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COMMENTS ON THE WING SHAPE OF THE HYPOTHETICAL PROAVIAN

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The origin of avian flight has been debated since Williston (1879) and Marsh (1880) proposed the competing cursorial and arboreal theories, respectively (reviews in Ostrom 1979 and Feduccia 1980). In the arboreal theory, powered flight evolved in a climbing proavian (hypothetical avian precursor) that glided from trees. The cursorial theory proposes that the transition to powered flight was via a ground-dwelling, running proavian. Unfortunately, the fossil record is sparse for the early stages of bird evolution. *Archaeopteryx* and the Triassic fossil discovered and identified as a bird by Sankar Chatterjee are the two oldest forms. Although geologically older, the Triassic fossil has not been described, evaluated, and put into the context of avian evolution at this time and so the functional stage prior to *Archaeopteryx* remains pre-eminent in the reconstruction of avian flight.

I present the hypothesis that the arboreal proavian wing had a low aspect ratio (Figure 1) and thus was the primitive condition for birds. I also comment on prior discussions of the wing shape of an arboreal proavis, including those by Saville (1957) and Peterson (1985), and suggest refinements for reconstructions by Böker (1935) and Tarsitano (1985).

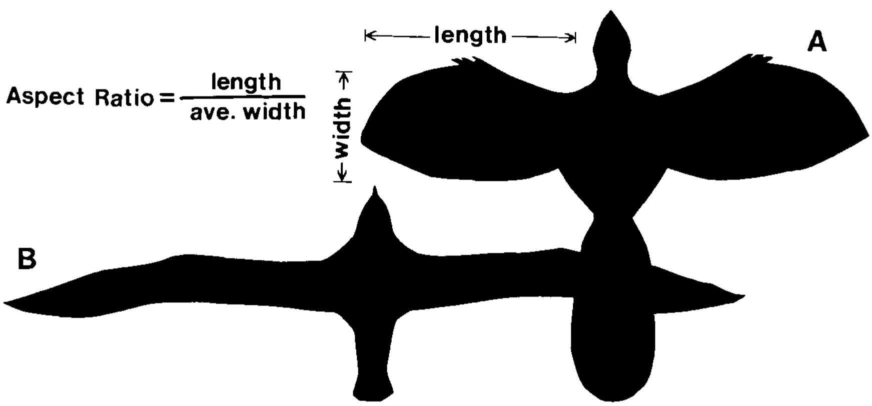

Figure 1. (A) A silhouette of *Archaeopteryx* (after Heilmann 1927, fig. 141) which has a wing with a low aspect ratio — short length and wide breadth. (B) An albatross silhouette has a high aspect ratio wing — longer length compared to breadth — and is better suited for gliding.

Environmental Influences. Although wings with high aspect ratios (Figure 1) are best for gliding due to the large amount of lift produced, they are not well suited for structurally complex environments such as wooded areas (Saville 1957). Birds with high aspect wings are not as maneuverable and require more clearance and an unobstructed flight path.

Energetics. High aspect ratio soaring wings of modern birds are probably advanced adaptations of fliers and are not likely to have evolved directly from small gliders. Increasing the aspect ratio increases the energy cost of flapping flight and can make take-off difficult (Rayner 1981). I suggest that it is improbable that a gliding proavis with a high aspect ratio would be able to overcome the energy costs during the transition to flying as easily as a glider with a low aspect ratio.

Morphological Advantages. Wings with low aspect ratios are advantageous due to the small surface area distally, in that the stress generated at the wing-tips is minimal. Also, wing area and hence stress increases toward the more robust medial joints (elbow and shoulder) resulting in increased stability for the bird (the center of lift on the individual wings are closer to the center of gravity in a bird with low aspect ratio wings) and minimal force applied to the thinner, less muscular wrist joint.

Additionally, low aspect ratio wings have a lower stalling speed at high angles of attack (high wing angle relative to direction of air movement), permitting slower speeds during takeoff, flight and landing. This is a beneficial characteristic for birds in an arboreal habitat.

Evolutionary Considerations. The transition to a flier from the hypothesized proavian glider would be less complex if the primitive wing form for birds was one with a low aspect ratio. The modification of the limb (increased length and distal stress modifications) from the primitive condition would then be relatively minor. A small wing-tip would also incur less stress during the transition to powered flight, since the widest arc of the limb is described by the wing-tip and it travels faster than any other part of the wing.

It is possible that the feather distribution of the proavian wing may be evolutionarily related to the pattern of primary remiges along the middle digit in modern birds. The feather pattern of the wing is consistent with the arboreal scenario in which the proavian wing was used for climbing as well as flight. The feathers on the trailing edge of the arm would be oriented away from the climbing surface, but feathers of the manus would have to be absent from the trailing edge of the lateral digit to avoid damage during climbing. Long feathers placed along the middle digit, however, would be protected by the lateral digits. This was discussed by Heilmann (1927) for the distal-lateral flight feathers in the Hoatzin (*Opisthocomus*), but it is also applicable to the trailing edge of the feathers of a proavian.

Peterson (1985:101) criticized the arboreal theory based on the wing shape of *Archaeopteryx*. He questions why *Archaeopteryx* had the wing typical of brushland birds (elliptical). The wing form of a gliding or soaring bird should be rectangular or pointed combined with a broad rounded tail.

This criticism illustrates such minor problems as: Which reconstruction or variant of the arboreal hypothesis is to be considered for criticism? For example, the tail in Figure I is not reconstructed as long and narrow as Peterson described. More important problems are that the environmental influences on the wing shape, and the robust nature of organisms are left unconsidered. The ability to glide is not contingent upon a high aspect ratio wing and its lack does not exclude gliding. Most birds can glide although some can glide better than others due to their specializations.

Saville (1957) concluded that the elliptical wing shape of *Archaeopteryx* is well suited for low-speeds in a wooded habitat. However, he considered wings with high aspect ratios to be phylogenetically primitive and that *Archaeopteryx* had an advanced wing morphology. He assumed the poor flight features of the modern Common Loon (*Gavia immer*) (high wing-loading, pointed wing-tips, poorly formed "slots" and small alulae) had to be primitive although the Gaviidae are of problematic phylogenetic relationships and numerous morphological specializations have since been recognized (Cracraft 1982). The reverse argument — that the elliptical wing is primitive — is more easily defended because this is the wing shape of *Archaeopteryx* and seems adapted for gliding flight in a structured environment.

Some proavian wing models (Figure 2) could be improved by reconsidering the wing shape in light of the environmental and structural constraints discussed earlier. The main surface area of the wing could be restored closer to the body, the feathers shortened, and the gap between the body and the wing closed. These modifications would decrease

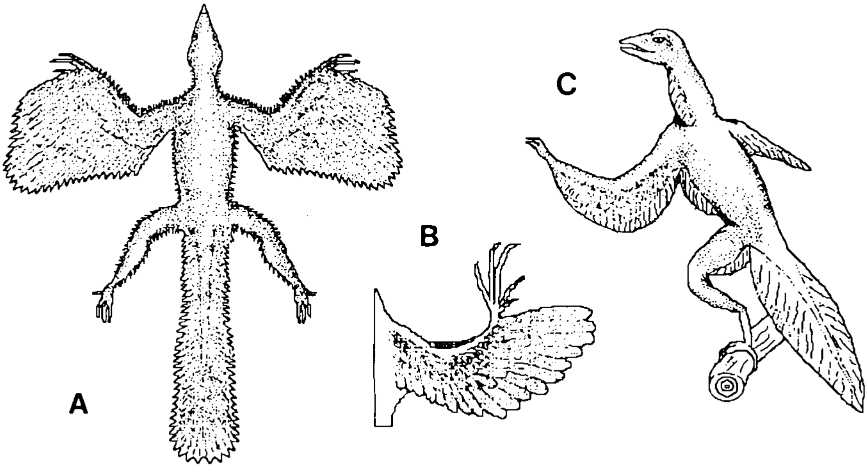

Figure 2. Reconstruction of proavis modified from (A) Tarsitano (1985, fig. 6) (B) Böker (1935, fig. 106A) and (C) Heilmann (1927, fig. 142).

the stress at the wing-tips and redistribute it along the more robust inner joints. The wing shape advanced by Heilmann (1927) for a proavian is constructed more along these lines (Figure 2), and avoids the novel design (compared to known gliders) advanced by Böker (1935) and Tarsitano (1985).

I consider the low aspect ratio wing to be the primitive avian condition. Although wings with high aspect ratios are better for gliding, they are a specialized adaptation of advanced birds which are not suitable for an arboreal habitat. They are also energetically expensive to flap. Wings with low aspect ratios concentrate the lift stresses toward the stronger inner joints, increase stability and allow slower airspeeds. This wing design is more compatible evolutionarily as there are fewer modifications necessary in the structure of the bone compared to a non-avian precursor, and the proavian also would have all the advantages associated with low aspect ratios.

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IN MEMORIUM: WILSON J. DINGUS

A long-time friend and valued charter member of the Kansas Ornithological Society, Wilson J. Dingus, died 5 March 1988. The funeral was held at Mound City, Kansas where he was born and where he had lived much of his life. His wife Eunice, whom he married in 1933 and who is also a charter member of the Society, survives him.

Wilson Dingus graduated from The University of Kansas and eventually became president of the Farmers' and Merchants' Bank in Mound City, a position that allowed him to indulge his passion for bird watching. He was regular at Society meetings and was treasurer from 1956 to 1958. Health problems caused him to retire in 1960. He and Eunice began touring the country towing a trailer, following the birds and returning home only to rest awhile and then set out again. Before they reluctantly gave up the trailer in 1976 and moved into a retirement center in Lenexa, Wilson had 551 species on his life list, Eunice 562, all in the 48 contiguous states. Eunice's higher total came about because Wilson could not climb to difficult places where more unusual birds might be found, but further listing ended when Eunice broke her ankle trying to add the Purple Sandpiper among the wet and slippery rocks of coastal Maine.

Wilson and Eunice will be remembered for their donation of 167 acres close by their beloved summer place, Windy Knob, near Mound City. This land was little disturbed from the time when Wilson's grandfather, Jasper Dingus, first settled in 1855. In 1952 Wilson and Eunice bought the first of four tracts of forest with a remarkably diverse flora. The presence of Pileated Woodpeckers contributed to their decision to preserve this unique area. In 1973 the Dingus Natural Area, as it was called, was deeded to The Nature Conservancy and in 1975 the KOS agreed to manage the site. A Dingus Natural Area Fund was set up to which Wilson and Eunice and others have contributed, providing funds for upkeep and protection.

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