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**An Early Cambrian Metanauplius**

# A Eucrustacean Metanauplius from the Lower Cambrian

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## Summary

A new eucrustacean arthropod, *Wujicaris muelleri* gen. et sp. nov., is represented by a Lower Cambrian early metanauplius of strikingly modern morphology despite being the oldest known fossil of such an early immature crustacean larva. The morphology of the metanauplius closely mirrors that of corresponding developmental stages of living barnacles and copepods [1, 2], and it is likely that its appendages had a similar function for feeding and locomotion. The metanauplius larva demonstrates remarkable stasis in morphology, life history, and lifestyle of (small) eucrustaceans over 525 million years, probably as a result of adaptation to a long-lasting physical niche and regime involving low Reynolds numbers and laminar current flow [3].

## Results

Crustaceans show wide diversity in morphology and mode of life. More than in other aquatic arthropods, their appendages have been modified as locomotory and feeding structures and exhibit marked adaptational variation [4] that is also reflected in molecular data [5]. Crustaceans are well represented throughout the fossil record of the last half a billion years, with hitherto two eucrustacean species known from even the Lower Cambrian [6, 7], some 525 million years old. “Orsten”-type lagerstätten have yielded Cambrian-aged three-dimensional fossils exquisitely preserved by phosphate impregnation, mainly of minute adult and larval growth stages of crustaceans [8, 9]. Based on Lower Cambrian Orsten-type material of larval specimens with soft parts preserved, recovered by acid etching of calcareous nodules, here we describe a new crustacean whose anatomy and functional morphology are strikingly similar to other more recent fossils and even to living eucrustaceans.

The specimens described here are assigned to Arthropoda, Eucrustacea, Entomostraca, *Wujicaris muelleri* gen. et sp. nov.

## Etymology

The new species is named after the town of Wuji, *caris* meaning shrimp, and in memory of Klaus J. Müller (February 6, 1923–March 12, 2010), the discoverer of the Orsten-type preservation.

## Material

The holotype is an almost complete specimen, Key Laboratory for Palaeobiology, Yunnan University, YKLP 11951 (body length ~270 μm; Figures 1A–1D). Paratypes (body length ranges from 250 to 270 μm) include a fragmentary specimen of a head shield with eyes, a labrum, and hypostomal spine, ventral side poorly preserved, YKLP 11952 (Figure 1E); an almost complete specimen, YKLP 11953 (Figures 1F and 1G); and a fragmentary specimen of the anterior part of a head shield with eyes, a tilted hypostome-labrum complex, and a squashed mandibular coxa, YKLP 11954. The material represents an early metanauplius developmental stage.

## Locality and Stratigraphy

All specimens used for this study were collected from the Xiaotan section, Yongshan, Yunnan Province, China (Yu’anshan Formation, *Eoredlichia-Wutingaspis* Biozone, upper Lower Cambrian of traditional usage). They co-occur with numerous bradoriid *Kunmingella douvillei* and lingulid brachiopods in a thin-bedded nodular limestone about 10 m above the bedding that has yielded eucrustacean *Yicaris dianensis* [6].

## Diagnosis

Semaphoront (developmental stage) of a eucrustacean characterized by a large, weakly domed, and laterally expanding head shield with the posterolateral margins converging into a posterodorsally projecting spine. The hypostome-labrum complex is fairly sclerotized, and has a pair of ovoid, putatively median eyes anteriorly and a long ventrally projecting spine centrally.

## Description

The growth stage has five appendage-bearing segments, the posterior-most of which houses the second maxilla on a hind body that lacks differentiation of thoracic segments. The head is covered by a large, subcircular, weakly domed shield that is wider than long and extends posteriorly to behind the first maxilla (Figures 1A–1G, 2, and 3A; see Movie S1, available online). The surface of the head shield is ornamented with fine papillate ridges arranged as elongate polygons (possible cell boundaries) (Figure 1F); posteriorly, it extends into a posterodorsally projecting spine (Figures 1A, 1C, 1D, 1F, 2, and 3A; Movie S1). A weakly defined plate-like suboval area, interpreted as a “dorsal organ” (see Discussion) [10, 11], occurs slightly anterior of the center of the head shield (Figures 1A, 1F, and 2; Movie S1).

Ventrally, the anterior body includes a prominent, elongate hypostome-labrum complex bearing a pair of elongate-ovoid, horizontally projecting, presumed eyes (Figures 1A, 1B, 1E, 1G, and 2). Adjacent to the point of insertion of the first antenna a large spine, at least 100 μm long, projects almost perpendicular from the raised median region of the hypostomal surface (Figures 1E and 2; Movie S1). The hypostome is confluent with the labrum, which is sharply bent ventrally and rounded distally (Figures 1B, 1E, and 1G). The postoral sternal surface bears a pair of weakly developed paragnath humps at the mandibular segment.

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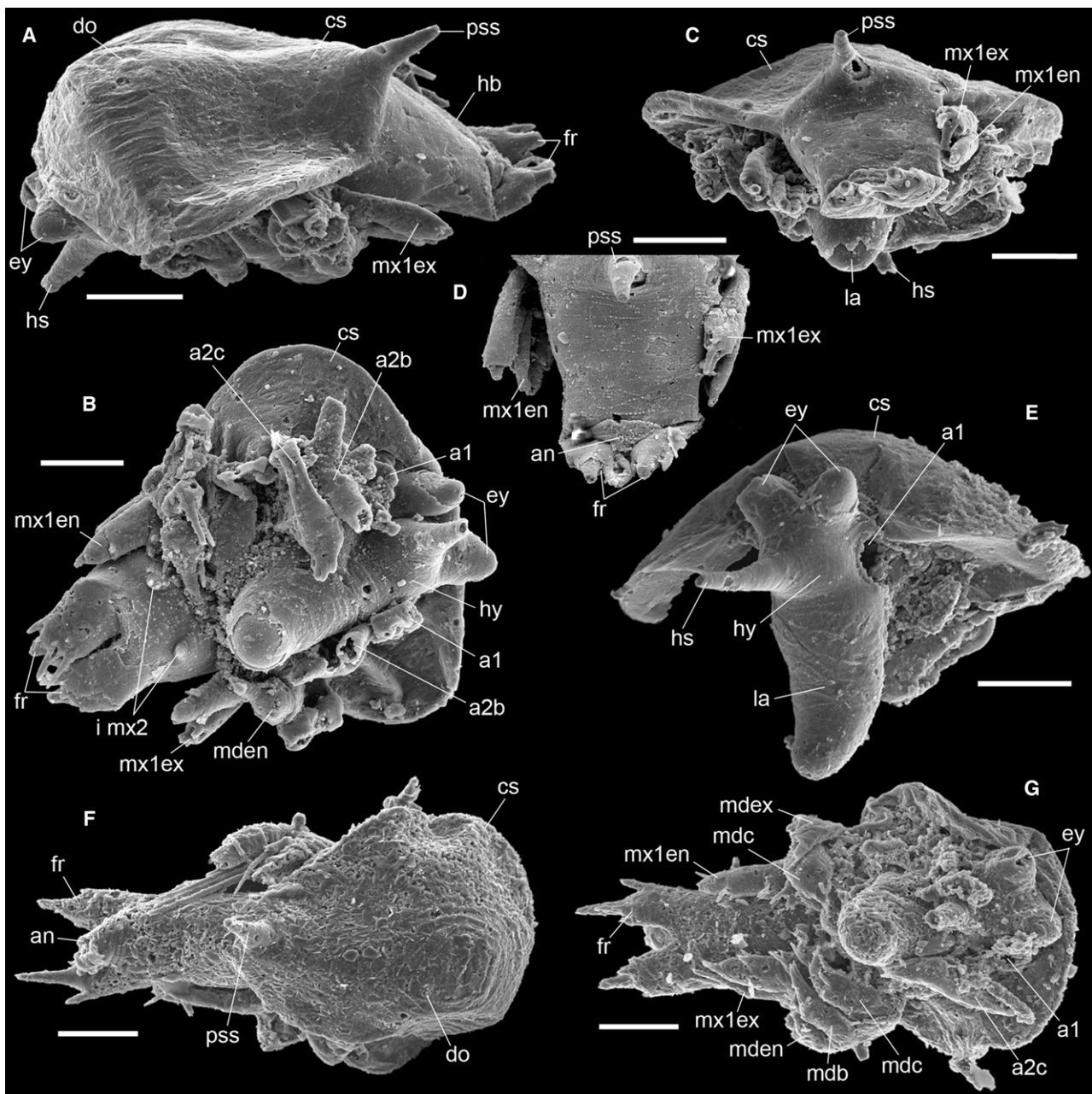


Figure 1. *W. muelleri*, Lower Cambrian, China

(A–D) Early metanauplius (holotype, YKLP 11951).

(A) Laterodorsal view displaying dorsal organ and probable median eyes protruding from underneath the head shield.

(B) Oblique ventral view.

(C) Posterior view.

(D) Dorsal view of hind body showing rows of tiny papillae on the cuticle.

(E) Fragment of an early metanauplius (YKLP 11952), anterolateral view displaying hypostome-labrum complex and a hole indicating the insertion area of the first antenna.

(F and G) Early metanauplius (YKLP 11953).

(F) Dorsal view showing the partially preserved anus.

(G) Ventral view.

Scale bars represent 100  $\mu\text{m}$  (A–C and E–G) and 50  $\mu\text{m}$  (D). The following abbreviations are used: a1, first antenna or its site of insertion; a2b, basipod of second antenna; a2c, coxa of second antenna; an, anus; cs, cephalic shield; do, dorsal organ; ey, eye(s); fr, furcal ramus (rami); hb, hind body; hs, hypostomal spine; hy, hypostome; i mx2, initial second maxilla; la, labrum; mdb, basipod of mandible; mdc, coxa of mandible; mden, endopod of mandible; mdex, exopod of mandible; mx1en, endopod of first maxilla; mx1ex, exopod of first maxilla; pss, posterior spine of head shield.

The first antenna (Figures 1E, 1G, and 2; Movie S1) arises at the lateral flanks of the hypostome; its large point of insertion indicates that it was well developed, but its fragmentary

preservation precludes a detailed description. The second antenna (Figures 1B, 1G, 2, and 3A; Movie S1) consists of a prominent, well-sclerotized coxa, four times as long as

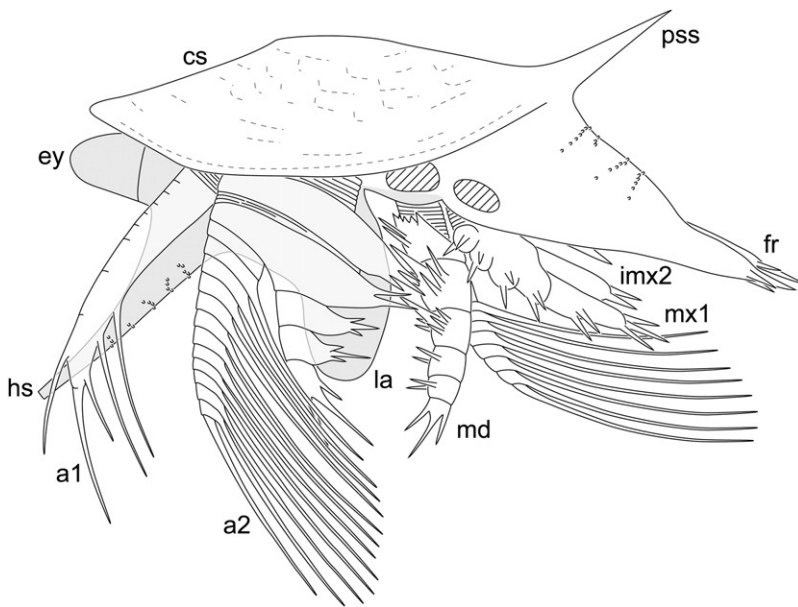


Figure 2. Reconstruction of the Metanauplius of *W. muelleri*, in Left Lateral View

Some parts unknown from *W. muelleri* (a1; and rami of a2) are added based on the morphology of other Cambrian eucrustacean larvae. Left mandible and left first maxilla are omitted (insertion sites indicated by stripped oval areas). The left first antenna and left second antenna are in part depicted as though transparent in order to emphasize the huge, sclerotized hypostome-labrum complex and the paragnaths (given in gray). Note the fine ornamentation on the hypostomal spine and hind body. Abbreviations are as in Figure 1 except: a2, second antenna; md, mandible; mx1, first maxilla.

wide and medially drawn out into an endite with a set of rigid, spine-like setae pointing toward the mouth underneath the posterior end of the labrum; a shorter and subtriangular basipod, bearing a median enditic elongation with setae; a three- or possibly four-segmented endopod (Figures 1B and 2; Movie S1) that arises mediodistally on the basipod; and an exopod posterolaterally, of which details are unknown. The mandible (Figures 1G and 2; Movie S1) has the same general design

and consists of a coxa that is much shorter than that of the second antenna, with a weakly developed pointed gnathobase bearing two gnathobasic setae anteriorly (as in feeding nauplii of living and fossil eucrustaceans); a subtriangular basipod proximomedially elongated into a prominent endite with spines and setae; an endopod about 60  $\mu\text{m}$  long, comprising three or four segments; and an exopod 90  $\mu\text{m}$  long, consisting of seven or eight annuli, of which at least the distal seven each bear a long seta. The first maxilla (Figures 1B, 1G, and 2; Movie S1) is slightly smaller than the mandible and arises ventrolaterally from the anterior end of the slightly ventrally bent hind body. Its basipod has three or four endites medially, each bearing two short setae. The cone-shaped, weakly two-segmented endopod is about 40  $\mu\text{m}$  long with

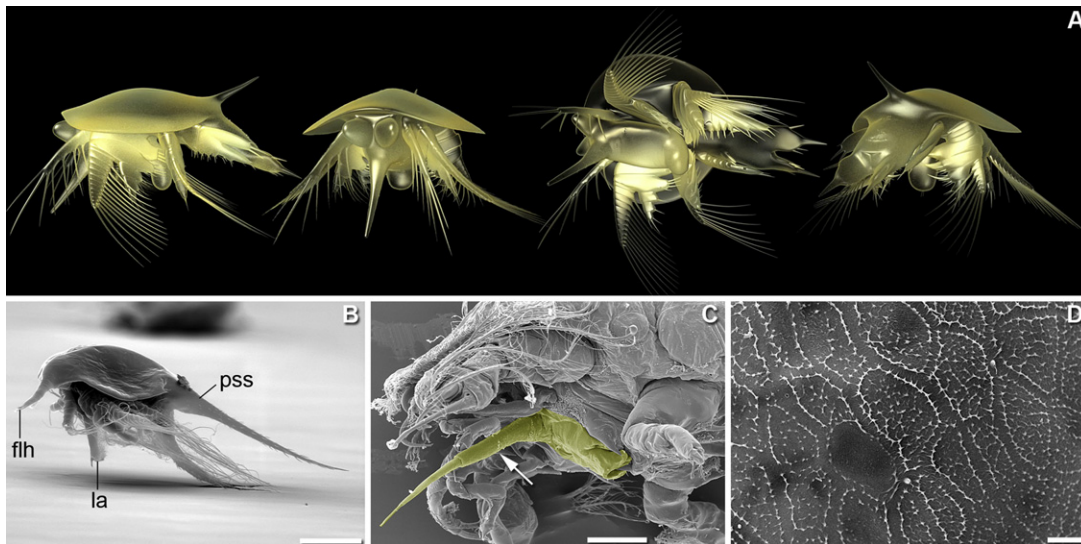


Figure 3. Model of *W. muelleri* and Modern Crustacean Larvae for Comparison

(A) Three-dimensional model of *Wujicaris muelleri* in lateral, anterolateral, ventrolateral, and posterolateral view (color pattern hypothetical). Stills are from Movie S1.

(B) Metanauplius 2 (of 5; also called “nauplius three”) of the cirripede *Capitulum mitella*, lateral view, displaying the large labrum, the characteristic posterior spine of the head shield, and shield margins merging into the body posteriorly (image courtesy of R. Kado and J.T. Høeg).

(C) Larva of *Argulus foliaceus* (Branchiura), ventral oblique view, displaying the preoral sting (color-enhanced) with a strongly sclerotized proximal cone (arrow) and a softer distal part.

(D) Ornamentation of the head shield of metanauplius 5 (of 5; also called “nauplius six”) of the cirripede *Ibla cumingi* (image courtesy of B.K.K. Chan and J.T. Høeg).

Scale bars represent 100  $\mu\text{m}$  (B), 50  $\mu\text{m}$  (C), and 10  $\mu\text{m}$  (D). Abbreviations are as in Figure 1, and flh denotes frontolateral horn (special feature of cirripede larvae).

two setae distally; the exopod is of similar shape and length, but is undivided and bears two or three short setae distally. Preservational factors prevent recognition of a proximal endite. The second maxilla is represented by one or two short, stout spines ventrally on the anterior third of the hind body (Figure 1B).

The hind body is subconical (Figures 1A, 1C, 1D, and 2; Movie S1), tapered, and progressively more flattened posteriorly in dorsoventral aspect, and it extends into a pair of “initial” (i.e., inarticulate) furcal rami (Figures 1B, 1F, 1G, and 2; Movie S1). Each ramus has five setae distally: two slender setae medially, a large spine-like seta centrally, an elongate seta sited laterally, and a tiny associate seta more ventrally. The anus is most likely located terminally on the hind body, immediately above the base of the furcal rami (Figures 1D and 1F; Movie S1). Fine pustulate ridges, arranged approximately into polygons, surface the hind body and the hypostome-labrum complex including the spine (Figure 1D).

## Discussion

In design, size, and developmental state of the appendages, total length, and in having inarticulate furcal rami with few terminal setae, the *Wujicaris muelleri* specimens are comparable to certain developmental stages of Cambrian eucrustaceans such as *Rehbachella kinnekullensis* [10] and *Bredocaris admirabilis* [12], and of living eucrustaceans such as Cephalocarida, Branchiopoda, and Maxillopoda, particularly copepods and cirripeds. *W. muelleri* is therefore assigned to the Eucrustacea (crown group Crustacea). The earliest developmental stages of all known Cambrian stem derivatives of the Crustacea each have four pairs of functional appendages, including an unspecialized trunk limb-like posterior-most limb [9, 13, 14]. The eucrustacean (ortho)nauplius has, however, only the three so-called naupliar appendages (first antenna, second antenna, and mandible). In subsequent development, over several metanaupliar stages, the first and second maxillae plus the trunk appendages originate as buds and change progressively into functional limbs. *W. muelleri* specimens have five appendages, but the first maxilla is little developed (individual elements of the rami are not clearly demarcated) and the second maxilla is only a tiny spine. That the first and second maxillae occur on the postnaupliar hind body and that the posterior end of the head shield is behind the first maxilla are further indicators that the specimens of *W. muelleri* represent an early metanauplius developmental stage.

The morphology and position of the circumscribed area dorsally on the head shield of *W. muelleri* (Figures 1A and 1E; Movie S1) resemble the shallow, smooth oval area—the osmoregulatory, so-called dorsal organ [11, 15]—of the head shield of early larvae of *R. kinnekullensis*, *B. admirabilis*, and living branchiopods. Early larvae of living maxillopods have like structures in a similar position, but verification of homology awaits further evidence [16–18]. A similar organ is not known in early larvae of malacostracans.

In the size of its naupliar appendages and the number of segments in the associate endopods and exopods, the *W. muelleri* metanauplius resembles metanauplius stages of living copepods and cirripeds even more closely than do comparable developmental stages of other Cambrian eucrustacean species. Furthermore, wide shallow head shields are not uncommon in eucrustacean larvae, as in copepods [1] and the branchiopod *Lynceus* [2]. Unlike the earliest larvae of

*R. kinnekullensis*, *B. admirabilis*, and some copepods, the *W. muelleri* metanauplius lacks a dorsocaudal spine on a supra-anal flap. In the ontogeny of most of those taxa the dorsocaudal spine progressively reduces in size and is lost, whereas in living branchiopod larvae the spine is absent from the beginning. By contrast, a spine like the one posteriorly on the head shield of the *W. muelleri* metanauplius is lacking in the larvae of all those taxa except the earliest larvae of living cirripeds (Figure 3B). In cirripeds, that shield spine shifts during ontogeny to become the dorsocaudal spine on the supra-anal flap, thus explaining the absence of the shield spine in later developmental stages and also accounting for the (intermediate) presence of the spine on the supra-anal flap, as in *R. kinnekullensis* and copepod larvae [10].

Another arresting feature of the *W. muelleri* metanauplius is the prominence of the hypostome-labrum complex and prelabral spine. In all specimens the latter is broken off distally, so it is uncertain whether or not it was simply a hollow tube. The only “spine” of comparable shape and size in larvae of other fossil and living eucrustaceans is the so-called preoral sting of the developmental stages of the parasitic branchiuran fish lice *Argulus* (Figure 3C) [19, 20], a structure that is rigid proximally and eversible distally [21]. The sinuous rows of fine papillae on the hypostome-labrum complex and hind body in *W. muelleri* are similar to surface ornament in larval cirripeds (Figures 1B, 1D, and 3D).

Fundamental aspects of the functional design of living crustacean larvae are also evident in the metanauplius of *W. muelleri*. As in the nauplii of cirripeds and copepods, the naupliar appendages of *W. muelleri* probably had a feeding plus locomotory function. The second antenna and mandible (Figure 1F; Movie S1) of the *W. muelleri* metanauplius are not as large as in living pelagic branchiopods and the Cambrian eucrustacean *Y. dianensis* [6]. This, in combination with the wide flat head shield, indicates that the *W. muelleri* metanauplius was, rather, probably epibenthic to benthic, comparable to living benthic copepod larvae [1]. Many, if not all, of the Cambrian Orsten (larval-stage) arthropods were possibly part of the meiofauna [22]. All aquatic animals smaller than about 2 mm, particularly the larvae, live in an environment characterized by low Reynolds numbers, where the water has laminar current flow and is “sticky” [3]. Nauplii and young metanauplii most likely adapted to such an environment by possessing specific structures, including multiannulated exopods, that facilitated special sweep-net mechanisms which combined feeding and locomotion functions [23–26]. Such adaptation, initiated by the stepwise acquisition of appropriate structures in the stem lineage of crustaceans [9], included the generation of flow currents to guide food to the mouth.

This dual feeding-locomotion mechanism, associated with a free-living but benthic lifestyle in a regime involving viscous flows, was apparently acquired in the Cambrian and has hardly changed over 525 million years. Moreover, that the metanauplius of *W. muelleri* is remarkably similar morphologically to living metanauplii, especially entomostracans, indicates that eucrustacean evolution was advanced even by early Cambrian times and that differences between living Crustacea are merely variations on a long-since established ground pattern.

## Experimental Procedures

The four Orsten-type specimens, along with thousands of phosphatized shelly fossils, were picked up through a stereomicroscope from the indissoluble residue left by dilute (5%) acetic acid dissolution of about 450 kg

of calcareous nodules collected from the type locality. Then their images illustrated here were taken with scanning electron microscopy (Phillips XL30ESEM).

#### Supplemental Information

Supplemental Information includes one movie and can be found with this article online at doi:10.1016/j.cub.2010.04.026.

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