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A Lower Cambrian merostome from Sweden

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With 2 plates and 3 figures in the text

Introduction

In addition to the considerable number of trilobite species known from the Lower Cambrian of several continents, a few other arthropods have been described. Particularly from North America several genera of bivalved carapaces have been referred to the crustaceans (Resser 1929). A better preserved form, *Protocaris marshi* Walcott, in addition to a bivalved carapace, has a multisegmented abdomen recalling *Hymenocaris* of the Middle Cambrian Burgess Shale (Walcott 1912).

Two Lower Cambrian genera have been referred to the merostomes. *Amiella prisca* Mansuy (1912, p. 31, Pl. 4, Fig. 6) from the *Redlichia* beds of China, is based on a very fragmentary specimen showing 6 segments of the pre-abdomen and 3 of the abdomen. Mansuy interpreted it as an eurypterid, but judging from the description and illustration, the arthropod fragment in my opinion may just as well or more probably belong under the Crustacea. The fragmentary state of preservation hardly permits a closer determination. *Roddya typa* Resser (1929, p. 14, Pl. 2, Fig. 5) from the Kinzers formation, Pennsylvania, U.S.A., has also been interpreted as a possible merostome. The fossil fragment consists of a small plate with certain elevations and surface ornamentation which hardly permits a determination.

The Order Aglaspida, the knowledge of which has been considerably increased in recent years by the work of Raasch (1939), ranges from the Middle Cambrian up into the Upper Ordovician (Caster and Macke 1952; Størmer 1955). The best-preserved specimens occur in the Trempealeau formation of Ohio. This formation is generally regarded as Upper Cambrian, but may belong to the lower part of the Tremadoc, hence forming the base of the Ordovician (Howell and Lochman 1939). Well preserved specimens of *Aglaspis* have revealed remnants of the appendages. The two orders Aglaspida and Xiphosuriida form the Subclass Xiphosura, which, together with the Subclass Eurypterida, constitutes the Class Merostomata.

From the Middle Cambrian Burgess Shale of British Columbia, Walcott (1911, 1912) described a number of merostome-like forms which he placed in the Merostomata. Owing to the excellent preservation, the structure of the appendages was indicated. The antennae and the trilobitan appendages deviate from the appendages known in the Merostomata. For this reason I suggested a new class of the Subphylum Chelicerata, the Merostomoidea, apparently equivalent to the Class Merostomata (Størmer 1944).

In discussing the phylogeny of the Merostomata, I have been inclined to regard (1952) the Merostomoidea as having branched off from the main arachnomorph

stem some time in the Precambrian. Somewhat later the Subphylum Chelicerata, forming one of the branches after the bifurcation, was split into the Arachnida and the Merostomata. The division of the merostome branch into the Xiphosura and Eurypterida was supposed to have occurred in Lower Cambrian time. From a phylogenetic point of view the discovery of a merostome in Lower Cambrian therefore deserves considerable attention.

The two merostome specimens described below were found at Kinnekulle in Västergötland in 1954. Count Hugo Hamilton fully appreciated the importance of the find and sent the specimens to the Swedish Museum of Natural History in Stockholm, and Professor E. A. Stensiö kindly invited me to describe the fossils. I wish to express my gratitude to Professor Stensiö for the opportunity of describing the fossils and to Count Hugo Hamilton and Dr. T. Örvig for valuable advice concerning the occurrence of the find.

Occurrence

The two specimens were found at Hjelmsäter, Kinnekulle, as loose boulders along the shore of lake Vänern. The boulders have evidently come from an abrasion escarpement close by. Along the shores of the lake the Precambrian peneplane is exposed. It is covered by a basal quartz conglomerate which introduces the Cambrian sequence. The conglomerate is succeeded by the Mickwitzia Sandstone (about 10 m) and above this by the Lingulid Sandstone (about 24 m; Hadding 1929; Westergård 1931, 1943).

The Mickwitzia Sandstone is fine-grained, light grey, and contains a certain amount of mica. After weathering it is more or less brownish-red. The sandstone contains *Mickwitzia monilifera* (LINRS.), *M. pretiosa* (LINRS.), *Volborthella tenuis* SCHMIDT, *Torellella laevigata* (LINRS.) and a number of remarkable trails and problematica (*Diplocraterion*, *Eophyton*, *Cruziana*, *Medusina* and others). The beds have been correlated with the *Holmia torelli* zone (Wærn 1952), thus representing the lower part of the Lower Cambrian.

The overlying Lingulid Sandstone, which is fine-grained and nearly white, weathers brownish-yellow to reddish. It contains *Obolella* (*Glyptias*) *favosa* (LINRS.), *Lingulella* sp. and trilobites fragments. The latter sandstone is generally correlated with the *Holmia kjerulfi* zone, probably of the middle part of the Lower Cambrian.

The boulders containing the merostomes consist apparently of light grey sandstone weathering brownish to reddish-yellow on account of the content of pyrite. The sandstone contains mica and small green grains, which are probably glauconite. According to verbal information from Count Hugo Hamilton, the escarpment from which the boulders evidently came, is about 20–30 m high and hence formed of both sandstones of which the lower one is mostly concealed by a tallus covered with vegetation. The loose boulders certainly belong to one of the Lower Cambrian sandstones. The colour and the content of mica suggest the lower one, the Mickwitzia Sandstone.

Preservation and preparation

The preservation is not good. The fossil specimens appear as moulds, and no traces of the shell (exoskeleton) or surface ornamentation are preserved. In certain cases the impression, the mould, has disappeared, too. Thus the hind portion of the 12th segment in the typoid (Pl. 2, Fig. 6) is not so well marked. The two specimens were

cleaned by means of chisels and automatic hammers, drills and a diamond saw. The matrix does not split easily from the mould. As mentioned below, the telson is missing in both specimens. Gradual removal of the matrix behind the 12th abdominal segment in both specimens did not reveal any traces of a telson, which was therefore probably lost before the animal became embedded in the sand.

Taxonomy

Class Merostomata DANA

?Subclass Xiphosura LATREILLE

? Order Aglaspida

Family Paleomeriidae STØRMER *n. fam.*

DIAGNOSIS OF FAMILY.—Large forms. Opisthosoma with 12 free segments, 12th segment trapezoid.

Genus ***Paleomerus*** STØRMER n. gen.

DERIVATION OF NAME.—παλαιός (Greek: old, ancient), μέρος (Greek: part).

TYPE SPECIES.—*Paleomerus hamiltoni* STØRMER n. sp.

DIAGNOSIS OF GENUS.—Dorsal exoskeleton (without telson), ovate, strongly inflated; prosoma parabolic with reniform antemedian compund eyes; opisthosoma with 12 strongly overlapping, movable tergites, 12th segment long, trapezoid; telson unknown. Lower Cambrian.

Paleomerus hamiltoni STØRMER n. gen. n. sp.

Pl. 1–2, Text-fig. 1–3.

DERIVATION OF NAME.—Species named after Count Hugo Hamilton.

HOLOTYPE.—No. Ar. 47071 of the collection in the Paleozoological Department of the Swedish Museum of Natural History in Stockholm.

TYPOID.—No. Ar. 47073 of the same collection.

DIAGNOSIS FOR SPECIES.—The same as for the genus.

GENERAL DESCRIPTION.—The dorsal exoskeleton is strongly inflated. The body, without telson, has an ovate outline. There is no noticeable trilobation of the body.

PROSOMA.—The short prosoma has a parabolic outline with a somewhat concave posterior border (Text-figs. 1, 2). The length of the prosoma is about 0.35–0.4 times the width. The convexity of the prosoma is strongest in front where the surface dips almost vertically towards the anterior border (Pl. 1, Fig. 2, Pl. 2, Fig. 1, 3). The anterior margin is apparently not elevated near the median line. No median lobe (cardiac lobe or glabella) is indicated. The postlateral angles of the prosoma are rounded and not prolonged into spines. No traces of median ocelli are seen, but this may be due to imperfect preservation. The lateral compound eyes are indicated by elevations on the prosomal surface. In the holotype the eye can best be seen on the right hand side; the greater part of the left eye is broken off, leaving only an imperfect

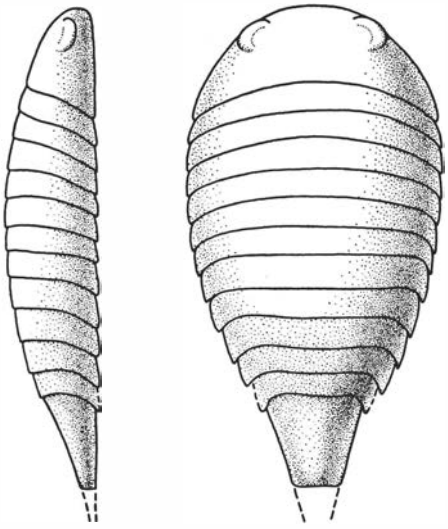

Fig. 1. *Paleomerus hamiltoni* STØRMER, n. gen., n. sp. Reconstruction. Lateral and dorsal view), 1 ×.

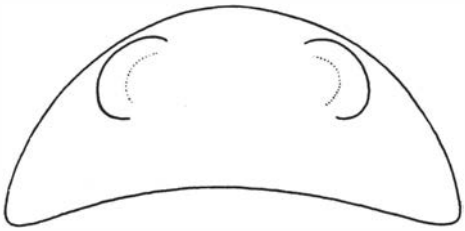

Fig. 2. *Paleomerus hamiltoni* STØRMER, n. gen., n. sp. Reconstruction of the prosoma. Dorsal, slightly anterior view. Median ocelli may have been present. $^4/_3$ ×.

outline. In the typoid the eyes are fairly well preserved on both sides. The compound eyes (Fig. 1) appear as antelateral reniform elevations almost reaching the anterior margin. The maximum length of the eye is about half the length of the prosoma. The longest axis across the two eyes converge in front, forming an angle of about 65°. The actual outline of the visual surface of the reniform eyes is difficult to make out; the upper, median surface conforms with the adjacent surface of the prosoma, but a faint suggestion of a median border is shown in Fig. 2.

OPISTHOSOMA.—In both specimens 12 abdominal segments are preserved. The opisthosoma increases sligthly in width towards the 3rd and 4th segments, then decreases again slightly, back to the 7th segment and thence more rapidly towards the hind border of the trapezoid 12th segment. The body is evenly convex, in longitudinal direction the holotype is more curved than the typoid except for the hind part where, in the latter, the 12th segment is bent downwards.

The tergites are all much alike, forming transverse bands with postlateral angles slightly prolonged (less typical in the anterior tergites which may have more rounded postlateral angles). The width of the 11th tergite is only a little more than $\frac{1}{3}$ of the greatest width of the abdomen. On the left side of the typoid the 7th tergite shows traces of a narrow lateral rim bordered by a shallow furrow, the width of which is about 0.14 times the length of the tergite. A strong overlapping of the tergites is characteristic, and about half the length of the 1st tergite is concealed under the prosoma (Pl. 1, Fig. 1, Pl. 2, Fig. 2). This is also more or less the case with the following 10 tergites, the degree of overlapping depending on the convexity of the body at the tergite concerned. The extensive overlapping of the tergites indicates a strong flexibility of the body. The power of rolling up as well as of lateral inflection was

probably present, the latter is also suggested by the lateral bending of the holotype (Pl. 1, Fig. 1) where the overlapping is different on both sides.

The tergites of the body had probably not developed any fully rigid articulation such as that found in trilobites and eurypterids. The loose articulation suggested in the present form may also have been characteristic of certain aglaspids (Raasch 1939, p. 64).

The 12th segment differs considerably from those in front. The outline, which is well defined in the holotype and indicated in the typoid, is trapezoid. The posterior transverse margin is not a line of fracture. The anterior margin is slightly concave (Pl. 2, Fig. 6) possibly with rounded anterolateral angles. The length of the anterior transverse margin is about $\frac{5}{3}$ the length of the posterior border and about $\frac{4}{3}$ the length of the segment. The 12th segment is not evenly convex, from the median line both sides slope gently towards the lateral margins, the median portion, however, is gently curved and does not form a median keel. The inflation diminishes towards the posterior border as may be seen in lateral view (Pl. 1, Fig. 2).

The abrupt transverse termination of the last segment suggests the presence of an unpreserved portion behind it, probably a lost telson, and, as mentioned above, no traces of such a segment were found during the successive cleaning of the two specimens. Judging from the general shape of the body and from the analogy of the aglaspids and eurypterids, the missing part of the body may have been a broad lanceolate or possibly a fan-shaped telson, the latter forming a horizontal tail fin.

DIMENSIONS.—Length (median) of body (without telson) in holotype and typoid 93 mm and 62 mm; greatest width 52 mm and 37 mm; lentgh of prosoma 15 mm and 12 mm, greatest width 45 mm and 34 mm.

HABITAT.—With no knowledge of the ventral appendage, it is difficult to say anything definite about the mode of life of the present arthropod. The lanceolate shape of the body would facilitate swift movements through the water, and the strong flexibility of the abdomen would be an advantage for rapid swimming and would enable the animal to make turns in any direction. The animal may then have been an able swimmer and could probably roll up to protect itself when lying on the sandy bottom of the sea. Other fossils in the sandstones, as well as the occurrence of the green mineral grains, probably glauconite, suggest a well ventilated marine environment.

AFFINITIES.—Because of the absence of ventral appendages, a comparison with other forms must be based exclusively on the morphology of the dorsal exoskeleton. We are here faced with a major difficulty, since the separation of the Class Merostomoidea (referred to the Subphylum Trilobitomorpha) from the Class Merostomata (referred to the Subphylum Chelicerata) is based chiefly on the structures of the appendages. In the following, a comparison, based on dorsal morphological features only, is made between *Paleomerus* and members of the Merostomoidea and Merostomata (subclasses Xiphosura and Eurypterida).

The MEROSTOMOIDEA comprise merostome-like forms (Størmer 1944) with apparently trilobitan appendages. Among the Middle Cambrian Burgess Shale forms, *Sidneya inexpectans* WALCOTT (1911) resembles the present species. The general outline of the body (Text-fig. 3*a*) is not dissimilar in both forms (a narrow postabdomen is sligtly more obvious in *Sidneya*), but the Canadian form deviates from *Paleomerus* in the shape of the prosoma, the absence of prominent, antemedian compound eyes,

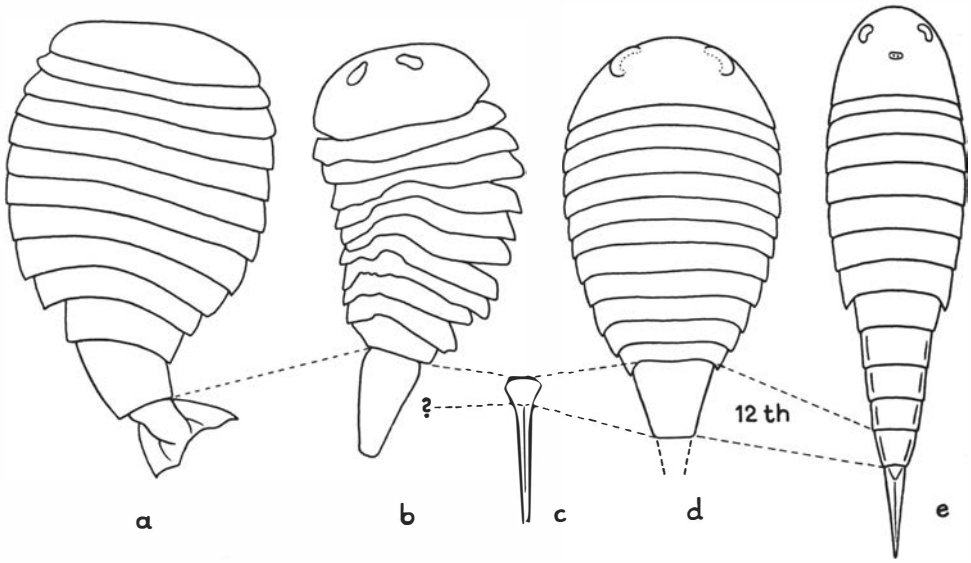

Fig. 3. A comparison between *a*, *Sidneya inexpectans* WALCOTT, Middle Cambrian, 1 × (after WALCOTT 1911); *b*, *Strabops thacheri* BEECHER, Upper Cambrian, $^1/_2$ × (after Beecher); *c*, *Aglaspides sculptilis* RAASCH, Uppermost Cambrian, $^1/_2$ × (after Raasch 1939); *d*, *Paleomerus hamiltoni* STØRMER n. g., n. sp., Lower Cambrian, $^3/_4$ ×; and *Hughmilleria norvegica* (KLÆR), Uppermost Silurian, $^3/_4$ × (after Størmer). Ordovician species of the genus less well-known.

and primarily in the presence of 11 instead of 12 free segments in front of the posterior portion. However, it must be mentioned that the nature of the posterior plate in *Sidneya* is not quite clear.

Among the MEROSTOMATA the AGLASPIDA of the Xiphosura, typical of the Cambrian, have several features in common with the present form. The Upper Cambrian *Strabops* (Beecher 1901) (Text-fig. 3*b*) has a similar outline to the body, anteromedian eyes and the same overlapping of the tergites, but an important difference is the presence of only 11 movable segments in front of the telson. The number of segments was correctly observed by Beecher in his original description in 1901. However, Clarke and Ruedemann (1912, p. 153), who had access both to the type and the relivio, claimed that there were 12 segments, a frontal one being pushed under the prosoma. They also disagreed with the compound eyes having an antemedian position. Raasch (1939, p. 45) carefully re-examined the material and found that it fully confirmed the results of Beecher regarding the position of the compound eyes and the number of movable segments in the abdomen. Beecher mentions the affinities between *Strabops* and the eurypterids, and this was strongly emphasized by Clarke and Ruedemann who assumed that both had 12 segments in the abdomen. They even regarded the Cambrian genus as a primitive eurypterid. Eleven movable segments between the prosoma and the telson is characteristic of Aglaspida. *Beckwithia* of the Middle Cambrian (Resser 1931) is an exception. Here we have 8 free segments, the posterior one being fused into a single continuous shield. Raasch (1939) assumes that the expanded anterior part of the telson in many aglaspids may represent an extra 12th segment incorporated (or fused with) the telson (l.c. Pl. 9, Fig. 3, Pl. 11, Fig. 12). If this is the case, the more or less trapezoidal anterior portion of the

telson corresponds to the similar segment in *Paleomerus* (comp. Text-Fig. 3*c*). Large compound eyes also occur in the Aglaspida. A comparison between the Aglaspida and the present form shows considerable resemblances which suggest a close relationship. There is, however, a difference in the number of free movable segments in the abdomen.

The EURYPTERIDA are not known before the ordovician (Deep Kill, Ruedemann 1934). The apparently primitive genus *Hughmilleria* (Text-fig. 3*e*) has much in common with *Paleomerus*. The lanceolate body is narrower, but the parabolic prosoma with reniform compound eyes is similar, and the number (12) of abdominal segments the same. A division of the abdomen into pre- and postabdomen such as in *Hughmilleria*, is of little significance, being absent from other eurypterids such as *Pterygotus* and *Eurypterus*. The pretelson or 12th abdominal segment of *Paleomerus* is, however, more prominent than the corresponding segment in *Hughmilleria*. A comparison between *Paleomerus* and the Eurypterida also reveals important common features. A difference may be seen in the general shape of the body and in the special development of the pretelson in the Cambrian form.

Paleomerus shows affinities both to members of the Class Merostomoidea and to the Class Merostomata. Although the appendages are unknown, the general morphological structures seem to point towards a closer relationship with the latter group. Among the Merostomata, the Cambro-Ordovician Order Aglaspida of the Subclass Xiphosura, has very similar general morphological features, the "habitus" being much the same. The definite difference, 11 instead of 12 free abdominal segments, is diminished by the possibility of one segment being incorporated in the telson. The fact that the Aglaspida are so old, geologically, may also suggest a closer connection. On the other hand, a relationship with the Subclass Eurypterida is also very evident. The plan of construction of the dorsal exoskeleton is much the same, although the general "habitus" may be somewhat different in addition to the marked difference in geological age.

A comparison with the Merostomata places *Paleomerus* as a more or less intermediate link between the two subclasses Xiphosura and Eurypterida. *Although the appendages are unknown, the general morphology of the dorsal exoskeleton of the new Lower Cambrian form suggests an ancestral form such as would be largely expected as an ancestor both of the Xiphosura and the Eurypterida.*

I have previously (Størmer 1952, Fig. 3) assumed that the bifurcation of the merostome stock into the two branches Xiphosura and Eurypterida, took place somewhere in the Lower Cambrian.

Provisionally I am inclined to place the new family Paleomeriidae in the Order Aglaspida. Further knowledge, particularly of the appendages, may favour another taxonomic position.

Summary

Two almost complete specimens of a new merostome have been found in the Lower Cambrian at Kinnekulle, Sweden. Previously, the earliest known merostome was one which occurs in the Middle Cambrian. The new form shows primitive morphological features indicating a zoological position between the Aglaspida and the Eurypterida. Judging from the dorsal structures, the species approaches a hypothetical common ancestor of both groups. For the new species, *Paleomerus hamiltoni*, a new family, Paleomeriidae, is suggested and placed provisionally in the Order Aglaspida of the Subclass Xiphosura.

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Explanation of plates

Plate I

Paleomerus hamiltoni STØRMER, n. gen. et n. sp. Holotype. No. Ar. 47071, Coll. Dept. of Paleozoology, Swedish Museum of Natural History, Stockholm. *1*, dorsal view; *2*, lateral; *3*, anterior. $^{4}/_{3}$ ×. LowerCambrian. Mickwitzia (or possibly Lingulid) Sandstone, Hjelmsäter, Kinnekulle, Västergötland, Sweden.

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Plate II

Paleomerus hamiltoni STORMER, n. gen. et n. sp. Typoid. No. Ar. 47073, Coll. Dept. of Paleozoology, Swedish Museum of Natural History, Stockholm. *2*, dorsal view; *1*, *3*, lateral; *4*, anterior; *5*, antedorsal; *6*, postdorsal. $^4/_3 \times$. Lower Cambrian. Mickwitzia (or possibly Lingulid) Sandstone, Hjelmsäter, Kinnekulle, Västergötland, Sweden.

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