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DOI: 10.1016/j.cub.2006.07.005

## Phylogeny: The Continuing Classificatory Conundrum of Chaetognaths

The phylogenetic conundrum posed by the Chaetognatha, a cryptic phylum consisting largely of planktonic predators, is the subject of two short papers in this issue of *Current Biology*. These analyses go some way towards defining the phylogenetic position of the chaetognaths, which possess features apparently spanning the protostome/deuterostome divide.

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It would be difficult to invent a more bizarre group of creatures than the chaetognaths or arrow worms, (literally ‘bristle jaws’). The chaetognaths are an ancient lineage of invertebrates that shares some characteristics with just about every other major invertebrate phylum and has consequently puzzled taxonomists ever since its original description in 1769. Darwin described chaetognaths as “remarkable for the obscurity of their affinities” and they have puzzled a succession of eminent zoologists ever since [1]. Though unfamiliar to most biologists, chaetognaths are typically the most abundant planktonic predators, sometimes accounting for more than 10% of zooplankton biomass and being outnumbered only by their major prey, the copepods. Approximately 20 genera have been described, containing more than 100 species ([2], see also: <http://academic.evergreen.edu/t/thuesene/chaetognaths/chaetognaths.htm>).

Although most chaetognaths are only a few mm in size and planktonic, there are some inshore benthic and deep-water species that may be much larger, up to 12 cm in length. The basic body plan

of the chaetognaths (Figure 1A,B) is relatively constant across the phylum, although details may vary considerably. The structure of the nervous system reveals little about the evolutionary affinities of

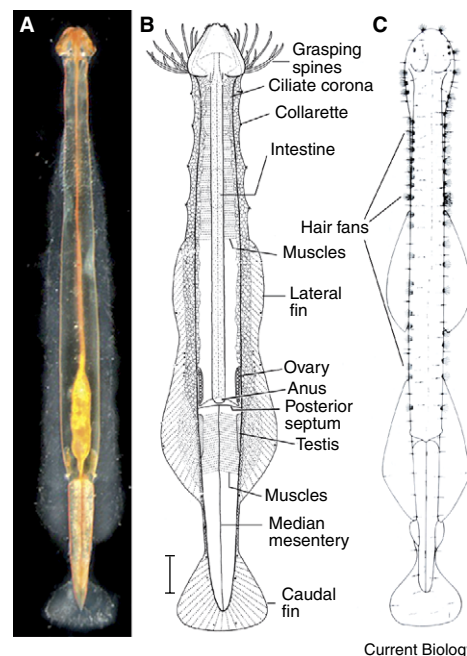
Figure 1. Chaetognath morphology.

(A) The deep water chaetognath *Eukrohnia* sp. from the Sargasso Sea (Photo courtesy Russ Hopcroft/UAF/NOAA/CoML). In contrast to most shallow water forms, this species is pigmented, making the internal organs easily visible. (B) This labelled drawing of the pelagic chaetognath, *Heterokrohnia*, provides a good introduction to the basic features of chaetognath anatomy. Some authors divide the body into head and trunk, while others add a tail, dividing the trunk at the posterior septum. There are three body cavities, which, together with the cuticle and the longitudinal muscles, form a hydrostatic skeleton. One or two pairs of longitudinal fins provide stabilisation, while the

flattened caudal fin provides locomotory power. There is no circulatory system and no specialised excretory system. The anterior grasping spines used in prey capture are shown spread, although they are normally folded under a hood, which presumably serves the dual purpose of protecting them and streamlining the head during swimming. Eggs are released into the thoracic coelomic space and sperm into the coelomic space of the tail. Modified from [20], with permission. (C) Drawing of *Sagitta hispida* showing the closely spaced hair fans which presumably provide the sensory input required for such complex behaviours as mating and prey capture. Modified with permission from [4].

chaetognaths, although it bears some resemblance to the nervous systems of nematodes, kinorhynchs and priapulids [1]. The age of the phylum is borne out by fossils from the Cambrian Burgess Shale which show a remarkable resemblance to modern chaetognaths [3] (Figure 2), suggesting chaetognaths have existed without major morphological change for at least 500 million years. Chaetognaths are unusual among marine invertebrates in that they are direct developers, hatching from the egg essentially as small adults rather than as a distinct larval stage.

Chaetognaths appear to rely mainly on vibrations for information



Current Biology

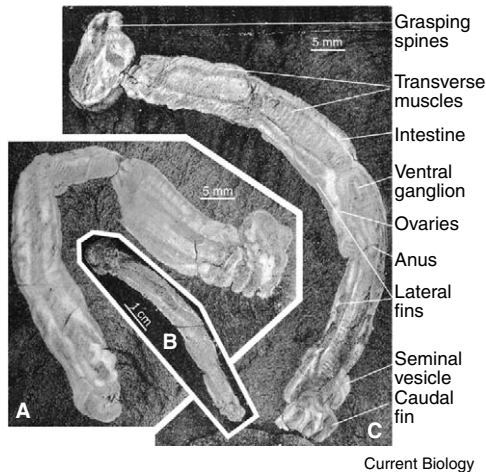


Figure 2. Fossil chaetognaths.

The assumption that modern chaetognaths epitomize an ancient and successful anatomical design, which has remained unchanged since the Cambrian, is confirmed by beautiful fossils from the Burgess Shale, such as this *Oesia disjuncta*, in which many modern anatomical features have been tentatively identified (A–C). Modified with permission from [3].

about their environment and they can hunt in darkness. Their vibration sense is mediated through fans of mechanoreceptive hairs [4] (Figure 1C) which apparently play critical roles in all behaviours. In addition to these hairs, chaetognaths have two eyes. In some genera the eyes are inverted, with the photoreceptor cells pointing inward and embedded in a single large pigment cell while in others the eyes are everted with the photoreceptors pointing outward. The eyes have relatively few receptor units and lack lenses, so they apparently are not image-forming. However, two features that appear to be unique to chaetognath eyes are the conical body, for which some have suggested an optical role, and the unusual lamellar organization of the distal segment of at least some species [5]. In addition, their photoreceptor cell is clearly ciliary, in contrast to the rhabdomeric photoreceptors found in many invertebrates. Based on this eye structure, chaetognaths should have an opsin characteristic of ciliary type eyes, thus adding to the other molecular evidence against ecdysozoan affinities.

#### Behaviour – Feeding, Sexual and Other Weirdness

Chaetognaths are remarkable killers that appear to hunt primarily by sensing vibration using the hair fans (<http://www.cc.mie-u.ac.jp/~sagitta/lab.html>). The chaetognath *Spadella cephaloptera* will attack a metal

or glass probe vibrating at an appropriate frequency and amplitude with the same ferocity as it will attack a copepod [6]. Chaetognaths swallow their prey whole and will apparently eat anything that can be accommodated in their mouth. As the chaetognath strikes its prey, the hood over the grasping spines is withdrawn, allowing them to fly outward and form a net that surrounds the prey and brings it into contact with the formidable teeth around the mouth. As if these impressive weapons weren't enough, at least some chaetognaths appear to use the potent neurotoxin tetrodotoxin to stun potential prey [7]. The exact source of the venom was not identified but it is most likely produced by symbiotic bacteria and injected from one of the structures surrounding the mouth.

Chaetognaths seem to spend most of their time gliding on their fins, until eventually they begin to sink. Sinking is counteracted by swimming with a series of short, rapid darts, followed by another glide. Some species show diurnal vertical migrations, tending to maintain themselves in a constant twilight zone. There is also a tendency for larger chaetognaths to occur at greater depths. According to Marshall [8], *Sagitta gazellae* in the Southern Ocean sink deeper in the water column as they mature, releasing their eggs at about 1000 m. The eggs are buoyant and float upward, hatching at about 250 m. The hatchlings spend the summer

months in the upper 100 m, descending to the 100–250 m zone during the winter.

All chaetognath species that have been studied are hermaphrodites with testes in the tail and ovaries in the posterior trunk, the latter maturing only after the tail coeloms are filled with sperm. Self-fertilization has been described in *Sagitta*, but it is unclear whether this occurs in nature. Mating specimens of *Spadella cephaloptera* become aligned head to tail in parallel and simultaneously exchange sperm packets [9], although one-way transfer has also been reported. The most amazing mating behaviour, starting with a dance and ending with a leap to deposit the sperm bundle or spermatophore, has been described for *Paraspadella gotoi* [10] (pictured at [http://www.uibk.ac.at/zoology/ultra/evol\\_ecol/former\\_research/paraspadella/mating/mating\\_behaviour.html](http://www.uibk.ac.at/zoology/ultra/evol_ecol/former_research/paraspadella/mating/mating_behaviour.html)). This complex behaviour is probably mediated by the mechanoreceptive hair fans [4].

Probably the strangest chaetognath of all is a deep-sea form, *Bathybelos typhlops*, described originally from a single specimen from a depth of 2,500 m in the Gulf of Mexico. This specimen showed many unusual features including rayless lateral fins, an elongated head and a dorsal nervous system, in contrast to the usual ventral one. *Bathybelos* is apparently a bottom-living form, living with the ventral side pressed into bottom sediments containing very low oxygen [11]. Chaetognaths lack a circulatory system, so their tissues are dependent on diffusion for oxygen. Under such conditions, there would presumably be selective pressure for the normally ventral nervous system to move dorsally. More specimens of benthic deep-water chaetognaths are eagerly awaited.

**Where Do Chaetognaths Fit in the Scheme of Living Things?**  
Ever since their discovery, the phylogenetic position of chaetognaths has posed

a conundrum. In particular, it has never been clear to which of the two major subdivisions of the animal kingdom they belong: Are chaetognaths protostomes or deuterostomes? Two short papers [12,13] appearing in this issue of *Current Biology* summarise some of the reasons for this obscurity and shed some light on chaetognath evolutionary affinities. By reporting moderate sized EST datasets for *Spadella cephaloptera* [12] and *Flaccisagittaenflata* [13] and applying some innovative methods of analysis, these papers significantly advance the field. The analyses in one of the papers [12] were based on 78 ribosomal protein sequences, using the novel approach of making comparisons with composite sequence collections consisting of the closest matching sequences across each of 14 animal phyla. The second paper [13] includes analyses based on 72 genes known from the previous work of Herve Philippe [14] to be appropriate for deep level phylogenetics.

Both analyses clearly demonstrate that chaetognaths are protostomes, despite showing deuterostome-like features of early embryonic development. However, their position within the protostomes remains unclear and controversial. In part, this reflects the debate still raging over acceptance of the 'new' phylogeny — the splitting of the protostomes into Ecdysozoa and Lophotrochozoa. It is hardly surprising that some of the 'minor' phyla, such as the chaetognaths, cannot yet be accurately placed when there is still disagreement over the broad framework, with many authors remaining unconvinced that the 'old' phylogeny needs revision. The new phylogeny recognizes a clade of moulting animals (the Ecdysozoa) within the protostomes, uniting some phyla previously considered to be only very distantly related (e.g. nematodes and arthropods), and also splits some traditional groupings (e.g. arthropods and annelids). At the core of the disagreement is the fact that the new phylogeny is revealed only with a specific and rather limited

gene set. The fact that 'blind' analyses based on many other genes are not consistent with the new phylogeny has led to its rejection by some authors.

As there appear to be some characteristic differences in the Hox clusters of lophotrochozoans and ecdysozoans this may be a fruitful and informative area for future work. Le Parco's group has done some preliminary work [15] on the *Spadella cephaloptera* Hox genes, but much more detailed analyses are clearly warranted.

Gene expression patterns could be another useful type of information for clarifying the evolutionary relationships of chaetognaths. Unfortunately, very few chaetognath gene expression patterns have been reported to date, and the take-home message from those that have, e.g. Brachyury [16], is that the chaetognaths are mainstream bilaterians. Hopefully the availability of the new EST datasets will lead to many more expression patterns being determined, which also could advance our understanding of several important aspects of chaetognath biology.

We have, as yet, a quite limited view of the biology of the phylum Chaetognatha as a whole and much of what we know, particularly concerning behaviour, is derived from a handful of genera. The only extensive molecular phylogenetic analyses conducted to date have been based on rDNA sequences [17] and are complicated by the presence of paralogous rDNA clusters. However, the mitochondrial genomes of *Spadella cephaloptera* [18] and *Paraspadella gotoi* [19] are highly diverged in spite of having common membership of a single family in one of the two recognised orders (and one of four clades based on rDNA sequence data; [17]). Given their major differences in mitochondrial gene arrangements, despite similar overall morphology, it seems likely that the chaetognaths are a genetically diverse phylum. More gene expression data, more sequences and anatomical analyses of more specimens,

particularly of benthic deep-water species, are eagerly awaited. It is humbling to note that in spite of all of the recent molecular progress we are still not far beyond the conclusion of Libbie Hyman [1] who concluded after a life spent studying invertebrate diversity, "It seems probable that the chaetognaths should be regarded as having diverged at an early stage from the primitive ancestor of the Bilateria".

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DOI: 10.1016/j.cub.2006.07.006

## Declarative Memory: Sleep Protects New Memories from Interference

Interference is one of the most fundamental phenomena in memory research: acquiring new memories causes forgetting of other, related memories. A new study shows that sleep, interposed between learning episodes, can mitigate the extent to which new (post-sleep) learning interferes with recall of previously acquired knowledge.

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How does the brain protect existing memories from being destroyed or distorted by new learning? This puzzle, labeled the stability-plasticity dilemma by [1], has been at the forefront of memory research for several decades. In the 1970s and 1980s, when researchers started to build explicit computer models of how the brain stores memories, they found that these neural network models of memory tend to show catastrophic levels of memory interference [2,3]: implanting new memories in the network causes distressingly fast forgetting of previously stored memories. This problem occurs because memories are stored in an overlapping fashion in these models, as they are in the brain. A given synapse might participate in storing multiple related memories (for example, memory for your breakfast today versus yesterday), so adjusting the strength of that synapse to strengthen one memory might distort another memory that relies on that synapse. While numerous psychological studies have demonstrated that new learning does, in fact, interfere with recall of

existing memories [4–6], it is also clear that the interference effects observed in behavioral studies are much smaller than those predicted by the simple neural network models mentioned above.

This discrepancy has led researchers to puzzle over what kinds of mechanisms (not present in these simple models) the brain might use to protect stored memories. Computational neuroscientists have come up with several different ideas about how the brain avoids catastrophic interference (for example, see [1,7,8]). One of the most intriguing of these ideas is that sleep might play a role in reinforcing and protecting existing knowledge. The gist of the idea is that sleep provides an opportunity for the brain to ‘think about what it already knows’, strengthening and potentially also refining existing memories so they are less likely to be disrupted by new learning. Some researchers [8] also have argued that learning during sleep can serve to repair damage to existing memories; just as a building with a crumbling infrastructure can be repaired (if it is accessed before it collapses), a damaged memory can be repaired so long as the memory is still

coherent enough to be accessed during sleep.

A new study by Ellenbogen *et al.* [9], published recently in *Current Biology*, directly explores the role of sleep in protecting new memories from interference. To accomplish this goal, the authors used the AB–AC word pair learning paradigm [10]. In this paradigm, subjects learn a set of word pairs, such as shoe–banana; call this the A–B set. Next, subjects learn a new set of word pairs, the A–C set, where the ‘A’ words from before are paired with new words, for example shoe–stapler. Later, subjects are given the ‘A’ words, such as shoe, and asked to recall both words that were paired with each ‘A’ word. Previous studies using this paradigm have found that learning the A–C items impairs subsequent recall of the A–B items [4,10].

To address the role of sleep in mitigating interference, Ellenbogen *et al.* [9] set up their study such that one group of subjects slept between learning the A–B pairs and learning the A–C pairs, and another group of subjects did not sleep during that interval; subjects were tested on A–B and A–C pairs after learning the A–C pairs. The experiment also included ‘no interference’ control conditions that were identical to the aforementioned conditions, except subjects did not learn any A–C items. The authors found that the negative effect of A–C learning on A–B recall was much smaller in the sleep condition than in the no-sleep condition. Thus, it appears that something happens during sleep — when interposed between A–B and A–C learning — that makes the A–B trace less vulnerable to interference.