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Introduction

In any kind of description of the history of a scientific field, there will be a fundamental narrative of uncertainly giving way to fact and theory, with unknowns and gaps in our knowledge being filled in and worked out. But perhaps inevitably, for every fact to hand or inference that can be made, there is another that was unknown or uncertain. Filling in one gap only tends to reveal another question that could not be answered, or perhaps even conceived of being answered, before that was known. Palaeontology is no different, though when dealing with dinosaurs, the pieces filling in those gaps do tend to be rather large.

In the late 1700s and early 1800s, a series of palaeontological finds of giant reptiles across the south of England heralded the beginnings of a new understanding of the bygone Earth. These animals lived in ancient seas and were soon christened with a barrage of now familiar names – *Ichthyosaurus*, *Plesiosaurus* and *Pliosaurus*, and less familiar ones such as *Temnodontosaurus*, *Opthalomosaurus* and *Cryptocleidus*. Plenty of fossil animals had already been discovered at this point, but these were primarily those of well-known living groups of mammals like elephants and hyenas, or shelly fossils like ammonites, which had obvious relatives in living squid and cuttlefish.

But now there was inarguable evidence of major types of animal unknown in the modern world, and from a geological era where many familiar animals such as birds and mammals were apparently absent. These finds indicated that there had once been an Age of Reptiles, something quite unlike anything that scientific minds of the time might have imagined. This proved to be a sensation, with the learned public flocking to hear lectures on these amazing new animals from the scientists of the day.

This was a time of great growth of the natural sciences in Europe. Although Charles Darwin's grand theory of evolution by means of natural selection was still decades from publication, the ideas of species changing over time, and that species or entire groups could have gone extinct and were no longer alive, were under discussion in scientific circles. New discoveries in biology, chemistry and physics were fuelling new concepts about the world, and entire fields such as geology were being established. The hearts of the great continents in the Americas, Africa, Asia and Australia were being explored, and old fables were being banished as new information made it back to the learned societies of London, Paris, Berlin and others. It was a near perfect time to investigate whole new groups of extinct animals.

Before too long, great reptiles that had lived on land started to be found and recognised, in addition to those from the seas. Not for them the sleek shapes, paddle-like fins and tails of the ocean-going animals; instead they possessed more normal reptilian walking limbs, which pointed to a terrestrial lifestyle. Although these were initially known from only a few, very fragmentary pieces, but researchers quickly realised that they were an entirely new group of animals. They were christened with the name 'Dinosauria'. Despite this is commonly translated as meaning 'terrible lizard', a more accurate version is probably 'fearfully great reptile', which better captures the spirit of how these animals were perceived.

When it was published in 1859, Darwin's *On the Origin of Species* gave the naturalists of the time an evolutionary framework to understanding life on Earth both past and present. Indeed, this was a time when the fields of geology and palaeontology were very much in their infancy.* Science was all about discovering new phenomena, new species, new elements, and identifying physical laws, and despite the huge efforts in all of these areas, the scaffold for understanding the past was still, at best, very limited. Add in a healthy dose of biblical literalism – since many naturalists were trained by, or even ordained in, the Church – and these infant sciences can be forgiven much for their early errors and confusion.

* The two fields were in fact broadly synonymous at this point and known for a time by the delightful name of 'undergroundology'.

Even so, what stood out early on was twofold: that so much information could be derived from so little data, and that so much more remained to be resolved. This apparent paradox is to be a running theme of this book; people seem to be consistently amazed at what palaeontologists are able to work out about dinosaurs from the limited resources of the fossil record, while being equally amazed at things that are unknown.

The second dinosaur

The famous *Iguanodon* serves as an example of what could be elucidated at the time from very little. This was only the second dinosaur to be named (the first being *Megalosaurus*), the honour going to an English doctor named Gideon Mantell, who had become fascinated by all things fossiliferous in the south of England. Although the *Megalosaurus* was originally known only from a small number of somewhat leaf-shaped teeth, these alone were enough for Mantell to work out quite a bit about his animal.

First off, the sheer size of these – some were several centimetres long – meant that they must have come from a large animal. Second, they were almost certainly from a reptile, given both the serrations to the edges (very common in reptiles, and almost unknown in mammals) and the fact that they were from a time known to be dominated by reptiles and devoid of large mammals. The teeth also had long roots, implying that they sat inside sockets in the jaws. This feature separated them from most other reptiles (though is seen in crocodiles), where the teeth are all but stuck to the jawbones and lack roots, but this aspect seems to have initially been overlooked.

Finally, the overall shape of the teeth, and especially the nature of the serrations, were very similar to those of various herbivorous lizards alive today. In particular, these were near identical to the modern iguanas, thus the origins of the name – *Iguanodon,* meaning 'iguana tooth'.* The wear on the teeth showed that the animal probably ate

* Mantell originally wanted to call his animal *Iguanosaurus*, but was dissuaded on the grounds that this was too much like calling it iguana-reptile, which is rather repetitive.

tough plants and these, and indeed large herbivores generally, are rare in aquatic systems. Collectively then, from only a few teeth, Mantell was able to work out that he had the remains of a very large herbivorous reptile, which lived on land, ate tough plants, and was like a lizard but also somewhat different. It was also dissimilar enough from other known species at the time to give it a new name, and so in 1825 he published this as: *Iguanodon atherfieldensis.*

That's really a lot of information from a few teeth and shows the kind of inductive work and comparative anatomy that still stands as part of the basic toolkit of palaeontologists today. Still, it left more than a bit to be resolved, with huge uncertainties over this creature's size and proportions. As to what its head looked like, the only thing they had to go on was its teeth, and there was virtually no real information about such things as its skin or colour.

Soon though, much of a skeleton was discovered, and what later became known as the 'Maidstone slab' or 'Mantell piece' made its way to him. Now the good doctor had more material to work with, and early descriptions of some other giant terrestrial reptiles were starting to appear, allowing for some comparisons and generalisations about them to be made. Most of these animals would eventually be identified as dinosaurs, but that term had yet to be coined, and it was not yet clear if these animals were truly distinct from, for example, various fossil crocodiles.

Iguanodon was indeed a large animal with robust and strong bones. The shape of the femur (thigh bone) was straight and demonstrated that the leg was held vertically under the body, giving it an upright posture like a bird or mammal, and not out to the side with a sprawling posture, such as a lizard or salamander. From this, Mantell inferred that these animals may have been quick, active and agile, an idea that was controversial at the time, but that turned out to be remarkably accurate from so little information.

Already, though, some details were creeping in that, with the wonderful clarity of hindsight, turned out to be in error. Mantell and his peers were sufficiently able anatomists that they could put a disarticulated skeleton back together and make some reasonable guesses about the form of missing pieces, so it's not like there were arms mixed with legs, or tails were put together backwards. However, in his sketch of how the animal may have looked, Mantell had the hips and shoulders, while in the right places, at the wrong angles. He reconstructed his new beast as a huge and squat quadruped, and an isolated spur of bone found with the specimen was suggested as a spike on the nose, giving the large animal a rhinoceros-like appearance.

This last issue is commonly cited to highlight the mistakes of the early palaeontologists, the accusation being made that they were indulging in some extravagant guesswork when they should not have been. However, this misses a couple of vital points about the work being done at this time and how people like Mantell were drawing on the limited available information; not only from the few fossils they had, but also from the rest of the natural world, which was still being uncovered.

Dinosaurs were different in various ways to the reptiles that came before them and the living birds, mammals and lizards to which various researchers would have been able to compare them. There were always going to be some unique features that would cause confusion and, lacking any other even vaguely complete dinosaurs for comparison, it was inevitable that unique traits would be hard to interpret. Context matters enormously. These early works were the first attempts to describe some truly new animals. Given that there were so few of them, and not an enormous pile of reference works available on other species, errors were predictable, and indeed credit must be given to the scientists, working as they were with such little information.

The second point that is overlooked, especially when it comes to the nose horn, is that Mantell was doing something entirely sensible. He wasn't comparing the larger and robust herbivore to a rhino directly, but to the iguanas. Many of them have bosses of bone on the nose, and one, the aptly named rhinoceros iguana, even has a pair of them stuck one behind the other. Mantell was well aware of this; he even included a sketch of the skull of one in a paper he wrote in 1841 and made the comparison rather explicitly. Lacking the evidence for large bipedal reptiles and stuck with an incomplete skeleton, it was entirely reasonable to propose a fully quadrupedal animal with such an adornment on the nose.

All in all, it was a brilliant start, but there was much more to come. Specimens of *Iguanodon* and other large terrestrial reptiles continued to accumulate, and scientific descriptions of the new teeth and bones appeared, allowing other researchers to add their input.

In 1842, Richard Owen, a legendary anatomist and the man who would later found the Natural History Museum in London, coined the name 'Dinosauria'. It was quite some claim to suggest that there was an important new group of reptiles out there, given that the dinosaurs at the time consisted of exactly three animals – *Iguanodon*, *Megalosaurus* and *Hylaeosaurs* – and none of them were known from especially complete remains – but time has shown that Owen was right to recognise that these were new and should all be grouped together.

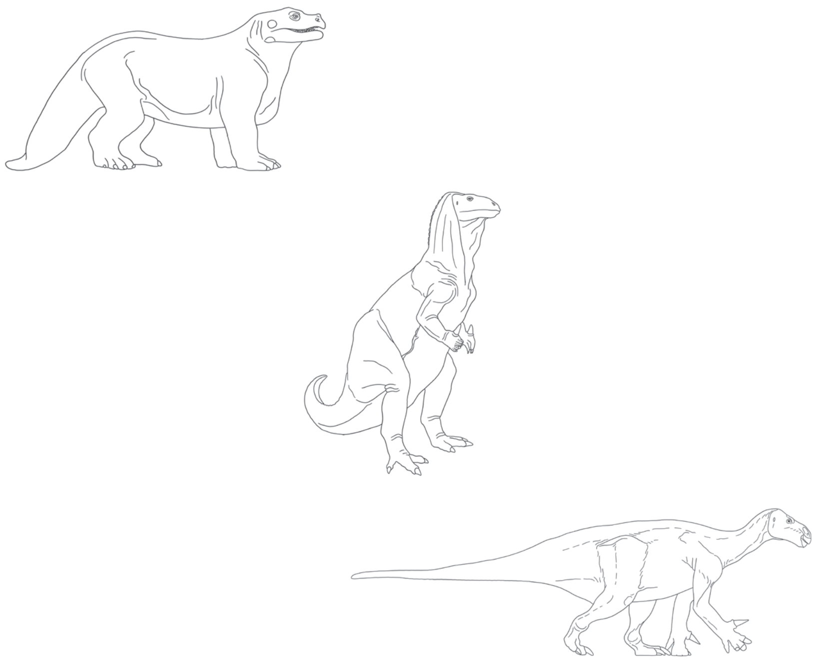
Several other animals were known at the time that would later be recognised as dinosaurs, and plenty would soon be added from other discoveries. However, this small triumvirate were enough to show that these animals truly were different and special compared to the other finds of the time. *Iguanodon*'s place in dinosaurian research was thus already assured, since it was the best represented of these newly recognised species. Looking back, it was a tremendous piece of insight from Owen to link these bits together as something special, but three fragmentary species, all from the south of England, would never provide sufficient information to say much about what dinosaurs were really like without much better specimens.

Happily, however, this problem was about to be greatly reduced thanks to a Belgian coal mine.

Skeletons by the dozen

In the year 1878, in the Walloonian town of Bernissart, a huge collection of dinosaur bones was discovered. Not only were there very large amounts of bones from a very large number of individuals, but complete and articulated specimens were unearthed, including the skulls. These animals were rapidly identified as belonging to *Iguanodon* (although it was given a new species name – *Iguanodon bernissartensis*), and thus between them and still more material that had been recovered in the UK, a new understanding of these animals was possible.

The nose horn was revealed to be a very unusual thumb, and presumably represented some kind of weapon. *Iguanodon*'s arms were rather like its legs in general form, though shorter and more slender, suggesting the animal, even if it was a quadruped, was rather less elephantine (or even rhinoceros-like) in stature and proportions. The tail was not quite as long or lizard-like as assumed, and the head was certainly not that of an iguana, however large.



The changing face of *Iguanodon* over the years. Left, based on the model displayed in London in the late 1800s; middle, a typical 'kangaroo' pose common from most of the 1900s; and right, a modern interpretation. Illustration by Scott Hartman, with left illustration based on the work of Benjamin Waterhouse Hawkins, and middle that of Zdeněk Burian.

Also novel was both the number of specimens and the fact that they appeared to have died together in a massive group (this has turned out not to be the case, and the Bernissart dinosaurs most likely represent the deaths of animals alone or in small groups over many years, rather than one mass mortality). Such a find suggested large groups of animals living together, which would again make them different from most modern reptiles and pointed to more complex behaviours among these ancient creatures.

Thus our understanding of *Iguanodon* took a major step forwards. Not the lumbering beast of the earliest reconstructions with the rhinoceros-like horn and huge columnar limbs (as exemplified by the famous reconstructions led by Richard Owen in London's Crystal Palace), but a svelte and perhaps agile animal, that moved in herds. The discoveries pointed to creatures that were far from simply being large lizards, but a truly special set of animals.*

Dinosaurs everywhere

By this time the Americas were yielding their own great trove of dinosaurs. Whole new types of dinosaur were being uncovered across the Atlantic, and those known from only scraps in Europe were now represented by whole skeletons. At the dawn of the twentieth century, animals like *Stegosaurus*, *Allosaurus*, *Diplodocus* and *Triceratops* were well known in scientific circles and even to the public, and were the subject of huge debates and fractious discussions among palaeontologists. Dinosaurs appeared from further afield too at this time, with specimens now being found in Tanzania, India, Mongolia and Brazil (and with the imperialist attitudes of the time, these were shipped straight to Europe).

In places there was painfully little evidence available to help resolve the outstanding questions or come down on one side or other of a disagreement: for all this new knowledge and improved understanding of the dinosaurs, it was clear that there was a huge amount that we did not know about them. Were dinosaurs warm or cold blooded? Why did they die out? How did they get so big? How many different species were there? And how and why did they evolve into the plethora of forms that were already known?

Darwin's theories were now accepted science and new ideas about evolution, extinction and adaptation were settling into the mind of researchers. New fields such as ecology and ethology would shortly

* Some modern studies suggest that these two animals were not just different species, but actually different genera. Thanks to a quirk of taxonomic history, the Belgian animal retains the name *Iguanodon*, whereas the British creature Mantell worked on is now called *Mantellisaurus* in his honour.

arise (or become recognised as fields in their own right), giving greater context, and opening up new aspects and depths to our ignorance. while presenting new possibilities for understanding.

In this twenty-first century there are more specimens, more researchers, and more techniques and technologies available than ever before. Both our understanding and our ignorance have multiplied. It would be something of an embarrassment to palaeontologists, given the abundance of tools available to us now, were this not a golden age for research, but we are standing on the shoulders of the wealth of data previously accumulated, the power of analyses available to modern scientists, and indeed the huge amount of history that has come before.

Previous generations of researchers made plenty of mistakes, but science is self-correcting (eventually). Modern science allows us to learn from these mistakes and not make them again (hopefully). And, of course, palaeontologists of the past got a lot right and generated much of the vast amounts of data that we can use. Indeed, such is the reliance of palaeontology on original descriptions and details of specimens that it is one of the few fields in the sciences that makes regular and copious use of research published not just decades, but even centuries ago.

Dinosaurs now number well over a thousand species and are known from thousands of skeletons and many hundreds of thousands of less complete ones, along with bones, teeth and footprints, with their fossils recovered on every continent. There are specimens with scales, feathers, claws and even internal organs intact (or at least impressions of them), and eggs, nests and burrows have been found. Juvenile dinosaurs and embryos have been described and some tantalising claims of original biological material that have survived tens of millions of years, if not yet quite proven, are certainly credible.

With such information comes the possibilities that have not so much eluded science as seemed redundant. It was natural to assume that some dinosaurs were camouflaged and others brightly coloured, that some had spots and others stripes, while males and females may have been dramatically different in colour. Such features are all but universal among modern animals like birds, mammals and reptiles, so were assumed to be the case for dinosaurs. Yet with no possible way of determining the colours or patterns of these animals, the point was moot – it was not that we didn't know the details for the dinosaurs so much that we never *could* know, so there was little value in wasting effort speculating about it.

There were some reasoned extrapolations that creatures like *Triceratops* with its advertising billboard of a shield on its head might be brightly coloured, and that smaller dinosaurs living in forests would have disruptive patterns to help hide them, but that was about it. With no way to actually test these ideas though, they remained as reasonable, but ultimately unknowable, speculations.

Now, however, the spectacular preservation of soft tissues in feathered dinosaurs from China and Brazil, coupled with high-resolution imaging, have allowed traces of pigments and patterns to be discerned for a small number of animals. In one sense we have a revolutionary new understanding of some species, and yet for every dinosaur for which we know the colour, there are hundreds that we do not. An area of dinosaur biology that used to be considered virtually beyond our grasp is now ripe with possibility. We know today that we can potentially know something, but that we do not know it – a stark shift that emphasises what we do not, and may never, know.

Many more issues of this type are coming to the fore – areas that had been abandoned intellectually as being impossible to engage with, owing to a lack of data, are becoming rich seams of research and new ideas. As each is mined and examined, yet more information is revealed and the grand framework of our understanding of dinosaurs is fleshed out a little more. Even if it is a web of information, which is more hole than strand, the fundamentals are clear. What awaits is the gaps to be filled in and we are at a time when we are likely to see many of these completed.

We will start, however, with the end.

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