A new species of the artiopodan arthropod *Acanthomeridion* from the lower Cambrian Chengjiang Lagerstätte, China, and the phylogenetic significance of the genus

Xianguang Hou*, Mark Williams*, Sarah Gabbot, David J. Siveter, Derek J. Siveter, Peiyun Cong, Xiaoya Ma, and Robert Sansom

*Yunnan Key Laboratory for Palaeobiology, Yunnan University, Kunming 650091, China; *Department of Geology, University of Leicester, Leicester LE1 7RH, UK; Earth Collections, Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, UK; Department of Earth Sciences, University of Oxford, South Parks Road, Oxford OX1 3PR, UK; The Natural History Museum, Cromwell Road, London SW7 5BD, UK; University of Manchester, Michael Smith Building, Dover Street, Manchester M13 9PT, UK

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New material of the rare arthropod *Acanthomeridion*, including *Acanthomeridion anacanthus* sp. nov., is described from the lower Cambrian Chengjiang biota, Yunnan Province, China. The material includes a specimen with paired gut diverticulae along the length of the mid-gut that resemble structures in other artiopodan arthropods such as naraoiids. Previous phylogenetic analyses have indicated a petalopleuran/xandarellid affinity for *Acanthomeridion*, but our analysis resolves *Acanthomeridion* outside the main subclades of the Artiopoda (Aglaspididae + Trilobita, Nektaspida, Cheloniellida + Xenopoda, Conciliterga, Petalopleura (including Xandarellida)) as the most basal artiopodan.

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**Keywords**: *Acanthomeridion*; Artiopodan; arthropod; Chengjiang; Cambrian; China

**Introduction**

Well over 200 species have been recorded from the lower Cambrian Chengjiang biota of Yunnan Province, China, with arthropods representing about a third of described species (Hou et al. 2004; Vannier 2007). These include many artiopodan arthropods (*sensu* Ortega-Hernández et al. 2013), a group that includes Aglaspididae + Trilobita, Nektaspida, Cheloniellida + Xenopoda, Conciliterga and Petalopleura (including Xandarellida). The taxonomic status and detailed phylogenetic relationships of many artiodactan taxa are in flux (for example, contrast the position of *Aglaspis* in the phylogenetic trees of Paterson et al. 2010 and Legg et al. 2013), possibly as a result of incomplete evidence of soft-part anatomy; this uncertainty includes *Acanthomeridion*, which was previously known only from a few specimens of the type species *Acanthomeridion serratum* Hou, Chen & Lu, 1989 (Fig. 1). Details of the soft anatomy of *A. serratum* are unknown, and in the absence of clear evidence for its taxonomic affinity Hou & Bergström (1997) established a separate family and order for *Acanthomeridion*.

Here we describe new material of *Acanthomeridion* from the Chengjiang biota, including a specimen with a partially preserved digestive tract, and another with a clear indication of what we interpret as a facial suture on the head shield. We also conduct a phylogenetic analysis of *Acanthomeridion* based on the analysis developed by Ortega-Hernández et al. (2013) to help resolve its wider relationships to other artiopodar arthropods.

**Material and methods**

All of the new material of *Acanthomeridion* recorded here comes from localities in the vicinity of Haikou, Kunming, Yunnan Province (see Hou et al. 2004, fig. 4.4). It comprises three dorsoventrally flattened specimens from Ercaicun, and a single dorsoventrally flattened specimen from Mafang that are referred to *Acanthomeridion anacanthus* sp. nov.; a single specimen from Jianshan, preserved dorsolaterally, that is designated as *Acanthomeridion* cf. *serratum*; and a specimen from Ercaicun described as *Acanthomeridion* from the Chengjiang biota, including a specimen with a scattered coating of red iron oxide (Fig. 2A–G). Type and
figured specimens are housed in the collections of the Yunnan Key Laboratory for Palaeobiology at Yunnan University (numbers YKLP 11112–11116, 11118 and 11119).

In order to help elucidate the digestive system of three specimens that preserve soft anatomy, we used a camera lucida attached to a Wild Heerbrug M10 microscope. The (weak) 3D morphology of specimens was also investigated with High Resolution X-ray Computed Tomography (HRXCT) at Leicester University using an XT225 Metris (Nikon) scanner, but we have not been able to resolve the morphology of the digestive tract using this method. Fossil material was imaged macrophotographically using Nikon Multiphot equipment with Micro-Nikkor lenses, adapted for use with a Canon 5D camera, and a Hitachi S-3600N scanning electron microscope (SEM) (Department of Geology, University of Leicester). Chemical analysis was undertaken using an Oxford INCA 350 EDX system, providing elemental mapping and point-and-ID spectrum. The system operated with a standard voltage of 15 kV; carbon was mapped using 5 kV.

**Preservation**

Specimen YKLP 11112 (see Figs 2B, 3B) was analysed using SEM backscatter and topographic modes. The majority of the fossil, especially towards the posterior and the periphery of the trunk, is preserved as an extremely thin white film, which is oxidized carbon. The red colouration of the fossil is a product of the scattering of iron oxides after pyrite (Gabbott *et al.* 2004; Forchielli *et al.* 2014); these are either anhedral microcrystals or poorly ordered frambooids. However, there are areas of the fossil that retain carbon as black patches of film that are cracked into polygonal shapes. The gut diverticulae appear as repeated black patches (Figs 2B, 3B), and SEM EDX imaging and analyses shows these are comprised of carbon with polygonal cracking and some associated iron oxides. The gut diverticulae do not show any relief, unlike in many naraoiid arthropods from the Chengjiang biota. Thus, in general the preservation of this specimen is typical of other arthropods in the Chengjiang biota, but it has more black carbon film than is evident in most of the arthropods.

**Systematic palaeontology**

*Artiopoda*

*Order incertae sedis*

*Family incertae sedis*

*Genus Acanthomeridion* Hou, Chen & Lu, 1989

*Type species.* *Acanthomeridion serratum* Hou, Chen & Lu, 1989.
Figure 2. Specimens of Acanthomeridion from the Chengjiang biota, from Ercaicun (A–C); Mafang (D, E); Jianshan (F, G). A, C, Acanthomeridion anacanthus sp. nov. A, dorsal view of exoskeleton (holotype YKLP 11116) with genal projection preserved on the left side of the head shield and remnants of the anterior end of the gut (arrowed, and see Fig. 3A); C, dorsal view of exoskeleton (YKLP 11113) with remnants of the anterior end of the gut preserved at the posterior end of the head shield (arrowed). B, Acanthomeridion cf. serratum: dorsal view of exoskeleton (YKLP 11112) with paired gut diverticulae exposed in the mid-gut area (see also Fig. 3B) where the plane of the rock has split through the specimen below the level of the exoskeleton. D, E, Acanthomeridion serratum, dorsal view of exoskeleton (YKLP 11118), and close-up of facial suture and detached free cheek. F, G, Acanthomeridion sp, dorsolaterally preserved specimen (YKLP 11119), entire exoskeleton and close-up of detached free cheek, respectively. Abbreviations: AR, axial region; FC, free cheek; FS, facial suture; GP, genal projection; MF, median furrow; MGD, mid-gut diverticula; PR, pleural region; PS, pleural spine; ToG, trace of gut. Scale bars = 2 mm.
Figure 3. Camera lucida interpretation of dorsal views of three specimens of Acanthomeridion anacanthus sp. nov. from Ercaicun (A, D, E) and a specimen from Mafang (C): A, holotype YKLP 11116; C, YKLP 11114; D, YKLP 11115; E, YKLP 11113. Labelled structures are discussed in the Systematic palaeontology section. B, Acanthomeridion cf. serratum, from Ercaicun, specimen YKLP 11112; the rock has split at a deep level through the specimen revealing anatomical structures beneath the exoskeleton that show a clear coupling between each tergite and a pair of gut diverticulae. This suggests that the number of somites and tergites are coupled in Acanthomeridion. Abbreviations: AR, axial region; GP, genal projection; HS, head shield; MF, median furrow; MGD, mid-gut diverticula; PR, pleural region; PS, pleural spine; T, trunk; ToG, trace of gut; TS, terminal spine. Scale bars = 5 mm.
**Diagnosis.** Artiopodans with a semi-elliptical head shield bearing short genal projections and, from a dorsal aspect, narrow free cheeks. Trunk composed of up to 12 tergites, with no differentiation between trunk and tailpiece, and terminating in a narrow, short or elongate terminal-spine. (Modified from Hou & Bergström 1997.)

*Acanthomeridion anacanthus* sp. nov.  
(Figs 2A, C, 3A, C–E)

**Diagnosis.** Species of *Acanthomeridion* with head shield about one-quarter the length of the body and trunk length twice that of the width. Trunk bears 12 tergites, the first partly covered by the head shield, and is parallel-sided to very weakly tapering posteriorly. The twelfth tergite is small and strongly curved to form a median furrow, from within which a narrow, short terminal spine projects. Each tergite has a pair of short pleural spines.

**Derivation of name.** Greek *an*, ‘without’, and *akanthos*, a prickly plant: alluding to the lack of pronounced pleural spines in the posteriormost tergites.

**Holotype.** Yunnan Key Laboratory for Palaeobiology, YKLP 11116 (Figs 2A, 3A), from Ercai, Haikou area, Kunming region; Yu’an Member, Chiungchussu Formation, *Eoredlichia-Wutingaspis* trilobite Biozone, Nangaoan Stage, lower Cambrian.

**Material.** Three specimens from Ercai and one specimen from Mafang, Haikou, Kunming, Yunnan Province, China.

**Measurements.** Total length of the exoskeleton is between 3.4 and 3.5 cm, and its width is between 1.5 and 1.75 cm. The head shield is between 0.7 and 0.95 cm long and up to 1.75 cm wide.

**Description.** The dorsal exoskeleton lacks biomineralization. The head shield is about one-quarter the length of the body and has a rounded anterior margin and short genal projections. The surface of the head shield is smooth and weakly convex both sagitally and transversely, lacking ornament or features that might represent exoskeleton bulges to accommodate eyes. The trunk has discrete axial and pleural regions and is composed of 12 tergites, the first being partly covered by the posterior margin of the head shield. The trunk tergites are well defined, they overlap each other, and each terminates laterally in a short posteriorly directed pleural spine (best developed in specimen YKLP11114, Fig. 3C). Overall the trunk is parallel-sided to very weakly abaxially convex, though some specimens are very weakly tapered posterior of tergite 7. There is no differentiation between trunk and tailpiece. The terminal tergite is small and strongly curved to form a median furrow, from within which a small terminal spine projects posteriorly (Figs 3D, 4).

**Remarks.** The four specimens of *Acanthomeridion anacanthus* are about twice as long as they are wide (3.4 to 3.5 cm long, and 1.5 to 1.75 cm wide). *Acanthomeridion anacanthus* differs from *A. serratum* by its greater number of trunk tergites (12 versus 11, see Fig. 3A, C) and by lacking the long spine-like pleural elongation of tergite 8, and especially 9 (see Fig. 1).

One specimen referred to as *A. cf. serratum* (Figs 2B, 3B) is narrower and approaches the proportions of *A.
serratum (being 3.4 cm long and 1.3 cm wide; the specimen of *A. serratum* in Figure 1 also has dimensions of 3.4 cm long and 1.3 cm wide). However, *A. cf. serratum* lacks the pleural elongations of tergites 8 and 9.

Hou & Bergstrom (1997, p. 38) described short curved lines occurring from about the mid-length of the head shield in *A. serratum* and extending forwards to the anterior margin; they considered these structures to represent dorsal sutures that defined narrow free cheeks, and this structure is evident in the holotype and other specimens of *A. serratum* (see Hou et al. 1989, fig. 3, pl. 3, figs 1, 2). These features are not evident in our specimens of *A. anacanthus*, possibly because they lie more marginal to the edge of the head shield, or because the plane through which the rock has split through the fossils has not captured these sutures. Similarly, in specimens of *A. serratum* these sutures are not always visible (Fig. 1). Nevertheless, a specimen preserved dorsolaterally and referred to *Acanthomeridion* sp. (Fig. 2F, G) confirms the presence of the suture line, with its free cheek detached from the main head shield, whilst a flattened specimen of *A. serratum* shows the suture line from a dorsal perspective near the edge of the shield, again with the free cheek detached (Fig. 2D, E).

No soft anatomy has previously been reported from *A. serratum*, but in the specimen referred to *A. cf. serratum* there are paired diverticulae along the whole of the mid-gut as far as it is preserved (Figs 2B, 3B). These do not show caeca at their terminations (cf. Vannier & Chen 2002; Vannier et al. 2014). A partial trace of the gut is

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**Figure 5.** Analysis of *Acanthomeridion* using the Ortega-Hernández et al. (2013) data set of artiopodan phylogeny: strict consensus of 35 trees with implied weighting ($k = 2$ following the original authors, length 25.75). *Acanthomeridion* is placed outside the main subclades as the most basal artiopodan.
also preserved in the head of at least two specimens of *A. anacanthus* (see Figs 2A, C, 3A, E), but it is not possible to differentiate four pairs of diverticulae seen, for example, in Cambrian naraoiids (e.g. Vannier & Chen 2002). There is no evidence for the development of an ‘arborescent’-type morphology for the anteriormost diverticulae. One of the specimens of *A. anacanthus* from Ercaicun shows the development of small circular nodes midway along both the ninth and tenth tergites on the left side of the exoskeleton (Fig. 2C, arrowed), but these structures are not observed on the corresponding side of the exoskeleton. The small terminal spine of *A. anacanthus* is only visible in one specimen, YKLP 11115 (Figs 3D, 4).

**Phylogenetic analysis**

A number of key characters remain unknown in *Acanthomeridion*, most notably information about the morphology of the cephalic appendages, the nature of attachment of the hypostome (see Stein et al. 2013, p. 29), and the anatomy of the trunk appendages (e.g. see Ortega-Hernández et al. 2013). Given this, our phylogenetic analysis is tentative, although we have applied cautious coding with respect to missing data so as to minimize biases (Sansom 2015). For our analysis, we resolved *Acanthomeridion* against the data set of artiopodan phylogeny (i.e. trilobitomorphs and vicissicaudates sensu Legg 2015) of Ortega-Hernández et al. (2013). Parsimony searches (1000 random replicates with TBR (tree bisection and reconnection) swapping in TNT (tree analysis using new technology); Goloboff et al. 2008a) found little resolution in the resulting strict consensus aside from monophyly of some subclades. Following the original authors (Ortega-Hernández et al. 2013), implied weighting was applied to mitigate the impact of homoplasy (Goloboff et al. 2008a, b). Reweighted analyses (*k* = 2, Fig. 5) recover a monophyletic Artiopoda comprised of five main clades: Aglaspidida + Trilobita, Nektaspida, Chelonellida + Xenopoda, Conciliterga, and Petalopleura (including Xandarellida). *Acanthomeridion* is placed outside the main subclades as the most basal artiopodan, close to the Chengjiang arthropod *Squamacula*. This placement is supported by the strongly curved posterior tergites and absence of a discrete tailpiece in *Acanthomeridion*, although these, like most other characters, are homoplasic to some degree (65% of 82 characters have a consistency index of less than 1). We recovered similar basal artiopodan placements for *Acanthomeridion* using the data sets of Paterson et al. (2010) and a reduced data set of Legg et al. (2012, i.e. the subset of trilobitomorph taxa and relevant characters). *Acanthomeridion* lacks evidence for eyes, eye slits and overlap of multiple trunk tergites by the head shield, making a petalopleuran/xandarellid affinity unlikely (Legg et al. 2013).

Many of the characters that would shed further light on the phylogenetic placement of *Acanthomeridion* (e.g. the nature of the appendages or the hypostome), and by extension the evolution of artiopodans, are not observable from the new or previously described material. Nevertheless, on the basis of currently available fossil data and phylogenetic data sets, the position of *Acanthomeridion* appears stable as a basal artiopodan. In many ways this is a reflection of its simple morphology relative to other arthropods. Aside from that, the shifting placement of trilobites resulting from the inclusion of *Acanthomeridion* (Fig. 5) indicates that the placement of major clades of artiopodans is very sensitive to taxon inclusion and coding (Legg et al. 2013; Ortega-Hernández et al. 2013; Stein et al. 2013).

The presence of a facial suture in *Acanthomeridion* suggests that this character may have evolved early in the artiopodan clade, and was secondarily lost in other artiopodan taxa, including the Aglaspidida (Fig. 5). In trilobites, which are more derived artiopodans in our analysis, the absence of a facial suture in the earliest trilobites (Olenellina) has been proposed as a primitive character, with later trilobites developing a facial suture (Lieberman 2002). If our interpretation of *Acanthomeridion* is correct, there are at least two possible likely scenarios: (1) that the facial suture was acquired independently in two different groups of artiopodans to facilitate moulting (trilobites and *Acanthomeridion*) and (2) that our placement of *Acanthomeridion* as a basal artiopodan is incorrect, reflecting a lack of anatomical information of its soft-part anatomy. There is a third possibility: if *Acanthomeridion* is basal, that the earliest Olenellina trilobites lost the facial suture, only to reacquire this character in Redlichina. However, this would appear the more unparsimonious and thus unlikely scenario, implying as it does that the facial suture persisted to the base of Trilobita, to then be lost in Olenellina but retained in Eutrilobita.

**Palaeoecology**

By analogy with naraoiids, the mid-gut of *Acanthomeri- don* was probably used for the chemical breakdown of food, as indicated by the serial paired diverticulae (see Vannier & Chen 2002). The Chengjiang seafloor was home to a great variety of epibenthic arthropods (Hou et al. 2004), and trace fossil evidence suggests that the sediment was crawled over and dug into by these animals. It is likely that, as is the case with most Chengjiang arthropods, *Acanthomeridion* lived amongst these epibenthic organisms. The absence of a well-developed visual system in *Acanthomeridion* suggests that it was not an active predator or a pelagic species. Assuming that the diverticulae of *Acanthomeridion* originally terminated in caeca, and given the difficulty of expelling large quantities of mud from guts with this morphological configuration,
Acanthomeridion was more likely a benthic scavenger, and less likely to be a mud-eater (see Vannier & Chen 2002).

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Supplemental data

Supplemental data to support the phylogenetic analyses (see Fig. 5) in this paper can be accessed here

ORCID

Peiyun Cong http://orcid.org/0000-0001-9910-6478
Robert Sansom http://orcid.org/0000-0003-1926-2556

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