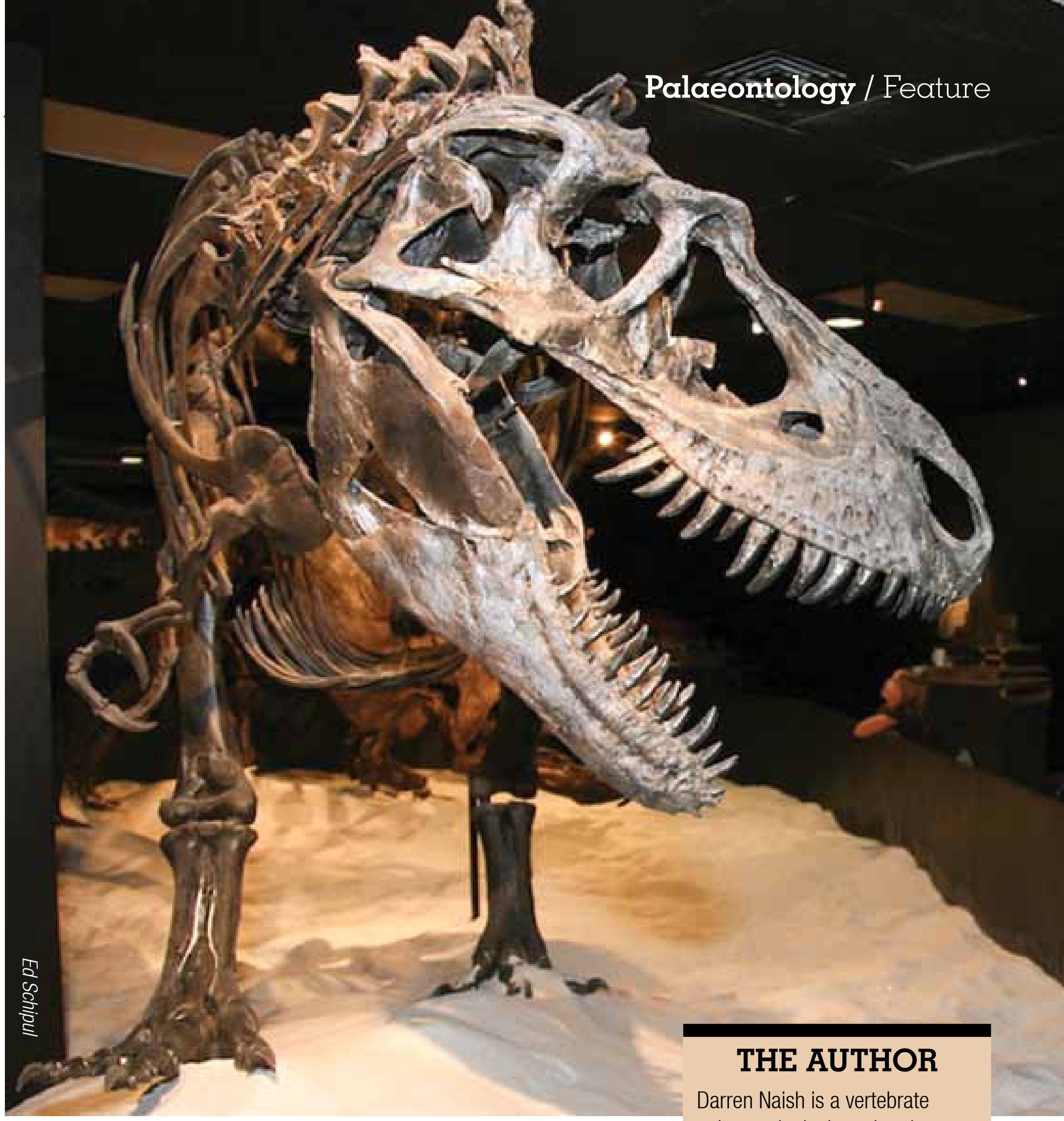
Palaeontology bites back…

In last month's *Laboratory News* Brian J. Ford suggested that dinosaurs were aquatic – here Darren Naish explains why this idea has the weight of consensus to battle with and why, in fact, dinosaurs do work



Ed Schipul

In April 2012, Brian J. Ford argued that the time is right for a "prehistoric revolution". Arguing that dinosaurs "don't work" on the basis of being too heavy to walk on land, he argued that dinosaurs – *all* dinosaurs, it seems – must have been aquatic and reliant on the support of water.

The appearance of this article so close to April 1st aroused considerable suspicion within the dinosaur research community, and adequate and wholly damning responses to Ford's article have already appeared online. Some are aggressive and question the abilities of a non-specialist to declare expertise in an area where there is no evidence of prior experience. Others state flatly that the data we have contradicts Ford's scenario in entirety, a contention with which I agree. My aim here is not necessarily to respond to Ford's proposal in a point-by-point rebuttal – I think that would be boring – but rather to give some idea of where we're at with respect to our knowledge of dinosaurs, all the while referring to Ford's proposal.

Dinosaurs are among the most famous and distinctive of animals. They were first named as a specific group of reptiles in 1842 following the discovery of various fragmentary remains in England. By the late 1800s, reasonably complete skeletons (mostly from the western states of the USA) had revealed the body plans of the bipedal, predatory theropods, the giant, long-necked sauropods, the plated stegosaurs, and the horned ceratopsians.

Dinosaurs were mostly neglected as objects of scientific research during the middle decades of the 20th century. However, a set of exciting ideas promoted during the late 1960s (namely, that dinosaurs were 'warm-blooded', that they lived on as birds, and that their story was one of success and innovation rather than failure and stagnation) fuelled a surge of interest known as the Dinosaur Renaissance.

Today, more people than ever are attracted to the study of dinosaurs and their world. An enormous number of new species (as many as 50) are discovered and named every year, and technology-led research is allowing dinosaur specialists to look anew at dinosaur skeletal and soft-tissue anatomy, to infer locomotory and feeding behaviour, and to correlate the dinosaur fossil record with data on changing sea levels, climatic gradients and tectonic events. The idea that palaeontologists sit in dusty labs and just peer at bones hasn't been true for decades, since much modern research involves CT-scanning, digital simulations of muscle and bone behaviour, the computer-assisted generation of phylogenetic hypotheses, and analyses of isotope geochemistry and bone, eggshell and feather microstructure. Descriptive analysis does, of course, still have its place. Much modern research is informed by work done on the biology and structure of living animals, and in fact dinosaur researchers have played key roles in an 'anatomical revolution' that is as much about understanding living animals as fossil ones.

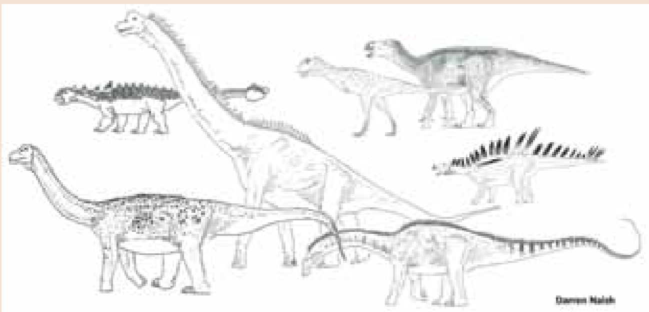
Dinosaurs were not the flabby-bodied, tail-dragging, swamp-dwelling dullards, destined for extinction, of stereotype. Articulated skeletons and the shapes of joints and muscle attachment scars show that dinosaurs were erect-limbed animals with narrow gaits, horizontal body postures, erect neck poses, and tails that were mostly held projecting horizontally and well up off the ground. Limb joint structure, musculature and trackways shows that dinosaurs were highly capable walkers and that many could run, though the speeds they could reach remain controversial.

Dinosaur hind limb, pelvic and tail muscles were enormous. It seems that the metabolic costs required to power these muscles provide evidence of endothermy or 'warm-bloodedness'[1]. Of course, the debate about dinosaur physiology continues, but the perpetual presence of dinosaurs in cool and even cold environments, combined with data indicating rapid and continuous growth, supports views that dinosaurs were indeed endothermic.

Many dinosaurs were large, sometimes stupendously so. The biggest theropods reached or exceeded 14m and 10 tons, and giant horned dinosaurs, duckbills and others also approached or ex- ▶

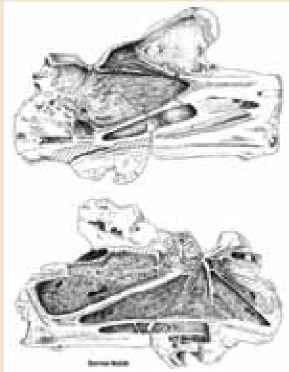
THE AUTHOR

Darren Naish is a vertebrate palaeontologist based at the University of Southampton. He works on predatory dinosaurs, pterosaurs and marine reptiles. His most recent book is *The Great Dinosaur Discoveries* (A&C Black). He blogs at Tetrapod Zoology, currently hosted by *Scientific American*.



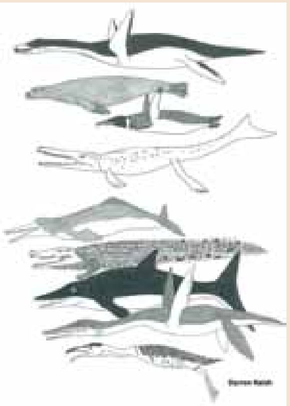
Just some of the body plans possessed by large Mesozoic dinosaurs. Sauropods were long-necked, quadrupedal giants while theropods were bipedal predators, sometimes with shortened forelimbs. Quadrupedal armoured dinosaurs – the ankylosaurs and stegosaurs – bristled with plates and spikes

Many dinosaurs (like this Stegosaurus, photographed at the IRSNB, Brussels) had enormous tails and enormous tail muscles. Articulated skeletons and data from living animals shows that these tails were held aloft and were not a problem for a successful life on land



Sauropod and theropod vertebrae possess cavities on their sides that open into larger chambers within. These are obvious in this diagram of a large sauropod neck vertebra. Based on comparison with birds, these cavities certainly housed air-filled sacs and tubes connected to the lungs

Bird-like theropod dinosaurs, like this deinonychosaur (left) and oviraptorosaur, were fully feathered and more bird-like than conventionally thought



A selection of aquatic and amphibious reptiles and mammals, including marine mammals, plesiosaurs, crocodilians and birds. Aquatic adaptations are obvious. They include tail flukes, flippers, paddle-like feet and torpedo-shaped bodies

ceeded 10 tons. The true giants are the sauropods. An average sauropod perhaps massed 15 tons or so, but the largest kinds (the current record-holder is *Amphicoelias*) were over 30m long and around or over 100 tons. These were the largest land animals that have ever existed. For comparison, the biggest land mammals (the rhino *Paraceratherium* and the largest mammoths) reached maximum weights of about 20 tons.

Interestingly, theropods and sauropods were not as heavy as might be expected, since their skeletons (and the rest of their bodies) were pneumatised by an air-sac system just like that present in birds. When pneumatisation is accounted for, sauropod mass estimates decrease by approximately 10%[2]. Extensive pneumatisation is obviously inconsistent with Ford's proposal of aquatic habits. In fact, one study specifically examined how sauropods might fare as swimmers once pneumatisation is taken into account. The conclusion: sauropods floated high in the water and were unstable and prone to tipping[3].

A substantial amount of anatomical data shows that birds are part of the dinosaur radiation, meaning that we have to refer to 'non-avian dinosaurs' or 'Mesozoic dinosaurs' when discussing the dinosaurs that lived before the end-Cretaceous extinction event. Bird-like, feathered Mesozoic theropods – all discovered since 1996 – demonstrate that feathers evolved deep within Theropoda. Many bird-like theropods had long, complex feathers on their arms and hands, hindlimbs and tails. Indeed, experts are now hard pressed to reliably distinguish those theropods typically regarded as 'early birds' (most famously, *Archaeopteryx*) from those typically considered 'bird-like dinosaurs'. Simple, filamentous feathers seem to have been one of the first steps in the evolution of feathering, and recent discoveries have shown that even some gigantic tyrannosaurs were covered in shaggy, filamentous pelts.

Any interpretation of a fossil animal's behaviour and ecology must take account of the palaeoenvironmental and sedimentological setting in which it occurs. A major criticism of Ford's proposal is that his idea was proposed in a vacuum. He assumed that we can look at dinosaur anatomy in the grossest, most superficial sense and make sweeping statements about ecology and habitat preference without considering other areas.

Dinosaur anatomy does not support the idea that they were aquatic animals (see below). Neither does sedimentological nor palaeoenvironmental data, all of which Ford ignored. As is well known, the majority of fossils are preserved in aquatic environments, since this is where sedimentation rates are highest and hence where bodies, bones and other organic remains are most usually buried and preserved. Many dinosaur fossils are indeed preserved in sediments that were deposited in water, but so are the fossilised remains of horses, bees and palm trees.

However, hundreds of other dinosaur fossils, representing species belonging to all major groups, are known from sediments deposited in undoubted terrestrial environments. Many are known from desert sands, and some of the world's richest dinosaur-bearing rock units are formed from sediments that were not deposited in wetlands, marshes or submerged regions, but in parklands, plains and semi-deserts. So far as we can tell from copious and much-studied sedimentological evidence, rivers, lakes and ponds were rare, small or even wholly absent from these places. Ford chose to remain wholly ignorant of this huge amount of palaeoenvironmental data.

What of Ford's claim that dinosaurs simply look like they must have spent their time in water? A lifestyle that involves wading, swimming or diving shapes an animal's body through evolution. Typical aquatic adaptations include paddle-like hands and feet, tails specialised for sculling, dense bones that contribute to buoyancy control, and eyes and nostrils positioned high up on the head.

It is very likely that dinosaurs were good swimmers. Their powerful, often long limbs and typically large, muscular tails almost certainly allowed them to make river or sea crossings when the need arose. On the basis of a similarity with modern groundbirds, I'm sure that even feathery, bird-like theropods were strong swimmers. Amphibious habits have been proposed for a few Mesozoic dinosaurs. An especially deep tail in the Jurassic theropod *Ceratosaurus*, and hippo-like body proportions in some horned dinosaurs and other herbivores, have been suggested to indicate water-going habits in these forms. Spinosaurid theropods have long, crocodile-like jaws and are thought to have been waterside predators that waded in the shallows, dipping their snout-tips into the water to grab large fish. And we know that several groups of Cretaceous birds – the foot-propelled hesperornithines in particular – took to aquatic life.

However, for the most part, Mesozoic dinosaurs do not exhibit any of the anatomical features associated with a lifestyle that involves wading or swimming. On the contrary, Mesozoic dinosaurs were obviously a terrestrial bunch, specialised for walking and running on land. Old ideas that sauropods and duckbills were swamp-bound, amphibious animals were countered decades ago by compelling research on the shapes of their bodies and limbs and on the environments they inhabited[4-6]. Data on tooth wear and trackways further demonstrates terrestrial habits for these animals.

Part of Ford's argument comes from his contention that large dinosaurs are simply too heavy to have walked on land. For a start, this ignores the existence of small and mid-sized dinosaurs, most of which exhibit the same body plans as their gargantuan relatives. It also ignores work by biomechanists who have demonstrated on the basis of bone and cartilage strength and other factors that even the biggest dinosaurs were well within the safety factors permitting locomotion on land[7].

Ford specifically stated that the tails of large dinosaurs were too heavy to permit terrestrial life. However, geometrical modelling performed by dinosaur specialists and utilising techniques somewhat more rigorous than Ford's technique of dunking toy dinosaurs in water most definitely does not find even the most substantial, most muscular dinosaurian tail to present any problem as goes terrestrial locomotion[3,8-10]. Furthermore, articulated, complete skeletons, the nature of the articulations between tail vertebrae, and our knowledge of passive tail support mechanisms in modern animals all show without doubt that the largest dinosaurs really could and did hold their enormous tails aloft, well up off the ground, no matter what Ford asserts.

There are numerous additional reasons for sticking with the consensus view that Mesozoic dinosaurs were predominantly terrestrial. Literally millions of dinosaur eggs are known from (mostly Cretaceous) rocks worldwide, all clearly preserved in terrestrial sediments. The vast majority of dinosaur tracks (of which millions are known) were made in exposed, terrestrial habitats, not on submerged mud as Ford suggested. Sedimentologists have published numerous works determining whether a sediment surface was exposed or submerged, and exposed surfaces are easily identifiable – they feature mud cracks, raindrop traces and mineral deposits that result from evaporation. Again, Ford's assertion that dinosaur tracks must have been made on submerged surfaces is naïve and ignores decades of research.

In conclusion, the effort of a non-specialist to declare the modern consensus on dinosaur behaviour and lifestyle to be flawed has clearly fallen flat. Anatomical, biomechanical, palaeoenvironmental and other lines of evidence contest the idea that dinosaurs might have been perpetually aquatic. Indeed, Ford's proposal is so wrong-headed and contrary to evidence and research that it hardly seems worth responding to. Some of my colleagues have argued that we should simply ignore this deviant opinion and not provide it with any further "oxygen of publicity". However, it is with the aim of 'undoing the damage' that I present this article. LN

REFERENCES

1. Pontzer, H., Allen, V. & Hutchinson, J. R. 2009. Biomechanics of running indicates endothermy in bipedal dinosaurs. PLoS ONE 4(11): e7783. doi:10.1371/journal.pone.0007783
2. Wedel, M. J. 2005. Postcranial skeletal pneumaticity in sauropods and its implications for mass estimates. In Wilson, J. A. & Curry-Rogers, K. (eds). The Sauropods: Evolution and Paleobiology. University of California Press (Berkeley), pp. 201-228.
3. Henderson D. M. 2003. Tipsy punters: sauropod dinosaur pneumaticity, buoyancy and aquatic habits. Proceedings of the Royal Society of London B
4. Ostrom, J. H. 1964. A reconsideration of the paleobiology of hadrosaurian dinosaurs. American Journal of Science 262, 975-997.
5. Bakker, R. T. 1971. Ecology of the brontosaurs. Nature 229, 172-174.
6. Coombs, W. P. 1975. Sauropod habits and habitats. Palaeogeography, Palaeoclimatology, Palaeoecology 17, 1-33.
7. Hokkanen, J. E. I. 1986. The size of the largest land animal. Journal of Theoretical Biology 188, 491-499.
8. Henderson, D. M. 1999. Estimating the masses and centers of mass of extinct animals by 3-D mathematical scaling. Paleobiology 25, 88-106.
9. Hutchinson, J. R. & Garcia, M. 2002. Tyrannosaurus was not a fast runner. Nature 415, 1018-1021.
10. Persons, W. S. & Currie, P. J. 2011. The tail of Tyrannosaurus: reassessing the size and locomotive importance of the M. caudofemoralis in non-avian theropods. The Anatomical Record 294, 119-131.

The hands of sauropods were peculiar, columnar structures. These are not the extremities of animals that regularly walked on soft, waterlogged substrates

Bipedal predatory dinosaurs like this Cryolophosaurus (photographed at the IRSNB, Brussels) were obviously terrestrial predators, good at running, that used their inward-facing, clawed hands and serrated teeth to catch and dispatch prey