A Duck Folded in Half

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A review of *Before the Backbone: views on the orgins of the vertebrate*s by Henry Gee. Chapman and Hall, 346 pp., £35.00, 8 August, 1996, 0 412 48300 9

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The evening of 22 August, 1799 was surely one of the less happy that Napoleon Bonaparte had known, for it was the eve of his departure from Egypt, and Alexandria lay battered at his heels. Unusually mindful of the mortality of empires made of mere soil, Buonaparte is said to have declared to the mathematician Gaspard Monge (one of a collection of savants he had brought to Egypt) that he would far rather be a Newton than an Alexander. To which Monge, perhaps appalled at such hubris from a soldier (even if he were the great Général), replied that no-one could attain the glory of Newton for there was only one world to discover. Not so, said Buonaparte, for there is still the "world of details" and the laws that govern them. A tender sentiment, and one which reflects well on this pre-eminent man of action being, intentionally so or not, curiously apposite of his expedition. For trailing Buonaparte out of Egypt came not only the Rosetta Stone, but a young Professor from the Muséum d'Histoire Naturelle in Paris: Etienne Geoffroy St Hilaire, a man whose mind was perfectly torrid with details and the drive to find laws in them.

The British took the Rosetta Stone, but allowed France to keep Geoffroy St Hilaire as well as his collection of crocodiles, ichneumons, and mummified ibises which he had threatened to burn rather than cede to the victors (the British High Command, perhaps mindful of how Alexandria strikes pyromaniacs, had wisely relented). It hardly needs saying that Geoffroy was one of Nature's romantics: ostensibly a descriptive anatomist, he investigated the devices by which Puffer fish inflate themselves, but did not shy from larger problems such as a deductive theory of the relationships between the "imponderable fluids" of the universe (light, electricity, nervous energy *etc.*), one of many profound pensées which never saw print. More usefully, it was also in Egypt that Geoffroy had the first glimmerings of what would become his *Philosophie anatomique* -- a grand scheme to demonstrate the fundamental unity in the construction of all animals.

Initially, the goal was a modest one. Geoffroy attempted to show that structures which appear in mammals were the same, only modified, as those which appear in other vertebrates such as fish, reptiles and amphibians. In other words, he attempted to identify what we now call homologues arguing, for example, that the opercular bones of fish (which cover the gills) were essentially the same as the tiny bones that make up the middle ears of mammals (the malleus, incus and stapes). Today this is a familiar kind of idea, usually presented in school texts as the notion that the wing of a bat, the flipper of dolphin, the hand of a chimpanzee *etc*. are all "the same". But opercular bones were small stuff for a truly synthetic thinker; Geoffroy went on to find homologies between the most wonderfully disparate structures in the most wildly different creatures. Confronted with the exoskeleton of an insect and the vertebrae of a fish, Geoffroy proposed that they were one and the same structure. To be sure, insects have an *exo*skeleton (meaning all their guts and things are inside their hard parts) while fish have an *endo*skeleton (bones are surrounded by tissue) but where other anatomists saw this is as ample reason to keep them distinct, he explained with the simple confidence of the true visionary that "every animal lives within or without its vertebral column." Not content with this application of his all-revealing system, he went on to show how the whole anatomy of a lobster was really very similar to that of a vertebrate -- if you only flipped it upside down. Where lobsters carry their major nerve cords on their ventral sides (bellies) and their major blood vessels on their dorsal sides (backs), the reverse is true for vertebrates. And then there was the curious case of cephalopods...if one took a duck and folded it in half backwards so that its tail touches its head (an exercise performed only on paper, I believe), did not its anatomy remarkably resemble that of a cuttlefish?

It did not. Geoffroy's speculations attracted the silken wrath of Baron Cuvier, greatest of living anatomists, and Geoffroy's powerful rival at the Muséum. The result was a debate in front of the Académie Française in 1829 which Geoffroy lost -- a duck doesn't look like a cuttlefish no matter how you bend it; even the homologies between fish opercula and the mammalian middle ear didn't bear serious scrutiny. Yet if the particular homologies that Geoffroy proposed seemed, even in his day, sometimes absurd, his general method was not. Different organisms *do* have structures that are somehow similar yet modified, and these similarities are well worth studying. Indeed, the idea of homology is today so commonplace and ubiquitous in biology (we speak of homology among DNA sequences as easily as we do of homology among tetrapod fore-limbs) that it is very easy to read into Geoffroy's claims an evolutionary meaning he did not intend. The homologies that Geoffroy saw, or thought he saw, were, as far as he was concerned, placed there by the Creator. It was the age of what would be called Transcendental Anatomy.

The Darwinian explanation for homologies -- that they are due to descent from common ancestors -- did not displace Transcendental Anatomy easily. At the British Museum (Natural History) Richard Owen promulgated a brilliant and detailed programme of comparative anatomy based firmly on the idea that the similarities among animals are due to correspondence to an ideal form -- an Archetype built to Divine Plan. For this, as well as his unattractive personality, he earned the enmity of Thomas Henry Huxley and a perpetual place as Arch-Fiend in the cosmology of all good Darwinians. (Though his successors at the South Kensington museum have remained at least partially loyal: there Owen's dark bronze statue glowers magnificently over the main gallery while the pristine marbles of Darwin and Huxley, originally placed nearby, now reside in the Museum Coffee-shop among a litter of crisp packets. Perhaps they had to make way for the *Diplodocus* which stands there instead.) Even so, the decades after the publication of the Origin of Species in

1859 saw a flourishing of anatomical studies in which Russian, German, British and, to some degree, American workers raced to work out the evolutionary relationships among the major animal groups, and translate the natural world into the enchanting new iconography of the evolutionary tree.

There are, depending on who's counting, some 36 major groups or phyla of animals. Some, such as the Arthropoda, are ubiquitous and familiar, but there are plenty of phyla more like the Ciliaphora -- which consists of microscopic species found only on the lips of Norwegian lobsters. All animals ultimately descend from a single common ancestor which was likely an animal too; the problem, then, was how. Did the animals arise from something that looked rather like a flatworm, or something that looked more like a jellyfish? Are scorpions closely related to insects, or is the resemblance merely superficial, a matter of adaptation rather than history? And, most pressing of all, where did the vertebrates come from? The particular interest of this last question must surely lie in the fact that we wish to know our own relatives among the myriad creatures that live on or under rocks in the sea. But I rather think that the problem of vertebrate origins was more pressing in the confident last decades of Victoria's reign when every Englishman believed himself the epigonos of all Nature's strivings. Today we are altogether more modest; Heroic vignettes of worms-that-got-backbones and fish-that-learned-to-walk no longer appeal. (Just this evening I have returned from the 4th Huxley lecture given at the Royal Society where Richard Dawkins emphatically dethroned us from our high evolutionary station; a tolerant audience seemed, if anything, rather pleased to hear it.)

Still, the problem of the origin of the vertebrates remains an important one for the simple reason that many zoologists have tried to solve it and all have failed. What makes this failure especially interesting, if rather unusual in the natural sciences, is that over the past 150 years someone, somewhere, has probably already hit upon the answer; it is just that he has been unable to convince all his colleagues of it. Henry Gee has written an excellent book explaining why this is so. To begin with, the problem of animal relationships is a tough one. The major animal phyla, including the vertebrates, are very ancient: at least 545 million years old (the beginning of the so-called Cambrian Explosion of animal diversity), but possibly as much as 1 billion years old. Either way, an awfully long time in which the marks of ancestry -- the homologies -- which zoologists use to identify relationships can become obscured by evolution. Furthermore, there is the problem of convergence: unrelated animal groups can evolve similar structures independently, and so deceive zoologists into seeing an ancestral relationship where there is none. These difficulties, so clear to us now, were much less so in the 1860's when it seemed as if an anatomical inventory of the animals would surely reveal some humble worm or other as the precursor to the vertebrates. For a time this hope seemed well justified. In 1866 Alexandr Kovalevsskii showed that a small, transparent animal called amphioxus had a dorsal nerve cord, pharyngeal gill slits and a notochord (a stiff rod of cartilage that runs the length of the animal above the nerve cord) -- absolutely unmistakably vertebrate features. He then went on to tell the Academy of Sciences in St

Petersburg that the tunicates (sea-squirts), an unprepossessing group of animals that live attached to rocks and which were thought to be related to snails, had larvae that resembled amphioxus in no small degree, indeed, remarkably resembled the tadpole of a frog! But was the tunicate a plausible ancestor of the vertebrates? Its adult was immobile and all but devoid of a brain (as, apparently, was amphioxus itself); *if* tunicates were related to vertebrates, surely they were degenerate offshoot from a more active proto-vertebrate stock rather than a plausible ancestor? And there were other candidates: in 1875 Anton Dohrn revived Geoffroy St Hilaire's idea of vertebrates being upside down relative to other animals, and pointed out that many annelid worms (e.g., earthworms) have well developed brains and, moreover, are segmented, just as vertebrates are, and tunicate larvae are not. Then, in 1886 William Bateson studied the development of a large mud-dwelling worm, quite unrelated to annelids, named *Balanoglossus*, and showed that it, too, had pharyngeal gill slits, a dorsal nerve cord and possibly even a notochord -- could this be the ancestor of the vertebrates?

As the century progressed, the hypotheses multiplied. Among the animals proposed as Vertebrate ancestors were tunicates, annelids, arthropods (especially scorpions), enteropneusts (*Balanoglossus*), tunicates, nemerteans, and, though Gee unaccountably misses this one, chaetognaths. The theories grew ever more elaborate and debate ever more acrimonious. Matters came to a head in 1909 at a meeting held at the Linnaean Society of London to celebrate the Golden Jubilee of the publication of the *Origin of Species.* The very rooms in which Darwin's and Wallace's papers on natural selection had first been read (to a famously apathetic audience) now rang with harsh words as the Professors of Comparative Anatomy squared off. One observer summed up the proceedings in the following way:

> "When we return home and our friends gleefully enquire, 'What of the Origin of the Vertebrates?', so far we seem to have no reply ready, except that the disputants agree on one single point, namely, that their opponents were all in wrong."

It may have been fun, but the disputes took their toll. The problem of vertebrate origins, and more generally, that of the evolutionary relationships of all the animal phyla, were coming to be seen as insoluble; the best young scientists were moving on to other problems. William Bateson of *Balanoglossus* fame left evolutionary speculations and took up the study of genetics. In America, Thomas Hunt Morgan, who had also studied *Balanoglossus*, took up culturing fruit-flies and proved the chromosome theory of inheritance. Twenty years later even undergraduates were no longer much interested in evolutionary problems. The late Sir Peter Medawar spoke for the up-to-date zoology undergraduate of the 1930's when confronted with Edwin Goodrich, Professor of Zoology at Oxford, and the greatest British vertebrate anatomist of his time:

> "Goodrich was a rather selfish little man...in spirit a member of the great generation of European comparative anatomists of the

> immediate post-Darwinian era...[He] saw himself as a revolutionary, a torch-bearer, the evangel of the new and exciting doctrine of organic evolution...By the time we became students, the revolution had been won and was now a matter of history to be found in the textbooks...[it] had already become a bore and was well on its way to becoming an abuse as revolutions so often do."

By then experimental biology was already mature. To do biology was not to dissect salamander limbs, but rather to transplant them. Not to compile interminable lists of species, but rather interminable lists of mutants. It was all rather depressing for the men who had stuffed, pinned, pickled and dissected their way through the animal kingdom.

Yet if the Darwinian faithful had felt oppressed by the coldly mechanistic sciences of the gene, the cell and the embryo (the Germans even called the latter *Entwicklungsmechanik*), they could have scarcely conceived the depths to which their fortunes would plunge. For in 1953 experimental biology begat a child, enchanting of aspect yet terrifying in its vigour: molecular biology. Triumphalist and omnivorous, molecular biologists proved boundless in their confidence and pitiless in their contempt for the Curators of the Dead. Worse, they didn't even care about animals -- preferring to lavish their youthful energies upon a fecal bacterium and one or two viruses. Later, emboldened by success, they took on baker's yeast and the fruit-fly. Today their bestiary includes one worm, one kind of aquatic toad, an aquarium fish, the domestic chicken, the house mouse -- a paltry enough sample of the 1,000,000 or so described animal species. Little wonder that E. O. Wilson, a man deeply enamoured of the plenitude of organic life, called the coming of these scientists "The Molecular Wars."

The comparative anatomists and systematists retreated. The great research universities had little space for them; provincial universities and natural history museums were more congenial places in which to labour long and lovingly over abyssal limpets, fossil echinoderms, and the 8,800 different species of ant. If the subject matter of their science harkened back to the previous century, so too, did its style: speculative, frequently philosophical, and, above all, disputatious. One such scientist is R. P. S. Jefferies of the Natural History Museum, London. Over the past 30 years he has constructed an elaborate theory which seeks to show that an utterly obscure group of extinct animals, usually thought to be echinoderms (starfish, sea-cucumbers and their kin) are, in fact, the direct ancestors of the vertebrates. Like all such theories, Jefferies' case rests upon identifying homologies between the anatomy of his fossils and that of true vertebrates. But he is handicapped in the Vertebrate Stakes: his champions are all quite extinct and so different from anything alive today that not even the cognoscenti can agree on which of the many orifices found in these fossils is the mouth and which the anus. Jefferies' theory is daunting in its detail and complexity, yet in the course of 86 pages Gee lays it out with all the grace, clarity, even wit, that the subject can possibly allow. But, oh, what a task it is! Here is Gee on the reconstruction of the fossil *Cothurnocytis*:

> "In this orientation, obverse becomes 'dorsal', reverse becomes 'ventral', and the hemicylindrical ossicles and the stylocone in the stele become ventral, directed towards the substratum."

The difficulty of performing such mental gymnastics on fossils that few have ever seen has ensured Jefferies a few followers, a few critics, and many who cannot be bothered to master the complexities of his argument; even Gee seems to love this theory only because he loves an underdog. So why did he lavish months (years?) on mastering it, clarifying its predictions, and making it all intelligible to a wider audience? The reason is simple: Jefferies might, just might, be right. Herein lies much of the charm of Gee's book. The names that populate its pages: Dohrn, Naef, Kovalevsskii, Lankester, Balfour, Garstang (and which give the book such a poignant air, so luminous they once were, and so forgotten they are now) suggest that it is a history of science where it is not, at least not in the modern sense. There is no talk here of the "formation of research networks", "disciplinary development", "the transforming of research programmes" and all the other apparatus that social-minded historians of science revel in. Gee's book is something better than that: it is simply a history of ideas, but ideas that still have life in them, that may still prove to be wrong or right, and may yet inspire beautiful new experiments. It is history of science with all the boring stuff left out.

Will we ever know the origin of the vertebrates? In a limited sense, yes. Predicting the pace and course of science is always a hazardous game, but I am confident that we will definitely know which living animal phylum is most closely related to the vertebrates within five years. That would be enough to send most of the theories that Gee has resurrected to the grave once and for all, indeed, he already re-inters several. Where previously the course of evolution was deduced from the comparison of anatomy, today it is done by comparison of gene sequences. The gain lies primarily in the huge amount of information that animal genomes contain: a typical evolutionary tree today might be based upon several hundred informative homologous characters (each character a nucleotide position); the classical trees were based upon two or three (each character an anatomical structure). In the last three years a few such gene-based trees have been produced for the vertebrates and their putative kin. They clearly show that amphioxus and tunicates are very closely related to vertebrates; *Balanoglossus* and echinoderms are somewhat more distantly related; arthropods, annelids, nemerteans, and chaetognaths are quite out of the picture. The problem is, at least in part, solved.

In 1894, William Bateson summarised the methods of his evolutionary minded colleagues: "'If,' say we with much circumlocution, 'the course of Nature followed the lines we say it did, then, in short, it did.' That is the sum of our argument." Cruel and accurate, and easily said by a man who has just dropped the subject. It is a sweet irony then, though not one I think that would have displeased Bateson, that his intellectual descendants -- those very molecular biologists enamoured of fruit-flies, the African clawed toad, and house mice -- have begun, in small but increasing numbers, to take up the evolutionary questions that he abandoned a hundred years ago. It was inevitable, really: the molecular biologist's bestiary, though small, is still just large enough to hint at answers to some of the forgotten questions of comparative anatomy. In 1995, a group of UCLA biologists identified part of the molecular machinery which distinguishes the dorsal (back) and ventral (belly) sides of a vertebrate (the African clawed toad) in the course of development. It was a beautiful result, but its true charm only became apparent when the two genes involved were compared to those that do the same job in the fruit-fly. They were the same (or to be precise, were the fly homologues of the toad's genes). But there was a twist: the gene that helps specify the dorsal side of the fly, specifies the ventral side in the African clawed toad; and the gene that specifies the ventral side of the fly, specifies the dorsal side of the toad. In other words, the molecular machinery of dorsal-ventral specification of a fly is, at least in part, the same as that of a toad, just inverted. Which, in essence, is what Geoffroy St Hilaire understood when in 1820 he saw that the anatomy of an lobster laid on its back was uncannily like that of a mammal on its four feet. Geoffroy supposed what molecular genetics is only beginning to show, that the enormous diversity of animal life conceals a deep fundamental unity. His *philosophie anatomique* failed because he lacked what we have now, a device that would translate the language of anatomical form into that of evolutionary history. What Geoffroy lacked, in fact, was his Rosetta Stone.