Revision of the late Ordovician trilobite *Holotrachelus punctillosus* (Törnquist, 1884) from Dalarna, Sweden

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Holotrachelus punctillosus from the Boda Limestone (Ashgill, Upper Ordovician) of Sweden is redescribed. The systematic position of this problematic species is discussed. Its distinctive morphology appears to be the result of an adaptation towards illaenid life habits. The pygidial morphology, with the extra-fulcral field developed as segmental pleural spines, makes an assignment possible to only four Ordovician groups, namely the Remopleuridioidea, Odontopleuroidea, Lichoidea and Cheiruroidea. Of these, the former three are so different that a direct affiliation is out of the question. Similarities with the Cheiruroidea are the more persuasive, particularly after a misinterpretation of the facial suture is corrected and some other problems are sorted out. It is suggested that the Holotrachelinae are placed within the Cheiruridae, where it may have special affinities to the Sphaerexochinae.

Key words: Trilobita, *Holotrachelus*, Proetida, Cheiruridae, Sphaerexochinae, Ordovician, Sweden.

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Introduction

Holotrachelus punctillosus is a distinctive Upper Ordovician trilobite with a smooth exoskeleton, an unusual hypostome, eight thoracic tergites and a poorly fused thorax-like pygidium that lacks a border. An examination of the systematic position of *Holotrachelus* reveals a combination of characters which does not fit properly the definitions of any existing high-level trilobite group. This superficially illaenacean-like species is also characterised by occurring almost exclusively with species of illaenaceans in 'pockets' within carbonate mounds (Suzuki & Bergström 1999). It is therefore tempting to believe that its unusual morphology indicates an adaptation similar to that of the co-existing illaenaceans. Material presently assigned to *Holotrachelus punctillosus* was first described by Wahlenberg (1818). He mistook the cranidium of this species for *Eobronteus laticauda* (Wahlenberg 1818). Since Wahlenberg's report, *H. punctillosus* has been referred to several different taxonomic groups. Other 19th century students have regarded the species variously as an asaphid (Dalman 1826), a bathyurid (Reed 1896), an illaenid (Holm 1898), a homalonotid calymenid (Törnquist 1884: author of the present species) or a cheirurid (Angelin 1854; see Warburg 1925: p. 147 for a detailed synonymy list). Only disarticulated sclerites were available to the above mentioned students. Subsequent to these conflicting interpretations, Warburg (1925) described the species in detail. Her description was largely based on an almost complete specimen with its hypostome detached but present beneath the cephalon. She erected a monotypic family Holotrachelidae for this unusual trilobite. Thus, Warburg (1925: p. 154) definitively rejected the idea of a relationship between *Holotrachelus* and any of the Illaenidae, Homalonotidae or Bathyuridae, although she did not state any reason for her judgment. Subsequently, several students have briefly commented on the taxonomic position of this genus. In the *Treatise on Invertebrate Paleontology part O* (Moore 1959), a rank of the group consisting of *Holotrachelus* alone was raised to superfamily level, and the Holotrachelacea was regarded as a member of the suborder Illaenina. Unfortunately, the only pygidium illustrated was a subadult one (Moore 1959: p. O381, fig. 289b). *Holotrachelus* has subsequently been regarded as closely related to the Proetidae or Bathyuridae (Bergström 1973), to be a derivative of bathyurids (Fortey in Lane & Thomas 1983), or as a member of the Holotracheloidea (Levman 1996; 'his' superfamily is a large group that contains the Cheirurina, Phacopina, Calymenina, Dalmanitoidea, and Illaenoidea). Finally, in the recent revision of the *Treatise* (Fortey in Kaesler 1997: p. 300), the genus is placed in the Bathyuroidea of the order Proetida.

The aim of this study is to describe and examine the systematic position of *Holotrachelus punctillosus*. As demonstrated by the variety of interpretations, it is difficult to recognize systematically significant characters because of the smooth nature of the exoskeleton. There are, however, hitherto unrecorded and overlooked characters such as the morphology of muscle scars and articulating devices and the character of the pleural spines in the pygidium.

Institutional abbreviations. — RM, Naturhistoriska Riksmuseet, Stockholm; UM, Paleontologiska Institutionen, Uppsala; LO, Geology Department, Lund University.

Geological setting

Holotrachelus punctillosus occurs in the Upper Ordovician Boda Limestone. This rock unit consists of a set of carbonate buildup masses of which now up to 20 are known in the Siljan district of Sweden (Fig. 1; Jaanusson 1979). An isolated Boda Limestone body has a thickness of up to about 100–140 m and a diameter of up to over 1 km (Jaanusson 1982). The facies is a massive pure limestone without obvious bedding, and stromatactis cavities and synsedimentary dykes occur frequently. The dominating facies is seemingly barren in nature and fossils are concentrated in patches, the so-called pockets. *Holotrachelus punctillosus* occurs richly in some pockets, just as do

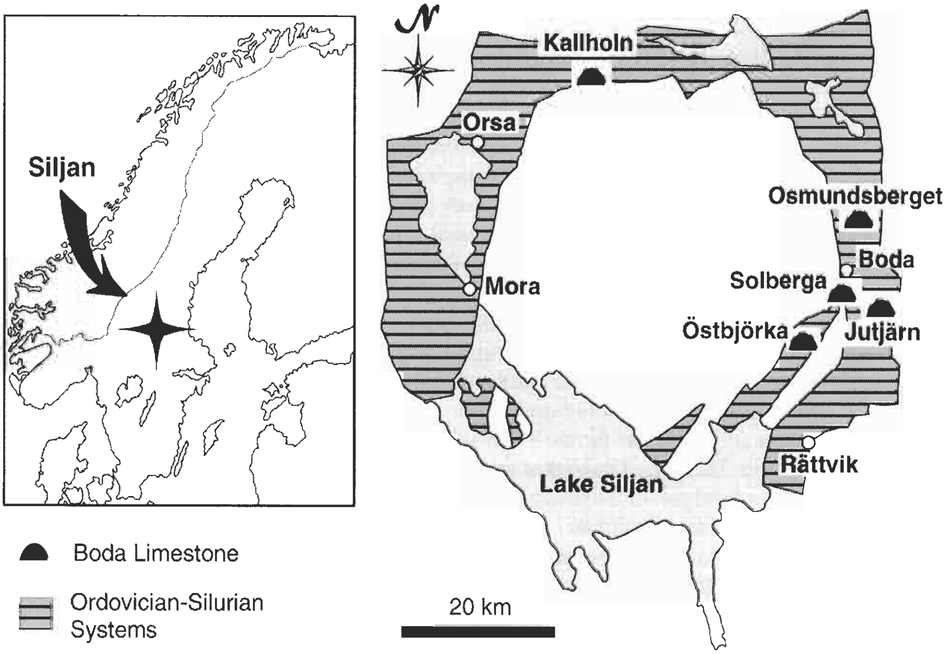

Fig. 1. Map of the Siljan district, Sweden, showing the distribution of Ordovician–Silurian rocks and occurences of the Boda Limestone.

several species of illaenaceans. A taphonomical study of the Boda Limestone trilobites was recently published by Suzuki & Bergström (1999).

Description

Genus *Holotrachelus* Holm, 1898

Holotrachelus punctillosus (Törnquist, 1884)

Entomostracites laticauda n. sp.; Wahlenberg 1818: p. 28, pl. 2: 7.
Cheirurus conformis n. sp.; Angelin 1854: p. 90, pl. 41: 15*.
Homalonotus punctillosus n. sp.; Törnquist 1884: p. 44, pl. 1: 46, 47, pl. 2: 1, 2.
Illaenus punctillosus (Törnquist); Holm 1898: p. 138, pl. 6: 1.
Illaenus (*Holotrachelus*) *punctillosus* n. subgen.; Törnquist 1919: p. 502.
Holotrachelus punctillosus (Törnquist); Warburg 1925: pp. 147–155, pl. 3: 16–25.
Holotrachelus punctillosus cilldaricus n. subsp.; Dean 1971: p. 58–60, pl. 24: 10, 12, pl. 25: 1–12, 14, non: pl. 24: 5, 7, 9, pl. 25: 13, 15.
Family undetermined (thoracic segment); Dean 1978: p. 109, pl. 46: 3.
Holotrachelus punctillosus (Törnquist); Owen 1981: p. 23–24, pl. 5: 11–16, 19.

Type specimens: In the Geology Department, Lund University, the following three cranidia described by Törnquist (1884) are kept as originals: LO 594T; LO 595t; LO 596t. Of these, I here select the best preserved and nearly complete cranidium, LO 595t, as the lectotype. The specimen is illustrated by Törnquist (1884: pl. 2: 1).

Authorship. — The confusing history of the authorship of the present genus and species (Warburg 1925: p. 152) was discussed by Owen (1981: p. 23), and is not dealt with herein.

Description. — The cephalon is semioval in shape (Fig. 2A, C), strongly convex with an evenly rounded margin (Fig. 2E, G). The cephalic border is fairly broad. The glabella is egg-shaped and strongly convex, distinctly set off from its surroundings. The eye lobes are situated laterally to the glabella about two fifths of its length from the anterior end. There is a pair of faint depressions, which are probably fossulae, on the anterolateral part of the glabella. A faint eye ridge is present. It is directed towards the supposed fossula but dies out before reaching the glabella. The facial suture is impossible to classify because of the absence of genal spines. There is no reason to follow the old '*Treatise*' (Moore 1959: p. O382) in regarding it as opisthoparian. A faint node at the posterior margin of the fixed cheek may represent a remnant of the genal spine (Fig. 2F). If so, the suture may be described as proparian. If not, it can be referred to as gonatoparian.

The number of thoracic tergites in an adult specimen is eight. The inner part of the thoracic pleura is widest at the third thoracic tergite. The thoracic axis is strongly convex in the most anterior segments, but less so more posteriorly (compare Fig. 3F and H). There is no furrow between the axial ring and the articulating half ring, but the latter is elevated (Fig. 3C, E, G: shadows behind the axial rings imply the condition). The pleural furrow has a 'V' shaped cross section especially in the anterior thoracic tergites (Fig. 3F). The furrow is shallower in the posterior tergites. It does not extend to the distal margin (Fig. 3E, F, H). The pleural extremity is much more pointed in the anterior tergites than posteriorly. The distal part of the pleura extends obliquely and ventrally in the first tergite, but is more horizontal towards the pygidium.

The doublure lacks panderian openings and hooks (Fig. 2L, M). The inner margin is concave in anterior tergites (Fig. 2M) but almost straight in posterior ones (Fig. 2L). In all tergites, the doublure covers the entire underside beyond the geniculation (Fig. 2L, M). The space between the doublure and the dorsal side is relatively voluminous (Fig. 2K–M). In the anteriormost thoracic segments the articulating facet is subtriangular (Figs. 3F, 7). The anterior margin of the facet is not parabolically curved as in so many other trilobites. Instead, the proximal part of this margin extends laterally to reach a rounded corner, from which the distal margin forms a concave curve (Figs. 3F, 7B). Contrasting with this situation, the facet on the posterior thoracic tergites is very small, indistinctly offset, and has a smoothly curved anterior margin (Figs. 3G, 7A).

In each tergite, a fulcral process is present at the inner end of the articulating facet (Fig. 3I), and a pivot joint at the anterior end of the axial furrow (Fig. 3G).

The pygidium is parabolic in outline. It includes four segments both in the axis and in the pleural part (note that the pygidium figured in Fig. 2J is an immature specimen with five segments). The fourth segment includes a triangular termination of the axis, presumably a post-segmental tip. The segmental portions are poorly fused. They easily come apart and may then be taken for thoracic tergites, to which they bear a striking similarity. The end of each pleura is abruptly truncated. A faint pleural furrow is developed in the inner part (Fig. 2J). There is no pygidial border. It is notable that the doublure is developed separately for each segment and is thus not continuous around the margin (Fig. 2K). As noted by Warburg (1925: p. 151), there is a structure reminiscent of an articulating half-ring in front of the 2nd and 3rd axial rings (Fig. 2J: white arrow). She called it a rudiment of the articulating half ring, and it is likely that her interpretation is correct.

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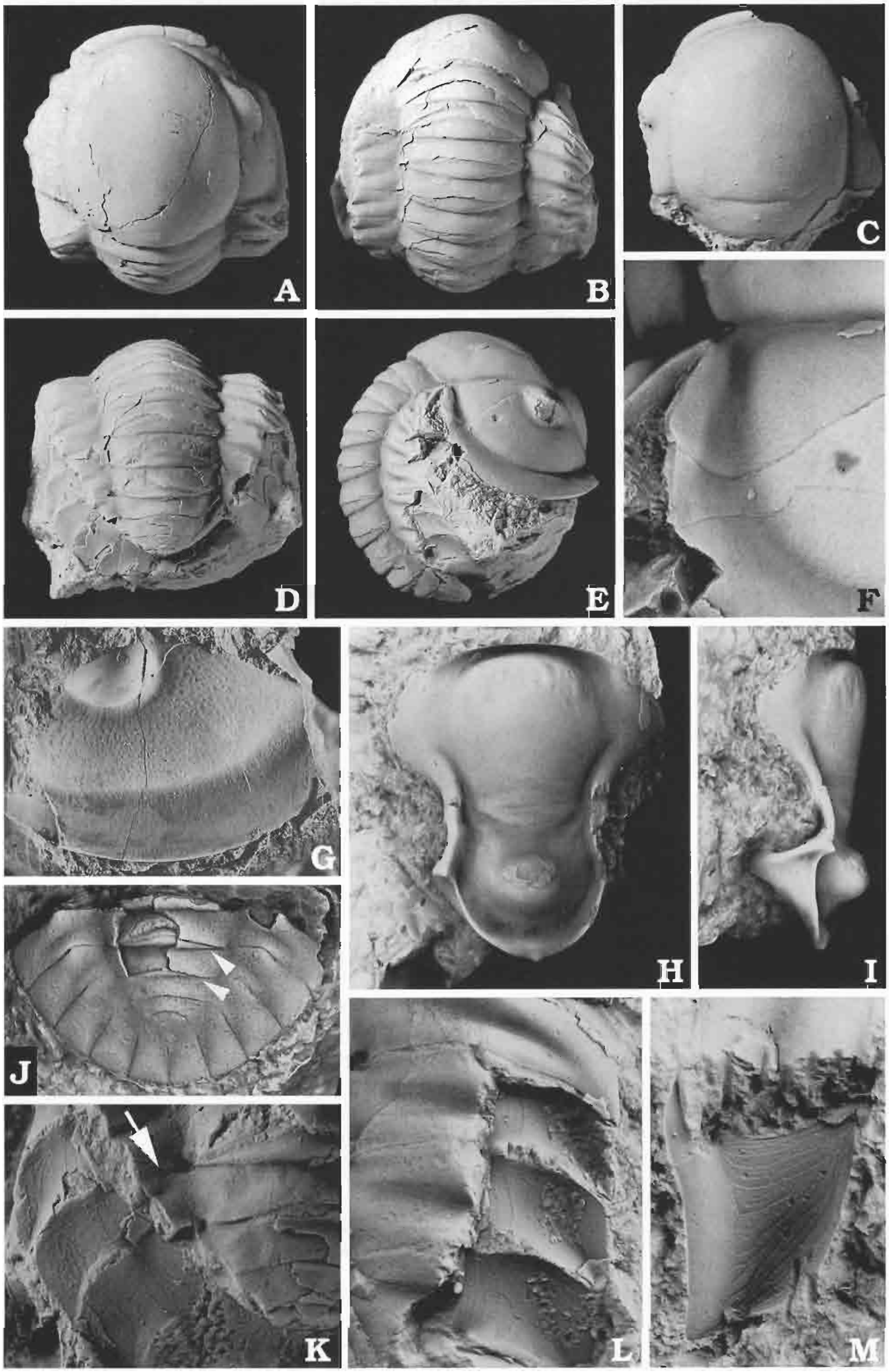
Fig. 2. *Holotrachelus punctillosus* (Törnquist, 1884). **A**, **B**, **D**, **E**. Cephalic, thoracic, pygidial dorsal views and side view of almost complete specimen. RM Ar. 45493; × 1.1. Kallholn. **C**. Smaller specimen with occipital furrow. Internal mould. RM Ar 57034; × 3.5. Jutjärn. **F**. Enlarged view of the posterior end of the facial suture with surroundings (same as Fig. 2E). RM Ar. 45493; × 3.4. Kallholn. **G**. Free cheek. Internal mould. RM Ar 57035; × 1.8. Jutjärn. **H**, **I**. Hypostome. Ventral and side views. Internal mould. RM Ar. 42879; × 3.3. Osmundsberget. Coll. E. Stensiö. **J**. Testiferous immature pygidium. UM ar. 517; × 1.6. Osmundsberget? This specimen was illustrated by Warburg (1925: pl. 3: 20). White arrows point at 'rudiments of articulating half rings'. **K**. Pygidial doublure, separate for individual segments. Specimen as **A**, **B**, **D**, **E**; × 3.5. White arrow marks the anterior end of the pygidium. **L**. Doublures in posterior thoracic tergites. Specimen as **A**, **B**, **D**, **E**; × 3.3. **M**. Doublure in an anterior thoracic tergite. RM Ar. 57036; × 4.5. Jutjärn.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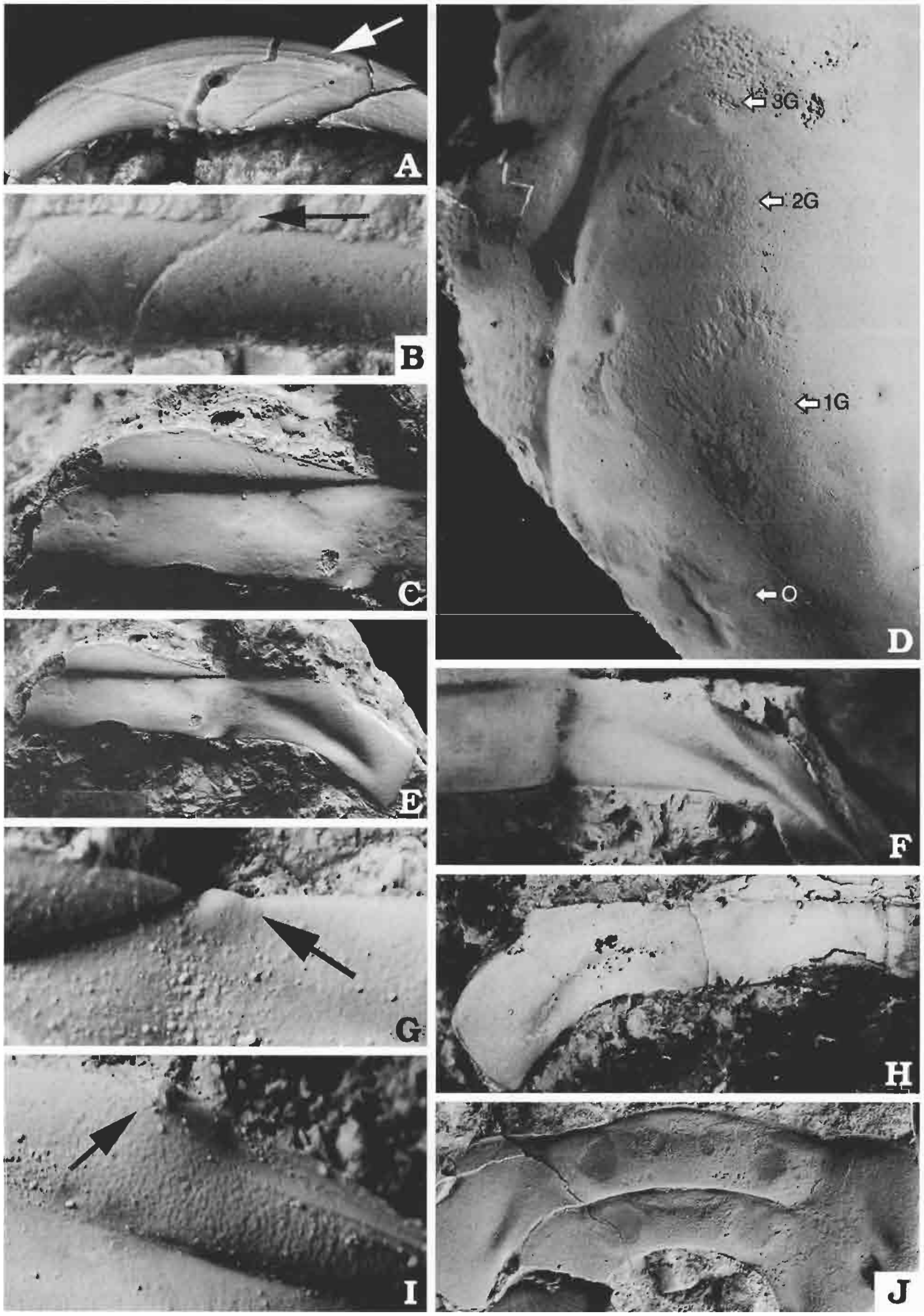

Fig. 3. *Holotrachelus punctillosus* (Törnquist, 1884). **A**. Ventral view of anterior part of rostral plate in the cephalic doublure; × 3.4. Specimen as Fig. 2A, B, D, E. White arrow marks the rostral suture. **B**. Posterior part of rostral plate, turned upwards and forwards on doublural roll. RM Ar. 47663; × 12. Kallholn. Coll. O. Isberg. Black arrow shows the hypostomal suture. **C**. Muscle scars in a thoracic axial ring; × 2.5. Kallholn.

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The hypostome has an hour-glass like outline and is slightly longer than wide (Fig. 2H, I). The anterior lobe is about two fifths of the maximum width. Its convexity is greatest anteriorly. The posterior lobe has a strong central rounded projection. The border is notably thick at the hypostome 'waist'. Posteriorly it comes to an abrupt end opposite the top of the posterior lobe. The anterior wing slopes gently and is fairly broad, about three fifths of the total length of the hypostome. The posterior wing extends vertically and deeply, forming almost a right-angled triangle (Fig. 2I). The embayment in front of it is large and has an almost right-angled delimitation. The hypostome ends posteriorly in a tiny acute projection. The anterior margin of the hypostome does not match the shape of the cephalic doublure (see also Moore 1959: p. O381, fig. 289c, d).

The anterior margin of the rostral plate is long, more than five times as long as that of the posterior margin, and midways between these the plate has a very narrow waist. The posterior half of the rostral plate curves strongly dorsally. Thus the anterior half is seen from below (Fig. 3A; anterior side up), but the posterior half only from behind (Fig. 3B; posterior side up).

Exoskeletal sculpture. — The external exoskeletal surface is granulose, but so finely that it appears smooth at first glance. Terrace lines have been observed only on the doublure (Figs. 2K–M, 3A). In the thorax, terrace lines are absent from surfaces which are overlapped by the articulating facet of the neighbouring tergite during enrolment (Fig. 2M). In the pygidium the lines are slightly sigmoidal to almost straight (Figs. 2K, 4), at a low angle to the inner and outer margins of the doublure.

Internal pattern. — Internal moulds of cranidia show five pairs of muscle scars (Figs. 3D, 4). The abbreviations of the muscle scars are those of Jaanusson (1954: fig. 5; see also Fig. 4). Two separate scars placed far anteriorly are both interpreted as representing 3G. One is subcircular, the other, lying closer to the margin, is narrow and elongate. The 2G scar is subtriangular in shape and lies at a level just in front of the eye lobe. The 1G and 0 pairs are of fairly complicated shape and more than twice as large as the others. The 1G has a subtriangular and highly digitated outline. In an internal mould figured in Fig. 3D, a distinct furrow is present in the 0 scar, which must represent the negative of a distinct ridge on the interior surface of the exoskeleton. This ridge extends backwards-inwards from the scar (see dark line in Fig. 4).

Fine pits seen in internal moulds cover the fixed and free cheeks except for the cephalic borders, but are absent in the glabella (Figs. 2G, 3D). This means that the interior surface is granulated. The granules are larger than the fine granules on the external surface and do not correspond to them in position.

Two pairs of muscle scars are recognised in the segments of the thorax and pygidium (Fig. 3C, J). These are smaller than the 0, 1G and 2G glabellar muscle scars. One is subcircular in shape with a highly digitated margin, the other is rectangular in shape (Figs. 3C, 4). The former is situated at the boundary between the articulating half ring and the axial ring; the latter is situated more laterally on the axial ring. In the pygidium, the former pair is much smaller and circular in shape.

Development. — As seen from the internal mould in Fig. 2C, the immature cranidium has an occipital furrow, which has disappeared in the adult (Fig. 2A). Similar losses with growth have also been described in Norwegian *Holotrachelus* by Owen (1981: pl. 5: 15, 16, 18). Smaller specimens tend to exhibit more strongly impressed occipital furrows than larger ones.

The cranidium tends to become less convex with size, and the most elevated part of the glabella is slightly flattened in large specimens.

One transitory pygidium is known (Fig. 2J; Warburg 1925: pl. 3: 20; Moore 1959: p. O381, fig. 289b). It has five segments, whereas adult pygidia have only four.

UM ar. 525. This specimen was illustrated by Warburg (1925: pl. 3: 22). **D**. Internal mould of a cranidium showing muscle scars and pitted structure in the fixed cheek. RM Ar. 57037; × 2.2. Jutjärn. **E**. Same as C. Entire view. Internal mould; × 1.5. **F**. Facet in an anterior thoracic tergite. Internal mould. RM Ar. 57038; × 3.1. Jutjärn. **G**. Axial articulating device (arrow). Internal mould. RM Ar. 57039; × 5. Jutjärn. **H**. Facet in a posterior thoracic tergite. Internal mould; × 2.1. RM Ar. 57040. **I**. Distal articulating device; × 10.5. Specimen as G. **J**. Fragmented pygidium with muscle scars. Internal mould. RM Ar. 57041; × 3.4. Jutjärn.

Morphological comparison with illaenid trilobites

As mentioned above, *Holotrachelus* has undergone strong modifications towards an illaenid-like morphology, perhaps as an adaptation to a similar mode of life. I will therefore try to 'peel off' the superficial 'illaenid polish' in order to identify systematically important characters. The first step involves a comparison with the illaenids.

In Fig. 4, *Holotrachelus punctillosus* is compared with *Stenopareia linnarssoni*, which is also common in pockets. Similarities include the following: (1) the proportion of total body length to cephalon is fairly small (about 2:1 to 3:1), (2) the cephalon has an almost spherical convexity, (3) the posterior part of the rostral plate is folded upwards and forwards, (4) the doublure has terrace lines, (5) there are notably large 0 and 1G muscle scars, and (6) the genal corner is rounded. Dissimilarities, which thus may be better as indicators of systematic affinities, include the following characters in *Holotrachelus*: (1) the presence of a preglabellar field and a cephalic border, (2) eight thoracic segments (nine in *S. linnarssoni*, but other illaenids have 8–10), (3) the unique slender shape of the hypostome (the illaenid hypostome is rounded), (4) segmental boundaries very distinct in the pygidium, (5) pygidial spines with separate doublures rather than an entire border (Fig. 4), (6) articulating devices (no fulcral process in *S. linnarssoni* or any other illaenacean), (7) a strong change in the morphology of the segmental pleural spines along the thorax (illaenacean segmental pleural spines are of more or less identical morphology along the thorax), and (8) the presence of oblique pleural furrows (no furrows in *S. linnarssoni* or any other illaenacean).

The development of the pleural area distal to the fulcrum (geniculation; point 5 above) is particularly interesting. It is developed as segmental pleural spines in the thorax of all trilobites, and in the pygidium of many early trilobites. In the pygidium of *Holotrachelus*, the corresponding distal pleural field is developed in the same way, with free segmental extremities. Each of them even has its own separate doublure (Figs. 4A, 5B). In most post-Early Ordovician trilobites, however, the corresponding distal pleural field forms a continuous rim of the pygidial shield. For instance, this is the case in proetids, bathyurids, illaenids, asaphids, phacopids, calymenids, trinucleids and harpids (Figs. 4B, 5C). In cases where there are spines, such as in taihungshaniids or dikelokephalinids, these are non-segmental spines. The only Ordovician groups with free segmental spines extending from the fulcral line are the Cheirurina, Odontopleurina, Lichina, Remopleuridoidea and possibly also Damesellacea (Fig. 5A). Thus we can distinguish two quite distinct pygidial morphologies characteristic of different high-rank groups of Ordovician trilobites, the development of the extra-fulcral field as segmental spines or as a continuous rim. *Holotrachelus* clearly belongs to the former category (Fig. 5).

The Remopleuridea are not included among the groups illustrated in the top rectangle of Fig. 5; they have no close phylogenetic relationship with *Holotrachelus*. One reason is the absence of a rostral plate in the former and its presence in the latter, another is the small pygidium with a terminal cleft rather than a terminal extension. The Lichina differ from *Holotrachelus* in lacking an eye ridge, in having a different glabellar (and glabellar muscle) arrangement, in having a different thoracic morphology including the articulating device, and in forming 'effacement' in a different way (see *Leiolichas illaenoides*: Thomas & Holloway 1988: pl. 10: 201, 202, 204, 207–210).

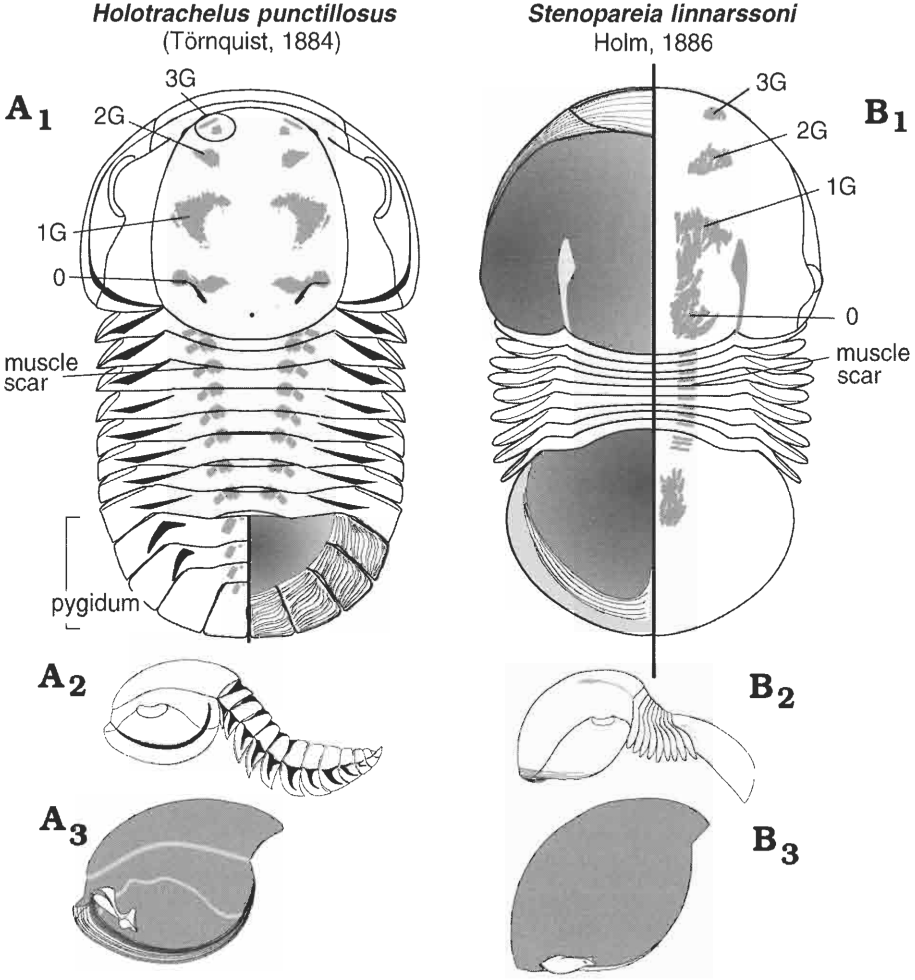

Fig. 4. Morphological comparison between *Holotrachelus punctillosus* (Törnquist, 1884) (**A**) and the illaenid *Stenopareia linnarssoni* Holm, 1886 (**B**). Dorsal view, in part combined with ventral view ($\mathbf{A}_1$, $\mathbf{B}_1$), side view ($\mathbf{A}_2$, $\mathbf{B}_2$), and cephalic cross section ($\mathbf{A}_3$, $\mathbf{B}_3$) with hypostomes in inferred position (cf. the displaced position illustrated by Whittington in Kaesler 1997: fig. 33). Dark markings in the axial area are muscle scars. Note how the extra-fulcral pleural area of the pygidium is developed as segmental pleural spines in *Holotrachelus*, but as a continuous pygidial rim in *Stenopareia*. 0, 1G–3G, muscle scars.

The Odontopleurina differ from *Holotrachelus* in the following fundamental characters: the complex glabellar morphology, fewer pygidial segments (1 to 2 as against 4), the apparent opisthoparian facial suture, the hypostomal morphology with a comparatively small anterior lobe, the details of the attachment of the hypostome to the cephalic ventral margin, and the spinosity of the body margins.

This leaves an affiliation of *Holotrachelus* with the Cheirurina as most plausible. However, since a bathyuroid (Order Proëtida) affinity is preferred in the revised '*Treatise on Invertebrate Paleontology*' (Fortey in Kaesler 1997: p. 300), such an alternative is considered below.

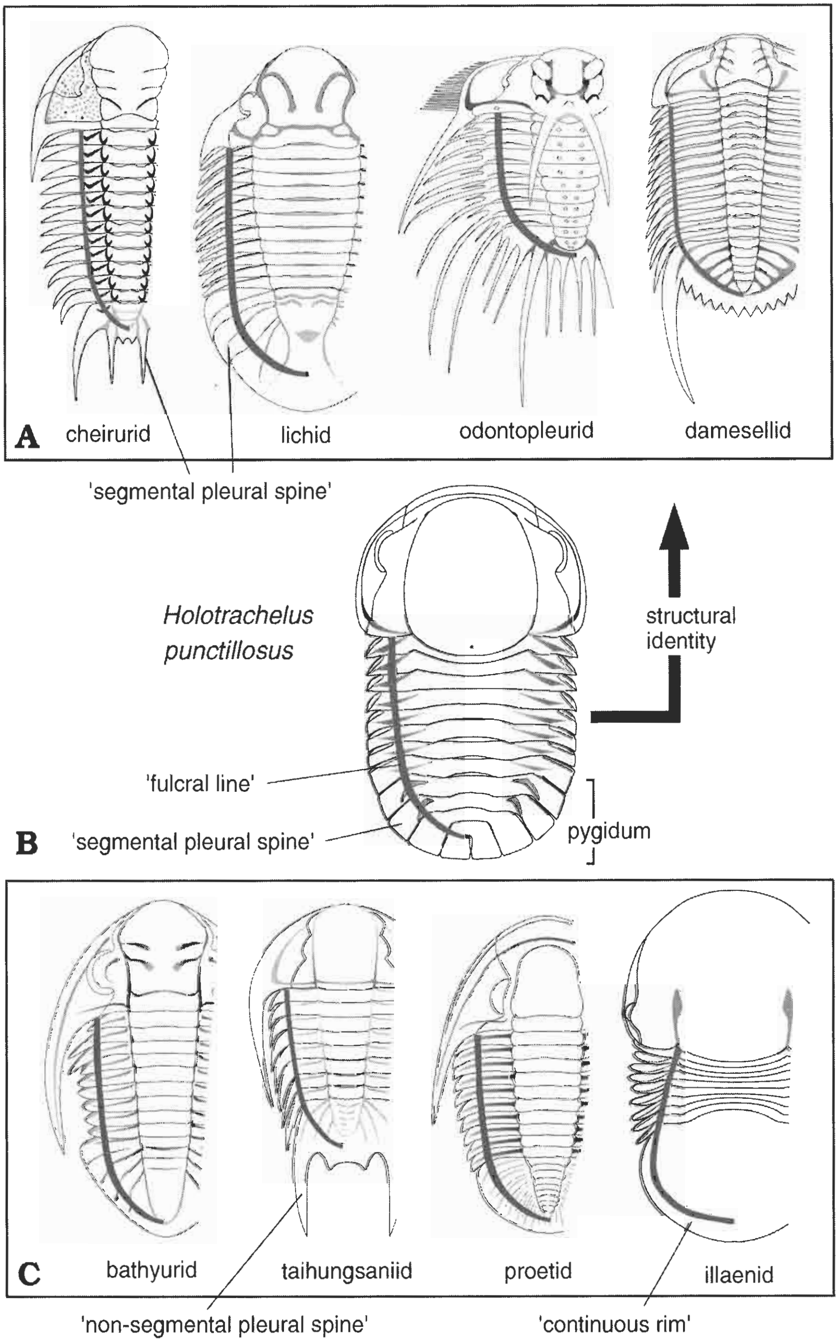

Fig. 5. Development of the pleural field distal to the 'fulcral line' in major groups of post-Early Ordovician trilobites (**A**, **C**), in comparison with *Holotrachelus punctillosus* (**B**). The 'fulcral line' is shown as a thick and dark grey line. The field distal to the 'fulcral line' consists of segmental spines in the thorax of all trilobites. In the pygidium, this field develops as segmental spines in the trilobite groups shown in **A**, but as a continuous rim in **C**. *Holotrachelus* clearly conforms with the trilobites shown in **A**.

Comparison with the Bathyuroidea

Bathyuroids are supposed to share with *Holotrachelus* an opisthoparian facial suture, the presence of a preglabellar field (although not in all bathyurid species), and the presence of terrace lines on the doublure. First, and as mentioned above, it should be noted that the suture of *Holotrachelus* can not be objectively described as being opisthoparian.

The most profound dissimilarity is found in the pygidium. As noted above, in *Holotrachelus* the segmentation of the pygidium stands out in a striking way, fusion between the segments is poor, and the outer pleural field (distal to the fulcrum) still consists of segmental pleural spines with separate doublures (Fig. 4 left). This is never so in any member of the Proetida as defined in the *Treatise*. Instead, the pygidium is a solid shield, always including the outer pleural field that corresponds to the pleural spines in the thorax.

Bathyurids have 9 or 10 thoracic tergites. In *Holotrachelus* the number is 8. In micropygous members of the Proetida there is only a slight morphological change through the thorax, whereas in nearly isopygous members the thoracic tergites are of almost identical morphology throughout the series. In *Holotrachelus*, there is a range from a pointed segmental pleural spine anteriorly to a blunt pleural extremity posteriorly. Moreover, the spines tilt downwards anteriorly in the pygidium, but are almost horizontal posteriorly. An additional difference is found in the thoracic doublure, which in *Holotrachelus*, but not in typical proetids, covers the underside of the entire segmental pleural spine (for bathyurids, see e.g. Whittington 1953: pl. 67: 27; for proetids, Whittington & Campbell 1967: pl. 2: 25; for otarionids, Whittington & Campbell 1967: pl. 4: 7). The Proetida also have a Panderian opening, which is absent in *Holotrachelus*, whereas the latter has articulating devices unknown in the Proetida.

Despite much variation within many trilobite groups, Fortey (1990) regarded the type of hypostomal attachment as being of prime importance for high level systematics, although it is often functionally related to the mode of enrolment (Bergström 1973). According to Fortey (1990), the presence of a preglabellar field indicates that the *Holotrachelus* hypostome is 'natant'. The natant condition is also considered to be an important character characteristic of the Proetida (Fortey 1990: fig. 19), although the hypostome may be attached to the cephalic doublure in both proetid and in bathyurid trilobites (Fortey 1990: fig. 1). In *Holotrachelus*, the posterior end of the rostral plate is bent dorsally and anteriorly towards the inner surface of the dorsal exoskeleton (Figs. 3A, B, 4). The mode of hypostomal attachment condition in this genus is most probably the same as in illaenids (see Fig. 4). Fortey (1990: fig. 11) noted that 'natant' hypostomes are of simple design. The *Holotrachelus* hypostome in this respect is typically non-natant, with a wide anterior margin and strong vertical posterior wings. It is therefore most probable that the hypostome in *Holotrachelus* was attached, perhaps flexibly so, to the doublure.

Neither the hypostome, nor the rostral plate of *Holotrachelus* shows any similarity to any member of the Proetida. Most particulary, a bathyurid rostral plate (see Ludvigsen 1979: pl. 5: 25, 26) exhibits a short anterior margin and a three to four times longer posterior one, while in *Holotrachelus* the anterior margin is more than five times longer than the posterior one.

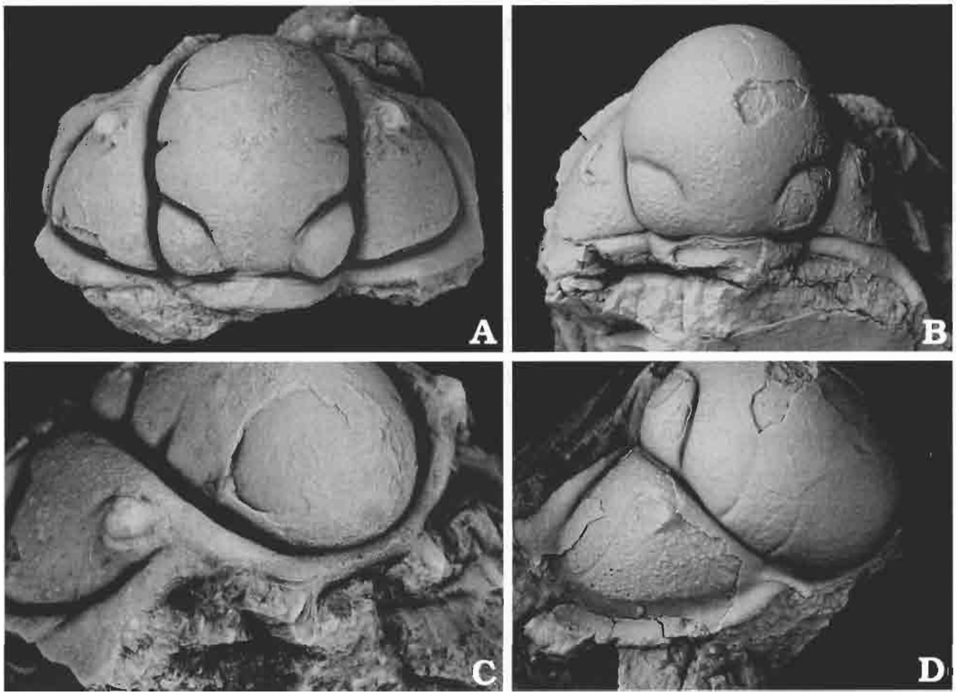

Fig. 6. Continuation of the fixed cheeks in front of the glabella as a 'preglabellar field'. **A**, **C**. *Cyrtometopus clavifrons*. RM Ar. 17911. Östergötland. Expansus or lower Raniceps beds. **A**. Dorsal cephalic view; × 2. **C**. Anteroblique view; × 2. **B**, **D**. *Pseudosphaerexochus tuberculatus*. UM ar. 663. This specimen was figured by Warburg (1925: pl. 10: 1–3). **B**. Dorsal cephalic view; × 2.2. **D**. Anteroblique view; × 2.3.

One of the characteristics of the Order Proetida is the possession of terrace lines on the doublure. However terrace lines were commonly present already in at least some Early Cambrian olenellid trilobites. Therefore their absence in some younger groups may be caused by suppression, whereas the presence (or the ability to form them) is just a plesiomorphy without much systematic significance. The terrace lines are also known to have had a functional significance (Schmalfuss 1981), and had also some relation to the sediment (Nielsen 1995: p. 67). Some trilobite groups possessed terrace lines only in larval stages (e.g., phacopids). As an example of variation within groups, the scutelluid genus *Planiscutellum* has well developed terrace lines over much of the pygidium, whereas the related *Scutellum* lacks such lines and instead has a granular ornament, very unusual in the order. It is quite obvious that we must be very cautious in using terrace lines as a strictly defining character in high level classification, although we may still use it as an indication.

Comparison with the Cheirurina

In the revised *Treatise* (Fortey in Kaesler 1997), the order Phacopida is taken to include the suborders Calymenina, Phacopina and Cheirurina. At first glance, *Holotrachelus* may appear unrelated to all three groups. However, the Cheiruridae (suborder

Cheirurina) and *Holotrachelus* share several characters. Such characters include: (1) marginal border present in the cephalon but absent in the pygidium, (2) proparian to gonatoparian facial suture (both states in cheirurids, best described as gonatoparian in *Holotrachelus*), (3) finely tuberculate inner surface of the cheeks, contrasting to the condition in the cephalic border and glabella, (4) an eye ridge (which may be only weakly developed), (5) a gradual shift in tergite morphology along the thorax, (6) a thoracic articulating device, (7) a complete doublural enclosure of the segmental pleural spines, (8) a visibly segmented pygidium; (9) rudiments of articulating half rings in the pygidium, (10) the extra-fulcral pleural field developed as segmental pleural spines in the pygidium.

Angelin (1854), who had only the pygidium available for study, regarded it as pertaining to the cheirurids, and it is easy to understand why. Some other characters of *Holotrachelus* are not shared with cheirurids. These include (1) the presence of a preglabellar field, (2) the shape of the segmental pleural spines, (3) the characteristic pleural furrow, and (4) the presence of terrace lines on the doublure.

Generally speaking, species of the Phacopida do not possess terrace lines on their doublure in the adult stage. However, as mentioned by Chatterton & Speyer in Kaesler (1997: p. 231), their larvae may have terrace lines on the doublure. This means that they had full potential to produce terrace lines. As mentioned above, terrace lines had significant functional meanings, as revealed by studies of recent crabs (Savazzi 1985). Illaenids differ from phacopids in having well developed terrace lines, possibly as a result of close contact between the skeletal surface and soft sediment (Bergström 1973; Westrop 1983). It would hardly be surprising if a cheirurid, having the genetic ability to form terrace lines and copying an illaenid mode of life and morphology, would also develop terrace lines in the adult.

The facial suture in *Holotrachelus* is different from that of most cheirurids if we consider the standard definition, but there are several cheirurid species with a closely comparable facial sutural course. Such species are found in the Sphaerexochinae and Eccoptochilinae (*sensu* Lane 1971). These subfamilies have a rounded lateral cephalic margin, and the facial suture seemingly crosses the posterior margin of the cephalon. Still, they are not regarded as being opisthoparian or gonatoparian, but proparian because they are cheirurids and 'should be' proparian. *Holotrachelus*, however, was not surmised to be a cheiruracean, and was therefore stated to be opisthoparian (although Warburg 1925 did not say so). In this respect, *Holotrachelus* is similar to the two cheirurid subfamilies mentioned. The position of the eye in the cheek is also the same, as is the presence of an eye ridge. Furthermore, there is a similarity in glabellar inflation and in the presence of an axial furrow.

The shape of the preglabellar field is related to the questions of the attachment of the hypostome, the rostral plate, and the glabellar morphology. *Cyrtometopus clavifrons* (Fig. 6A, D) from the Middle Ordovician of Öland, and *Pseudosphaerexochus conformis* (Fig. 6B, D) from the Ashgillian Boda Limestone may serve as illustrative examples. In both of these a ridge originating from the fixed cheek extends between the facial suture and the glabella and surrounds the anterior end of the latter. A field extending around the glabella between the cheek fields is called a preglabellar field in all non-cheirurid trilobites, but in cheirurids it is called a border. A similar preglabellar area of a fixed cheek origin is also recognised in *Cyrtometopella askerensis* (see

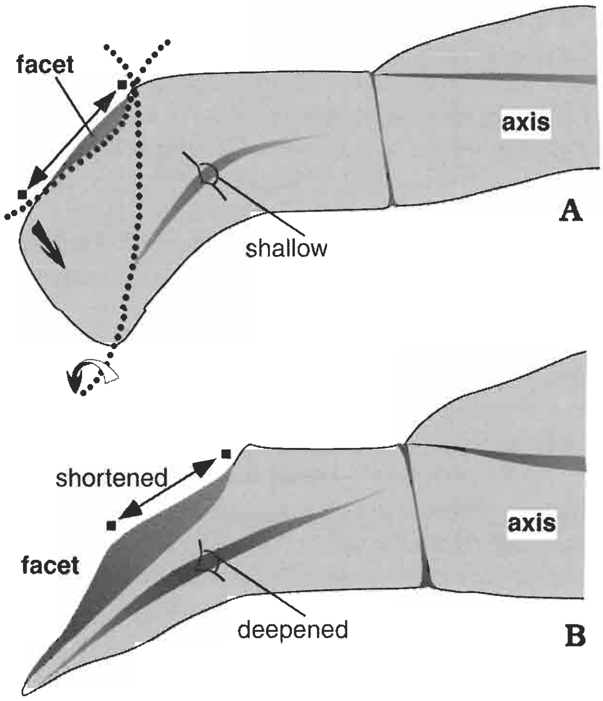

Fig. 7. Interpretation of the morphological differences between anteriorly and posteriorly situated thoracic tergites. **A**. Posterior thoracic tergite. **B**. Anterior thoracic tergite.

Nikolaisen 1961: pl. 1: 5, the proximal part of the true cephalic border is somewhat hidden under the fixed cheek anterior to the eye lobe). Also in case of *Remipyga*, a clear preglabellar field, in the sense that it is a field continuous with the fixed cheeks, is recognised without being cut by any marginal furrow (Whittington 1954: pl. 54: 8, 10–12). We do not know at present how the peculiar situation in some cheirurids arose, in which the free cheek does not seem to fit properly at the front end, and where it is a matter of taste whether the ridge in front of the glabella is called a preglabellar field or a marginal border, or perhaps preglabellar field plus marginal border. There is even the possibility that the ridge, or part of it, corresponds to the eye ridge of other trilobites. There is no way we can say that the genetic constitution would not be able to mould the *Holotrachelus* situation from such an origin.

Among cheirurids, a ventrally situated rostral plate is known only from *Actinopeltis* (Kielan 1959: fig. 7). This genus is difficult to place in a specific cheirurid subfamily (Lane 1971: p. 9). In the case of *Holotrachelus*, the rostral plate is situated not only ventrally, but its posterior half is bent dorsally and forwards on the doublure roll. With this kind of doublure roll and high attachment of the hypostome, the glabella can not be too close to the margin. In this way a need for a short preglabellar field has arisen (see Fig. 4).

As stated above, there is a strong morphological gradation along the thorax in *Holotrachelus*. Particular cheirurid species likewise have a gradation with segmental pleural spines pointing transversely in the anterior part of the thorax and posteriorly in

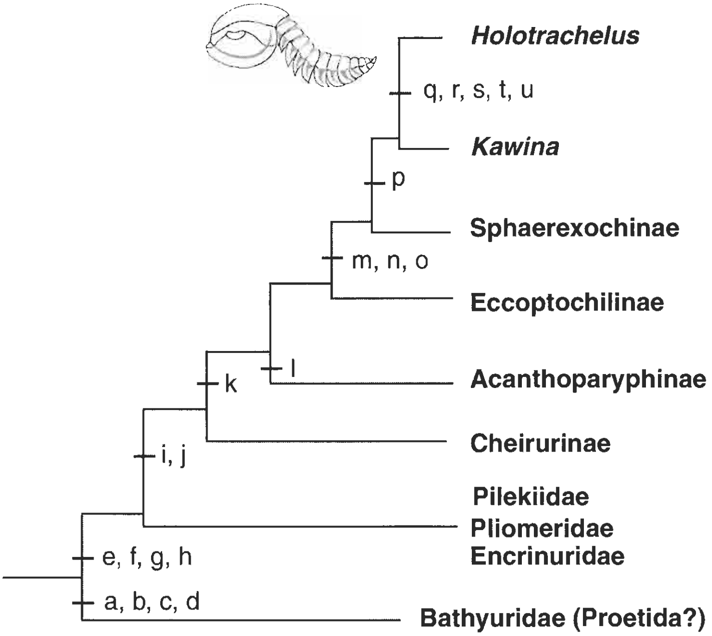

Fig. 8. Cladogram showing the suggested position of *Holotrachelus* within the Cheirurina. Letters denote morphological characters. a, extra-fulcral pleural area forms continuous pygidial rim; b, pygidial border; c, opisthoparian facial suture (plesiomorphic); d, loss of eye ridge; e, extra-fulcral pleural area forms spines in pygidium (plesiomorphic); f, border in cephalon but not in pygidium; g, doublure entirely covers underside of segmental pleural spine; h, doublural terrace lines in immature stages; i, 1S furrow relatively deeply impressed, extends obliquely; j, strong gradual morphological transition among thoracic tergites; k, glabellar inflation; l, reduction in pygidial segmental numbers; m, facial suture more or less gonatoparian; n, dorsal surface smooth; o, reduction of genal spine; p, strong overlap between adjoining thoracic segmental pleural spines; q, terrace lines in the doublure; r, reduction of the number of thoracic tergites; s, enlarged cephalic muscle attachment area; t, gradual modification of pleural 'facets' along thorax; u, narrow preglabellar field.

the rear (see Whittington 1954: pl. 20: 2). Moreover the tilt of the segmental pleural spine can change. Most cheirurids have no articulating facet between successive segmental pleural spines in the enrolled trilobite. However, *Kawina* has relatively large facets (see Whittington 1963: pl. 26: 8). According to Lane (1971), *Kawina* belongs to the Sphaerexochinae.

It is notable that *Kawina* has a pygidium that is strikingly similar to that of *Holotrachelus*. However, *Kawina* is longitudinally extended and has 12 thoracic segments, whereas *Holotrachelus* has acquired a short, illaenid-like body with only 8 thoracic segments. Typical Cheiruridae normally have 9–12 thoracic segments. However, variability is indeed part of the characteristics of the suborder, as indicated by ranges such as 8–19 segments in the thorax and 2–16 pleural ribs and about 1–30 axial rings in the pygidium. With this background, the number of thoracic tergites in *Holotrachelus* can not be an argument aginst cheirurid affinities.

An odd feature of the pleura is that there are two distal corners (Fig. 7). The posterior corner constitutes the tip of the pleural spine in the most anterior segments. In the posterior segments the distal tip is blunt, so that both corners are at the lateral edge of the exoskeleton. The posterior tergites apparently represent the least altered state from a developmental point of view, because each tergite is first formed by being set off from the pygidium. The anterior condition therefore is derived from the posterior one, at least from an ontogenetic point of view. How this transition comes about is shown by the gradual transition from tergite to tergite (see Fig. 7). The facet (delimited by a dotted line) successively becomes larger as a result of a shift of its distal termination from the anterior corner to the posterior one (arrows). Simultaneously the posterior corner grows into the pointed tip that is seen in the anterior tergites, and the pleural furrow deepens until it has a V-shaped cross section. This furrow strengthens the otherwise flat pleura, and is thus an alternative for the strongly vaulted and therefore strong construction of the pleura that is found in typical cheirurids. Again the almost extreme plasticity of the Cheirurina as a whole should be pointed out: there is quite a variety of pleural morphologies in the suborder, indeed a strong reminder that we should not be surprised to find still other unusual solution.

As noted above, the characters of *Holotrachelus* that have not undergone an 'illaenid polish' point decisively towards a cheirurid affinity. The characters, which do not fit with the cheirurid standard definitions, can also be interpreted toward a cheirurid affinity. Thus regarding the supposed differences in the presence or absence of a preglabellar field and in the course of the facial suture, it appears that much or all of the difference lies in different usages of terminology. *Holotrachelus* appears to have been derived from a cheirurid stock with a swollen glabella, almost smooth surface and no genal spines. Particular similarities are seen in the Sphaerexochinae. However, since the exact phylogenetic position is still unknown, I suggest a separate grouping in a downgraded monotypic subfamily Holotrachelinae of the Cheiruridae. *Holotrachelus* is very similar in gross morphology to the cheirurid *Kawina* which ranges from the Lower to the Middle Ordovician (see Whittington 1963: pl. 27: 1). *Kawina* specimens occur in profusion in a chaotic boulder which seems to be of a Boda Limestone type of pure whitish limestone (Whittington 1963: p. 11). The following unique correspondences are further indications supporting the idea of an affinity between *Holotrachelus* and sphaerexochinids including *Kawina*. These are the occurrence of *Kawina* and *Holotrachelus* in pure limestone buildup bodies, and the presence of distinct thoracic facets in the two species, an unusual character for the Cheiruridae. Fig. 8 is an attempt to show a possible phylogenetic position and the evolutionary modifications in a cladogram.

Comments on *Holotrachelus punctillosus cilldaricus*

Dean (1971) established a new subspecies of this species, *H. punctillosus cilldaricus*, from the Kildare Limestone. He noted that the most significant differences between the two are in the shape of the hypostome. In Dean's form, it is granulose, and the sub-conical median tubercle is placed more anteriorly than in the Boda form. The abrupt posterior end of the thick border which is recognised in the Boda form is absent in the Kildare form. There is no evidence for the association of the hypostome with *Holotrachelus* in the Chair of Kildare Limestone. Dean's locality no. 14, where a hypostome (holotype), a pygidium and two cranidia of *H. punctillosus cilldaricus* have been found, yielded several other species. It is a general observation that dorsally smooth trilobites do not have highly granulose hypostomes. I therefore feel strong doubts about associating the hypostome with *Holotrachelus*. In the case of the Boda *Holotrachelus*, Warburg (1925: p. 153) found a detached hypostome just underneath of a dead specimen, in addition to isolated hypostomes in a pocket with many fragments of *H. punctillosus*. In this case, the association is not in doubt. Considering the above arguments I include this subspecies to the synonymy of *H. punctillosus* (see p. 333).

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Rewizja późnoordowickiego trylobita *Holotrachelus punctillosus* (Törnquist, 1884) z Dalarna, Szwecja

YUTARO SUZUKI

Streszczenie

W pracy przedstawiono redeskrypcję trylobita *Holotrachelus punctillosus,* pochodzącego ze szwedzkich wapieni Boda (aszgil, górny ordowik) i omówiono pozycję systematyczną tego problematycznego gatunku. Jego charakterystyczna morfologia wydaje się być związana z przystosowaniem do trybu życia typowego dla Illaenidae. Morfologia pygidium, z polem pozawidełkowym rozwiniętym w postaci członowanych kolców pleuralnych, umożliwia zaliczenie holotrachelusa do jednej z czterech ordowickich nadrodzin: Remopleuridioidea, Odontopleuroidea, Lichoidea lub Cheiruroidea. *Holotrachelus* wykazuje największe podobieństwo do Cheiruroidea, zwłaszcza po skorygowaniu mylnej interpretacji szwu policzkowego. Autor sugeruje, że Holotrachelinae należy umieścić w obrębie Cheiruridae, przy czym najbliższe pokrewieństwa mogą je łączyć ze Sphaerexochinae.