

Evidence That '4-Winged' Paravian Dinosaurs May Have Used Hindlimb Feathers For Brooding

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ABSTRACT

Recent fossil discoveries have revealed a substantial number of theropod dinosaurs possessing feathers of various forms on their hind limbs, including some specimens with long, pennaceous, 'wing' feathers on their tibiae and tarsi, similar to the flight-capable primary and secondary feathers of birds. Several investigators have proposed that these leg feathers may have had roles in flight in some species, or in gliding, and have suggested models of '4-winged' flight or gliding locomotion. However, as we first pointed out in 1998, pennaceous feathers in modern birds and non-flying dinosaurs can rationally be ascribed brooding, as well as flight functions. Here we present evidence gleaned from our studies of a number of fossils that possess hind-limb feathers, as well as two examples of nesting *Citipati*. Taken together, these fossils allow us to develop a model of brooding postures that make use of pennaceous hindlimb feathers to cover and incubate eggs and hatchlings. In the case of *Citipati*, two well preserved individuals sitting on nests with large egg clutches (IGM-100/979, IGM-100/1004) clearly demonstrate a lack of complete coverage of the eggs by the animals' bodies and limbs. We previously showed that pennaceous feathers would have aided the coverage of eggs near the ulna and manus. We also noted a deficiency of egg coverage at the rear quarters laterally adjacent to the pelvis and tail. Here we demonstrate how pennaceous feathers, recently described on the tibiae and tarsi of several non-flying theropods and some primitive birds as well, could have served very effectively to cover eggs in these rear quarter positions. In recent literature, considerable attention has been given to possible flight-related or visual display related functions for hindlimb pennaceous feathers, while their nest-covering capabilities have been neglected. As with forelimb feathers, we conclude that pennaceous hindlimb feathers could have evolved primarily for the purpose of brooding, without requiring selective pressure for other uses such as flight or display. Hopefully our observations will bring a better balance to the understanding of potential functions of hindlimb feathers in non-flying, ground-dwelling, bipedal dinosaurs, and perhaps in primitive birds as well.

INTRODUCTION: THE BROODING-TO-FLIGHT HYPOTHESIS

The original proposal of our 'Brooding-to-Flight' concept was presented at Dinofest 98. We used fossil evidence from nesting oviraptorid dinosaurs, combined with observations of modern bird brooding behavior, to establish the concept that feathered dinosaurs may have developed wing-like forelimb feathers in order to enhance brooding success (Hopp and Orsen, 2004). Figure 1, taken from that publication, illustrates the central concept that slow, incremental, evolutionary lengthening of pennaceous feathers along the rear edge of the ulna and manus would have been advantageous at every stage of lengthening, to provide improved coverage for eggs within a nest, or to cover nestlings once they were hatched. This idea provided an alternative to the two competing theories of wing evolution at the time, the Arboreal Theory, in which animals leaping from trees evolved wing feathers for improved gliding, and the Cursorial Theory, in which ground-dwelling bipedal dinosaurs evolved wing feathers to help them remain airborne when they leapt upwards. The preponderance of fossil evidence supports the cursorial nature of bird predecessors, but neither theory has been unequivocally proven, and neither theory rules out our brooding-to-flight concept.

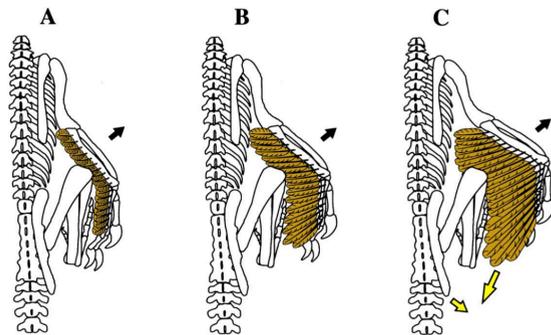


Figure 1. Incremental wing feather lengthening. The skeleton of a nesting *Citipati* was used to illustrate wing feather evolution from a hypothetical short-feathered ancestor (A) through an intermediate stage (B) to the final posture in the *Citipati* fossil (C). As the feathers lengthened through a series of mutations, the forelimb was able to move outward (solid arrows) to cover larger broods. The yellow arrows, however, indicate an area at the rear quarter where coverage of the nest would have remained inadequate.

One observation that tends to validate our hypothesis is modern birds' dual use of wing feathers for both flight and brooding (reviewed thoroughly in Hopp & Orsen, 2004). Our innovation was simply to suggest that the order of evolution was brooding first and flight second. This theory has met both support and disagreement but perhaps most tellingly, Dr. John Ostrom, the original proponent of birds evolving from theropod dinosaurs, stated that our idea filled the last hole in his theory (Ostrom, 1998, personal communication). The three panels in Figure 1 illustrate the gradual evolutionary lengthening of pennaceous feathers on the ulna and manus. However, they also illustrate a problem we noted at the time. In panel C, arrows at the rear quarter indicate that there was apparently no way to shelter eggs laid in that sector, and yet *Citipati* and other oviraptorids laid eggs all the way around the circumference of their nests.

REVISING THE THEORY BASED ON NEW FOSSILS

A two-species model. Since 1998 a significant number of new theropod dinosaur fossils with preserved feathers have been described, including some with extensive feather coverage on their hindlimbs. To explore the relationship between these leg feathers and brooding, we pursued a modeling strategy based on the best available fossil evidence: the exquisitely preserved fossils of the oviraptorid *Citipati* on its nest, and the finely preserved feathers of early birds and paravian dinosaurs like *Microaptor*. It would have been preferable to use the feathers and nests of the same species, but to date there have been no discoveries of *Citipati* feathers, nor *Microaptor* nests. Nevertheless, many new fossils of feathered theropods and early birds have been described, and some of these newer fossils provide excellent data to answer our question regarding the rear quarter. In particular, those theropods described as 'four-winged' animals represent, to us, the answer to the rear-quarter brooding issue. Conceivably, the hindlimb 'wings' of 'four-winged' theropods may have had nothing to do with flight or gliding but were a response to evolutionary selective pressure to improve coverage of eggs or hatchlings at the rear quarter of the nest.

FEATHER VARIATIONS AMONG FOSSIL BIRDS AND DINOSAURS

With the concepts above in mind, we considered the evidence in the fossil record of feather variations among ancient birds as well as theropod dinosaurs, as to the evolution of form and function in hindlimb feathers.

Sapeornis. Figure 2 shows a fossil of *Sapeornis*, an advanced Cretaceous avialan with 'wings' on its hindlimbs (Zheng, 2013). These feathers were described as pennaceous, and stiffened by quill shafts that enabled them to point in the required direction(s) for their use(s). Other fossils with large forelimb wings led to suggestions these feathers were used to assist in thermal soaring (Serrano, 2017) or as ornaments for display (O'Connor, 2015). However, we suggest brooding could have been their primary purpose, because their form and location are ideally suited for sheltering eggs or hatchlings at the rear-quarter gap shown in Figure 1.

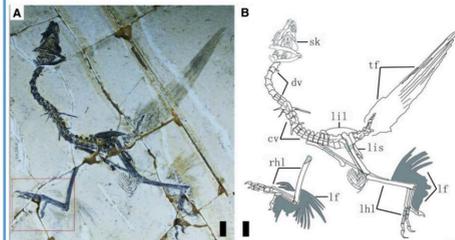


Figure 2. *Sapeornis*, a feather-footed avialan. (A) The prepared fossil, showing traces of hindlimb feathers. (B) The authors' interpretation of skeletal and feather elements of the fossil; tf, tail feathers; lf, leg feathers.

Figure 3. *Pelopenna*, a feather-footed maniraptoran.

Although most of this fossil is missing, the feathers radiating from the metatarsus create a fan that would have been ideal for covering eggs or hatchlings in a nest. Panel (a) is the prepared fossil; (b) diagram of the bones and feathers (grey areas); (c) microscopic view of the inset from (b); (d) diagram of pennaceous feather forms identified in (c).

***Pelopenna*.** Xu and Zhang (2005) described a fossil of an isolated maniraptoran theropod foot with extensive pennaceous feathers on the metatarsus (Figure 3). They noted the presence of rachi, rami, and hooklets diagnostic of pennaceous feather structure, and also an additional layer of shorter feathers superimposed on the longer ones, analogous to covert feathers overlapping the primary and secondary feathers on the wings of birds.

***Microaptor*.** Many well-preserved fossils of the dromaeosaurid, *Microaptor*, possess pennaceous feathers on both fore- and hindlimbs. Figure 4 shows an example of one such fossil, which, along with others, has led to life restorations of the animal as a four-winged glider or flyer (Xu, 2003; Li, 2012). However, the means by which these 'wings' would have assisted in flight remains a matter of debate (Dyke, 2013; Li, 2012).



Figure 4. *Microaptor* fossil with hindlimb feathers. The fossil shows traces of both forelimb and hindlimb pennaceous feathers (white arrows). Hindlimb pennaceous feathers originate on both the tibiotarsus and metatarsus. Black arrows indicate areas where feather impressions were obliterated during preparation of the bones.

BROODING BY FOUR-WINGED DINOSAURS

***Microaptor* as a brooder.** In Figure 5 we consider the brooding capabilities of the four wings of *Microaptor* on a hypothetical nest. Starting from the published restoration of *Microaptor* as a four-winged glider (Li, 2012) we have adapted the posture only slightly to demonstrate how the four wings could have combined very adequately to cover a nest of eggs arranged similarly to those in a well-preserved oviraptorid nest fossil (Wiemann, 2017). The shape and placement of the hindlimb wings seem ideally suited for covering eggs at the rear quarters. While *Microaptor* nests remain undiscovered, nests of the closely related *Troodon formosus* are quite similar to those of oviraptorids (Varricchio, 1997; Tanaka et al., 2018). Therefore it is reasonable to assume that *Microaptor* nests were also similar to these known specimens.

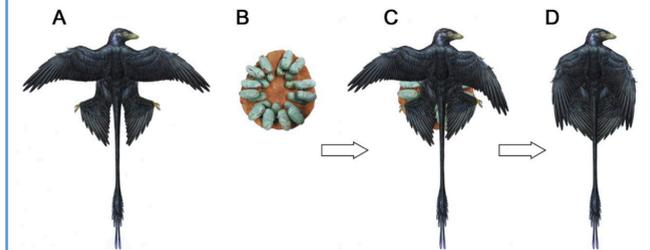


Figure 5. Gliding vs brooding *Microaptor*. Panel A is Ellison's restoration of *Microaptor* in a gliding posture based on compiled data from eight individual *Microaptor* fossils (Li, 2012). Panel B is a fossilized clutch of *Heyuannia luangi* oviraptorid eggs (Wiemann, 2017). The nest has been resized to match *Microaptor*'s smaller body for modeling purposes. Panel C, *Microaptor* settling onto the nest. Some eggs are still partially exposed. Panel D, *Microaptor* fully settled onto the nest. Note that the overlap of tail, hindlimb feathers, and forelimb feathers makes a complete cover to shelter the eggs. To make this figure, the pennaceous feathers illustrated by Ellison were rotated into position without altering their proportions as shown in Panel A.

Tanaka et al. also compared fossil nests of different oviraptorids and concluded that the animals' weight was born in the center of the nest, and that smaller species placed their feet inside while larger species may have rested only the pubic boot in the empty center of the nest to avoid crushing the eggs. Given this 'feet-inside' orientation for small animals, it would have been physically impossible for *Microaptor* to sit within a nest without covering eggs with its hindlimb feathers. Hence, evidence for hindlimb feather use in brooding is equally plausible to evidence for four-winged flying models, which invoke observable climbing, leaping, flapping, or gliding behaviors. On the other hand, the notion that *Microaptor*'s hindlimb feathers were involved in nesting is supported simply by observed fossil nest shapes and observed locations of its fossilized pennaceous feathers.

FOUR-WINGED DINOSAURS—A NEW MODEL BASED ON NEW EVIDENCE

With the preceding concepts in mind, we sought to gain more insight into the evolution of form and function in hindlimb feathers by looking at detailed models. Figure 6 schematizes the forelimb and hindlimb feathers of *Microaptor* using a color spectrum to aid interpretation (but not to imply such colors existed on *Microaptor*, which has been proposed to have solid black and/or iridescent coloration).

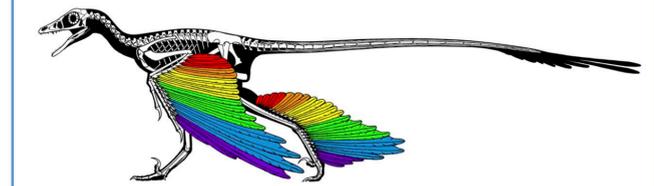


Figure 6. Schematic of *Microaptor*'s pennaceous feathers in color. Note that the colors are arranged similarly on the fore- and hindlimbs, with red and orange proximally on the ulna and tibia, yellow and green at the wrist and ankle, and blue and purple on the manus and pes. The skeletal restoration used here is a slight modification of the accurate skeletal profile created by Scott Hartman (2015). The rainbow color scheme on fore- and hindlimb feathers is used again on *Citipati* in Figure 7 for the purpose of comparison.

RE-EXAMINING CITIPATI NEST FOSSILS

Figure 7 updates our original model (Figure 1), of a feathered brooding *Citipati*, to include hindlimb feathers filling the gap at the rear quarter. The skeletal model is based on the posture of two nesting *Citipati* (Norell, 1995; Norell, 2018). Although neither *Citipati* fossil preserved any trace of feathers, feather occurrence on the forelimbs of the basal oviraptorid *Caudipteryx* (Ji, 1998) strongly suggests their presence. No fossil evidence is known for hindlimb feathers in an oviraptorid (thus far), but we place them there in the interest of modeling their applicability to brooding. Clearly, if such feathers existed on *Citipati*, they would have been well suited to cover eggs or hatchlings at the rear quarter of the nest. The combination of the feathered 'lid' over the nest, with the animal's body heat (or cooling) suggests the eggs were incubated in an efficient, temperature-controlled environment, in which both fore- and hindlimb feathers played crucial roles. This in turn provides a rationale for the entire evolutionary development of pennaceous feathers on fore- and hindlimbs, without invoking either flight or gliding at any stage in the process.

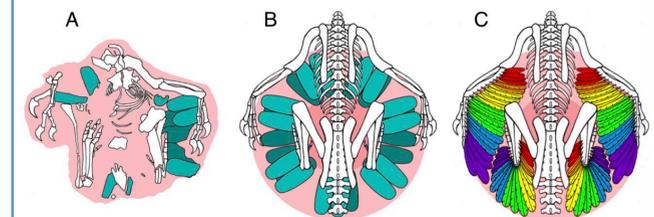


Figure 7. *Microaptor*'s feathers applied to a nesting *Citipati*. The rainbow color scheme is the same as *Microaptor* in Figure 6, but the feathers are superimposed on the *Citipati* skeleton. Panel A traces the outlines of the fossilized bones and eggs of *Citipati* 'Big Mama' (Norell, 1995). Panel B is a restoration of the skeleton and completion of the clutch of eggs based on both 'Big Mama' and 'Big Auntie' (Norell, 2018). The pink ring under the animal in B and C emphasizes the location of the eggs in a nearly symmetrical ring. Panel C demonstrates how *Microaptor*-like forelimb and hindlimb feathers would combine to completely cover the ring where the eggs were located. Slight gaps are left for clarity in C, but it is understood that slightly longer feathers would have created overlaps to completely seal the nest.

ACKNOWLEDGMENTS AND CONTACT INFORMATION

In memory of John Ostrom, with gratitude for his personal support of our brooding-to-flight hypothesis at the time of its original publication.

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Web address to download this poster and/or a copy of our previous brooding-to-flight paper: (Hopp & Orsen, 2004): <http://thomas-hopp.com/THscience4.html>



GENETICS OF FEATHER-FOOTED BIRDS



Figure 8. Ice Pigeon breed of *Columba livia*. The animal possesses both forelimb and hindlimb wings, not unlike some dinosaurs and early birds. This breed dramatically illustrates the power of the *Pitx1* and *Tbx5* loci, which can impose this phenotype onto a wild-type, scale-footed pigeon in two generations. Conceivably, such radical alterations of phenotype could have occurred many times among various lineages of paravian dinosaurs, and early avians as well. Photo credit: Graham Manning, Wikimedia.

Rapid gain and loss of feather-footed phenotypes. Research into modern bird genomes yields insight into mechanisms by which scales on legs and feet can interchange with pennaceous feathers on birds, and presumably their paravian dinosaur ancestors. Domyan & Shapiro (2017) reviewed the recently-sequenced genome of the rock dove, *Columba livia*, which includes a variety of domestic breeds like the Ice Pigeon (Figure 8). Molecular genetic studies have shown that mutations at just two limb-bud regulatory loci, *Pitx1* and *Tbx5*, can alter leg scales into pennaceous feathers in the Ice Pigeon and other similar breeds. The underlying mutations do not simply alter the fate of individual epidermal placodes as was once thought, but instead alter hindlimb identity itself. In F2 laboratory crosses, genetic markers for *Pitx1* co-segregate with the extent of feather coverage on the foot while *Tbx5* co-segregates with the feather length. Inter-species comparisons suggest these gene loci were present in the dinosaurian predecessors of birds and therefore could have played roles in the variation of hindlimb feather patterns seen in paravian dinosaur fossils. Furthermore, the ease with which these mutations alter scaled feet into feathered hindlimbs suggests that mutational variations of hindlimb feathers could have arisen many times during the tens of millions of years of feathered theropod evolution.

Plasticity of hindlimb wing feathers. While the fossil record offers little evidence why hindlimb feathers were lost in most bird lineages, we suggest that, as forelimb feathers lengthened sufficiently for flight in volant paravian dinosaurs and early birds, they superseded hindlimb feathers for covering the rear quarters of nests. Referring to the yellow arrows in Figure 1, it is likely that as primary wing feathers lengthened they projected farther into the rear quarter area, making hindlimb feathers redundant for brooding. Released from selective pressure, foot and shank feathers were free to interchange with scales by rapid mutations of *Pitx1* and *Tbx5*. This in turn allowed hindlimbs to revert to the efficient scaly running legs of their cursorial dinosaurian ancestors, or to evolve other specialized functions like perching, paddling in water, or grasping prey without the hindrance of feathers. Alternatively, some present-day hawks and owls retain feathers on their shanks or feet, demonstrating the continuing diversity of hindlimb feather patterns.

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