Abstracts from the 2004 Lyell Meeting

DINOSAUR PALAEOBIOLOGY

A joint meeting of the Geological Society of London, the Palaeontological Association and the Linnean Society.

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The Evolution of the Dinosauria

David B. Norman (Sedgwick Museum of Earth Sciences, University of Cambridge, UK)

It is very probable that the first dinosaurs appeared on Earth during the Late Triassic. The actual fossil record of dinosaurs begins in the latest part of the Carnian stage (c. 225 Ma) of the Late Triassic, at which time they had already differentiated into the two major clades: Ornithischia and Saurischia.

Early representatives of the Dinosauria are, generally speaking, medium-sized animals (1-3 m long) characterised by being bipedal and possessing elongate hindlimbs that were moved vertically beneath the body on either side of the midline (in what is described as parasagittal motion). This style of motion permitted these animals to move their limbs very effectively: giving them a long stride and thus the ability to move very quickly over the ground, as well as offering the alternative strategy of allowing the hindlimbs to act as vertical pillars that were capable of supporting great body weight.

The characteristically dinosaurian limb posture is linked directly with a number of diagnostic dinosaurian features: the feet are narrow and the toes, which point forward, tend to be symmetrically arranged about a midline axis; the feet are digitigrade (dinosaurs walk by balancing on their toes alone, rather than using the entire length of the foot – as in the case of the human foot); the ankle and knee joints form simple uni-axial hinges; and the upper end of the femur (thigh bone), possesses an in-turned articular head. The in-turned femoral head fits into a deep (open-backed) cup-shaped socket (acetabulum) on the pelvis, above which is found a prominent, curved shelf of bone (the supracetabular crest) which buttresses the hip socket against the vertical forces exerted by the head of the femur. Related to these features, the attachment of the pelvis to the vertebral column is reinforced through an increased number of sacral ribs, and the lower pelvic bones (ischium and pubis) are generally narrow and elongated primarily to maintain the mechanical advantage of their associated hindlimb-moving muscles.

The significance of the highly distinctive saurischian and ornithischian pelvic constructions will be discussed briefly. This will be followed by an overview of the patterns of appearance, diversification and subsequent extinction, of many of the principal dinosaurian clades (phylogenetic lineages) throughout the remainder of the Mesozoic Era and the subtle, but overarching, influence of the tectonic evolution of the Earth during this, primarily dinosaurian, Era.

In summary, the Late Triassic is dominated primarily by medium-sized, bipedal, carnivorous saurischians (theropods), abundant, facultatively bipedal, herbivorous saurischians (sauropodomorphs) and relatively rare bipedal ornithischians. The Jurassic records a significant diversification of sauropodomorphs and some ornithischians, while the Cretaceous Period is notable for the relative decline in overall sauropodomorph diversity (although this is a decidedly geographically variable phenomenon), and a comparatively spectacular diversification of theropod and ornithischian dinosaurs right through to the end of the Cretaceous. The abrupt termination of an ecologically dominant and clearly vigorously evolving set of lineages, represented by the non-avian dinosaurs, by the event at the close of the Cretaceous Period represents one of the most stark examples of a punctuation mark in the story of life on Earth.

The Biogeographic History of Dinosaurs

Paul Upchurch (University College London)

The biogeographic history of dinosaurs has received considerable attention but remains controversial. Few studies have applied a rigorous biogeographic method to a large data-set or evaluated the statistical significance of their results. Nevertheless, the recent influx of data on dinosaur distributions and phylogeny makes a review of dinosaur biogeography feasible and timely.

Several dinosaur groups became widespread during their Late Triassic radiations. This is consistent with the existence of Pangaea at this time. However, we do not see a cosmopolitan fauna at the generic or specific level across Pangaea: this suggests that, after an initial "global" dispersal some vicariance occurred. During the Early and Middle Jurassic, eustatic and tectonic events led to the isolation of Asia, and then the separation of North America from Gondwana, resulting in statistically significant levels of vicariance. This explains why many Asian dinosaurs are the most basal forms in their clades. Furthermore, similarities between the Late Jurassic faunas of North America and Africa, which have previously been explained in terms of dispersal, are more plausibly interpreted as vicariance. Vicariance events also occurred during the Late Jurassic and Early Cretaceous as Gondwana fragmented, first into western and eastern portions and then the separate continents we know today. Thus, there is a consistently closer relationship between South American and African forms relative to organisms elsewhere in Gondwana. Marine regression during the Aptian-Albian created a connection between Europe and Asia allowing the geodispersal of many dinosaur groups. The Late Cretaceous has not yet produced a statistically significant level of pattern repetition and so biogeographic interpretation remains preliminary. Nevertheless, the strong similarities between North America and Asia are consistent with the formation of a land connection across the north Pacific during the early Late Cretaceous. There is also growing evidence that South America formed a new connection with eastern Gondwana via Antarctica at this time.

These results have several implications for our understanding of dinosaur evolution. First, the presence of vicariance signals contradicts many hypotheses for dinosaur distributions based on dispersal, and thus resolves many conflicts between biogeography and palaeogeography. Second, biogeographic patterns can make predictions about the distribution histories of individual clades, such as the proposal that diplodocid sauropods are an endemic radiation restricted to the Late Jurassic of North America. Finally, the presence of vicariance patterns that match the sequence and timing of Pangaean fragmentation indicates that many dinosaur clades had diversified by the late Early Jurassic, somewhat earlier than the fossil record indicates directly.

The Dinosaurian Origin of Birds - A State-of-the-art Review.

Angela C. Milner (Natural History Museum, London)

Archaeopteryx, from the latest Jurassic of Germany, is the earliest known bird. It has long been regarded as an example of evolution in action by virtue of a suite of skeletal features shared with maniraptoran theropod dinosaurs, yet it possesses impressions of modern asymmetrical flight feathers. The wing feathers have a configuration of primary and secondary flight feathers identical to those of modern birds suggesting that *Archaeopteryx* had some powered flight capability. It is thus a key taxon in the investigation of the dinosaurian origin of birds and the origin of flight. However, it provides no clues as to how feathers evolved although they must, logically, have been present in the dinosaur lineage that gave rise to birds. That has now been demonstrated by a series of spectacular discoveries in the last ten years from an Early Cretaceous lagerstätten in Liaoning Province, China. Several taxa of feathered dinosaurs have provided the 'missing' feather evidence and stimulated debate about feather origins, feather development and feather function. Representatives of several lineages of small coelurosaurian dinosaurs are present in the Liaoning assemblage and allow the evolution of feathers to be mapped onto theropod phylogeny.

Most of the feathered dinosaurs from Liaoning were not capable of flight. However, a small arboreal form, *Microraptor*, adds new fuel to the controversial debate over whether flight began from the ground up or the trees down, and recent studies on ground living modern birds have generated new ideas on how birds became airborne. The Liaoning assemblage also includes a range of primitive true flying birds that show how elaboration of the flight apparatus developed beyond the *Archaeopteryx* stage.

The Liaoning discoveries have demonstrated that that most obvious defining character of birds - feathers – is no longer an avian exclusive. So what makes a bird a bird? Recent computed tomography and three-dimensional reconstruction of the braincase and brain of *Archaeopteryx* may provide some new characters by which birds can be distinguished from feathered dinosaurs.

Dinosaur Herbivory: from functional morphology to macroevolution

Paul M. Barrett (Natural History Museum, London)

In terms of species-richness and biomass, herbivorous dinosaurs were the dominant terrestrial vertebrates of the Mesozoic Era. Dinosaurs were primitively carnivorous (inheriting this condition from their archosaurian ancestors), but herbivory appeared in multiple dinosaur lineages early in the evolution of the group and may have arisen via various omnivorous intermediate stages. Plants are a difficult food source and require either significant oral or digestive processing to release the meagre amounts of nutrients that they contain. In order to deal with these problems, dinosaurs possessed a wide range of adaptations to herbivory. Many of these were concentrated in the skull and dentition, but herbivory also affected the postcranial morphology of these animals.

The levels of structural organisation displayed by the functional complexes associated with dinosaur herbivory ranged from rather simple feeding systems that were not too dissimilar from those of living herbivorous lizards (such as those seen in prosauropods and stegosaurs) to those that approached or surpassed those known in extant herbivorous mammals (such as those of ornithopods). These adaptations included: complex jaw movements; development of dental batteries; presence of a precise occlusion; cheeks; and changes in limb proportions and neck function. Dinosaur herbivores occupy a much broader range of morphospace than their carnivorous relatives.

In addition to providing information on functional morphology and palaeobiology, the varied character complexes associated with herbivory offer the potential for macroevolutionary and palaeoecological insights. These include: possible coevolutionary interactions with food plants; effects of feeding adaptations on the diversity and evolution of various dinosaur groups; and also investigation of more general macroevolutionary phenomena such as correlated progression, ‘key adaptations’ and ‘major adaptive zones’.

Biomechanical Approaches to Feeding, Skull Form and Function in Carnivorous Dinosaurs

Emily J. Rayfield (University of Cambridge, UK)

Theropod dinosaur feeding habits are traditionally viewed as conservative in comparison to the range of unique cranial and dental adaptations utilized by ornithischian dinosaurs. Recent research, particularly using biomechanical analysis, is however, currently uncovering a range of dietary specialisations in the arguably less morphologically diverse non-avian theropods. Here, I present an overview of recent biomechanical research into form, function and feeding in carnivorous Theropoda. Such analysis offers insight not only into the feeding behaviour of specific theropod taxa, but also the evolutionary pressures driving cranial design across the group as a whole.

Primary fossil evidence provides us with our most direct inferences of feeding: cannibalism, coprolites and bite marks are discussed in the context of prey preference and feeding behaviour. Comparative studies offer tantalising insights into the nature of feeding in particular taxa. For example, the cranial morphology of the so-called 'crocodile-mimic' spinosaurids alludes to a piscivorous lifestyle. Such hypotheses demand to be tested by further biomechanical means in the future.

'Traditional' biomechanical approaches such as adductor muscle reconstruction, lever-arm mechanics and bending strength analysis have proved immensely valuable in estimating and elucidating theropod bite forces, cranial strength and construction parameters, such as orbit and fenestration dimensions and also mandibular adaptation. Morphometrics has offered insight into cranium-specific niche partitioning and dimensional shifts in skull evolution.

The engineering/orthopaedic technique Finite Element Analysis (FEA) permits an assessment of cranial stress, strain and strength in response to external loads, such as bite and muscular forces. FEA has been used to infer cranial mechanical performance and possible feeding behaviour in the skulls of *Allosaurus fragilis* and *Tyrannosaurus rex*, and these results are discussed here. Such FE-models allow the adaptive significance of particular cranial features to be identified, and have implications for the significance of patent (open) sutures in the crania of large theropods.

Stability and Agility in Dinosaurs

Donald M. Henderson (University of Calgary, Canada)

The combination of large size and large mass in most dinosaurs would have exerted a strong effect on what they were capable of as living, moving organisms. Lacking living examples of animals with sizes equal to those of dinosaurs, investigating aspects of stability and agility in dinosaurian locomotion can be done using ideas and techniques from physics and engineering.

A basic requirement for any animal is that it be able to balance and remain stable while standing still or walking, and determining the centre of mass (CM) of a dinosaur is a key component in understanding how they did this. Knowing the position of the CM can also lead to the testing of restorations of dinosaurs to see if a proposed restoration would have permitted the animal to have walked without becoming unstable. Examining the stance of a dinosaur and the position of its CM relative to its limb sockets can also reveal whether the animal was a biped, a quadruped, or something in between.

Given that dinosaurian body masses span at least five orders of magnitude, a study of the patterns of phylogenetic increases in body size reveals allometric changes in body shape that suggest strategies for maintaining levels of agility that would be impossible if growth was isometric. These changes are especially marked in the bipedal dinosaurs such as the carnivorous theropods and the herbivorous ornithopods where bodies become deeper and wider, and tails become relatively shorter with increasing body size. This has the effect that body mass becomes concentrated towards the hips and trunk region, and results in relatively lower rotational inertia about a vertical axis. A reduced rotational inertia for an animal enables it to pivot and change direction much more quickly, which has implications for both predators and their prey.

Dinosaur eggs and babies: facts versus fiction.

Eric Buffetaut (CNRS, Paris, France)

Dinosaur eggs were first discovered in the Upper Cretaceous of southern France in the mid-nineteenth century by Philippe Matheron and Jean-Jacques Pouech, and an initial study of eggshell microstructure was published by Paul Gervais in 1877. However, dinosaur eggs first attracted widespread attention in the 1920s with the much publicised discoveries of the American Museum of Natural History expeditions to the Gobi Desert. Starting in the 1960s, systematic investigations in the field and laboratory have shown that fossil eggs are extremely common in some Mesozoic formations, ranging in age from Triassic to terminal Cretaceous.

A major difficulty faced by studies on fossil eggs is that the identity of the egg-layer can be strictly ascertained only when an identifiable embryo is present within the egg. Although a number of fossil embryos have been reported from various parts of the world, the vast majority of fossil eggs are not associated with embryonic remains. A detailed parataxonomy of fossil eggs was established in the 1980s and 1990s, but many “ootaxa” are still insufficiently linked to taxa based on skeletal remains. This problem has been compounded by misidentifications of embryos or purported egg-layers, the best known example being that of the supposed *Protoceratops* eggs from the Gobi which turned out to be those of the theropod *Oviraptor*. Similarly, embryos long referred to the ornithopod *Orodromeus* were shown to belong to the theropod *Troodon*. An enduring problem is that of megaloolithid eggs, which are clearly associated with titanosaurid sauropods in Argentina, but may be associated with hadrosaurids in Romania.

Nesting behaviour in dinosaurs is still incompletely known, despite several well-publicised studies, as egg-laying patterns are not always easily discernible. Clutches arranged in circles have been reported from southern France, but are probably an artefact of excavation. Most dinosaurs seem to have laid their eggs in tightly assembled clutches, and in some cases these may have been buried. Brooding is well documented in oviraptorosaurs (which some authors suggest may have been birds rather than dinosaurs). Histological evidence suggests that hatchlings of some dinosaurs were precocial, while others may have been altricial. Hatchlings and babies are known from various dinosaur groups and provide interesting evidence about growth rates (which appear to have been fast) and patterns.

Purported evidence of dinosaur decline prior to extinction based on a supposed increase of pathological eggshells in latest Cretaceous formations in southern France has been shown to be erroneous. Attempts to use dinosaur eggshells as stratigraphic markers in southern France have been only moderately convincing, as the reported succession of eggshell types bears little resemblance to evidence based on skeletal elements.

Extinction of the dinosaurs

Michael J. Benton (University of Bristol, UK)

According to many, the extinction of the dinosaurs is now fully known. However, not much has changed since 1980 in fact.

Of course, the impact hypothesis of Alvarez *et al*. (1980) has not been rejected, and in fact has been reinforced by substantial, and unpredicted, evidence - shocked quartz, glass spherules with the geochemistry of sedimentary rocks, stishovite, direct evidence of flash freezing, zoning of the impact products in concentric circles leading out from the proto-Caribbean, and indeed a crater. The Chicxulub crater is of the predicted size, it is in roughly the predicted place, and the fallout and tsunami materials are as would be predicted. So the impact model is multiply confirmed, and the hypothesis in the Alvarez *et al*. (1980) paper turns out to have been one of the most daring scientific hypotheses ever – the authors took a huge risk, laying themselves open to easy refutation – and yet they have not been successfully refuted, despite numerous efforts to do so.

The simple impact story is weakened by suggestions that the extinctions of foraminifera and other microfossil groups occur at times other than the impact horizon, and that the impact in fact had little to do with the demise of various life forms. This rather strains credulity, but the conflicts between different biostratigraphers ought to be resolvable.

So, barring a small number of persistent critics, the impact model is accepted by a majority of earth scientists. But did this cause the extinction of the dinosaurs and, if so, how? Again, it would seem incredible if there were no linkage between the impact and the extinction. The coincidence of timing is strongly suggestive. However, there are three outstanding areas for exploration; the pattern of the die-off, quality of the record, and the biotic consequences of impact.

(1) *The pattern of the die-off*. It is well documented that two large-scale attempts to document huge numbers of fossils through the Hell Creek Formation in Montana failed to find agreement. Peter Sheehan and colleagues found evidence for catastrophic extinction (i.e. survival of most dinosaurian species right to the last inch of the Maastrichtian, and their instant disappearance at one horizon), while David Archibald and colleagues found evidence for longer-term or gradual decline. This dispute might suggest that the question will never be resolved. What geological succession could be more appropriate, and how many more specimens have to be counted in order to provide convincing evidence one way or the other?

(2) *Quality of the record*. One issue in the Sheehan vs. Archibald debate was that of quality. How perfect does one expect the fossil record to be, and to what extent can one calculate probability measures and apply correction factors? Studies of ammonite diversity up to the K/T boundary suggest that the more one collects the more one finds. However, intensity of collection effort is also an important factor in avoiding the mistake of failing to identify a decline in abundance, if not of diversity. Patchy collecting and gaps in the rock record can either make a catastrophic extinction pattern seem gradual or a gradual pattern seem catastrophic respectively.

(3) *Biotic consequences of impact*. Very little attention has been given to killing models. How can an impact, and its physical environmental consequences, cause mass dying? All we have for comparison are volcanic eruptions and other essentially local-scale phenomena. Many K/T researchers believe it was enough to establish that impact had occurred, and to determine the consequences. However, it is hard to kill many species worldwide. The killing models have yet to be developed.

Dinosaur Taphonomy – Applications to Interpreting Sedimentology

Jon Noad (Shell International, Rijswijk, Netherlands)

Dinosaurs have received an enormous amount of attention in the media throughout the last century, far in excess of their palaeontological significance. However, beyond the detailed anatomical work, taphonomic studies have helped to reconstruct their day-to-day lifestyles and behaviour. Work on associated footprints, nests, coprolites, skin impressions, as well as other dinosaurian trace fossils, has led to great advances in this understanding.

However, taphonomy works both ways. Of course these fossils and ichnofossils can be used to reconstruct saurian behaviour. They also have the potential to be used, in association with sedimentary structures, to elucidate the depositional environment in which they were deposited or formed. The changes in style of skeletal preservation through time can be used to indicate changes in fluvial character, while the presence or absence of nests can provide palaeoclimatic data. Footprints can show the state of the substrate at the time dinosaurs traversed a locality, while their absence, in the presence of common carcasses, may also yield information on potentially arid settings. Bone and footprint orientation can also provide information relating to palaeocurrents or palaeorelief.

Field data from the USA, Europe and South Africa will be presented to show how the taphonomy of the largest land animals ever to roam the planet can provide a surprisingly valuable tool in the Mesozoic sedimentologist's armoury.

A new basal ornithischian from the Upper Elliot Formation of Southern Africa

Richard Butler (Department of Earth Sciences, University of Cambridge / The Natural History Museum, London)

The Upper Elliot Formation of Lesotho and Southern Africa is lowermost Jurassic (Hettangian) in age and contains one of the oldest reasonably well documented faunas of ornithischian dinosaurs, currently best represented by the 'fabrosaurid' /Lesothosaurus diagnosticus/, and the heterodontosaurids /Heterodontosaurus tuck/i and /Abrictosaurus consors/. The literature contains persistent references to a large undescribed 'fabrosaurid' from the Upper Elliot Formation. New work on material from the Natural History Museum (London) and the South African Museum (Cape Town) has allowed the recognition of this 'large fabrosaurid' as a distinct genus, distinguishable from /Lesothosaurus/ and the heterodontosaurids by a suite of autapomorphies including the presence of a distinct tab-like obturator process on the ischium. This new taxon increases the known diversity of basal ornithischians, and gives new insights into character evolution at the base of the ornithischian clade.

Thecodontosaurus: Preparing a Vulnerable Dinosaur Specimen

Remmert Schouten (University of Bristol)

Many fossils are especially vulnerable and require specific attention. Discovering a fossil is more often than not relatively easy. After that comes the preparation. For very vulnerable fossils and tough matrixes the fossil can be protected with a wax for protection during the preparation. Material from a small dinosaur from Bristol, Thecodontosaurus antiquus, (Morris, 1840) is taken as an example here, and in particular a partial jaw. Specimens of Thecodontosaurus were first found in the 1830s, and further material came to light in the 1980s. Preservation is unusual: the fossils occur in a cave breccia, containing blocks of Carboniferous limestone (cave wall), bones, and red (Triassic-age) paleosol as a matrix. This combination makes it impossible to use acid techniques in preparation, and fine-scale mechanical preparation is essential.