The Lower Ordovician trilobite Megistaspis (Rhinoferus) hyorrhina (Leuchtenberg, 1843) (Trilobita) in Norway, with notes on its autecology

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The occurrence in the Arenig of the Oslo Region of the typically east Baltic trilobite *Megistaspis (Rhinoferus) hyorrhina* (Leuchtenberg, 1843) is confirmed. The Norwegian specimens exhibit a range of variation just as wide as that seen in the east Baltic. The visual field is estimated and found to overlap posteriorly and 20° above horizontal. The glabellar tubercle in asaphids is considered to have functioned as a pressure-sensitive organ. The swelling of the posterior part of the glabella in some specimens, may have been to lift this organ as high as possible. This interpretation, together with the elevated eyes and the flattened exoskeleton, suggest a shallow infaunal life habit.

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Introduction

Megistaspis (Rhinoferus) hyorrhina (Leuchtenberg, 1843) has previously been considered a typical eastern Baltic species, common on the island of Öland, but rare in central Sweden and absent from the deeper-water environment of the Oslo Region (Tjernvik & Johansson 1980, p. 189). Recently, Nielsen (1995, p. 150) recorded and figured a pygidium of *Megistaspis (Rhinoferus)* cf. *hyorrhina* (Leuchtenberg 1843) from the Lysaker Member of the Huk Formation (upper subzone of the *M. limbata* Zone) at Slemmestad. He considered this pygidium to correspond «in all preserved features to *M. hyorrhina* as described by Schmidt (1906)», but treated it «*as M. (R.)* cf. *hyorrhina* in the absence of cephalic material». He also mentioned two other pygidia of this species from Slemmestad in the collections of the Paleontological Museum, Oslo. The latter specimens are very poorly preserved; they may or may not be conspecific.

At Vestfossen in 1997, a student, Ståle Melbye, found an almost complete specimen of *M. hyorrhina* which, together with specimens found by the second author and museum material from Paleontologisk Museum, Oslo, prompted the present study. The quality of some of the material makes it possible to discuss some of its ecological features.

Material

An almost complete, articulated specimen (PMO 162.658-659), from Skarahaugen, Vestfossen, Øvre Eiker. The specimen was found one metre above the base of the Lysaker Member (Huk Formation) (see Owen et al. 1990, p.13). This level corresponds to the lower part of the upper subzone of the *Megistaspis limbata* Zone of Nielsen (1995, p. 38). Additional material consists of two pygidia, each with five associated thoracic segments from the collections of Paleontologisk Museum, Oslo; one from Krekling Farm, Øvre Eiker (PMO 83486-83487) and one from an unknown locality, probably somewhere near Vestfossen (PMO 162.660). This material derives from an unknown level within the Lysaker Mbr. Five new cranidia were found by the junior author, three at Skarahaugen to the west of Vestfossen (PMO 162.661,162.663 and 162.665), one at Såsen east of Vestfossen (PMO 162.662) and one at Stavlum, Krekling (PMO 162.664) (for localities, see Fig. 1). All are from approximately the same level as the complete specimen. All specimens are housed in the Paleontologisk Museum, University of Oslo, Norway (PMO).

The East Baltic specimens illustrated by Schmidt (1906) on pl. III, figs. 1, 1a, 1b, 1c, 8, 10 and 11 are missing from Russian museum collections. The rest of his illustrated specimens (pl. II, fig. 10; pl. III, figs 2-7, 9) are housed in the Central Scientific Research Geological Exploration Museum (CNIGR) in St. Petersburg, Russia (Bruton et al. 1997, p. 56-57, p. 95). They have not been studied.

Associated fauna

The beds in which the Norwegian material was collected (100-140 cm above the base of the member), consist of very muddy limestones, and yield numerous orthid brachiopods and beyrichiacean ostracods (Brøgger, 1882, Öpik, 1939) together with complete exoskeletons of the trilobite *Ptychopyge excavata-zonata* (Angelin, 1854). Most of the latter seem to be the remains of dead animals rather than moults. *Asaphus (Asaphus) lepidurus* Nieszkowski, 1859, and *Megistaspis (Megistaspidella) acuticauda* (Angelin, 1854) are less common in this bed, but about 30 cm higher in the section, *A. lepidurus* is very common in the Vestfossen area (hundreds of complete specimens), and its abundance exceeds that seen in Estonia, although it is also very abundant in the uppermost part of the Volkhov Stage in Russian sections (A.T. Nielsen pers. comm.).

Description

The complete specimen (Fig. 2A-D) is slightly damaged anteriorly and posteriorly. It is seemingly more elongated than the specimens figured by Schmidt (1906; pl. 2, fig. 10; pl. 3, fig. 1-11). It is 109 mm long, but lacks the posteriormost part of the pygidium and a very small part of the anterior margin.

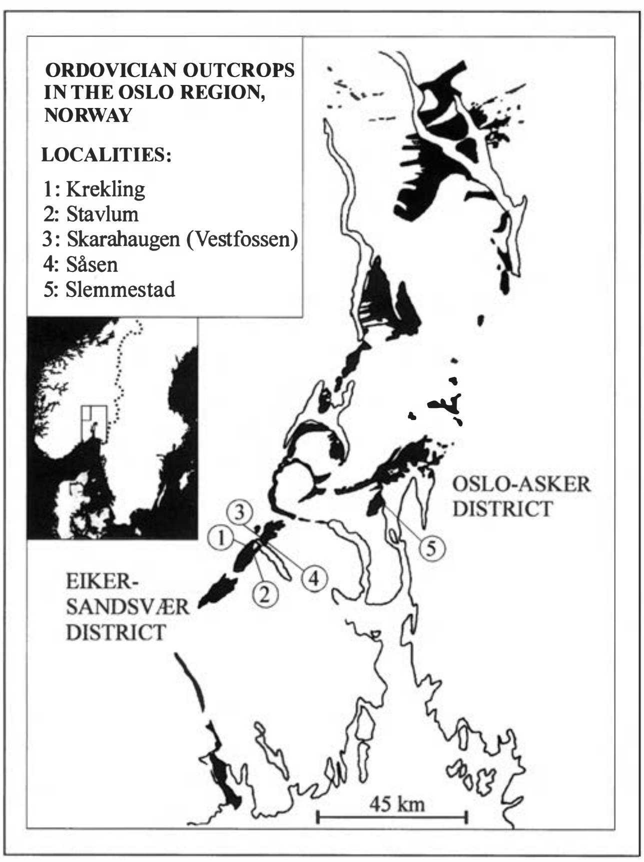

Fig. 1. Map of the Ordovician outcrops in the Oslo Region. Numbers correspond to the localities mentioned in the text.

The ratio (glabellar length : cranidial length) varies between 0.62 to 0.65 in the east Baltic material illustrated by Schmidt (1906). In the Norwegian material this ratio falls into two groups; the three best preserved cranidia have a value of 0.51-0.52, the three flattened and damaged cranidia are grouped at around 0.57-0.6. The preglabellar field is thus longer in the Norwegian specimens. A median depression in the preglabellar area is present. The tips of the fixigena range from bluntly rounded to more pointed. The anterior branches of the facial suture diverge in front of the eyes and bend inwards at the level of the anterior margin of the glabella. Two to three pairs of glabellar furrows are visible, the posterior pair being most distinct and located directly inside the palpebral lobes. The glabella is unusual for megistaspids in that it bears a prominent glabellar node of variable size.

The eyes are relatively small in proportion to the cephalon. Only in the specimens with the smallest glabellar nodes do the palpebral lobes rise above the top of the glabella.

The occipital furrow is only visible as slight depressions laterally, which are bent slightly forward as in other megistaspids. The posterior border furrow is only weakly developed. The occipital ring is wider (transv.) than the fixed cheeks. In specimens with the most prominent glabellar node, the node is elongated onto the occipital ring, thus totally overgrowing the medial part of the occipital furrow. In these specimens the posterior border furrow is absent.

The free cheeks run steeply downward from the eye to a lateral, horizontal border which tapers posteriorly towards the genal spine. The genal spines are rather robust, reaching to the fourth thoracic segment, bending evenly inwards and somewhat upwards at the posterior end, with a very sharp point.

The pygidium is parabolic in outline. The length:width ratio varies between 0.75 and 0.85 in Schmidt's figured material. In most of the Norwegian pygidia the posterior margin is damaged, but they yield approximately the same values. In the Norwegian material the axis occupies probably about 90 % of the total pygidial length, while in the material figured by Schmidt (1906) this varies between 72 % and 83 %. The axis is of equal width along all the thorax, narrowing rapidly in the anterior 5-6 axial rings of the pygidium, and then maintains equal width to the posterior end but seems to widen in the posteriormost part in flattened specimens. This is an effect of the profile of the axis; anteri-

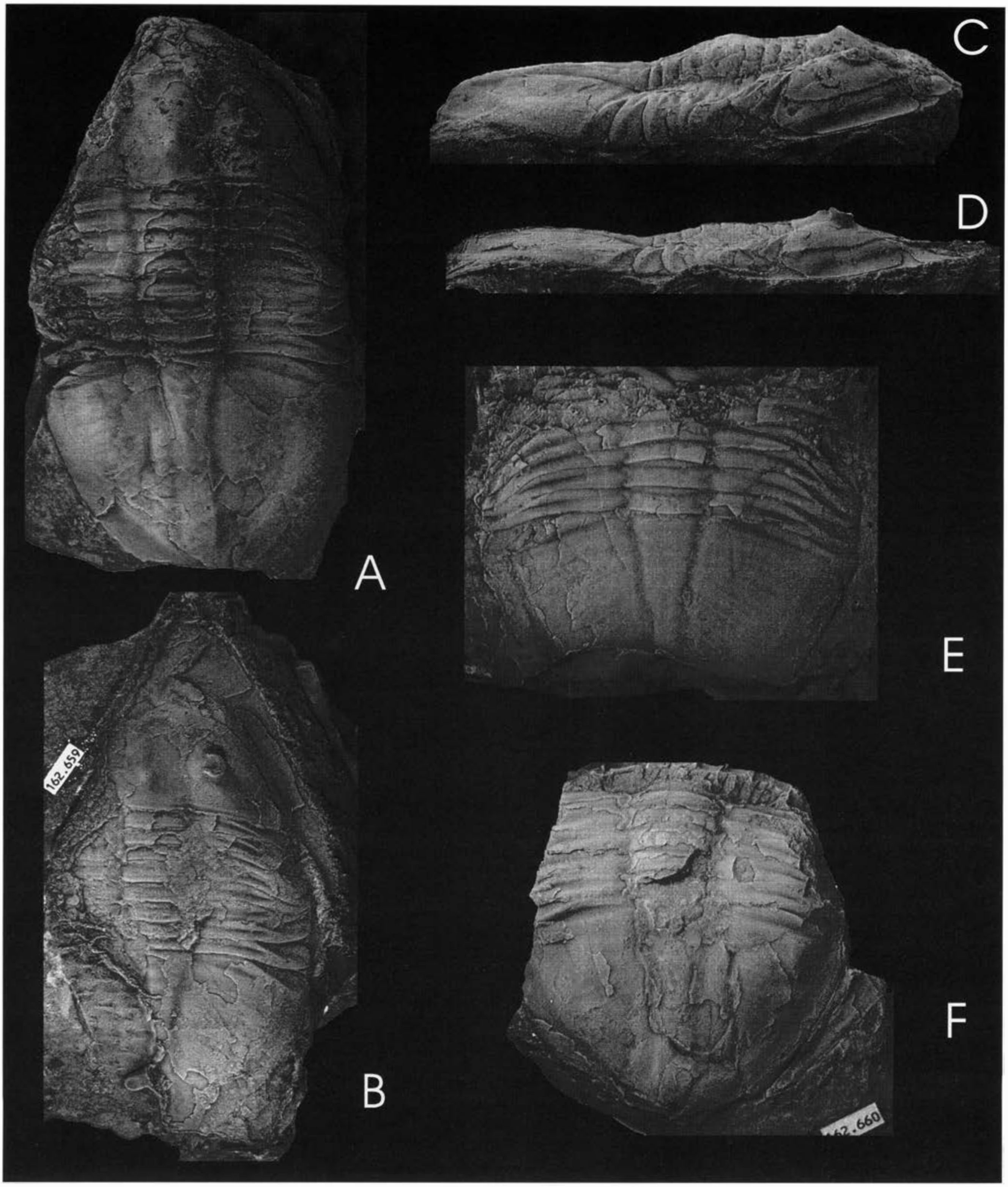

Fig. 2. Megistaspis (Rhinoferus) hyorrhina (Leuchtenberg, 1843). A-D: Dorsal and right lateral views of entire specimen (X 0.9); A,C: PMO 162.658 (part); B,D: PMO 162.659 (counterpart and latex cast). Huk Fm. (Lysaker Member, 1m above top of Huk Member), Skarahaugen, Vestfossen. Coll. Ståle Melbye 15/4/1997. E. Dorsal view of latex cast of pygidium with 5 segments (X 0,8). PMO 83486. Loose block from the Huk Fm. (Lysaker Member), road cutting, Krekling farm, Krekling, Eiker. Coll. S. Skjeseth 9/7/1954. F: Dorsal view of latex cast of pygidium with 5 segments (X 0,9). PMO 162.660. Huk Fm. (Lysaker Member), Locality unknown, probably near Vestfossen.

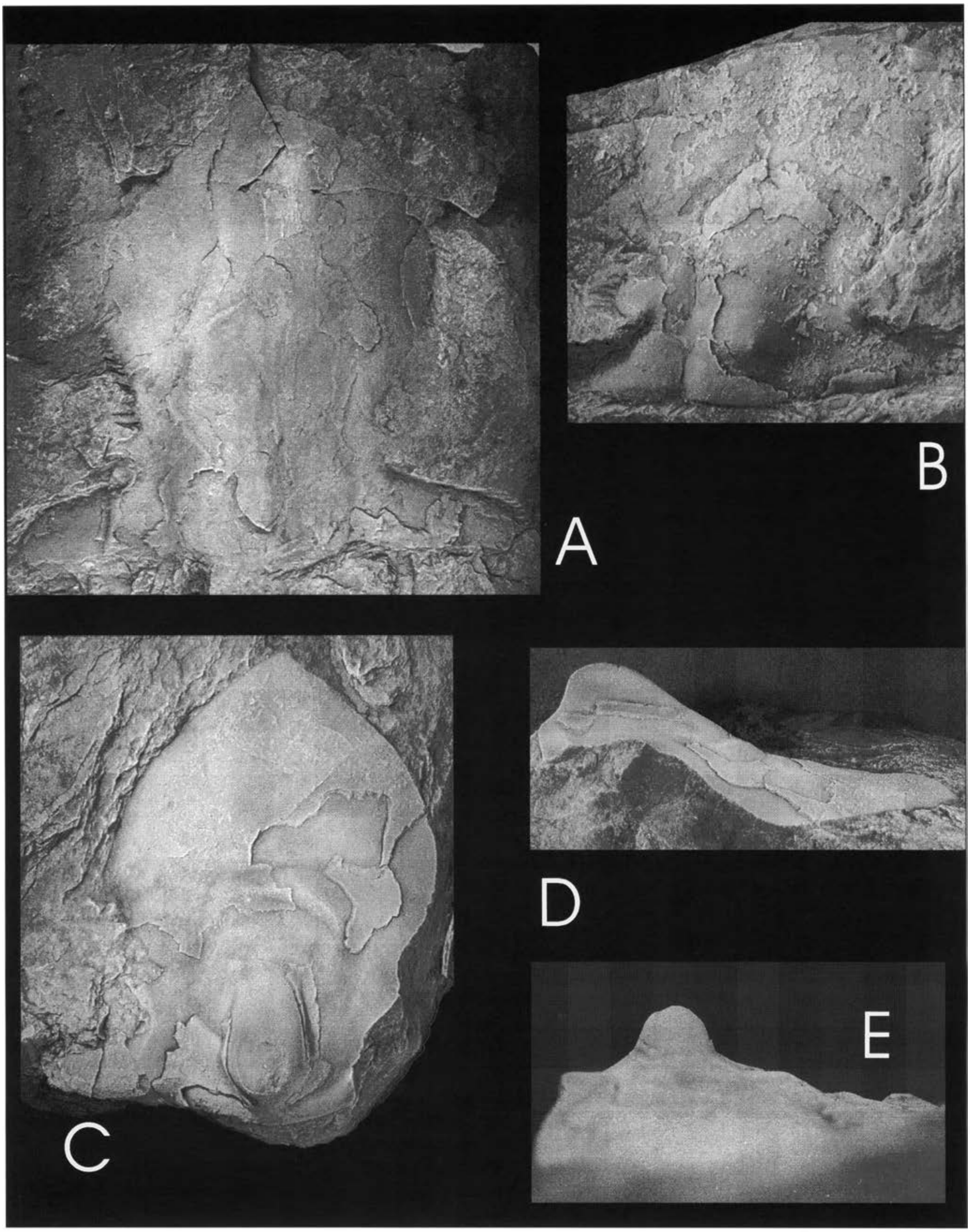

Fig. 3. Megistaspis (Rhinoferus) hyorrhina (Leuchtenberg, 1843). A: Dorsal view of large, flattened cranidium with ridge-like glabellar node (X 0,6). PMO 162.662. Loose block from the Huk Fm. (Lysaker Member), Såsen, Vestfossen. Coll. M. Høyberget. B: Dorsal view of small cranidium with pointed glabellar node (natural size). PMO 162.664. Huk Fm. (Lysaker Member, approx. 2.5 m above the top of the Tøyen Fm.), Stavlum, Fiskum. Coll. M. Høyberget 1997. C-E: Dorsal, lateral and frontal views of large cranidium with bulbous glabellar node (X 0,8). PMO 162.661. Huk Fm. (Lysaker Member, approx. 2.5 m above the top of the Tøyen Fm.), Skaratoppen, Vestfossen. Coll. M. Høyberget 1994.

orly and posteriorly it is raised above the pleural fields, while the median part is almost level with the pleural fields. The posterior axial rings are indistinct. The pleural fields have 9-10 pairs of very low ribs which end at the paradoublural line. Pleural furrows are mostly effaced, except the anteriormost one, while the interpleural furrows are more visible as thin ridges rising above the surface. The articulating facets are large. A concave border is present on all sides, widening posteriorly. The doublure seems to be of approximately uniform width along the whole margin, with terrace lines rather widely spaced, being slightly less than 1 mm apart.

Distribution

All Norwegian specimens are from the upper subzone of the *Megistaspis limbata* Zone. Geographically, they are all from the Eiker-Sandsvær district on the western rim of the Oslo Region, except the three pygidia mentioned by Nielsen (1995, p. 151), which are from Slemmestad (central Oslo Region). In central Sweden, it is occasionally present in the *M. limbata* Zone and it is common in the same zone on Öland. On Öland, the same, or a similar species is also found in the older *M. simon* Zone (Nielsen 1995, p. 150). In the eastern Baltic Region, the species occurs in the lower Volkhov Stage

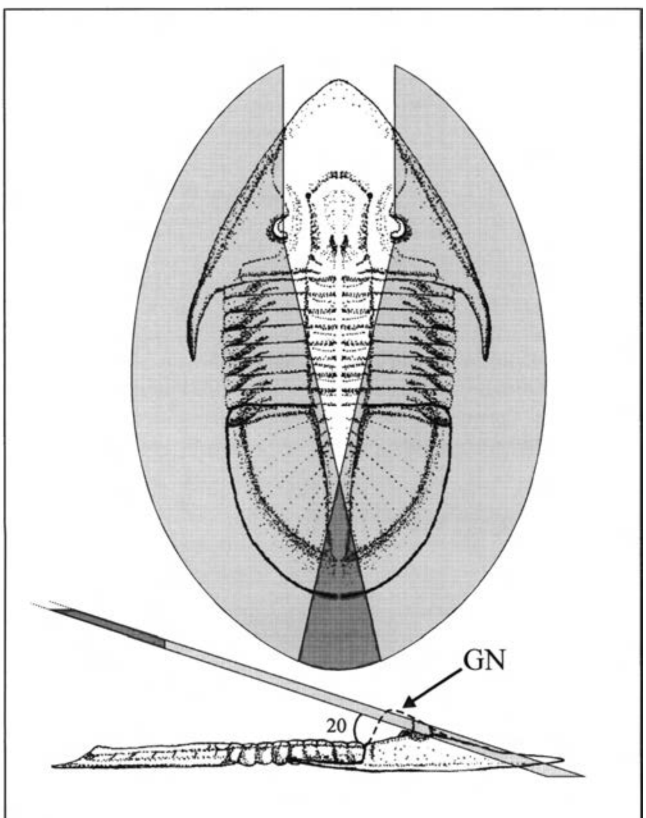

Fig. 4. Dorsal and lateral reconstruction of the visual field of Megistaspis (Rhinoferus) hyorrhina based on PMO 162.658-659. Darker colour indicates overlapping fields. The dotted line marked GN is the outline of the glabella in the most swollen specimens.

(BIIα-β, *M. simon-M. limbata zones*), and becomes more frequent in the upper part of this stage (BIIγ, *Asaphus expansus Zone*) (Schmidt 1906, p. 31).

Ecological remarks

Effaced furrows

Nielsen (1995, p. 65, 104) noted that in species of *Megistaspis* the development of the cephalic posterior border furrow differs between specimens found in shallow waters and those found in deeper water environments. This furrow is prominent in east Baltic specimens, but is less so in Scandinavian ones. He related this and other character variations to environmental factors, perhaps in part reflecting the firmness of the sediment. In the case of the occipital furrow, it is almost effaced in the Norwegian specimens of *M. hyorrhina,* while east Baltic specimens have a deep and prominent furrow. It is interesting to note that the cranidium of *M. hyorrhina* from Öland, figured by Bohlin (1955, pl. 3, fig. 10), has an effaced cephalic posterior border furrow, while the occipital furrow is continuous across the midline, and thus seems to be intermediate between the East Baltic and Norwegian morphology. It is about the same size as the cranidium of the whole Norwegian specimen (Fig. 2A-D), so the difference should not be size-related.

Cuticular thickness and moulting

East Baltic pygidia illustrated by Schmidt (1906, pl. 3, figs 1a, 1b, 5a, 6a, 7, 8) seem to be less compressed, with segmentation better visible than those from Norway. In the latter, the pygidia appear more flattened and wrinkled than do the cranidia, which might suggest that they are relatively newly moulted specimens, in which a fully calcified cuticula had not been achieved. Contrary to this idea, two specimens consist of pygidium and five attached thoracic segments; these are just as flattened as the other pygidia, but are most probably shed exuvia. This may indicate that, in life, the cuticula actually was thicker and more robust in the cephalon than in the pygidium.

The two specimens of pygidium and five attached thoracic segments might possibly suggest that during moulting, this posterior region of the animal separated as a unit from the anterior parts, leaving the anterior section to be shed somewhere else. The suture between the third and the fourth thoracic segment may thus have been a constant zone of weakness. A specimen of *Megistaspis (Megistaspidella) triangularis* (Schmidt, 1906) collected by the junior author from the same beds as the material of *M. (R.) hyorrhina,* also consists of pygidium with five attached thoracic segments. A similar pattern of pygidium plus some thoracic segments is commonly found in many species (J. Bergström *pers. com.*). Although it is dangerous to generalize from so few specimens, it may be a pattern worth looking for among different trilobite groups.

Visual field (see Fig. 4)

As in most asaphids, *M. hyorrhina* had a restricted visual field. This has been calculated from a latex cast of PMO 162.659 (Fig. 2B, D). The light falling through the c-axis of the crystals making up the lenses, will be perceived by the animal only if striking the surface of the lens at right angles. Thus the horizontal visual field can be approximated by extrapolating 90° from the surface of the eye. On this assumption, the visual field extends from straight forward, and posteriorly to approximately 15° past the axis, a total field of about 195° to each side, overlapping posteriorly but not anteriorly. Vertically, the visual fields extend from the anterior margin of the animal, backwards and upwards, covering a narrow band sloping about 20° above the horizontal.

Glabellar node

The glabellar node is much more variable in *M. hyorrhina* than in other megistaspids. The Norwegian specimens show that the node varies between a pointed form (Fig. 2C, 3B), a more ridge-like form (Fig 3A) and a thick, blunt node (Fig. 3C-E). This variation was recognised by Schmidt, who (1906, p. 35) erected a number of variants, seemingly mostly based on this varying development of the glabellar node. Var. *typica* has the largest knob, the knob in var. *kolenkoi* is smaller, var. *mickwitzi* has a small, rounded knob and var. *stacyi* has only a normal, small tubercle. Schmidt followed such a "lumping" approach because of the great variety and the number of intermediate stages he found. It is interesting that almost the full range of variation is seen in the few Norwegian specimens. Following Balashova (1976), Nielsen (1995 p. 105) listed these varieties as separate species, but this is not maintained here since the same variation is displayed in the small number of Norwegian specimens. Most of the specimens come from approximately the same bed at localities close to each other.

Dimorphism as a cause for the variation is not plausible due to all the intermediate stages. One could imagine the node growing in size as the animal got older, but all the specimens figured here are of roughly the same size; the least prominent node is actually found on the largest cranidium.

A swelling of the anterior portion of the glabella in supposedly predatory or scavenging trilobites such as asaphids has been taken to facilitate accommodation of larger prey (Fortey & Owens 1999, p. 556). *Megistaspis (Rhinoferus) gibba* (Schmidt, 1898) is an east Baltic asaphid with just such a swelling of the anterior glabellar lobes. The hypostome of *M. hyorrhina* figured by Schmidt (1906, pl. 3, fig. 2) does not seem to have a radically different shape from other megistaspids, but it does have the median notch typical of *Megistaspis (Megistaspis)*, and not the pointed rear margin as seen in M. *(Megistaspidella)* (Jaanusson 1956, p. 70, 73). The hypostome of *M. gibba* is unfortunately unknown, but if found might shed light on the ecological significance of such an anteriorly inflated glabella.

In *M. (R.) hyorrhina* the glabellar swelling occurs not in the anterior glabella, but in the posteriormost lobe, beneath the glabellar tubercle. In at least some asaphids, e. g. *Niobe* and *Ogygiocaris* (Fortey & Clarkson 1976, p.104), and other forms such as odontopleurids (Whittington 1997, fig. 72.2), phillipsinellids (Bruton 1976, plate 105, fig. 8) and styginids (Whittington 1965, p. 297), this tubercle has four symmetrically disposed pits, similar to the median sensorial complex in the living syncarid crustacea; Laverack et al. (1996) considered this organ to function as a pressure sensor. Thus, if the analogy is correct, the raised position of this tubercle in some specimens of *M. hyorrhina* could indicate increased sensitivity to the pressure waves of an approaching predator. Alternatively, the raised position could enable the animal to be buried while keeping the organ above the sediment. This is in agreement with the rather strongly elevated position of the eyes in this species.

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