DISPATCH

Evolution: The Battle of the First Animals

Ctenophores or 'comb-jellies' are marine animals whose relationship to other phyla is uncertain, yet important for understanding major steps in animal evolution. Fossil ctenophores from the Cambrian indicate that ctenophores may have evolved from a sessile, cnidarian-like ancestor.

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The origin and earliest evolution of animals has been the subject of open warfare in the natural sciences in recent decades. One important battlefield has been the unresolved relationship between five animal groups — ctenophores, cnidarians, placozoans, poriferans, and bilaterians (essentially all other animals). This (phylogenetic) Battle of the Five Armies is as cacophonous and confusing as anything that Peter Jackson produced in recent years [1]. Yet an uneasy truce has recently emerged concerning the position of the sponges (Porifera), returning to the antebellum state with a monophyletic group of sponges at the base of animal evolution [2-5]. Otherwise, there is little resolution. These five animal groups are highly derived, with over 500 million years separating their origination from their modern anatomy. The ctenophores are particularly rogue and querulous, with their molecular sequence seemingly switching sides so often that its true allegiance is difficult to discern [6,7]. Fortunately, we also have fossils. These provide another tangible record of evolution, and are particularly abundant and well preserved during the first major burst of animal evolution, the Cambrian explosion. A new study in this issue of *Current Biology* by Yang Zhao, Jakob Vinther and colleagues [8] describes bizarre Cambrian fossils and places them in the ctenophore stem lineage, forming a close alliance between ctenophores and cnidarians.

The fossils of the Cambrian explosion, found at sites such as Burgess Shale and Chengjiang Biota, are renowned not only for their exquisite preservation of soft-bodied animals in fine anatomical detail, but also because of their enigmatic nature. The most famous of these are the 'bizarre crab' *Anomalocaris* and the 'mind-bending' *Hallucigenia*. The fossils described by Zhao and colleagues [8] are just as enigmatic, marking this work as an important contribution to the field owing to the detailed descriptions and images of a new taxon, *Daihua sanqiong*, and of enlightening new specimens of previously described taxa, including *Xianguangia*, *Dinomischus* and *Siphusauctum*. This last taxon has colloquially been called the 'tulip animal', which is a fairly accurate visual description of its overall anatomy [9]. The tulip-shaped body of *Siphusauctum* consists of a narrow stem topped by a rounded, bulbous main body chamber, which contains the mouth and gut, and is adorned with 'petals' represented by six radially-arranged tentacles covered in rows of hair-like protrusions, or cilia [8,9]. *Siphusauctum* was previously identified as a bilaterian but could not be placed in any specific phylum [9]. Another taxon that has yet to find a home in any animal phylum is *Dinomischus*, which is also tulip-like but has a sclerotized organic skeleton not found in the entirely soft-bodied *Siphusauctum* [9]. The new taxon *Daihua* and the previously described *Xianguangia* [10] are both stalkless, but have a sclerotized organic skeleton supporting an expanded body region with long tentacles bearing pinnules with rows of cilia [8]. *Xianguangia* had previously been placed in the stem lineage of Cnidaria [10].

By comparing these enigmatic fossil taxa with definitive ctenophores, the phylogenetic analysis of Zhao and colleagues [8] places *Xianguangia*, *Daihua*, *Dinomischus* and *Siphusauctum* in the stem lineage to ctenophores. The resulting scenario of evolution suggests that ctenophores originated from sessile benthic, sea anemone-like ancestors, with *Xianguangia* then *Daihua* branching off basally, followed by the stalked *Siphusauctum* and *Dinomischus*, before the evolution of pelagic ctenophores. This sequence of events requires numerous major anatomical transitions. The main body chamber is progressively reduced and the organic skeleton lost, and the ciliary organs are relocated from the tentacles to the external surface of the body to form the comb rows that characterise ctenophores. These interpretations will no doubt be contentious, because the scenario requires extreme morphological saltation. What this means for the evolution of the gut, which in cnidarians consists of a digestive sac whereas in ctenophores is a unidirectional tube, is not addressed. Most astonishing of all is the presence of mesenteries, sheet-like partitions of the internal body cavity that were hitherto a defining character of cnidarians, in the stem-lineage of ctenophores, stretching the definitions of these phyla to breaking point. Support for their theory is suggested by the authors to be found in the ctenophore developmental series, which shows a comparable pattern of emergence of the ctenes during the early developmental stages, and the progressive displacement of the centralized nervous system posteriorly during development, coherent with the reduction of the calyx in their proposed evolutionary transition.

The sessile to free-swimming evolutionary transition in the stem lineage of Ctenophora described by Zhao and colleagues [8] does not consider the fact that modern benthic ctenophores, though rare, do exist. These bottom-dwelling ctenophores, known as Platyctenida, typically lack comb rows and superficially resemble flatworms. Molecular studies suggest that benthic ctenophores are not basal, meaning they returned to a benthic lifestyle secondarily [3,11,12]. The recent sequencing of the mitochondrial genome of three Platyctenida taxa revealed that evolutionary rates were extremely fast in this phylum, and that the mitochondrial genome was extremely reduced in size and rearranged in gene order [5]. The genetic difference between pelagic and benthic ctenophores is actually far greater than the difference between humans and sea urchins. This creates difficulties in resolving the position of the ctenophores in the animal tree of life using molecular analyses, because of the systematic error that causes long genetic sequences to be probabilistically aligned with other long sequences rather than with shorter ones, leading to long branch attraction. Fossils are the best way to break up these long genetic branches [13]. By showing that basal stem lineage ctenophores look very much like sea anemones, the palaeontological analysis of Zhao and colleagues [8] provides strong support for a sister-group relationship between ctenophores and cnidarians. This relationship has been found previously using mainly morphological datasets, such that both taxa were previously grouped together as 'Coelenterata' [14]. Molecular phylogenetic analyses have, however, not provided strong support for this grouping.

Zhao and colleagues [8] suggest a plausible evolutionary scenario for the emergence of the highly derived ctenophores by taking a comprehensive approach drawing on multiple fossils from several localities and styles of preservation. This approach follows other recent studies focused on the palaeontological chronicle of different animal phyla, in particular sponges, cnidarians and arthropods [15–17]. These studies are converging on a stable timeline for the Cambrian explosion. Stem lineages diversified during the Cambrian, leading to the construction of the modern crown groups, and originated no earlier than the very end of the preceding Ediacaran period, approximately 550 million years ago [8, 15-18]. As is the case with the arthropods, cnidarians and sponges, putative ctenophore fossils from the

Ediacaran period were re-examined, and their ctenophore affinities rejected by Zhao and colleagues [8]. Early molecular clock analyses suggested that there must be a deep Precambrian root for the origin of animals, but this no longer seems conceivable given the exhaustive approach taken to studying the fossil record, which has yet to recover any definitive Precambrian animal fossils. More recent molecular clock analyses also suggest a latest Ediacaran or early Cambrian origination of animals [19, 20], in line with these detailed paleontological studies [8, 15-17]. The ultimate goal in this field is to understand the mechanisms underlying the Cambrian Explosion, which requires both a clear timeline of the sequence of events, and resolution of the interrelationships of the earliest diverging animal phyla.

So when the dust settles and the bodies are strewn across the battlefield, who is left standing? The Coelenterata, a scarred old warrior from ages past, having survived the molecular onslaught stand proud once more — a small but important battle as we await the wars to come.

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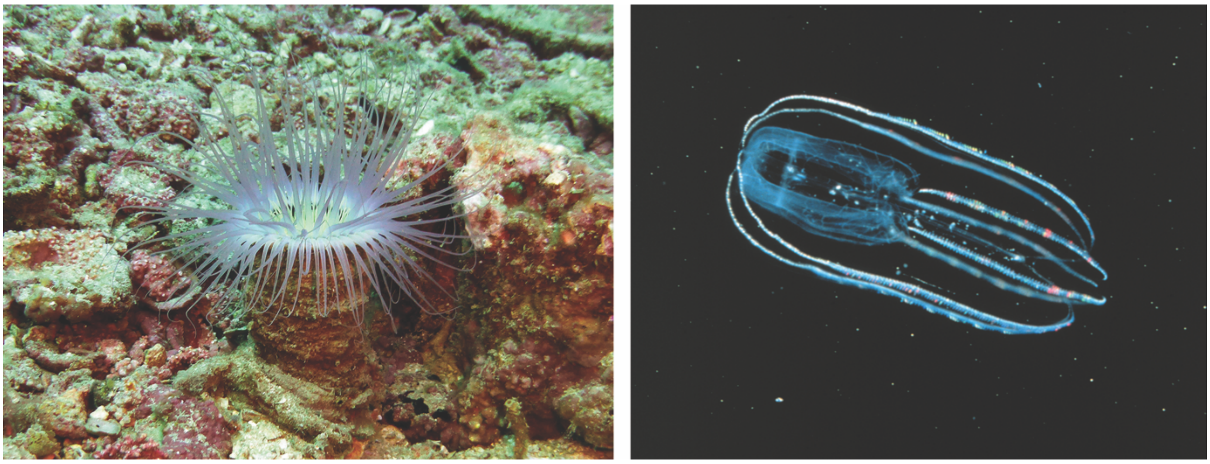

Figure 1: Could the tentacles of this tube-dwelling anemone (left) have evolved into the comb rows seen in this ctenophore (right)? Zhao et al. [8] use exceptionally preserved Cambrian Explosion fossils to reconstruct ctenophore origins, suggesting they evolved from sessile, polyp-like suspension feeders, similar to cnidarians (left photo: Amada44, Wikimedia Commons; right photo: OAR/National Undersea Research Program (NURP)”