

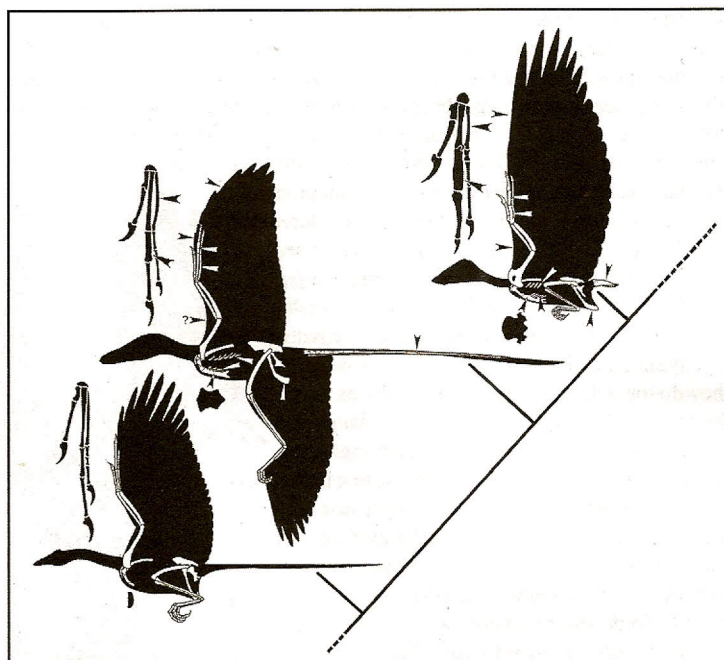
Screaming Biplane Dromaeosaurs of the Air

Written & illustrated by
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It is questionable whether anyone even speculated that some dinosaurs were feathered until Ostrom detailed the evidence that birds descended from predatory avian theropods a third of a century ago. The first illustration of a feathered dinosaur was a nice little study of a well ensconced *Syntarsus* dashing down a dune slope in pursuit of a gliding lizard in Robert Bakker's classic "Dinosaur Renaissance" article in the April 1975 *Scientific American* by Sarah Landry (can also be seen in the *Scientific American Book of the Dinosaur* I edited). My first feathered dinosaur was executed shortly after, an inappropriately shaggy *Allosaurus* attacking a herd of *Diplodocus*. I was soon doing a host of small theropods in feathers. Despite the logic of feather insulation on the group ancestral birds and showing evidence of a high level energetics, images of feathered avian theropods were often harshly and unscientifically criticized as unscientific in view of the lack of evidence for their presence, ignoring the equal fact that no one had found scales on the little dinosaurs either.

In the 1980s I further proposed that the most bird-like, avian theropods - dromaeosaurs, troodonts, oviraptorosaurs, and later therizinosaurids - were not just close to birds and the origin of flight, but were secondarily flightless and closer to modern birds than feathered *Archaeopteryx*. If so these dinosaurs should have been as feathered as living flightless birds. Clues were to be seen in quarry photographs of the famed fighting *Velociraptor* (and *Protoceratops*) skeleton in which ossified uncinates processes on the ribs and big sternal plates of the sort typical of modern birds but absent in *Archaeopteryx* were in view. And just why did dromaeosaurids have a pterosaur like tail, and folding arms anyway? Other features ally the bird like avian theropods with derived birds. But an over reliance by most researchers on cladistic methods which are inherently ill suited for coping with the extensive reversals associated with the loss of flight caused the hypothesis to be neglected. I was even compelled to remove the rib uncinates from my *Deinonychus* skeleton when it was published in the January 1993 *National Geographic*. Since then uncinates have shown up on dozens of dromaeosaur and other avian theropod skeletons.

Nowadays, since the explosion of fossils from the Chinese Early Cretaceous Jehol - which could have been uncovered in the 1920s and 30s which would have resulted in Knight doing feathered dinosaurs - the presence of feathers on small avian theropods has become conventional wisdom except for the diminutive and dwindling cabal of opponents to the dinosaur-bird connection. Relatively simple filaments that probably represent early feathers have been found on moderately advanced avian theropods such as *Sinosauropteryx*. The same are present on the much more bird-like therizinosaur *Beipiaosaurus*, but the remains are too incomplete to tell what else it may have had. More interesting is the oviraptorosaur relative *Caudipteryx*, which sports fully developed, complex pennaceous feathers on its hands and short tail. The hand feathers are too small and symmetrical to generate lift, and they



Above: Proposed relationships based on flight adaptations of preserved skeletons and feathers of *Archaeopteryx*, a generalized *Sinornithosaurus*, and *Confuciusornis*, with arrows indicating derived adaptations not present in *Archaeopteryx* as described in text. Not to scale.

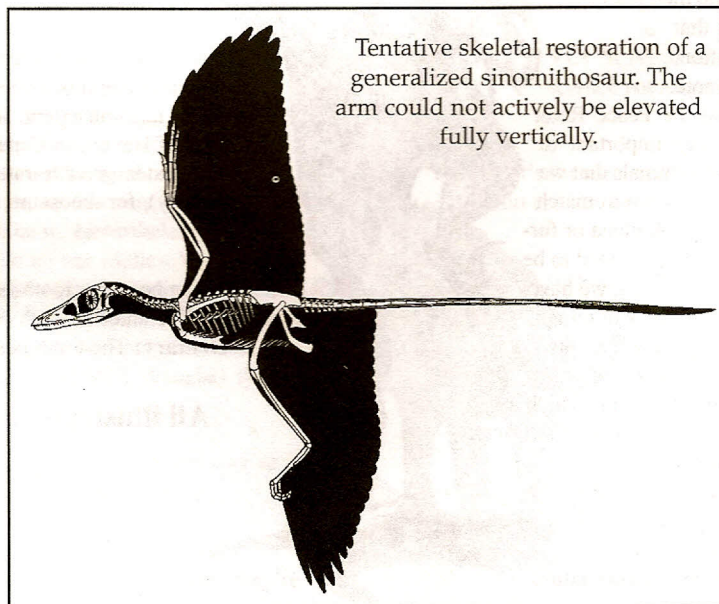
appear to represent the remnants of wings converted to display devices.

But most spectacular by far are the feathers found on a series of small Jehol dromaeosaurs that range in mass from 0.15 to 3 kilograms. Labeled *Sinornithosaurus*, *Microraptor* and *Cryptovolans*, they are so similar that I suspect they are species of one genus, and they are referred to as sinornithosaurs. A number of good skeletons were published, but the feathers were not that well preserved. Yet I noticed that the central finger of these creatures were flattened and expanded at the base, the same way the fingers of birds are in order to streamline the hand while improving the support for the large primary feathers that make up the outer wing. *Archaeopteryx* lacks such finger expansion, so I rushed an appendix into *Dinosaurs of the Air* suggesting that sinornithosaurs inherited the modified finger from flying ancestors.

I was closer than I knew. In *Nature* a new sinornithosaur specimen was described which seemed to show big, asymmetrical flight feathers coming off the legs, but not the arms. Odd. After seeing the same specimen Stephen Czerkas concluded in *Feathered Dinosaurs and the Origins of Flight* that

the feathers were actually coming off the folded arm instead of the legs. He was half right. In the January 23rd *Nature* another complete skeleton showing fully developed flight feathers arrayed along both arms and legs solved the confusion. Because the outer arm and leg feathers are asymmetrical as in flying birds, there is no doubt their primary purpose was generating thrust and/or lift for flight.

The question is what kind of flight. Flight is merely progressing through the air by means of an airfoil; it includes everything from simple gliding through soaring to powered flight. In accord with conventional phylogenetics the *Nature* authors proposed that the Cretaceous dromaeosaurs were basal to the Jurassic initiated *Archaeopteryx*-modern bird clade, and



Tentative skeletal restoration of a generalized sinornithosaur. The arm could not actively be elevated fully vertically.

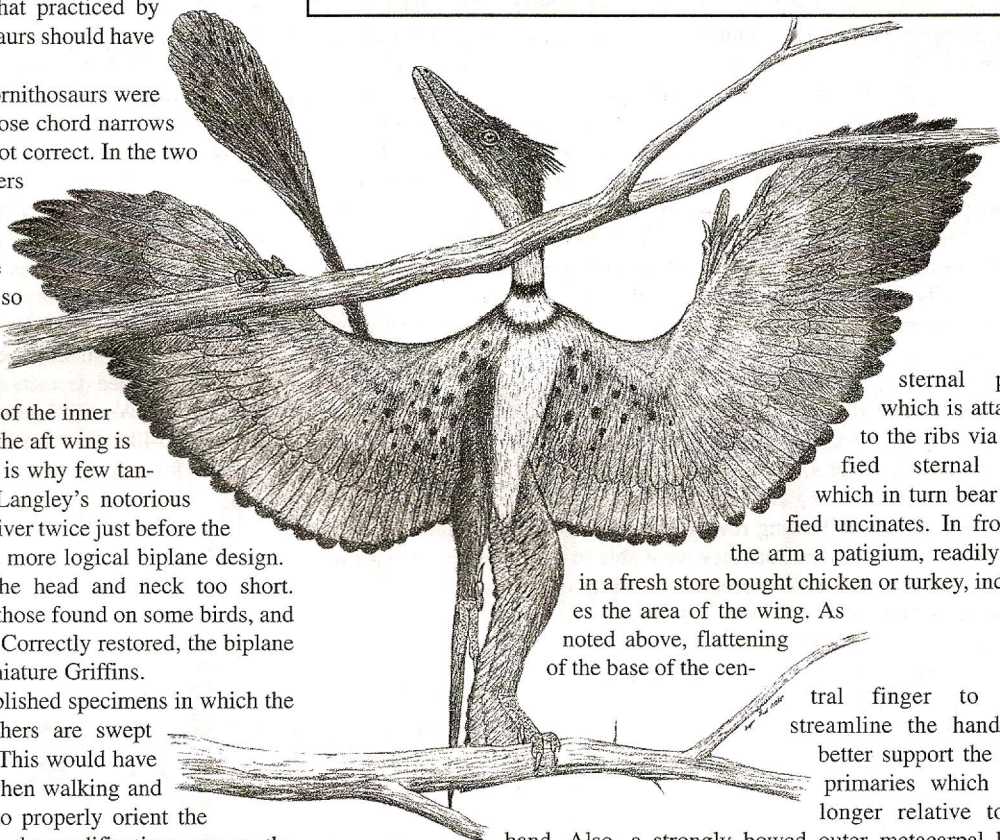
the Jehol taxa were gliders that represent a protoflight stage in the transition from classic dinosaurs to birds. But if the idea that dromaeosaurs achieved a level of flight more sophisticated than that practiced by *Archaeopteryx* is correct then the sinornithosaurs should have been well beyond the gliding stage.

Warning to artists. In *Nature* the aerial sinornithosaurs were restored with tandem arm and leg wings whose chord narrows strongly progressing proximally, but this is not correct. In the two published specimens in which the arm feathers are preserved, sediment damage obscures the length of the inner arm feathers, but in both cases the mid wing secondaries appear to be longer than the ulna, as is usual in birds. If so the forewing chord was probably fairly constant along the entire length of the wing in the typical avian manner. The proximal leg feathers are also very long. The broad chord of the inner wings are aerodynamically inefficient when the aft wing is in the turbulent wake of the fore plane. This is why few tandem biplanes have been built, one being Langley's notorious Aerodrome which ditched into the Potomac river twice just before the Wright Brothers pattered into the air with a more logical biplane design. The *Nature* restoration also shows both the head and neck too short. Pennaceous feathers formed a head crest like those found on some birds, and on some accidentally prophetic restorations. Correctly restored, the biplane sinornithosaurs are rather reminiscent of miniature Griffins.

One perplexing point is that in the two published specimens in which the foot feathers are well preserved, the feathers are swept strongly inwards relative to the metatarsals. This would have cleared the long feathers from the ground when walking and running, but would have made it difficult to properly orient the flight feathers in the airstream. The foot lacks the modifications seen on the flattened main finger to firmly anchor the primaries, and birds can use dermal muscles to erect feathers over much of their body. It is therefore possible that the foot feathers were mobile, and could be swept outwards relative to the foot when flying, and folded up when not. Sinornithosaur legs, particularly the feet, were much less streamlined than the arm with its flattened hand, and pelvic anatomy is not modified to support well developed flapping muscles. The feathers behind the thigh and shank also seem repositionable judging from differences in the three published legs, which are folded in one and not the other two. In other dinosaurs and birds a cylindrical femoral head prevents the legs from sprawling, and articulated *Archaeopteryx* specimens are consistently preserved on their sides. In a growing number of sinornithosaur skeletons the articulated legs are sprawled, and their femoral heads were spherical, a most unusual adaptation for a dinosaur that allowed the hindwing to be held horizontal. Elevation above horizontal is more questionable. In *Archaeopteryx* and sinornithosaurs the arm could be strongly elevated, but probably not as vertically as more derived birds.

Gliding is relatively simple and requires only a modest sized airfoil that can be held and manipulated in the airstream, even body flattening snakes can be good gliders. preavian protoflier gliders should be less well adapted for flight than *Archaeopteryx*, whose fully developed wings were proportionally large as those of modern birds, and had enlarged areas for flight muscle attachment and other skeletal adaptations suitable for a crude level of powered flight (see *Dinosaurs of the Air* for more details). More derived birds such as the Jehol confuciusornithids further improved powered flight with a set of adaptations still seen in modern fliers. Enlarged flight muscles are anchored upon a much larger

Living in the Jehol forests, *Sinornithosaurus* appears to have adapted for climbing. Compare to original version in *Dinosaurs of the Air*



sternal plate, which is attached to the ribs via ossified sternal ribs which in turn bear ossified uncinate. In front of the arm a patigium, readily seen in a fresh store bought chicken or turkey, increases the area of the wing. As noted above, flattening of the base of the cen-

tral finger to both streamline the hand and better support the outer primaries which were longer relative to the

hand. Also, a strongly bowed outer metacarpal better supports the inner fan of primaries. Under the pelvis is a strongly swept back distal end of the pubis that flattens and streamlines the body. Confuciusornithids didn't have them, but other advanced birds have alula feathers on the thumb which act as leading edge slots to help control airflow over the wing during slow speed maneuvers.

In no respect were sinornithosaurs less adapted for flight than *Archaeopteryx*, and they possessed all of the above advanced flight adaptations not found in the latter, except I'm not entirely certain that a patigium is present. Far larger than that of *Archaeopteryx*, the fused sinornithosaur sternal plate was almost as well developed as in the latter, while public retroversion and lengthening of the primaries was less extreme. Because both wings were equally big, the loading (wing area/mass ratio) of the arm wing alone was about the same in sinornithosaurs and *Archaeopteryx*, being in the middle of the avian range (see figure). Adding the leg wing doubles the wing area, placing the flying dinosaurs among the most lightly loaded soaring birds. Other flight features, such as retroversion of the coracoid and development of its acrocoracoid in the shoulder girdle, were as well developed as in *Archaeopteryx*, indicating a similar grade wing elevator complex. Although longer than that of *Archaeopteryx*, the dromaeosaur's tail with its ossified tendons was specialized for flight in the manner otherwise seen only in the long tailed rhamphorhynchoid pterosaurs, themselves sophisticated powered fliers. The flight adaptations of sinornithosaurs were much better developed than those seen in any glider, and were intermediate to those of *Archaeopteryx* on the one hand and confuciusornithids and rhamphorhynchoids on the other.

The phylogenetic hypothesis that dromaeosaur dinosaurs are more derived than *Archaeopteryx* is correspondingly supported, in

The biplane sinornithosaurs soon adapted for a fairly advanced level of flight, and may have engaged in aerial displays and combat using both sets of wings

which case basal birds mimicked pterosaurs by passing through a long-tailed pterosaur like grade of flight before adopting the more dynamic short-tailed version seen in pterodactyls and modern birds. The biplane form may represent a basal avian condition, or a dromaeosaur specialization. Less parsimoniously but definitely possible, basal dromaeosaurs may have evolved a sophisticated level of flight independent of the *Archaeopteryx*-modern bird clade, in the process becoming unique biplanes while converging with rhamphorhynchoid tail. In either case larger, shorter armed, and more derived, terrestrial dromaeosaurs such as *Dromaeosaurus*, *Bambiraptor*, *Deinonychus*, *Velociraptor* and even bigger bodied examples lost the ability to fly, at least in the adults. This means that features that most have viewed as adaptations (less correctly called preadaptations) for flight that originally developed for terrestrial predation - large brains, overlapping fields of vision, sternal plates, folding arms, pterosaur like tails, and complex pennaceous feathers - actually evolved in the context of flight and arboreality, some being retained for hunting on the ground. If this is correct, then it is a mistake to restore other small theropods with complex contour feathers; they may have been limited to simpler filaments.

Because the flight of *Archaeopteryx* and confuciusornithids is not observable, and because no living birds are biplanes, restoring sinornithosaur flight is difficult. Big heads bearing rows of serrated teeth, hook-clawed hands, and sickle-clawed toes indicate they were able to dispatch prey as large as or larger than themselves. The presence of wings on even the legs indicates that aerial and arboreal habitats were frequented more often than terrestrial environs, and this is compatible both with the long grasping fingers and toes with their large claws, and with the heavily forested nature of the wet, lake dominated Jehol habitat. When power flying with the arm wings, presumably over modest distances considering the grade of flight adaptation, the less streamlined legs may have been folded out of the airstream. If the leg wings did not produce too much drag they may have been deployed to allow lightly loaded soaring in search of prey over longer distances. In this case the fore and hindwings can be envisioned as forming a shallow X with a few degrees of dihedral and anhedral respectively to clear the aft set from wake turbulence. When diving upon prey whether the latter be in the air (birds and pterosaurs), trees (more birds and pterosaurs as well as mammals and lizards), or on the ground (including such small dinosaurs as caudipterygians and psittacosaurids), the hindwings could be employed as auxiliary control surfaces whose lift and drag compensated for the lack of greater aerodynamic sophistication of the forewings seen in modern raptors. The sinornithosaurs' inflight ability to transform between monoplane and biplane configurations is reminiscent of the pre-WW II Nikitin-Sevchenko IS-1 experimental fighter, which could fold the lower wing into the upper to improve speed, and extend the lower wing for take-off, landing, and extra maneuverability during dogfights. Not practical with our crude 20th century machines, it worked for flying dinosaurs. The leg wings could have also been used for display as well, but the same is true of the forewings as they are in many birds, and neither set evolved for this purpose.

Being relatively derived fliers, the sinornithosaur's do not provide direct evidence of the earliest stages of dinosaur-avian flight, although their arboreality is compatible with a

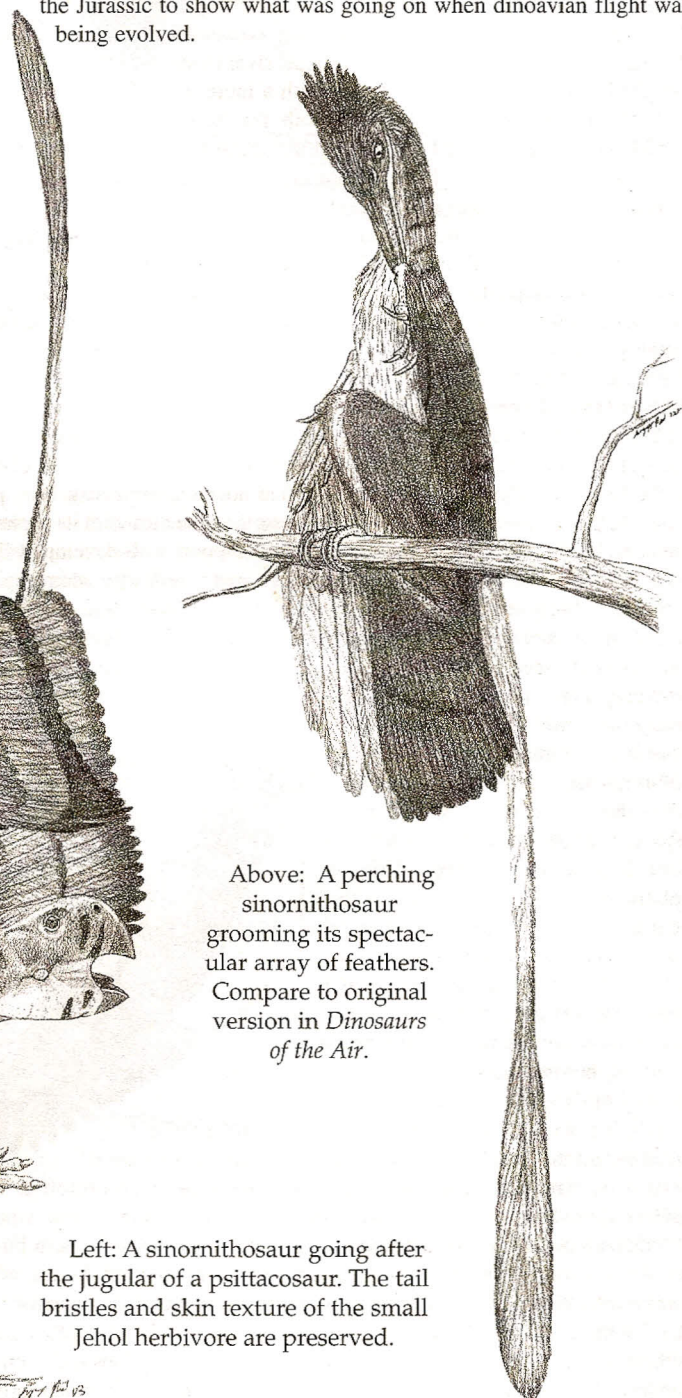
strong climbing component to its origin.

Dromaeosaur like teeth found in the Jurassic are similar in size to those of sinornithosaurs, hinting that their style of aerial hunting first appeared at the middle of the Mesozoic, while the presence of small bodied, big armed, sickle-clawed, long tailed Late Cretaceous

Rahonavis suggests it continued to the end of the era, when it disappeared in the general K/T extinction. Oh well.

In a phylogenetic panic in the face of dromaeosaurs with fully blown feather wings, some in the anti-dinosaur camp are starting to claim that the same dinosaurs they have spent so much time denying are relatives of birds, are instead birds not at all related to dinosaurs after all! The basic policy is that if a fossil has unambiguous feathers on it, it's a bird and not a dinosaur. The flying dromaeosaurs may have been birds even more than *Archaeopteryx*, but they were also true dinosaurs. Sinornithosaurs can be viewed as the hawks of our time, perching in trees waiting for something to come by, or patrolling in the air on one or two pairs of wings depending upon the aerodynamic situation, then diving upon their hapless victims, using their strange leg wings to control the last seconds of the attack, then using the sickle claws to lethally wound the prey. They may have operated alone or perhaps in small packs of the air.

The Jehol lake bed deposits are hyperproductive, immense, and have barely been tapped. We will be learning a lot more about flying dromaeosaurs and other bird-like dinosaurs. What we now need are similar deposits from the Jurassic to show what was going on when dinoavian flight was being evolved.



Above: A perching sinornithosaur grooming its spectacular array of feathers. Compare to original version in *Dinosaurs of the Air*.

Left: A sinornithosaur going after the jugular of a psittacosaur. The tail bristles and skin texture of the small Jehol herbivore are preserved.