At present, the Charnian fauna (and its correlatives overseas) remains a unique assemblage of very late Precambrian forerunners to the rest of the fossil record, possibly Cnidarians (Coelenterates), possibly not. Only much more research both in Charnwood Forest and in far-off lands will provide any answers.

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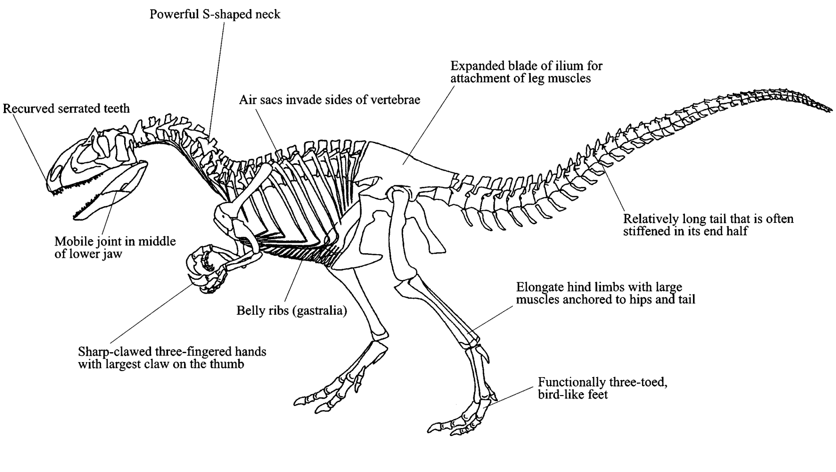
Fig. 11. A short length of possible 'worm' trail. Length 25 mm.

Fig. 12. *Teichichnus* burrows on a Swithland slate gravestone. (Photo: Helen Boynton.)

Fossils explained 27: Theropod dinosaurs

Theropods are a group of bipedal dinosaurs characterized by the presence of sharp, recurved claws on powerful, grasping hands; a lower jaw with a flexible joint half-way along its length; functionally three-toed, bird-like feet; and serrated, blade-like teeth. All theropods share a uniform body design (Fig. 1) with a short, relatively stiff body supported by long legs, a gently upward-curving neck, an elongate tail and strong, dextrous forelimbs. This design ranged in size from the 1 m length of compsognathid coelurosaurs to the 14 m or more of the biggest carnosaurs and tyrannosaurids. Sizes upward of 15 m for certain theropod specimens, reported in the popular press, have yet to be officially substantiated.

Fig. 1. The most characteristic parts of the theropod skeleton, labelled on the Upper Jurassic North American allosaurid *Allosaurus*. The skeleton is 9 m in total length.



Theropods were predominantly predatory in behaviour and were the dominant predatory animals on land for most of the Mesozoic. A Middle Jurassic English theropod, *Megalosaurus*, was the first dinosaur ever to be awarded a scientific name (first published by James Parkinson in 1822), and the first to be scientifically described (by William Buckland in 1824). Together with the herbivores *Iguanodon* and *Hylaeosaurus*, *Megalosaurus* was further notable in that its unusual features first led Sir Richard Owen to recognize dinosaurs as a properly unique group of reptiles in 1842.

Morphology

Various lines of evidence show that theropods moved with their backbones held horizontally, and with the tail held straight out behind for use as a dynamic stabilizer (Figs 1, 2). As in other dinosaurs and related groups of reptiles, some muscles for the theropod hindlimb anchored themselves to the tail. However, in some advanced theropods this hindlimb musculature was modified so that the tail was no longer needed for muscle attachment. It could therefore be reduced in length, a trend that was carried to its extreme in modern, virtually tailless birds which are part of the theropod radiation (see below).

Theropod necks articulated in gentle S-curves and the skulls carried upon them varied in design from long and low crocodile-like shapes, exemplified best by spinosauroids like *Baryonyx* from the Lower Cretaceous of England, to the short, deep parrot-like skulls of oviraptorosaurs (Figs 3–5). Big theropods that specialized in hunting other large dinosaurs generally had very deep, elongate heads that were so proportionally gigantic they have earned these beasts the accolade 'walking skulls'. In the biggest tyrannosaurids and carcharodontosaurids, animals with body lengths of around 13 m, the skulls exceeded 1.5 m in length. All theropod skulls were lightened by 'windows' in the side and by invasive air sacs which pneumaticized certain of the skull bones.

Bipedality allowed theropods to employ their forelimbs as weapons in predation and a defining characteristic of this group is the possession of trenchant, recurved hand claws. Although primitive theropods had four or five fingers, it is always the three inner ones that bear the large claws (Fig. 2). During their evolution, theropods lost digits from the hand and lost them in a characteristic pattern, going from the outside (digit 5) inward. This digit loss was carried to its extreme in Upper Cretaceous tyrannosaurids, which only had digits 1 and 2, and alvarezsaurids, which only had digit 1. Based on evidence from fossil trackways made by theropod ancestors, a few workers think that advanced theropods lacked digit 1, a pattern of digit loss that has also been advocated for birds. This issue is still controversial and is contradicted by the sequence of digit loss seen in the fossils.

Like nearly all dinosaurs, theropods walked with their ankles high up off the ground and were digitigrade – that is, they walked only on their toes (Fig. 1). New discoveries of fully articulated theropod feet show that the theropod hallux, the small, elevated first digit of the foot, was not reversed as it is in birds. However, trackways indicate that it was fairly mobile and, as is the case in birds, smaller theropods may well have used the hallux when climbing. There is no reason why smaller-bodied theropods could not have climbed in trees (Fig. 6), given that many modern animals, including bears, tree kangaroos and goats, are able climbers yet lack the flexible sharp-clawed digits of theropods.

Theropod integument

Large theropods were covered in scaly skin. Skin impressions from *Carnotaurus*, a large Patagonian abelisauroid, reveal keeled, conical protuberances spaced evenly across the animal's side. Other theropods, such as *Ceratosaurus* from the Upper Jurassic of North America and Africa, are known to have possessed a row of bony scutes along the back-

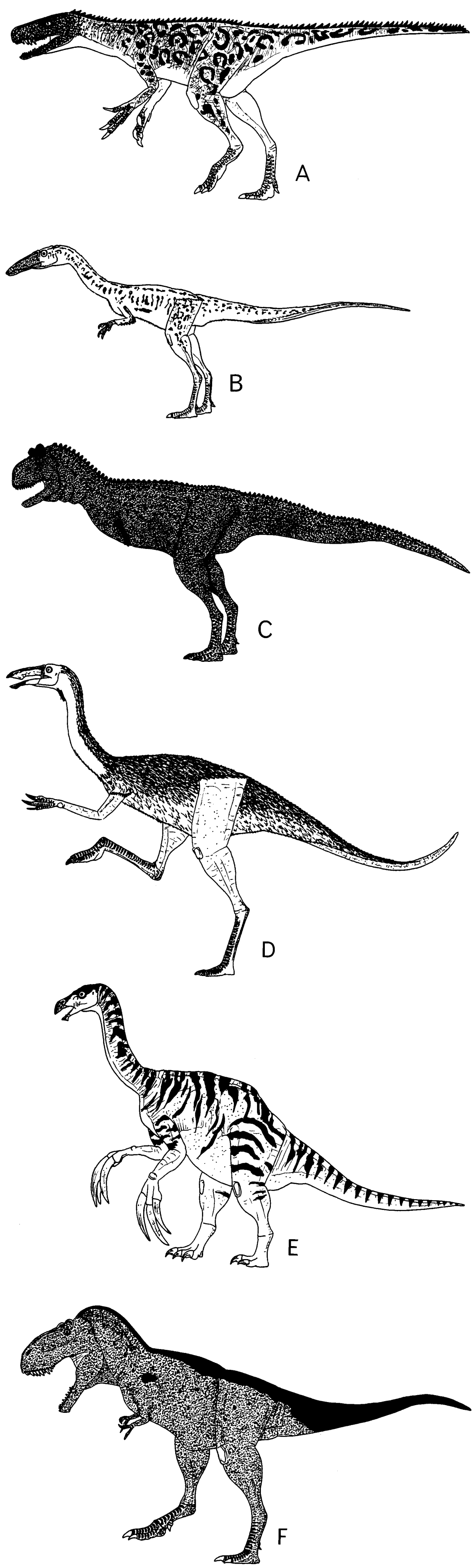


Fig. 2. Life restorations of a diversity of theropods. (A) Upper Triassic herrerasaurid *Herrerasaurus ischigualastensis* from Argentina (total length 4 m). (B) Upper Triassic coelophysoid *Coelophysis bauri* from southern North America (total length 3 m). (C) Middle Cretaceous abelisauroid *Carnotaurus sastrei* from Argentina (total length 5 m). (D) Upper Cretaceous ornithomimid *Gallimimus bullatus* from Mongolia (total length 6 m). (E) Upper Cretaceous therizinosauroid *Erlikosaurus andrewsi* from Mongolia (total length 4 m). (F) Upper Cretaceous tyrannosaurid *Tyrannosaurus rex* from North America (total length 13 m).

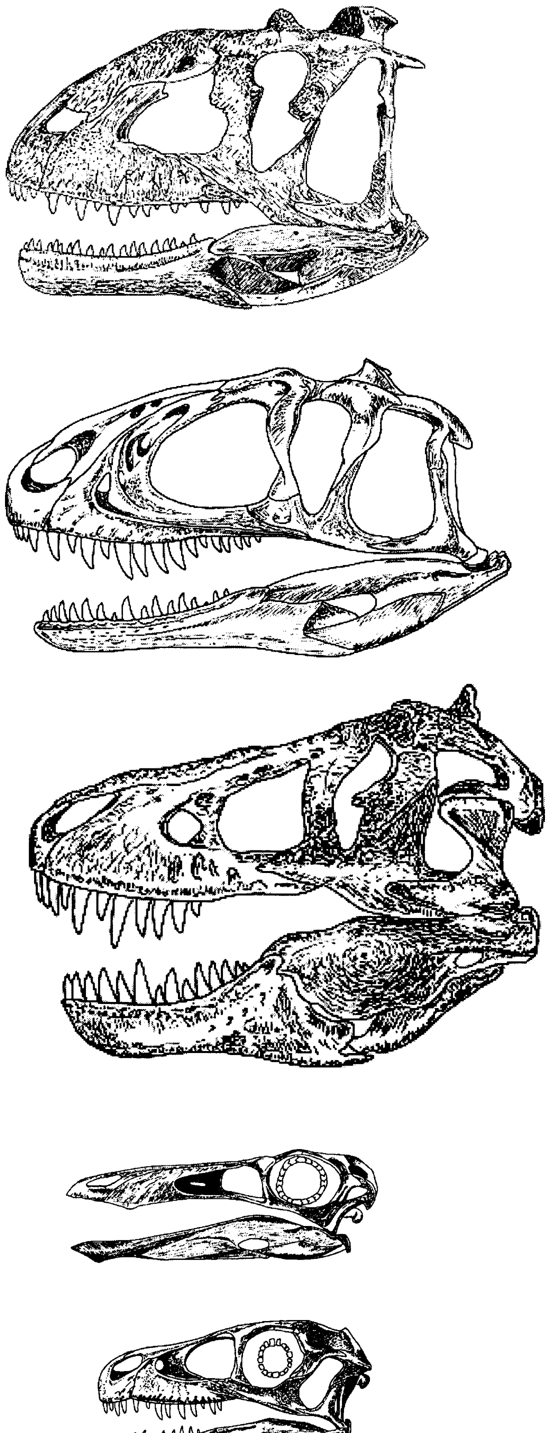


Fig. 3. Diversity within the skulls of theropods. From top to bottom: the abelisauroid *Majungatholus atopus* (Upper Cretaceous of Madagascar), the allosauroid *Sinraptor dongi* (Upper Jurassic of China), the tyrannosaurid *Tyrannosaurus rex* (Upper Cretaceous of North America), the ornithomimosaur *Gallimimus bullatus* (Upper Cretaceous of Mongolia) and the dromaeosaurid *Dromaeosaurus albertensis* (Upper Cretaceous of Canada). Not drawn to the same scale throughout. Redrawn from Paul (1988), Currie & Zhao (1994), Currie (1995) and Sampson and others (1998).

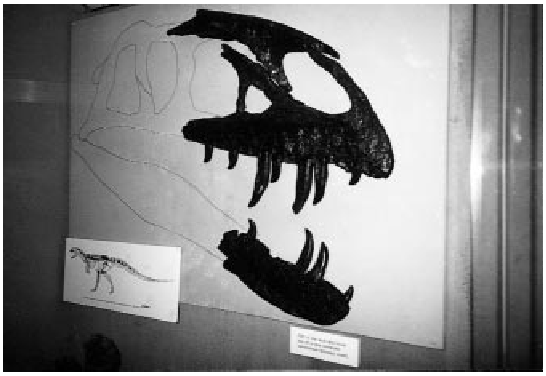


Fig. 4. Incomplete skull of the Lower Cretaceous allosauroid *Neovenator salerii* from the Isle of Wight. The teeth have slipped out of their sockets and thus look longer than they would have been in life. The complete skull would have been about 80 cm long. Published with the permission of the Isle of Wight Council (Museum of Isle of Wight Geology, Sandown).

bone. Because of the close relationship between birds and other coelurosaurs, and because of the possible need for an insulating integument in these possibly endothermic ('warm blooded') animals, it has often been suggested that some theropods were feathered (Fig. 6). True feathers and feather-like structures have now been discovered on Lower Cretaceous theropods from China, proving that feathers of both downy and vaned type appeared in theropods prior to the evolution of birds. However, detailed studies that would reveal whether or not these structures are made of the same unique material as are bird feathers have yet to be performed. Some theropod trackways, most notably those made when the animals rested on the ground, arguably preserve traces of hair or feather-like structures.

Theropod teeth

An important character of theropods is a set of laterally compressed, recurved and serrated teeth. A keel, or carina, runs along the anterior and posterior margin of the tooth and is usually (but not always) serrated. Serrations, as can be observed today in sharks and predatory lizards, aid in cutting through tissues, and vary in proportional size and morphology depending on preferred prey. In theropod teeth we measure the number of serrations for every 5 mm. This can be as fine as the 37 serrations per 5 mm in *Baryonyx*. At the other extreme, in troodontids there may be as few as 17 denticles on the entire tooth. These very coarse serrations recall those seen in herbivorous lizards and dinosaurs, and suggest that troodontids may have eaten plants on occasion. Some other groups of theropod, notably ornithomimids, include toothless species equipped with sharp-edged beaks. The shape of their beaks, and their lack of curving hand or foot claws, suggests that they were predominantly herbivorous.

Tyrannosaurids differ from other theropods in possessing stout, thickened teeth that are not laterally compressed. Tyrannosaurids share with other broad-snouted coelurosaurs, such as troodontids, upper jaw teeth where the anterior keel has migrated to the posterior surface of the tooth, resulting in a triangular or D-shaped cross-section. This has been interpreted as either a shared feature indicating a close evolutionary relationship or a convergent response to a similar broad-snouted condition.

Some studies show that theropods often broke their teeth. Shed theropod teeth, which were at the end of the natural 'lifespan' in the theropod's jaws, are not uncommonly found alongside skeletons of herbivorous dinosaurs and presumably were broken off while the theropod was feeding. Spiral fractures in shed teeth show that they broke during a bite. Theropod fossils often preserve worn tooth-tips where the teeth had repeatedly contacted bone and, in extreme cases, broken teeth have been worn down to blunt stubs. Most theropods probably did not bite bone to break them open, but swallowed them whole. This may have been hazardous; it has recently been asserted that the only known speci-

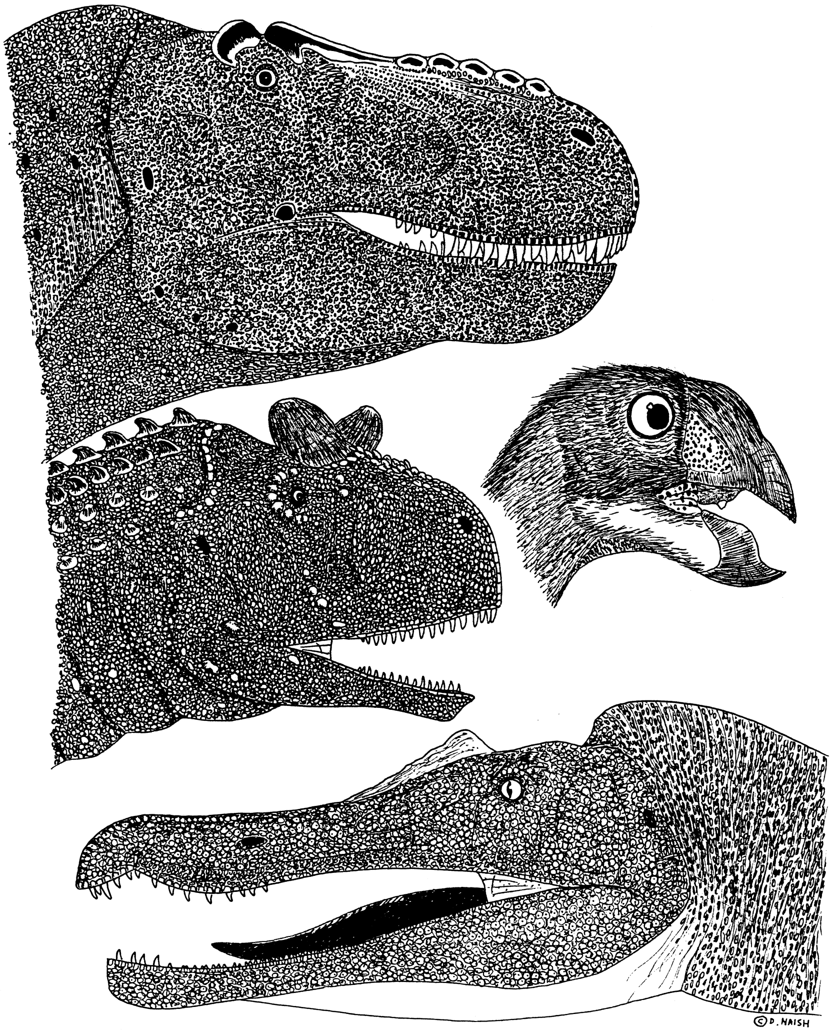


Fig. 5. Diversity in the heads of theropods. At the top, the tyrannosaurid *Tyrannosaurus rex* (Upper Cretaceous of North America); middle left, the abelisauroid *Carnotaurus sastrei* (Middle Cretaceous of Argentina); middle right, the oviraptorosaur *Ingenia yanshini* (Upper Cretaceous of Mongolia); bottom, the spinosauroid *Baryonyx walkeri* (Middle Cretaceous of Europe). Not drawn to the same scale throughout.

men of *Cryolophosaurus*, a Lower Jurassic carnosaur from Antarctica, choked to death on bones that got stuck in its throat. However, a gigantic coprolite from the latest Upper Cretaceous of Saskatchewan, ostensibly from a *Tyrannosaurus*, contains abundant bone fragments, suggesting that tyrannosaurids, at least, did crunch up bones before swallowing. This is in accord with their unique tooth morphology.

Theropod diversity

At present, most workers recognize two main groups of theropod, 'ceratosaurs' and tetanurans (Table 1). A number of primitive predatory dinosaurs from the Upper Triassic, *Eoraptor* and the herrerasaurids, are regarded by some as basal theropods, but by others as near, or even as distant, relatives.

Ceratosaurs are characterized by specially fused leg and pelvic bones, and often have raised crests or horns on the skull. A group of mostly small-bodied, lithe and slim ceratosaurs, the coelophysoids, are known from Upper Triassic and Lower Jurassic rocks. In some ways, coelophysoids are among the best known of all theropods because certain species are preserved *en masse* after having perished in mass death events. Why these animals – representatives of the genera *Coelophysis* (from Ghost Ranch, New Mexico) and *Syntarsus* (from South Africa) – all died together in these assemblages is unknown, but all manner of mechanisms have been suggested, including flash floods, suffocation via volcanic ash clouds, forest fires and even accidental poisonings.

Fig. 6. New discoveries in Lower Cretaceous rocks of China reveal that feathers are not unique to birds, but were also present in certain other theropod groups. In this speculative restoration, entitled 'The New Chinese Revolution' and reproduced with the permission of the artist, Luis V. Rey, predatory dromaeosaurids harry a large, long-necked therizinosauroid. The small compsognathid *Sinosauropteryx* flees in the foreground. The birds in the tree represent male and female specimens of *Changchengornis*.

Neoceratosaurs are the second ceratosaurian group. They were mostly large-bodied Upper Jurassic and Cretaceous forms. A group of neoceratosaurs called abelisauroids appear to have been the most important group of theropods in Cretaceous South America, a landmass thought to have been an island continent. The dominance of abelisauroids here, when tetanurans were the prevalent theropods everywhere else, has therefore been likened to the ecological dominance of Australia by marsupials. However, there is now good evidence that some groups of tetanuran theropods were living in Cretaceous South America alongside the abelisauroids.

The characters that unite coelophysoids and neoceratosaurs as ceratosaurs are not particularly convincing. In many ways, the big neoceratosaurs are more like tetanurans, such as megalosaurs and allosaurs, than they are like coelophysoids. For example, neoceratosaurs and tetanurans share strap-shaped shoulder blades, five sacral vertebrae and big, deep skulls. This all suggests that the ceratosaurs are an unnatural grouping.

Tetanurans represent the most diverse group of theropods and, except perhaps in South America, were the dominant theropods of the Cretaceous. Tetanurans differ from more primitive theropods in having a three-fingered (tridactyl) hand, a skull where all of the teeth are in front of the eye socket, an expanded 'boot' at the end of the pubis and a tail held stiff in its end half by interlocking processes. Tetanurans include the large-bodied carnosaurs, like *Allosaurus* and *Megalosaurus*, and the coelurosaurs. Coelurosaurs include pheasant-sized compsognathids, beaked ostrich-like ornithomimids, parrot-headed oviraptorosaurs, and predatory dromaeosaurids and troodontids. Both latter groups were equipped with a raised second toe which supported a sickle-shaped claw and, unlike other theropods, must have walked on just two of their toes. It is now evident that tyrannosaurids, previously regarded as carnosaurs, are gigantic coelurosaurs.

Certain coelurosaurs exhibit all of the features later modified by birds for use in flight including a wishbone (furcula), elongate forelimbs, large breastbone (sternum), reduced tail and extensively pneumaticized bone. Thus a very robust body of evidence indicates that birds are part of the tetanuran radiation and are close relatives of coelurosaurs such as the dromaeosaurids. So theropods survived the end Cretaceous extinction event and became one of the most species-rich tetrapod groups in the Cenozoic, the birds (= Aves Linnaeus in Table 1).

Table 1. A taxonomic scheme for the Theropoda. Certain aspects of theropod phylogeny are much disputed, the interrelationships among the coelurosaurian taxa especially. Current standing of the Carnosauria is also controversial and the group may be artificial. The most important names in this scheme are printed in bold.

Theropoda Marsh
- *Eoraptor* Sereno and others
- Herrerasauridae Benedetto
- **Neotheropoda** Bakker
  - 'Ceratosaurs'
    - Coelophysoidea Paul
    - Neoceratosauria Novas
    - *Ceratosaurus* Marsh
    - Abelisauroidea Bonaparte & Novas
  - **Tetanurae** Gauthier
    - **Carnosauria** von Huene
    - Megalosauroidea Huxley
    - Spinosauroidea Stromer
    - Allosauroidea Marsh
    - **Coelurosauria** von Huene
    - Tyrannosauridae Osborn
    - Compsognathidae Cope
    - Oviraptorosauria Barsbold
    - Therizinosauroidea Maleev
    - Ornithomimosauria Barsbold
    - **Maniraptora** Gauthier
      - Deinonychosauria Colbert & Russell
        - Troodontidae Gilmore
        - Dromaeosauridae Matthew & Brown
        - Aves Linnaeus

Theropod lifestyles

Theropods of all kinds frequently preserve injuries inflicted upon them by other theropods. Broken and rehealed bones, including ribs, ankles and tail vertebrae, are common, as are bite marks. In some cases, such wounds may have resulted from combat induced by social disputes. In other cases, theropods may have been predating on others or cannibalizing carcasses. A recently discovered *Velociraptor* skull had been pierced by *Velociraptor* teeth, almost certainly inflicted during a killing bite to the brain. The large, probably female *Tyrannosaurus* referred to as 'Sue' possessed a catalogue of healed injuries, including a broken fibula, broken ribs, damaged upper arm, and mangled left side of face. This animal must have been in a miserable state before its death.

All theropods probably reproduced by laying eggs and it may not have been possible for them to have evolved viviparity. However, until recently, theropod eggs were all but unknown. Oviraptorosaurs, originally interpreted as egg eaters, are now known to have been defending the nests they were originally thought to have plundered and several specimens are preserved in brooding postures on top of egg-filled nests. It seems that some theropods, perhaps most or all of them, constructed crater-like nests which they either brooded or filled with rotting vegetation. Post-hatching parental strategies in theropods are unknown; babies may have been cared for by their parents, or they may have been totally independent. Although pack-hunting social behaviour has been suggested for some theropods, it is poorly founded and not provable. However, there is no reason why theropods could not have practised various social strategies depending on species and maybe some did employ group hunting strategies. Big-skulled theropods, like carnosaurs and tyrannosaurids, are thought to have hunted using the 'land shark' technique – that is, they may have ambushed prey from cover and taken haemorrhaging bites from the flank or thigh. The prey would have been debilitated and weakened by shock and blood loss.

Some of the adult coelophysoids at Ghost Ranch have baby coelophysoids preserved within their stomachs. These babies are not embryos; they are simply too large and too well developed. Instead, this is clear evidence of cannibalism within these dinosaurs, a behaviour we would have predicted for theropods given its prevalence in living carnivorous animals, but which was not previously 'observed', in action as it were, in the fossil record.

It has been suggested that, by examining the morphology of the hips and the insertion points for the muscles around the cloaca, theropods can be sexed. This has been tested in tyrannosaurids, and results indicate that females were bigger and more robust than males. However, this is arguable and based on a very small data set. Coelophysoid species also come in large, robust and smaller, gracile versions, a pattern consistent with sexual dimorphism, but at present we do not know if the bigger, more robust individuals were the males or the females. Both alternatives are possible.

Suggestions for further reading

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Branch line

Collecting, 1840s style

These days, we are very conscious of codes of conduct governing whatever we are tempted to do in the way of collecting, whether it be fossils or minerals. Most codes are seeking to curb our enthusiasms, possibly overstating the case for 'conservation' in the hope that a self-discipline will emerge which will see prized localities survive for the future generations. It hasn't always been so. An interesting insight into acquiring fossils from the classic cliffs of Sheppey is given in a letter published in *Magazine of Natural History* in 1840, which seems worth reprinting. Originally, it was regarded as 'useful' by the editor of the magazine, Edward Charlesworth, himself a collector, who might be judged to have overstepped the reasonable mark. Here it is as published:

'Mr Editor, I have been so frequently applied to by geologists, as to the best mode of collecting the fossils of the London Clay from the Isle of Sheppey, that I am induced to send you a few hints as to the mode of collecting in that locality. Although one of the most accessible, it is probably the least known of any of the rich geological fields that are within a short distance of the metropolis. As a trip to this interesting spot can be accomplished by an absence from London of only three days, and yet the collector be amply laden with fossils on his return, I will endeavour to put your readers in possession of the best mode of conducting such an excursion. The best conveyance is by the Southend and Sheerness steam packets, which leave from London Bridge on Tuesdays, Thursdays and Saturdays, at 11 o'clock in the morning, and reach Sheerness about 4 or 5 o'clock in the afternoon. The town is divided into two parts – the one contained within the limits of the garrison being designated the Bluetown, while that beyond the fortifications to the north-east is designated the Miletown – and it is to this portion that I should recommend the visitor to proceed, and to take up his quarters either at the *Royal Hotel*, or at the *Wellington*; the latter is an exceedingly snug and comfortable house, and is the one which I have resorted to for many years. After having established yourself in your inn, request the Boots to desire the attendance of Mr Hays (better known perhaps by the name Paddy Hays) from whom you may purchase, at a very reasonable rate, some good fossils, such as crabs, lobsters, heads and portions of fishes, and numerous species of fossil fruits. Our traveller will then have accomplished all that can be done towards the acquisition of fossils until the following morning; there not being, I believe any other collector in town from whom purchases can be made.

On the following morning, I should recommend an early breakfast, as a considerable extent of ground is to be traversed. It is advisable to go provided with five or six sheets of soft paper, to wrap fragile specimens in, and a few cotton or linen bags, of about four or five inches in diameter, to separate the larger from the small fossils; the whole can be carried in a good sized blue bag or haversack, no chisel or hammer being necessary on this occasion. If our geologist has a desire to view the great section of the London Clay, afforded by the cliffs of the north shore of Sheppey, and is content with comparatively few fossils which he may be able to procure by his own exertions, he may proceed in the following manner – Leaving Sheerness by the new town, he will pass along the sea wall, towards Minster, until he reaches Scapsgate, where the cliffs begin to rise from the low lands of the western end of Sheppey. A few cottages are scattered round this point, some of the inhabitants of which work upon the beach either collecting cement stones or pyrites, the latter being better known by the name of copperas. To these, applications should be made to know if they have any 'curiosities', and very frequently excellent specimens, and at a small price, will be thus procured. From this point the route will then be beneath the cliffs upon the shingle, amidst which, dark patches, 10 or 15 yards in length, will be observed, composed of nodules of pyrites, intermixed with pyritised fragments of branches of trees in great abundance. It is at such spots that the numerous and beautiful specimens of fossil fruits are found; but to ensure success, the collector must be content to go upon his knees, and carefully search among the fragments. The whole of the beach, from about the parallel of Minster church to Warden Point, abounds with these patches of pyrites, and I have by this means obtained in the course of a morning upwards of one hundred fine fruits of various sizes. Care must be taken in such an investigation of the coast that it be undertaken during the falling tide, or unpleasant consequences may arise from