Scansoriopteryx nestlings by Stephen A. Czerkas

AN ARBOREAL MANIRAPTORAN FROM NORTHEAST CHINA

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Abstract

The small skeleton of a juvenile saurischian resembling a theropod with maniraptoran characters, including a semilunate distal carpal block, is described as an arboreal precursor to birds. Although most closely allied to *Archaeopteryx*, numerous characters throughout the skeleton reflect a more basal developmental stage. The manus is equipped with a robust, hypertrophied third digit unprecedented among the Saurischia. This specimen represents a previously unknown lineage of arboreal dinosaurs which sheds new insights for interpreting the origin of birds as well as theropod dinosaurs.

INTRODUCTION

INTERPRETATIONS REGARDING the origin of birds have been intensely divided by speculating that the ancestral form which led towards Aves was either a terrestrial dinosaur (Gauthier and Padian, 1984; Ostrom, 1976), or an arboreal archosaur (Bock, 1986; Feduccia, 1996; Martin, 1991). Proponents of the cursorial theory have maintained that the evolution of flight among birds could not have taken place within an arboreal environment by excluding dinosaurs as having been terrestrial animals incapable of climbing. In similar fashion, but reaching a different conclusion, the proponents of the arboreal theory have dismissed dinosaurs as being ancestral to birds for the same reason of not being able to climb. Supporters of the arboreal theory suggest that the ancestors of birds must be non-dinosaurian archosaurs which would have evolved from an unknown basal archosaur (thecodont), and as such the similarities found between birds and dinosaurs are regarded as convergent rather than directly inherited (Feduccia, 1996). Detractors of the non-dinosaurian ancestry of birds claim that *Archaeopteryx* was primarily a terrestrial animal with little or no capability of flight (Burgers and Chiappe, 1999; Chiappe, 1995; Gauthier, 1986; Ostrom, 1974; Padian and Chiappe, 1998). Therefore, according to this interpretation, the evidence from the fossil record does not support the theory of pre-avian arboreal archosaurs existing or playing a role in the origin of birds. However, fossils of arboreal reptiles from the Mesozoic are extremely rare, and their lack of discovery may be due to preservational biases instead of their actual nonexistence. Also, the physical characteristics that might demonstrate an arboreal ability are not always self-evident or unequivocal, resulting in critics of the arboreal theory to have claimed that there is no "evidence" to demonstrate that climbing played a role in the evolution of flight (Ostrom, 1986). Furthermore, the application of cladistics, or phylogenetic analysis, has generated a broad consensus in accepting birds as being derived from theropod dinosaurs, notably from within the Maniraptora (Gauthier, 1986). The specimen described below challenges the popular and widely held dogma of a dinosaur/bird relationship by presenting the strongest evidence discovered so far that the ancestors of birds were uniquely adapted for an arboreal lifestyle involving the ability to climb. Whether one considers this animal to be a theropod, or a basal saurischian of pre-theropod status depends on the interpretation of unique characters which must have been retained either from the primitive state prior to the development of theropods, or from arboreal theropods that mimic the ancestral condition. Still, regardless of how these characters are considered, it does not change the outcome that such an animal appears to represent, not only a precursor to the earliest known bird, *Archaeopteryx*, but also that the ancestors of birds lived among the trees.

SYSTEMATIC DESCRIPTION

Archosauria Cope 1869
Saurischia Seely 1887
Maniraptora Gauthier 1986
Scansoriopterygidae, fam. nov.
Scansoriopteryx heilmanni, gen. et sp. nov.

The systematic description of *Scansoriopteryx* depends upon whether certain characters are considered as truly plesiomorphic, or as derived reversals that only resemble primitive conditions secondarily. The main distinction between the two interpretations is that *Scansoriopteryx* was derived either from a pre-theropod saurischian ancestor, or from a theropod. The first scenario suggests that the ancestral forms which led to *Scansoriopteryx* were basal saurischians from the Middle Triassic, or earlier, before theropods had appeared. The second option would suggest that *Scansoriopteryx* appeared much later in time from a theropod lineage which, in becoming arboreal, developed massive reversals secondarily resembling primitive characteristics. The basal saurischian relationship is seen here as being the more parsimonious interpretation.

ETYMOLOGY

Scansoriopteryx means "climbing wing", *Scansori-* from scandere (Latin) for "climb", and *-pteryx* (Greek) for "feather, wing"; *Heilmanni*, in honor of Gerhard Heilmann, the pioneer of avian paleontological studies who championed the concept of birds being derived from an arboreal ancestry.

DIAGNOSIS

Scansoriopteryx heilmanni is the only known saurischian, or theropod, which has the third digit of the manus elongated to nearly twice that of the second digit. *Scansoriopteryx* closely resembles *Archaeopteryx*, but differs in the following: a definite contact between an elongate ventral process of the postorbital and the ascending process of the jugal; the lower jaw is equipped with a large fenestra; the tail has a greater development in the articulation of the zygapophyses. The pelvis is similar to that of *Archaeopteryx* in having the same number of sacrals and general shape of the ilia, but differs in having a small, unexpanded pubic peduncle; a significantly short pubis which is not retroverted; longer ischia; and an acetabulum which is not entirely perforated. Also unlike *Archaeopteryx*, the posterior end of the scapula is expanded; separate clavicles are present instead of a furcula; and the foot is more capable of perching as indicated by its having a longer hallux, and the reduced lengths of the middle phalanges in digits III and IV of the pes.

DISCUSSION

In April, 2000, at the Florida Symposium on Dinosaur/Bird Evolution presented by the Graves Museum of Archaeology and Natural History, the fossil of *Scansoriopteryx* was initially presented as an "arboreal theropod". However, this terminology is an apparent contradiction in terms as according to definition, "theropods" do not climb. Also, according to Gauthier (1986), theropods are united as a group by having the second digit of the manus as being the longest. Since the third digit in the manus of *Scansoriopteryx* is much longer than the second, it must either represent a highly derived specialization from that of typical theropods, or must represent a pre-theropod status. The combination of the third digit having a more elongate and robust third metacarpal; together with phalanges that become progressively shorter distally, as well as the numerous primitive characteristics throughout the body collectively suggest that these are not aberrant reversals but reflect true plesiomorphic conditions. Therefore, *Scansoriopteryx* is more parsimoniously regarded as being a saurischian of "pre-theropod" status, instead of as a true theropod.

While *Archaeopteryx* has remained the most primitive, basal bird known to Science for the past 140 years, there has been considerable debate and at times heated controversies as to what the precursor of *Archaeopteryx* was like and how the evolution of avian flight began. *Scansoriopteryx* most closely resembles *Archaeopteryx* in its number of caudal vertebrae, basic structure of the tail, sacral vertebrae, shape of the ilia, the length of forelimb, and general morphology of the skull. The most significant differences between the two animals are characters which would ordinarily be considered as primitive.

However, this determination is complicated by the ontogenetic level of the animal which appears to be that of a nestling perhaps only two to three weeks of age. Whereas it is well known that primitive characters in the structure of the shoulder complex and forelimbs associated with flight development are often retained in the early ontogenetic stages of extant birds, these seemingly ancestral traits are lost during the normal growth of modern birds, or secondarily retained among flightless forms (Olson, 1973). Therefore, while it is conceivable that some of the primitive characters found in *Scansoriopteryx* might reflect its ancestral condition, these characters might have continued to develop during its maturity. On the other hand, it is also plausible that the primitive characters of *Scansoriopteryx* are not simply reflective of a juvenile stage in being undeveloped and actually were retained throughout the life of the animal. Only the discovery of a fully mature specimen may resolve this issue.

Nonetheless, unlike that in *Archaeopteryx*, the pubis is not only directed forward as in saurischians, but it is also remarkably reminiscent in its short length and proportions to that of thecodonts like *Marasuchus (= Lagosuchus*). In addition, the acetabulum is not as fully perforated as in any known theropod; the ilia are widely set apart; and the pubic peduncle is very small and unexpanded which are all consistent with being extremely primitive compared to theropods. While the rod-like clavicles are separate and it could be argued that this is a reversal from being a true furcula, as seen in ratites, there is no such analogy for interpreting the expanded caudal end of the scapula as being a reversal. Instead, the flared end of the scapula once lost in birds remains slender and unexpanded even among flightless forms. This signifies that the scapula of *Scansoriopteryx* is truly more primitive than that of *Archaeopteryx*, and that the short coracoid and separated rodlike clavicles are more likely to be plesiomorphic and not reversals, or the result of neoteny.

Especially revealing towards the possible functions of the forelimbs is that in spite of the juvenile status of *Scansoriopteryx*, its elongate forelimbs are inconsistent with those of modern day hatchlings of birds which initially have smaller forelimbs than the hindlimbs. This suggests that both the forelimbs and hindlimbs were crucial in the locomotion of *Scansoriopteryx*. And though clearly incapable of powered flight, the length of the forelimbs must have provided a necessary function even at this early stage of development. Furthermore, the anisodactyl structure of the pes is well adapted for perching and an arboreal lifestyle more so than *Archaeopteryx* or any dinosaur. Also, the stiffened tail may also have been used as a tail prop (Chatterjee, 1997) much like the stiff rectrices of trunk-climbing birds such as woodpeckers (Picidae), creeper (Certhiidae) and wood creepers (Dendrocolaptidae). Altogether, these adaptations in conjunction with the unique characters of the manus, demonstrate that *Scansoriopteryx* was better equipped for climbing than any previously known theropod.

Comparison with any animals that have hands which even vaguely resemble the disproportionately elongated digits seen in *Scansoriopteryx* all indicate that climbing was surely possible. As can be seen in the manus of the extant iguanid, *Corytophanes*, the total length of digit III is longer than digit II. But compared to that of *Scansoriopteryx*, the proximal phalanges of

Corytophanes are shorter than the penultimate phalange, which is a parallel development to that of all theropods except *Scansoriopteryx*. It is significant to note that without such a reduction of the proximal phalanges, the proportional length of this digit would be essentially that of *Scansoriopteryx*. Altogether, this demonstrates that just as shorter digits correlate towards being adapted to a more terrestrial lifestyle, the elongated third digit of the manus in *Scansoriopteryx* is all the more ideally suited for climbing in conjunction with the disproportionate lengths of the first two digits.

Similar displacement of the claws can readily be found among the most arboreal members of various iguanas and agamids which also have elongated third (and fourth) digits. This disproportionate length of the digits further insures a strong grip and greater likelihood of catching onto widely spread branches or irregular surfaces.

Seeing as how extant birds such as the baby *Hoatzin* are equipped with only two clawed digits on their manus and are capable of climbing, it would be without merit to suggest that *Scansoriopteryx* could not have climbed as well, or even better having had the advantage of the elongated third digit.

The evidence of such an unequivocal arboreal theropod is unprecedented and presents an irreconcilable paradox to the cursorial theory of the origin of birds. Phylogenetically, this remains a major contradiction to current analyses regardless of whether the arboreal adaptations are considered plesiomorphic or highly derived. Either way, *Scansoriopteryx* strongly supports the theory that the origin of birds and avian flight came from the "trees down".

Scansoriopteryx does not appear to have been capable of flight even though its forelimbs are comparable in length to the wings of *Archaeopteryx*. The shoulder girdle is incompletely known, but no derived adaptations indicating the ability of flight are discernible, and the separate clavicles indicate that *Scansoriopteryx* could not fly even as well as *Archaeopteryx*. While neither fully volant or strictly terrestrial in its habits, *Scansoriopteryx* appears to represent the arboreal "Proavian" stage of bird origins of which Heilmann (1927), Abel (1911) and Osborn (1900) speculated upon so long ago. To what extent *Scansoriopteryx* could have leapt about, or even glided amid its arboreal setting would be highly conjectural. However, since other arboreal reptiles living today demonstrate considerable feats of leaping from branch to branch, or tree to tree, it is wholly plausible that *Scansoriopteryx* was capable of leaping and perhaps gliding.

Scansoriopteryx is clearly more primitive than *Archaeopteryx* in many respects such as its saurischian-style pelvis which has remarkably short pubes; elongate and robust ischia; and comparatively small pubic peduncles. These primitive features further suggest that the nearly closed acetabulum is not a reversal, but a true plesiomorphic condition.

When *Sinornis* was discovered, it created the impression that the avian pes became adapted for perching sometime not long after *Archaeopteryx* (Sereno, 1992). This was also in accord with the popular "ground up" concept of birds origins. However, as with *Sinornis*, the pes of *Scansoriopteryx* is also clearly that of a perching animal although not one which could fly. This suggests that perching in an avian manner appeared before *Archaeopteryx* and not as a result after the development of more advanced flight abilities occurred. In the case of *Archaeopteryx*, its pes may reflect the adaptive changes towards becoming more cursorial instead of becoming more arboreal. Since the tendency of birds becoming flightless is so prevalent, becoming more terrestrial could have existed any level within the evolution of birds from anytime after *Archaeopteryx*, or even before. In this context, the origin of the split first metatarsal among theropods may well be attributed to having been derived from arboreal ancestors that were capable of perching but which may not have become volant to any degree (Olshevsky, 1992). Whether initially volant or not, the more cursorial descendants would have lost the adaptations for perching such as having shorter mid-phalanges and a reversed hallux. The pes of *Scansoriopteryx* tends to support this speculation that all true theropods are derived from ancestors which were arboreal.

The down-like integumentary impressions preserved around parts of the skeleton, and especially around the forearm and manus suggest that a more fully grown *Scansoriopteryx* may have had more fully developed flight feathers of some sort which may have aided it while leaping and gliding. Whether or not these would have been as asymmetrical as in fully volant birds remains unknown, but hopefully the discovery of an adult *Scansoriopteryx* might someday confirm this speculation. Still, since the wrist of *Scansoriopteryx* was equipped with a distinct semilunate carpal, this indicates that the movements of the hand would have been essentially like that of a bird-like fashion and any feathers extending from the manus would have been beneficial in the balance and steering of the animal while gliding or jumping. There is a clearly progressive relationship between the evolution of the unique restriction of movement of the avian wrist and the benefits derived from it, (Vazquez, 1992; Czerkas and Xu, this volume) which the cursorial theory does not sufficiently account for. However, as an arboreal glider even at the most basal development as seen with *Scansoriopteryx*, the avian motion of the wrist would have enabled it to steer and balance itself essentially like a bird through the forces of air resistance, though not with the high degree of efficiency seen in modern birds.

While *Scansoriopteryx* represents an arboreal precursor of *Archaeopteryx*, in essence it also represents a "proto-maniraptoran". This suggests that dromaeosaurs and other maniraptors are derived from arboreal ancestors which had already achieved the ability to glide or possibly fly at least to some extent. Therefore, the primitive semilunate wrist articulation evolved in concert with the gliding, incipient stages of becoming volant and need not be treated as being either inexplicable or due to evolutionary influences unassociated directly with flight.

It is well known that within Aves, there is a strong tendency of becoming secondarily flightless as demonstrated by the fossil record (Feduccia, 1996) and by studies of extant birds (Olsen, 1973). This tendency of losing the ability to fly has not been widely acknowledged or studied in any great detail with regards to Mesozoic birds or bird-like dinosaurs. That there may well be a connection to certain theropods as being secondarily flightless was suggested by Greg Paul (1988), but with little notice. And though largely ignored, this tendency of becoming more terrestrial must have been possible, if not likely, to have occurred over time among the arboreal ancestors such as *Scansoriopteryx* and basal birds (Olshevsky, 1992; Paul, 2002). As such, this would account for the primitive avian characters found among maniraptorans and other "bird-like" dinosaurs in a more parsimonious manner than the cursorial theory, or how current phylogenetic analyses are structured (Padian, Hutchinson and Holtz, Jr., 1999).

Regardless of whether the hypertrophied third digit is considered a highly derived reversal, or as a plesiomorphic retention of a true ancestral condition, the implications as to how *Scansoriopteryx* affects our understanding of the origin of birds remain critically instrumental. The evidence is overwhelming that an animal such as *Scansoriopteryx* represents either an arboreal lineage of theropods, or a "pre-theropod" lineage of saurischian archosaurs which could climb. In either case, the argument that birds must have evolved from the "ground up" is disputed and becomes an inappropriate scenario.

With the discovery of *Scansoriopteryx*, the concept of birds evolving "from the trees down" is certainly supported more than the "ground up" scenario. However, the relationship between dinosaurs and birds is not exactly what either contingent have claimed. The cursorial theory has maintained that all theropods, including maniraptorans were strictly terrestrial. But the interpretation of *Scansoriopteryx* as being ancestral to maniraptorans would suggest that they became cursorial late and independently from true theropods. What this indicates is while some theropods may have become cursorial from arboreal ancestors prior to the maniraptoran stage of development, the maniraptorans became cursorial much later after having achieved some degree of gliding or actual flight capabilities. Therefore, while the "trees down" supporters have been more correct in attributing arboreality to the origin of birds, they have also been incorrect in accepting maniraptorans as non-avian theropods which only resemble birds by independent convergence.

With *Scansoriopteryx* as representing the most primitive ancestor to birds, the reduction of the third digit as seen in *Archaeopteryx* and other maniraptorans happened independently of theropods and after the development of gliding had been achieved. Contrary to both camps of thought of either "ground up" or "trees down", this would remove maniraptorans from being considered true theropods and place them as direct descendants of arboreal avian ancestors. These avian ancestors cannot be considered as having been derived from theropods, or as true theropods themselves, because actual theropods lost the elongated length of the third digit when they became cursorial. *Scansoriopteryx* is the sole representative of the avian lineage which stems from a basal ancestral stock of arboreal saurischians. Whether these saurischians can be considered dinosaurs depends on the definition of what a "dinosaur" is. However, while birds did not necessarily evolve from dinosaurs as widely believed from cursorial theropods, dinosaurs may be related to the avian lineage in being derived from a common ancestor within the earliest stages of saurischian archosaurs.

The discovery of *Scansoriopteryx* further demonstrates the incomplete nature of the fossil record and the complexities this creates especially when objectivity is obfuscated by the misleading confines of preconceived dogma. When *Scansoriopteryx*, or its ancestors took to the trees remains unknown. But that such an important lineage could be entirely represented by only a single, diminutive fossil further demonstrates the possibility, if not probability, that an unknown number of arboreal archosaurs existed and await their discovery. This needs to be taken into account when assessing whether *Scansoriopteryx* is a highly derived maniraptoran which would require massive reversals and atypical behavior, or whether *Scansoriopteryx* could be derived directly from a previously unknown lineage of arboreal saurischians that could have thrived among the treetops from the very origins of dinosaurs. Perhaps only additional specimens of arboreal archosaurs from earlier periods in time will finally resolve this issue. But regardless of when archosaurs took to the trees, the discovery of *Scansoriopteryx* challenges the widely held dogma regarding the terrestrial nature for the dinosaurian origin of birds by placing the ancestral forms within an arboreal setting.

Based solely upon its skeletal morphology, it would not be so surprising or unexpected to find such a primitive looking animal as *Scansoriopteryx* from much earlier periods of time dating from the Middle Triassic or even further back into the Permian. But that this sole representative fossil is known from strata pertaining to the Late Jurassic or Early Cretaceous suggests that *Scansoriopteryx* was somewhat like a "living fossil" in its own time. That it co-existed along with the likes of *Archaeopteryx*, dromaeosaurs, *Confuciusornis*, *Archaeovolans* and other basal birds demonstrates that there was a far greater diversity of avian and pre-avian forms which could have thrived together throughout the first half of the Mesozoic.