

A Cambrian fossil from the Chengjiang fauna sharing characters with gilled lobopodians and radiodontans

Jianni Liu (✉ liujianni@126.com)

Early Life Institute <https://orcid.org/0000-0001-6326-3180>

Jason A. Dunlop

Museum für Naturkunde - Leibniz-Institut für Evolutions- und Biodiversitätsforschung

Michael Steiner

Freie Universität Berlin

Degan Shu

Northwest University

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Abstract

Background: Lobopodians are worm-like animals with simple legs. Probably representing a grade of organization, rather than an explicit clade, some lobopodians are thought to have given rise to both Euarthropoda and Onychophora (velvet worms). Another subset has been referred to as gilled lobopodians, and are characterized by flap-like appendages along the trunk and large, raptorial forelimbs. These animals probably include the ancestors of another important Cambrian group, the Radiodonta: large predatory or filter-feeding stem-arthropods such as *Anomalocaris*.

Results: *Parvibellus atavus* gen. et sp. nov. from the Early Cambrian Chengjiang fauna of China is a small fossil preserving a distinct cephalic region bearing a pair of lateral projections and a circular, ventral mouth. The trunk bears eleven pairs of flap-like appendages and a short pair of terminal projections. A circular ventral mouth is also seen in Radiodonta and in some gilled lobopodians. *Parvibellus atavus*, gilled lobopodians and radiodontans also share the character of flap-like appendages along the trunk. However, the new fossil differs from radiodontans and gilled lobopodians by its small size and the absence of enlarged and/or raptorial frontal appendages. It also differs from gilled lobopodians in lacking ventral lobopod limbs, and from radiodontans in lacking stalked eyes.

Conclusions: *Parvibellus atavus* expresses a unique combination of characters among Cambrian arthropods, and could be part of an early radiation of nektonic stem-Euarthropoda. Lobopodians have emerged as a diverse grade of proto-arthropods ('worms with legs'), walking on the substrate of the early Palaeozoic seas. The new fossil hints at a similarly diverse fauna of nektonic (swimming) stem-group arthropods in the Cambrian, from which gilled lobopodians and radiodontans may have evolved.

Background

Cambrian fossils offer unique insights into the early stages of animal evolution. Two groups of particular significance, both of which first appear in the Cambrian, are lobopodians and radiodontans. Lobopodians have been characterised as 'worms with legs' and are thought to include the ancestors of both the modern velvet worms (Onychophora) and probably arthropods too (Euarthropoda). For overviews see, e.g. Liu & Dunlop [1] and Smith & Ortega-Hernández [2], and references therein [1, 2]. A remarkable lineage belonging to the euarthropod stem-group is the Radiodonta, which is usually characterised by a ring-like mouth (or oral cone)-albeit absent in some taxa [3, 4]-a pair of large and sometimes raptorial frontal appendages, and a series of flaps along the body which are presumed to have been used for swimming [5]. Some radiodontans achieved body lengths of more than two metres [6], rendering them among the largest Early Palaeozoic animals. Based on the armature of the frontal appendages and evolutionary trends from active predation through to suspension feeding has been proposed [7, 8].

Other genera of Cambrian stem-group euarthropods such as *Opabinia* Walcott, 1912 from the Burgess Shale of Canada, and *Kerygmachela* Budd, 1993 and *Pambdelurion* Budd, 1997 from the Sirius Passet of Greenland, have been referred to as gilled lobopodians. They could represent transitional forms between

the lobopodian grade of organisation and the radiodontans [9–12]. Here, we describe a new fossil from the Early Cambrian Chengjiang fauna of China revealing a combination of characters consistent with a lineage which may have been close to the origins of gilled lobopodians and/or radiodontans.

Results

Systematic palaeontology

Lower stem-EUARTHROPODA *sensu*[12]

PARVIBELLUS gen. nov.

Type and only species

Parvibellus atavus gen. et sp. nov., by monotypy.

Diagnosis

Cephalic region subcircular with paired lateral projections and a large circular ventral mouth. Cephalic region clearly differentiated from trunk, which bears eleven pairs of suboval lateral flaps generally decreasing in sized from anterior to posterior; trunk terminating in a short pair of projections.

Derivation of name

From the Latin *parvus* (small) and *bellus* (cute) in recognition of its size and engaging appearance.

Parvibellusatavus gen. et sp. nov.

(Figs. 1–2)

Diagnosis

As for the genus.

Derivation of name

From the Latin *atavus* (ancestor), referring to its great age and the possibility that other nektonic stem-euarthropods could have evolved from this body plan.

Holotype and only known specimen

ELI-EJ 048A/B, part and counterpart. From the Chengjiang Biota, Erjie, Haikou, Yunnan, south-western China. Early Cambrian (Series 2, Stage 3), from the Yu'an-shan (Heilinpu) Formation (*Wutingaspis-Eoredlichia* Zone).

Description

Complete fossil in ventral view. Total body length 5.25 mm. Body clearly divided into a subcircular cephalic region (length 1.18 mm, maximum width 1.38 mm) and a longer trunk (length 4.07 mm). Cephalic region with paired projections emerging from anterior third and directed laterally and slightly posteriorly. Lateral projections 0.51 mm long, basal width 0.26 mm, tapering slightly from proximal to distal. Ventral surface of cephalic region dominated by large, circular mouth region. Mouth area consists of two circles, both composed of rings of plates; diameter of outer ring 0.6 mm, of inner ring 0.18 mm (Figs. 2,4B). About ten plates in outer ring and several tiny plates in inner ring, but plates are not well preserved. Trunk width ca. 1.03 mm, preserving hints of transverse segmentation and possible median gut trace. Trunk mostly straight, bending slightly to the left posteriorly (Fig. 1). Trunk bears eleven pairs of flap-like projections along its entire length. Individual flaps suboval to subtriangular in outline; transition from trunk to flap indistinct, but flap length ranging from ca. 0.82 mm to 0.27 mm. Trunk flaps 3–4 largest, with subsequent flaps becoming successively smaller towards posterior end (Figs. 1; 4A,C). Anterior pair of flaps separate from the rest and project more laterally. Other flaps orientated postero-laterally and overlapping slightly. Disposition of the flaps gives the entire trunk a broadly oval outline in overview; maximum preserved width of entire animal ca. 2.37 mm. Trunk terminates in a pair of short projections (left one mostly missing), or furcae, length 0.25 mm (Figs. 1; 4A,C).

Discussion

The preserved morphology of *Parvibellus atavus* gen. et sp. nov. appears to be unique among the animals found so far at Chengjiang, and from comparable Cambrian to Ordovician Lagerstätte. In overview, the fossil is fairly small (length ca. 5 mm), with a distinct cephalic region bearing a single pair of tapering lateral projections (Fig. 1). The mouth is circular, possibly formed from circlets of plates, and located ventrally in the middle of the cephalic region (Fig. 2). Any plate dentition is equivocal. There is no evidence that the lateral projections represent stalked eyes, i.e. they are not bulbous at the tips, and these same projections are neither articulated into limb podomeres nor enlarged or raptorial with either spines or setae. A sensory function as antennae seems plausible. The trunk expresses at best only weak ventral segmentation, but clearly bears eleven pairs of flap-like appendages (Fig. 1A) along its length with the flaps often overlapping slightly, especially towards the posterior end. In life these flaps probably sloped below the flap behind it, a condition also seen in, e.g., the radiodontan *Anomalocaris* Whiteaves, 1892 where it may have been an adaptation for swimming [5] through enabling the entire lateral body margin function as a single fin flap. In the new fossil there is no evidence for ventral leg-like appendages (i.e. lobopods) associated with these flaps. The trunk terminates in a pair of short projections.

A possible interpretation of this fossil is an early instar of a radiodontan in which the circular ventral mouth and flaps along the trunk are present, but the stalked eyes and raptorial frontal appendages have not yet developed. Arguing against this is the fact that unequivocal juvenile radiodontans such as the ca. 18 mm long specimen of *Lyrarapax unguispinus* Cong et al., 2014 described by Liu et al. [13] resemble adults (cf. [3]) and have fully developed stalked eyes and spiny frontal appendages. If the new fossil were a juvenile radiodontan, it would imply a fundamental shift in their morphology during early post-embryonic development. Lobopodian affinities also appear unlikely as the fossil lacks an elongate, worm-

like body. The closest match among the known lobopodians would be *Aysheaia pedunculata* Walcott, 1911 which also has laterally projecting (albeit here branching) frontal appendages and ten pairs of fairly broad lobopod limbs [1, 14]. By contrast, the trunk appendages of our new fossil appear flap-like (Fig. 1), with a degree of overlap in life typical for a nektonic animal (see above), and are thus inconsistent with a function as walking appendages. Furthermore, none of the Early Palaeozoic lobopodians are known to have a ventral mouth [1], although it should be noted that a mouth in this position is present in modern velvet worms (Onychophora).

Comparisons with gilled lobopodians and radiodontans

The circular ventral mouth consisting of two putative rings, together with the flap-like appendages along the trunk could support affinities with radiodontans. Budd [9] recognised an 'AOPK' group comprising *Anomalocaris* (a radiodontan), plus the gilled lobopodians *Opabinia*, *Pambdelurion* and *Kerygmachela*. These taxa share the presence of lateral lobes and enlarged frontal appendages. Several subsequent studies also recovered gilled lobopodians close to Radiodonta ([7, 15]; [6]: supplementary data), Ortega-Hernández [12] noted that the gilled lobopodians probably represent a grade, rather than a clade, and that within this assemblage the position of the mouth may have shifted from an anterior position (*Kerygmachela*) to a ventral position (*Pambdelurion*, Radiodonta).

Also important are the trunk appendages. *Parvibellus atavus* gen. et sp. nov. reveals eleven pairs of flaps (Fig. 1A), exactly matching the count in *Pambdelurion* and *Kerygmachela* [9, 16] and at least some radiodontans where the complete body is known [6, 17]. Other radiodontans have been described with eight to ten pairs of trunk flaps [3, 8, 18], while *Opabinia* has fifteen. Additionally, *Opabinia*, *Pambdelurion* and *Kerygmachela* have all been interpreted as having both lateral flaps and lobopod limbs [9, 10]—hence the name gilled lobopodians—although at least in *Opabinia* the lobopod limbs are less obvious and have not been universally accepted [19]. Radiodontans were traditionally assumed to have lost the lobopod limbs and retained only the flaps. Van Roy et al. [6], see also [11], proposed that radiodontans actually possessed both dorsal and ventral flaps: the dorsal flaps homologous with the flaps of the gilled lobopodians, the ventral flaps homologous with their stubby lobopodian limbs. In this hypothesis these dorsal/ventral structures may eventually have evolved into the typical arthropod biramous limb ([6]: Fig. 4).

Affinities of *Parvibellus*

So where could *Parvibellus atavus* gen. et sp. nov. fit into these evolutionary scenarios? A cephalic region bearing a single pair of appendages suggests it belongs to the lower stem-Euarthropoda *sensu* [12]. As noted above, the circular ventral mouth and eleven pairs of lateral flaps are strongly reminiscent of radiodontans, and similar flaps are also seen in gilled lobopodians. A ventral mouth is also present in *Pambdelurion* [20]. The cephalic projections in the new fossil are primarily orientated laterally and are not demonstrably raptorial. In this sense they differ from the more anteriorly directed and spiny frontal appendages of at least *Pambdelurion*, *Kerygmachela* and the radiodontans; *Opabinia*, by contrast, has a

proboscis. There is no evidence in the new fossil for stalked eyes projecting laterally as in radiodontans. *Pambdelurion* and *Kerygmachela* have been reconstructed without eyes [9, 16], while *Opabinia* has an unusual pattern of five stalked eyes on the dorsal surface. The dorsal surface of the new fossil, and any eyes it may have borne, remains equivocal. Finally, at 5 mm in body length the new fossil is noticeably smaller than both the gilled lobopodians (*Opabinia* ca. 7 cm, *Pambdelurion* ca. 29 cm, *Kerygmachela* ca. 18 cm) and the radiodontans (ca. 20 cm as adults up to more than 2 metres).

One solution would be to place the new fossil as sister-group to the clade encompassing the gilled lobopodians and the radiodontans: the 'AOPK' group *sensu* Budd [9] (Fig. 3A). This entire lineage could be defined by the acquisition of lateral flaps and, presumably, a shift from walking to swimming as the primary mode of locomotion. The gilled lobopodians and radiodontans could be further characterised by their larger body size and a probably predatory lifestyle facilitated by the development of a large, raptorial forelimbs. The implication would be that the lateral cephalic projections in the new fossil are homologous with the radiodontan frontal appendages. The problem with this hypothesis is the apparent absence of lobopodian limbs in *Parvibellus atavus* gen. et sp. nov. Either lobopod limbs were present in the new fossil, but have not been preserved, or there were at least two independent losses and/or transformations (*sensu* Van Roy et al. [6]) of these lobopod appendages. Placing the new fossil higher in the tree as, for example, sister-group to Radiodonta (Fig. 3B), could be reconciled with only a single loss of the lobopod limbs, but would require a reversal with respect to the enlargement and modification of the frontal appendages.

Conclusions

The present material does not allow us to unequivocally resolve the phylogenetic position of *Parvibellus atavus* gen. et sp. nov. Further discoveries may reveal other taxa with character combinations bridging the gap between lobopodians and radiodontans, and this may help in placing the new fossil more robustly. The important message here is that there were small, swimming arthropods in the Chengjiang biota (Fig. 4) with a fairly simple grade of organisation from which other, more complex, body plans could have evolved. Just as lobopodians seem to have been a diverse grade of animals with walking appendages associated with several individual morphologies [1], so there may have been a similar nektonic grade of lower stem-group arthropods in the Early Cambrian whose diversity and relationships remain to be explored.

Methods

The new specimen was studied under a Leica stereomicroscope M125 and drawn with a *camera lucida* attachment. Both low angle light and immersion in alcohol proved useful for resolving details. Energy-dispersive spectroscopy (EDS) analyses of the specimen without coating were conducted on a ZEISS-Supra40VP environmental scanning electron microscope with an Inca(EDS) system and X-max 50 mm² detector at the FU Berlin. Brightness/contrast and the tone of all images were refined by optimizing the levels in Adobe Photoshop CC 2014. The figures were prepared with Coral Draw X7. Systematic

terminology follows Ortega-Hernández [12]. Panarthropoda refers to a clade including Euarthropoda, Onychophora and Tardigrada. Euarthropoda *sensu* Lankester, 1904 consists of the clade including the most recent common ancestor of extant chelicerates, myriapods, and pancrustaceans and all of its descendants, to the exclusion of Onychophora and Tardigrada.

Abbreviations

ce: cephalic region; cm: circular mouth; flp: flap-like projections; fu: furcae; ir: inner ring; lp: lateral projections; or: outer ring; pl: plates; tr: trunk;ts, trunk segmentations.

Declarations

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Availability of data and materials

The datasets supporting the conclusions of this article are included within the article. The fossils are deposited in the Early Life Institute (ELI) of the Northwest University, Xi'an, China under the repository number EJ 048A/B.

Authors' contributions

JL and DS collected and prepared the fossils, JL and MS took the SEM images, and JL and JAD wrote the manuscript. JL made the camera lucida drawings and photographed the specimens. All authors contributed to data interpretation and manuscript writing. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

Author details

¹State Key Laboratory of Continental Dynamics and Shaanxi Key Laboratory of Early Life and Environment, Department of Geology, Northwest University, Xi'an, 710069, PR China

²Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity at the Humboldt University Berlin, D-10115 Berlin, Germany

³Department of Earth Science, Freie Universität Berlin, D-12249, Berlin, Germany

⁴School of Earth Sciences and Resources, China University of Geosciences (Beijing), 100083, PR China

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Figures

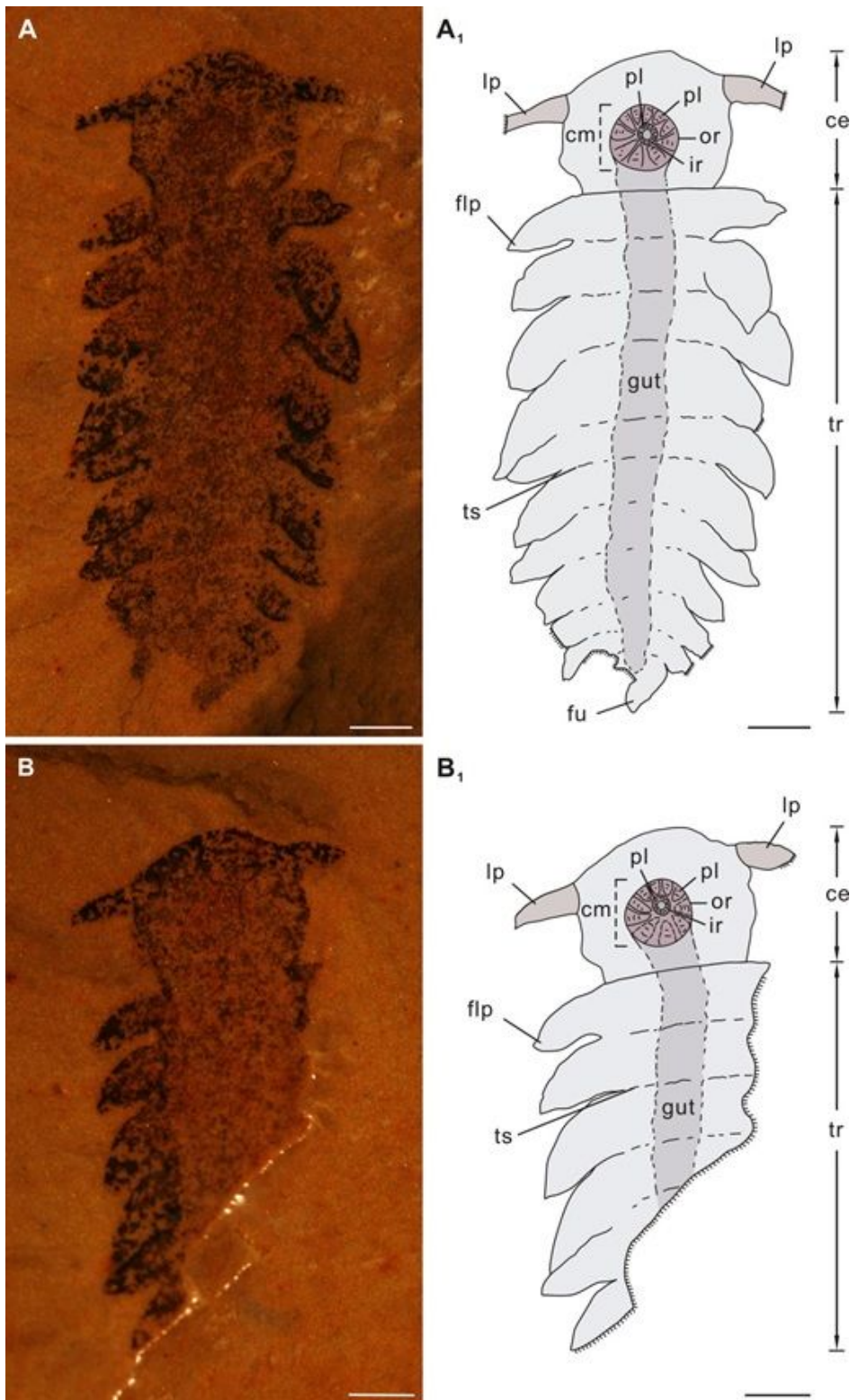


Figure 1

Parvibellus atavus gen. et sp. nov. Holotype (ELI-EJ 048A/B) and only known specimen of a new lower stem-euarthropod from the Chengjiang fauna of China preserved in ventral view, revealing a distinct cephalic region with lateral projections and a circular ventral mouth and a trunk with eleven pairs of flap-like appendages. A and A1 Part of a near-complete specimen (ELI-EJ 048) and interpretative drawing. B and B1 Counterpart (mirrored) and interpretative drawing. Scale bars 0.5 mm.

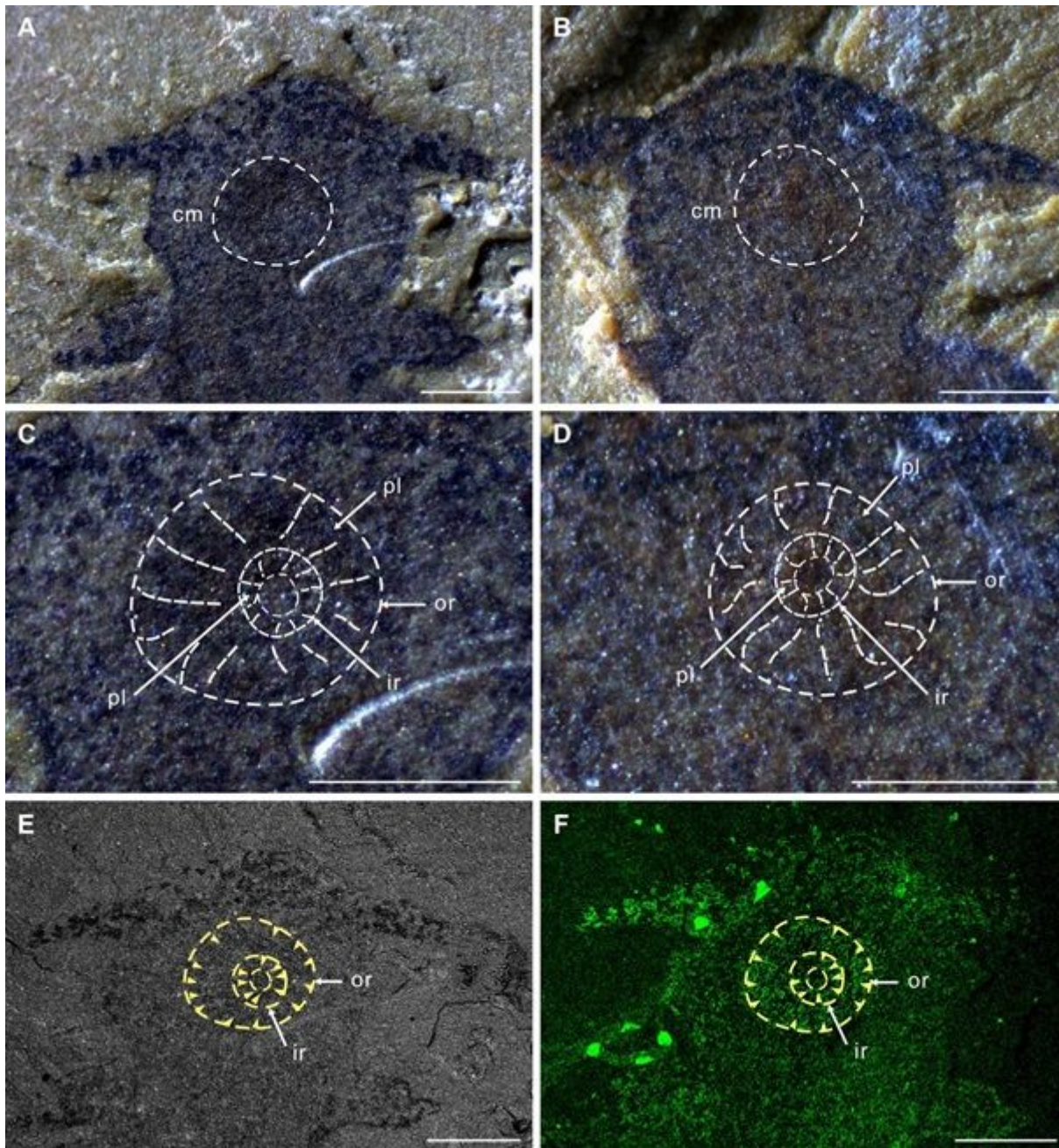


Figure 2

Enlargement of head region of *Parvibellus atavus*. A and B: Photographs of part and counterpart. C and D: Outlines of circular mouth with plates. E and F: Back scattered electron micrographs and Iron element map of part, showing the outer ring (or), inner ring (ir) and plates (yellow arrowheads). Scale bar: A, B, E, F, 0.5mm; C, D, 0.1 mm.

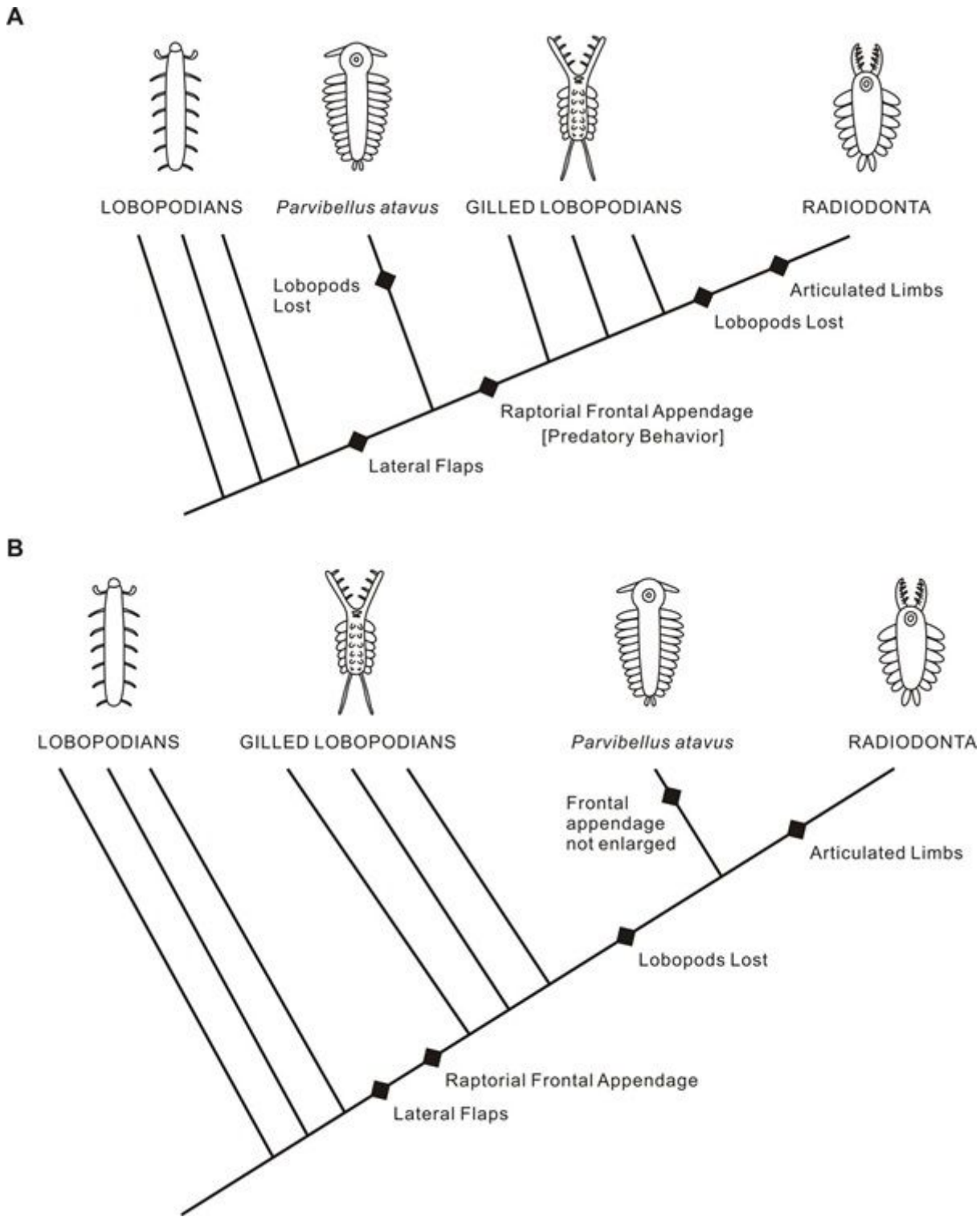


Figure 3

Two possible evolutionary scenarios for *Parvibellus atavus*. A, sister group to the “AOPK” group sensu Budd. B, sister-group to Radiodonta. See text for details.

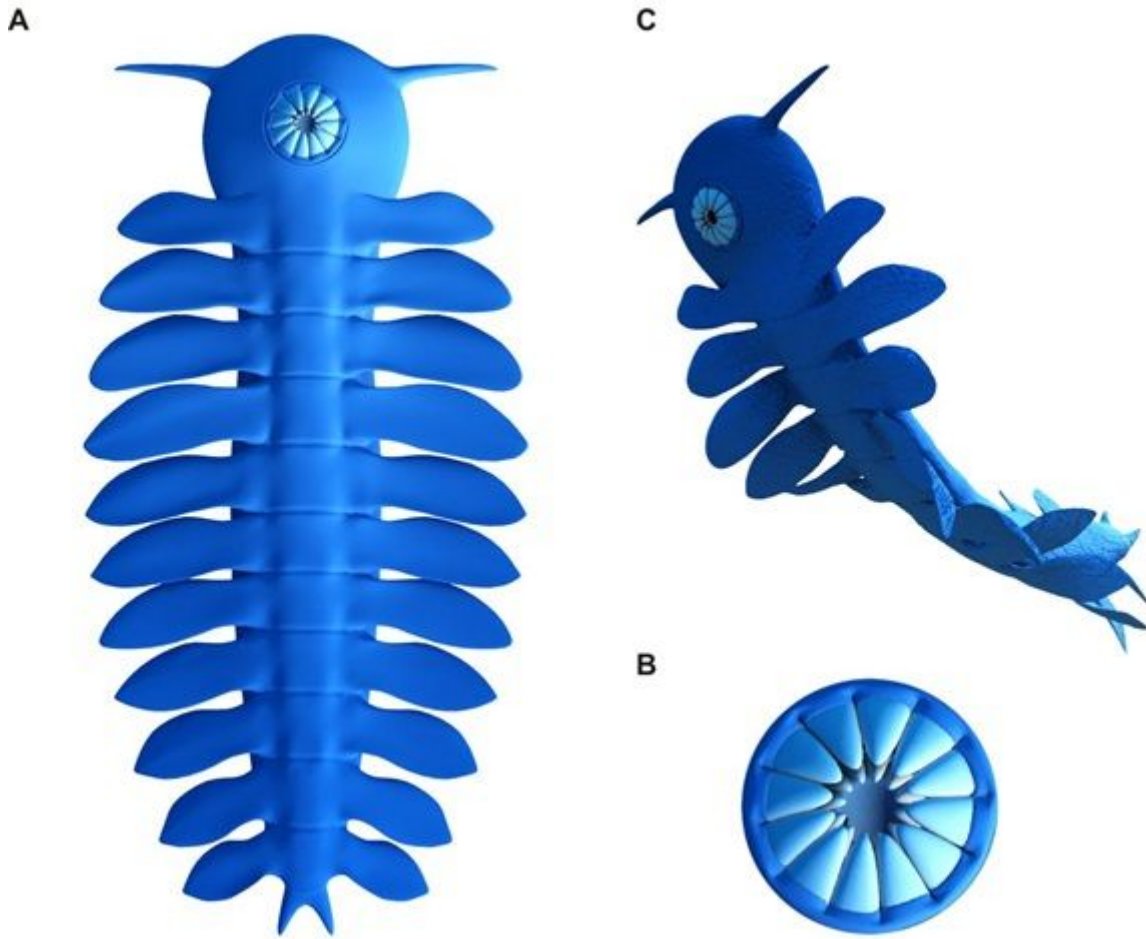


Figure 4

Reconstruction of *Parvibellus atavus*. A, Complete body in ventral view. B, Circular mouth with plates in ventral view, showing the out ring and inner ring. C, Artistic representation of the animal swimming in life.