An Early Cambrian stem polychaete with pygidial cirri

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The oldest annelid fossils are polychaetes from the Cambrian Period. They are representatives of the annelid stem group and thus vital in any discussion of how we polarize the evolution of the crown group. Here, we describe a fossil polychaete from the Early Cambrian Sirius Passet fauna, Pygocirrus butyricampum gen. et sp. nov., with structures identified as pygidial cirri, which are recorded for the first time from Cambrian annelids. The body is slender and has biramous parapodia with chaetae organized in laterally oriented bundles. The presence of pygidial cirri is one of the characters that hitherto has defined the annelid crown group, which diversified during the Cambrian-Ordovician transition. The newly described fossil shows that this character had already developed within the total group by the Early Cambrian.

Keywords: Annelida; Polychaeta; Cambrian; fossil; pygidial cirri

1. INTRODUCTION

Polychaetes (Annelida) are common constituents of modern marine habitats. With their distinctive segmented body plan and lateral appendages, called parapodia, which usually have two bundles of chitinous bristles (neuro- and notochaetae), they display several modes of life, for example, as epibenthic predators and scavengers, infaunal burrowers, sessile filter feeders and pelagic predators and planktotrophs [1]. The clitellates, which include the more familiar earthworms and leeches, evolved within the annelids and have invaded most freshwater and terrestrial habitats. Annelid cirri (polychaete with pygidial cirri on the part (figure 1), Geological Museum of Copenhagen, MGUH 29288. Paratype: part and counterpart (electronic supplementary material, figure S1), MGUH 29289.

(c) Diagnosis

Annelid with biramous parapodia, each ramus containing seven to 10 laterally oriented capillary chaetae. One pair of pygidial cirri present.

2. SYSTEMATIC DESCRIPTION
crown group Lophotrochozoa Halanych et al. 1995 stem group Annelida Lamarck 1909 Pygocirrus butyricampum gen. et sp. nov.

(a) Etymology

Pygo: for pygidium (Latin), terminal body region—and cirrus: thread, used for a tendril-like appendage in zoology.

This species is named in honour of Dr Nicholas Butterfield (Department of Earth Sciences, Cambridge University, UK) in recognition of his work on Cambrian metazoan palynomorphs. Butyrum: butter and campus: field; butyricampum is a noun in apposition.

(b) Locality and material

Sirius Passet, North Greenland, Lower Cambrian (possibly Atdabanian [14]). Collected from the exposure of a very fissile dark shale unit within the Buen Formation, with abundant fossils preserved as two-dimensional reflective films. Holotype: part and counterpart (figure 1), Geological Museum of Copenhagen, MGUH 29288. Paratype: part and counterpart (electronic supplementary material, figure S1), MGUH 29289.

(c) Diagnosis

Annelid with biramous parapodia, each ramus containing seven to 10 laterally oriented capillary chaetae. One pair of pygidial cirri present.

(d) Description

The holotype is a posterior fragment, lacking the head and an unknown, but presumably small, number of anterior chaetigers. The preserved body is 14 mm long excluding pygidial cirri, and 1.2 mm wide without parapodia, 1.7 mm with parapodia and 5.3 mm with parapodia and chaetae. A total of 14 chaetigers are present. The median body region is straight-sided and with preserved pygidial cirri, and discuss its implications for our understanding of evolution towards the annelid crown group.

Mazon Creek fauna [8–10] and the largely undescribed Cretaceous Hakel polychaete fauna [11,12].

The oldest known fossil polychaete is Phragmochaeta canicularis Conway Morris and Peel, 2008 from the Early Cambrian Sirius Passet fauna [13]. In this paper, we describe a new genus and species, Pygocirrus butyricampum gen. et sp. nov., from the same locality and with preserved pygidial cirri, and discuss its implications for our understanding of evolution towards the annelid crown group.
The paratype is a median fragment with 10 chaetigers; it is 11.3 mm long, 1.7 mm wide lacking well-preserved parapodia and 9.5 mm wide with parapodia and chaetae. Neither specimen shows any sign that dorsal cirri, ventral cirri or aciculae were present. The paratype is more decayed than the holotype: some of the parapodia are partially detached from the body and show no evidence of aciculae.

3. DISCUSSION
The presence of pygidial cirri in *P. butyricampum* is unique among annelids known from the Cambrian Period. Therefore, although the species description provided here is incomplete (the anterior end is unknown), this form marks the origin of an important character for our understanding of annelid evolution. Pygidial cirri are widely distributed among modern annelids and have been considered one of the key autapomorphies of polychaetes [15,16]. The consistent result that clitellates (which lack pygidal cirri) are derived from within the polychaetes [16–19] indicates that this feature is one of the characteristics of the phylum as a whole.

Understanding the phylogenetic relationships among major subclades of annelid polychaetes has been problematic owing to major conflicts between molecular systematics and morphology, e.g. [20], although recent published research displays a high degree of agreement between the two [19]. This contribution supports the recognition of two major groups. The first is Sedentaria (including the Clitellata), which contains groups that have grooved peristomial palps for food collection or are infaunal burrowers lacking large external head appendages (broadly conforming to Canalipalpata + Scolecida, both *sensu* [21], as well as Clitellata). The second major group is Errantia (as with Sedentaria, originally introduced in De Quatrefages [22]), most members of which have non-grooved, sensory prostomial palps and are often motile surface dwellers; this group consists mainly of the Aciculata, *sensu* [21], with the addition of Orbiniidae. The exact position of some groups remains problematic in this analysis, such as the ectoparasitic Myzostomidae and the Chaetopteridae, which are placed at the base of the annelids, below the sipunculans. Other studies that relied on less homoplastic characters such as rare genomic changes [23] have indicated that Sipuncula is the sister group of Annelida, as a separate phylum [18,24], which suggests that the position of myzostomids and

Figure 1. *Pygocirrus butyricampum* sp. et gen. nov. Holotype MGUH 29288. From Sirius Passet, North Greenland, Early Cambrian. (a) Part and (b) corresponding interpretive camera lucida drawing; numbering denotes individual parapodia. (c) Counterpart and (d) corresponding interpretive camera lucida drawing. (e) Parapodium, detail of area indicated in (b). (f) Two chaetal bundles emerging from a parapodium, detail of anterior area indicated in (d). (g) The pygidial cirri on the counterpart, detail of posterior area indicated in (d). Scale bars, (a–d) 5 mm; (e–g) 1 mm.
chaetopterids below sipunculans is erroneous: they exhibit features that suggest an aciculate and canalipalpate affinity, respectively. This would also be in agreement with the fossil evidence, as crown group sipunculans are known from the Early Cambrian Chengjiang fauna of South China [25], which is similar in age to the Sirius Passet fauna. Thus, the primitive morphology of crown annelids can be reconstructed as an animal with anterior non-grooved palps, pygidial cirri, nuchal organs and parapodia that contain two bundles of simple chaetae [15,16].

The diverse polychaete fauna from the Burgess Shale includes a number of stem annelids [6]. These forms all have elaborate, usually biramous, parapodia with simple chaetae and many forms exhibit anterior (presumably prostomial) palps and thus conform to the expected presence of these characters in the ancestral annelid, except that they all lack pygidial cirri. The fossil Cambrian annelids therefore enable us to polarize the morphology of the ancestral annelid body plan as a surface dwelling errant worm with palps and biramous parapodia, but without compound chaetae or aciculae. None of these forms exhibit unequivocal pygidial cirri like those in P. butyricampum [6]. A cladistic analysis (electronic supplementary material, S2) finds that P. butyricampum resolves at a node above Canadia from the Burgess Shale in a polytomy with the crown group. While nothing is known about the anterior region of this new species, we predict that it also possesses sensory palps and might be located in a more derived position on the annelid stem lineage than the forms hitherto known from the Cambrian (figure 2). While it could be argued that it belongs to the crown group, we hypothesize that it diverged further down the lineage subverting the crown group. It has been argued that the crown group diverged in the Late Cambrian/Early Ordovician [6,26].

Continued studies of annelids from the Cambrian Period will provide more detail to our emerging picture of the appearance of apomorphic morphological characters among forms preceding the origin of the crown group near the Cambrian–Ordovician transition.

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