

Gill rays of primitive vertebrate *Yunnanozoon* from Early Cambrian: a first record

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Abstract Yunnanozoans (including *Yunnanozoon* and *Haikouella*) are important representatives of the primitive vertebrates in the Early Cambrian Chengjiang fauna. For Yunnanozoans, we know less about *Yunnanozoon* than about *Haikouella* due to the poor preservation of *Yunnanozoon*. Up to now, there have been some reports that *Haikouella* had developed gill rays, while there have been no reports on *Yunnanozoon*. In this paper, we described our new findings of the distinct gill rays of *Yunnanozoon lividum* based on new well-preserved material collected from the Lower Cambrian Maotianshan Shale in Xiaolantian of Yunnan Province, China. This study provides new data on the evolutionary relationship of the primitive vertebrates and their early evolution.

Keywords gill rays, *Yunnanozoon*, *Haikouella*, Early Cambrian, Yunnan

1 Introduction

The research on the origin of vertebrates is one of the most important topics in palaeontology. However, we currently know little about ancestral vertebrates due to the limited fossil cases. Up to now, most studies of ancestral vertebrates have been done based on the Middle Cambrian *Pikaia* from the Burgess Shale (Walcott, 1911; Conway Morris and Whittington, 1979; Briggs et al., 1994) and the conodonts with poorly-known soft tissues (Briggs, 1983; Donoghue et al., 2000). Some problematic animals from the Burgess Shale (e.g. *Odontogriphus*, *Nectocaris*) recently deemed to have a close relationship with chordates are interpreted with a mollusk affinity

(Chen et al., 2005). Thus, we know much less about the origin of vertebrates especially those from the Early Cambrian before a series of important findings from the Early Cambrian Chengjiang fauna. Recently, diverse chordates have been described from Chengjiang fauna (ca. 525 Ma) such as tunicate (Chen et al., 2003) and abundant primitive vertebrates (Chen et al., 1995, 1999; Shu et al., 1996 a, b, 1999, 2003 a, b; Hou et al., 2002; Shu, 2003; Zhang and Hou, 2004).

Yunnanozoon was first interpreted as a problematic animal (Hou et al., 1991). Some researchers subsequently suggested that it was in fact a chordate based on the new observation of some well-preserved materials that revealed several critical characteristics such as pharyngeal cavity, branchial arches, and notochord (Chen et al., 1995; Dzik, 1995). Thus, *Yunnanozoon lividum* is the first Early Cambrian chordate from the Chengjiang fauna. Shu et al. (1996 b) suggested that *Yunnanozoon* was a hemichordate based on some structures of *Yunnanozoon* such as collar and proboscis. This was argued by Chen and Li (1997) with new morphological revision and discussion. More than 300 well-preserved specimens of *Haikouella lanceolata* have been collected near the Ercai village, Haikou, Kunming City of Yunnan Province, China. The *Haikouella lanceolata* displayed remarkable similarities to *Yunnanozoon lividum*, which indicated their close evolutionary relationship (Chen et al., 1999). It was thought that *Haikouella* belonged to a craniate based on its distinct cephalopharyngeal region formed by brains, eyes, neural cord, aortas, and hearts etc. (Chen et al., 1999). Chen and Li (2000) suggested *Haikouella* was a crown-group vertebrate, but it was more like a cristozoa, the sister group or stem-group vertebrate (Holland and Chen, 2001) or sister group of craniates (Mallatt and Chen, 2003). However, Shu et al. (2003 b) described a new form of *Haikouella* (*H. jianshanensis*) and considered it as an extinct deuterostome. Furthermore, he suggested that Yunnanozoans displayed a similar evolutionary

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stage with hemichordate or as the sister group of Vetulicolia (Shu, 2003).

The arguments of the systematic position of *Yunnanozoon* have so far never been unified with three major different opinions: (1) it was generally placed in deuterostome (e.g. Shu et al., 2003); (2) it was an uncertain taxon (e.g. Hou et al., 2004); (3) it was a chordate (even a vertebrate), which was agreed by most researchers (e.g. Chen et al., 1995, 1999; Dzik, 1995, 2000; Luo et al., 1999; Holland and Cheng, 2001; Cheng and Qian, 2002; Mallatt and Chen, 2003; Chen, 2004). Thus, further morphological studies may be helpful in understanding the phylogenetic position and evolutionary relationship of *Yunnanozoon*.

2 Materials and analysis

The described materials of *Yunnanozoon* were mainly collected from Ma'anshan of Chengjiang County. Most of them had a small body and were largely preserved in one bedding plane, overlapped each other and partly decayed exhibiting poorly-preserved features. The verified structures of *Yunnanozoon* were described from a few other larger specimens. Our recent excavation in the site near the Xiaolantian Village, Chengjiang County, Yunnan Province, China yielded rather rich soft-bodied fossils that included some new forms and well-preserved *Yunnanozoon* (Fig. 1 A–D). All of the fossils have been deposited at the Chengjiang Fauna National Geopark.

We collected more than 10 new specimens which were preserved as black films. One of them, a complete specimen, was mentioned by Chen (2004). He considered that *Y. lividum* may have a pair of large lateral eyes (Fig. 1 D; Chen, 2004 Fig. 516, 517). However, this structure is probably represented by an anterior branchial vessel that resembles lateral parts of the so-called collar (Shu et al., 1996b). The branchial arches of *Y. lividum* are armed with ca. 20 discs that resemble those from larval lamprey (Mallatt and Chen, 2003). This seems different from the long gill rays of *H. lanceolata*. The gill rays of *H. jianshanensis* are distinctly visible as a flattened structure (Shu et al., 2003 b). However, so far it is unclear whether *Yunnanozoon* has gill rays. Dzik (2000) supposed that the gill rays of *Yunnanozoon* pointed to the pharyngeal cavity. The gill rays are also clearly displayed in the above materials (Fig. 1 B). They are flat and pointed topically, as long as the width of branchial arches but distinctly shorter than those of *Haikouella*. These gill rays seem pointed inwards for supporting filtrate function.

Yunnanozoon and *Haikouella* were both filter feeders. They draw food particles into the pharyngeal cavity by beating buccal tentacles (e.g. *Haikouella*). The food particles (and probably oxygen) are retained on the

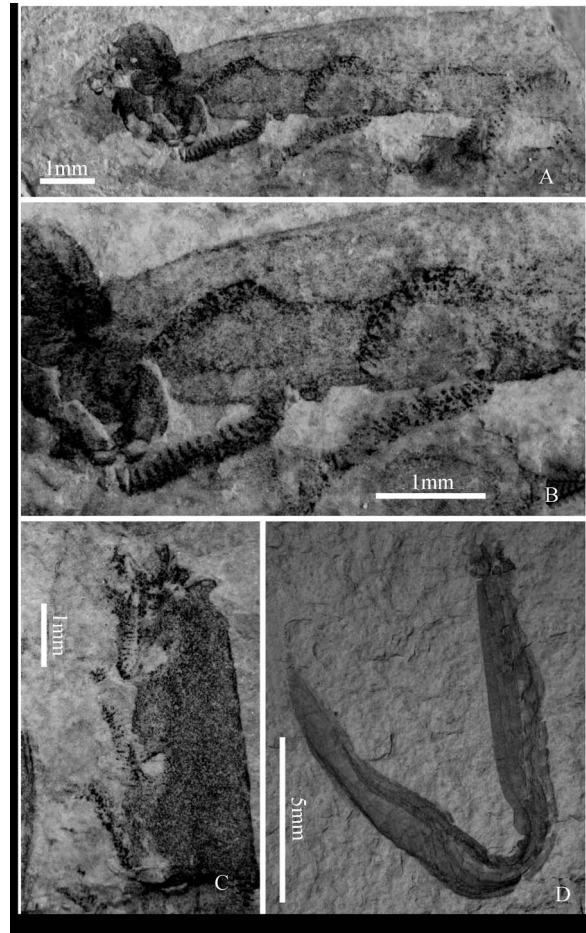


Fig. 1 *Yunnanozoon lividum* from the Lower Cambrian Maotianshan Shale of Xiaolantian, Chengjiang County, Yunnan Province, China. Note: A: a specimen (CFM0008 a) preserved the anterior section of animal showing the branchial arches with gill rays; B: enlargement of A, showing the details of gill rays; C: a specimen (CFM00194 a) showing the branchial arches with gill rays; D: a twisted complete specimen (CJM049) showing the general morphology.

mucus of gill rays produced by the endostyle, and the water exits via the atriopore. The gill rays were well-developed in *Yunnanozoon* and *Haikouella* unlike the recent amphioxus and larval lamprey. Such structure may increase the surface area for filtering and breathing, which represents a primitive character. The paired gill rays suggest a heterogeneous structure with that of fishes (Mallatt and Chen, 2003).

3 Morphological comparison between *Yunnanozoon* and *Haikouella*

The morphology of *Yunnanozoon* and *Haikouella* remarkably resemble each other (e.g. the general shuttle-like body shape, paired branchial arches in developed pharyngeal cavity, circa 24 dorsal myosepta with nearly straight shape, a large notochord (or

protovertebrae) located relatively ventrally and tapering towards both ends). Moreover, their colors also resembled (black-brownish or black-purplish). Chen et al. (1999) considered that the appearance of gill rays was different between *Yunnanozoon* and *Haikouella*. Thus, the finding of gill rays of *Yunnanozoon* provides an additional similarity with *Haikouella*. Although *Yunnanozoon* may bear a pair of lateral eyes like *H. lanceolata* (Chen et al., 1999; Mallatt and Chen, 2003), the large and protruding eyes of *Yunnanozoon* described by Chen (2004) are suspicious. Several structures of *H. lanceolata* such as aortas, neural cord, brain, and caudal projection have so far never been found in *Y. lividum*. However, these structures are not regarded as differences between them, because the different appearance of these structures probably results from preservation. *Yunnanozoon* and *Haikouella* (*H. jianshanensis* is not compared here because its most detailed structures are still poorly-known) display differences in the following four characteristics (Fig. 2).

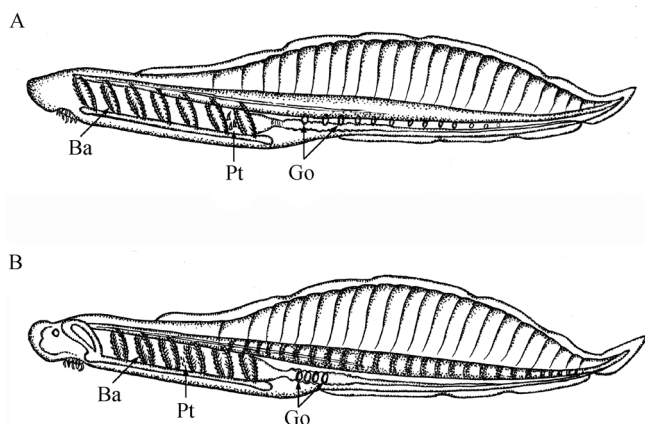


Fig. 2 Morphological comparison of *Yunnanozoon lividum* and *Haikouella lanceolata*. A: reconstruction of *Y. lividum*; B: reconstruction of *H. lanceolata*. Ba: branchial arches; Go: gonad; Pt: pharyngeal denticle.

(1) The general body shape. The anterior region of *H. lanceolata* is distinctly wider than its posterior region. The posterior region forms a sail-like outline indicated by the dorsoventrally compressed animals (Chen et al., 1999). However, the twisted specimens of *Y. lividum* (see Chen and Li, 1997, Fig. 1; Chen, 2004, Fig. 516) show that its width is gradually changed. The broad anterior region of *H. lanceolata* and *Y. lividum* indicate that they belong to benthic animals unlike a burrower (e.g. amphioxus) and a strong swimmer (e.g. lamprey).

(2) The number of branchial arches. The number of branchial arches in *Yunnanozoon* and *Haikouella* are stable. *Haikouella* has 6 branchial arches. Both ends of branchial arches respectively attach to the branchial hearts on the ventral aorta and two dorsal aortas. A

mandibular artery derives from the anterior end of the ventral aorta (Chen et al., 1999; Mallatt and Chen, 2003). There are 7 pairs of branchial arches developed in *Yunnanozoon*. The small number of branchial arches indicates a primitive structure (Donoghue et al., 2000).

(3) The number and arrangement of gonads. Both *Yunnanozoon* and *Haikouella* bear the rounded and paired gonads arranged laterally in the post pharyngeal cavity region. *H. lanceolata* has 4 pairs of gonads with equal sizes that range between 5–7 myosepta (corresponding to the 6th and 7th myomeres; Chen et al., 1999). *Y. lividum* bears circa 13 pairs of gonads. Each pair compliably corresponds to one myomere (the first gonad pair corresponding to the 6th myomeres). The size of the gonads decrease gradually (Chen and Li, 1997; Chen, 2004). A similar feature is interpreted as a spiral gut in *H. jianshanensis* (Shu et al., 2003 b), but the midgut of *H. lanceolata* exhibit distinct wavy margins (Chen et al., 1999).

(4) The location of pharyngeal denticles. Both *Yunnanozoon* and *Haikouella* develop a mineralized pharyngeal denticle assemblage in their pharyngeal cavity. These denticles are very small and slightly curved with a simple taper shape. They were probably original regularly arranged but displayed a disordered arrangement by compression. The pharyngeal denticles of *H. lanceolata* are tiny (ca. 100 μ m long) which locate near the third branchial arches (Chen et al., 1999). The pharyngeal denticles of *Y. lividum* are relatively large (the biggest is nearly 1 mm long) which are armed between the 6th–7th branchial arches (Chen and Li, 1997). Chen and Qian (2002) suggested that some taxa of protoconodonts (e.g. *Protocanthocordylodus simoni*) represented the earliest chordate with a mineralized part, even the earliest vertebrate and the common ancestor of the two fronts. Some researchers believe that some other taxa of protoconodonts such as *Protoherzina* and *Mongolodus* are probably the grasping spines of chaetognath (e.g. Szaniawski, 2002; Vannier et al., 2005). The compressed fossil of chaetognath has been already described from the Lower Cambrian Maotianshan Shale (e.g. Chen and Huang, 2002). Thus, the above description confirms that the protoconodont is a polyphyletic group. Nevertheless, various metazoans bearing complex wimble/spine shape structures have occurred in the Early Cambrian. Thus, more detailed and extensive studies are necessary.

To summarize, the morphology of *Yunnanozoon* and *Haikouella* distinctly resemble each other. They are clearly distinguished by the number of branchial arches (7 pairs in *Yunnanozoon* and 6 pairs in *Haikouella*), but such difference is blurry in many incomplete specimens. *Yunnanozoon* displays a very close evolutionary relationship with *Haikouella* on the basis of the above analyses and comparison. The two represent very primitive vertebrates although *Yunnanozoon* was formerly considered as

a cephalochorate (Chen et al., 1995). The in-depth study of *Yunnanozoon* based on additional well-preserved material is very important, which may reveal more detailed structures and phylogenetic relationships.

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