	12	7,5	1,5	?	?	8	?	6	4,5	121	?
RL1343	C. clavifrons	L25A	11,5	?	10	6,5	1,5	4	1,5	?	?	4,5	5	116,5	30
RL961	C. clavifrons	L23E	15,5	30	13,5	8,5	2	?	?	9	?	6,5	5	122	34
RL1322	C. clavifrons	L25A	11	?	10	6,5	1,5	4,5	2	?	?	4,5	3,5	125	?
RL176	C. clavifrons	L22C	18,5	34,5	16	10,5	2,5	7,5	3,5	?	?	7,5	6,5	119,5	?
RL1004	C. clavifrons	L23E	7,5	?	6,5	4	1	2,5	1,5	?	?	3	2,5	?	?
RL1336	C. clavifrons	L25A	14,5	?	13	8,5	2	6,5	2,5	?	?	6,5	4,5	116,5	?
RL163	C. clavifrons	L22C	18,5	?	16,5	9,5	2	?	3,5	?	?	7,5	?	?	?
RL340	C. clavifrons	L23A	13,5	?	11	8,5	2	5	2	?	?	6	4	?	?
RL1181	C. clavifrons	L24C	16	?	13,5	?	2	6	2	?	?	7	?	?	?
RL320	C. clavifrons	L23A	?	?	?	?	?	6	2	8,5	?	?	4	?	?
RL160	C. clavifrons	L22C	9	15	7,5	4,5	1,5	3,5	1,5	5,5	?	3,5	2,5	121	?
RL160	C. clavifrons	L22C	12,5	?	10,5	6,5	1,5	?	2	?	?	5	?	124	?
RL397	C. clavifrons	L23A	19,5	?	17,5	?	?	?	?	?	?	8	?	120	?
RL847	C. clavifrons	L23D	9	?	8	5	1	3,5	1	5,5	?	3,5	2,5	120	?
RL4523	C. clavifrons	L31B	?	?	?	?	1,5	3,5	1,5	6	?	4	2,5	?	?
RL4442	C. clavifrons	L30A	15	?	13,5	?	?	?	?	?	?	6,5	?	114,5	?
RL4060	C. clavifrons	L28B	?	?	15	?	?	?	?	?	?	7,5	?	?	?
RL4315	K. paraspinosis	L29C	7,5	?	6,5	4	1	2	1	?	?	3	2	121,5	?
RL2200	K. paraspinosis	L25J	9,5	15	8	5	1,5	2,5	1	5,5	?	4	2,5	123	12
RL1809	K. paraspinosis	L25G	6,5	9,5	5,5	3,5	1	1,5	0,5	3	?	2,5	1,5	122	?
RL3758	K. paraspinosis	L27E	7,5	11,5	6,5	4	1	2	1	3,5	?	3	1,5	126,5	?
RL2859	K. paraspinosis	L26D	5	8,5	4,5	3	1	1	0,5	2,5	?	2	1	123	11,5
RL4256	K. paraspinosis	L29C	8	?	6,5	?	1	2	1,5	?	?	3,5	?	116	?
RL2849	K. paraspinosis	L26D	6	8	4,5	2,5	1	?	?	?	?	2,5	?	126	?
RL3620	K. paraspinosis	L27B	7	?	6	4	1	2	1	?	?	3	?	122	?
RL1783	K. paraspinosis	L25G	8,5	?	7,5	?	1	2	1	?	?	3	?	125	?
RL2682	K. paraspinosis	L26C	7,5	13	6,5	4,5	1	2,5	1	4,5	?	3,5	2,5	122	?
RL3806	K. paraspinosis	L27E	5,5	9	4,5	3	1	1,5	1	3	?	2,5	1	128,5	15
RL3148	K. paraspinosis	L26F	4,1	?	3,6	2,4	0,5	1,1	0,5	?	?	1,7	?	117	?
RL1769	K. paraspinosis	L25G	6,5	9,5	5,5	3,5	1	1,5	1	3	1,5	2,5	1,5	122	?
RL2331	K. paraspinosis	L25K	?	13	?	4,5	1,5	2,5	1	4,5	2,5	3,5	2	?	?
RL1787	K. paraspinosis	L25G	?	13	?	?	?	2	1	4,5	?	?	?	?	?
RL3784	K. paraspinosis	L27E	3,3	?	2,8	1,8	0,5	0,7	0,3	?	?	1,2	0,6	120	?
RL1800	K. paraspinosis	L25G	4,3	7,5	3,7	2,6	0,6	1,1	0,5	2,5	1,6	1,8	1	128	?
RL2085	K. paraspinosis	L25I	9,5	?	8	5,5	1,5	?	?	?	?	4	?	131	?

Appendix 2
Morphometric measurements on the cranidium of *Cyrtometopus clavifrons* in Scandinavia.

Sample	Taxon	Locality	Stratigraphic index	Ai	W	Wo
A.564	*C. clavifrons*	Norway	BIIβ	107	?	?
A.1022	*C. clavifrons*	Norway	BIIβ-BIIγ (Lower)	116	?	?
A.1042	*C. clavifrons*	Norway	BIIβ-BIIγ (Lower)	114	?	?
A.1017	*C. clavifrons*	Norway	BIIβ-BIIγ (Lower)	114	?	?
A.327	*C. clavifrons*	Norway	BIIγ (Upper)	122	?	?
A.293	*C. clavifrons*	Norway	BIIγ (Upper)	111	?	?
A.384	*C. clavifrons*	Norway	BIIIα	108	?	?
K.1347	*C. clavifrons*	Sweden	BIIIα	114	~23,5	~6
PMO 1994	*C. clavifrons*	Norway	BIIβ-BIIIα	116	38	10
PMO 66338	*C. clavifrons*	Norway	BIIβ-BIIIα	?	26,5	7,5
PMO S.1601	*C. clavifrons*	Norway	BIIβ-BIIIα	102	?	?
PMO 106.073	*C. clavifrons*	Norway	BIIIγ-C1a	?	17,5	5
PMO 106.065	*C. clavifrons*	Norway	BIIIγ-C1a	?	29,5	~7,5
PMO 102.474	*C. clavifrons*	Norway	BIIIγ-C1a	114	16	4
PMO 105.984	*C. clavifrons*	Norway	BIIIγ-C1a	?	22	6,5
PMO 102.454	*C. clavifrons*	Norway	BIIIγ-C1a	116	?	?

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Artiklen præsenterer en taksonomisk gennemgang af to midt ordoviciske trilobitarter, *Cyrtometopus clavifrons* Angelin, 1854, og *Krattaspis paraspinosis* n.sp., tilhørende underfamilien Cyrtometopinae. Undersøgelsen er hovedsageligt baseret på materiale indsamlet fra kalk- og mergelaflejringer ved bifloden Lynna´s udmunding cirka 150 kilometer øst for Skt. Petersborg, NV Rusland, men er suppleret med materiale af *Cyrtometopus clavifrons* fra Oslo området i Norge. *Krattaspis paraspinosus* n.sp. udgør den yngste art indenfor slægten. Den er morfologisk nærmere søsterslægten *Cyrtometopus* end slægtens andre arter og synes dermed at understøtte at *Cyrtometopus* nedstammer fra *Krattaspis* således som foreslået af Pärnaste (2003, s. 245). Undersøgelser af vækstændringer hos både *K. paraspinosus* og *C. clavifrons* indikerer en fremadrykning af øjets relative pladsering på hovedet i forhold til dyrets størrelse. Dette er modsat af hvad der ses hos andre repræsentanter af familien Cheiruridae.

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