130 years of tree-climbing dinosaurs:
Archaeopteryx, ‘arbrosauras’ and the origin of avian flight

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Abstract: The idea that small predatory dinosaurs might have climbed trees is rather popular today. However, it isn't a new idea and has been suggested several times over the years. Some ideas about tree-climbing dinosaurs are downright ridiculous; others are reasonable and comparisons with living animals imply that some dinosaurs were able climbers.

The dinosaurs of today are up to all sorts of things. They have been seen mating, climbing mountains and even playing in the snow: giants like sauropods and Tyrannosaurus have been witnessed leaping, balancing erect on their tails and pushing down trees. I refer of course to the explosion of dynamic artwork that has followed in the wake of the 'dinosaur renaissance' inspired by Robert Bakker. Arguing that large dinosaurs were not constrained by their bulky, Bakker’s 'renaissance' has promoted artistic speculation that is often controversial in the light of studies on animal form, function and behaviour.

The downside of all this is that dinosaurs have sometimes been visualised as behaving in downright unlikely ways. In Bakker's 1995 book Raptor Red, theropod dinosaurs excavate subterranean tunnels and a dromaeosaur has a nervous breakdown when one of its babies dies. On the other hand, comparisons between dinosaurs and living animals have increased. Group-hunting or mobbing strategies, for example, have been proposed for predatory theropods, acoustic advertisement has been suggested for hadrosaurs, aggresive head-shoving behaviours have been advocated for horned dinosaurs, among others.

Many living small and medium-sized predators climb trees: they can do this because they have flexible fingers and toes, sharp claws and a good sense of balance. Accordingly, the dinosaur ‘renaissance’ has promoted the idea that small dinosaurs – particularly theropods – could climb trees. Today this notion is becoming increasingly popular and there are now scientists who argue both that certain theropods were specialised for tree climbing (scansoriality), and that this lifestyle was integral to the evolution of birds.

A history of tree-climbing dinosaurs

It would be misleading, however, to think that ideas about tree-climbing dinosaurs originated during this ‘renaissance’. Such ideas are actually almost as old as the recognition of dinosaurs themselves. In the 1830s, Gideon Mantell reconstructed Iguanodon standing on a branch as if it were a tree-dwelling iguana. The Isle of Wight palaeontologist Reverend William Fox, famous for his discoveries of the Wealden Group dinosaurs Hypsilophodon and Polacanthus, suggested in 1866 that the small theropod Comampusaurus oweni was scansorial. Fox appears to have based this idea on the lightweight, pneumatic structure of the C. oweni specimen. Fox’s suggestion, overlooked until recently, may constitute the earliest written suggestion of tree-climbing habits for a non-avian dinosaur.

During the 1930s, at a time when the small ornithopod Hypsilophodon was thought of as arboreal, Swinton advocated a climbing ability in small theropods. The arboreal lifestyle promoted for Hypsilophodon by Swinton was disproved by Galton in 1971. However, Galton did note that some other small dinosaurs, including theropods, could have been tree-climbers.

Excepting the work of some Russian palaeontologists (see below), however, the notion of scansoriality in theropods was only really brought to the fore by Bakker and Paul. Paul’s 1988 illustration of Ornitholestes in a tree is perhaps the ultimate iconographic representation of the whole ‘climbing dinosaur’ movement, and as such has always attracted attention, both negative and positive. In criticising Paul and the whole idea of feathered, tree climbing dinosaurs, ornithologist Alan Feduccia referred to this piece as a ‘wild speculation’. Paul has proposed that birds evolved from small climbing theropods that were adept hunters both on the ground and in bushes and trees. He also continues to argue that bird-like coelurosaurs are themselves flightless birds that evolved secondarily terrestrial habits from Archaeopteryx-like ancestors. Meanwhile, in 1993 and at the height of Jurassic Park fever, Bakker regarded the theropods Pragmagnostus and Velociraptor, as proficient climbers, and in Raptor Red there is even a part where the Utahraptor family climb trees in order to escape a flood. Such views found their way into Michael Crichton’s book where the evil dromaeosaurs pursue the fleeing humans into the trees.

Paul’s argument about secondary flightlessness in certain theropods has been elaborated upon by writers and researcher George...
Olchovsky. Olchovsky has argued that features seen in dinosaurs (particularly theropods) such as pneumatic bones, stiffened tails, feathers and a reduction in digits have no conceivable adaptive 'value' except as features reflecting arboreal life, and that all dinosaurs were enlarged, terrestrial descendants of small arboreal dinosaurs which themselves were the direct ancestors of birds.

If such a model is in any way correct, there must be numerous small climbing theropods currently missing from the fossil record. Olchovsky has occasionally compared such hypothetical dinosaurs to the arborousaurus postulated by Dougal Dixon in his thought-provoking The New Dinosaurs (1988). Arboosaurous were diminutive arboreal theropods, sometimes capable of gliding that, in Dixon's speculative scenario, take the place of small birds and arboreal mammals. Dixon also invented tree-dwelling ornithodorns that mimic real animals including koalas, pandas and hornbills. As for the presence of real, Mesozoic arboosaurs, Olchovsky and his colleagues argue that their presence is indicated by the fossil footprint record - according to recent work by Martin Lockley, the Mesozoic trackway record includes innumerable tiny prints made by very small dinosaurs. The numerous tiny theropod teeth now on record are also interpreted by Olchovsky as potential evidence for miniature tree-climbing 'dino-birds'.

Surprisingly, it has at times been suggested that certain giant theropods were tree-climbers. In 1970, Russian palaeontologist Anatoly Rozhdestvensky concluded that Deinonychus, a giant ornithomimosaur (ostrich-dinosaur) known only from its 2.4 m long arms, was an arboreal 'sloth-dinosaur' that had a shortened tail and hindlimbs. Rozhdestvensky based this idea on both the general form of the Deinonychus forelimbs - as in all ornithomimosauress these are very elongate and with slim fingers of equal length, recalling vaguely the forelimbs of climbing sloths - and the fact that the palms faced inwards, again as they do in sloths.

However, inward-facing palms and elongate forelimbs are seen widely in theropods and probably do not correlate with a climbing ability. Furthermore, Deinonychus is only known from the Nemegt Formation. This preserves a fairly and environment where large trees are presumed to have been rare or absent. Finally, the size of its arms indicates that Deinonychus was huge, maybe weighing 10 tons or more. For comparison, the largest known arboreal mammals, extinct giant orang-utans and Madagascan lemurs, did not exceed 350 kg. In Rozhdestvensky's view, arboreal environments of the Upper Cretaceous may have been somewhat crowded - he did not just regard Deinonychus as arboreal but argued that all ornithomimosauress were scavengial. After Deinonychus, the biggest of these is Gallimimus bullatus, also of the Nemegt Formation. Gallimimus grew to 6 m and about 500 kg.

The idea that ornithomimosauress were scavengial or arboreal is hard to accept. These dinosaurs were built somewhat like long-tailed ostriches and their lengthy hindlimbs, shortened toes and hoof-like claws indicate that they were terrestrial cursorial, not climbers. While their arms may have functioned somewhat like those of tree sloths and could have been used in gathering vegetation, they were comparatively very weakly muscled, have straightened rather than hooked claws, and do not look useful for supporting weight if their owner were a climber.

Nevertheless, the idea of tree-climbing ornithomimosauress was resurrected by Chatterjee in 1995, who argued that a climbing mode of life was primitive for coelurosauress. This was then used to explain the evolution within the group of enhanced vision, increased brain size, and increasing flexibility of the wrists and fingers. In 1999 Chatterjee advocated Sinosauropteryx, the Chinese 'feathered' compsognathid, as a climber and proposed that its hair-like integumentary filaments acted like a parachute as it leapt from trees, thus representing one of the first steps towards the evolution of flight. In particular Chatterjee has viewed dromaeosaurids as specialised climbers that used their enlarged foot claws, stiffened tail and sharply clawed hands for vertical climbing on tree trunks.

Vertical climbing for dromaeosaurids was also advocated by Svend Palm who published his ideas in a 1997 booklet. Palm thought that the presence of straight-trunked cycadeoids in the Mesozoic was important to the evolution of climbing dinosaurs and that dromaeosaurids and early birds evolved a scavengial ability to exploit the crowns of these plants as places in which they could nest and take refuge. As Palm notes, this idea has a historical precedent in the illustrations of Gerhard Heilmann. Though Heilmann's 1926 The Origin of Birds includes discussions and restorations of conifer-climbing habits in protobirds, Heilmann had earlier illustrated these animals vertically ascending cycadeoid trunks.

**Archaeopteryx: its claws and the origin of flight**

Strict arboreality for Archaeopteryx, a bird identical in many of its features to dromaeosaurid theropods, was first suggested by Hurst in 1893. More recently, it has been strongly argued for by Feduccia (1993) and the mammallogist Derek Yalden (1997), who have compared the curvature and sharpness of the hand and foot claws of Archaeopteryx with those of living animals. Both conclude that, in its foot claws, Archaeopteryx most resembles perching birds and, in its hand claws, trunk-climbing birds.

These conclusions are disputed by those advocating a terrestrial origin for avian flight. One argument is that, because its closest coelurosaurian relatives were terrestrial, cursorial predators, Archaeopteryx was too. This is not convincing because some of these other coelurosaurs may have been scavengial. A second argument concerns the near treeless palaeoenvironment that has been reconstructed for the Solnhofen islands on which Archaeopteryx is thought to have lived (Archaeopteryx and other Solnhofen
fossils are recovered from marine deposits, and thus any attempt at depicting the Solnhofen islands is extremely speculative). If there were no trees here, how could Archaeopteryx have been arboreal? While there is no evidence for huge trees at Solnhofen, there apparently were trees including 3m conifers and ginkgoes.

Finally, the claw curvature data itself has been questioned. Some workers have argued that claws of similar curvature to those of Archaeopteryx are seen on the hands of certain other theropods. Notably, however, strongly curved foot claws like those of Archaeopteryx are not seen in other theropods, excepting the sickle claws of dromaeosaurids. Also, if claws like those of Archaeopteryx are seen in other theropods, might this indicate that these theropods were climbing as well? Despite claims to the contrary, the hand claws of theropods like tyrannosaurids and allosaurids are not as sharply curved or laterally compressed as those of Archaeopteryx: it is, notably, small coelurosauras like dromaeosaurids and oviraptorsids that come closest. Data on claw curvature has also been confused by the discovery that some cliff-dwelling birds (puffins) have claw curvature as marked as tree climbers. Peters and Gorgner used this data to suggest that Archaeopteryx was not necessarily arboreal. Clearly, however, this does not demonstrate that it was not arboreal and the absence of cliff-like habitats from Solnhofen makes this alternative unlikely.

Archaeopteryx does have a comparatively large and fully reversed hallux that is positioned low down on the foot. Though not as well developed as in modern climbing birds, this would clearly have assisted in climbing, as would the sharp claws. Similarly, muscle and ligament attachment sites on the feet of Archaeopteryx are much less developed than in modern climbing birds. While these indicate that it was not as good at grasping as living arboreal birds, they do not prove that it could not climb. There is therefore no reason why Archaeopteryx could not have climbed, and there is reasonable evidence showing that it did, even if it was primarily terrestrial as some palaeontologists insist. A climbing ability in Archaeopteryx, and in coelurosauras generally in fact, suggests that bird flight did evolve in the trees.

What living animals tell us

Exclusively arboreal animals are often anatomically distinctive with specialised hands, feet and tails that are not suited for locomotion on the ground. Prehensile tails, seen in some lizards and snakes, arboreal salamanders and various mammals, are generally clear indicators of a climbing ability. Arboreal marsupials, some primates and chameleons also have unusual 'pincer-hands' used for grasping. Finally, many climbing animals have partially rotatable ankles that are adapted so that their owners can hang from branches or climb down tree trunks.

No non-avian theropod exhibits such arboreal specialisations, thus none appears to have been truly arboreal. However, scansorial habits appear likely in small theropods given the morphology of living scansorial animals. In extant mammals, it is essentially those taxa that have flexible digits and/or sharp claws that are capable of climbing. Like small theropods, scansorial mammals have sharp claws, palms that can face inward, and a good sense of balance. By using these simple features to predict which groups of eutherian mammals might be capable of climbing, I predicted a climbing ability in 16 out of 33 analysed groups. These predictions could then be tested by looking at behaviour. Of the 16 groups predicted to be capable of climbing, all 16 are. This might indicate that suggestions of scansoriality in fossil animals, based only on morphological features like those used in this test, are largely accurate.

However, the behaviour of living animals also shows that, as has recently been said of armadillo life habits, 'Anatomy is not destiny'. Three groups not predicted to include scansorial taxa actually do:

- canids, artiodactyls and hyracoids. It is well known that some animals exhibit behaviour that we would not predict from their morphology, meaning that we must be cautious when setting constraints on the behaviour of extinct forms.

Conclusions, and a final perspective

The fact that non-avian dinosaurs lack all of the features seen in living arboreal animals indicates that we have not yet discovered a fully arboreal dinosaur. Why not? Maybe such animals did exist and simply remain unrepresented by fossils. Ostensibly arboreal Triassic reptiles are known and include drepanosaurids like Megalancosaurus.
and the possible archosaur Longisquama. In the Upper Cretaceous and Cainozoic, scorpionoid and arboREAL birds such as avaroid enantiornithines, rollers, mousebirds, parrots and trogons are well represented. The question is - where are the Jurassic and Lower Cretaceous archosaurs?

One possible answer is that small pterosaurs, lizards and mammals like dryolestoids were the dominant arboREAL animals at this time. If so, dinosaurs may only have begun their arboREAL 'career' with the earliest birds, currently represented only by Late Jurassic Archeopteryx. Another possible answer is that arboREAL theropods are known, but we have not recognised them as such. Though many living climbing animals exhibit morphological features that indicate their lifestyle, others do not. Hyraxes, grey foxes, goats and some lizards do not exhibit climbing specialisations and we probably would not predict from their fossils that they regularly climb (but they do).

Throughout the Mesozoic, it seems that small, sharp-clawed theropods were wholly capable of climbing and could well have used arboREAL environments as much as modern predators like cats, mustelids or monitor lizards. In the Late Jurassic, specialised climbing features are evident in the bird Archeopteryx and the origin of bird flight probably owes itself to the scorable abilities of small theropods.

Addendum: Since this article was written a brief note has appeared on an apparently arboREAL theropod. The specimen, a complete skeleton of a tiny juvenile, is from the Lower Cretaceous of China and has a unique robust, elongate third finger. We await the full description with great interest.

References