Palaeogeography, Palaeoclimatology, Palaeoecology 398 (2014) 4–15

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Cambrian lobopodians: A review of recent progress in our understanding of their morphology and evolution

Jianni Liu [a,*], Jason A. Dunlop [b,1]

[a] Early Life Institute, The Key Laboratory of Continental Dynamics, Department of Geology, Northwest University, Xi'an 710069, China
[b] Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin, D-10115 Berlin, Germany

ARTICLE INFO

Article history:
Received 13 February 2013
Received in revised form 26 April 2013
Accepted 6 June 2013
Available online 15 June 2013

Keywords:
Cambrian
Lobopodians
Evolution

ABSTRACT

Lobopodians are an important group of organisms which appeared during the Cambrian Explosion. The underlying morphology is invariably a worm-like body bearing multiple pairs of legs. Yet in detail these animals preserve a range of morphologies and have attracted much paleontological attention; particularly since this assemblage probably includes the ancestors of living velvet worms (Onychophora), water bear (Tardigrada) and arthropods (Arthropoda). In recent years, knowledge of Cambrian lobopodians has increased dramatically based on numerous new records. However, there have been few comprehensive reviews of these animals since Ramsköld & Chen's study in 1998. In the present paper, new insights into Cambrian lobopodians are presented. The legs of *Aysheaia pedunculata* have a strong attachment with the body, like those of lobopodians in the Chengjiang Fauna. *Hallucigenia fortis* has a pair of eyes, two pairs of tentacles are observed in the 'neck' region while a bivalved head shield is unequivocally lacking. Some new characters for, and the orientation of, *Hallucigenia sparsa* are discussed. Longitudinal wrinkles on the body of *Xenusion auerswalde* are regarded here as putative muscles. *Cardiodictyon sinicum* bears doublure structures at the anterior margin of head and a pair of eye spots; the shape of dorsal plates is also reinterpreted. *Onychodictyon* has a pair of anterior appendages, but no sclerotized head shield. The affinities of *Miraluolishania haikouensis* are clarified and the proposal that *M. haikouensis* is a junior synonym of *Luolishania longicruris* is refuted. The large lobopodians, *Kerygmachela*, *Jianshanopodia* and *Megadictyon* – all with frontal appendages, gill-like limbs and tree-like or lamellate-like branches – may be swimming predators.

1. Introduction

Since the last comprehensive studies of Cambrian lobopodians (e.g. Ramsköld and Chen, 1998; Budd, 1999; Bergström & Hou, 2001), much new morphological information on the Chinese Chengjiang material in particular has come to light; some of it published by Liu et al. (2004, 2006, 2007, 2008, 2011a,b). These data – together with advances in our understanding of other Cambrian lobopodians – are summarized here on a genus by genus basis, including a reinterpretation of several features. Since relationships between the various taxa remain in a state of flux, we present the lobopodians in a largely chronological sequence here based on when the taxa were established.

2. Material and methods

Lobopodian specimens were examined either from the first author's personal collection, or from museum material; in particular from the Smithsonian Institution, Washington (USA), the Geological Museum, Copenhagen (Denmark), and the Museum für Naturkunde Berlin (Germany). These investigations were supplemented by a review of the literature and individual specimens and/or publications are documented in detail below. The fossils were photographed with Olympus camera through the ocular of an Olympus SZX12 stereomicroscope. Drawings were made with a camera lucida on an Olympus SZX9 stereomicroscope. Figures were prepared with Adobe Photoshop CS3 and Coral Draw 11.

3. Results and discussion

3.1. Aysheaia

3.1.1. Aysheaia pedunculata

Aysheaia pedunculata Walcott, 1911 was originally described as a fossil annelid worm from the Middle Cambrian Burgess Shale of Canada. It was subsequently re-interpreted as a velvet worm (Onychophora) – or a close relative thereof – by authors such as Brues (1923), Walton (1927), Hutchinson (1930), Walcott (1931), Whittington (1978) and Robison (1985). It was also compared with tardigrades (Delle Cave and Simonetta, 1975). *A. pedunculata* is a worm-like animal, ranging from 1 to 6 cm in length and about 5 mm in width, bearing ten pairs of clawed,

* Corresponding author. Tel./fax: +86 29 88303706.
E-mail addresses: liujianni@126.com (J. Liu), Jason.dunlop@mfn-berlin.de (J.A. Dunlop).
[1] Tel.: +49 30 2093 8516; fax: +49 30 2093 8528.

0031-0182/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.palaeo.2013.06.008

spiny limbs on the ventro-lateral side of its body. Based on observations of specimens of *A. pedunculata* (specimens 365608 and 83942A) in the Smithsonian Institution, we found one pair of sub-rounded structures per body segment on the dorsal–lateral side of *A. pedunculata* (Fig. 1A–D), which suggests to us that the legs had a strong attachment to the body, similar to those of lobopodians found in the Chinese Chengjiang Fauna such as *Paucipodia* and *Miraluolishania* (see Sections 3.8 & 3.11). The whole morphology of *A. pedunculata* is somehow similar to *Onychodictyon ferox* (see Section 3.6) in that both of them bear tubercles on the trunk and limbs, the lobe-like limbs are short and stubby and the frontal appendages of *A. pedunculata* are similar to feathery, antenniform appendages of '*O. ferox*' (Fig. 1A–D, Ou et al., 2012, figs. 2c–e, see below for a discussion of *Onychodictyon*).

3.2. Hallucigenia

3.2.1. Hallucigenia sparsa

This iconic species was described as *Canadia sparsa* Walcott, 1911 and, like *Aysheaia pedunculata*, was originally interpreted as an annelid worm. Another specimen was illustrated twenty years later (Walcott, 1931). Detailed study by Conway Morris (1977) demonstrated that this material did not belong to *Canadia*, or to the annelids at all. Conway Morris' famous reconstruction showed a rather bizarre animal, walking on spines and with dorsal tentacles interpreted as a feeding apparatus. He named the new genus *Hallucigenia* because of its 'dreamlike' appearance and also in recognition of its uncertain affinities. The subsequent discovery of similar-looking lobopodians in the exceptionally preserved Lower Cambrian Chengjiang Fauna of China (see below) suggested that the previous reconstruction was upside down: the spines of *H. sparsa* were actually designed to protect the dorsal surface of the animal. New data showed that the supposed tentacles represented just one row of a series of paired legs; the other row being buried in the matrix (cf. Ramsköld and Hou, 1991; Ramsköld, 1992). The anteroposterior orientation was also reversed, with the former swollen 'head' interpreted as possible decay fluids seeping from the body (Ramsköld, 1992).

Based on observations of specimens of *H. sparsa* in the Smithsonian Institute, we can largely accept the morphological description of Conway Morris, albeit with the orientation sensu Ramsköld. However, the location of first pair of legs in *H. sparsa* is still debatable. Ramsköld (1992) recognized three pairs of tentacles in the 'neck' region, with no corresponding legs below the first pair of spines. Later Ramsköld and Chen (1998) proposed that there are two pairs of tentacles in the 'neck' region while the third pair of tentacles represents the first pair of legs and in turn corresponds to the first pair of spines. Obviously, the problem is which (and where) are the first pair of legs?

Morphologically, the three pairs of tentacles are much more slender than the legs and they lack annulations or distal claws. Thus the third pair of tentacles should probably not be treated as the first pair of legs. However, topologically each pair of spines corresponds with a pair of legs, and in this scenario the third pair of tentacles would indeed correspond with being the first pair of legs, since they are located

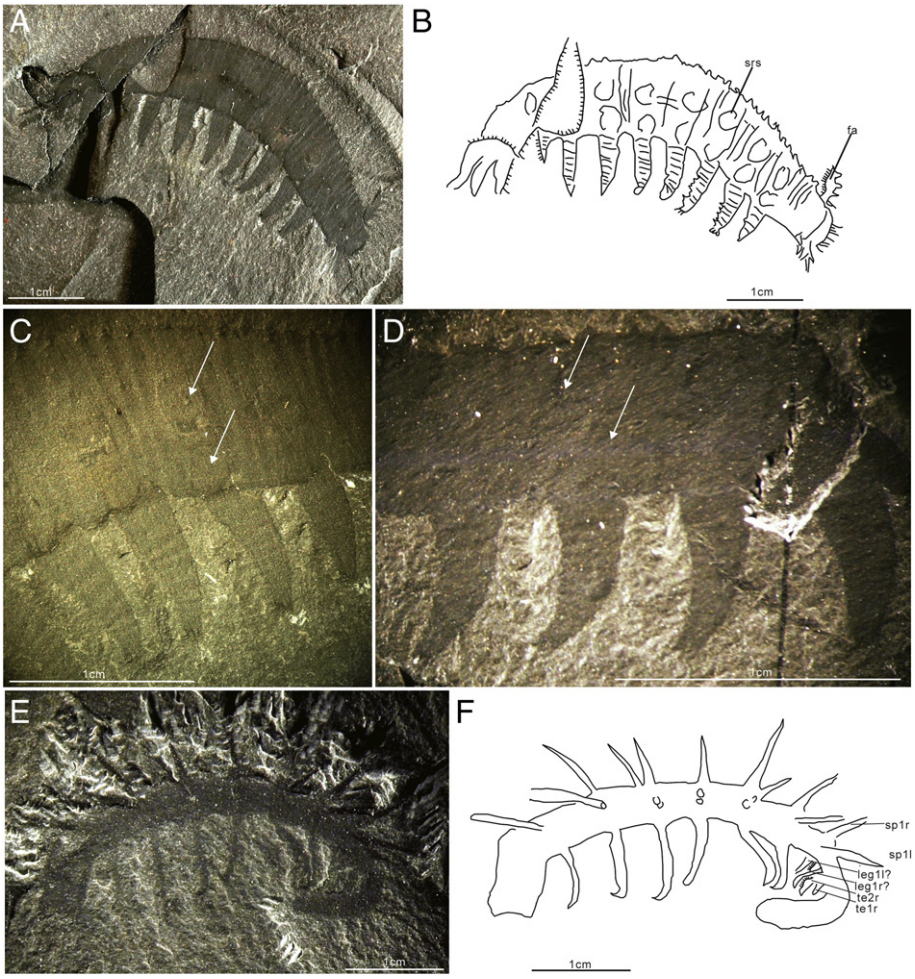

Fig. 1. *Aysheaia pedunculata* Walcott, 1911 and *Hallucigenia sparsa* Conway Morris, 1977, from Burgess Shale. A. Complete specimen of *A. pedunculata* 365608 with one pair of sub-rounded structures and a pair of frontal appendages. B. *Camera lucida* drawing of specimen 365608. C, D. Enlargement of specimens 365608 and 83942A, arrows indicate sub-rounded structures. E. Specimen of *H. sparsa* 198658. F. *Camera lucida* of specimen of *H. sparsa* 198658; showing the three pair of tentacles. Abbreviations are as follows: fa: frontal appendages; sp.: spine; spl: the left spine; spr: the right spine; srs: sub-rounded structures; te: tentacle.