Available online at www.sciencedirect.com
ScienceDirect
ELSEVIER
Palaeogeography, Palaeoclimatology, Palaeoecology 254 (2007) 307–316
PALAEO
www.elsevier.com/locate/palaeo

Diverse pelagic predators from the Chengjiang Lagerstätte and the establishment of modern-style pelagic ecosystems in the early Cambrian

Shixue Hu [a,c,*], Michael Steiner [c], Maoyan Zhu [b], Bernd-Dietrich Erdtmann [c], Huilin Luo [a], Liangzhong Chen [a], Bernd Weber [d]

[a] *Yunnan Institute of Geological Science, No. 87 Dongfeng Lane, Dongfeng Donglu, Kunming 650051, Yunnan Province, China*
[b] *Nanjing Institute of Geology and Palaeontology, 39 East Beijing Road, Nanjing 210008, Jiangsu Province, China*
[c] *Technische Universität Berlin, ACK 14, Ackerstrasse 71-76, D-13355 Berlin, Germany*
[d] *Institute für Geologische Wissenschaften, Freie Universität, Malteserstrasse 74-100, D-12249 Berlin, Germany*

Accepted 5 March 2007

Abstract

New information obtained from exceptionally preserved nonmineralized fossils in the Chengjiang Lagerstätte indicates the presence of diverse pelagic predators in the early Cambrian, including ctenophores (*Maotianoascus octonarius* Chen and Zhou, *Trigoides aclis* Luo and Hu, *Botafasciculus ramificans* Hou et al., and a new species, *Yunnanoascus haikouensis* gen. et sp. nov.), chaetognaths (*Protosagitta spinosa* Hu = *Eognathacantha ercainella* Chen and Huang), eldoniids (*Stellostomites eumorphus* Sun and Hou, and *Rotadiscus grandis* Sun and Hou), and epipelagic nektonic arthropod predators (e.g., *Isoxys*), as well as some meroplankton (e.g., *Anomalocaris* and *Amplectobelua*). Trophic analysis of the early Cambrian pelagic community of the Chengjiang Biota reveals a phytoplankton-based food web with a complex trophic structure containing at least three (probably four) trophic levels. A complex, modern-style pelagic ecosystem may have been developed by the time of early Cambrian.

Keywords: Pelagic; Predators; Chengjiang Lagerstätte; Early Cambrian; Pelagic ecosystem

1. Introduction

The early history of pelagic organisms and their ecology has remained relatively obscure until recently. Despite the ongoing dispute on the affinities of Precambrian medusa-like Ediacara-type fossils (see Glaessner, 1984), it has been suggested that the pelagic realm remained unexploited until the Late Cambrian (Signor and Vermeij, 1994; Rigby and Milsom, 2000; but see Briggs and Whittington, 1985; Fortey, 1985; Babcock, 2003). This hypothesis has been challenged during the last decade. The discovery of fossil mesozooplankton, represented by a filter-feeding crustacean from the early Cambrian (Butterfield, 1994) reflects the harvesting of plankton and a fundamental shift in the trophic structure of ancient communities (Butterfield, 1997, 2001). Other studies (e.g., Fortey, 1985; Vannier and Chen, 2000; Babcock, 2003) also indicate an early colonization of the pelagic realm in the Early Cambrian. Conway

* Corresponding author. Yunnan Institute of Geological Science, No. 87 Dongfeng Lane, Dongfeng Donglu, Kunming 650051, Yunnan Province, China. Tel.: +86 871 3188877.
E-mail address: hushixue@hotmail.com (S. Hu).

0031-0182/$ - see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.palaeo.2007.03.044

Morris (1979) and Briggs and Whittington (1985) even earlier recognized a pelagic assemblage from the Middle Cambrian Burgess Shale fauna. Despite some progress, made largely from interpretations of a few pelagic faunal elements, our knowledge about early pelagic ecosystems still remains limited. Butterfield (2001), for example, presented the hypothesis of a simple and short food web and a top-down model with trophic cascades in the Cambrian. However, this model requires scrutiny.

The Chengjiang Lagerstätte, which occurs in the middle and upper Yu'anshan Formation (Cambrian Series 2) in eastern Yunnan, China, contains abundant exceptionally preserved nonmineralized fossils that have been assigned to more than 10 animal phyla (Chen et al., 1996, 2002). Among these fossils, most taxa have been described but not yet comprehensively reviewed, particularly in terms of feeding strategies and lifestyle. The aim of the present study is to investigate the presence of pelagic faunal components and the structure of a pelagic ecosystem based on new information from the Chengjiang Lagerstätte.

2. Pelagic predators from the Chengjiang Lagerstätte

2.1. Ctenophores

Chen et al. (1996) reported two species of ctenophores from the Chengjiang Biota, which they later (Chen and Zhou, 1997) described and named as *Maotianoascus octonarius* and *Sinoascus papillatus*. However, the assignment of *S. papillatus* to the ctenophores remains questionable because of poor preservation of the specimens. The single described specimen of *Sinoascus* shows no critical characters such as comb-rows and the aboral globular or capsule structure, which are diagnostic for this animal group. The body of *Maotianoascus* (Fig. 1B, E) is globular and walled with eight comb-rows. Orally beyond the globular body is a skirt-like structure surrounding the inferred position of the mouth. The more prominent appearance of the comb-rows may mimic a more lobate structure and the specimens may be distorted and incomplete. Although Hou et al. (2004) reconstructed *Maotianoascus* as a strongly lobate form, with 16 comb-rows and without the previously reported skirt-like extension at the oral pole, it is more probable that the species had a more globular morphology with eight comb-rows, as indicated by Chen and Zhou (1997) and Dzik (2002).

Another species, *Trigoides aclis* (Fig. 1A), known from the Haikou area, Yunnan, China was first considered as a ctenophore by Chen et al. (2002), although it was originally misidentified as the head shield of an arthropod (Luo et al., 1999). This animal has four major flap-like lobes, which are arranged longitudinally, and probably four less prominent lobes (of which only three can be recognized in the only available specimen) carrying broad comb-rows. The flap-like lobes also carry ctene-like structures, which are less distinct. These may represent ciliary bands comparable with those in auricles of the modern Lobata. Four bag-like extensions are present on the oral pole. However, no tentacles have been observed.

Petalilium latus, which was also suggested as belonging to the ctenophores by Chen et al. (2002), shows no significant characters supporting such a placement. Thus, its affinity remains uncertain.

A new fossil animal, *Yunnanoascus haikouensis* gen. et sp. nov., which is probably a new ctenophore, is reported herein (Fig. 1C, F, G; Fig. 2) and has ca. 16 comb-rows. The presence of comb-rows indicates its ctenophoran affinity (Fig. 1G). Tentatively a predatory mode of life similar to that of *Maotianoascus octonarius* is proposed.

Both *Maotianoascus* and *Trigoides* have a dome-like structure on the aboral pole (called "capsule-like dome" or "dome-shaped organ" by Chen and Zhou, 1997). The structure ranges from 3 to 5 mm in height and 2 mm in width. A similar structure, termed "capsule structure", was also reported from the Middle Cambrian ctenophore *Ctenorhabdotus capulus* (Conway Morris and Collins, 1996) and interpreted tentatively as a statocyst-containing dome. Conway Morris and Collins (1996) noted the large size of the dome compared with the domes of some modern ctenophores, which are composed of fused cilia. However, an exceptionally prominent dome also exists in larvae of some modern ctenophores, where the dome comprises approximately 1/10 of the body size of the entire larva (Conway Morris and Collins, 1996; Martindale, 2002). Based on our observations of Chengjiang fossils, we interpret this structure as homologous to the dome in extant ctenophores. Although no primarily mineralized structures could be detected yet in the fossil dome-structures, it might have functioned as in the modern examples to house the statocysts.

Besides the three species discussed above, *Botafasciculus ramificans* (Hou et al., 1999, 2004) from the Chengjiang Lagerstätte can possibly also be assigned to the ctenophores. This species has eight externally directed longitudinal lobes with regular spines. Although originally classified as uncertain taxa (Hou et al., 1999, 2004), we reinterpret it as a possible ctenophore owing to its general resemblance to other ctenophores from both the Chengjiang Lagerstätte and the Burgess Shale. This resemblance is especially expressed by the presence of the aboral dome-like structure, which is clearly visible in