Giant Predators from the Cambrian of China

Derek E. G. Briggs

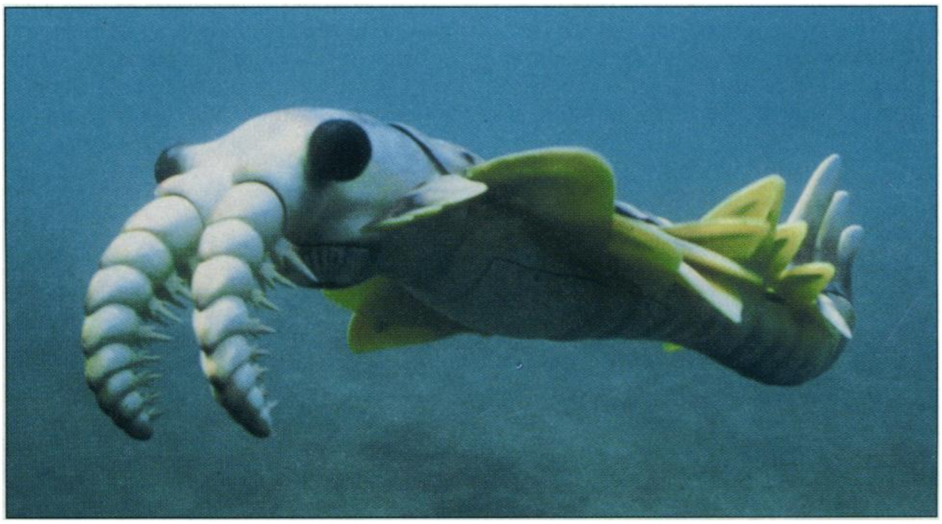
Just 15 years ago, the Cambrian animal *Anomalocaris* was little known, its legacy confined to isolated limbs found in the Burgess Shale and a few other localities in North America (*1*). Now, as reported on p. 1304 of this issue, this creature turns out to be representative of a diverse group of giant Cambrian predators that ranged as far as Europe, Australia, and China (*2*).

The unfolding story of the anomalocaridids (the group including *Anomalocaris* and its near relatives) is almost as unlikely as the animal itself. When isolated *Anomalocaris* appendages were first discovered near the end of the last century, they were thought to be the trunk of a shrimp-like arthropod. This mistake was not rectified until 1979 (*1*). In the meantime, examples of a second isolated appendage—with more complex, spiny, blade-like projections—were described from the Burgess Shale by Walcott, who mistakenly regarded it as part of the large arthropod *Sidneyia* (*3*). These two types of limb must have had a tough decay-resistant cuticle to account for their preservation in the absence of any body. Although the appendages testified to a giant predator, the nature of the animal remained a mystery until specimens preserving the body with the limbs at the front of the head were discovered in Burgess Shale material. These revealed the large eyes and a series of overlapping flaps or lobes on each side of the tapering trunk (see photo). More recently, specimens preserving a tail fan have been found (*4*). Most remarkable, however, was the discovery that the jaw of these anomalocaridids consisted of a circlet of plates that was originally described by Walcott as a jellyfish! There appear to be three genera of these animals in the Burgess Shale, although new material awaits description, and the distinctions between them have yet to be completely unraveled (*4*).

The discovery of complete (*5*) anomalocaridids in the older Early Cambrian Chengjiang fauna of China (*2*) indicates a greater diversity of these predators than previously imagined (adding a new species of *Anomalocaris* and two new unnamed genera). The length of the largest of the new forms is estimated to have reached a staggering 2 meters, although it is so far known only from the jaws. While all anomalocaridids appear to have been predators, the form of the jaws, and of the raptorial appendages at the front of the head, varies. The appendages of the two more completely known Chinese forms are equipped with long dagger-like proximal spines and, like *A. canadensis* from the Burgess Shale, they clearly grasped relatively large animals. The appendages of *Peytoia* have long blade-like projections graduated in length to rake the sediment surface (*1*), whereas the limbs of a new *Anomalocaris* from the Cambrian of Australia are arrayed with spinules that appear suited to capturing much smaller animals by filtering (*6*). Thus, the anomalocaridids had evolved a range of predation strategies even by the Early Cambrian.

The new Chinese *Anomalocaris* (see drawing) has a large tail fan, prompting speculation that swimming might have involved undulations of the body in the carangiform mode used by some fish (*2*). This is unlikely, however, because the largest trunk flaps are in the middle of the body rather than at the posterior, where they would generate the greatest thrust. Equally, the flexibility of the body would have been limited by the relatively long segments. It is more likely that anomalocaridids swam by moving the trunk flaps up and down like a series of hydrofoils or underwater wings (*7*). Limbs or fins used in this manner, however,

Portrait of a predator. Camera lucida drawing of *Anomalocaris* (*2*).



No shrimp. Swimming model of *Anomalocaris canadensis* made for Nippon Hoso Kyokai (NHK) (Japan Broadcasting Corporation) by Buildup Co., Ltd., for a television documentary on the Cambrian radiation (The Great Experiment) as part of their series, "Planet of Life." The life-size model is 70 cm in length. [Photograph courtesy of T. Fujisawa, NHK, Tokyo]

The author is in the Department of Geology, University of Bristol, Bristol BS8 1RJ, United Kingdom.

normally occur in one or two pairs, not in an overlapping series. The flaps in anomalocaridids were attached to the body along a broad base, sloping gently downward to the rear, each one overlapping that in front. They must have moved in a metachronal rhythm, a wave passing from front to rear along the length of the trunk.

The hypothesis that *Anomalocaris* swam in this way received strong support recently through experiments on the movement and maneuverability of a life-size (70 cm by 40 cm), remotely controlled model (see photo). The lobes were constructed with a thickened anterior margin and thin flexible trailing edge (a hydrofoil cross section). A stiff bar running through the anterior part of each lobe moved up and down in a single plane normal to the body axis. A rotating rod running the length of the body, powered by a battery-driven electric motor, moved the lobes in a continuous sequence. This resulted in the progression of propulsive waves along the body from front to rear, the 11 swimming lobes accommodating about one and one-third of a wave at any time.

Hydrofoils (underwater wings) generate thrust in both parts of the swimming stroke (unlike limbs operating as oars, which have a separate power and recovery element). The long basal attachment of the flexible lobes to the body of the model resulted in an automatic adjustment of the angle of attack in both the up and down stroke. Backward thrust was guaranteed during the upstroke because of the inclined line of attachment of each lobe, and it was enhanced by the convexity of their upper surface, induced by the resistance of the water. This resistance caused the lower surface to become convex during the downstroke, once again ensuring backward thrust. Thus, as long as the stiffened leading edge of successive lobes moves up and down in a metachronal rhythm, their shape and attachment ensure that the resultant wave will propel the animal along and generate lift. The model swam smoothly in the water without rolling. A slight tendency to pitch was evident when the model was allowed to swim on the surface, but this was dampened out once it was underwater.

The left and right series of flaps on the model moved in phase. When the propulsive wave was reversed so that it moved forward instead of backward along the body, the model stalled and dropped in the water as a result of the loss of lift. It then began to move backward in a manner that would have facilitated the capture of prey with the grasping appendages of *Anomalocaris*. Reversing was slower and less efficient, however, because the stiffened anterior edge of the flaps prevented them from acquiring an optimal angle of attack to propel the animal backward. Movement of the flaps of the animal itself, however, may have been more sophisticated, and the opposite lobes of a pair may have moved independently (in opposite phase or even direction), thus allowing the animal to turn in the water.

A propulsive wave is used for swimming by fish and squid with a single continuous fin running the length of the body. Anomalocaridids differ, however, in that a series of overlapping flaps is involved. Not only was their method of locomotion unusual, so too was the morphology of the jaw (*2*, *7*). Thus a number of functional strategies found in the Cambrian have subsequently disappeared; the anomalocaridids provide one example, the tubular carapace and three-fluked tail of the arthropod *Odaraia* another (*8*). Nonetheless, the volume of morphospace occupied (morphological disparity) is approximately equal in the Cambrian and Recent (*9*), suggesting that functional and developmental constraints were established by the Cambrian.

The affinities of *Anomalocaris* have long proved problematic. As long as only the segmented anterior appendages were known, its identification as an arthropod was accepted without question. The discovery of the entire animal, revealing a jaw apparatus and trunk flaps unknown among living arthropods, prompted speculation about separate origins. As new discoveries reveal a greater diversity of anomalocaridids, their importance as a separate group increases. Cladistic analysis (*10*) indicates that *Opabinia* belongs in the same clade, which is a sister group to the arthropods, but the relationship of *Kerygmachela* (*11*) is less certain because the preservation of the specimens makes some features of the morphology difficult to interpret. A phylogenetic analysis of anomalocaridids (incorporating the evidence of all the new forms), together with the arthropods *sensu stricto* and other related taxa, is now needed rather than a debate about whether they consititute a phylum or subphylum of the Arthropoda.

References and Notes

1. D. E. G. Briggs, *Palaeontology* **22**, 631 (1979).
2. J.-Y. Chen, L. Ramsköld, G.-Q. Zhou, *Science* **264**, 1304 (1994).
3. C. D. Walcott, *Smithson. Misc. Collect.* **57**, 17 (1911).
4. D. H. Collins, *Fifth North American Paleontological Convention*, Chicago, 1992, *Abstr. Prgm.* **66** (1992).
5. Isolated appendages of *Anomalocaris* were reported from Chengjiang by X.-G. Hou and J. Bergström, in *The Early Evolution of Metazoa and the Significance of Problematic Taxa*, A. M. Simonetta and S. Conway Morris, Eds. (Cambridge Univ. Press, New York, 1992), pp. 179–187.
6. B. McHenry and A. Yates, *Rec. South Aust. Mus.* **26**, 77 (1993); C. Nedin, personal communication.
7. H. B. Whittington and D. E. G. Briggs, *Philos. Trans. R. Soc. London Ser. B* **309**, 569 (1985).
8. D. E. G. Briggs, *ibid.* **291**, 541 (1981).
9. This equality was revealed by analyses of the arthropods, by far the largest group and therefore arguably a proxy for the metazoans as a whole [D. E. G. Briggs, R. A. Fortey, M. A. Wills, *Science* **256**, 1670 (1992); M. A. Wills, D. E. G. Briggs, R. A. Fortey, *Paleobiology*, **20**, 93 (1994)].
10. M. A. Wills, D. E. G. Briggs, R. A. Fortey, in preparation.
11. G. Budd, *Nature* **364**, 709 (1993).

12. I am grateful to NHK (Japan Broadcasting Corporation) for access to their model and to C. Nedin, H. B. Whittington, and M. A. Wills for discussion.