

Early Cambrian origin of modern food webs: evidence from predator arrow worms

J. Vannier^{1,*}, M. Steiner², E. Renvoisé³, S.-X. Hu⁴ and J.-P. Casanova⁵

¹Université de Lyon, Université Lyon 1, UMR 5125 du CNRS 'Paléoenvironnements et Paléobiosphère', Campus Scientifique de la Doua, Bâtiment Géode, 2, rue Raphaël Dubois, 69622 Villeurbanne, France

²Technische Universität Berlin, Sekr. ACK 14, Ackerstrasse 71-76, 13355 Berlin, Germany

³Université de Bourgogne, UMR Biogéosciences, 6, boulevard Gabriel, 21000 Dijon, France

⁴Yunnan Institute of Geological Science, 131 Baita Road, 650011 Kunming, China

⁵Université de Provence, ER 'Biodiversité et Environnement', 13331 Marseille, Cedex 3, France

Although palaeontological evidence from exceptional biota demonstrates the existence of diverse marine communities in the Early Cambrian (approx. 540–520 Myr ago), little is known concerning the functioning of the marine ecosystem, especially its trophic structure and the full range of ecological niches colonized by the fauna. The presence of a diverse zooplankton in Early Cambrian oceans is still an open issue. Here we provide compelling evidence that chaetognaths, an important element of modern zooplankton, were present in the Early Cambrian Chengjiang biota with morphologies almost identical to Recent forms. New information obtained from the lowermost Cambrian of China added to previous studies provide convincing evidence that protoconodont-bearing animals also belonged to chaetognaths. Chaetognaths were probably widespread and diverse in the earliest Cambrian. The obvious raptorial function of their circumoral apparatuses (grasping spines) places them among the earliest active predator metazoans. Morphology, body ratios and distribution suggest that the ancestral chaetognaths were planktonic with possible ecological preferences for hyperbenthic niches close to the sea bottom. Our results point to the early introduction of prey–predator relationships into the pelagic realm, and to the increase of trophic complexity (three-level structure) during the Precambrian–Cambrian transition, thus laying the foundations of present-day marine food chains.

Keywords: Cambrian; fossil-lagerstätte; chaetognaths; predation; plankton; food chain

1. ARROW WORMS: KEY RECENT ZOOPLANKTON WITH AN OBSCURE EVOLUTIONARY HISTORY

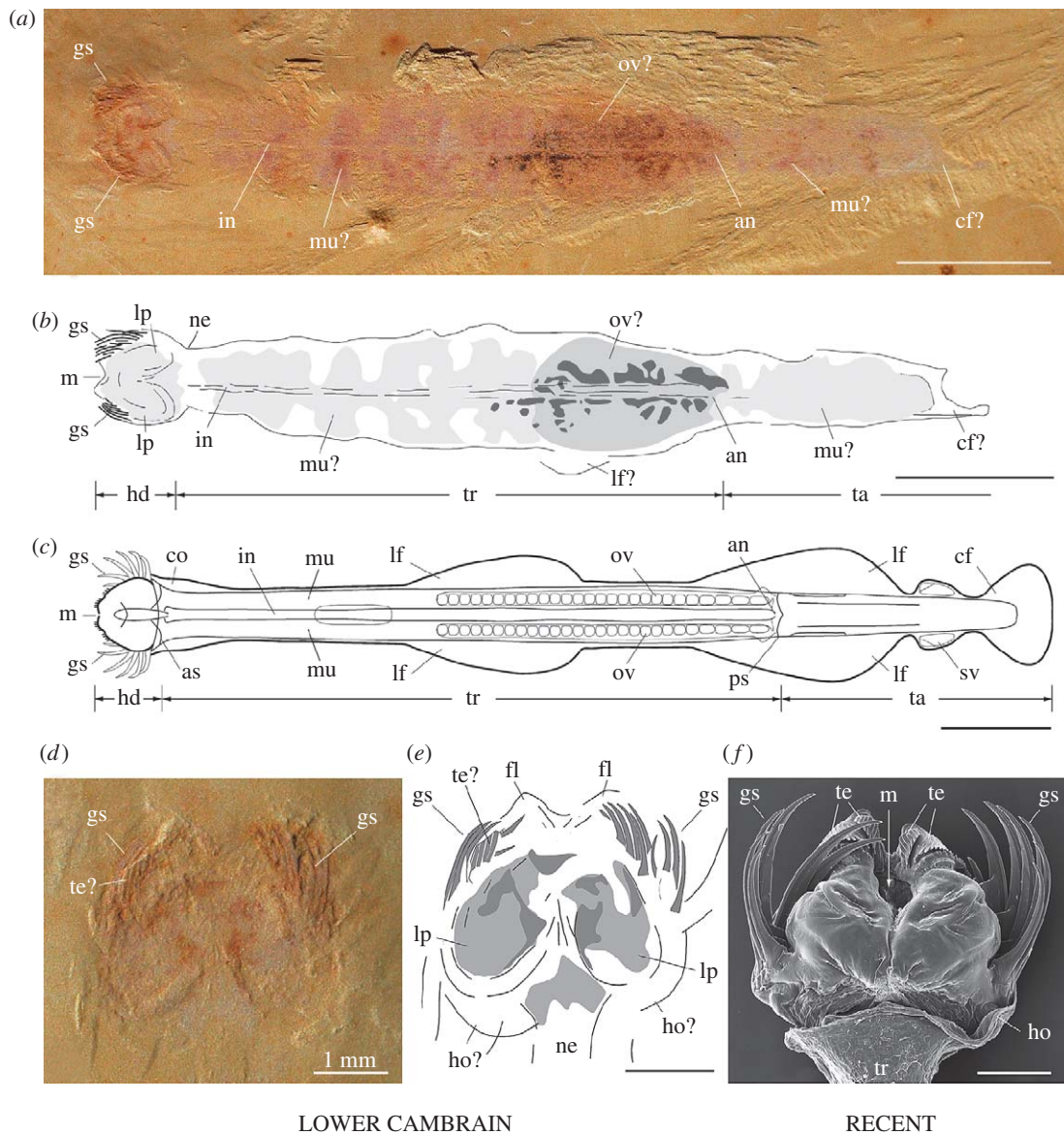
Chaetognaths ('arrow worms') are tiny (adults approx. 2–120 mm long), extremely prolific animals that are often second only to copepod crustaceans in terms of abundance and biomass in the world's oceans (5–15% biomass; Longhurst 1985). They play an important role in the marine trophic web both as consumers and as a food source for larger animals. Their bodies are streamlined, almost translucent and divided into head, trunk and tail regions by internal transverse septa. Their only hard parts with high potential for being fossilized are chitinous circumoral grasping spines and teeth (gs and te, respectively, in figure 1f) attached to lateral plates composed of collagen-like material. These three elements form a powerful feeding apparatus. Chaetognaths are predators and feed on a variety of mesoplanktonic organisms, their most frequent prey being copepod crustaceans (Terazaki 2000). Prey is detected by ciliary receptors, captured by the crown of spines, and forced into the mouth by the teeth. Although the majority of present-day chaetognaths are permanently pelagic (e.g. *Sagitta*), a few species are epibenthic and can attach to the substrate. Swimming involving rapid dorsoventral undula-

tions of the body alternates with motionless and passive sinking in the water column.

The evolutionary origin of chaetognaths has long been a subject of debate, but recent molecular studies (mitochondrial genes; Helfenbein *et al.* 2004; Papillon *et al.* 2004) suggest strong affinities with protostomes. The fossil record of Chaetognatha is extremely patchy and the evolutionary history of the group is still obscure. The oldest putative ancestors of the group are two specimens, both from the Early Cambrian Chengjiang biota: (i) *Eognathacantha ercainella* Chen and Huang (Chen & Huang 2002) is poorly preserved, making the recognition of most diagnostic features used for chaetognaths questionable (e.g. head), and (ii) *Protosagitta spinosa* Hu, first briefly reported in Chen *et al.* (2002) is fully described in the present paper (figure 1). The presence of chaetognaths in the Middle Cambrian Burgess Shale has long been discussed (e.g. *Oesia*, *Amiskwia*; Walcott 1911; Conway Morris 1977; Butterfield 2003; Szaniawski 2005) but needs confirmation from the study of unpublished material (D. E. G. Briggs 2005, personal communication). There is a lack of fossil data concerning the group until the Early Carboniferous (phosphatic concretion with numerous chaetognath grasping spines; Doguzhaeva *et al.* 2002). Chaetognaths possibly occur in the Upper Carboniferous Mazon Creek Lagerstätte (Schram 1973), but the very poor preservation of their body features allows no accurate interpretation. Another important set of fossil evidence

* Author for correspondence (jean.vannier@univ-lyon1.fr).

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LOWER CAMBRAIN

RECENT

Figure 1. Lower Cambrian and Recent chaetognaths. (a), (b), (d), (e) *Protosagitta spinosa* from the Chengjiang biota (Yu'anshan Formation, Ercaicun near Kunming, Yunnan Province, China, coll. Yunnan Institute of Geological Science, Kunming, no. Che-f-1001), general morphology and head. (c) Recent *Sagitta hispida*. (f) head of *Sagitta nagae*, Recent, Pacific Ocean (Suruga Bay, Japan), ventral view. Coloured areas (mainly iron iron oxide) represented by grey tones. an, anus; as, anterior septum; cf, caudal fin; co, collar; fl, frontal lobe; gs, grasping spines; hd, head; ho, hood; in, intestine; lf, lateral fin; lp, lateral plate; m, mouth; mu, muscles; ne, neck; ov, ovary; ps, posterior septum; sv, seminal vesicle; ta, tail; te, teeth; tr, trunk. Scale bars, 5 mm in (a), (b), 1 mm in (c)–(e) and 200 µm in (f).

that is discussed in the present paper comes from recurved spine-like small shelly fossils (SSF) known as protoconodonts (Bengtson 1976, 1983). Protoconodonts are abundant in the Cambrian of many regions and have been convincingly interpreted as the possible elements of chaetognath grasping apparatuses (e.g. Szaniawski 1980, 1982, 1983, 2002; Andres 1988; Azmi 1996).

2. SMALL PREDATORS FROM DEEP TIME: FOSSIL EVIDENCE

(a) An undoubted Early Cambrian chaetognath from the Chengjiang biota

Protosagitta spinosa Hu is a chaetognath from the Lower Cambrian Yu'anshan Formation (Chengjiang biota; Hou *et al.* 2004), Yunnan Province, China. It is approximately 35 mm long and is preserved in weathered yellowish mudstones (figure 1a). Most external and internal features

are defined by coloured mineral coating, mainly iron oxide possibly derived from an original pyrite composition (Gabbott *et al.* 2004). Calcium and phosphate are virtually absent both in the fossil and in the surrounding matrix (energy dispersive spectroscopy analysis). Elemental mapping of the grasping spines reveals a composition with dominantly Fe and O, minor P content and a lack of Ca. The body is clearly divided into three parts, with a short head (10% of the body length), a cylindrical trunk and a more slender tail whose distal part is missing. A superficial constriction (neck) marks the junction between head and trunk. The narrow digestive tract runs axially in the trunk and terminates at the boundary between trunk and tail. No fin system is present except the remains of possible caudal and lateral flaps.

The head shows two symmetrical sets of lateral grasping spines, and elliptical features interpreted here as the trace of lateral plates and associated muscles.

One set of spines has at least eight elements, each with a recurved shaft and a wider base (best preserved spine, 1.2 mm long). The opposite set of grasping spines is more closely packed and single elements more difficult to discern. Straight bar-like features below the left set of spines are interpreted as possible teeth (figure 1*d–f*). Most of the trunk and tail regions are filled with irregular pinkish to reddish patches that may represent original muscle masses. In Recent chaetognaths, longitudinal muscles comprise approximately 80% of the tissue volume (Shinn 1997; Casanova & Duvert 2002). The posterior part of the trunk of *P. spinosa* has a brownish elliptical area that contrasts with the overall pale colour of the fossil specimen. This area lies in the same position as the ovaries of Recent chaetognaths and may represent the outline of the fluid-containing space originally occupied by oocytes (figure 1*b,c*). The trunk of Recent chaetognaths contains no organs apart from the intestine and the ovaries.

It has been demonstrated (Gabbott *et al.* 2004) that pyritization controlled by nucleation crystal growth rates was largely responsible for replicating numerous types of non-mineralized tissues of Chengjiang animals, and that the type of pyrite mineralization reflects the more or less decay-susceptible nature of the tissues involved. Although SEM observations of the iron oxide coating of our unique specimen were not allowed, we suppose that colour differences observed in the fossil chaetognath express differences in the original tissue composition of the animal (e.g. chitinous grasping spines, more labile muscles and possible ovarian structures). In numerous key aspects of its morphology (overall streamlined shape, body division, bilateral symmetry, head armed with grasping spines and assumed teeth, muscles and ovaries), this fossil chaetognath is almost identical to Recent species (figure 1). Although unique, this specimen brings firm evidence that the chaetognath body plan was established in the Early Cambrian and confirms previous assumptions based on poorly preserved material (Chen & Huang 2002; *E. ercainella*). Whether *P. spinosa* and *E. ercainella*, both from the Yu'an-shan Formation, are conspecific is uncertain. Most differences observed between the two forms (e.g. tail and fin structure) may result from preservation factors.

Chaetognaths have long been assumed to be present in the Middle Cambrian Burgess Shale, with two plausible candidates, namely *Amiskwia sagittiformis* Walcott 1911 and *Oesia disjuncta* Walcott 1911. Although these two forms, especially *Oesia*, indeed superficially resemble Recent chaetognaths (overall shape, tissue distribution; Butterfield 1990, 2003; Szaniawski 2005), we see strong objections against their placement within the Chaetognatha, especially the lack of clear evidence of a grasping apparatus, the posterior location of the anus and the prominent cephalic tentacles of *Amiskwia*. The idea that the ancestral chaetognaths may have possessed distinctive features (Conway Morris 1977) is not confirmed by the Early Cambrian *P. spinosa* from Chengjiang. This displays no major difference from Recent chaetognaths (figure 1).

(b) Lowermost Cambrian chaetognaths: evidence from protoconodonts

A series of detailed studies have provided convincing evidence that protoconodont elements were likely to be the grasping spines of ancestral chaetognaths or animals

closely related to them (e.g. Szaniawski 1982, 1983, 2002; Andres 1988; Azmi 1996). The fact that chaetognaths are now firmly recognized in the Lower Cambrian of China (figure 1) revives this important issue and calls for an updated review. New key information (e.g. natural clusters and distribution) is given here from material collected over the Yangtze Platform of South China, especially at Kuanchuanpu, Hexi (both South Shaanxi), Shatan and Xinli (both North Sichuan) in the basal Cambrian of the *Anabarites trisulcatus–Protohertzina anabarica* Biozone (Steiner *et al.* 2003, 2004).

- (i) Both protoconodont elements and grasping spines of Recent chaetognaths have a recurved conical shape, a well-developed base, an internal cavity reaching the apex and longitudinal ornament (figure 2*a,b,e,f*; Nagasawa & Marumo 1973; Müller & Hinz 1991; Moreno & Kapp 2003; Qian *et al.* 2004). The size ranges of *P. anabarica* (length 1.0–2.5 mm), *Protohertzina unguiformis* (length 1.6–2.9 mm) and *Mongolodus longispinus* (length 0.4–1.3 mm) studied herein (basal Cambrian, China) are similar to that of Recent chaetognath grasping spines (length 0.3–2 mm).
- (ii) The wall of chaetognath grasping spines has a thick middle layer formed by closely packed fibrils of chitin (figure 3*a,b*) and thin inner and outer layers. A similar three-layered structure is present in all protoconodonts and is remarkably preserved in *Phakelodus* from Upper Cambrian of Poland (Szaniawski 1983, 2002). Similarly, the middle layer (approx. 50 µm thick) of *P. anabarica* from the basal Cambrian of China has a fibrous phosphatic fabric with elongated, imbricated crystallites running parallel to the shaft axis. The assumed outer layer (approx. 10 µm) is featureless with dominant apatite microspherules. The inner layer is often thickened by secondary phosphate growth (figure 3*c,d*).
- (iii) Chaetognath grasping spines grow through the combined secretion of pulp cells and anchor cells, and by basal accretion (Shinn 1997). This growth mode produces discrete oblique increments along the external surface of the shaft that are also visible in protoconodonts (e.g. Szaniawski 1983, 2002; Andres 1988; Müller & Hinz-Schallreuter 1998).
- (iv) The most compelling evidence that protoconodonts were indeed the elements of a grasping apparatus comes from natural clusters in acid residues (three-dimensional preservation; figure 2*b–d*) or flattened in shales (electronic supplementary material 3). These natural clusters typically consist of crescent-like half-apparatuses with 2–13 elements. More rarely, these assemblages are found in two symmetrical sets that strongly recall the bilateral series of grasping spines (4–14 each; figure 1*f*) that surround the mouth of modern chaetognaths. Protoconodont elements within individual clusters display moderate size and shape variations (Müller & Andres 1976; Müller & Hinz 1991) comparable with those observed in chaetognath apparatuses. A well-preserved *Mongolodus* cluster from the basal Cambrian of China is shown here (figure 2*c,d*). It has five hooks oriented in the same

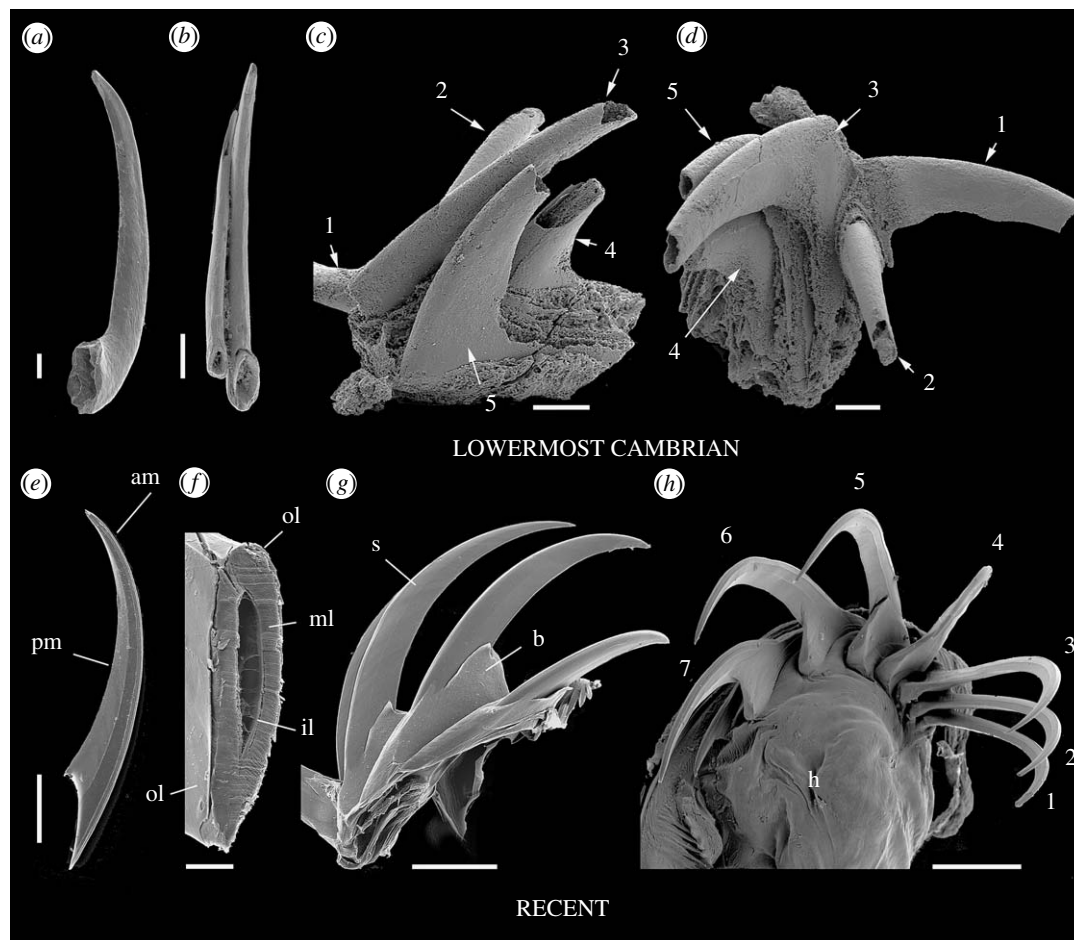


Figure 2. Protoconodonts from the lowermost Cambrian Kuanchuanpu Formation, Hexi Shaanxi Province, China (a)–(b) and Kuanchuanpu (c)–(d), both, and grasping apparatus of Recent chaetognaths (e)–(h). (a), (b) *Protohertzina unguiformis*, isolated element and natural cluster (coll. TU Berlin, no. He22-Re and He22-195, respectively). (c), (d) *Mongolodus longispinus*, cluster of five elements seen in different orientations (Kua125-166). (e) *Sagitta nagae* (base removed by NaOH dissolution). (f) *Eukrohnia hamata*, transverse section through grasping spine showing details of chitinous structure. (g), (h) Dissected cluster of grasping spines of *Sagitta ferox* and half-apparatus of *Sagitta lyra*. am, anterior margin; b, base; h, head; il, inner layer; ml, middle layer; ol, outer layer; pm, posterior margin; s, shaft. Protoconodonts were obtained, along with other small shelly fossils, by digestion of phosphatic carbonates in 10% buffered acetic acid and hand-picked from residues under the binocular microscope. Scale bars, 200 μm in (b)–(d), (g) and (h), 100 μm in (a) and (e), and 20 μm in (f).

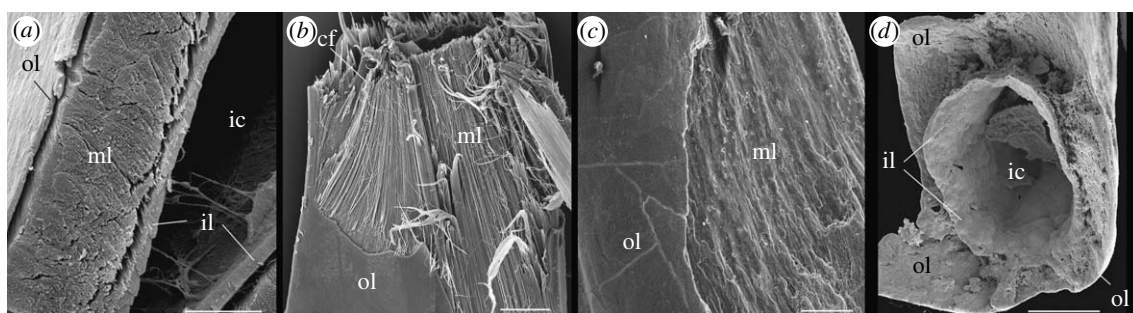


Figure 3. Wall microstructure of Recent chaetognath grasping spines (a, b) and lowermost Cambrian protoconodonts (c, d), from the Kuanchuanpu Formation, Hexi, Shaanxi Province, China. (a) *Eukrohnia hamata*, three-layered chitinous structure. (b) *Sagitta lyra*, exfoliated distal part showing chitin fibrils. (c) *Protohertzina anabarica* showing fibrous structure of middle layer. (d) *P. unguiformis*, basal part showing inner and outer layers. cf, chitin fibrils; ic, inner cavity; il, inner layer; ml, middle layer; ol, outer layer. Scale bars, 5 μm in (a), 10 μm in (b) 20 μm in (c), and 100 μm in (d).

direction and all inserted within a single basal structure. This cluster is unlikely to result from the cementation of isolated elements deposited in sediment and, instead, is represented as a natural feature closely resembling the half-grasping apparatus of a chaetognath (figure 2g). The lacunar phosphatized structure that surrounds the base of the hooks is reminiscent of the basal electron-lucent

cuticle of chaetognath grasping spines (Shinn 1997), which clearly supports the view that protoconodont hooks, similar to chaetognath spines, had a soft tissue basal support structure. Similar *Mongolodus* clusters with only two to four elements occur in the lowermost Cambrian of northern India (Azmi 1996). The presence of possible teeth associated with protoconodont

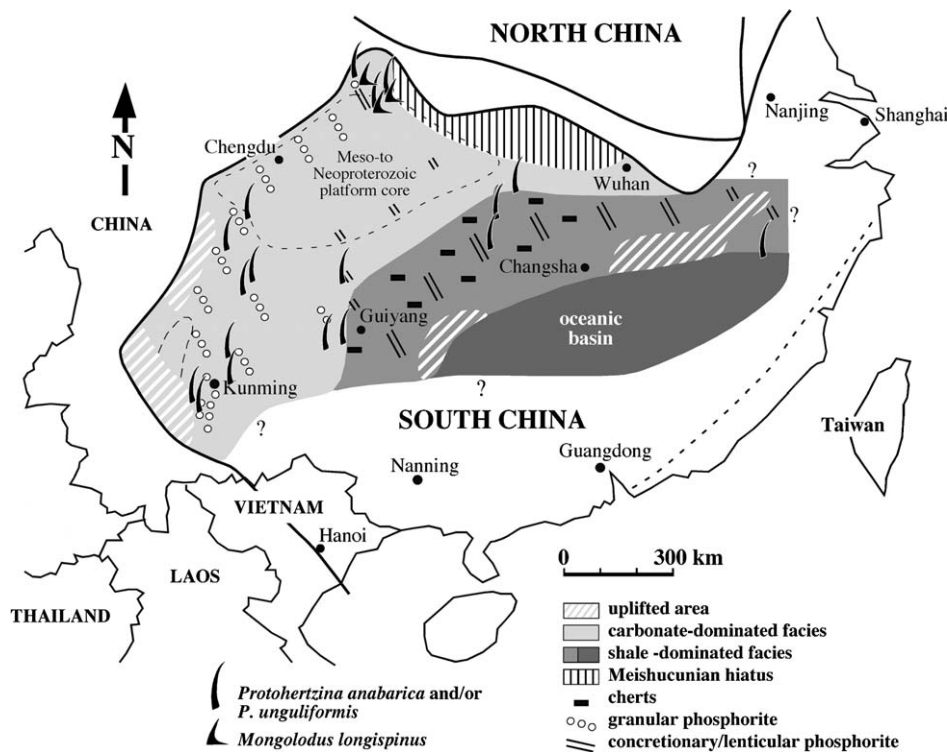


Figure 4. Facies reconstruction and distribution of protoconodonts over the Yang Tze Platform, South China, for the earliest Cambrian (Meishucunian Stage). *Protohertzina anabarica*, *P. unguiformis* and *Mongolodus longispinus*.

natural clusters (Szaniawski 2002) also supports the chaetognath affinities of protoconodonts.

- (v) The grasping apparatus of the chaetognath from the Chengjiang biota (*P. spinosa*; figure 1) closely resembles protoconodont clusters by its size (electronic supplementary material 3) and its closely packed crescent-like arrangement.

It becomes clear from these five lines of morphological evidence that the animals bearing protoconodont sclerites were chaetognaths or belonged to a group closely related to them. The obvious raptorial function of their apparatus and their lowermost Cambrian occurrence place the chaetognaths *s.l.* among the earliest marine predators (Szaniawski 2002). The complexity of their feeding apparatus, involving sclerites and associated muscle and neuronal systems, points to the Precambrian origin of the group. Chaetognaths were obviously not restricted to the single species from the Chengjiang biota (figure 1) and were already abundant, widespread and diverse in the earliest Cambrian (electronic supplementary material 3; Qian *et al.* 2004). *Protohertzina unguiformis* (figure 2*a,b*) represents up to 3.6% of the SSF assemblages in southern Shaanxi (up to 1400 specimens per kilogram of rock).

3. CHAETOGNATHS IN THE EARLY CAMBRIAN FOOD CHAIN

Morphology, biometrics and distribution patterns support a pelagic rather than a benthic lifestyle for the Early Cambrian chaetognaths *s.l.* Some Recent benthic chaetognaths use adhesive organs to attach to solid substrates (Kapp 1991; Shinn 1997). No such features are present in the Chengjiang specimen (figure 1). The musculature of Recent chaetognaths is essentially longitudinal and concentrated in the trunk and in the tail (Bone & Duvert 1991). Additional transverse muscles, present in all Recent

benthic chaetognath species, could not be discerned in the Chengjiang specimen. The relative lengths of the trunk and the tail vary between Recent benthic and pelagic chaetognath species (Shinn 1997; Casanova 1999). We calculated the body ratios of 52 pelagic and 12 benthic Recent species and those of the two specimens from the Chengjiang biota. Multivariate analysis displays a benthic and a pelagic group for the Recent species and places the Cambrian specimens within the pelagic group (electronic supplementary material 1 and 2). The chaetognaths from the Chengjiang biota are preserved in mudstones deposited in a shallow-water environment (approx. 50–200 m depth; Hou *et al.* 2004; Hu 2005). Protoconodonts are recorded worldwide (electronic supplementary material 3). *Protohertzina* occurs around the margins of several major Early Cambrian palaeocontinents, such as Laurentia, Siberia, Kazakhstan, Mongolia and South China, and its two species, *P. anabarica* and *P. unguiformis* (figure 2*a,b*), have a widespread occurrence over the Yang Tze Platform, being associated with both shallow and deeper water lithofacies (figure 4). These distribution patterns suggest wide oceanic dispersal capabilities and infer a pelagic lifestyle.

Recent arrow worms achieve predation by their grasping apparatus (spines and teeth) in addition to neurotoxins, thus possibly explaining their ability to capture relatively large prey (e.g. fish larvae; Thuesen & Bieri 1987; Thuesen *et al.* 1988). The presence of a similar feeding apparatus (grasping spines and teeth; figures 1*d,e*, 2*i,j*) in the Early Cambrian ancestors of the group is consistent with a function for the capture of small motile or drifting prey of possibly several millimetres long. The exact ecological niche of these early predators is difficult to ascertain but was obviously determined by the availability of prey in the water column. Evidence for potential prey, such as mesozooplankton (0.2–20 mm) in the Early Cambrian oceans is sparse and limited to possible filter-feeding crustacean-like organisms

(Butterfield 1994, 2001a,b) and small bivalved arthropods (Steiner *et al.* 1993) found in deeper water black shales. Other swimmers and drifters, such as *Isoxys* (Vannier & Chen 2001), anomalocaridids (Vannier & Chen 2005), ctenophores (Chen & Zhou 1997) and medusoids (Zhu *et al.* 2002) were mostly larger (greater than 20 mm) and nektonic, and fall beyond the size range of potential prey for chaetognaths. We think that hyperbenthic niches (approx. 1–10 m above bottom) may have provided Early Cambrian predator chaetognaths and protoconodont animals with an abundant food source, such as tiny arthropods (e.g. bradoriids and copepod-like *Ercaia*; Shu *et al.* 1999; Chen *et al.* 2001) and the possible meroplanktonic larval stages of various animal groups (e.g. naraoiid arthropods; Zhang *et al.* 2003). Arthropods account for more than 60% of the species found in the Chengjiang biota (Hou *et al.* 2004). Our hypothesis is supported by the fact that Recent hyperbenthic communities are intensively exploited for food by mature chaetognaths. For example, submersible dives using video recordings revealed extremely high concentrations of *Parasagitta elegans* in the hyperbenthic zone within a few metres of the bottom in Conception Bay, Newfoundland (Choe & Deibel 2000). That Early Cambrian chaetognaths lived in the epipelagic and mesopelagic zones remains a plausible alternative. However, no fossil evidence supports the idea that this part of the water column may have provided a suitable and sufficient food source for chaetognaths.

Based on fossil evidence from phytoplankton and assumed filter-feeding pelagic arthropods, Butterfield (1994, 2001a,b) suggested that the introduction of herbivorous zooplankton in the water column during the P–C transition considerably modified the structure of the early marine ecosystem. The introduction of this new tier is likely to have triggered a cascade of effects on the primary production, the phytoplankton evolution (e.g. Knoll 1994) and, eventually, set up the first coupling between pelagos and benthos (e.g. via faecal pellets; Butterfield 2001a,b). Our results suggest that the complexity of the trophic structure may have reached an even more advanced level during the Precambrian–Cambrian transition with the construction of a three-level trophic structure (primary producers, herbivorous and predator mesozooplankton). The widespread introduction of prey–predator relationships into the pelagic realm during the P–C transition via the chaetognaths seems to represent another important innovation in the tiering and functioning of early marine ecosystem that may have laid the foundations of modern-style marine food chains. Other potential pelagic consumers, such as macrozooplankton (e.g. ctenophores and eldoniids) and nekton (e.g. early chordates, vetulicolids and arthropods), were certainly inhabiting the water column, although very little is known of their exact lifestyles, diet and feeding strategies. There remains the crucial and unresolved question of when and how metazoans entered the plankton (Rigby & Milsom 1996). This key event may have resulted from different factors, such as possible changes in larval development (e.g. meroplanktonic stages) and pressure from benthic predators (Butterfield 1997). Hyperbenthic niches close to the sea bottom may have represented transitional habitats for the pioneer invaders of the water column (e.g. chaetognaths) and a step towards a subsequent and extensive occupation of the pelagic realm.

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REFERENCES

- Andres, D. 1988 Strukturen, Apparate und Phylogenie primitiver Conodonten. *Palaeontographica Abt. A* **200**, 105–152.
- Azmi, R. J. 1996 Evidence for soft tissue basal support in earliest Cambrian protoconodonts from the Lesser Himalaya: conodont function and affinity. In *Contributions to the 15th Indian Colloquium on Micropalaeontology and Stratigraphy, Dehra Dun* (ed. J. Pandey, R. J. Azmi, A. Bhandari, & A. Dave), pp. 457–463. Dehra Dun, India: Wadia Institute of Himalayan Geology.
- Bengtson, S. 1976 The structure of some Middle Cambrian conodonts, and the early evolution of conodont structure and function. *Lethaia* **9**, 185–206.
- Bengtson, S. 1983 The early history of the Conodonta. *Fossils and Strata* **15**, 5–19.
- Bone, Q. & Duvert, M. 1991 Locomotion and buoyancy. In *The biology of chaetognaths* (ed. Q. Bone, H. Kapp & A. C. Pierrot-Bults), pp. 32–44. Oxford, UK: Oxford University Press.
- Butterfield, N. J. 1990 Organic preservation of non-mineralizing organisms and the taphonomy of the Burgess Shale. *Paleobiology* **16**, 272–286.
- Butterfield, N. J. 1994 Burgess Shale-type fossils from a Lower Cambrian shallow shelf sequence in northwestern Canada. *Nature* **369**, 477–479. (doi:10.1038/369477a0)
- Butterfield, N. J. 1997 Plankton ecology and the Proterozoic–Phanerozoic transition. *Paleobiology* **23**, 247–262.
- Butterfield, N. J. 2001a Ecology and evolution of Cambrian plankton. In *The ecology of the Cambrian radiation* (ed. A. Y. Zhuravlev & R. Riding), pp. 200–216. New York, NY: Columbia University Press.
- Butterfield, N. J. 2001b Cambrian food webs. In *Palaebio* **II** (ed. D. E. G. Briggs & P. R. Crowther), pp. 40–43. Oxford, UK: Blackwell Science.
- Butterfield, N. J. 2003 Exceptional fossil preservation and the Cambrian explosion. *Integr. Comp. Biol.* **43**, 166–177. (doi:10.1093/icb/43.1.166)
- Casanova, J. P. 1999 Chaetognatha. In *South Atlantic Zooplankton* (ed. D. Boltovskoy), pp. 1353–1374. Leiden, Germany: Backhuys Publishers.
- Casanova, J.-P. & Duvert, M. 2002 Comparative studies and evolution of muscles in chaetognaths. *Mar. Biol.* **141**, 925–938. (doi:10.1007/s00227-002-0889-3)
- Chen, J.-Y. & Huang, D.-Y. 2002 A possible Lower Cambrian chaetognath (arrow worm). *Science* **298**, 187. (doi:10.1126/science.1075059)
- Chen, J.-Y. & Zhou, G.-Q. 1997 Biology of the Chengjiang fauna. *Bull. Nat. Mus. Nat. Sci.* **10**, 11–105.
- Chen, J.-Y., Vannier, J. & Huang, D.-Y. 2001 The origin of crustaceans: new evidence from the Early Cambrian of China. *Proc. R. Soc. B* **268**, 2181–2187. (doi:10.1098/rspb.2001.1779)
- Chen, L.-Z., Luo, H.-L., Hu, S.-X., Yin, J.-Y., Jiang, Z.-W., Wu, Z.-L., Li, F. & Chen, A.-L. 2002 *Early Cambrian Chengjiang Fauna in Eastern Yunnan, China*. Kunming, China: Yunnan Science and Technology Press.
- Choe, N. & Deibel, D. 2000 Seasonal vertical distribution and population dynamics of the chaetognath *Parasagitta*

- elegans* in the water column and hyperbenthic zone of Conception Bay, Newfoundland. *Mar. Biol.* **137**, 847–885. (doi:10.1007/s002270000413)
- Conway Morris, S. 1977 A redescription of the Middle Cambrian worm *Amiskwia sagittiformis* Walcott from the Burgess Shale of British Columbia. *Paläontologische Zeitschrift* **51**, 271–287.
- Doguzhaeva, L. A., Mutvei, H. & Mapes, R. H. 2002 Chaetognath grasping spines from the Upper Mississippian of Arkansas (USA). *Acta Palaeontologica Polonica* **47**, 421–430.
- Gabbott, S. E., Hou, X.-G., Norry, M. & Siveter, D. J. 2004 Preservation of Early Cambrian animals of the Chengjiang biota. *Geology* **32**, 901–904. (doi:10.1130/G20640.1)
- Helfenbein, K. G., Fourcade, H. M., Vanjani, R. G. & Boore, J. L. 2004 The mitochondrial genome of *Paraspadella gotoi* is highly reduced and reveals that chaetognaths are a sister group of protostomes. *Proc. Natl Acad. Sci. USA* **101**, 10 639–10 643. (doi:10.1073/pnas.0400941101)
- Hou, X.-G., Aldridge, R. J., Bergström, J., Siveter, D. J., Siveter, D. J. & Feng, X.-H. 2004 *The Cambrian Fossils of Chengjiang, China*. Malden, MA: Blackwell Publishing.
- Hu, S. X. 2005 Taphonomy and palaeoecology of the Early Cambrian Chengjiang Biota from Eastern Yunnan, China. *Berliner Paläobiologische Abhandlungen* **7**, 1–197.
- Kapp, H. 1991 Morphology and anatomy. In *The biology of Chaetognaths* (ed. Q. Bone, H. Kapp & A. C. Pierrot-Bults), pp. 5–17. Oxford, UK: Oxford University Press.
- Knoll, A. H. 1994 Proterozoic and Early Cambrian protists: evidence for accelerating evolutionary tempo. *Proc. Natl Acad. Sci. USA* **91**, 6743–6750. (doi:10.1073/pnas.91.15.6743)
- Longhurst, A. 1985 The structure and evolution of plankton communities. *Prog. Oceanogr.* **15**, 1–35. (doi:10.1016/0079-6611(85)90036-9)
- Moreno, I. & Kapp, H. 2003 Structures of grasping spines and teeth in three species of chaetognaths from Antarctic waters. *Polar Biol.* **26**, 143–150.
- Müller, K. J. & Andres, D. A. 1976 Eine Conodontengruppe von *Prooneotodus tenuis* (Müller, 1959) in natürlichem Zusammenhang aus dem Oberen Kambrium von Schweden. *Paläontologische Zeitschrift* **50**, 193–200.
- Müller, K. J. & Hinz, I. 1991 Upper Cambrian conodonts from Sweden. *Fossils and Strata* **28**, 1–153.
- Müller, K. J. & Hinz-Schallreuter, I. 1998 Internal structure of Cambrian conodonts. *Ź. Paleontol.* **72**, 91–112.
- Nagasawa, S. & Marumo, R. 1973 Structure of grasping spines of six chaetognath species observed by scanning electron microscopy. *Bull. Plankton Soc. Jpn* **19**, 5–15.
- Papillon, D., Perez, Y., Caubit, X. & Le Parco, Y. 2004 Identification of chaetognaths as protostomes is supported by the analysis of their mitochondrial genome. *Mol. Biol. Evol.* **21**, 2122–2129. (doi:10.1093/molbev/msh229)
- Qian, Y., Li, G.-X., Zhu, M.-Y., Steiner, M. & Erdtmann, B.-D. 2004 Early Cambrian protoconodonts and conodont-like fossils from China: taxonomic revisions and stratigraphic implications. *Prog. Nat. Sci.* **14**, 173–180. (doi:10.1080/10020070412331343321)
- Rigby, S. & Milsom, C. 1996 Benthic origin of zooplankton: an environmentally determined macroevolutionary effect. *Geology* **24**, 52–54. (doi:10.1130/0091-7613(1996)024<0052:BOOZAE>2.3.CO;2)
- Schram, F. R. 1973 Pseudocoelomates and a nemertine from the Illinois Pennsylvanian. *Ź. Pal.* **47**, 985–989.
- Shinn, G. L. 1997 Chaetognatha. In *Microscopic anatomy of invertebrates*, vol. 15 (ed. F. W. Harrison & E. E. Ruppert) *Hemichordata, Chaetognatha and the invertebrate chordates*, pp. 103–220. New York, NY: Wiley.
- Shu, D.-G., Vannier, J., Luo, H.-L., Chen, L., Zhang, X.-L. & Hu, S.-X. 1999 The anatomy and lifestyle of *Kunmingella* (Arthropoda, Bradiorida) from the Chengjiang fossil Lagerstätte (early Cambrian; southern China). *Lethaia* **42**, 279–298.
- Steiner, M., Mehl, D., Reitner, J. & Erdtmann, B.-D. 1993 Oldest entirely preserved sponges and other fossils from the lowermost Cambrian and a new facies reconstruction of the Yangtze Platform (China). *Berliner Geowiss. Abh.* **9**, 293–329.
- Steiner, M., Li, G.-X., Qian, Y., Zhu, M.-Y. & Erdtmann, B.-D. 2003 Lower Cambrian small shelly faunas from Zhejiang (China) and their biostratigraphical implications. *Prog. Nat. Sci.* **13**, 852–860. (doi:10.1080/10020070312331344550)
- Steiner, M., Li, G.-X., Qian, Y. & Zhu, M.-Y. 2004 Lower Cambrian Small Shelly Fossils of northern Sichuan and southern Shaanxi (China), and their biostratigraphic importance. *Geobios* **37**, 259–275. (doi:10.1016/j.geobios.2003.08.001)
- Szaniawski, H. 1980 Fused clusters of paraconodonts. In *Abstracts of the 2nd European Conodont Symposium (ECOS II)* (ed. H. P. Schönlaub) *Abhandlungen der Geologischen Landesanstalt Wien*, vol. 35.
- Szaniawski, H. 1982 Chaetognath grasping spines recognized among Cambrian protoconodonts. *Ź. Paleontol.* **56**, 806–810.
- Szaniawski, H. 1983 Structure of protoconodont elements. *Fossils and Strata* **15**, 21–27.
- Szaniawski, H. 2002 New evidence for the protoconodont origin of chaetognaths. *Acta Palaeontologica Polonica* **47**, 405–419.
- Szaniawski, H. 2005 Cambrian chaetognaths recognized in Burgess Shale fossils. *Acta Pal. Polonica* **50**, 1–8.
- Terazaki, M. 2000 Feeding of carnivorous zooplankton, chaetognaths in the Pacific. In *Dynamics and characterization of marine organic matter* (ed. N. Handa, E. Tanoue & T. Hama), pp. 257–276. Dordrecht, The Netherlands: Kluwer Academic.
- Thuesen, E. V. & Bieri, R. 1987 Tooth structure and buccal pores in the chaetognath *Flacisagitta hexaptera* and their relation to the capture of fish larvae and copepods. *Can. Ź. Zool.* **65**, 181–187.
- Thuesen, E. V., Kogue, K., Hashimoto, K. & Nemoto, T. 1998 Poison arrow worms: a tetrodotoxin venom in the marine phylum Chaetognatha. *Ź. Exp. Mar. Biol. Ecol.* **116**, 249–256. (doi:10.1016/0022-0981(88)90030-5)
- Vannier, J. & Chen, J.-Y. 2001 The Early Cambrian colonization of pelagic niches exemplified by *Isoxys* (Arthropoda). *Lethaia* **33**, 295–311.
- Vannier, J. & Chen, J.-Y. 2005 Early Cambrian food chain: new evidence from fossil aggregates in the Maotianshan Shale Biota, SW China. *Palaios* **20**, 3–26. (doi:10.2110/palo.2003.p03-40)
- Walcott, C. D. 1911 Cambrian Geology and Paleontology II, No.5—Middle Cambrian annelids. *Smithsonian Misc. Coll.* **57**, 109–144.
- Zhang, X.-L., Han, J., Zhang, Z.-F., Liu, H.-Q. & Shu, D.-G. 2003 Reconsideration of the supposed naraoiid larva from the Early Cambrian Chengjiang Lagerstätte, South China. *Palaeontology* **46**, 447–465. (doi:10.1111/1475-4983.00307)
- Zhu, M.-Y., Zhao, Y.-L. & Chen, J.-Y. 2002 Revision of the Cambrian medusiform animals *Stellostomites eumorphus* Sun et Hou and *Pararotadiscus guizhouensis* (Zhao et Zhu) from South China. *Geobios* **35**, 165–185. (doi:10.1016/S0016-6995(02)00025-6)