On the origins of birds: the sequence of character acquisition in the evolution of avian flight

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Assessment of competing theories for the evolution of avian flight is problematic, and tends to rest too heavily on reconstruction of the mode of life of one or a few specimens representing still fewer species. A more powerful method is to compare the sequence of character acquisition predicted by the various theories with the empirical sequence provided by cladistic phylogeny. Arboreal and cursorial theories incorrectly predict the sequence of character acquisition for several key features of avian evolution. We propose an alternative 'pouncing proavis' model for the evolution of flight. As well as being both biologically and evolutionarily plausible, the pouncing proavis model correctly predicts the evolutionary sequence of all five key features marking the evolution of birds.

Keywords: *Archaeopteryx*; flight; dinosaur; cursorial; arboreal; pouncing proavis

1. INTRODUCTION

The paradoxical mosaic of reptilian and avian characters seen in *Archaeopteryx* has permitted fundamentally different reconstructions of its way of life. Subsets of these characters have been used to support both cursorial and arboreal scenarios for the origin of avian flight. As the validity of competing hypotheses often rests upon speculative reconstruction of the mode of life of a species, perhaps represented by only a single specimen, several authors have suggested that such scenarios are fundamentally untestable (Gee 1998; Bock 1985).

However, different scenarios often predict different sequences of character acquisition. Comparison of predicted sequences with the empirical sequence provided by cladistic phylogeny permits evolutionary scenarios to be rigorously tested against one another (Ahlberg & Millner 1994; Balmford *et al.* 1993; Marden & Kramer 1995; Thomas & Norberg 1996). As phylogenies improve, the validity of competing evolutionary scenarios can be reassessed in the same objective fashion in which they were first tested. Recent fossil finds have revolutionized our understanding of avian phylogeny (Chiappe 1995; Garner & Thomas 1998; Gauthier 1986; Thomas & Garner 1998) and revealed the presence of supposedly avian characters deep within their theropod ancestry (Chen *et al.* 1998; Gauthier 1986; Padian & Chiappe 1998). The time seems ripe for assessing the validity of the cursorial and arboreal hypotheses in terms of the sequence of character acquisition they each predict.

2. ARBOREAL AND CURSorial PREDICTIONS

(a) *Ancestral state*

Matching predicted and cladistic sequences of character acquisition requires that we define the phylogenetic frame of reference within which we are to work. Specifying the ancestral state from which the predicted sequence is expected to run provides us with this frame of reference. We take as our starting point the ancestral node marking the divergence of theropods with aerodynamic (lift or drag producing) surfaces from a sister group lacking such surfaces. The integumentary structures of *Sinosauropteryx* do not form aerodynamic surfaces (Chen *et al.* 1998), although the feathers of *Protarchaeopteryx* clearly do. In the absence of any evidence that dromaeosaurs possessed aerodynamic surfaces, the presently unresolved trichotomy between *Protarchaeopteryx*, Dromaeosauridae, and a clade consisting of *Caudipteryx* and *Avialae* (Qiang *et al.* 1998) forms the starting point for the analysis (figure 1). Like the cladistic sequence of character acquisition, the character states of this ancestral node are liable to modification as phylogenies improve. We regard this as a strength of the method, not a weakness.

Both arboreal and cursorial theories make strong predictions about this ancestral state. The arboreal theory predicts that arboreality evolved concomitant with, or prior to, the appearance of aerodynamic feathers. Even if *Archaeopteryx* was arboreal, it is clear that neither *Protarchaeopteryx* nor *Caudipteryx*, or any known dromaeosaur, were arboreal. Aerodynamic surfaces appear much earlier in avian evolution than even the putative arboreal adaptations of *Archaeopteryx*. Indisputable evidence of arboreality does not appear until *Iberomesornis*, which possesses a fully reversed hallux typical of perching birds (Sereno & Rao 1992; but see Feduccia 1993). If the wings of *Caudipteryx* are homologous as aerodynamic surfaces

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Figure 1. Cladogram showing the phylogenetic sequence of characters discussed in this paper. (Based on Qiang *et al.* 1998; Padian 1998; Sanz *et al.* 1995.)

with those of *Archaeopteryx*, then the arboreal theory can tell us nothing about the early evolution of wings, unless we consider *Caudipteryx* to represent a secondary loss of arboreality. The cursorial theory, by contrast, predicts that the ancestral node was occupied by an active cursorial biped, which is clearly compatible with everything we know about theropod evolution.

(b) Feather asymmetry

Much weight, and much confusion, has been attached to the importance of feather asymmetry (Feduccia & Tordoff 1979; Norberg 1985, 1995; Speakman & Thomson 1994, 1995). At its simplest level, vane asymmetry is necessary for self-stability of any feather the rachis of which is orientated across the airflow. This applies whether the airflow is generated passively through gliding, or actively through flapping (Norberg 1985). For a flat, rectangular lifting surface, the centre of pressure lies approximately one-quarter of the chord behind the leading edge. If this point lies ahead of the rotational axis of the feather (i.e. the rachis), as in a symmetrical feather, then the feather will be unstable. Any rotation increasing the angle of attack will increase the lifting force acting ahead of the axis of rotation, causing the feather to stall. Likewise any nose-down rotation of the feather will be propagated through positive feedback as the lifting force decreases.

A symmetrical feather can therefore only operate as a useful lifting surface if both rachis and socket are able to resist any torsional forces generated, or if the rachis is orientated parallel to the airflow (like the inner secondaries or central rectrices of modern birds, which are invariably more symmetrical than the primaries or outer rectrices, respectively). Thus, both gliding birds and powered fliers, possess asymmetrical primaries and only flightless birds lose this asymmetry (Speakman & Thomson 1994, 1995). Since arboreal and cursorial

theories both consider flight to have been the selective force driving the evolution of the wing, both require that any feathers orientated across the airflow be asymmetrical as soon as they appear.

The remiges (wing feathers) and rectrices (tail feathers) of *Caudipteryx* are symmetrical. No remiges are preserved in the holotype of *Protarchaeopteryx*, but its rectrices are symmetrical (Qiang *et al.* 1998). The rectrices of *Caudipteryx* and *Protarchaeopteryx* have tapering rachides with basal diameters of 0.74 mm and 1.5 mm, respectively, which could not possibly have resisted the torsional forces associated with the movement of such large animals through the air, if the rectrices were orientated across the airflow. The rectrices of *Protarchaeopteryx* appear dislocated from the caudal vertebrae, but the feathers of *Caudipteryx* are preserved in a position which suggests that the rectrices would have been orientated at an acute angle to the airflow, and the remiges obliquely so. The second most distal remex of *Caudipteryx* is symmetrical, but if the wings were being used to generate lift, there would have been strong selection for the more distal feathers to be asymmetrical. Neither arboreal nor cursorial theories can accommodate these observations unless *Caudipteryx* is considered secondarily flightless.

(c) Placement of the wings

With few exceptions, the wings of flying tetrapods are continuous with the body wall. This permits the wings to operate as a single functional unit, increasing aerodynamic efficiency at the cost of reducing induced power. Useful aerodynamic force is generated by imparting momentum to a volume of air, which is accelerated in a downwash behind the wing's trailing edge. The impulse of the reaction force pushing the wing upwards and forwards is dependent on the momentum imparted to this downwash of air (mass $\times$ velocity).

Figure 2. Aerodynamic consequences of distal versus proximal placement of incipient flight surfaces. Flight surface area is identical in both examples. Potential lifting surfaces are shaded. The lever arm (L) of the lifting surface is shown for each. (a) Proximal placement, continuous with body wall. The two flight surfaces form a continuous wing, with the body contributing functional area. The aspect ratio (AR , wing span divided by the mean wing chord) of 3.39 is higher than in figure 2b. The lever arm and turning moment (force $\times$ lever arm) are small. This arrangement gives an efficient gliding wing, with a high lift-to-drag ratio, but a weak power stroke and poor orientational control. (b) Distal placement. Each flight surface forms a separate low AR wing ($AR = 1.89$ for each wing) with a low lift-to-drag ratio. The lever arm and turning moment are large. This arrangement confers a high degree of orientational control and a strong power stroke, at the expense of flight efficiency.

For any single wing in a steady airstream, an elliptic distribution of lift across the wing span is optimal in terms of the drag associated with the generation of a given total lift (i.e. efficiency measured as lift-to-drag ratio). This is because the pressure difference generated by a wing must decrease to zero at the wing tips and by the rate of change of momentum of the air (mV per unit time). Dividing a wing of given span into subsections inevitably increases drag because even if each section maintains an elliptic lift distribution, the subsections must induce higher downwash velocities than a continuous single wing of the same total span in order to achieve the same total lift (Thomas & Hedenström 1998).

Gliding wings are under strong selection for flight efficiency (i.e. a high lift-to-drag ratio), and we would therefore expect wings evolved for this purpose to be continuous with the body wall (figure 2). The arboreal theory and run-jump-glide version of the cursorial theory therefore predict that the avian flight surface should evolve either proximally to distally along the forelimb, or in concert along its length. In each case the wing is expected to be continuous with the body wall from the outset. By contrast, the flapping start version of the cursorial theory requires the wing to produce high power for take-off, and therefore predicts that the flight surface should develop distally on the forelimb. This maximizes the wing's leverage against the air, and its speed of movement during the downstroke. The wing need only become continuous with the body wall once there is selection for improved flight efficiency.

All 14 preserved remiges of *Caudipteryx* are attached to the second digit of the manus. Despite excellent preservation of these, the rectrices and the plumulaceous feathers covering the body, no secondaries are preserved along the ulna. The remiges of *Caudipteryx* are relatively shorter than in modern birds and *Archaeopteryx* (Qiang *et al.* 1998), making it unlikely that the incipient flight surface extended to the body wall. Symmetry of the feathers would further prohibit orientation of the remiges across the airflow from the manus to the body wall. Dorsal reconstructions of *Archaeopteryx* (Yalden 1984) show an extensive gap between the most proximal secondary and the body wall, arising because the humerus is relatively longer in *Archaeopteryx* than in modern birds. Yalden (1984) suggests that this gap would have been filled by tertials attaching to the humerus, as in modern birds. However, microscopic examination of the London and Berlin specimens reveals no evidence of tertials in either, despite excellent preservation of the other flight feathers. Indeed the flight feathers in the Berlin specimen are preserved right up to the elbow, but no feathers are present beyond that point. Tertials could have been removed in preparation but even the earliest drawing of the Berlin specimen, supposedly showing a complete covering of contour feathers since prepared away (Ostrom 1985; Feduccia 1996), fails to show any feathers in the correct position and orientation to be tertials.

Given the great and sudden improvement in flight efficiency that would accrue from making the wing continuous with the body wall, it is unlikely that flight efficiency was a significant selective pressure in wing evolution in either *Archaeopteryx* or *Caudipteryx*. The placement of their flight surfaces therefore does not sit comfortably with either the arboreal theory or the run-jump-glide version of the cursorial theory, but is more consistent with the flapping-start version of the latter.

(d) Weight reduction

For an arboreal glider, great selective advantage is attached to lightening the body, since this decreases both sink rate and horizontal airspeed. This reduces the impact force of landing, and allows more time for active correction of the flight path. Similar selective advantages apply under the run-jump-glide version of the cursorial theory. Moreover, a jumping cursor will be able to jump higher and glide further if it reduces its weight. Under the

flapping-start version of the cursorial theory, lightening the body reduces the power necessary for take-off and flight. Both arboreal and cursorial theories therefore predict that weight-reducing adaptations should appear at an early stage of avian evolution, simultaneous with other adaptations for flight.

Pneumatized bones are probably plesiomorphic in birds, being present in dromaeosaurs such as *Deinonychus*. Other weight-reducing adaptations of the skeleton, such as reduction of the tail to a pygostyle, loss of teeth and reduction of the bony elements of the skull do not appear until *Iberomesornis*, *Enantiornithes* and *Ornithurae* (Gauthier 1986; Chiappe 1995). *Protarchaeopteryx robusta* was a rather heavily built maniraptoran, and the two specimens of *Caudipteryx* are unique among theropods in possessing gastroliths (Qiang *et al.* 1998). Weight reduction was clearly not a significant selective pressure for either *Caudipteryx* or *Protarchaeopteryx*, and we are forced to conclude that lightening of the skeleton occurred much later in avian evolution than either arboreal or cursorial theories would predict.

(e) *Transition from theropodan to avian gait*

Theropod dinosaurs were highly efficient bipedal cursors, the muscle mass of which was concentrated around the hindlimbs, pelvic girdle and tail. As in modern lizards, bipedal locomotion probably required the body to be counterbalanced around the hips, with the large caudifemoralis muscle pitching the body upwards (Gatesy & Dial 1996). Indeed, bipedal lizards such as *Basiliscus* cannot run if their tail is partially amputated (Snyder 1962). By contrast, modern birds are highly efficient fliers and the majority of their muscle mass is associated with the forelimbs and pectoral girdle. As a result, the centre of gravity of birds lies well in front of the acetabulum (Alexander 1983) and much further forward than in a non-avian theropod (Gatesy & Dial 1996). This is reflected in the bobbing gait of birds, in which tonic muscles pull the caudal end of the massively enlarged, shoehorn-shaped synsacrum anteriorly towards the femora (Pennycuik 1986), allowing the synsacrum to work as a lever to resist forward toppling forces.

The transition from theropodan to avian gait is therefore expected to occur as the pectoral girdle and associated muscles become hypertrophied under selection for powered flight. Under the flapping-start version of the cursorial theory, in which the wing evolves under selection for powered flight, modification of the pelvic girdle and hind limbs is expected to occur simultaneously with the appearance of an aerodynamic wing. Under the arboreal theory and run-jump-glide version of the cursorial theory, the wing first evolves under selection for gliding flight. Major rearrangement of the pelvic girdle and hindlimbs is therefore not expected to occur until substantial modification of the pectoral girdle has occurred. Modification of the pelvic girdle will be accompanied by significant reduction of the tail, as the caudifemoralis muscle loses its pivotal role in terrestrial locomotion (Gatesy & Dial 1996).

Reduction of the tail to a pygostyle is not seen until *Iberomesornis*, which also possesses adaptations for powered flight, such as the possession of strut-like coracoids and an ulna longer than the humerus (figure 1). Further reduction

of the pygostyle, fusion of the pelvic elements and possession of a synsacrum with more than eight vertebrae do not appear until the divergence of the *Enantiornithes* and *Ornithurae*, concomitant with the appearance of further adaptations for powered flight (Chiappe 1995). The transition from theropodan to avian gait therefore occurs at a much later stage of avian evolution than predicted by the flapping-start version of the cursorial theory. Both the arboreal theory and the run-jump-glide version of the cursorial theory correctly predict the late appearance of modifications of the pelvic region associated with the change in gait.

3. THE POUNCING PROAVIS MODEL

We now introduce a new hypothesis for the origin of avian flight: the pouncing proavis hypothesis. It is distinct from both cursorial and arboreal theories because it proposes that locomotor control, rather than some direct attribute of flight such as speed or efficiency, was the selective pressure that initiated the evolution of flight in birds.

We propose that birds evolved from predators that specialized in ambush from elevated sites, using their raptorial hindlimbs in a leaping attack. Drag-based, and later lift-based, mechanisms evolved under selection for improved control of body position and locomotion during the aerial part of the attack. Selection for enhanced lift-based control led to improved lift coefficients, incidentally turning a pounce into a swoop as lift production increased. Selection for greater swooping range would finally lead to the origin of true flight.

Caple *et al.*'s (1983) model of a bipedal animal using incipient flight surfaces to control a leap from the ground was found to be an energetically feasible lifestyle under conservative estimates of the calorific value of the insect prey that the jump was intended to catch. Our modification of their model, in which gravity assists, rather than opposes, the leaping attack, is more robust still, requiring no quantitative assumptions regarding the cost:benefit ratio of a single successful capture during a jump. It is assumed that the energetic costs of climbing to the ambush site (a large rock, for example) are small. The pouncing proavis model is therefore both biologically and evolutionarily plausible. Indeed, the initial selective advantage of increasing the area of an incipient flight surface is much greater when under selection for enhanced control than when under selection for improved locomotor efficiency (Caple *et al.* 1983).

(a) *Ancestral state*

No special adaptations are required for leaping in a bipedal runner. The major difference between the two modes of locomotion is that the propulsive force is laterally symmetrical during bipedal leaping (where both feet push off the ground together), but laterally asymmetrical during bipedal running (where the feet push off the ground alternately). No special adaptations are required to withstand large symmetrical, as opposed to asymmetrical, forces (Hildebrand 1995). We would therefore expect our leaping biped to look no different to the bipedal cursor which we have identified as the ancestral state from which the evolution of avian

flight began (figure 1). The first stage of the pouncing proavis scenario is therefore fully compatible with the ancestral state as empirically determined from the fossil record.

(b) *Feather asymmetry*

A leaping animal has three potential sources of control: inertial, drag-based and lift-based mechanisms. Inertial control, achieved by swinging the limbs in an appropriate manner, is available to any animal with sufficiently long or heavy limbs. The principle is the same as that used by humans, which swing their arms to maintain stability while running. Drag-based control is available to any animal with an aerodynamic surface, irrespective of whether that surface creates useful lift (Caple *et al.* 1983). We therefore predict that feathers need be neither asymmetrical nor pennaceous to form an effective control surface. Indeed, since the only metastable position for a symmetrical vane is perpendicular to the airflow, drag is maximized by having symmetrical feathers. For an animal using a drag-based control mechanism, symmetrical feathers would form a more effective control surface than asymmetrical feathers. Under the pouncing proavis scenario, vane asymmetry evolves after the appearance of incipient flight surfaces, as part of a more efficient lift-based control mechanism.

For reasons outlined earlier, the symmetrical wing and tail feathers of *Caudipteryx* look to be ideal as drag-inducing flaps, but rather poor as lifting surfaces. Good modern analogues exist for such a drag-based control mechanism—fledgling owls hunt in this manner before they can fly (M. G. Wilson, personal communication). Vane asymmetry in the remiges of *Archaeopteryx* is as compatible with the feathers forming part of a lift-based control system as it is with their forming a true flying wing. Once again, good modern analogues exist for such a lift-based control mechanism—kestrels and other small raptors, and many species of owl swoop down upon their prey from elevated ambush sites in a controlled fall (Snow & Perrins 1998).

(c) *Placement of the wings*

Simple lever mechanics dictates that both drag-based and lift-based control mechanisms are most effective when the control surfaces are distally placed (figure 2). Optimum aileron theory further confirms this result for lift-based mechanisms (Nickel & Wohlfahrt 1994). The pouncing proavis model therefore predicts that the development of incipient flight surfaces will occur at the extremities of the forelimbs and tail, since the development of control surfaces on the hindlimbs would tend to compromise the predatory stroke. The distally placed remiges and rectrices of *Caudipteryx* make this a perfect model for a predatory animal using a drag-based mechanism to control its descent upon its prey.

(d) *Weight reduction*

Unlike arboreal and cursorial theories for the evolution of avian flight, the pouncing proavis scenario does not predict that weight reduction should be a significant selective pressure from the first appearance of incipient flight surfaces. Both drag-based and lift-based control mechanisms will slow a pouncing animal's descent in the

absence of any weight-reducing adaptations. Ambush success will represent a trade-off between maintaining an element of surprise (requiring a swift descent) and having sufficient time to make the necessary control movements (requiring a slower descent). We would therefore expect body weight to be under stabilizing, rather than directional, selection, and no special adaptations to decrease body weight are expected during the early stages of the model. Significant lightening of the body will only begin when swooping is sufficiently advanced that the emphasis of selection shifts from control of descent to increased locomotive flight efficiency. The late appearance of weight-reducing synapomorphies observed in avian evolution fits well with this prediction of the pouncing proavis scenario.

(e) *Transition from theropodan to avian gait*

Under the pouncing proavis model, the evolution of powered flight and accompanying modification of gait do not occur until late in the evolutionary sequence, long after the appearance of wings. This corresponds well with the late appearance in avian evolution of gross rearrangement of the pelvic region, together with adaptations of the pectoral girdle for powered flight.

In summary, the pouncing proavis model correctly predicts the sequence of character acquisition for all five of the key features of avian evolution identified above. Arboreal and cursorial theories incorrectly predict the sequence of character acquisition for at least three of these five features (table 1). We are led to reject the arboreal and cursorial models in favour of the pouncing proavis theory.

4. AVIAN EVOLUTION: A PARADOX LOST

In addition to successfully predicting the observed sequence of character acquisition in avian evolution, the pouncing proavis theory also resolves three key paradoxes left unresolved by both arboreal and cursorial models.

(a) *Mosaical evolution of Archaeopteryx*

First, neither model explains the mosaic of characters seen in *Archaeopteryx*, where an otherwise unremarkable theropod skeleton possesses a fully feathered wing. Indeed, both arboreal and cursorial models predict the coevolution of a whole suite of skeletal and non-skeletal characters associated with flight (see above). The pouncing proavis theory, on the other hand, directly predicts the evolution of an *Archaeopteryx*-like grade of organization through continued selection for enhanced control of body position during a jump or controlled fall.

(b) *Coexistence of early and mid-grades of avian organization*

Second, the presence of *Protarchaeopteryx* and *Caudipteryx* in deposits dated to the Late Jurassic or Early Cretaceous (Smith *et al.* 1995, 1998) indicates that aerodynamically feathered, proavian grades of organization persisted until at least this time. Other putatively feathered forms, such as *Rahona*, representing an *Archaeopteryx*-like grade of organization (Forster *et al.* 1998), persist into the Late

Table 1. *Summary of predicted and observed sequences of character acquisition*

(Correct predictions are given in bold. Only the pouncing proavis theory correctly predicts the order of evolution for all five characters.)

feature	cladistic sequence	arboreal theory	cursorial theory run-jump-glide version	cursorial theory flapping-start version	pouncing proavis theory
ancestral state	bipedal cursor	arboreal	cursor	bipedal cursor	leaping cursor (with some climbing ability)
feather asymmetry	vane asymmetry evolves after the appearance of an aerodynamic wing	vane asymmetry evolves simultaneously with the appearance of an aerodynamic wing	vane asymmetry evolves simultaneously with the appearance of an aerodynamic wing	vane asymmetry evolves simultaneously with the appearance of an aerodynamic wing	vane asymmetry appears after the appearance of an aerodynamic wing
placement of the wings	flight surfaces first appear distally on the forelimbs, separated from the body wall	wings evolve proximally to distally, or in concert along the length of the forelimb; always continuous with the body wall	wings evolve proximally to distally, or in concert along the length of the forelimb; always continuous with the body wall	flight surfaces appear distally on the forelimbs, only later becoming continuous with the body wall	flight surfaces appear distally on the forelimbs, only later becoming continuous with the body wall
weight reduction	weight-reducing synapomorphies do not appear until after <i>Archaeopteryx</i> , as wing efficiency improves	weight-reducing synapomorphies evolve simultaneously with the appearance of an aerodynamic wing	weight-reducing synapomorphies evolve simultaneously with the appearance of an aerodynamic wing	weight-reducing synapomorphies evolve simultaneously with the appearance of an aerodynamic wing	weight-reducing synapomorphies appear after the evolution of an aerodynamic wing, under selection for flight efficiency
transition from theropodan to avian gait	transition to avian gait occurs late in avian evolution, simultaneously with adaptations for powered flight	transition to avian gait occurs late in avian evolution, simultaneously with adaptations for powered flight	transition to avian gait occurs late in avian evolution, simultaneously with adaptations for powered flight	transition to avian gait occurs simultaneously with the evolution of an aerodynamic wing	transition to avian gait occurs late in avian evolution, simultaneously with adaptations for powered flight

Cretaceous. Both arboreal and cursorial models view the early evolution of birds as a series of progressive improvements in flying ability. If so, proavian and *Archaeopteryx*-like grades of organization would not be expected to coexist with more advanced grades, as later and more improved animals should competitively exclude earlier forms. The persistence of proavian and *Archaeopteryx*-like grades well into the Cretaceous argues against such a view. Moreover, *Rahona* is known from the same locality and horizon as *Vorona* (Forster *et al.* 1998); a bird considered more derived than *Iberomesornis* (Forster *et al.* 1996). This suggests that *Archaeopteryx*-like forms were not only cotemporal with more advanced grades, but lived sympatrically with them.

By contrast, the pouncing proavis theory predicts that animals up to an *Archaeopteryx*-like grade of organization were under selection for enhanced control, rather than improved locomotive efficiency during flight. Later grades would be under selection for improved flight efficiency, allowing expansion into a more recognizably avian niche. Flying forms would be unlikely to compete

with earlier pouncing grades, permitting the two to live sympatrically. Progressive improvements in flying ability would lead us to predict a sudden and rapid turnover of flying forms through competitive exclusion of less advanced fliers. Although absence of evidence is not evidence of absence, especially where the vagaries of the fossil record are concerned, this is indeed what we see where successive strata are exposed in the same locality. *Confuciusornis*, a genus comprising at least three species (Hou 1996), is very numerous in the Yixian Formation of Liaoning Province, China, but absent from overlying Neocomian deposits, in which more advanced flying birds such as *Sinornis* first appear.

(c) *The primitive perfection of feathers*

The evolution of feathers presents a third paradox for models proposing that aerodynamic feathers evolved under selection for lift production. It is hard to see how useful lift could be produced by a feather any less complex than those of modern birds: without barbules to hold together adjacent barbs the integrity of the vane

would be lost. The pouncing proavis theory, however, proposes that selection for drag-based control initiated the evolution of aerodynamic feathers.

Drag on a cylinder is maximized when the cylinder's long axis is orientated perpendicular to the flow (Zdravkovich 1997). This requires a certain degree of flexural stiffness. The integumentary (scale or hair-like) structures from which feathers derived would therefore have become thicker and stiffer under selection for drag-based control. Selection to maximize the strength to mass ratio would lead to the evolution of a tubular cross-section of any axial structures. Continued selection for increased drag would lead first to their roughening and later to the development of lateral extensions (barbs) from the central axis. A planar vane-like arrangement is inevitable if the barbs are held perpendicular to the flow to maximize drag. Though the vane need not be solid to produce drag, the development of barbules would allow individual barbs to provide structural support for one another, minimizing bending. The resulting vaned feather, evolved solely under selection for increased drag, would be fully aerodynamic and capable of producing useful lift.

5. CONCLUSIONS

With the rapid development of our knowledge of the avian fossil record, it has become apparent that neither cursorial nor arboreal theories can account for the complex pattern of character acquisition seen during the evolution of birds (table 1). Despite the biological plausibility (or implausibility) of either theory, the fact that neither can predict the observed sequence of character acquisition forces us to reject both as adequate scenarios for the evolution of birds. The pouncing proavis model, on the other hand, predicts the observed pattern of character acquisition, has good modern analogues for several stages, and explains three key paradoxes of avian evolution left unresolved by either of the conventional theories.

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