A brief history of dinosaur paleobiology

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First finds

The first dinosaur bones must have been found in ancient times, but no record was kept. In Medieval times, philosophers commented on fossil shells and sharks' teeth which they had seen, and they debated the origin of these strange stones. Were these stony petrifactions in any way related to modern shells and fishes, or were they simply odd pebbles that happened to look like the remains of plants and animals? A popular view was that fossils were 'sports of nature' formed in the rocks by plastic forces. [The nature of these plastic forces was never made clear.] The first dinosaur bone to be described was found while this debate raged, and the line of argument followed by its describer is revealing.

Robert Plot, Professor of 'Chymistry' at the University of Oxford was known to be preparing a monumental book on the 'Natural history of Oxfordshire', and local naturalists sent him unusual specimens to include. These included a weighty specimen that had been collected in a shallow limestone quarry at Cornwell in north Oxfordshire. Plot illustrated the specimen in a figure that also contained illustrations of numerous other strangely-shaped stones, some of which he interpreted as preserved kidneys, hearts, and feet of humans. His interpretation of the rock from Cornwell was, however, quite different.

Plot saw that the specimen looked like a bone. It had a broken end which was circular, and seemed to have a hollow core which was full of sand. The fractured surface round the core showed clear porous patterns exactly as in bone, and the shape of the opposite end, with its two large rounded processes, was just like the knee end of a thigh bone. Despite the seemingly mystical interpretations that Plot gave to many of the other stones illustrated in his book, he seemed to have no doubts about his giant bone. Then, Plot went through a discussion of the kind of creature that could have produced such a monster bone. He stated that it came from a animal that was larger than an ox or horse, and considered the possibility that it might have come from an elephant brought to Britain by the Romans. He ruled out that possibility since the bone was even bigger than that of an elephant.

Plot's final decision was that the Cornwell bone came from a giant man or woman. He referred to mythical, historical, and Biblical authority in support of this interpretation ('there were giants in those days'). After a promising discussion, Plot's final decision to identify the bone as human might seem perverse to us, but recall that no-one at the time had an inkling of the former existence of dinosaurs and other extraordinary animals in the history of the earth. Indeed, there was no acceptance of the idea that some plants and animals might have become extinct, since that would imply that God had made a mistake, nor was there any idea that the earth was very old.

Plot's bone can be identified from his illustration as the lower end of the thigh bone of *Megalosaurus*, a dinosaur that is now relatively well known from the Middle Jurassic of Oxfordshire. Plot's specimen is now lost, but there is a twist in the tail. It was illustrated again in 1763 by R. Brookes, and he named it *Scrotum humanum* in honour of its appearance. This is the first named dinosaur, although unfortunately the name has never been used seriously.

The idea of extinction

Extinction seems a very obvious aspect of nature to us now, but in the seventeenth and eighteenth centuries, this was not the case. By 1700, most naturalists accepted that fossils truly represented the remains of ancient organisms that had somehow been buried and turned to stone. One big question remained: were these the remnants of extinct plants and animals? From 1750 to 1800, there was a heated debate about the possibility of extinction. Up to 1750, most naturalists believed that fossils represented species that were either known still living, or would soon be found in some of the hitherto unexplored parts of the world. Isolated fossil bones of vertebrates, backboned animals, had been found in Ireland, Britain, France, and elsewhere, but none of these shook the faith of naturalists that extinction had not happened.

Everything changed in the 1750s, when explorers in North America began to dig up the remains of elephants (mastodons and mammoths), and sent some of the bones to Paris and London. There, distinguished anatomists and naturalists, such as William Hunter, Georges Louis Leclerc, Comte de Buffon, and others debated the specimens. As more and more specimens were found, and as more of the Americas were explored, it became clear that these truly were remains of recently-extinct forms. Baron Georges Cuvier of the Muséum d'Histoire Naturelle in Paris was instrumental in clarifying this question. He showed, in a series of books and papers from 1796 onwards that the fossil elephants, and giant mammal bones from Russia, South America, and other parts of the world, represented extinct species.

The vastness of geological time

The mammoths, mastodons, and giant ground sloths of the late 18th century were obviously not very ancient fossils. The bones were still in good condition, and the skeletons were often quite complete. Geologists were happy to accept that some of these animals had perhaps died out only a few thousand years ago.

Other fossils seemed much more ancient, however. The bone or shell material seemed to be filled with crystalline minerals, often calcite, quartz, or iron oxide, and these minerals must have taken some time to enter the pores and solidify. In many cases, the fossils seemed to come from plants and animals with no obvious living relatives. Geologists debated the true antiquity of the Earth during the late 18th century, but the outlines of what had happened in the past became clear only from 1800 onwards.

The first breakthrough came in the writings of James Hutton (1726-1797), a Scottish agriculturalist and naturalist. In his *Theory of the Earth* (1795), he argued that the Earth was enormously ancient, based on his observations of modern-day processes. Hutton observed the rates of accumulation of sediments, and the rates of erosion by mountain streams in his native Scotland, and he believed that such processes must always have been equally slow. Hutton then compared modern rates of processes with the vast piles of rocks he saw in cliffs around Scotland, and the depth and ruggedness of the mountains. At slow rates of deposition and erosion, these features must have taken huge amounts of time, presumably millions of years, to form. Hutton's book is immensely dull, and readers in his day also found it so. Luckily his work was popularised by James Playfair, and the idea of an ancient earth spread rapidly among naturalists and philosophers.

The antiquity of the earth was a theme developed by later geologists, among them Charles Lyell (1797-1875), another Scot. In his highly influential *Principles of Geology* (1830), he spread his net wide, and called on examples from all over Europe ot show how landscapes had changed, coasts had moved vast distances, and fossils were found abundantly everywhere. Lyell especially championed Hutton's application of modern processes to the interpretation of the past, the principle of uniformitarianism, or 'the present is the key to the past'. Between 1795 and 1830, practical field geologists had begun to produce geological maps, and to divide up the sedimentary rocks according to their fossils. This marked the beginning of geology as a science, and particularly the beginning of the modern international geological time scale.

<u>Making sense of the first dinosaurs</u>

The first dinosaur discoveries, from 1818 to 1840, began to paint a portrait of an astonishing fauna of giant reptiles in the Mesozoic. The dinosaurs, found first in England, and then elsewhere in Europe and, after 1850, on every other continent, showed early naturalists that whole assemblages of plants and animals, quite unlike anything now living, had existed in the past. How were paleontologists to interpret these extraordinary giant bones that seemed to be quite unlike those of any living animal?

Georges Cuvier provided the method, in the new science of comparative anatomy, a discipline in which he established new standards of precision. He carried out a painstaking comparison of every bone of a fossil form, and noted similarities and differences between equivalent elements in the skeletons of a variety of extinct and living forms. He found that the shapes of bones indicated the purposes for which they were used and the relationships of the animals in question. By the 1820s, Cuvier had honed his skills in comparative anatomy to such a pitch of perfection that it was said he could identify any animal from a single bone, and that he could reconstruct any unknown fossil form from a single bone.

Bones of a large meat-eating dinosaur came to light north of Oxford about 1818, and they were taken to William Buckland (1784-1856), Professor of Geology at the University of Oxford, and Dean of Christ Church. It was not uncommon for churchmen to combine their careers with science in those days. Buckland was shown some collections of bones and teeth of a large meat-eating reptile about 1818, but he could not identify the bones, and he showed them to Cuvier in Paris, and to other experts. In the end, Buckland classified the animal as a giant reptile, probably a lizard, and he estimated it had been 40 feet (12 m) long in life. After six years of consideration, Buckland finally published a description of the bones in 1824, and he stated that they came from a giant reptile which he named Megalosaurus ('big reptile'). This was the first dinosaur to be described.

At the same time, independently, Gideon Mantell ((1790-1852), a country physician in Sussex, was amassing large collections of Mesozoic fossils. During a visit to a patient near Cuckfield, so the story goes, his wife Mary, who had come with him, picked up some large teeth from a pile of road-builders' rubble. Mantell realised the teeth came from some large plant-eating animal, and when he sent them to Cuvier, the great French anatomist assured him that the animal must have been a rhinoceros. Then, Mantell compared the teeth with those of other modern animals in the Hunterian Museum in London, and a student there, Samuel Stutchbury, showed him that they were like the teeth of a modern plant-eating lizard, the iguana, only they were much bigger. So, Mantell described the second dinosaur, named by him *Iguanodon* ('iguana tooth') in 1825, based on the teeth, and some other bones he had found since.

William Buckland and Gideon Mantell had great difficulty interpreting these early dinosaur bones since there were no modern animals like them. In the end, they decided that *Megalosaurus* and *Iguanodon* were giant lizards. The third dinosaur to be named, *Hylaeosaurus*, came to light in southern England in the same Wealden beds that had produced *Iguanodon*. It was named in 1833. Further dinosaurs were named in the 1830s, including two from the Triassic: *Thecodontosaurus* was named in 1836 by Henry Riley and William Stutchbury from Bristol, SW England, and *Plateosaurus* in 1837 by Hermann von Meyer from southern Germany. It was only later that paleontologists realised these were both prosauropods (basal sauropodomorphs) and, in fact, closely related. So, by 1840, a number of different dinosaurs had been named, and these included a theropod (*Megalosaurus*), two basal sauropodomorphs (*Thecodontosaurus* and *Plateosaurus*), an ornithopod (*Iguanodon*), and an ankylosaur (*Hylaeosaurus*). In 1841, Richard Owen named the first sauropod, *Cetiosaurus*. But still no-one knew what these extraordinary giant beasts were.

Richard Owen and the 'Mammalian Dinosaurs'

Richard Owen (1804-1892), Professor of Anatomy at the Royal College of Surgeons in London, was set the task of reviewing everything that was then known about the giant reptiles of the land, sea, and air. He had some difficulty in understanding the land reptiles: some were clearly crocodiles, others were small and lizard-like, but there were all those giant 'lizards'. What was he to do? At first, he tried to shoe-horn them all into existing groups. So, some were overblown lizards, others were crocodiles, and yet others were something in between. Finally, he turned that idea on its head when, in 1842, he argued that some of them at least represented a new group, which he called the Dinosauria (meaning 'fearfully great reptiles'), characterized by being terrestrial, being huge, and by having more than two vertebrae in the sacrum (most reptiles have two elements of the backbone which attach to the hip girdle; dinosaurs have three to seven). Owen argued that the dinosaurs were bulky quadrupedal reptiles that had many advanced mammal-like features. But he included only *Megalosaurus*, *Iguanodon*, and *Hylaeosaurus* in the group. The others were left as giant lizards and crocodiles.

In 1851, a huge exhibition of technical, scientific, and trade goods was held in the centre of London. The Great Exhibition was the biggest show of its kind, and it showed all the wonders of British industry - the steam engines, railways, massive new factory works and products, the fruits, minerals, and fibres from the British Empire. It was housed in a vast metal and glass structure, the biggest ever built. When the exhibition was over, the people wanted to preserve the vast glass house, and it was taken apart, and set up at a new location in south London. There, known as the Crystal Palace, a new public park was created for the enjoyment and education of the citizens. Prince Albert, Queen Victoria's husband, was keenly interested in science, and he wanted the park to reflect all the latest knowledge. He turned to Sir Richard Owen, as he then was, and they developed a scheme to illustrate the geological history of the Earth in the park. Great rock formations were to be brought in from around the land and set up in the correct sequence. Lakes were excavated, and massive hydraulic schemes were to operate the water levels, creating floods and tides.

The highpoint of the geological garden was to be a set of life-sized models of the ancient creatures that Owen had helped to interpret. There were models of ancient fishes, amphibians, marine reptiles, flying reptiles, and, of course, dinosaurs. The sculptor Waterhouse Hawkins was engaged, and he designed the structures. Each dinosaur was to be sculpted in concrete over a hollow framework built from steel and bricks. These were to be some of the first 'artificial' sculptures in the world. Everything was ready by the end of 1853, and a great dinner was held inside the model of the *Iguanodon*, before the top was fitted. At the beginning of 1854, the public were able to see the Crystal Palace dinosaurs, and they were amazed. This was the first 'dinosaur craze'. Pictures of Owen's marvels were made and sold as posters. Copies appeared in the popular illustrated newspapers, and small-scale models, made from plaster or bronze could be purchased as souvenirs. Dino-mania is nothing new!

But why did Owen make these first life models of dinosaurs so mammal-like? They look very odd to us. Partly, it was because, at that point, he did not have any complete skeletons. The first five or six dinosaurs from Europe were based on isolated bones. But, careful historical study by Adrian Desmond of London has shown that Owen had an ulterior motive. He had mixed views about evolution, and certainly did not accept that life had evolved from simple to complex organisms - the principle of progressionism. He believed that the fossil record showed many cases of *degeneration*, that is a kind of reversal of evolution, where plants or animals were once highly complex and advanced, and degenerated to a more primitive state. He believed that modern reptiles were degenerate, the mere inferior relics of a once much more glorious past. So, we have large, possibly warm-blooded, mammal-like dinosaurs in the Mesozoic, and miserable, cold, slimy, creeping lizards and crocodiles today, sad remnants of a once-great dynasty.

Progression and evolution were hot topics in the 1850s, and dinosaurs played their part. The debate about progressionism is forgotten now, but not so evolution. It is important to understand where evolution enters the picture in the history of dinosaur studies.

Evolution

The theory of evolution by natural selection was proposed by Charles Darwin in 1859. Darwin had come to this theory after a long voyage of discovery in the early 1830s, both literally and figuratively. He set sail as gentleman naturalist on board the survey ship 'Beagle' with the generally-held views of his day, that life had been created, and that species did not change. He had, after all, been brought up as a traditional Christian, and he was training to become a Minister of the Church. He came back from his voyage of discovery as a convinced evolutionist. Darwin did not propose the idea of evolution: this view had been championed by distinguished French naturalists, such as Buffon and Lamarck, during the eighteenth century. Their idea was that species were not fixed, and that they could change in some way through time, although they were unclear about how this happened. That is all evolution means, literally 'unrolling' or change.

Palaeontologists throughout Europe had also been gathering evidence that pointed to some kind of change, or progression of life through time. They found simple fossils in older rocks, then fishes, then reptiles, then mammals, showing, they thought, some kind of sequence of development. Whether this progression meant that there had been a series of separate creations and extinctions, or whether ancient fossil forms had somehow changed, was debated in a general way. This was the progressionism that Owen railed against.

During the voyage of the 'Beagle', Darwin saw and collected numerous examples of fossil mammals from South America, and these confirmed that the fossil forms resembled mammals still living in South America. If life had been created, why should there be apparent evidence of some relationship between extinct and living animals in one part of the world? When he visited the Galapagos islands, Darwin saw that the plants and animals there were like those on the South American mainland. Why should that be, if life had been created? He saw also that the tortoises and finches on each of the dozen or so islands in the Galapagos group looked very similar to each other, and yet he observed that there were clear differences from island to island. When he showed his collection of bird skins to an ornithologist on his return, he was assured that the finches were all different species. Darwin had to admit the impossible; species were not immutable: if species were not permanent, then that meant they could evolve and split. This meant that God had not created all life in one act. All life could have evolved from a single common ancestor, and the vastness of geological time was already available for this process to take place.

The final brick was fitted into Darwin's shocking new edifice, when he read 'An essay on the principle of population', written by Thomas Malthus, an economist. This showed how human populations always breed faster than the increase in available food, and that certain processes must come into play to maintain the correct level of population. Darwin saw that this idea applied to animals and plants which all produce too many young to survive, and, in general, only the strongest survive. The features that enable them to survive (bigger teeth, stronger legs, brighter feathers) must be inherited in some way, and they are passed on to their offspring. In time, the make-up of the whole population may change, or evolve, in the direction of the features that most promote survival at the time. This is natural selection.

Looking at the diversity of life today, the countless millions of living species, and looking back over the history of life, admittedly only patchily known in the 1830s, Darwin could see a single principle at work. Species could evolve and split. In time, those species themselves could change further and split, and over countless millions of years, a single population of simple organisms could have diversified into many species. A group like the dinosaurs could have arisen from a single ancestor which, if well adapted to the prevailing conditions, would survive and multiply. Over time, as new opportunities presented themselves, and with the vast potential for reproduction and variation, any kind of evolutionary change could be imagined: increase in body size, change from bipedalism to quadrupedalism, change in diet, or change in habitat.

<u>Missing links; Archaeopteryx</u>

In his 'On the origin of species', Darwin devoted two chapters to paleontological questions. He realized that fossils could provide critical evidence that evolution had actually happened: after all, looking at geographic distributions of modern plants and animals and talking to animal breeders could show how evolution might have happened, but the time dimension is essential to show it really happened. But Darwin was also very concerned about the completeness of the fossil record, and this is still an important question today, In other words, how much of the history of life is actually documented by the fossils we know: ninety percent, fifty percent, or less than one percent? It was impossible for Darwin to answer that question, and it is still a knotty problem. But what Darwin most hoped for was a spectacular 'missing link', some fossil that was exactly mid-way between two living groups. He didn't have long to wait.

In 1860, quarrymen found an isolated feather in a limestone quarry near Solnhofen in Bavaria, southern Germany. The quarries produced so-called lithographic limestone, that is, a very high-quality limestone that broke naturally into perfectly flat sheets. It was used for making lithographs, printing plates for intricate engraved pictures in books. The rocks were known to be Jurassic in age, probably latest Jurassic (now dated at about 150 million years old). This was unmistakeable evidence for the oldest fossil bird by a long way, and it was named *Archaeopteryx lithographica* by Hermann von Meyer (1801-1869), the father of German vertebrate paleontology, who had named *Plateosaurus* in 1837. The name means 'Ancient wing from the lithographic limestone'. The feather proved that birds had lived in the Mesozoic, but it did not show what kind of bird.

A year later, an even more dramatic discovery was made, a complete skeleton of *Archaeopteryx*. This was the perfect missing link, and Darwin could not have asked for a better one: it had the jaws and teeth, the long bony tail, and the strong hand with claws of a reptile, but it also had wings and feathers, so it must be a bird. Carl Häberlein, a physician in the nearby town of Pappenheim, obtained the specimen from the quarrymen. He was a keen fossil collector, and the poor workmen often paid for his medical services with fossils. But Häberlein realised this was something better than the usual fishes and plant fronds that they brought him. He offered it for sale, and several major museums around Europe made strenuous efforts to obtain it. In the end, Richard Owen was able to buy it, and the rest of Häberlein's collection, for £700. This first skeletal specimen of *Archaeopteryx*, now known as the 'London' specimen, to distinguish it from others that were found later, shows the wings outstretched, the neck bent round, and much of the skull and braincase. In 1862, £700 was a great deal of money certainly, but the specimen is essentially priceless now.

A German paleontologist, Andreas Wagner, published a brief account of the skeleton in 1861, and Owen prepared a full account, which was published in 1863. Wagner bitterly opposed any kind of evolutionary interpretation of the specimen, and Owen followed suit, although perhaps less strongly. He interpreted it as a bird, but did not draw the obvious evolutionary conclusions. His younger rival, Thomas Henry Huxley (1825-1895) had no such scruples. Huxley had already stood up as 'Darwin's bulldog' to argue the case for evolution, and here was the perfect ammunition. Huxley saw that *Archaeopteryx* had the skeleton of a small theropod dinosaur, and he never wavered from that view, which is the current view, that birds evolved directly from small flesh-eating dinosaurs. The small theropod *Compsognathus* had also just been reported from the Solnhofen limestones, and it was the perfect comparative animal. Plucked of its feathers, Huxley declared, *Archaeopteryx* is a small dinosaur.

A second *Archaeopteryx* skeleton, complete with feathers, came to light in 1877, and was acquired by the natural history museum in Berlin. In the twentieth century, a further five specimens were found, one in an old collection which had been described in 1855 as a pterosaur, but four entirely new finds. An attempt in the 1980s to declare that *Archaeopteryx* was a fake, an amalgam of a genuine small theropod dinosaur skeleton with feathers printed around the sides, ignored the fact that there are numerous specimens, and indeed the finest and closest examination showed that they are genuine fossils.

Dinosaur discoveries up to 1850 had relied on chance finds, usually by quarry men, in Europe. These discoveries continued, with important new finds in southern England, France, and Germany, but attention shifted to North America in the late 1850s, as the first reports were made of fantastic new discoveries across the Atlantic.

Joseph Leidy and the first American dinosaurs

Dinosaur footprints had been discovered in New England earlier in the nineteenth century, although they were thought to have been made by giant birds. The first specimen was found, famously, by a schoolboy, Pliny Moody, on his parent's farm in Massachusetts about 1800, three-toed prints in red Triassic sandstone. [He is probably remembered partly for his discovery, partly for his splendid name.] Such footprints were common in the Triassic rocks of the eastern seaboard of North America, and collectors assembled many specimens. They were studied first by Edward Hitchcock, President of Amherst College, and State Geologist for Massachusetts, who summarized his views in 1858 in his book 'Ichnology of New England'. He called the footprints 'ornithichnites' ('bird footprints'), and pictured their maker as a large flightless ostrich-like bird, perhaps 12-15 ft. (3-4 m) tall. His insight was the first inkling that Owen had been wrong in his vision of dinosaurs, but Hitchcock was right for the wrong reasons. The maker was indeed a large lightly-built biped, but it was a dinosaur, not a modern-style bird.

The first dinosaur bones from North America were modest enough, a few teeth collected by an official geological survey team operating in Montana in the year 1855. They were described in 1856 by Joseph Leidy (1823-1891), Professor of Anatomy at the University of Pennsylvania. Small beginnings. However, two years later, Leidy was able to report a much more significant find, a nearly complete skeleton of a large plant-eating dinosaur from Haddonfield, New Jersey, which he named *Hadrosaurus*. Leidy realised that *Hadrosaurus* was related to *Iguanodon*, but it was younger in age. Most significant was the fact that the skeleton was more complete than anything yet known from Europe, and it proved for the first time that this dinosaur at least stood on its hind legs. Owen's Crystal Palace models had already had their day: Leidy's announcement soon showed that many, if not most, dinosaurs had been bipeds. But he didn't get the pose quite right.

The skeleton of *Hadrosaurus* was mounted in the Philadelphia Academy of Natural Sciences by Joseph Leidy in the 1860s. He chose to show it in 'kangaroo pose', that is, with its backbone nearly vertical, the tail bent hard along the ground, and the arms held out to the front. This was, however, a reasonable assumption for the time. Remember that by 1858, only 15 or so dinosaurs had been described around the world, and *Hadrosaurus* was the first relatively complete one. Among modern animals, Leidy looked at humans, ostriches, and kangaroos. Obviously *Hadrosaurus* was not fully upright as we are: it had a long tail for some reason. The ostrich lacks this kind of tail, so he chose the kangaroo, which does have a powerful tail for balancing. We now know that dinosaurs could not easily have adopted the 'kangaroo pose'. Their tails, for one thing, did not have a natural bending point midway along the length, as in kangaroos. To mount the skeletons this way, the tail had to be broken and forced out of joint.

Leidy's *Hadrosaurus* inspired a strong wish among the citizens of New York that they should have their own Crystal Palace-style dinosaur museum, but bigger and better, of course, than Owen's establishment in London. Plans for a 'Palaeozoic Park' in Central Park were prepared, and Waterhouse Hawkins, Owen's sculptor, came over from England to build the models. All the dinosaurs were to be shown in bipedal pose, a dramatic improvement on Owen's quadrupedal designs of only five years before. Waterhouse Hawkins set up his workshop, and began to build the concrete dinosaurs. Drawings from the time show *Hadrosaurus* as a tall slender biped. Other wonderful beasts were constructed. But a gang of thugs wrecked the workshop and smashed the models. This was part of a violent phase in local politics in New York City, and the ruffians were almost certainly members of Boss Tweed's gang, who were protecting their patch in the city, The wrecked frames and concrete debris were buried in Central Park, where they still reside, and so the first American paleontological theme park bit the dust.

<u>Cope and Marsh and the 'Great American bone wars'</u>

The North American bone wars began in earnest in the 1870s, with the rise of Cope and Marsh. Edward Drinker Cope (1840-1897) was a Quaker, taught by Leidy in Philadelphia, and his interests spanned paleontology and herpetology, the study of modern amphibians and reptiles. Cope toured Europe in 1862, to improve his education, and to visit the museums. He taught for a while at Haverford College, but did not enjoy that, and soon became a scientist of independent means, living from his family wealth. In his lifetime, Cope wrote thousands of technical papers on fossil and modern reptiles, and he named over 1000 new species. This is a record that will probably never be beaten (and that is probably not a bad thing). Cope was brilliant, aggressive, socially inept, and utterly obsessed. He was impatient, and leapt from project to project: this gave him an encyclopedic knowledge of nearly everything in natural history, but he often made mistakes. When Cope died, he donated his body to science, and his skull is sometimes reckoned to be the type specimen of the human species, Homo sapiens, his dearest wish.

Othniel Charles Marsh (1831-1899) was also an enthusiastic paleontologist, but his education followed a more patrician course. He was educated at Yale University, and in the early 1860s spent three years in Europe. In 1866, his wealthy uncle George Peabody was persuaded to donate $150,000 to Yale University to establish a natural history museum. Thus was born the Peabody Museum. Marsh was appointed Professor of Paleontology, an unpaid position, and he relied on his uncle's fortune for financial support for the rest of his life. Marsh was much calmer than Cope, and he worked slowly and methodically. He was somewhat aloof and overbearing. He employed many 'assistants', who in fact did much of his work for him. Whereas Cope wrote every word himself, many of Marsh's famous monographs were 'ghost-written' by poorly paid aspiring young naturalists he had taken under his wing.

Cope and Marsh met first during their respective European tours, and for a time they worked together in a friendly manner, both of them collecting and describing a range of fossil reptiles and mammals, first from the East Coast, and then from the new territories of the Midwest of the United States. Their rivalry began about 1870. Cope had shown Marsh some fossil beds in New Jersey, but found later that he could not collect anything from the sites because Marsh was paying the workmen more for any finds they made. Then, Marsh noticed, during a visit to Philadelphia, that Cope had mounted a skeleton of the marine plesiosaur *Elasmosaurus* with its head on the end of the long thin tail, instead of at the other end. Supposedly, when Marsh told him of his error, Cope's pride was so hurt that he swore lifelong enmity. The enmity was a constant and major force for the remaining years of their lives.

The Cope vs. Marsh fight developed into the famous 'bone wars' of the late nineteenth century. It might seem, today, that the North American continent is big enough for two dinosaur paleontologists. They certainly found enough new dinosaur sites and dinosaur specimens to keep both of them, and armies of assistants, busy for decades. However, the ambitions of both men led them to compete with each other for the best finds. Each of them had enough money to buy fossils from local collectors, and to employ teams of excavators who operated in the Midwest. The excavators at first were the tough workmen who lived in wild conditions building the great railroads across America. These men were used to hard work, but they were not trained paleontologists. Nevertheless, Cope and Marsh found that they were resourceful, that they had a good eye for bones, and that they did not have to paid much. When word came through that a survey team had found some fossil bones, Cope's and Marsh's agents would gather a team of fieldworkers, and have them work day and night removing bones at speed. Some of these operations were in dangerous country, and the field men were armed against attack. At times, they worked through winter, removing bones in appalling conditions of ice, snow, and blizzard. It's no wonder that a huge amount of damage was done by these speedy operations. Inferior bones were smashed in the field, and the good ones were hacked out with such speed, and with none of the careful mapping, strengthening, and packaging that is commonplace today.

Marsh's crews can be credited, though, with inventing the 'plaster jacket', the mainstay of modern dinosaur collecting. They found that bones fell to bits when they were lifted from the rock. Thinking of typical medical practise, they realised that a strengthening structure could be built rapidly by coating the bones in plaster of Paris. This plaster comes as a powder, which is simply mixed to a paste with water. It then soon sets hard. By inserting strengthening materials in to the plaster, the bones were permanently preserved. Sackcloth (burlap) is commonly used and, for larger bones, wooden struts are set into the plaster cast to assist dragging (like runners of a sledge) or as carrying handles.

Dinosaur and mammal bones were loaded into boxcars and sent east by rail when possible, where Cope and Marsh fell on the packing cases, tearing them open, and describing the new dinosaurs and other wonderful beasts in haste. They rushed their manuscripts to their editors and published new dinosaur names as fast as the presses could roll. Each man had his own journal, Marsh the *American Journal of Science*, Cope the *Proceedings of the Natural History Society of Philadelphia*. A brief description would be written and delivered to the presses the same day. It would be typeset, checked, and published in two or three days. Their papers often appear at the ends of the monthly issues of those journals as supplements, tagged on in the day or two before they were mailed to subscribers. Even a day could make a difference: a rule of biological nomenclature is that the first name to be given to a new plant, animal, or fossil is the name that everyone uses. So, if Cope could beat Marsh by a day, his name would stand, the other would fall. Working at such speed, mistakes were made, and certainly neither man had the time to carry out a full-scale study of many of the wonderful new dinosaurs they were bringing to light. It took Cope or Marsh less than a week to unpack and describe a new dinosaur. Today, it typically takes three or four years to remove the bones from the rock, conserve them adequately, draw everything, carry out the intricate anatomical interpretations, and prepare drawings and photographs.

Thanks to Cope and Marsh we have many of the famous North American dinosaurs - *Allosaurus*, *Apatosaurus* (= *Brontosaurus*), *Camarasaurus*, *Camptosaurus*, *Ceratosaurus*, *Diplodocus*, *Stegosaurus*, and *Triceratops*. These men also opened up the famous dinosaur sites of Utah, Colorado, the Dakotas, and Montana. At the same time, their collectors investigated younger rock layers, and turned up spectacular finds of fossil mammals and birds, which were also shipped back east, and avidly described by Marsh and Cope.

The mass burial at Bernissart

Many new dinosaurs were found in Europe in the late nineteenth century, but one attracted much attention. This was the discovery of the mass grave of dozens of skeletons of *Iguanodon* found at Bernissart in Belgium. In 1877, coal miners working a deep shaft, more than 300m below the surface, came upon large bones in the roof of a cutting. The mining company contacted scientists in Brussels, who were able to identify the remains as belonging to *Iguanodon* by examining the isolated teeth. Normal mining operations were stopped, and paleontologists from the Royal Museum of Natural

History moved in, and supervised the careful excavation of 39 skeletons of *Iguanodon*, most of them essentially complete, as well as the skeleton of a meat-eating megalosaurid, fishes, turtles, crocodilians, insects, and plants.

Louis Dollo (1857-1931) was appointed as museum assistant at the Royal Museum in Brussels in 1882, and he was given the job of sorting, preparing, and describing the astonishing Bernissart dinosaur collection. The job took him most of the rest of his life. He supervised the cleaning of the skeletons, not an easy task, since the bones were damp, and cracked. The museum technicians had to use a terrifying cocktail of varnishes and glues to strengthen the bones, and this has led to endless conservation problems today. If the Victorian varnish is removed, the bones decay and crumble, and yet today they look unpleasantly shiny and damaged beneath the thick covering of glue. For the first time in Europe, Dollo was able to reconstruct some complete dinosaur skeletons in natural pose, efforts that rivalled those of Leidy, Cope, and Marsh in North America.

Dollo announced his results to the scientific world through a series of dozens of papers about the Bernissart *Iguanodons*, and the associated faunas. He was one of the first paleontologists to consider the biology of the dinosaurs - how they lived - rather than merely giving them a name, and moving on rapidly to the next specimen, as was more the habit of his contemporaries. The new *Iguanodon* skeletons were more complete than anything yet found in England, and Dollo was able to solve a long-standing problem concerning the correct location of a conical pointed bone. Mantell thought this was a nose horn, and indeed Owen reconstructed *Iguanodon* in the 1850s in his Crystal Palace models with the bone mounted on the snout. The new skeletons from Bernissart showed that the mystery bone was a specialized thumb claw, used presumably for defence, or in fighting for mates.

<u>After Cope and Marsh; the Morrison Formation</u>

Cope and Marsh died in the 1890s, but they had trained a new generation of bone hunters. Their discoveries had also inspired the American people, and new museums were built in several cities to house the huge skeletons. Millionaires stepped in to fund the work, and major expeditions went out all over North America, especially in the mid-western United States and in Alberta, Canada. The first focus of attention was the Late Jurassic Morrison Formation

The early excavations by Cope's and Marsh's collectors had been motivated by a desire to excavate as many giant bones as possible in the shortest possible time, and the men who did the digging, and their methods, were often extraordinarily crude. New approaches were introduced in 1897, when the first American Museum expedition entered the area, and work on the Morrison Formation this century has revealed a great deal about the life of the Late Jurassic.

The American Museum of Natural History continued operations in the Morrison Formation until 1905, and during that time sent many tonnes of bones back to the fledgling museum in New York. These provided a basis for one of the world's best dinosaur collections, and many of the Morrison dinosaurs collected around 1900 form the core of present exhibitions.

Other museums were looking towards the Morrison Formation about 1900 as a quick source of spectacular dinosaur specimens. The Carnegie Museum had been set up in Pittsburgh from donations by Andrew Carnegie, a Scotsman who had made his fortune making steel. Earl Douglass, on the staff of the Carnegie Museum, first devoted his efforts to collecting Tertiary mammals in Montana and Utah. In 1908, he was visited in the field by W. J. Holland, the director of the Carnegie Museum, and he suggested to Douglass that they should perhaps look at some Jurassic rocks in the vicinity. This they did, and very soon Douglass stumbled upon a perfect *Diplodocus* femur, lying isolated at the bottom of a ravine.

Douglass returned to the locality the following year, in arid canyonlands close to the western border of Colorado with Utah. His brief was to find the precise source of the *Diplodocus* femur, and to assess whether the site could be excavated. After many days of prospecting, marching up and down the dry canyons, Douglass hit paydirt. He spotted some vertebrae of a big dinosaur in articulation, and this proved that this was an undisturbed dinosaur bonebed. Douglass wrote to his director, Holland, and together they excavated the skeleton represented by the vertebrae, later to be named *Apatosaurus louisae* in honour of Carnegie's wife.

With this encouragement, Carnegie donated the dollars necessary for large-scale excavations. Earl Douglass decided to remain at the site, and to work there full-time. He used the money to hire workmen locally and to buy heavy equipment for the task of removing rock, and of moving the bones out. His wife, delightfully named Pearl Douglass, joined him in the remote corner of the Colorado-Utah border where the first bones were found, and the family remained there for many years. The nearest town, Vernal, Utah, was 30km away, so Douglass set up a homestead and built a log cabin right on the bone quarry. His excavations lasted from 1909 to 1923. During this time, Douglass and his crews excavated hundreds of skeletons, which are now in the Carnegie Museum, and even after so much effort, the bonebed showed no sign of running out.

Douglass unearthed skeletons of the sauropod *Apatosaurus*, the first find from the site, as well as the longer sauropod *Diplodocus*, the plated *Stegosaurus*, the bipedal ornithopod *Camptosaurus*, and the predatory *Allosaurus*. These dinosaurs had been found by Cope and Marsh before, but no site in the Morrison Formation had produced multiple skeletons of each form in a single locality. Douglass collected twenty complete skeletons, and isolated remains of a further 300 individual dinosaurs.

Douglass was at first puzzled by the immense richness of the site. How had such a diversity of dinosaur skeletons ended up in one place? He realised that these animals could not all have come here and died by some catastrophe: there were too many of them, and the range of species represented was too great. Douglass suggested that he had chanced upon an ancient sandbar that lay in the middle of some great meandering river in the Late Jurassic, and that the skeletons were accumulated by normal river action. Carcasses of animals that had died upstream were washed along, and eventually ran aground on the bar, where the flesh rotted, and where they were eventually buried under more sand brought down by the river.

One of the best finds from the quarry was a complete skeleton of Diplodocus, which Holland named *Diplodocus carnegiei* in honour of his patron. This greatly pleased

Carnegie, who had always said he wanted his museum crews to find a dinosaur 'as big as a barn'. He was so pleased indeed that he decided the world should see his new dinosaur, and he ordered that the whole thing should be cast in plaster bone by bone. Duplicates of the skeleton were made, and prepared for shipment to the leading museums of the world. Dr Holland followed the specimens as they were sent out, and he, and the dinosaurs, were received with acclaim and obvious pleasure, by the directors of the British Museum in London, the Musée d'Histoire Naturelle in Paris, the Senckenberg Museum in Frankfurt-am-Main, the Royal Museum in Vienna,, the University Museum of Natural History in La Plata, Argentina, and the Museum in Mexico City. The casts are still on show in most of these institutions (indeed they are so large that they would be hard to dispose of).

Further dramatic dinosaur discoveries in the Morrison Formation included a skeleton of the short-snouted sauropod *Camarasaurus*, collected by the Carnegie Museum team in 1922, near the end of their long series of excavations. This skeleton created a stir since it was small, a mere 5 metres long. Large sauropods were by 1922 quite familiar, but the new *Camarasaurus* was exciting since it was a juvenile. During this time, the Carnegie Museum recognised the longer-term value of their quarry to the nation, and after much lobbying of the government by Holland, the site was named Dinosaur National Monument in 1915, and preserved for posterity. It is now a living museum, covered with a building, where a small part of Douglass' sandbar is still actively worked in front of visitors.

Dinosaurs of the Late Cretaceous: Canada and USA

Following the leads set up by Cope and Marsh, paleontologists began seriously exploring the rich dinosaur beds of Alberta, Canada in the early twentieth century. About 1910, two collecting groups set out along the Red Deer River, to collect dinosaur skeletons. Although the field men were working for money, and the more they found, the more they would earn, this collecting proceeded without the animosity that had existed been the parties working for Marsh and Cope.

The Red Deer River cuts deep canyons through the Late Cretaceous sediments of southern Alberta. Climatic conditions are desert-like for most of the year, and there is very little vegetation other than scrubby bushes. Every year, there are torrential rains, and huge rivers of water cut through the canyon walls, creating classic badland scenery (bad for farmers; good for fossil-hunters). The two collecting teams were led by Barnum Brown, acting for the American Museum of Natural History, and Charles H. Sternberg, working for several institutions, but especially the Geological Survey and the National Museum of Canada, and the Royal Ontario Museum. All these institutions wanted to acquire dinosaur skeletons, and the Canadians in particular wished to build collections of their own dinosaurs.

Barnum Brown invented a new collecting technique. He built a large wooden barge, and floated downstream in 1910 and 1911, tying up here and there, and venturing up side canyons looking for shards of bone. When he found a good prospect, he and his team excavated the bones, and loaded the plaster packages on to the barge. They were later offloaded and sent east to New York. The Canadian Government was aware of Brown's discoveries, and they decided to secure some dinosaurs for their own fledgling museums. They hired Charles Sternberg, a commercial collector, who operated at times with the help of some or all of his sons, George, Charles, and Levi. The Sternbergs set off for the Red Deer River in 1912, and they found rich dinosaur beds around Drumheller and Steveville. The Sternbergs and Barnum Brown returned in 1913, and trips continued until 1917. During this time, both teams found dozens of complete skeletons of dinosaurs at various levels in the Late Cretaceous, which are now assigned to the Santonian, Campanian, and Maastrichtian. This sequence through time is one of the most important aspects of the Alberta collecting, since it showed for the first time that it might be possible to track dinosaur evolution in one area through a long time span.

The biggest dinosaur expedition

One of the biggest bone-hunting expeditions ever was mounted by German paleontologists in what is now Tanzania, then German East Africa. The fauna is large, consisting of three meat-eaters and six plant-eaters, and they created a sensation when their skeletons were first exhibited in Berlin about 1920. The first finds were made in 1907 in what was then German East Africa at a locality called Tendaguru, four days march inland from the important coastal port of Lindi.

The locality was discovered by W. B. Sattler, an engineer working for the Lindi Prospecting Company, as he searched for valuable mineral resources. He found pieces of gigantic fossil bones weathering out on the surface of the baking scrubland. Sattler reported back to the director of the company, and he in turn told Professor Eberhard Fraas, who happened to be in the colony at the time. Fraas was a noted paleontologist, who had created his reputation describing Triassic fossil reptiles from Germany, and he had also worked on the early prosauropod *Plateosaurus* (see pages 76-77). Fraas visited the Tendaguru site, and he clearly recognised its huge potential. He collected some good specimens to take back to Stuttgart, and he showed them to various museum curators. Dr W. Branca, director of the Berlin Museum was enthusiastic, and he set about raising funds for an expedition.

Branca, and his colleagues, succeeded in raising the huge sum of 200,000 marks from the government, from various scientific organisations, and from wealthy local donors. This allowed him to mount a substantial expedition, which was planned to run from 190 to 1911, under the leadership of Dr Werner Janensch, curator of fossil reptiles at the Berlin Museum, and with the assistance of Dr Edwin Hennig. In the end, the expedition also ran in 1912, but under the leadership then of Dr Hans Reck.

The expedition was on a larger scale than anything mounted before. In the first season at Tendaguru, 170 native labourers were employed, and this rose to 400 in the second season, and 500 in the third and fourth. These huge numbers of workers were accompanied by their families, so the German dinosaur expedition at at Tendaguru involved an encampment of 700-900 people. This created enormous logistical problems in obtaining enough food and water, and in maintaining the operation.

The labourers dug numerous pits all over the site which ran from Tendaguru hill to Tendaguru village, a site spanning about 3 km. Most of the bones were very large, but they were fractured and had to be protected. The finds were mapped, measured, and then encased in plaster for then long journey to the coast. Teams of workmen carried the bones on their heads, or slung on poles, for the four-day trek to Lindi, where they were shipped out to Germany. In the first three years of the expedition, 4300 loads of fossil bones were sent out, weighing a total of 200 tonnes. During the fourth year, a further 50 tonnes were shipped out.

In Berlin, the long process of cleaning the bones began, and this lasted for many decades. As the materials were cleaned up, the huge skeletons were mounted in the Humboldt Museum in Berlin, where they may still be seen, and the new species were described up to the 1960s by Janensch, Hennig, and others. The Berlin specimen of Brachiosaurus the largest complete dinosaur skeleton in the world.

China and Mongolia

Dinosaurs from Asia were found sporadically at first. Specimens from China were collected up to the 1920s by American, French, and Swedish priests and explorers. The first good Chinese dinosaur skeleton, *Mandschurosaurus*, was found in Manchuria, then under Russian control, and was sent back to St Petersburg in 1917. Asiatic dinosaurs really hit the headlines in 1922, 1923, and 1925, when an American expedition, led by Roy Chapman Andrews, returned from Mongolia with spectacular dinosaur specimens, skeletons of the small ceratopsian *Protoceratops* with nests containing eggs, the extraordinary slender meat-eaters, *Saurornithoides*, *Velociraptor*, and *Oviraptor*.

The expedition had been sent out by Henry Fairfield Osborn, the Director of the American Museum of Natural History, in the hope of finding early human fossils, but it came back with evidence for one of the best dinosaur-hunting areas in the world. Mongolia was little known in the West, but Vladimir A. Obruchev, a distinguished Russian paleontologist, had found a rhinoceros tooth there in 1892. This suggested that rocks of the right age to hold fossil humans might be there. Andrews raised money and bought numerous cars and other equipment, and a caravan of vehicles and camels set off from China in early 1922, crossed the border into Mongolia, and headed north towards Ulanbaatar, the capital. The expedition was led by Andrews, and the chief paleontologist was Walter Granger. They made discoveries early on, first at a site called Iren Dabasu, on the road to Ulanbaatar, where they found Cretaceous mammals and dinosaurs. They visited Ulanbaatar briefly, and then set off west into the Gobi Desert.

After some weeks of exploring the Gobi Desert, and a few discoveries, the expedition turned east again, heading back to China. One day, the vehicles drew up on the edge of a large eroded basin formed in red sandstones, a site they named 'Flaming Cliffs', and now officially called Bayan Zag. The collectors found abundant dinosaur bones and eggs, but they then had to head home. The expedition returned in 1923, fired by enthusiasm, and they were able to spend adequate time at Iren Dabasu and at Bayan Zag. They collected bones of several extraordinary new dinosaurs. There were dozens of specimens of the small ceratopsian *Protoceratops*, and, most dramatically of all, these were associated with several nests containing elongate eggs arranged in neat circles. When Andrews and his crew returned to New York, and announced the collections of *Protoceratops* with their nests, they created a sensation. Dinosaur eggs had been found as isolated remains in the Late Cretaceous of southern France in the nineteenth century, but these were the first complete nests.

The Americans returned to the Gobi Desert in 1925, and during their three expeditions they amassed large numbers of specimens. Apart from *Protoceratops*, they found small theropods such as *Saurornithoides* and *Oviraptor*. Later expeditions to Mongolia were mounted by the Russians in 1946, 1947, and 1949, and they found new dinosaurs, especially *Tarbosaurus*, a relative of the North American *Tyrannosaurus* and the hadrosaur *Saurolophus*, also a North American form. Polish expeditions operated in Mongolia in the 1960s, and the American Museum of Natural History began a second series of expeditions in the 1990s, all of which have been crowned with astonishing new discoveries.

Later finds: the 1940s, 1950s, and 1960s

Dinosaur paleontology went through a recession during the middle decades of the twentieth century. Major expeditions were run by Russian, Chinese, and Polish teams. Some important discoveries were made in more well explored parts of the world. For example, John Ostrom found skeletons of *Deinonychus* in the Mid Cretaceous of Montana in 1964, and this marked the beginning of a revolution in understanding of theropod dinosaurs, and a revival of interest in Huxley's old idea that birds evolved from theropod dinosaurs.

Further isolated discoveries were made up to 1950 in North Africa (Egypt, Tunisia, Morocco, Niger), Brazil, and Argentina. Initially, the work was stimulated by expeditions mounted mainly by European and North American institutions, keen to acquire exotic specimens, and keen to expand their scientific reputations. Increasingly, during this time, countries in Asia, Africa, and South America established their own geological surveys, universities, and museums, and the focus shifted to locally-based experts. By 1950, dinosaurs had been found on every continent, except one, Antarctica, and more than 500 dinosaur species had been named. This was a dramatic rate of discovery when it is recalled that dinosaur hunting on a large scale began only after 1850.

However, very little dramatically new work was published during these decades on dinosaur paleobiology. The view of dinosaurs had become rather stagnant. Most scientists, and the public, saw them as broken-down overblown animals that pretty well deserved to go extinct. Dinosaurs, metabolically, were giant lizards, cold-blooded, stupid, and slow. Paleontologists concentrated on economic areas of their subject, particularly the rapidly advancing field of biostratigraphy: oil companies around the world employed paleontologists to date the rocks they drilled through. Dinosaurs were kids' stuff, not serious, not interesting. I have made a detailed survey of publications on one of the hottest dinosaur topics of all, their extinction at the end of the Cretaceous, and I found that only two or three papers on this topic were published each year up to the 1970s, when the annual total rose to 10-15, and the total is now probably several hundred per year, since 1980.

Dinosaur renaissance

Bob Bakker in 1975 penned an article in *Scientific American* entitled 'Dinosaur renaissance'. Never a man to hide behind false modesty, he was drawing attention to the fact that something amazing was happening in the field of dinosaurian paleobiology. Suddenly dinosaurs were sexy again, bright young geologists and biologists wanted to work on dinosaurs. Publications about dinosaurs were burgeoning, and in all the serious scientific journals. Museums were hiring paleontologists again; expeditions were setting out and finding amazing new species of dinosaurs. What had happened?

It was a two- or three-step process. First came Bakker (1970s), then came the impact extinction hypothesis (1980s), and then came computerized cladistics (1990s). All three shook up dinosaurian paleobiology. All three had been on the boil since the 1960s, and they burst on the scene neatly at the beginning of each of the last three decades of the twentieth century. All three were interdisciplinary. All three affected the professionals profoundly, but all three were also played out largely in public.

Bob Bakker was a student of John Ostrom's at Yale in the late 1960s. He was working on dinosaurian posture at the same time as Ostrom was completing his descriptions of the startling *Deinonychus*, and beginning to have ideas about bird origins. Both Ostrom and Bakker saw that *Deinonychus* was no slouch. Here was a small dinosaur, with powerful limbs, and clearly adapted for rapid movement. Its flick-knife toe claws were clearly not designed for scraping moss off tree trunks. Here was a dinosaur that leapt and slashed its prey. It had stiffening ossified ligaments along its tail: this implied balancing. *Deinonychus* could stand on one leg, rotating, and positioning itself as it slashed with the other foot. This required fine coordination, excellent eyesight, and a powerful motor area in the brain. Later evidence suggested that *Deinonychus* hunted much larger prey, such as the ornithopod *Tenontosaurus*, presumably by pack hunting. Social behavior of this kind required communication and more brain power. Perhaps dinosaurs were not overblown lizards after all. Maybe Richard Owen had been right in 1842 to see dinosaurs as mammal-like in many ways (even if he held this view for the wrong reasons).

This was all very daring. The message that something was afoot in professional dinosaurian circles came out to a wider public through Bob Bakker's artwork. He had a fine eye, and produced excellent vigorous pencil sketches. His first major piece was a frontispiece to John Ostrom's monograph on *Deinonychus*, published in 1969. Normally, a monograph like this would be read with interest by professional colleagues, but would not impact on a wider audience. However, *Deinonychus* was such a vigorous and vicious little beast, Ostrom's descriptions and illustrations of the skeletal anatomy were so thorough and stimulating, and Bakker's vision of *Deinonychus* in life was so startling, that the news got out. Pictures were published widely in popular science magazines and newspapers. There was a new excitement.

A key to the renaissance was the reposturing of dinosaurs. Bakker saw that *Deinonychus* had to be shown with a horizontal backbone, not vertical, as Leidy had thought. Dinosaurs should be modeled on see-saws, not kangaroos. The stiffening rods down the tail showed that the tail had to be held out vertically. This meant that there was no choice but to make the whole body horizontal. Another young student, Peter Galton, recently arrived in Connecticut from England, showed that this new horizontal posture had to apply to the bipedal ornithopods too. Some of them had stiffening ligaments over the hips and tail. A horizontal dinosaur meant business. It was a go-faster posture. It was heading somewhere, whereas Leidy's vertical kangaroo-dinosaur couldn't really budge. But it wasn't only posture that Bakker, and other young turks, changed. There was also their thermal physiology.

Were the dinosaurs warm-blooded?

Were dinosaurs warm-blooded or not. How can such a question be answered without a time machine and a giant rectal thermometer? The debate began virtually with the invention of the group. In 1842, when Richard Owen coined the name 'Dinosauria', he speculated that these giant reptiles had been rather mammal-like in their physiology, and very different from living reptiles, such as lizards and crocodiles. Owen clearly thought that dinosaurs were able to control their body temperature to some extent, and to keep it high.

Modern animals divide up into two main categories in terms of temperature control. The ectotherms, like fishes and reptiles, generally use only external means to control their body temperature. So, lizards bask on rocks to raise their temperatures, or hide in holes to cool down. The endotherms, like birds and mammals, can maintain warm body temperatures by internal means, by burning up food and by a complex feed-back mechanism that heats and cools the body to maintain temperature at a precise level. A change of only a few degrees can be critical, as in humans, whereas ectotherm body temperatures may vary by 20oC or more each day. The second distinction in modern animals is between poikilotherms and homeotherms. Poikilotherms have variable body temperatures, and homeotherms have constant body temperatures. Lizards are clearly poikilothermic ectotherms, and birds and mammals are generally endothermic homeotherms. But poikilotherm does not equal ectotherm, or homeotherm equal endotherm. The four terms are necessary because fishes are generally ectothermic homeotherms: their body temperature is constant, although controlled externally, since then temperature of the sea does not change much. Bats and hummingbirds are poikilothermic endotherms, since they can switch off their expensive heating system at night, or in winter. What were the dinosaurs?

Until 1970, dinosaurs were thought to be sluggish cold-blooded reptiles, in other words, ectothermic and poikilothermic, despite Owen's classic ideas. Then in 1970, Bob Bakker, extending his revised view of dinosaurs, marshalled a range of evidence that dinosaurs had been endothermic homeotherms. He noted these points, among others:

(1) dinosaurs have complex bone structure with evidence of constant remodelling, a bone feature seen in modern mammals, but not in reptiles;

(2) dinosaurs have an upright posture, as in modern mammals and birds;

(3) dinosaurs evidently had active lifestyles, or at least the small theropods certainly did;

(4) predator-prey ratios of dinosaurs show more in common with those of mammals than with those of modern reptiles;

(5) dinosaurs are found in polar regions.

Bakker's collection of evidence shows some of the ingenuity paleontologists must employ in their efforts to understand the past, drawing here on the physiology and anatomy of modern animals, bone histology, paleoecology, and paleogeography.

There was a furious debate about Bakker's proposals in the 1970s and 1980s. Much of his evidence was equivocal, and did not stand up to strong scrutiny. Further study of bone structures has shown that the dinosaur and mammal pattern is associated with large size and fast growth rather than simply with endothermy. Upright posture does not necessitate endothermy, nor does an active lifestyle (think of insects or small lizards). Predator-prey ratios for dinosaurs do suggest that the predators were endothermic, but there are serious problems in trying to calculate such paleoecological measures in a precise manner. Dinosaurs are found in regions that lay near the poles in the Jurassic and Cretaceous, but there were apparently no polar ice caps in the Mesozoic, and so conditions were not cold.

The debate isn't over. Most paleontologists accept that large dinosaurs were inertial (or mass) homeotherms. This means they were certainly warm-blooded in a commonsense meaning of the term, but they achieved their warmbloodedness (= homeothermy) simply by being huge: it takes a giant lardbag weeks to cool down and warm up. But the small theropods, like *Deinonychus*, might well have been mammalian endotherms, eating high-protein food in large quantities and generating high resting metabolic rates. New studies of isotopes in the 1990s have tended to confirm this: different mass states of oxygen can give indications of ancient temperatures. In a study on *Tyrannosaurus*, ribs indicated temperatures some 4oC higher than in peripheral parts, like fingers and toes. Maybe this giant flesh-eater kept its core regions hotter than external temperatures. or maybe not. Another set of studies in the 1990s revealed that dinosaurs lack nasal turbinates. These are paper-thin bones that occur inside the nasal cavities of modern mammals and birds. They support complex infoldings of the nasal tissues, and they function as heat exchangers (radiators), heating up cold air as it is breathed in, and cooling hot air before it is breathed out.

Impact extinctions

The second boost to dinosaurian paleobiology came in 1980, with the publication of one of the most daring papers in earth sciences of the twentieth century. The paper was published by a Nobel laureate in physics, Luis Alvarez, and colleagues from Berkeley, California, and in it they proposed that the dinosaurs died out as a result of the impact of an asteroid, a giant meteorite, measuring 10 km across. The impact happened 65 million years ago, at the boundary between the Cretaceous and Tertiary periods, and it is known in shorthand as the 'KT event'.

Over the years, hundreds of theories for the disappearance of the dinosaurs had been proposed, and yet none had gained general acceptance. The problem was that many of the ideas took no account of what actually happened: it wasn't only the dinosaurs that disappeared, but also pterosaurs, marine reptiles, ammonoids, belemnites, rudists, and much of the marine plankton. There had been another problem: the extinction of the dinosaurs was not really regarded as a serious scientific problem, just a kid's problem or a kind of parlour game. Alvarez and colleagues made people sit up and take notice, and within a few years, cosmologists, astronomers, physicists, geophysicists, volcanologists, mineralogists, climatologists, ecologists, mathematicians, and other 'serious' scientists wanted to be in on the act. Dinosaur extinction had become a huge interdisciplinary research problem, attracting thousands of dollars of research money.

This intensity of research on the KT event reflected the breadth of Alvarez's vision. His idea was that the impact caused massive extinctions by throwing up a vast dust cloud which blocked out the sun and prevented photosynthesis, and hence plants died off, followed by herbivores, and then carnivores. The dust cloud also prevented the sun's heat reaching the earth, and there was a short freezing episode.

There are three key pieces of evidence for the impact hypothesis, an iridium anomaly worldwide at the KT boundary, and associated shocked quartz and glassy spherules. Iridium is a platinum-group element that is rare on the Earth's crust, and reaches the Earth from space in meteorites. At the KT boundary, that rate increased dramatically, giving an iridium spike. Many localities have also yielded shocked quartz, grains of quartz bearing crisscrossing lines produced by the pressure of an impact, as well as glassy spherules produced by melting at the impact site. A catastrophic extinction is indicated by sudden plankton and other marine extinctions in certain sections, and by abrupt shifts in pollen ratios at some KT boundaries. Alvarez had only the iridium spike at a couple of localities, one in Italy and one in Denmark, but that was enough for him to propose his dramatic idea. Work since has confirmed what he proposed in a dramatic way.

The impact model was strengthened by the discovery, in 1990, of the impact site, the Chicxulub Crater in Mexico. This is big enough (200 km diameter) for a 10km asteroid, and there is strong evidence for impact fallout and tsunamis (tidal waves) all round the Proto-Caribbean. This is the smoking gun, but the debate isn't over yet: paleontologists still have to explain how the impact actually caused the selective extinctions that occurred 65 million years ago. There are also other bits of evidence that don't quite fit, or which may suggest a more complex set of events 65 million years ago. First, there was major volcanic activity at just this time. The Deccan Traps in India represent a vast outpouring of lava which occurred over the 2-3 Myr. spanning the KT boundary. Vast eruptions like this can themselves cause extinction. In addition, it is clear that many of the groups that died out at the KT boundary had actually begun to decline long before the boundary. Either they knew the impact was coming, and turned up their toes in good time, or there were other processes going on: major long-term volcanism can cause major climatic fluctuations, and climates were certainly becoming cooler in North America.

Like the Bakker/ endothermy phenomenon of the 1970s, the KT impact hypothesis of the 1980s is still a wide open research topic, and far from full explanation. The last of the triumvirate is the computerized cladistic revolution.

<u>The 1990s: computerized cladistics</u>

Cladistics might at first seem an arcane book-keeping method, and hardly the stuff of revolutions. The methods were developed in the 1950s and 1960s by a German entomologist, Willi Hennig, and they were picked up only slowly in the late 1960s and 1970s by paleontologists. There were huge fights about the implications of the new methods, but they are now well established. Basically, Hennig present biologists and paleontologists with a scientific method for reconstructing evolutionary trees. Up to 1960, systematists (the scientists who try to understand the diversity of life) were regarded as half-artists, half-scientists. Only by years of careful study could you get a feel for the true classification and pattern of evolution of a particular group. This kind of intensive training and careful work is still absolutely essential, but the method is now a science, not an art.

Hennig's great insight was so obvious that it sounds like nothing at all: systematists should use only derived characters in classification. In sorting out a group of parrots, for example, it's not helpful to note that they all have wings and beaks - those are primitive characters found in all birds. Equally, it might not be helpful to classify them simply by colour. After all there are other birds that are red, green, or blue, but entirely unrelated. Focus instead on specific features of the anatomy found in subgroups of your sample. Perhaps six or seven species of parrots all share a particular shape of the lower jaw, or a specific structure on the thigh bone. Characters are coded in data matrices, with species on the x-axis, characters along the y-axis. In a typical study, the data matrix might contain 60-70 characters coded for 10-20 species. What to do next?

Hennig worked through his data matrices by hand, and so too did most systematists until about 1985. You looked for any pair of species that shared a lot of characters, and then paired them off. Then you found a third species that was closer to that pair than to any others, and it joined the group (the clade). Then you added a fourth, the next most similar, and so on. In 1985, computer programs for doing this became available. Early versions had to be run on clunky old mainframe computers. After 1985, they were rejigged for use on PCs (the most popular, PAUP, worked best on Macs). Paleontologists quickly invested their $50 (that is the size of research funding paleontologists can just about afford), and they set to. From one or two cladograms a year in the 1980s, typical dinosaur paleontology journals now contain hundreds.

The computerized cladistic revolution really took hold after 1990. Early dinosaur cladograms of the 1980s were reanalyzed. Data matrices grew to gargantuan proportions. Monthly, new cladograms of major dinosaurian groups appeared. Much attention focused on the theropods. Ostrom's intuition of the 1960s and 1970s that birds were dinosaurs was proved time and time again. *Archaeopteryx* shares dozens of intricately complex anatomical features of its skull and skeleton with dinosaurs. The debate moved on to which was the most closely related dinosaur to birds. These debates continue today, with radical cladistic revisions of theropods and sauropods published about 2000, and more in the pipeline.

Does this matter? Is it all a trend? Computerized cladistics matters because it is a *method*, it exposes the workings of the practitioners, and it is available to all. Debates about dinosaurian phylogeny up to 1980 were about prejudice. Evidence could be found for anything (and some diehards who operate in the old mindset, continue to look for obscure bits of evidence that birds are not dinosaurs). The computer cladist after 1990 had to lay her/himself on the line and expose every detail of the reasoning. Anyone could pick over the evidence and tear it to shreds (and they did/ do with huge glee). The computerized cladistic method encouraged a new kind of research study. Young graduate students embarked on ambitious systematic projects on dinosaurs, projects of a kind that would not have been undertaken twenty years ago. They tried to see every specimen of some particular group often traveling very widely, and they scrutinized the specimens in more detail than had ever been done before in search of the elusive characters that might reveal the true phylogeny. The end products have an authoritativeness that is admirable.

The computerized cladistic revolution of the 1990s, added to the KT impact revolution of the 1980s, and the Bakkerian revolution of the 1970s, have all conspired to make dinosaur paleontology a burgeoning field. The newfound interest in these kinds of paleobiological, systematic, and theoretical studies has been matched by a startling renaissance in fieldwork.

<u>Dinosaur finds since 1970s</u>

In North America, spectacular discoveries include some giant sauropods, whose precise size cannot be estimated since the specimens are incomplete, but which have all been said to exceed the length of *Diplodocus* (30m): *Supersaurus* and *Ultrasaurus* were named from bones found in Dry Mesa Quarry, in southern Colorado in the 1970s. An even larger sauropod, *Seismosaurus*, was named in the 1980s from monstrous bones excavated in central New Mexico, at the southern limit of the Morrison Formation. This animal has not been fully described, but it is estimated to have measured over 40m in length.

Long-term collecting by Jack Horner and his colleagues in the Montana Badlands since the 1970s has turned up yet another series of dramatic discoveries. He located a dinosaur nesting ground where hadrosaurs, or duckbilled ornithopods, had apparently returned year after year to lay their eggs. Horner found numerous nests on an elevated patch of ground, and by digging through the sediments of the site, which he named Egg Mountain, he found that the same hadrosaur species had built nests here time after time. The nests were shallow hollows scraped in the ground, and the eggs were apparently tended by the parents and older offspring, since he found skeletons of all age groups associated with the nests. He suggests that dinosaurs showed intelligent parental care, and he named the new hadrosaur *Maiasaura*, or 'good mother reptile'.

A third new area of research in North America has been the study of dinosaur footprints, and especially megatrackways. These are sites, often extending over tens or hundreds of kilometres, covered with dinosaur tracks. Martin Lockley of the University of Colorado has shown that there are Late Jurassic and Cretaceous horizons that can be traced along the western shore of the Mid-American Seaway, where great herds of dinosaurs (especially sauropods and ornithopods) hiked from north to south, perhaps migrating 1000-3000 km each year as climates and food sources changed.

Dinosaurs had been excavated in Europe during the early decades of the twentieth century. Friedrich von Huene, for example, carried out excavations of mass burials of *Plateosaurus* in the Late Triassic of southern Germany during the 1920s. At the same time, Baron Franz Nopcsa, an unusual man by any score, studied the latest Cretaceous dinosaurs of Romania, while making brilliant interpretations of dinosaurian paleobiology. A dramatic discovery was the finding of *Baryonyx* in 1983. Against the odds, here was an extraordinary new dinosaur found within the commuter belt around London. *Baryonyx*, with its massive slashing claw, and long slender jaws with tiny teeth, was hard to interpret. It appears to have fed on fishes, and is most closely related to the North African spinosaurids.

The modern phase of dinosaur collecting in Asia began perhaps in the 1960s, when Polish paleontologists forged a link with their colleagues in Ulaanbaatar, and a series of Polish-Mongolian expeditions took place. These expeditions were spectacularly successful, turning up more specimens of the classic Mongolian Late Cretaceous dinosaurs *Protoceratops*, *Oviraptor*, *Velociraptor*, also *Tarbosaurus*, but also some new sauropod specimens, *Opisthocoelicaudia* and *Nemegtosaurus*, and an extraordinary specimen which has come to be known as the 'fighting dinosaurs'. This specimen preserves a skeleton of the lightweight flesheater *Velociraptor* with its claws seemingly locked into the bony headshield of a *Protoceratops*. Were the two fighting, *Protoceratops* perhaps defending its nest from a raid by *Velociraptor*, or is this merely a chance association of two skeletons? The Polish-Mongolian expeditions scored another coup in turning up dozens of beautiful skeletons of the tiny mammals that lived side by side with the dinosaurs. Previous expeditions had yielded a few mammal skeletons, but no-one had previously collected carefully enough to be able to bring such beautiful delicate fossils back to the lab.

Dinosaur collecting in Mongolia has continued since the 1970s by Mongolian and Russian paleontologists, and, in the 1990s, by a renewed collaboration between Mongolians and the American Museum of Natural History. The recent Mongolian-American expeditions have turned up *Mononykus*, billed as a large flightless bird, but possibly an aberrant theropod dinosaur. They have also shown that the theropod Oviraptor, far from being an 'egg thief' was actually found near nests with eggs since it was incubating its own eggs. Discoveries in Inner Mongolia, which is part of northern China, have resolved a long-standing problem of saurischian systematics. Strange long sickle-like claws from Mongolia were named *Therizinosaurus* in in the 1950s by Russian paleontologists. In the 1960s and 1970s, Polish and Mongolian paleontologists found a new group of plant-eating theropods that they called segnosaurs. Discoveries by the Sino-Canadian expeditions to Inner Mongolia in the 1990s proved that these two groups were one, the therizinosaurs, and that these were some of the most bizarre theropods of all: not only plant-eating, but armed with long claws for scraping food together, and with a skeleton that made them look like a cross between a giant gorilla and a ground sloth - Godzilla truly lives in eastern Asia!

Dinosaur study began to expand seriously in China about 1965, with the establishment of several museums, and the training of a new generation of paleontologists. Since then, dinosaurs have been found in Jurassic and Cretaceous rocks in China, and 100 or more species have been reported. The rate of collection of new dinosaurs in China shows no sign of slowing down. The latest efforts have focused on the spectacular Early Cretaceous sites of Liaoning which have yielded spectacularly well-preserved plants, fishes, and reptiles. Birds with feathers have been found there, and, most astonishing, in the 1990s, several dinosaurs came to light that were equipped with feathers. These feathered dinosaurs included forms close to the German *Compsognathus*, therizinosaurs, and others.

Dinosaurs had been found in Argentina and Brazil before, but young paleontologists in both countries began to find more material in the 1960s, and the pace has quickened especially in the 1990s, with dramatic new finds of the world's oldest dinosaurs in the Late Triassic of Argentina (*Eoraptor*, *Herrerasaurus*), and whole faunas of new forms from the Jurassic and Cretaceous. The Late Cretaceous dinosaurs of South America in particular are important, since some forms are unique to that continent. The latest finds from Argentina include *Giganotosaurus*, a theropod that was possibly larger than *Tyrannosaurus*.

In Africa, sporadic collecting has turned up dinosaurs from north to south, and east to west. Recent American expeditions to Niger, and other parts of the Sahara, have shown that Cretaceous dinosaurs of Africa still had some affinities with North America, even though Africa was virtually an island by then. Unusual African forms include the spinosaurids, long-snouted theropods that might have been fish-eaters, distributed over North Africa, South America, and Europe. The Late Triassic and Early Jurassic dinosaurs of South Africa, first found about 1850, were further explored, and some new specimens came to light. Extensive collecting in the latest Cretaceous of Madagascar has turned up titanosaurid sauropods, abelisaurid theropods, and other forms that prove a close land link to South America, but putative isolation from the African mainland.

Polar dinosaurs have long exerted a fascination. Bakker used Arctic finds to bolster his view that warm-blooded dinosaurs happily lived in polar regions. While some paleobiologists pictured dinosaurs happily skipping through the snowdrifts, others preferred to consider that they migrated away in winter. New finds in Australia have re-opened the discussion of polar conditions. Work by Pat and Tom Rich at Dinosaur Cove in South Australia, has turned up a restricted fauna of mainly small dinosaurs. That part of Australia lay within the Antarctic Circle during the Cretaceous: did they live through the icy winter, or migrate north? This is part of a wider debate about Mesozoic paleoclimates: were temperature pretty uniform from Equator to poles, or were winters severe around the north and south poles?

The final piece of the jigsaw of dinosaur distribution was completed in the 1990s with the discovery of several dinosaurs in the Jurassic and Cretaceous of Antarctica. Dinosaurs are now known from every continent on earth.