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The Middle Cambrian paradoxidid trilobite *Hydrocephalus* from Jämtland, central Sweden

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ABSTRACT:

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A new paradoxidid species, *Hydrocephalus vikensis*, is described from the lower Middle Cambrian *praecurrens* Zone in Jämtland, central Sweden. It is contrasted with typical *Hydrocephalus* species and shows features that recall *Paradoxides*. The genus *Hydrocephalus* BARRANDE is discussed; the validity of the related genus *Rejkocephalus* KORDULE is considered to be doubtful. The associated fauna is listed and an agnostoid that differs slightly from *Condylopyge regia* (SJÖGREN) is illustrated.

Key words: Middle Cambrian, Jämtland, Biostratigraphy, Trilobites, Baltica.

INTRODUCTION

Thanks to the work of WESTERGÅRD (1936, 1946, 1948, 1950, 1953), the majority of trilobites from the Middle Cambrian of Sweden have been systematically described and well illustrated, but despite this several of the species of Paradoxididae known from Sweden have not received modern revision. In 1936 WESTERGÅRD had reported on the fauna of the 'Oelandicus Beds' of Öland, from which he described seven named species of paradoxidids and four unnamed taxa; but later, at the end of his working life, he had perforce to leave the rest of the Swedish paradoxididids unrevised (WESTERGÅRD 1953, p. 34) and for many of those species one has to rely on older papers, such as those of LINNARSSON (1877, 1879, 1882).

The present study was initiated by Thomas WEIDNER's discovery of new material from strata in central Jämtland that are equivalent to the Bårstad Member of the Borgholm Formation (the upper part of the 'Oelandicus Beds') of Öland, southern Sweden. It includes a hitherto undescribed species attributed to the paradoxidid genus *Hydrocephalus* BARRANDE, a species that is not known from Öland.

The term 'Middle Cambrian' used above follows the long-standing but not precisely defined usage of 20th century workers, that corresponds approximately to the stratigraphical range of 'paradoxidian' trilobites. At the time of writing the Cambrian Subcommission is working to subdivide the Cambrian System more precisely into four series, of which the lower two series correspond to the Lower Cambrian as traditionally construed; the third series ranges through all of the traditional Middle Cambrian; and the fourth, the formally defined Furongian Series, corresponds to the all of the traditional Upper Cambrian with the exception of its lowermost part (BABCOCK & *al*. 2005). In this paper we deal with fossils from the lower part of the as yet unnamed Third Series. Although this series is not yet precisely defined, it is agreed that it will be subdivided into three stages, referred to as the 5th, 6th and 7th stages of the Cambrian, and of these the 6th stage has formally been designated the Drumian Stage. Whichever level is adopted from among those being considered for the base of the Third

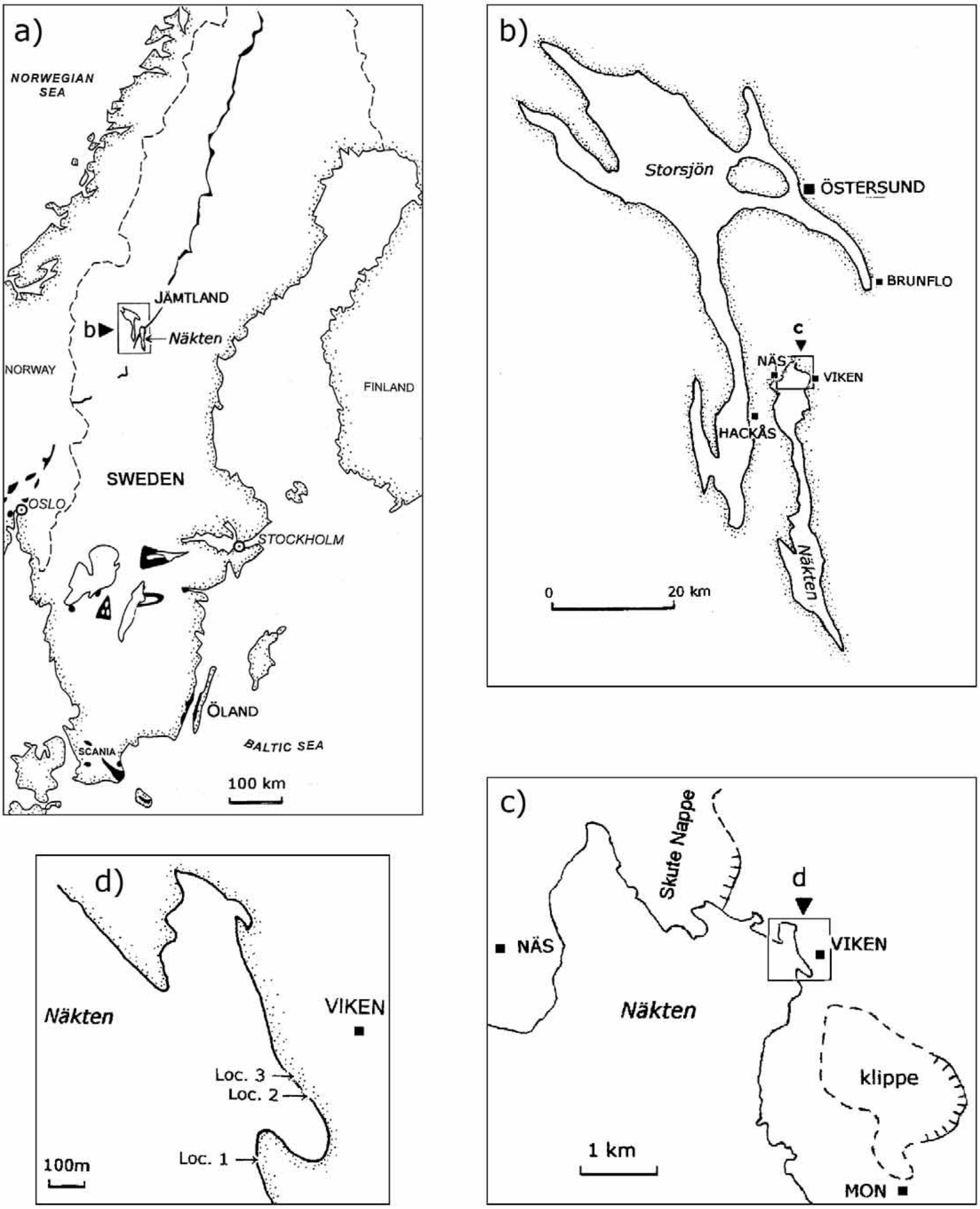

Fig. 1. **a** – Sweden, with Cambrian outcrops shown in black (after AXHEIMER 2006), showing the area of Figure 1b; **b** – The area around the lakes Näkten and Storsjön, Jämtland, showing places mentioned in the text; **c** – The northern end of Näkten. The lines of the Skute Nappe and the outlying klippe are taken from THORSLUND (1940); **d** – The positions of Locs 1-3 in the autochthon on the shore of Näkten near Viken

Series (GEYER 2005), the material we discuss here is from the upper part of the unnamed 5th stage.

STRATIGRAPHICAL SETTING

THORSLUND (1940) investigated a considerable area along the Caledonian thrust front in south-central Jämtland and one of his maps showed the geology of the area between Brunflo and the lake Näkten (THORSLUND 1940, pl. 14). His study was primarily concerned with the Chasmops Beds (mid-Ordovician). BERGSTRÖM (1980) reviewed the Middle and Upper Cambrian strata in the area, drawing on additional information from boreholes. He recorded that the autochthonous beds of the *Acadoparadoxides* (*Baltoparadoxides*) *oelandicus* Superzone (formerly termed 'Stage'), which are up to 20 m thick, form the greater part of the Middle Cambrian in the area. The basal part of the *oelandicus* Superzone may be developed as coarse sandstone, but the bulk of the strata are composed of grey mudstone, sometimes shaly, with more massive silty beds with a small content of carbonate. More recently KARIS & STRÖMBERG (1998), in describing the geological map of Jämtland, used the name Kläppeskiffer (Kläppe Shale) to include both the fine-grained siltstones of the *oelandicus* Superzone and the overlying black kerogenous mudstones of mid Middle and Late Cambrian age, referable to the middle and upper stages of the Third Series and the Furongian. In southern Sweden, especially Öland, the correlative strata were reviewed and formalised by NIELSEN & SCHOVSBO (2006), but we do not claim to extend their nomenclature from southern Sweden to Jämtland, and in the present paper we use the old term 'Oelandicus Beds' to refer to the grey siltstones of the Kläppeskiffer, to the exclusion of the overlying black mudstones.

LOCALITY

The trilobites discussed below were found close to Viken, a hamlet near the north-east corner of Näkten, 14 km SW of Brunflo and 20 km south of Östersund, Jämtland (Text-fig. 1). THORSLUND (1940, p. 60-61; fig. 35) identified the strata around Viken as autochthonous Cambrian strata, locally strongly folded, overlain by Ordovician, and partly covered by a klippe of Ordovician rocks. To the north-west, the Skute Nappe, the lowest nappe of the Caledonian thrust front, is mapped as reaching the northern shore of Näkten less than 1.5 km to the north-west of Viken (Text-fig. 1c). This nappe includes Cambrian and Ordovician strata of comparable age to the autochthonous strata.

The fossils were collected by Thomas WEIDNER in 2004 and 2005 from fairly flat-lying autochthonous Cambrian strata (Oelandicus Beds) near the shore. Some are from concretionary lenses extracted from deeply weathered shale of the slope down to the lake, and others are from loose blocks of very local origin on the shore. Most of the specimens of *Hydrocephalus vikensis* described here came from a large concretion at Loc. 2 in Text-figure 1d. Several specimens were found at Loc. 1, including fairly complete but deformed axial shields in mudstone, though some isolated sclerites are well preserved. The preservation of specimens in the more massive silty beds is locally good and in partial relief, whilst the mudstone specimens are rather flattened and may be slightly crushed; some of the cracks in the trilobite exoskeletons were presumably caused by compaction and evidently formed before lithification (Pl. 1, Fig. 3). Although most specimens are unaffected by local tectonism, some specimens are slightly deformed (Pl. 1, Figs 11, 15). We used calculations based on deformed right-angles, as described by COOPER (1990), to infer that the strain-ellipse in the plane of bedding has an eccentricity of about 1.1.

During 2004-2005 Thomas WEIDNER collected additional specimens of *Hydrocephalus vikensis* in situ from autochthonous Oelandicus Beds at Travbana ('trotting race course'), at Hackås, 8 km south-west of Viken. His subsequent investigations in 2007 have shown that *H. vikensis* occurs throughout the autochthonous Oelandicus Beds of Jämtland at all localities between Brunflo in the north and Hackås in the south, and that it has also been observed in allochtonous strata on Tåsjö-mountain in Ångermanland.

AGE AND CORRELATION

The fauna from Viken localities 1, 2 and 3 includes:
Condylopyge aff. *regia* (SJÖGREN): Locs 1, 3 (Pl. 1, Figs 5-10)

Peronopsis fallax (LINNARSSON): Locs 1, 3
Ptychagnostus praecurrens (WESTERGÅRD): Locs 1, 2, 3 (Pl. 1, Figs 1-4)
Burlingia sp.: Loc. 1
Ellipsocephalus polytomus (LINNARSSON): Locs 1, 2, 3
Acadoparadoxides (*A.?*) *pinus* (WESTERGÅRD): Loc. 3
A. (*Baltoparadoxides*) *bidentatus* (WESTERGÅRD): Locs 1, 2.
A. (*Baltoparadoxides*) *oelandicus* (SJÖGREN): Loc. 3
Eccaparadoxides torelli (WESTERGÅRD): Locs 1, 2
Hydrocephalus vikensis sp. nov.: Locs 1, 2, 3? (Pls 1-3)

A very similar fauna was collected at the Travbana locality.

Compared with the succession in the Mosseberga and Båstad members of the Borgholm Formation in Öland (NIELSEN & SCHOVSBO 2006), the presence of *Pt. praecurrens*, *P. fallax* and *A.* (*A.*?) *pinus* indicate the *praecurrens* Zone (*pinus* Zone, A2 of WESTERGÅRD 1946, pp. 98-100) in the upper part of the *oelandicus* Superzone. *Eccaparadoxides torelli* is also recorded only from the *pinus* Zone, whilst *E. polytomus*, *A.* (*Baltoparadoxides*) *oelandicus* and possibly *A.* (*Baltoparadoxides*) *bidentatus* are recorded in Öland from both the lower *Eccaparadoxides insularis* Zone (A1) as well as the upper A2 zone (WESTERGÅRD 1953, pp. 36-38).

The presence of a species close to *C. regia* appears anomalous because in Öland *C. regia* is confined to the *insularis* Zone (WESTERGÅRD 1936, p. 27). However, there are differences between the specimens from Öland and those from Jämtland, which, though slight, indicate variant forms that may have slightly different stratigraphic ranges.

In view of the stratigraphical importance accorded to these agnostoids, some examples are figured here. The specimens of *Ptychagnostus praecurrens* (Pl. 1, Figs 1-4) are within the range of variation illustrated by WESTERGÅRD (1946, pl. 9, figs 9-14). Among our specimens of *Condylopyge* aff. *regia* (Pl. 1, Figs 5-10), the cephala appear identical with those from Öland illustrated by WESTERGÅRD 1936 (pl. 1, figs 1-3), but the pygidia differ because the posterior end of the axis is more pointed and is slightly longer (Pl. 1, Figs 8, 10); also the axis is narrowest just anterior to the axial tubercle and widens backwards by about 10%, whereas in *C. regia* from Öland the axis is more nearly parallel-sided. Dr L. WICKSTRÖM of Sveriges Geologisk Undersökning, Uppsala, kindly loaned some specimens of *Condylopyge* from Jämtland that WESTERGÅRD had identified as *C. regia*. We find that those specimens (Text-fig. 2a-c) are just like our specimens from Viken (Pl. 1, Figs 5-10), and differ in the same ways from the typical form from Öland. Although the sharply rounded ends of the pygidial axes figured here recall those of *Condylopyge cruzensis* LIÑAN & GOZALO (1986, pl. 1, figs 1-8), that species lacks the backward expansion of the pygidial axis and it has a longer postaxial field. We conclude that the species of *Condylopyge* from Viken and other places in Jämtland, though closest to *C. regia*, is slightly different and should be distinguished under open nomenclature as *C.* aff. *regia*, and we presume that it does not necessarily occur at the same horizon as the specimens from Öland. As the supposed presence of the *insularis* zone (A1) in Jämtland is based primarily on the presence of boulders containing *C. regia* (WESTERGÅRD 1946, p. 18), that inference is now cast into doubt by our observation that in Jämtland the variant form *C.* aff. *regia* occurs with *P. praecurrens* and *A. pinus*, which are representatives of the *pinus* Zone (A2) in Öland; the presence of the *insularis* Zone in central Jämtland remains to be established.

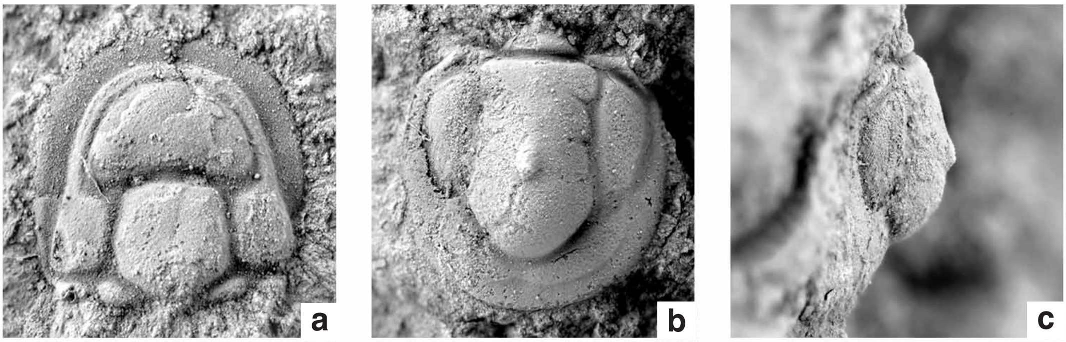

Fig. 2. Specimens from Jämtland recorded by WESTERGÅRD (1946) as *Condylopyge regia* (SJÖGREN, 1872), but here transferred to *C.* aff. *regia*, all figures magnified × 10. **a** – cephalon collected by THORSLUND from Fäste, Hackås, SGU 9476; **b**, **c** – top and side views of a pygidium collected by WESTERGÅRD from Brunflo station, SGU 9477

REPOSITORIES

The holotype and part of the paratype material of *Hydrocephalus vikensis* is deposited in the Palaeozoological collections of the Swedish Museum of Natural History (Naturhistoriska Riksmuseet), Stockholm (abbreviation NRM-PZ). Additional specimens, including some other paratypes, are in the collections of the Palaeontological Department, The Natural History Museum, London (abbreviation NHM). The two specimens in Text-fig. 2 are held in the collections of the Sveriges Geologisk Undersökning, Uppsala (SGU).

TERMINOLOGY

The terminology follows that of WHITTINGTON & *al.* (1997). The symbols used for specifying points on the facial sutures are Greek letters, following WHITTINGTON & *al.* (1997, p. 6, fig. 3).

SYSTEMATIC PALAEONTOLOGY

Family Paradoxididae HAWLE & CORDA, 1847

DIAGNOSIS: See DEAN & RUSHTON *in* WHITTINGTON & *al.* 1997, p. 471.

Hydrocephalus BARRANDE, 1846

TYPE SPECIES: *Hydrocephalus carens* BARRANDE, 1846.

DIAGNOSIS: See ŠNAJDR 1987, p. 100, and DEAN & RUSHTON in WHITTINGTON & *al*. 1997, p. 476.

REMARKS: *Hydrocephalus carens* was originally based on meraspid stages which are now considered to be the early growth stages of a large paradoxidid that was known to BARRANDE as *Paradoxides spinosus* BOECK sp. (ŠUF 1926; ŠNAJDR 1958). Although the lectotype of *H. carens* (ŠNAJDR 1958, pl. 24, fig. 32) is a meraspid a little over 3 mm long with the cranidium 1.8 mm long, it is representative of a species that grew to more than 200 mm in length (ŠNAJDR 1958, pl. 30) and of very different appearance. ŠNAJDR figured juvenile specimens of *H. carens* with cranidia up to 6 mm long and two giant specimens with cranidia 60 mm or more in length. Specimens of intermediate size were figured by HORNÝ & BASTL (1970, pl. 2, fig. 3, cranidium about 44 mm long) and WHITTINGTON (1990, figs 22 and 26, cranidia about 32 mm and 36 mm long). A slightly smaller example is figured here (Pl. 2, Fig. 2).

ŠNAJDR (1858) described and figured four Czech species of *Hydrocephalus*: *H. carens, H. minor* (BOECK, 1827), *H. rotundatus* (BARRANDE, 1846) and *H. lyelli* (BARRANDE, 1852), and he also referred *Paradoxides hicksii* SALTER, 1866 and *P. hicksii palpebrosus* LINNARSSON, 1879 to the genus. In 1987 ŠNAJDR described a new subspecies, *H. minor petrin*, and additionally referred *Paradoxides sjoegreni* LINNARSSON, 1877 and *P. eopinus* SOLOVJEV, 1969 to *Hydrocephalus*, but he indicated that *H. rotundatus* and *H. lyelli* should be transferred to a new genus. This idea was effected by KORDULE (1990) who proposed *Rejkocephalus* and made *Paradoxides rotundatus* BARRANDE, 1846 the type species. He remarked on the close relationship of *Rejkocephalus* and *Hydrocephalus*, and indeed the diagnoses of *Hydrocephalus* by ŠNAJDR (1987) and of *Rejkocephalus* by KORDULE (1990) are almost identical apart from their respective accounts of the pygidia – that of *Hydrocephalus* being transverse, with length 2/3 of width, with an entire margin, and that of *Rejkocephalus* being longer than wide with the axis no more than half the pygidial length, and having a much wider doublure and a pair of posteromarginal spines.

KORDULE (1990, p. 57) followed ŠUF (1926) in regarding *Paradoxides rotundatus* as synonymous with the junior but more completely known species *P. lyelli*, and used features of the latter in formulating his diagnosis of *Rejkocephalus*. There are, however, several differences between those species, which lead to doubt in recognising *Rejkocephalus*. In BARRANDE's figured syntype* (= lectotype) of *R. rotundatus* (BARRANDE 1852, pl. 14, fig. 24; ŠNAJDR 1958, pl. 18, fig. 1), the frontal area is relatively

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* BARRANDE (1846) did not specify the holotype of *Paradoxides rotundatus*, and as he had more than one specimen, monotypy does not apply; see HORNÝ & BASTL 1970, p. 269. However, following the I.C.Z.N. Code (1999), Article 74.6, ŠNAJDR (1958, p. 141), having used the term "holotype" for BARRANDE's figured syntype, is deemed thereby to have selected it as the lectotype.

broad sagittally, about three times as long as the corresponding length in *lyelli* in which it is very narrow (Šnajdr 1958, pl. 18, figs 1 and 5). In the lectotype of *rotundatus* the posterior margin of the gena is nearly transverse and the inner spine angle of the librigena is obtuse, whereas in *lyelli* the posterior margin is bent forward outside point ω on the facial suture, and the inner spine angle is acute (Šuf 1926, pl. 4, figs 4, 6; Šnajdr 1958, pl. 19, fig. 13). The posterior segments of the thorax of *rotundatus* have relatively short and curved tips, and do not extend farther back than the posterior margin of the pygidium which (as figured by Barrande and Šnajdr) is entire; in *lyelli* the posterior segments are longer, sharper and straight, and reach as far or farther back than the posterior spines of the more elongated pygidium of that species. Kordule (1990, p. 57) stated that the marginal spines of the lectotype of *rotundatus* are broken off but that their traces are observable under suitable conditions, though he did not illustrate this feature. His observation implies, however, that in *rotundatus* the pygidial spines extend farther back than the posterior thoracic spines, unlike the corresponding spines in *lyelli*. A further difference of more doubtful significance is the presence of swellings adaxial of each palpebral lobe of *rotundatus*, a feature recognised as unique by Barrande (1852, pl. 14, fig. 24) and shown in Šnajdr's figure of the Barrande's specimen (1958, pl. 18, fig. 1). These swellings are not seen on any figured specimen of *lyelli.* It may be that they are merely parasitic galls (neoplasms; see Šnajdr 1958, pl. 42) and are not of systematic value. Until all these differences have been evaluated, the two species in question cannot be regarded as synonymous, and if they are not synonyms, *Rejkocephalus* must be based primarily on *rotundatus*, rather than on *lyelli*.

Hydrocephalus vikensis sp. nov.
(Pl. 1, Figs 11-15; Pl. 2, Figs 1, 3-8; Pl. 3, Figs 1?, 2?, 3-5, 6?, 7?, 8-19)

NAME: From Viken, the type locality, and the suffix *–ensis* signifying 'from that place'.

HOLOTYPE: Axial shield no. NRM-PZ Ar60130a-b (Pl. 1, Fig. 11) showing all parts in fairly good preservation. It is slightly deformed and the cranidium is shown retrodeformed in Pl. 2, Fig 4.

MATERIAL: Two small dorsal shields, 13 axial shields (i.e. those lacking librigenae), some incomplete; about 30 cranidia, some juvenile or doubtful, 15 librigenae, 17 hypostomata of which five are associated with rostra; about 10 thoraces and thoracopyga and 14 isolated pygidia. Most are from Viken Loc. 2, several from Loc. 1, and a few are from Travbana, Hackås, 8 km SW of Viken.

DIAGNOSIS: Small *Hydrocephalus* (up to about 100 mm long, so far as known) with relatively long and thick palpebral lobes and short postocular sutures; thorax with 17 segments having long and sharply spinose tips; pygidium a little wider than long (c. 1.3:1), with narrow doublure.

DESCRIPTION: Cranidium wider than long. Glabellar length (including LO) about 4/3 of its maximum width; glabella widens forward from LO to S1, then widens more strongly to attain 1.5 times the basal width at the level at which the inner end of the palpebral-ocular ridge reaches the axial furrow (Pl. 2, Figs 1, 4). Anterior outline of the glabella approximately semicircular, lateral outline gently concave. LO with a small median tubercle towards its posterior edge (Pl. 2, Fig. 6). SO bowed gently forwards medially. S1 directed obliquely inwards and slightly backwards, with gentle forwardly-concave curvature, joined weakly across the mid-line of glabella (sometimes deepened by dorso-ventral crushing), confluent with axial furrow (Pl. 2, Fig. 4); S2 transverse, with very gentle forwardly-convex curvature, not joined across glabella or only very weakly so, barely confluent with axial furrow; S3 and S4 not evident. Surface smooth, except the frontal lobe of glabella, which in some specimens shows weak cuesta-style terrace lines sub-concentric with anterior outline, with the steeper slope facing posteriorly.

Preocular fixigenae (β-β) about as wide as the width across the palpebral lobes (δ-δ). Anterior border short, shorter exsagittally than LO, becoming very short at sagittal line; has about 4 terrace lines roughly parallel to the anterior margin. No preglabellar field, except in small specimens (cranidia <6 mm long; Pl. 3, Fig. 3). A weak ridge (*facial line* of Whitehouse (1939, p. 189), or *pre-ocular facial line* of Zhang & *al*. 1980, figs 48, 49, 51) is commonly seen just within, and subparallel to, the preocular suture (Pl. 2, Fig. 1; Pl. 3, Fig. 3). Palpebral lobe has a length between 0.3 and 0.4 of glabella, but is proportionately longer in the smallest specimens; unevenly curved, thickens backwards, more sharply curved at posterior end (Pl. 1, Fig. 11); anterior end (γ) set abaxially from axial furrow, extends forwards and inwards as an ocular ridge to reach the axial furrow opposite the widest part of the glabella (Pl. 3, Fig. 3); posterior end of palpebral lobe (ε) set above and just forward of posterior border furrow (Pl. 2, Fig. 6). Interocular genae are subtriangular. Postocular sutures short, straight, oblique outward and backwards (Pl. 2, Fig. 4); the length δ-ω is about the same as the sagittal length of LO. Postocular genae consist of narrow border and border furrow, extend as widely (ω-ω) as preocular genae, but less far in small specimens.

Librigenae with ocular incisure roughly twice as long as preocular or postocular suture (Pl. 1, Fig. 12; Pl. 2, Fig. 3). Border and doublure narrower than the minimum width of the genal field between the border furrow and the ocular incisure. Genal spine at least as long as the rest of the librigena, inner spine angle 90° or more. With the librigena in position on the cephalon, its posterior margin and that of the cranidium appear to have formed a roughly transverse line (Pl. 1, Fig. 13). Lateral border of librigena bears about 7 cuesta-style terrace lines, their steeper slope facing upwards and adaxially.

Hypostome has maximum width 4/3 of sagittal length. Middle body rounded in front, narrows backwards to a subparallel-sided posterior portion that is 2/3 of maximum width, ending in a pair of short spines that point backwards and outwards, behind which the border bends adaxially to form a transverse posterior margin. The middle body has a whorl of fine terrace-lines. Rostra are associated with some hypostomes but are not seen to be fused with them. They are narrow and appear tubular from below, and are about 1.6 times wider than the transverse width of their associated hypostomes. About 7 terrace-lines on rostrum, their steeper slope facing forwards.

Thorax of 17 segments, seen in 6 thoraces 20 to 40 mm long. The axial lobe tapers such that the last ring is half the transverse width of the first. The axial rings have an anastomosing pattern of subtransverse cuesta-style terrace lines, their steeper side facing backwards (anterior segment in Pl. 3, Fig. 19). The pleurae are transverse adaxially and are about as wide as the corresponding axial ring, but abaxially curve abruptly back and slightly outwards, forming slender pointed spines, which have a few terrace lines on their upper surface (Pl. 1, Figs 11, 14); the spine on the second segment is generally much the same length as those on the first or third segment, but may be slightly longer in small specimens (Pl. 2, Fig. 8). Posteriorly the pleural spines become progressively longer, the last three extending farther back than the posterior edge of the pygidium; the last segment tends to bend round the pygidium and may incline slightly inwards towards the axial line (Pl. 2, Fig. 8). The doublure of the pleural spines is observed at a distance from the axial furrow about equal to the transverse width of the corresponding axial ring (Pl. 1, Fig. 13), but the details are poorly seen. Some segments show thoracic articulation similar to that observed by WHITTINGTON (1990) in *Hydrocephalus carens*, with an articulating projection at the outer end of the transverse proximal part of the pleura (arrowed in Pl. 1, Fig. 14). The narrow flange developed on the frontal edge of the pleura adaxially from the projection, as described by WHITTINGTON (1990, fig. 21), was not observed; the appearance of such a flange in Plate 1, Figure 14 actually represents the thickness of the exoskeleton, where this has flaked away, and the counterpart shows no flange.

Pygidium small, length about three-quarters of width, rounded, or may be truncate posteriorly or somewhat angulate (Pl. 3, Figs 14-19). Axis (excluding articulating half-ring) a little more than half the length and width of the pygidium; one distinct axial ring seen and often a weak second one, and a short rounded or bluntly conical terminal part. Pleural regions fairly flat but with a narrow downward-sloping rim posteriorly (Pl. 3, Figs 14, 16); one short pleural furrow weakly indicated. Margin entire, without spines (apart from the teratological specimen shown in Pl. 3, Fig. 17); doublure narrow, extending forwards only about 1/3 of the length of the post-axial field (Pl. 3, Fig. 18).

ONTOGENY: Little is known of the ontogeny of *Hydrocephalus vikensis*. In a small holaspid (Pl. 1, Fig. 13), which has a cephalon just under 7 mm long, the glabella encroaches on the anterior border, as is typical of holaspids of *Hydrocephalus*. In a slightly smaller cranidium (Pl. 3, Fig. 3), 6.1 mm long, there is still a trace of the preglabellar field.

The early growth stages of *Hydrocephalus carens* are striking: they have a subcircular glabella that occupies almost the whole cranidium (Šnajdr 1958, text-fig. 23, pl. 24), but in the meraspid development, the glabella rapidly contracts from the frontal margin and then more slowly grows forward again, reaching towards the anterior edge of the cranidium (Šnajdr 1958, text-fig. 25), whilst gradually assuming a more typical holaspid form (Šnajdr 1958, text-fig. 24, pl. 25). Apart from *H. carens,* the species that Šnajdr retained in *Hydrocephalus* have not been illustrated showing a 'hydrocephalus' larval stage, except, in part, the smallest example of *H. minor* (Šnajdr 1958, pl. 23, fig. 1) with a cranidium 1.6 mm long. In a larger specimen, with a cranidium 2.9 mm long (Šnajdr 1958, pl. 23, fig. 2), the glabella is inflated but fixigenae are present and a narrow preglabellar field has developed between the glabella and the frontal border.

It is not known whether two meraspid cranidia (Pl. 3, Figs 1, 2) collected at Viken Loc. 1 are referable to *H. vikensis* or one of the other paradoxidids that are found, though much more rarely, at Viken. The smaller meraspid (Pl. 3, Fig. 1), 2.7 mm long, has a glabella that widens forwards, a long preglabellar field and a narrow but clearly delimited border; it appears that the longitudinal ridge in front of the glabella is an original feature but is obscure because the specimen is cracked there. It does not resemble any early growth stage of *H. carens*, but is more like meraspids of the same size referred "in all probability" to *Baltoparadoxides oelandicus* (Westergård 1936, pl. 2, fig. 1) and *Acadoparadoxides pinus* (Westergård 1936, pl. 5, fig. 6); it differs from those in the forward widening of the glabella and the slight backward thickening of the palpebral lobes. The widening of the glabella and narrow frontal border are more like those seen in *Paradoxides gracilis* (Šnajdr 1958, text-fig. 18 (1) and pl. 12, fig. 2); Adrian Rushton has observed similar features in meraspid cranidia of *P. paradoxissimus* about 3 mm long from Hunneberg, south-central Sweden, and additionally some of those have a longitudinal preglabellar ridge.

A second specimen (Pl. 3, Fig. 2), 4.2 mm long, has a short preglabellar ridge; in this it resembles a meraspid cranidium of *Acadoparadoxides pinus* 3.6 mm long (Westergård 1936, pl. 5, fig. 6), though it differs in other ways, such as the forward widening of the glabella. The slightly pointed frontal outline of the glabella and the preglabellar ridge recall meraspid and holaspid cranidia of some species of the ellipsocephalid genera *Lermontovia* Suvorova and *Bergeroniellus* Lermontova figured by Suvorova (1956, p. 53, fig. 18 and p. 71, fig. 23), but none of those have the well marked transglabellar furrows of *Hydrocephalus* or *Paradoxides*.

If these two specimens are meraspids of *Hydrocephalus vikensis*, the ontogeny of that species appears to have differed from that of the type of the genus, *H. carens*, and resembles some *Paradoxides*. The significance of this is not yet clear, but, as Fletcher & *al.* (2005, p. 319) emphasised, the larval stages of paradoxidids are not widely enough known for ontogenetic features to be used in classifying putative species of *Hydrocephalus*.

COMPARISON: This species is placed in *Hydrocephalus* because the glabellar outline, the glabellar furrows, the medial narrowing of the frontal area, the form of the thoracic segments and the pygidium are all typical of the genus, and the hypostome is not fused to the rostrum in large specimens. *H. vikensis* differs from typical *Hydrocephalus* in having relatively long palpebral lobes and short postocular sutures.

The present species differs from *Hydrocephalus carens* and *H. minor* in having 17 thoracic segments (rather than 18) and a less transverse pygidium. It otherwise generally resembles *H. minor* (Šnajdr 1958, pl. 23), but shows several differences: the palpebral lobe is less curved and thicker posteriorly, and extends nearer to the posterior border furrow, so the postocular suture is shorter. The occipital node lies farther back on the occipital ring. The posterior margin of the gena is straighter, and the inner spine angle is obtuse rather than acute. The hypostome is wider anteriorly and narrows backwards more than it does in *H. minor*. The elongation of the spine on the second thoracic segment (Pl. 2, Fig. 8) is less prevalent than in specimens of *H. minor* of comparable size (Pl. 2, Fig. 9). The pygidium is less transverse than those of *H. minor minor* and *H. minor petrin* figured by Šnajdr (1987, pl. 1, figs 4-6, pl. 2, figs 4, 5), the pleural fields are more distinctly furrowed and the doublure is narrower posteriorly. Evidently in *H. minor* the posterior thoracic segment overlies the lateral edges of the pygidium, so what is exposed on a thoracopygon looks more nearly circular (Pl. 3, Fig. 20) than the isolated pygidia. In *H. vikensis* the posterior pleurae scarcely overlap the pygidium (Pl. 3, Fig. 19).

Comparison of the cranidium with that of *H. carens* of comparable size is not so clear, but it appears that in *H. vikensis* S1 and S2 are less distinctly transglabellar than in *H. carens*; the anterior border is more distinct in larger specimens (Pl. 2, Figs 1, 2) and is narrower exsagittally, and the postocular suture is shorter; the posterior margin of the gena is more transverse (Pl. 1, Fig. 13; cf. BARRANDE 1852, pl. 12, fig. 1) and the inner spine angle is not acute (ŠNAJDR 1958, pl. 27, fig. 5). The pygidial axis is shorter than in *H. carens*, the anterior pleural furrow is fainter and the doublure is less broad.

Of the Swedish paradoxidids, the most similar is *Paradoxides sjoegreni* LINNARSSON, as revised by WESTERGÅRD (1936, p. 41, pls 9, 10), which ŠNAJDR (1987) transferred to *Hydrocephalus*. *H. vikensis* differs from *H. sjoegreni* because S3 (if present) is weaker and S4 is not seen; the occipital tubercle lies farther back on LO; the palpebral lobe is longer and thicker than that of *H. sjoegreni*, its anterior end extending farther forwards into an eye-ridge and the posterior end lying closer to the posterior border furrow. WESTERGÅRD (1936, p. 42) noted that in larger cranidia of *H. sjoegreni* the anterior border furrow may become weak or obliterated, but the new species (which is not known to approach the size of a large *H. sjoegreni*), shows no such feature. The thorax of *H. sjoegreni* has the same number of segments as *H. vikensis*, but the posterior spines are not so long. The pygidium of *H. sjoegreni* is subquadrate, widens backwards and has a considerably longer axis than *H. vikensis*.

WESTERGÅRD (1936, pl 7, figs 10, 11, 13) figured two unnamed pygidia, "*Paradoxides* sp. No. 2" and "*Paradoxides* sp. No. 4". No.2 is fairly typical of *Hydrocephalus*, e.g. *H. carens*, in its transverse shape. It differs from *H. vikensis*, having better-marked pleural furrows and a wider doublure. No. 4 is very like some pygidia of *H. vikensis*, but the doublure is considerably wider posteriorly.

Other species assigned to *Hydrocephalus* are less similar: *Paradoxides eopinus* SOLOVJEV, 1969 as figured by JEGOROVA & *al.* 1976 (pl. 45. figs 6, 7, 9, 10, and pl. 46, figs 4-9) resembles *H. vikensis* in that the palpebral lobe extends forward into an eye-ridge; however it differs from *H. vikensis*, and all other species of *Hydrocephalus*, because the glabella does not encroach on the frontal border, but is separated from it by a preglabellar field (albeit a short one), even in large cranidia. *Hydrocephalus donayrei* LIÑAN & GOZALO (1986, pl. 22, fig. 4, pl. 23, figs 1-5) is a typical *Hydrocephalus* characterised by a short palpebral lobe and an unusually long postocular suture. The librigena in their pl. 23, fig. 3, though deformed, appears to have had an acute inner spine angle.

Although *Hydrocephalus vikensis* differs from all *Paradoxides* species because its hypostome is not fused to the rostrum and the pygidium is wider than long and has a pair of pleural furrows, some cranidial features recall species of *Paradoxides*. In particular, the shape and length of the palpebral lobes and the presence of eye-ridges resemble those of *P. paradoxissimus* (WAHLENBERG). *H. vikensis* differs from *P. paradoxissimus* in the glabellar outline, which is more rounded frontally and more concave laterally, but a cranidium from Loc. 1 (Pl. 3, Fig. 7), provisionally assigned to *H. vikensis*, has straighter axial furrows, like *P. paradoxissimus*. The shape of the glabella in *H. vikensis* is generally more like that of *Paradoxides jemtlandicus*, as revised by RUSHTON (2006), but it has longer and more protuberant palpebral lobes than *P. jemtlandicus*, and differs in having a distinct occipital tubercle.

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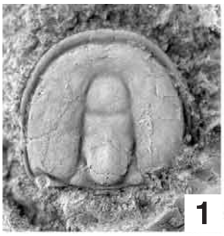
PLATE 1

1-4 – *Ptychagnostus praecurrens* (WESTERGÅRD, 1936); all × 5. 1 – cephalon NHM It27184(1), Loc. 3; 2, 3 – pygidium NHM It27185; side and top views, Loc. 3; 4 – pygidium NHM It27186, Loc. 2.

5-10 – *Condylopyge* aff. *regia* (SJÖGREN, 1872); all from Loc. 1, all × 8. 5 – cephalon NHM It27187(1); 6, 7 – cephalon NHM It27188, side and top views; 8, 9 – pygidium NHM It27189, top and side views; 10 – pygidium NHM It27190.

11-15 – *Hydrocephalus vikensis* sp. nov.; all from Loc 2. 11, 14 – **holotype**, axial shield NRM-PZ Ar60130a, × 1.5; and enlargement of thoracic segments 3-4, showing the articulating projection on segment 2 (arrowed), × 6; see also Pl. 2, Fig. 4; 12 – librigena, NRM-PZ Ar 60131e, exfoliated mould showing the ventral doublure, × 1; 13 – latex cast of small dorsal shield, NRM-PZ Ar 60131b, displaying the doublure of the pleural spines, × 1.5; 15 – latex cast of slab NHM It27191b(1) to (4), showing an axial shield (1), a cranidium (2), a hypostome with rostrum (3) and a librigena (4), approximately natural size (the slab shows slight deformation and the photograph is here retrodeformed).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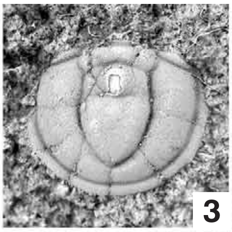
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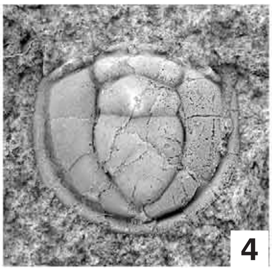
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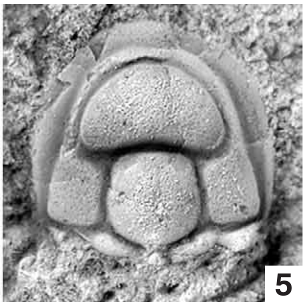
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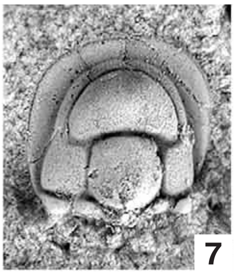
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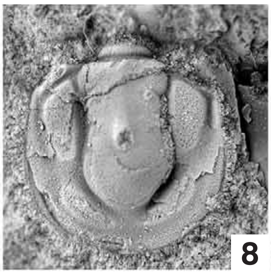
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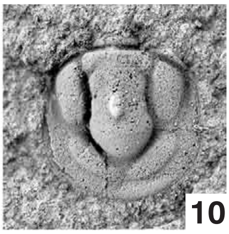
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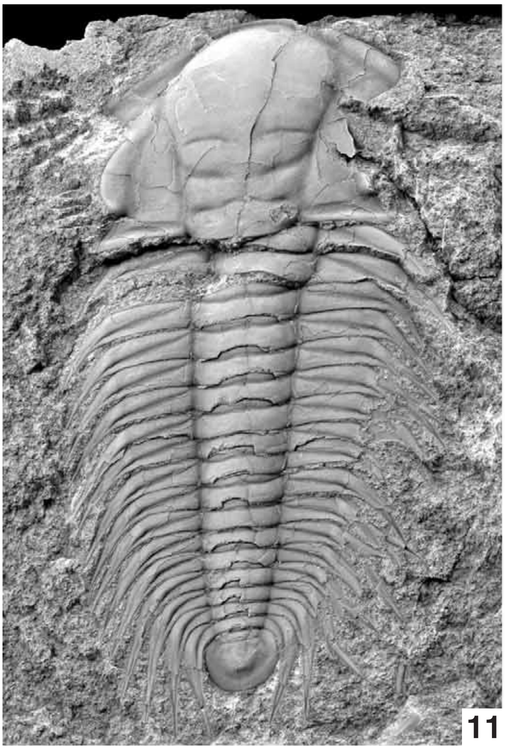
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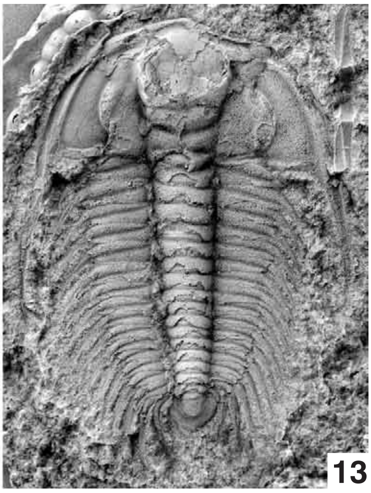
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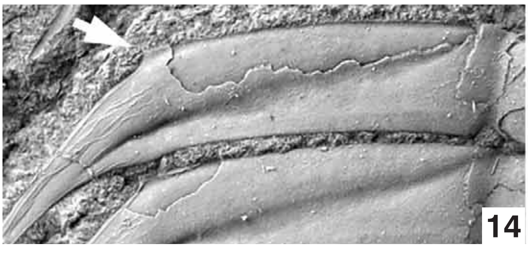
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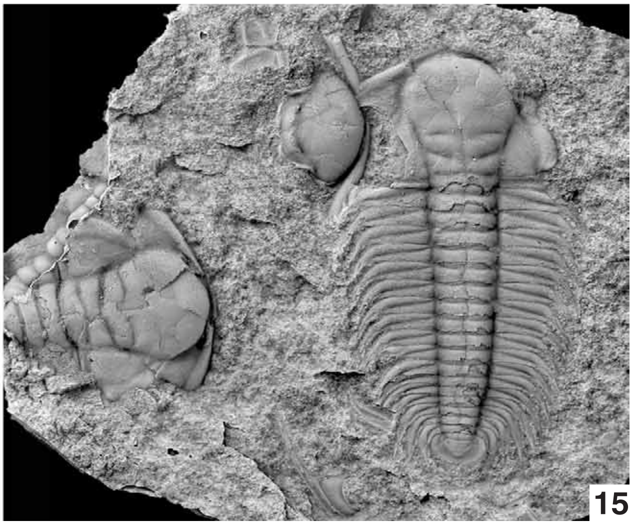
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PLATE 2

1, 3-8 – *Hydrocephalus vikensis* sp. nov.; 1 – NRM-PZ Ar 60130c-f, with three cranidia and a hypostome, Loc. 2, × 1. 3 – librigena, latex cast of NRM-PZ Ar 60131c, Loc. 2, × 1.5; 4 – cranidium of **holotype**, NRM-PZ Ar 60130a (see Pl. 1, Fig. 11), Loc. 2, here retrodeformed and enlarged to approximately × 2; 5-7 – cranidium NHM It27192, Loc. 2, front, top and right side view, × 2; 8 – thoracopygon, latex cast of NHM It27193, Loc. 1, × 3; the pleural spine of the second segment is slightly elongated and the pygidium is asymmetrical.

2 – *Hydrocephalus* carens BARRANDE, 1846; internal mould of frontally compressed cranidium from Skryje, Bohemia, NHM 42445, × 1.

9 – *Hydrocephalus minor* (BOECK, 1827); latex cast of laterally compressed axial shield from Jince, Bohemia, NHM 42443, × 2.


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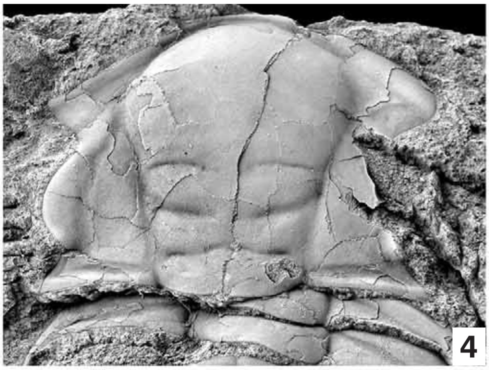
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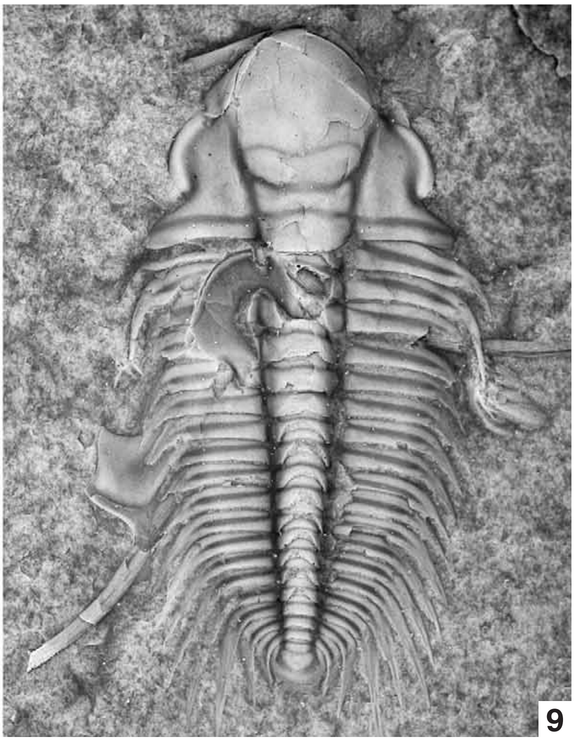
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PLATE 3

1, 2 – Meraspid cranidia doubtfully referred to *Hydrocephalus vikensis* sp. nov.; 1 – latex cast of specimen 2.7 mm long, NHM It27184(2), Loc. 3, × 10; 2 – cranidium 4.2 mm long, NHM It27187(2), Loc. 1, × 5.

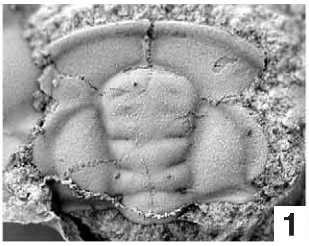
3-8 – *Hydrocephalus vikensis* sp. nov.; cranidia from Loc. 2; 3 – cranidium 6 mm long, showing short preglabellar field, NRM-PZ Ar 60132c, × 4; 4, 5 – latex casts of nos NHM It27194b and NRM-PZ Ar 60131f, both lacking preglabellar fields, both × 2; 6, 7 – two small cranidia doubtfully assigned to *Hydrocephalus vikensis*, nos. NHM It27195 and NHM It27196(1), both × 3; 8 – cranidium with thoracic segments, NHM It27197, × 1.

9-13 – Hypostomata assigned to *Hydrocephalus vikensis*; 9 – NHM It27198, Loc.1, × 4; 10 – NHM It27199, Loc. 1, × 5; 11, 12 – specimen with rostrum, latex cast, and external mould NRM-PZ Ar 60132a, with large internal mould, NRM-PZ Ar 60132b, Loc. 2, × 2; 13 – latex cast, NRM-PZ Ar 60131h, Loc. 2, × 2.

14-18 – Pygidia of *Hydrocephalus vikensis* sp. nov.; all × 6; 14, 15 – nos NHM It27200 and It27201, both Loc. 2; 16, 17 – nos NRM-PZ Ar 60133 and Ar 60134, both Loc 1, the latter with a teratologically fused thoracic pleura forming a marginal spine; 18 – large pygidium showing narrow doublure, NHM It27202, from Travbana.

19 – *Hydrocephalus vikensis* sp. nov.; pygidium with four thoracic segments, NRM-PZ Ar 60135, Loc. 1, × 4.

20 – *Hydrocephalus minor* (Boeck, 1827); pygidium with posterior thoracic segments, Jince, Bohemia, NHM 42443 (see Pl. 2, Fig. 9), × 4.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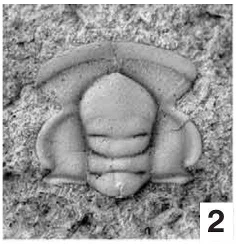
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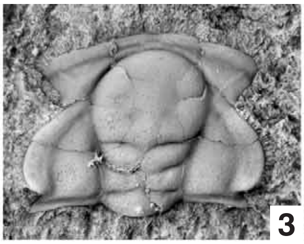
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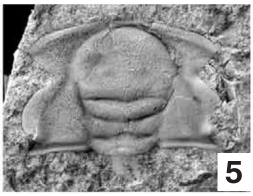
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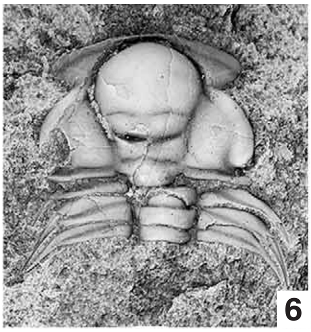
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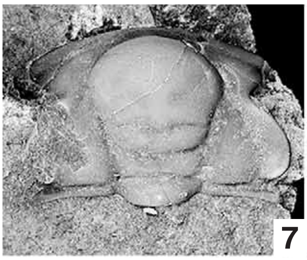
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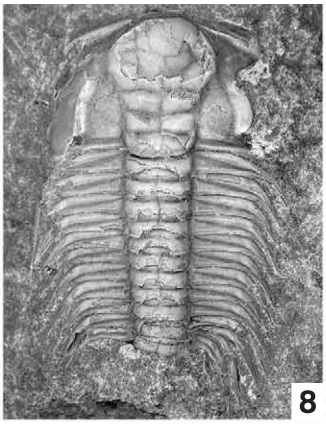
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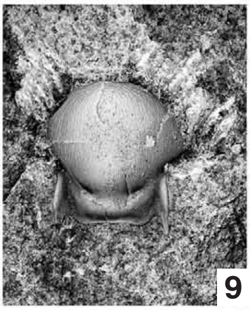
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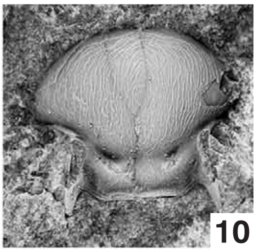
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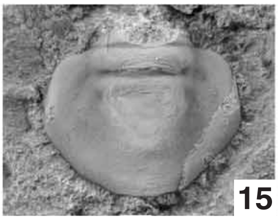
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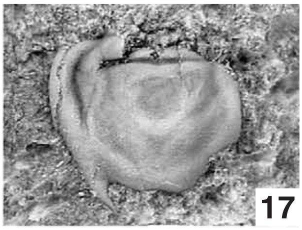
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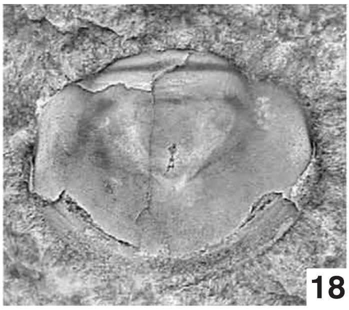
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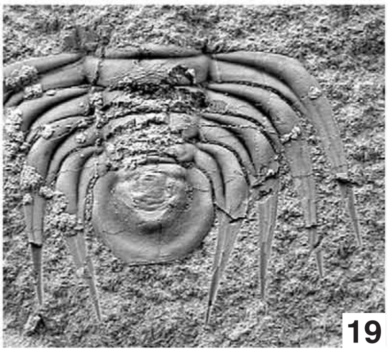
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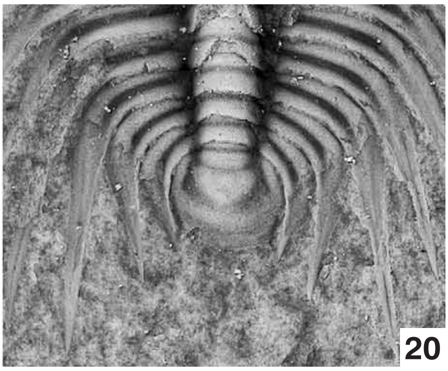
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