

Gravity-defying Behaviors: Identifying Models for Protoaves¹

NICHOLAS R. GEIST^{2,*} AND ALAN FEDUCCIA[†]

^{*}Department of Zoology, 3029 Cordley Hall, Oregon State University, Corvallis, OR 97331-2914

[†]Department of Biology, 304 Coker Hall, University of North Carolina, Chapel Hill, NC 27599-3280

SYNOPSIS. Most current phylogenetic hypotheses based upon cladistic methodology assert that birds are the direct descendants of derived maniraptoran theropod dinosaurs, and that the origin of avian flight necessarily developed within a terrestrial context (*i.e.*, from the “ground up”). Most theoretical aerodynamic and energetic models or chronologically appropriate fossil data do not support these hypotheses for the evolution of powered flight. The more traditional model for the origin of flight derives birds from among small arboreal early Mesozoic archosaurs (“thecodonts”). According to this model, protoavian ancestors developed flight in the trees via a series of intermediate stages, such as leaping, parachuting, gliding, and flapping. This model benefits from the assemblage of living and extinct arboreal vertebrates that engage in analogous non-powered aerial activities using elevation as a source of gravitational energy. Recent reports of “feathered theropods” notwithstanding, the evolution of birds from any known group of maniraptoran theropods remains equivocal.

INTRODUCTION

There are few viable scenarios for the origin of powered flight in the reptilian ancestors of birds. Protoavians may have taken flight by leaping or falling from high places, such as trees or cliffs, or, alternately, they may have generated sufficient energy from running and leaping off the ground to become, and eventually remain, airborne. The latter scenario, commonly referred to as the cursorial (or “ground-up”) theory for the origin of flight is not supported by living taxa that demonstrate an intermediate cursorial/aerial habit. The cursorial scenario for the origin of flight is based largely upon cladistic analyses that link protobirds to derived Late Cretaceous theropod dinosaurs (Ostrom, 1975; Gautier, 1984; Padian, 1985; Chiappe, 1995; Ji *et al.*, 1998) without taking account of a variety of contradictory biophysical constraints (Tarsitano, 1985; Bock, 1965, 1985; Rayner, 1985a, 1986, 1991; Ruben *et al.*, 1997, 1999).

On the other hand, the alternative evolutionary scenario for the genesis of avian flight, the arboreal (or “trees-down”) the-

ory, is consistent with the reservoir of potential energy provided by gravity available to tree-living animals. Additionally, this model has the advantage of being supported by numerous relevant extant vertebrate models for the intermediate stages of its evolution (Norberg, 1991; Feduccia, 1999). In this scenario, small archosaurian protobirds are hypothesized to have gone through a sequence of gravity-dependant aerial activities, such as jumping, parachuting, and gliding, which eventually culminated in powered flight.

Also, unlike the ground-up theory, which lacks chronologically and biophysically appropriate intermediate fossil forms, there exist numerous fossils of small, arboreal, reptilian gliders preserved from across the Permo-Triassic barrier (Carroll, 1978, 1988).

PHYSICAL CONSTRAINTS ON PROTOFLYERS

Arboreal scenarios for the evolution of vertebrate flight originate with Darwin's hypothetical gliding model for the origin of flight in bats (1859). Marsh (1880) first promoted an arboreal hypothesis for avian flight. This theory, and subsequent elaborations, was bolstered by the publication of *The Origin of Birds* by Heilmann (1926).

Most compelling contemporary biome-

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² E-mail: nick.geist@sonoma.edu

chanical arguments for the initial stages in the origin of avian flight list two prerequisites, a) small size, and b) elevation. The macroevolutionary transition from a reptilian ancestor resulting in avian flight may reasonably be explained if it can be demonstrated that there is a clear adaptive advantage at each intermediate (microevolutionary) stage (Bock, 1965, 1985). According to this scenario, the progressive elongation and elaboration of reptilian scales to feathers must necessarily have afforded fitness benefits to the organisms at each step. For a small tree dweller, the benefits are clear; any elaboration of the integument that increases surface area, especially along the limbs or flanks of the body, would tend to increase drag, slowing the rate of descent during a fall (Tarsitano, 1985). The development of a propatagium, a membrane extending between the shoulder and forearm that is essential to flight in extant birds (Brown and Cogley, 1996) would have further increased lift and control in early parachuting protobirds. Lengthening the scales further and flattening the limbs and bodies of small protoavians would have allowed them to improve their parachuting capability while increasing aerodynamic maneuverability, eventually resulting in more adept gliding performance. However, the adaptive aerodynamic advantages provided by such minimal, incremental increases in the length of the scales in very early protobirds would have been unavailable to larger animals. The more massive an organism is, the less effect a minor enhancement of surface area will have on diminishing the rate or angle of a fall. This is concisely explained by the large Reynolds numbers (Re's) characteristic of larger organisms moving through air (*e.g.*, birds and bats have Re's in the range of 10^4 to 10^5 ; aircraft operate at Re's in the hundreds of millions). High Reynolds numbers, typical of larger flying organisms, reflect the mass-related dominance of inertial forces over the viscosity-induced drag of the aerial medium (Nachtigall, 1977; Norberg, 1990). Significantly, the largest living gliding mammals (*e.g.*, colugos) weigh not more than 1.75 kg (Nowak, 1991), and this may approximate the upper limit for gliders.

PROBLEMS WITH A CURSORIAL DINOSAURIAN ORIGIN OF FLIGHT

The first widely distributed theory for a terrestrial origin of avian flight was that of Nopsca (1907, 1923). A number of other "ground-up" scenarios have since been offered in recent decades (Ostrom, 1979; Padian, 1982; Caple, 1983). Most of this work derives birds from theropod dinosaurs, with the latest phylogeny drawing birds from "feathered, ground-living, bipedal dinosaurs" (Ji *et al.*, 1998).

Implications inferred from cladistic analyses notwithstanding, the cursorial model is untenable on mechanistic, energetic, and ecological grounds (Norberg, 1990; Rayner, 1985a, 1988). The greatest constraint on a cursorial origin of flight is the inability of small terrestrial organisms to run fast enough and jump high enough to glide in a way that could have evolved into flapping, powered flight. Theoretical calculations suggest that to initiate powered flight, a terrestrial organism must run at a velocity at least equal to that achieved at its optimal glide angle (Rayner, 1985b). Accordingly, a small (0.2 kg) running animal must be able to sustain speeds of approximately 6 m/s (~ 22 km/hr) to achieve gliding angles consistent with the initiation of flapping flight. Though a number of small living reptiles and birds may reach this threshold speed during bouts of anaerobic activity lasting only a few seconds; aerobically sustainable speeds are much slower (Ruben, 1993; Bennett, 1982). Significantly, the top running speed of *Archaeopteryx* has been estimated to have approximated around 2.5 m/s, or about 9 km/hr (Thulborn and Hamley, 1985), and top speeds for small bipedal dinosaurs, estimated from trackway evidence, were in the range of 3.3–4.4 m/sec (12–16 km/hr) (Farlow and Chapman, 1997). In any case, the transition from running to gliding necessarily results in a decrease in velocity—a strategy counterproductive for either prey capture or predator avoidance.

In an attempt to circumvent the theoretical biophysical constraints on ground-up flight, it has been suggested that *Archaeopteryx* may have been able to compensate for the apparent "velocity gap" by flapping

its wings while running (Burgers and Chiappe, 1999). The calculations supporting this hypothesis are based on the assumption that *Archaeopteryx* was primarily a terrestrial animal, rather than an arboreal form, an argument inconsistent with morphology of its feet and claw arc geometry. In fact, the pes claw arc curvature of *Archaeopteryx* falls within the range of perching birds, and well outside the range of ground dwellers (Feduccia, 1993b). Additionally, the reversed hallux of *Archaeopteryx* is a feature associated with an arboreal, perching habit in modern birds. Significantly, a reversed hallux is a hindrance to primarily cursorial birds, and has been repeatedly lost or reduced in these forms (Feduccia, 1999).

A variation on the cursorial theory, *i.e.*, the terrestrial leaping, or “fluttering,” model for the origin of avian flight, argues that flapping, powered flight developed directly from running and leaping in small, cursorial forms, rather than gliding intermediates. Furthermore, adherents of this theory suggest that the transition from gliding to flapping flight is aerodynamically impossible (Caple *et al.*, 1983, 1984; Balda *et al.*, 1985). According to these scenarios, feathers developed at the distal ends of the forelimbs of small terrestrial bipeds to enhance stability when leaping for insect prey, and subsequent additional selection for wing development resulted from increased stability during high speed running. Even if this hypothetical cursorial avian ancestor could run at a speed necessary to initiate flight, the immediate loss of power resulting from a leap would slow it down below the required threshold velocity. Therefore, the low forward speeds of a fluttering protobird during these initial aerial forays would have required a hovering-type of wingbeat, the most energetically and aerodynamically complex and demanding form of flight (Rayner, 1988).

The *de novo* origin of such a mechanically and behaviorally complicated form of flight in the immediate ancestors of birds, especially without having been preceded by a gliding stage, seems highly unlikely. Moreover, the transition from gliding intermediate to powered, flapping flight in hy-

pothetical arboreal avian ancestors has been shown to be aerodynamically advantageous at each evolutionary step (Norberg, 1985, 1986; *contra* Balda *et al.*, 1985). This model demonstrates that a net thrust force can be produced even in the slightest flapping motions of a gliding animal without loss of lift. Selection pressure was probably high for the increased control, stability, and maneuverability produced by such flapping motions in gliding protobirds (Norberg, 1991). Significantly, neither flapping motions to increase leap length nor extension of the forelimbs for balance are used during running by primarily terrestrial birds (Bock, 1985).

Current cladistic analyses fail to account for the basic physical constraints that rule out known theropods, all of which were terrestrial cursors, as avian ancestors. More specifically, the basic theropodan bauplan is inconsistent with the requirements for arboreality and flight. The mass of even the smallest known mature coelurosaurs, in the range of ~5 kg (*i.e.*, compsognathids), is incompatible with the initial stages of flight in an arboreal avian ancestor (Tarsitano, 1985, 1991). Furthermore, the non-aerodynamic, stereotypically deep, laterally-compressed body shape of theropods, characterized by the relatively long, narrow, vertical to subvertical pubes, and the long, stiffened, counterbalancing tail typical of derived maniraptorans, is antithetical to arboreality. Additionally, the forelimbs of theropods are inevitably shorter than the hindlimbs—a condition opposite to that of volant birds (Feduccia, 1999). Nevertheless, the theropod theory for the ancestry of birds continues to have many supporters.

Advocates of a coelurosaurian ancestor of birds have argued that the recently described fossil *Rahonavis ostromi* from Madagascar represents a combination of derived avian and theropod characteristics that strongly supports a theropodan ancestry for birds (Forster *et al.*, 1998). *Rahonavis* is said to possess an avian “elongate, feathered ulna” coupled with a typically theropodan vertical pubis that has a “well-developed hypopubic cup.” However, close examination of *Rahonavis* refutes the presence of an *Archaeopteryx*-like hypopubic

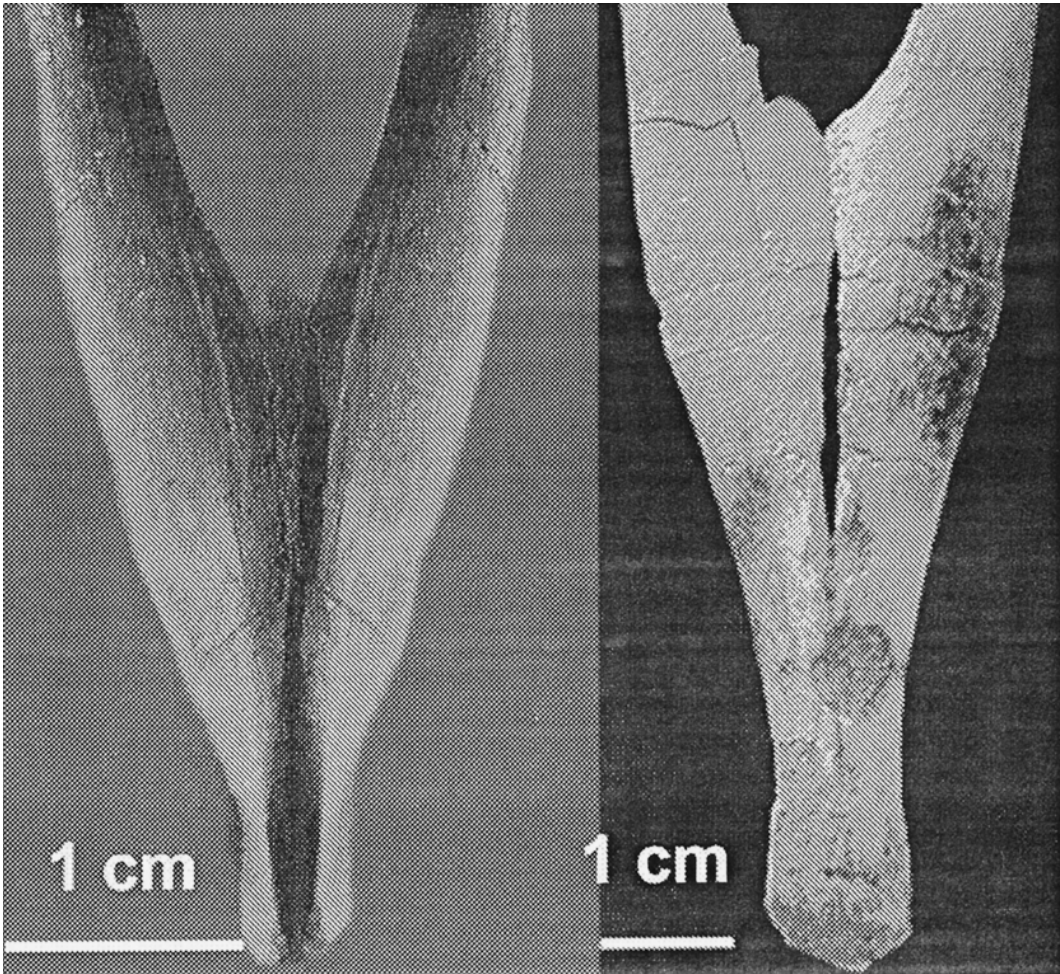


FIG. 1. Anterior view of the distal pubic “boot” of *Rahonavis* (left) and the maniraptoran theropod dinosaur *Velociraptor* (right). Both pubes are vertically to subvertically oriented and exhibit the stereotypical laterally compressed, theropodan morphology.

cup (Geist, 1999, unpublished observations). The hypopubic cup, a transversely flattened, spatulate elaboration of the distal pubis, was associated with specializations of the suprapubic musculature tightly linked to arboreality in early birds (Ruben *et al.*, 1997). Rather, the pelvic girdle of *Rahonavis* is typically theropodan, with a deep, laterally compressed, vertical pubis, complete with distal boot (Fig. 1). The presence of the hypopubic cup in *Archaeopteryx* and other early Mesozoic birds, rather than the typically coelurosaurian laterally compressed pelves with sagittally elongated pubic boot, is likely to represent a suite of

morphological features distinguishing early birds from theropods (Fig. 2). The distinctly non-avian structure of the pelvic girdle of *Rahonavis* lends credence to the possibility that this fossil may represent a chimera composed of the hind quarters of a small theropod and forelimbs of a bird, a possibility acknowledged by the authors (Forster *et al.*, 1998). Significantly, a wingless fossil of the similarly sized enantiornithine bird *Vorona* was unearthed within the same quarry in close proximity to *Rahonavis* (Forster *et al.*, 1998; Gibbons, 1998).

Recent descriptions of the “protofeathered” theropod *Sinosauropteryx prima*

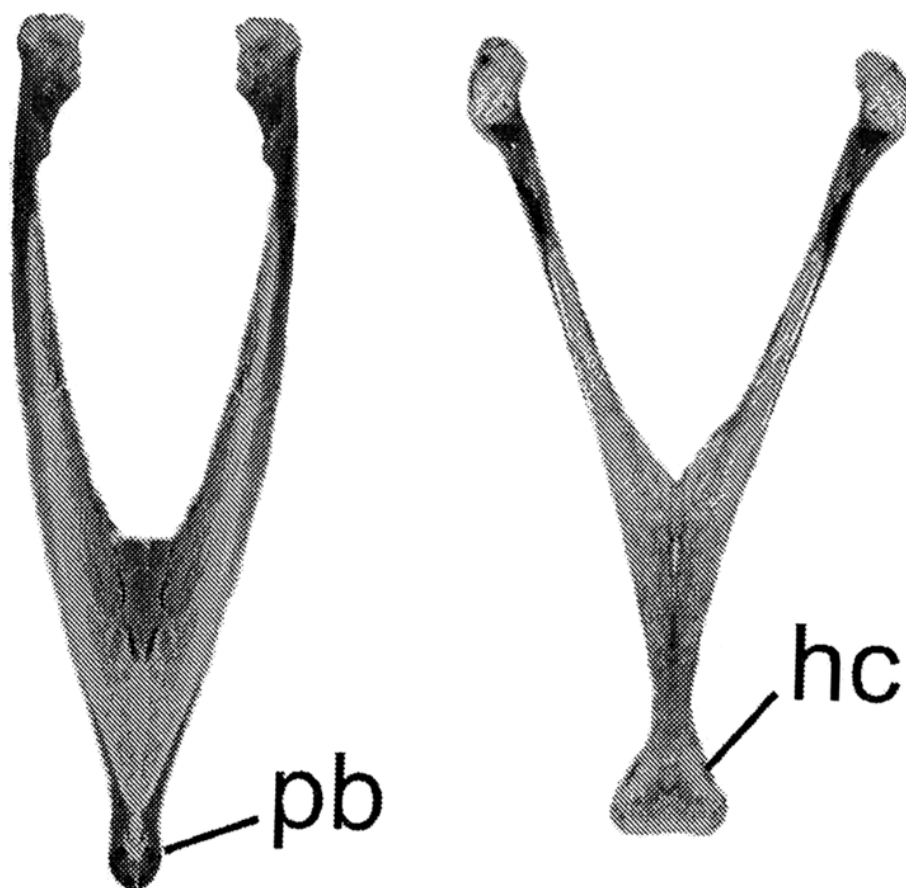


FIG. 2. Posterior view of the pubes of *Rahonavis* (left) and the London *Archaeopteryx* (right). The distal extremity of the pubes of *Archaeopteryx* and other early Mesozoic birds forms a broad, spatulate, hypopubic cup, a structure functionally linked to arboreality that is unknown in theropods. Abbreviations: hc, hypopubic cup; pb, pubic boot.

(Chen et al., 1998), and a putative feathered theropod (e.g., *Caudipteryx*) (Ji et al., 1998), claim to close the phylogenetic gap between birds and dinosaurs even further; however, these assertions are based upon equivocal evidence. The fibrous integumentary structures associated with the fossils of the small compsognathid theropod *Sinosauropteryx*, which have been described as having formed a downy external coat of “protofeathers,” are virtually indistinguishable from the elaborate bundles of dermal collagenous fibers frequently seen along the dorsal midline of many living reptiles (Geist, unpublished observations; Gibbons, 1998). Another of the supposed feathered theropods, *Caudipteryx zoui* may just as

reasonably be interpreted as having been a secondarily flightless bird (Jones et al., 2000). A number of non-theropodan, derived avian features of *Caudipteryx*, including a shortened, incipiently fused tail (“protopygostyle”), a ventrally oriented foramen magnum, vaned feather structure, along with questionable identifications of crucial characters of the skull (e.g., the nature of the quadrate-quadratojugal complex), make the theropodan classification of these fossils unwarranted.

Phylogenetic hypotheses for the origin of birds that are based solely upon cladistic analysis have resulted in interpretations that are in stark contrast to the various data from fossils and biophysical limitations. Signifi-

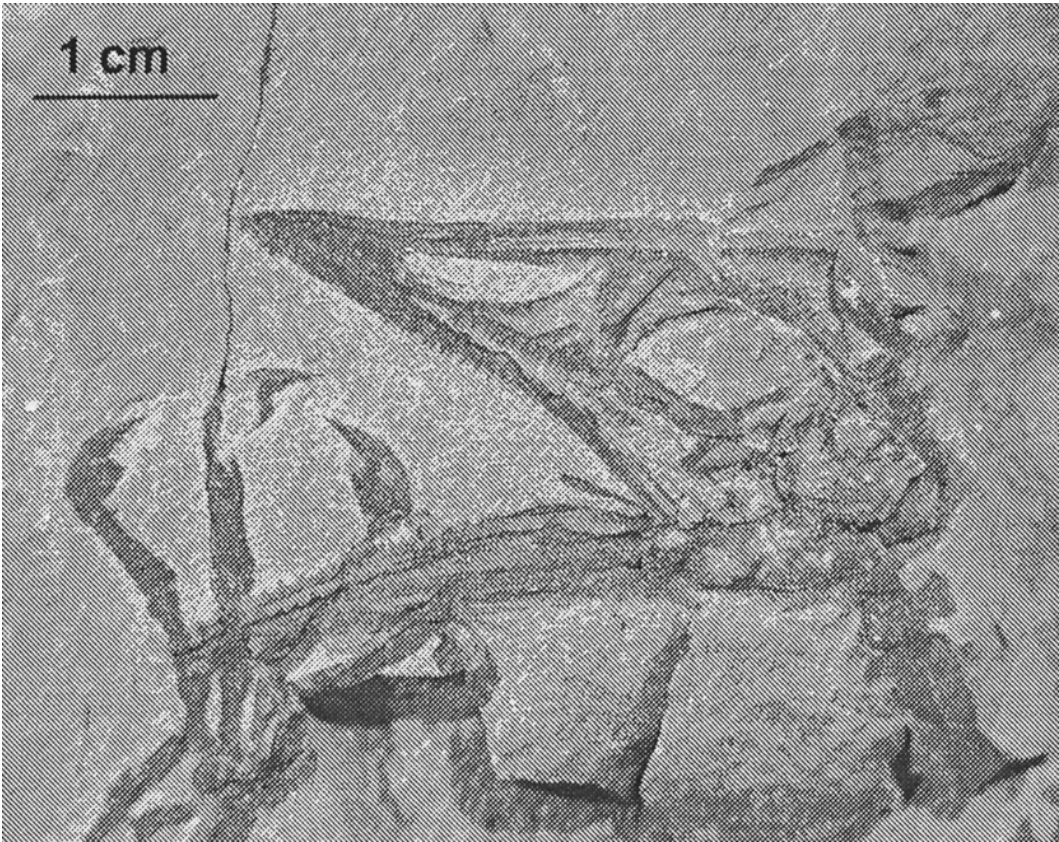


FIG. 3. The strikingly bird-like head of *Megalancosaurus*. The posteroventral position of the foramen magnum is similar to that of birds and unlike the posterior orientation typical of theropods. Note the beak-like snout and the exceptionally large, bird-like orbits. As with the rest of the skeleton, the skull is extremely lightly built. The articulated left manus exhibits several scansorial adaptations, including semi-opposable, sharp-clawed digits and well-developed flexor tubercles.

cantly, a cladistic analysis of pterosaur relationships dictated that they were a sister group of dinosaurs (Padian, 1984) and, therefore, evolved “from small, active, bipedal terrestrial predecessors” (Padian, 1991). This phylogenetic interpretation constrained the biomechanical analysis of terrestrial locomotion in basal pterosaurs, resulting in the conclusion that the hindlimbs of the earliest forms were necessarily held in an upright, bipedal, parasagittal posture and digitigrade stance like that of theropods. As with cladistically-based phylogenies that derive birds from maniraptoran theropods, this interpretation necessitated a terrestrial, cursorial origin of pterosaur flight. However, compelling fossil evidence for obligate quadripedal, plantigrade walk-

ing in basal pterosaurs has rendered these cladistically-based assertions of bipedality and “ground-up” flight untenable.

Analysis of fossils of the rhamphorhynchoid pterosaur *Sordes pilosus* has revealed the presence of an extensive uropatagium, a flight membrane extending between the hindlimbs and tail (Unwin and Bakhurina, 1994). This finding implies that *Sordes* probably could not have walked with an erect, bidepal posture. In addition, the recent discovery of a three-dimensionally preserved, articulated foot of the basal pterosaur *Dimorphodon* confirms obligate quadripedality and plantigrade stance as primitive features of the group (Clark *et al.*, 1998). These data are consistent with putative pterosaur footprints showing impres-

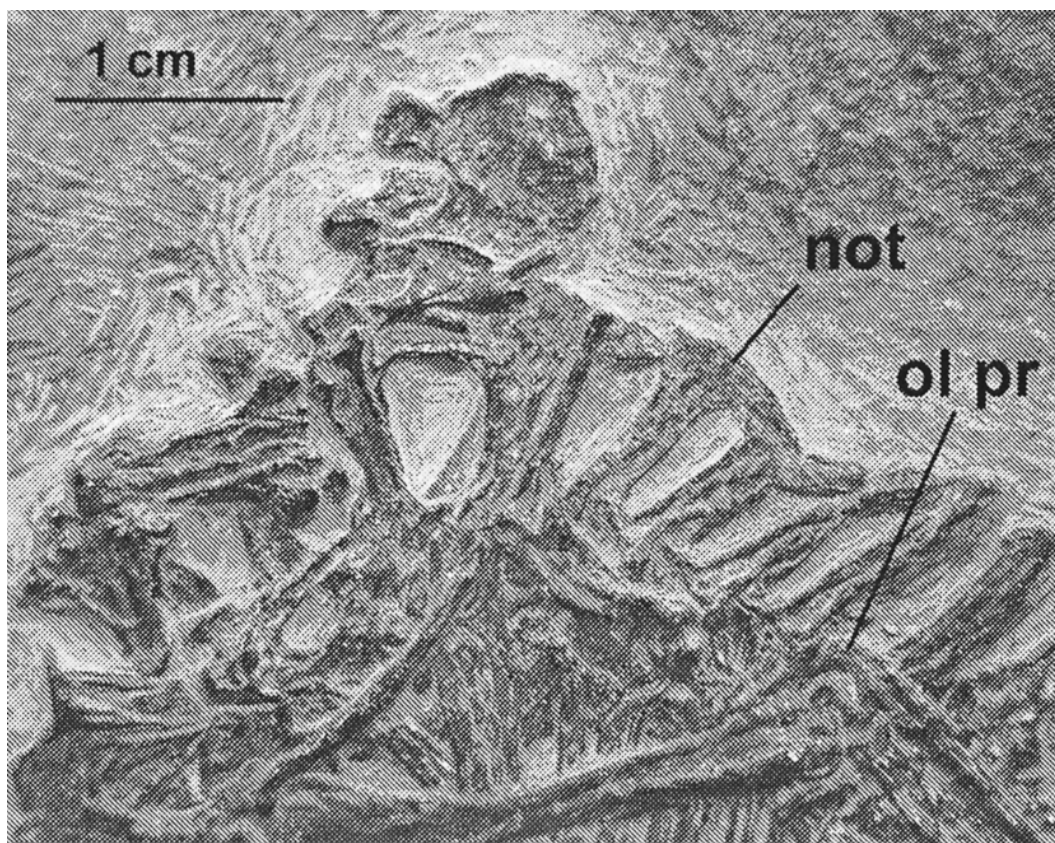


FIG. 4. Gliding adaptations in the trunk and forelimb skeleton of *Megalancosaurus*. Left lateral view of anterior trunk region. Note excavation of ribs and neural spines; virtually all elements of the axial skeleton of *Megalancosaurus* are lightened. The trunk is stiffened at the pectoral girdle by a notarium formed from fusion of the elongate neural spines of 4 dorsal vertebrae. Note the robust olecranon process of the ulna and shallow olecranon fossa of the humerus that limited extension of the elbow. Inability to fully extend the elbow, coupled with the presence of a tubercular process on the anterior aspect of the scapula analogous to the site of origin of the avian propatagium, indicates the probable presence of a propatagial membrane in *Megalancosaurus*. Abbreviations: not., notarium; ol. pr., olecranon process of the ulna.

sions of the entire sole of the foot (Lockley *et al.*, 1995; Bennett, 1997). These data illustrate the potential pitfalls of any philosophical/functional approach based upon strict adherence to a particular phylogenetic interpretation that limits the use of available evidence in paleontological reconstructions.

LIVING MODELS FOR THE PROTOAVES

In attempting to reconstruct a plausible scenario for the origin of avian flight, one can look to the diverse array of living and fossil vertebrates that have used gravity to engage in airborne activities. In the absence of adequate fossil evidence, such extant forms can serve as structural analogs that

can provide a basis for alternative hypotheses of mechanical function in protoflyers. Though there are few true parachuters (descent angle >45 degrees) among extant vertebrates, there are numerous living gliders (descent angle <45 degrees) representing independent evolution of non-powered flight in five vertebrate classes (Feduccia, 1999, Norberg, 1990).

Aerial amphibians include the “flying frogs” of the families Hylidae and Rhacophoridae from Southeast Asia, Australasia, and Central and South America. These animals use the webbing between their toes as flight surfaces, while sometimes flattening their bodies to enhance aerodynamic effect.

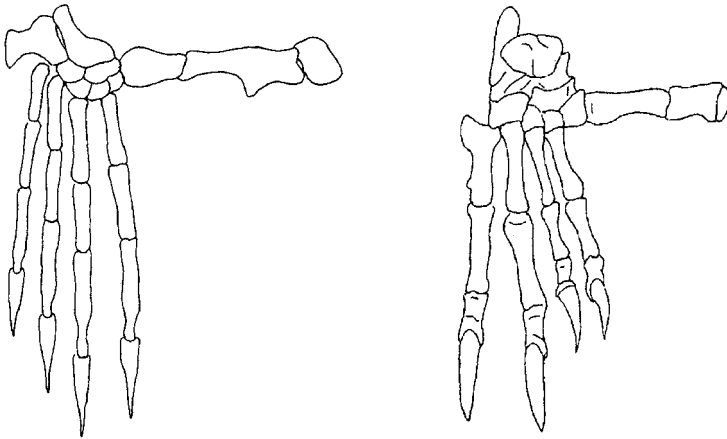


FIG. 5. Comparison of the hind feet of *Megalancosaurus* (left), and the gliding marsupial *Petaurus* (right). Note the similarities between the first toes of both animals. In *Petaurus*, the highly modified first toe serves as a primary attachment site for extensive patagial gliding membranes (modified from Renesto, 1994).

For example, during a glide, the Malaysian flying frog *Rhacophorus nigropalmatus* extends its limbs and webbed toes to slow and reduce the angle of its descent. These amphibians are relatively maneuverable gliders (Emerson and Koehl, 1990), a characteristic that is likely to be adaptive as a predator avoidance device as well as protecting the frog from injury in accidental falls.

Parachuting reptiles include *Ptychozoon*, the “flying gecko,” and the Bornean colubrid snake *Chrysopelea*. Perhaps the most efficient reptilian flyers are found among the twenty or so species of the agamid lizard genus *Draco*, skilled gliders known from the Malay Peninsula and western Pacific islands. The flight surface of these lizards is formed by a membrane stretched across 6 elongated ribs, an aerodynamic feature that allows *Draco* excellent maneuverability while gliding distances up to 60 meters.

Three mammalian orders, the marsupials, dermopterans, and rodents, have independently evolved arboreal gliding forms that use a skin flap stretched between the fore and hind limbs (Nowak, 1991). The marsupial gliders include three genera of flying petaurids of Australia (sometimes placed in the family Phalangeridae): *Petaurus*, *Petauroides*, and *Acrobates* (Nowak, 1991). The Southeast Asian order Dermoptera consists

of a single family (Cynocephalidae), and genus (*Cynocephalus*), with 2 species. Known as colugos, or flying lemurs, these animals have a large gliding membrane attached to the neck and sides of the body. This membrane is better developed than in any other volant mammal, even forming webbing between the fingers, toes, and tail. The membrane is so extensive that it renders them virtually helpless on the ground (Lekagul and McNeely, 1977).

Aerial adaptations are common in the Rodentia, with twelve genera of the broadly distributed family Sciuridae, and three genera of the African family Anomaluridae that glide. In addition, a number of arboreal primates from both the Old and New World have developed parachuting abilities. Two lemurs of the genus *Propithecus*, commonly known as sifakas, not only have a small patagium, or “gliding membrane,” analogous to that of birds, between the forearm and body, but also appear to use a thick, posteriorly-directed mat of fur on the forearms as a flight surface (Feduccia, 1993). These arboreal lemurs use their patagial and fur “wings” to slow descent and accomplish safe landings in branch-to-branch leaps that may span more than 10 m. Several New World primates also display semi-aerial adaptations. Among these are the highly arboreal sakis of genus *Pitheca*,

known to leap and “glide” in a flying squirrel-like manner. Sakis can maneuver accurately while airborne to a target tree trunk, often adjusting their bodies so that they glide upwards at a steep angle just before contact (Moynihan, 1976).

One hypothesized selective advantage to parachuting or gliding animals is predator-avoidance (Bock, 1965, 1986), while another is the maximization of net energy gain during foraging from trees or cliffs (R. A. Norberg, 1983). Even the early, steep parachuting leaps of the first proto-birds would have reduced the time and energy required for foraging, and an increased wing surface area would have slowed the descent while providing enhanced gliding performance and improving the likelihood of a safe landing (Norberg, 1991).

A PLETHORA OF FOSSIL GLIDING REPTILES

The fossil record indicates that a diverse radiation of small arboreal diapsid reptiles with gliding adaptations proliferated across the Permo-Triassic boundary. Among them are early diapsids from the Upper Permian of the family Coelurosauravidae, and Upper Triassic “dawn lizards” of the family Kuehneosauridae (Carroll, 1978; Evans, 1982; Robinson, 1962; Colbert, 1970). In these reptilian gliders, elongated ribs, or, as described in the recent reanalysis of *Coelurosauravus*, a radially-oriented set of hollow, dermal, bony rods, probably supported a horizontal, aerodynamic membrane analogous to that of the living glider *Draco* (Carroll, 1988; Frey *et al.*, 1997). Other unique adaptations for gliding are seen in several fossil reptiles from the Late Triassic of Kirghizia (Sharov, 1970, 1971). The small (~20 mm), lizard-like *Sharovipteryx* (*Podopteryx*) *mirabilis* stretched a patagial membrane between its relatively elongate hindlimbs and tail, as well as possibly having had a smaller wing surface between forelimbs and its body (Gans *et al.*, 1987). Sharov also described the bizarre pseudosuchian reptile *Longisquama* from the same deposits. Named for the row of tremendously elongated, feather-like appendages on its back, *Longisquama* could apparently fold these structures down like the wings of

a butterfly to form a gliding surface (Haubold and Buffetaut, 1987). This diverse fossil assemblage of small arboreal reptiles documents that a wide range of non-powered gliding adaptations appeared prior to the evolution of vertebrate powered flight.

The small Late Triassic thecodont *Megalancosaurus preonensis* of Northern Italy (Calvaria, *et al.*, 1980) is an especially bird-like archosaurian reptile that may provide valuable insight into the morphology of protoavians (Feduccia and Wild, 1993). *Megalancosaurus* exhibits a suite of arboreal characteristics, including long limbs with opposable digits, sharp, mobile claws, tarsi and pedes similar to those of arboreal mammals, and a long, possibly prehensile tail (Renesto, 1994; *contra* Padian and Chiappe, 1997). The strap-like scapula is more bird-like than that of any other known archosaur. The anterior limbs, without manus, are, like those of *Archaeopteryx* and other volant birds, longer than the hindlimbs minus pedes—a condition never exhibited by theropods. The exceptionally light, bird-like head was positioned on a long mobile neck composed of six or seven elongate cervical vertebrae. The skull has a number of very bird-like features, including a posteroventrally positioned foramen magnum, relatively large orbits, and a tapered beak-like snout with small isodont teeth set in sockets (Fig. 3). Although Renesto (1994) states that “there is no evidence that *Megalancosaurus* was a glider,” first-hand reexamination of the specimens indicates the likelihood that *Megalancosaurus* was a patagial glider (Geist, unpublished observations). These attributes include long anterior limbs with only partially extendable elbow, long and mobile rudder-like tail, notarium formed by 4 dorsal vertebrae, and a skeleton lightened by excavation of nearly every axial element (Fig. 4). Additionally, the first toe of *Megalancosaurus* exhibits “striking similarities with that of some phalangeriids (petaurids)” (Renesto, 1994). In these marsupial gliders, as in *Megalancosaurus*, the highly modified first toe is clawless and probably of little use in climbing. In *Petaurus*, this toe serves as a primary attachment site for the extensive patagial gliding membrane (Fig. 5). Though

probably not the avian ancestor, *Megalanacosaurus* represents a chronologically and biophysically plausible model for a gliding stage through which birds must have passed.

CONCLUSIONS

Current cladistically based hypotheses derive birds from coelurosaurian dinosaurs. This proposed relationship is based primarily on the anatomical similarities between the urvogel *Archaeopteryx* and Late Cretaceous maniraptoran theropod dinosaurs (e.g., *Velociraptor*), forms that postdate *Archaeopteryx* by at least 50–60 million years. Since all known theropods were terrestrial cursorial forms, such a relationship implies that flight must have originated from the ground up, an idea that is not supported by biophysical, ecological, or chronologically appropriate fossil data. Recent reports of fossils, which claim to further cement the bird–dinosaur relationship, must be regarded with skepticism. The partial fossil of *Rahonavis ostromi* has been described as a primitive bird that retains characteristics indicating a theropod ancestry, yet reevaluation of several key features of the pelvis support suggestions that this fossil may represent a chimera composed of the hind parts of a theropod with the forelimbs of a primitive bird found preserved in the same deposits nearby. The spectacular recent reports of “feathered theropods” from China are also dubious. First-hand examination of the fossils reveals that certain key characteristics claimed to bolster the dinosaurian nature of these forms are questionable, while other characters tend to support classification of these fossils as post-*Archaeopteryx*, secondarily flightless birds (Ruben and Jones, 2000; Jones *et al.*, 2000).

If the dinosaurian ancestry of birds is untenable, are there reasonable alternatives from the fossil record? The plethora of small gliding thecodonts that proliferated during the Late Permian and throughout the Triassic were arboreal, as are the many living parachuting and gliding vertebrates that use the energy provided by gravity to take to the air. Some of these Mesozoic animals, such as the strikingly bird-like archosaur

Megalanacosaurus, though they are unlikely to have been the actual avian ancestor, may represent an evolutionary grade through which the ancestors of birds passed on the way to developing powered flight. Such forms provide us with a biophysically and ecologically relevant model for the early stages leading to the evolution of the flapping flight of birds.

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