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A new specimen of *Paleomerus hamiltoni* (Arthropoda; Arachnomorpha)

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ABSTRACT: A fourth specimen of the enigmatic Lower Cambrian arthropod *Paleomerus hamiltoni* is described from the Mickwitzia Sandstone of Sweden. The nature of the telson of *P. hamiltoni* was previously unknown and it has been assumed that the abdomen consisted of 12 segments, the posterior-most being elongate and tapering. This new material constitutes a mould of the entire animal and a cast of the posterior-most abdominal segment and telson, proving that the abdomen consists of 11 segments and a short, tapering telson, which was previously misinterpreted as the twelfth abdominal segment. The presence of 11 abdominal segments in *P. hamiltoni* eliminates significant differences between it and *Strabops thacheri*, supporting assignment to Strabopidae and rendering the family Paleomeridae redundant.

KEY WORDS: Atdabanian, Cambrian, Strabopidae, telson.

Paleomerus hamiltoni is one of the oldest known arthropods. It was used as an outgroup by Dunlop & Selden (1997) and Anderson & Selden (1997) in their phylogenetic analysis of early chelicerates. As such, it may occupy an important position between stem-group chelicerates and other arachnomorph arthropod groups such as the trilobites. *Paleomerus hamiltoni* was described by Størmer (1956; see also Størmer 1955) from the Lower Cambrian Mickwitzia Sandstone of Kinnekulle, Sweden, based on two incomplete specimens. Størmer (1956) believed that the posterior-most tagma (telson hereafter) of his two specimens was missing, and concluded that *P. hamiltoni* had 12 abdominal segments and a telson. An additional specimen described by Bergström (1971) did not cast any light upon the 'missing' telson of *Paleomerus*. Bergström (1971) discussed whether *P. hamiltoni* had 11 or 12 abdominal segments, and suggested 11 to be most likely, based on comparisons with *Strabops thacheri* Beecher (1901). Subsequently, Dunlop & Selden (1997) and Anderson & Selden (1997) coded *Paleomerus* as having 11 abdominal segments. The present paper describes a new specimen preserving the entire telson, conclusively proving that *P. hamiltoni* has 11 abdominal segments and a broad, triangular telson.

The new specimen is a poorly preserved mould presented to the authors by Mr J. Ahlgren. It was found on the beach of lake Vänern, directly west of Hällekis, 10 km north of Hjelmsäter, where the three previous specimens were found (Størmer 1956; Bergström 1971). As with earlier specimens, it was found in an erratic and abraded block, and is preserved in the same buff-coloured, coarse sandstone, presumed by Størmer (1956) and Bergström (1971) to have been derived from the lower part of the Mickwitzia Sandstone. This sandstone has long been known to be Lower Cambrian and has been confined to the Lower Atdabanian by analyses of acritarchs (Bergström & Gee 1985; Moczydłowska 1989; Moczydłowska & Vidal 1988). Preservation of the new specimen is similar to the previous specimens. The cast is preserved in dark, fine-grained sandstone while the mould is lighter in colour and is preserved in a more coarse-grained sandstone.

Support for assigning this specimen to *P. hamiltoni*, in addition to being from the same formation and almost the same locality, can be found in the morphological similarities with the holotype described by Størmer (1956). This is evident by the overall similarities in shape between the two specimens; the L/W ratio (length divided by width) of the carapace in this specimen is around 0.4 (but is incompletely preserved anteriorly and laterally because of erosion), quite similar to the L/W ratio of 0·33 in the more complete holotype. Bergström (1971) noted that the carapace had the same length as the anterior three segments of the abdomen, which is also evident in this specimen, despite poorly preserved segment boundaries. Faint segmentation is observed on the right-hand side of the specimen, and the segment lengths are comparable to those found in the holotype. The segmentation is also seen anterior to the telson on the cast, and segment lengths of these and the tapering ratio of the telson are also comparable with those of the holotype.

1. Material and methods

The carapace and abdomen of the specimen are preserved as an external mould, while the telson and part of the last abdominal segment are also preserved as an internal cast, which remained in the mould prior to preparation. As in the other three specimens, no trace of the original exoskeleton is preserved. The internal cast is composed of a grey, very fine-grained sandstone, easily distinguishable from the coarse, buff-coloured quartzitic sandstone of the mould. The cast of the telson was loosened by repeated freezing and thawing, and removed from the mould with a small hammer. Photographs were prepared with low-angle surrounding light and without any coating of the specimen. The specimen is reposited in the Paleontologisk Museum, Oslo (PMO), Norway, under the catalogue numbers PMO 201.957 (mould) and PMO 201.957a (cast).

2. Systematic palaeontology

Arachnomorpha Heider, 1913
Order Strabopida, Hou & Bergström, 1997
Family Strabopidae Gerhardt, 1932
Paleomerus hamiltoni Størmer, 1956

Remarks. Similarities between *P. hamiltoni* and *Strabops thacheri* Beecher (1901) were discussed by Bergström (1971), who noted that the only feature separating these genera is eye

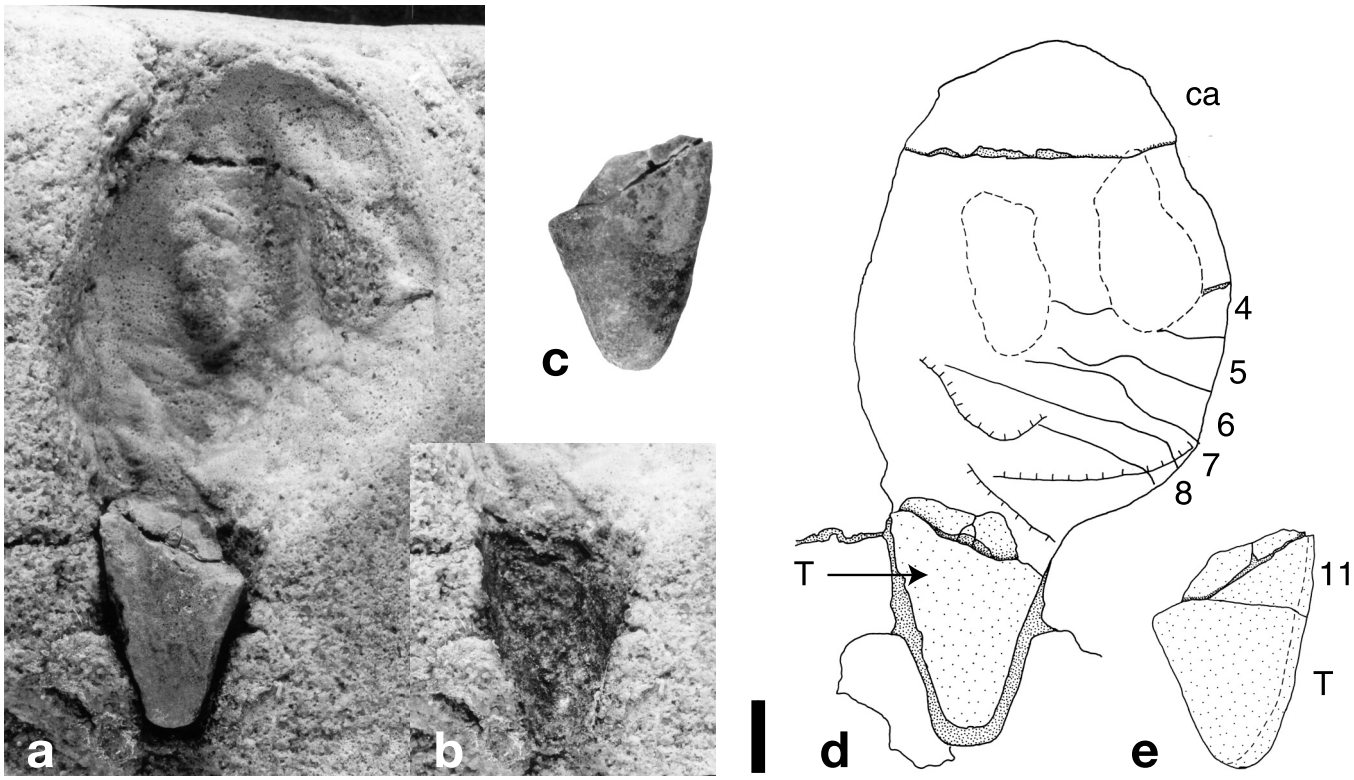

Figure 1 *Paleomerus hamiltoni*: (a) photograph of PMO 201.957, ventral view before removal of telson mould; (b) photograph of posterior region of PMO 201.957, ventral view after removal of telson mould; (c) photograph of PMO 201.957a, dorsal view of telson cast with attached abdominal segment 11; (d) *camera lucida* drawing of PMO 201.957, ventral view; (e) *camera lucida* drawing of PMO 201.957a, dorsal view. Key: (ca) carapace; (T) telson; (4–8, 11) abdominal segment numbers. Scale bar = 10 mm.

position. An additional difference noted here is that the telson of *P. hamiltoni* is relatively shorter and broader than in *S. thacheri*. Presumed differences in opisthosomal segment numbers are here shown to be erroneous. The present authors place *P. hamiltoni* and a second species, *P. makowskii* Orlowski, 1983, in the same family as *S. thacheri*, rather than in the family Paleomeridae Størmer, 1956, a classification that was based on the assumed presence of 12 abdominal segments (Størmer 1955, 1956; Orlowski 1983). Paleomeridae should therefore be abandoned. We note that some authors (e.g. Jensen 1990, p. 30) have tentatively suggested that *P. hamiltoni* should be assigned to *Strabops*, but we hesitate to do so because of the difference in eye position and telson length. Hou & Bergström (1997) assigned *Neostrabops martini* Caster & Macke, 1952 to the family, but the present authors agree with Dunlop & Selden (1997) that carapace shape is more suggestive of it being a cheloniellid. Arachnomorpha was erected by Heider (1913) to include trilobites and chelicerates, but was expanded by Størmer (1944) to include most non-bivalved Cambrian problematica (e.g. many Burgess Shale and Chengjiang fossils such as *Leanchoilia* Walcott, 1912, *Emeraldella* Walcott, 1912 and *Molaria* Walcott, 1912.

3. Description and discussion

The carapace is separated from the abdomen by a marked line that is considerably less well-preserved than in the holotype, and cannot provide any new information. Abdominal segment boundaries are best preserved on the right side of the specimen (Fig. 1d). The abdomen is distorted, but is highly domed and undifferentiated, as in the holotype. There are two areas where the abdomen has been partially collapsed (stippled in Fig. 1d). The left of these is just left of the axis of the animal and has three lobes with separation similar to those seen in the segments (Fig. 1a). These could be the areas of attachment of three pairs of appendages, which would be appendages 3, 4 and 5. However, it is also possible that they represent poorly-preserved segment boundaries of the collapsed segments (3 through 5). All new information from this specimen relates to the telson, which is short, broad and triangular (tapering posteriorly). Similarities between the telson (Fig. 1c, e) and the twelfth segment of the holotype described by Størmer (1956) suggest the latter to be the anterior two-thirds of the telson, as proposed by Bergström (1971), and coded by Dunlop & Selden (1997) and Anderson & Selden (1997), and confirm that *P. hamiltoni* has only 11 abdominal segments. A line on the dorsal surface of the cast (Fig. 1e) is interpreted as the boundary between the eleventh segment and the telson. The rounded termination of the cast of the telson was originally completely surrounded by coarse sandstone, but the posterior part of the mould was removed during preparation. The presence of 11 abdominal segments in *P. hamiltoni* suggests the twelfth segment reported by Orlowski (1983) in *P. makowskii* is probably an incomplete telson. *Paleomerus hamiltoni* is reconstructed (Fig. 2) from Størmer (1956) and the new information from the specimen described here.

4. Affinities

Cambrian arachnomorph arthropods with 11 abdominal segments include the following taxa: *Alalcomenaeus* Simonetta, 1970 and *Leanchoilia* Walcott, 1912. Both have a 'great appendage', two biramous prosomal appendages and a fan-shaped telson (Bruton & Whittington 1983; Briggs & Collins 1999). *Sanctacaris uncata* Briggs & Collins, 1988 has at least six pairs of biramous prosomal appendages and a fan-shaped

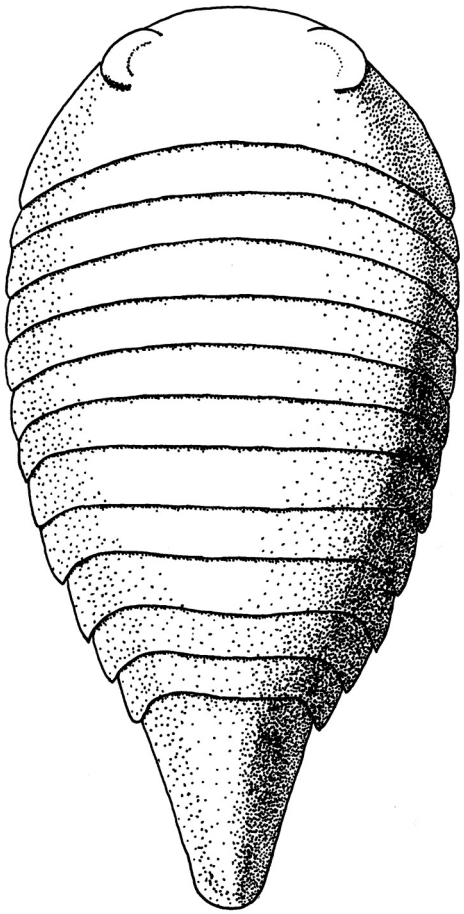

Figure 2 Reconstruction of *Paleomerus hamiltoni*. Complete dorsal view based on the specimen figured herein, combined with those figured by Størmer (1956) and Bergström (1971).

telson. Aglaspidids have four (or five) ?uniramous prosomal appendages (Briggs *et al*. 1979), paired ventral plates and a styliform telson.

Paleomerus hamiltoni is closely related to the poorly known *Strabops thacheri*, with which it shares a short carapace, 11 abdominal segments and a broad conical telson. Appendages of strabopids are unknown, but because of the short length of their carapace, Bergström (1971) suggested that they probably had fewer than seven pairs of prosomal appendages, although the present authors think that even this may be an overestimate. As in most other Cambrian arachnomorph arthropods, the undifferentiated abdomen probably carried a pair of biramous appendages on each segment and the abdominal lateral margins of the holotype suggest that the segments were trilobite-like with appendages, rather than annulate. Dunlop & Selden (1997) concluded that the removal of *Paleomerus* and *Strabops* from the Aglaspidida is supported by the lack of aglaspidid apomorphies (e.g. lack of genal spines) in these forms. This conclusion is supported by the presence of a short, triangular telson in *Paleomerus*, which is in contrast to the long styliform telson of aglaspidids (Hesselbo, 1992). However, they suggest that aglaspidids may be derived from a *Paleomerus*/*Strabops*-like lineage because of the generalised body plan of the Strabopidae. Anderson & Selden (1997, character 22) and Dunlop & Selden (1997, character 12) also concluded that the presence of 11 abdominal segments unites *Lemoneites* spp. Flower, 1968 and the synziphosurines *Weinbergina opitzi* Richter & Richter, 1929 and *Legrandella lombardii* Eldredge, 1974 (also *Paleomerus*, *Strabops* and the aglaspidids in Dunlop & Selden). However, *Lemoneites* spp. is particularly problematic because of the fragmentary nature of the material (R.M., personal observation) and a subsequent study of *Weinbergina* by Anderson *et al*. (1998) has indicated that it has 10 rather than 11 abdominal segments, suggesting that a restudy of *Legrandella* is required. Without further material preserving the ventral structures of strabopids, their phylogenetic position will be difficult to determine.

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