Contents

Acknowledgements	ix
Preface	xi
Introduction	Ι
1. Extinction	II
2. Origins and Relationships	23
3. Preservation	39
4. Diversity	55
5. Evolutionary Patterns	73
6. Habitats and Environments	87
7. Anatomy	97
8. Mechanics and Movement	109
9. Physiology	123
10. Coverings	135
11. Appearance	149
12. Reproduction	163
13. Behaviour	175
14. Ecology	189
15. Dinosaur Descendants	203
16. Research and Communication	211
17. Coda	223
References	239
Index	241

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.

HOW FAST DID T. rex RUN?

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'.

INTRODUCTION

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.

HOW FAST DID T. rex RUN?

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

INTRODUCTION

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.

HOW FAST DID T. rex RUN?

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.

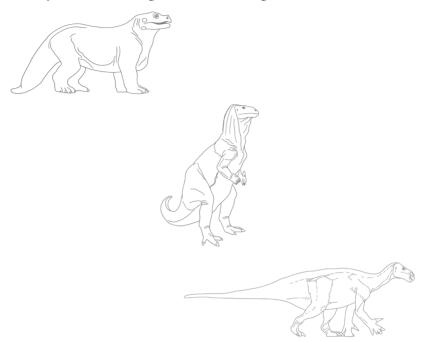
Skeletons by the dozen

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

INTRODUCTION

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.

HOW FAST DID T. rex RUN?

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.

INTRODUCTION

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

HOW FAST DID T. rex RUN?

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.

Index

Page numbers in **bold** refer to illustrations.

А

abelisaurs 59, 61, 70, 186 activity times 95 Africa 24, 66, 89-90, 91, 194-5; see also specific country 'Age of Reptiles' name 12 agility 117-18 Ajkaceratops 83 Alamosaurus 89 alligators 34, 93, 113, 127, 127, 143-4, 177 allosaurs 59, 107, 145 Allosaurus 8, 30, 182, 185 Alvarez, Luis and Walter 14 alvarezsaurs 61, 70, 79, 121, 159, 197 Amargasaurs 64 amber 217 amniotes 27 Amphicoelias 51, 52 anatomy 97, 107-8 data from bones 98–9 digestive systems 105-6 fat deposits 105 function of features 106-7 furculae 101 importance 98-9

joints 110-11 mechanics and movement see biomechanics: movement missing data problems 102 muscle composition 104-5 retrodeformation 99-100 skulls 99, 100 small bones, missing 100 tails see tails Anchiornis 153-6, 160 ankylosaurs 46, 65, 66, 121, 156, 166, 182-3, 190 Ankylosaurus 32, 77 apatosaurs 64 Apatosaurus 64 appearance colouration and patterning see colouration and patterning and communication 181-2 crests 149, 160-2 Edmontosaurus 160, 161 eye shape and colour 158-9 eyelashes 159 facial discs 159 feathers see feathered dinosaurs; feathers

HOW FAST DID T. rex RUN?

mouth bristles 159 wattles and combs 160–2 *Archaeopteryx* 30, 34, 43, 53, 101, 195, 205, 215, 216 archosaur group 28–9, 30, 216 Arctic and Antarctic regions 25, 93, 105, 207 *Argentinosaurus* 77 armour 136, 137–8 arms 107, 109, 186 Asia 82, 83; *see also specific country* asteroid extinction theory (K-Pg) 14–17, **15**

В

Balaur 205 beaks 62, 141-2, 206 behaviours carnivores 183-6 communication 181-3 competition 181-2 daily rhythms 186-7 feeding ecology 180-1 fighting 167-8, 182-3 future discoveries 227 herbivores 182-3 intelligence 176-7 social 177-81, 179 Belgium 6-8 biological species concept 69 biomechanics 109, 122 agility 117-18 climbing 119-20 digging 120-1 feeding 190 flight, powered 118–19 future discoveries 227

jumping 119 limits of large size 112-14 mating 117 necks 115-16 posture 116-17 swimming and floating 120, 121 tails 115 walking and running 117-18 weight 110-12 bipedalism 23, 30, 31, 62, 65, 81, 101, 116-17 birds ancient representatives 206-9 appearance 159-60 diversification 81 evolutionary pathway 30, 31, 33-4, 79-80, 205-6, 215-16 feathers 127, 128, 142-3 furculae 101 intelligence 176 K-Pg event, impact of 19-20, 209-10 living dinosaurs xn, 203 Mesozoic 62 muscle composition 104 number of species 55 paedomorphosis 79-80 powered flight 118-19, 203-5 and pterosaurs 207-9 reproduction 163-4, 168, 169-70, 171 scales 143 thermophysiology 127, 128 Vegavis 206-7, 208 Boreaopelta 156 'bottom-up' effect 197-8 brachiosaurs 33, 64

INDEX

Brachiosaurus 30, 31, 33, 64 brain size and structure 176–7, 187 Brazil 8, 10, 24–5, 27, 142 breathing, circular 217 *Brontosaurus* 31, 64 Buckland, William 13

С

camouflage 94-5, 150, 152-3, 155, 157 CAMP (Central Atlantic Magmatic Province) volcanic events 29-30 Canada 15, 44, 89, 142, 160, 161, 216 Carcharodontosaurus 195 carnivores see theropods Centrosaurus 100 ceratopsians 67, 77, 83, 99, 100, 104, 120, 157, 166, 167; see also specific species ceratosaurs 59, 141-2 Ceratosaurus 59 chimeras 50 China Anchiornis 153 feathered dinosaurs 10, 44, 119, 142, 203, 216 horned dinosaurs 83 Lystrosaurus 25,63 nests and eggs 170 ornithischians 83 oviraptorosaurs 170 pterosaurs 90 research investment 214 Shantungosaurus 49

Sinosauropteryx 151-2 sites 90, 93, 103, 194, 216 stegosaurs 80 trackways 179 tree trunk fossils 93,94 clades 30-2, 32 claws 107, 138-9, 186, 190-1 climate 41, 90–1, 95–6, 105, 124, 126, 127, 128 climbing 119-20 coelophysids 59 Coelophysis 59 colouration and patterning 9-10, 162 age differences 155 Anchiornis 153-6 camouflage 95, 152-3, 157 change, ability to 156 countershading 152-3 environmental context 155 eves 158 function of colour 156-61 future discoveries 155-6 gender differences 154-5 melanosomes 150-2 research difficulties 152 scales 156 Sinosauropteryx 151-2 stereotypes 149-50 variation within species 154 warning and mimicry 157-8 combs 160-2 communication, animal 135, 181-3 communication of research 218-22 competition 74, 78-9, 84, 181-2, 192-3, 197

HOW FAST DID T. rex RUN?

compsognathids 60, 151-2, 195 Compsognathus 60 computer modelling 44, 46, 109, 111, **121**, 218–20, **220** cooling strategies 128-9 Cope, E.D. 51 courtship and mating 117, 166-9 coverings 147-8 armour 137-8 beaks 141-2 claws 138-9 feathers see feathered dinosaurs: feathers filaments 145-7 keratin 137-8 lips 139-41 new discoveries 135 scales 135, 136-9, 143-4, 147 skin 135, 136-9 spikes 137-8 unguals 138 cranks 222n crests 149, 160-2 Cretaceous Period 12-13 crocodiles 3, 4, 34, 89, 125, 126, 140, 156, 171, 174, 195, 217 crocodilians 28-9, 34, 89-90, 126-7, 140, 149, 161, 177, 195 CT scans 213, 218 Cuvier, Baron Georges 13

D

daily rhythms 186–7 Darwin, Charles 2 decay 41–2, 71 Deccan Trap, India 18 *Deinocheirus* 77 deserts 42, 105 dicraeosaurs 64 diet 3-4, 81-2, 105-6, 130-1, 190-3, 194-5, 196-7 digestive systems 105-6, 130 digging 120-1 Dilong 220 'Dinosauria' name 2,6 dinosauromorphs 24-7, 26, 28, 74 diplodocids 63-4 Diplodocus 8, 13, 30, 63, 138, 190 diseases 131-2, 199-201, 200 diversity 58 compared to living animal groups 56-7,67 discoveries 67-8 evolutionary patterns 80-2 islands 70-1 missing species 70-2, 103 number of species 55, 68–9 ornithischians 65-7 rainforests 71 sauropods 62-5 species, recognition of 69-70 theropods 57, 59-62 undiscovered species 71-2 domination 27-30 Doyle, Sir Arthur Conan 13n dromaeosaurs 33-4, 62, 79, 105, 138-9, 159-60, 186, 204, 205 drones 222 droughts 77, 96, 194

Е

ears 187 ecology 189, 201 diet 190–3

244

INDEX

ecosystems 193-6 future discoveries 227-8 interactions 197-9 niche partitioning 192-3 parasites and diseases 131-2, 199-201, 200 population density 192 population regulators 198 specialist/generalist feeding 196-7 'top-down' and 'bottom-up' effects 197-8 ecosystem control 197-8 ecosystems 92-4, 94, 192-6 Edmontosaurus 160, 161 eggs 164, 169-72, 170 encephalisation quotient (EQ) 176-7 England see United Kingdom environment see climate; ecosystems; habitats Euoplocephalus 121 Europe 83, 226; see also specific country evolution, theory of 2 evolutionary-developmental (evo-devo) biology 215, 217-18 evolutionary patterns co-evolution with plants 82 diversity increasing 80-2 environmental impacts 73 locations 82-3 size, changes in 74-80, 76 species duration 84-5 species extinctions 84 speed 74

evolutionary relationships 30, 33–8, 145 extinction, Permian-era 27 extinction, survival of 19–21, 75, 78, 209–10 extinction theories, mass 11–12 asteroid theory 14–17, **15** infection 199–200 Victorian Era 12, 13–14 volcanic destruction theory 18–19 extinction, Triassic-period 28, 29–30 eyelashes 159 eyes 158–9, 186

F

face scales 139 facial discs 159 family trees 33-6 fat deposits 105 feathered dinosaurs 30, 43, 53, 60, 102, 107, 128, 142-3, 144-5, 147-8, 215-16 feathers 128, 142-7, 159-60, 215-16 fighting 167-8, 182-3 filaments 145-8, 147, 216-17 flight, powered 118–19, 203–5 floods 96 footprints 45-8, 136 fossilisation 40, 41-2 frills 99, 166 furculae 101 future discoveries 26, 71-2, 85, 117, 180, 215-18, 226-8

HOW FAST DID T. rex RUN?

G

Galloanseriformes 207 gastroliths 191 geology – palaeontology links 2, 12 Germany 43, 51, 53, 59, 63, 142, 195–6, 216 giantism 77*n* gigantohomeothermy 125, 129–30 *Gigantoraptor* 77 *Gigantosaurus* 77 *Giraffatitan* 64, 110 gliders 34, 62, 79, 93, 101–2, 120, 156, 159–60, 204 growth rate 125–6, **127**

Η

habitats 87 activity times 95 climatic and seasonal influences 90-1,95-6 colour 95 and dinosaur size 88-92 dinosaur ubiquity across 89-90 ecosystem changes 90-1 ecosystems 92-4,94 light 94-5 hadrosaurs 32, 66-7, 77, 91, 116, 132, 136, 137, 160, 170, 172, 196 hearing 187 Hennig, Willi 35 herbivores 30, 81-2; see also ornithischians; sauropods Hesperornithes 210 heterodontosaurs 65 heterotherms 123-4, 127-8 hibernation 93, 94, 124, 127 hips 24, 31

homeotherms 123, 124, 125, 130 horns 74, 137, 167 Hungary 83 hunting/scavenging 183–6, 192, 198 Huxley,Thomas Henry 36 *Hylaeosaurus* 6

I

ichnology 47 *Iguanodon* 3–6, 6–8, **7**, 12–13, 66 iguanodontids 66, 137, 138, 191 India 8, 18 Indonesia 18 injuries and infections 131–2, **132**, 199–201, **200** integument 135 intelligence 176–7 iridium 14, 15, **15** islands 70–2, 195–6, 205 isotope analysis 91–2 Italy 44, 105–6

J

Jinguofortis 206 jumping 119 *Jurassic Park* series 59, 132, 149, 199 Jurassic Period 12

Κ

K-Pg extinction theory 14–17, **15** keratin 137–8, 141, 143, 156 Keynes, John Maynard xii *Kulindadromeus* 146–7, **147**

L Lagerstaetten beds 43–4, 100*n*, 159

246

INDEX

light 94–5 Limusaurus 141–2 lips 139–42 lizards 31, 126, 139, 156, 163–4, 217 Lufengosaurus 63 Lystrosaurus 25

Μ

Mallon, Jordan 164n mamenchisaurs 63 Mamenchisaurus 103, 116 Mantell, Gideon 3-5, 13 Mantellisaurus 8n mass mortalities 49-50 mass mortality sites 178-9, 185, 194, 199 mass/weight 45, 75, 77, 110-12, 113*n*, 114, 115 mating 117, 166-9 medullary bones 164 megalosaurs 59-60 Megalosaurus 3, 6, 13 melanosomes 150-2, 156 Mesozoic Era 12-13 Mexico 15-16,89 Microraptor 102 migration 88-9, 90-2, 180 mimicry 157-8 molecular palaeontology 226-7 Mongolia 8, 61, 144-5, 180 mouth bristles 159 movement 77-8, 101, 109, 117-22; see also biomechanics muscle composition 104-5 museums 50-4, 219, 220 Myanmar 217

Ν

naming rules 61*n* necks 31, 115–16, 129 nests and eggs 164, 169–72, **170** niche partitioning 192–3 Niger 89–90, 104 *Nigersaurus* 190 North Africa 194–5 North America 8, 15, 64, 82, 83, 89, 127, 144–5, 226; see also Canada; United States North Korea 142 number of species 55, 68–9 *Nyasasaurus* 24, 25, 27

Ο

On the Origin of Species (Darwin) 2 origins 223 difficulties determining 23 dinosauromorphs 24-7, 26 evolution and domination 27-30 evolutionary relationships 30 first dinosaurs 23-7, 26 Nyasasaurus 24, 25, 27 ornithischian-saurischian split 36-8 ornithischians 32; see also specific group beaks 141 camouflage 156 claws 138 climbing 120 digging 121 diversity 65-7 filaments 145-7, 147, 148, 216-17 finds 49, 103 groups 65-7 origins 83

HOW FAST DID T. rex RUN?

ornithischian-saurischian split 36 - 8overview 32 pubis 31 scales 147, 148 size 49,75 tails 115 teeth 142 ornithomimosaurs 60, 77, 104 ornithopods 66 Ornithoscleida 36-8 Oryctodromeus 121 Ouranosaurus 66, 105 Oviraptor 142, 191 oviraptorosaurs 61, 70, 77, 79, 142, 159, 170, 191 Owen, Richard 6, 8

Р

pachycephalosaurs 67 paedomorphosis 79-80 palaeognaths 207 palaeontology, early 1-9 palynology 92-3 Pangea 25 Parasaurolophus 132 parasites and diseases 131-2, 199-201, 200 parental care 172-4 patterning see colouration and patterning Pelicanimimus 60 Permian-era mass extinction 27 phalluses 169 photogrammetry 218-19 physiology 133 digestion 130

growth rate 125-6, 127 injuries and infections 131-2, 132 temperature see thermophysiology venom 132-3 Pisanosaurus 83 plant ecosystems 92-4, 94 plant evolution 82,87 Plateosaurus 63 pneumatic bones 111 pollen, fossil 92-3 posture 4, 28, 115, 116–17 preservation of remains burial 42 climatic events 95-6 data limitations 39-40 environmental conditions 41-2 footprints 45-8 Lagerstaetten-type deposits 43-4 movement of remains 48-50 museums 50-4 requirements 41 soft tissues 43-4 taphonomic history, tracing 48-50 prosauropods 31, 62, 81, 101, 116 Protoceratops 180 Psittacosaurus 146, 156 Pteranodon 209 pterosaurs 13, 28–9, 90, 118, 145n, 195, 207-9 public engagement 220-2

Q

quadrupedalism 23, 31, 62, 65, 81, 102, 116–17

248

INDEX

quartz, shocked 15, 16

R

rainforests 41, 42, 71 rebbachisaurids 64 record keeping 53 reproduction 163, 174 and communication 182 courtship and mating 117, 166-9 egg-laying 164 evolutionary and ecological impacts 173 growth and maturity 174 males and females 163-6 nests and eggs 164, 169-72, 170 parental care 172–4 phalluses 169, 169n sexual dimorphism 164-6 research; see also research technology communication of results 218 - 22evolutionary-developmental (evo-devo) biology 215, 217-18 finding and accessing relevant papers 211-12 funding 98, 214, 220, 222 future discoveries 215-18 new fields 215 non-academic researchers 222 public engagement 220-2 researcher numbers 68, 214 research technology 3D imaging and printing 218-10.220 communication 212, 218, 220-1 computer modelling 44, 46, 109,

111, **121**, 122, 218–20, **220** drones 222 genetics 35 molecular palaeontology 226–7 photogrammetry 218–19 scans of fossils 40, 99–100, 152, 187, **208**, 213–14, 218, **220** Romania 70, 205 Russia 25, 146–7, 216–17

S

saltasaurs 65 saurischians 31: see also sauropodomorphs; sauropods; theropods Sauropelta 121 sauropodomorphs 30, 31, 32, 36, 51, 62-3, 75, 101, 138, 148; see also prosauropods; *specific group*; specific species sauropods 36-7; see also specific species claws 120, 138 diversity 63-5 epoch 77 evolutionary relationships 33, 81 feeding ecology 190, 192-3 finds 90, 99, 103 footprints 46 groups 63-5 intelligence 176, 177 migration 91 muscle composition 104 necks 115-16 new discoveries 113n posture 116-17 size 31, 112, 113

249

HOW FAST DID T. rex RUN?

thermophysiology 129-30 scales 135, 136-9, 143-4, 146-8, 147, 156, **161** scans of fossils 40, 99-100, 152, 187, 208, 213-14, 218, 220 scansoriopterygids 61-2, 70, 204 scavenging 183-6 Scipionyx 44, 105-6 senses 158-9, 186-7 sexual dimorphism 164-6 Shantungosaurus 49,77 Shunosaurus 63, 103 Sinornithosaurus 132 Sinosauropteryx 151-2 size 3, 30, 31, 32, 74-80, 76, 81, 88-92, 112-14; see also mass/ weight skin 135, 136-9, 144-5 smell, sense of 187 snakes 124, 126, 156, 163-4 social behaviours 177-81, 179 soft tissues 40, 43-4, 47-8, 104-6, 217 South Africa 25, 83 South America 8, 24-5, 64, 65, 70, 83; see also specific country specialist/generalist feeding 196-9 species duration/extinction 84-5 species, missing 43, 67-70, 71, 103 species, number of 9, 55-6, 68-9 species, recognition of 69, 103 speed 4, 117-18 spikes 137-8 Spinophorosaurus 104 spinosaurs 59-60, 81, 102 Spinosaurus 30, 51, 59, 77, 102, 105, 194, 195

stegosaurs 65–6, 80, 84 *Stegosaurus* 8, 32, 65–6, 193 swimming and floating 120, **121**

Т

tails 31, 101-2, 103-4, 115, 159-60, **161**. 182-3 Tanzania 8, 24, 64 taphonomy 40-50 technology see research technology teeth 3-4, 91-2, 141, 142, 190, 101 temperature, body see thermophysiology Thecodontosaurus 51 therizinosaurs 60-1, 139 thermophysiology age-related 129-30 cooling strategies 128-9 and dietary needs 130-1 gigantohomeothermy 125, 129-30 hibernation and torpor 124 high body temperatures 126-8 homeotherms and heterotherms 123 - 4surface-area-to-volume ratios 124-5 theropods **32**; see also specific group; specific species anatomy 31, 101, 107, 138, 141-2 ancestors of birds 31, 33-4, 79-80, 205-6 climbing 119 courtship and mating 167, 168

INDEX

diet 194-5 diversity 57, 59–62 feathers 142-3, 144-5, 147, 159, 160 groups 59-62 herbivory, switch to 81-2 hunting/scavenging 183-6, 198 intelligence 176 on islands 195 Late Cretaceous period 77 nests and eggs 170 Ornithoscleida proposal 36-8 overview 30 size 75, 77, 79, 112-13 social behaviours 179 thermophysiology 127, 128 3D imaging and printing 99, 218-19, 220 thyreophoreans 65-6 titanosaurs 64, 65, 70, 77, 89, 171 'top-down' effect 197-8 torpor 124 trace fossils 47 trackways 45-7, 115, 178-80, 179 Transylvania 70 Triassic Period 12 Triassic-period extinction 28, 29-30 Triceratops 8, 10, 13, 32, 67, 77, 146, 167 Trichomonas 199 troodontids 33-4, 62, 79, 153-5, 160, 176, 186, 187, 190-1, 204, 205 tyrannosaurs 3D scans 220

anatomy 107, 141 feathers and/or scales 142, 144-5, 147 finds 228 hunting 184, 186, 191-2 injuries and infections 167, 182-3, 199, 200 lips 141 muscle composition 104-5 overview 60 size 77-8 thermophysiology 128 tracing ancestry of 82 Tyrannosaurus epoch 77 feathers and/or scales 144-5 finds 47-8,99 geographic range 89 injuries and infections 200 intelligence 176n sexual dimorphism 164n size 111, 113, 114 smell, sense of 187n speed and agility 117-18 T. rex ix-x, 111, 200

U

unguals 138 United Kingdom 1, 3–6, 25, 27, 51, 82, 83, 220–1, 223 United States 25, 27, 64, 89, 113, 168, 193–4, 226

V

Vegavis 206–7, **208** *Velociraptor* 30, 105, 142 Venezuela 25

HOW FAST DID T. rex RUN?

venom 132–3	weight/mass 45, 75, 77, 110-12,
vision 158–9, 186	113 <i>n</i> , 114, 115
volcanic extinction events 18-19,	
28, 29–30	Х
	X-ray scanning 152, 187, 213
W	X-ray videos 46
warning colouration/patterning	
157-8	Y
wattles 160–2	<i>Yi</i> 62