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RAPID COMMUNICATION

A restudy of *Utahcaris orion* (Euarthropoda) from the Spence Shale (Middle Cambrian, Utah, USA)

DAVID A. LEGG*† & STEVE PATES‡

*Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW
‡Department of Zoology, University of Oxford, The Tinbergen Building, South Parks Road, Oxford OX1 3PS, UK

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Abstract

Utahcaris orion Conway Morris & Robison, 1988, from the lower middle Cambrian (Series 3, Stage 5) Spence Shale Member situated in Utah, USA, is redescribed based on a restudy of the original material. Newly recognized features, including ventral lateral eyes, trunk appendages, and a bulbous cephalic shield with subtriangular extension, reinforce similarities with *Sanctacaris uncata* from the middle Cambrian Burgess Shale. Both are assigned to the new family, Sanctacarididae. Sanctacaridids represent the oldest chelicerates. Their ecology and that of their nearest non-chelicerate relatives indicate that Chelicerata were plesiomorphically predatory.

Keywords: Langston Formation, Wellsville Mountains, *Sidneyia*, ambush predation, Chelicerata.

1. Introduction

Burgess Shale-type deposits (BSTs) provide an unrivalled view on early animal groups during the so-called 'Cambrian explosion'. This event is best documented in particularly prolific sites, such as the lower Cambrian Chengjiang biota of China (Hou *et al*. 2004), and middle Cambrian Burgess Shale of Canada (Briggs, Erwin & Collier, 1994); however, numerous other sites with their own unique faunas are known throughout the Cambrian (Hagadorn, 2002), and contain potentially significant components for tracking the progress of the 'Cambrian explosion'. One such deposit, the lower middle Cambrian (Series 3, Stage 5) Spence Shale, located in northern Utah, USA, is situated within the *Glossopleura* Assemblage Zone (Robison, 1976), and is thus marginally older than the Burgess Shale Formation. The Spence Shale contains a diverse biota including algae (Robison, 1991), sponges (Rigby, 1978, 1983), brachiopods (Robison, 1964), eldoniids (Conway Morris & Robison, 1988), stem-molluscs (Babcock & Robison, 1988; Conway Morris *et al*. in press), cycloneuralians (Robison, 1969; Conway Morris & Robison, 1986), deuterostomes (Ubaghs & Robison, 1985, 1988; Sprinkle & Collins, 2006; Conway Morris *et al*. in press), lobopodians (Conway Morris & Robison, 1988), and a variety of arthropods including trilobites (Resser, 1939; Gunther & Gunther, 1981) and non-trilobites. The latter include carapace-bearing arthropods (Robison & Richards, 1981; Briggs & Robison, 1984), megacheirans (Robison, 1991; Briggs *et al*. 2008; Conway Morris *et al*. 2015), xenopods (Briggs & Robison, 1984), and the enigmatic taxa *Meristosoma paradoxum* (Robison & Wiley, 1995) and *Utahcaris orion* (Conway Morris & Robison, 1988).

Utahcaris orion has frequently been compared to *Sanctacaris uncata* Briggs & Collins, 1988, from the Kicking Horse Member of the Burgess Shale Formation (Conway Morris & Robison, 1988; Bousfield, 1995; Paterson *et al*. 2008, 2016), with which it shares a number of features, specifically an elongate, paddle-shaped telson and 11 trunk somites. *Sanctacaris* was recently identified as belonging to the crown-group of chelicerates (Legg, 2014), and thus *Utahcaris* potentially represents one of the oldest representatives of this clade. In order to decipher the relationships of *Utahcaris*, material attributed to this taxon is re-examined.

2. Material and methods

Just two specimens of *Utahcaris orion*, from the Wellsville Mountains in Utah, are known; the holotype, KUMIP (University of Kansas Natural History Museum) 204784 (Fig. 1), collected by Benjamin F. Dattilo from Antimony Canyon, and KUMIP 204785 (Fig. 2), collected by Robert and Nancy Meyers from Miners Hollow. KUMIP 204784 is dorsoventrally compressed and preserves most of the dorsal morphology, including a near-complete cephalon with a phosphatized gut with contents. The smaller individual, KUMIP 204785, is preserved in a lateral-oblique orientation and, like the holotype, possesses a near-complete cephalon and a complete complement of tergites, tipped with an elongate paddle-like telson. Specimens were photographed both wet and dry, under polarized lighting, using a Canon EOS 500D digital SLR Camera with a Canon EF-S 60 mm Macro Lens, which was controlled using the EOS Utility 2.8.1.0 program for remote shooting.

3. Systematic palaeontology

Phylum EUARTHROPODA Lankester, 1904
Subphylum CHELICERATA Heymons, 1901
Family Sanctacarididae nom. nov.

Type genus. Sanctacaris Briggs & Collins, 1988, designated herein.

Other genera. Utahcaris Conway Morris & Robison, 1988, and *Wisangocaris barbarahardyae* Jago, Garcia-Bellído & Gehling. in press.

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†Author for correspondence: david.legg@oum.ox.ac.uk

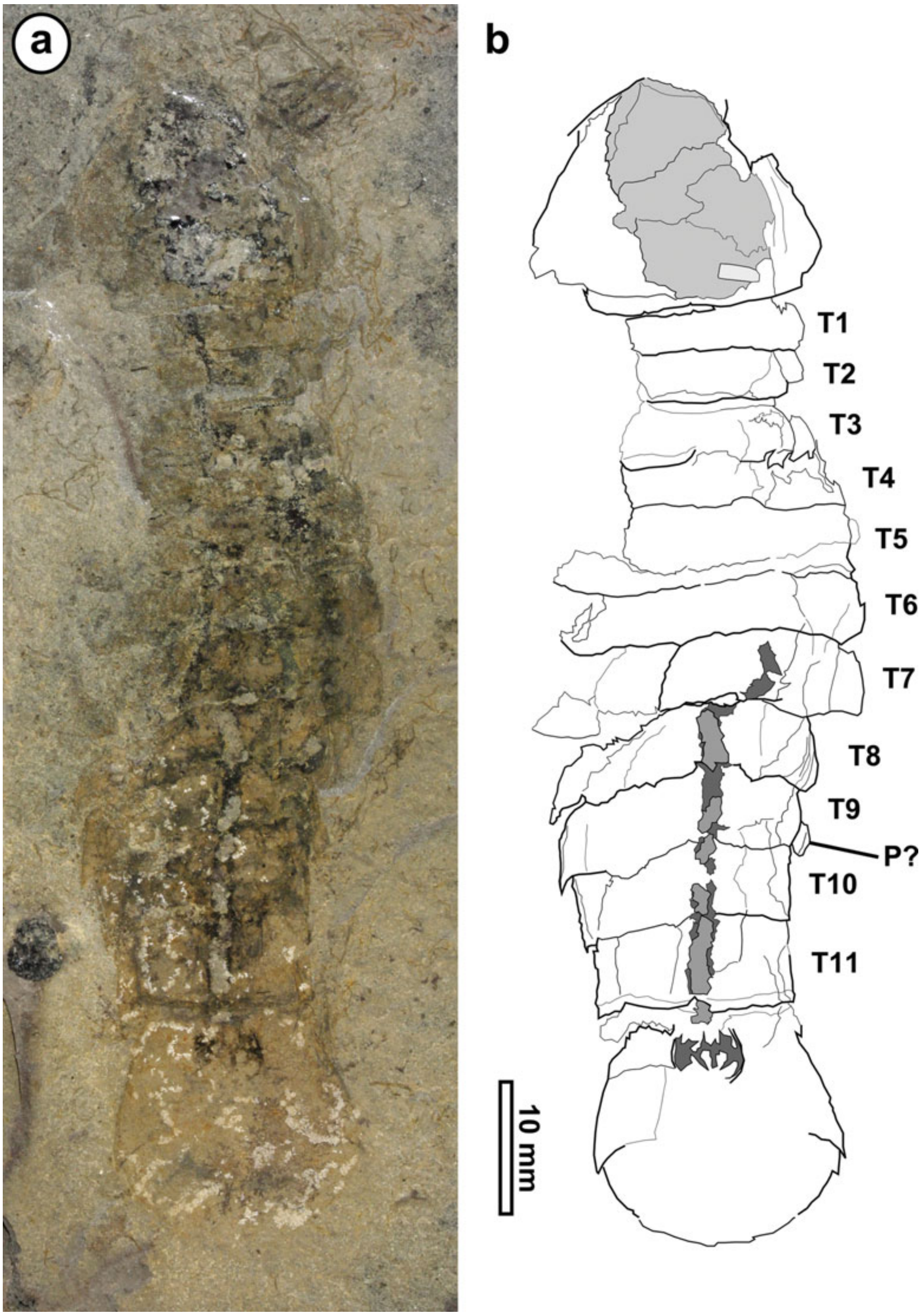

Figure 1. (Colour online) KUMIP 204784a, holotype of *Utahcaris orion* Conway Morris & Robison, 1988. (a) Part, photographed using polarized lighting, and (b) accompanying camera lucida drawing. Gut content is coloured grey. Abbreviations: P? – putative podomere; and T1–T11 – trunk tergites 1–11.

Diagnosis. Arthropods with a highly vaulted and bulbous cephalon possessing expansive lateral margins and ventral eyes situated close to the anterolateral cephalic margin, a trunk composed of 11 trunk segments, the most posterior of which lack extensive pleurae, and a paddle-shaped telson with lateral spines towards the posterolateral margin.

Remarks. As part of a recent restudy of *Sanctacaris*, Legg (2014) conducted an extensive phylogenetic analysis which resolved this taxon as the oldest crown-group chelicerate. To this analysis *Utahcaris* and *Wisangocaris* were added herein using the coding provided in the online supplementary materials (S1 and S2). This analysis resolved *Wisangocaris* and *Utahcaris* as successive sister-taxon of *Sanctacaris*, within the stem-lineage of Euchelicerata (Fig. 3), the clade composed of modern horseshoe crab, arachnids, their most recent common ancestor, and all its descendants. Given the morphological similarities and close relationships of *Utahcaris*, *Wisangocaris* and *Sanctacaris*, as resolved in the phylogenetic analysis, these taxa are assigned to a new family, Sanctacarididae, for which the more completely known taxon *Sanctacaris* is designated type genus.

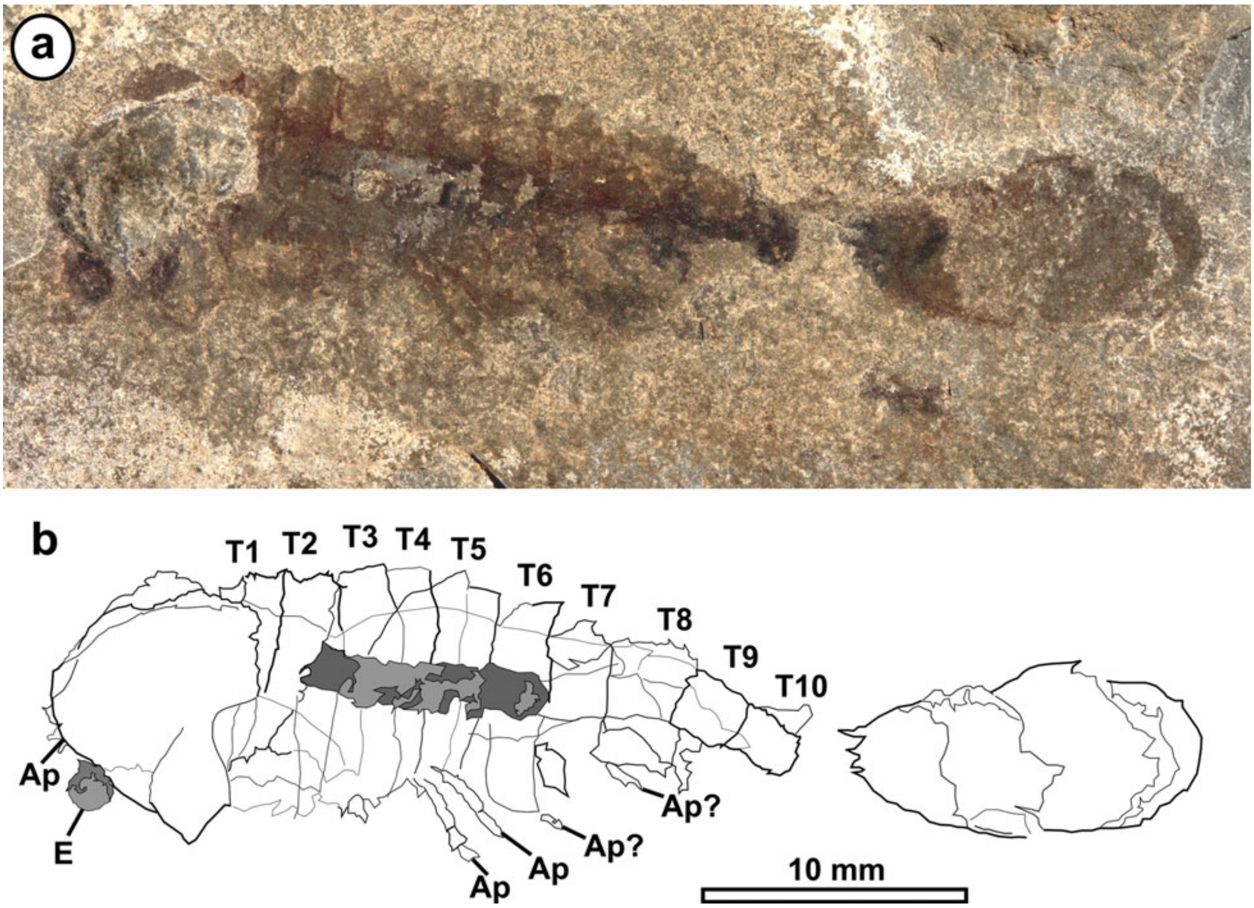

Figure 2. (Colour online) KUMIP 204785a, additional specimen of *Utahcaris orion* Conway Morris & Robison, 1988. (a) Part, photographed using polarized lighting, and (b) accompanying camera lucida drawing. Gut content and eyes are coloured grey. Abbreviations: Ap – appendages; E – eye; and T1–T10 – trunk tergites 1–10.

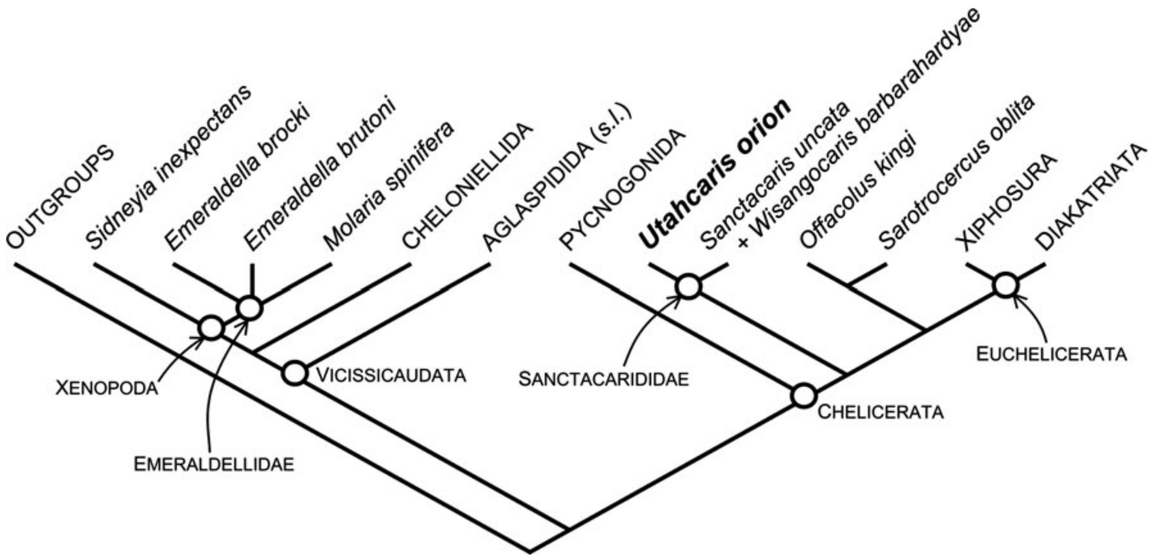

Figure 3. The phylogenetic position of *Utahcaris orion* as resolved in this study. An abbreviated consensus tree of 35 Most Parsimonious Trees of 146.67015 steps (CI = 0.497; RI = 0.867), produced using New Technology Search Options in TNT v. 1.1. (Goloboff, Farris & Nixon, 2008), with implied character weighting ($k = 3$).

Genus *Utahcaris* Conway Morris & Robison, 1988

Type species. Utahcaris orion Conway Morris & Robison, 1988 (by monotypy).

Diagnosis. Sanctacaridid with a cephalic shield that is subtriangular in dorsal aspect, a trunk composed of 11 segments, lacking paired carinae, and a two-segmented abdomen differentiated from the more anterior tergites by a lack of extensive pleurae (emended from Conway Morris & Robison, 1988, p. 30).

Remarks. In its original description, *Utahcaris* was compared to both *Sanctacaris*, and the leanchoiliid megacheirans *Actaeus* Simonetta, 1970, *Alalcomenaeus* Simonetta, 1970, and *Leanchoilia* Walcott, 1912. However, besides the number of trunk tergites, and the presence of a paddle-shaped telson in *Alalcomenaeus*, *Utahcaris* shares few features with leanchoiliids, instead bearing more similarity to *Sanctacaris*. For instance, leanchoiliids lack an abdomen; instead their posterior tergites bear reduced pleurae which become progressively more flexed towards the posterior of the animal. It should be noted that although *Sanctacaris* has at times been allied with megacheiran arthropods (e.g. Budd, 2002), based mainly on the erroneous interpretation of its frontal appendages (see discussion in Legg, 2014), few recent phylogenetic analyses have supported this assignment, instead resolving megacheirans outside crown-group Euarthropoda and resolving *Sanctacaris* within the crown-group amongst vicissicaudates (Legg, Sutton & Edgecombe, 2013) or within crown-group chelicerates (Legg, 2014).

With viccissicaudates, *Utahcaris* shares a posteriorly differentiated abdomen (Ortega-Hernández, Legg & Braddy, 2013). It differs from most, however, in possessing two segments rather than three, as seen in *Sidneyia* Walcott, 1911 (Bruton, 1981), or one, as seen in *Emeraldella* Walcott, 1912 (Stein & Selden, 2012), cheloniellids (Ortega-Hernández, Legg & Braddy, 2013) and *Sanctacaris* (Briggs & Collins, 1988; Legg, 2014). *Utahcaris* also differs from the latter, and *Wisangocaris*, in lacking paired tergal carinae. It is this combination of features which confirms its status as a separate taxon.

Utahcaris orion Conway Morris & Robison, 1988
Figures 1 and 2

Holotype. KUMIP 204784, by original designation.

Paratype. KUMIP 204785, designated herein.

Diagnosis. As for genus.

Description. The majority of new information regarding this taxon was retrieved from KUMIP 204785 (Fig. 2). KUMIP 204784 (Fig. 1) and KUMIP 204785 (Fig. 2) measure 87 mm, and 44 mm, from the anteriormost tip of their cephalic shield to the posteriormost tip of their telson, respectively.

Although incompletely preserved in the holotype, the cephalic shield appears subtriangular in dorsal aspect, with a pointed anterior margin, a gently rounded posterolateral margin and a straight posterior margin with a poorly developed medial emargination (Fig. 1). The centre of the cephalic shield of KUMIP 204784 possesses a slight convexity which may be due to the underlying phosphatized gut content, although it is thought to be a genuine feature based on comparisons with KUMIP 204785, which, although lacking noticeable relief, appears to have a bulbous cephalic shield (Fig. 2); this bulbous region is flanked on either side by subtriangular pleural extension (Fig. 2). An enlarged, circular compound eye is present under the anterolateral margin of KUMIP 204785 (Fig. 2). Although very poorly preserved, the remnants of cephalic appendages can be observed in KUMIP 204785 (Fig. 2).

Eleven trunk segments can be observed in KUMIP 204784 (Fig. 1). Tergites show little overlap and a slight convexity, although the exact extent of both is difficult to determine based on the available specimens, both of which show considerable post-mortem deformation. The trunk of KUMIP 204784 shows noticeable torsion, and the majority of anterior tergite pleura are missing; however, lateral pleura can be observed on the posterior thoracic tergite, namely tergites 8 and 9 (Fig. 1). These pleura are posteriorly flexed with a subtriangular posterolateral margin (Fig. 1). The pleura of the posterior two trunk somites are extremely reduced, with tergite 11 lacking subtriangular pleural extensions altogether (Fig. 1). The two posteriormost somites are further distinguished from the anterior ones in being more elongate, with tergite 11 nearly twice as long as tergite 1. Poorly preserved appendages are present beneath trunk segments 4–7 of KUMIP 204785 (Fig. 2). The presence of gnathobases and the number of podomeres could not be determined.

A simple gut, lacking accessory glands, runs through the length of the trunk, terminating in an anus between segment 11 and the telson (Fig. 1). The paddle-like telson of *Utahcaris* is long, accounting for 20 % of total body length in KUMIP 204784, and 31 % of total body length in KUMIP 204785, subcircular and possesses a strongly curved posterior margin (Figs 1, 2). The posterolateral margins are characterized by subtriangular margins which extend into the telson interior (Fig. 1). A second pair of less prominent spines is present halfway between the last trunk tergite and the more posterior telson spines (Fig. 1).

Discussion. The description of *Utahcaris* presented herein differs from the original of Conway Morris & Robison (1988) in a number of key aspects. Specifically, the original describers found no evidence for lateral eyes or appendages, which, although poorly preserved, give additional insight into the ecology of this taxon (see below). The bulbous nature of the cephalon, with its subtriangular posterolateral extension is recognized for the first time, and along with the anterolateral position of the ventral eyes, further strengthens similarities to the slightly younger *Sanctacaris uncata*. Given the sister-taxon relationship of these taxa, and *Wisangocaris*, as resolved in the phylogenetic analysis herein, this means that these taxa represent the oldest currently named chelicerates.

Remarks. Our restudy of *Utahcaris* revealed a number of previously unrecognized features of KUMIP 204785, specifically regarding the morphology of the cephalon, including its bulbous nature and the presence of ventral eyes under the anterolateral margin, and the presence of appendages, which are otherwise lacking from the holotype.

4. Discussion

A number of features of *Utahcaris*, and other sanctacaridids, indicate they were active predators, or at least scavengers, first and foremost of which is the putative gut content. Identified as fragmented trilobite remains in the original description (Conway Morris & Robison, 1988), phosphatized elements are clearly visible in the cephalic region of *Utahcaris* (Fig. 1). The affinity of these remains could not be deciphered, however, due to the fragmentary nature of this material, although it is almost certainly biogenic and therefore indicative of a durophagous lifestyle. The presence of this material led Skovsted *et al.* (2007) to infer the presence of robust gnathobases in *Utahcaris*, although none were observed in the present study; they are, however, unequivocally present in closely related taxa, namely *Sanctacaris* (Briggs & Collins, 1988; Legg, 2014).

The presence of enlarged lateral eyes, and an elongate paddle-shaped telson, at least in the smaller of the two specimens, is further indicative of an active, potentially predatory, lifestyle. A paddle-like telson, also associated with elongate posterior trunk somites, is observed in a number of taxa thought to represent active and agile swimmers, including pterygotid eurypterids (Plotnick & Baumiller, 1988), and the Cambrian carapace-bearing arthropods *Nereocaris* (Legg *et al*. 2012), *Jugatacaris* (Fu & Zhang, 2011) and *Pectocaris* (Hou, Bergström & Xu, 2004). The combination of a few elongate trunk somites and a flat paddle-like telson is seen in modern crustaceans (Krasne & Wine, 1987), in which it serves to provide thrust for rapid escape from predation; however, in a putatively predatory taxon it may indicate a preference for ambush attack rather than active pursuit of prey.

The presence of a predatory lifestyle in the oldest chelicerates, and their nearest outgroups, namely the vicissicaudates (Legg, 2014) such as *Sidneyia* (Zacai, Vannier & Lerosey-Aubril, in press), indicates that this lifestyle was plesiomorphic for Chelicerata, and has proven so successful that it is maintained by the majority of its members, and may have been instrumental in their origin and proliferation during the 'Cambrian explosion'.

5. Conclusions

This restudy of *Utahcaris orion*, and the discovery of newly recognized features such as ventral marginal eyes, lends further credence to suggestions of sanctacaridid affinities for this taxon and its status as an active predator. Its phylogenetic position, as sister-taxon to *Sanctacaris uncata*, within the euchelicerate stem-lineage, makes *Utahcaris* and *Wisangocaris*, the oldest currently recognized crown-group chelicerates, and suggests a pleiomorphically predatory ecology for this clade.

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Supplementary material

To view supplementary material for this article, please visit http://dx.doi.org/10.1017/S0016756816000789.

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