

## HISTORICAL PERSPECTIVE

# Adaptations for Gliding in the Lizard *Draco*<sup>1</sup>

Edwin H. Colbert

## INTRODUCTION

In connection with the detailed description of a Triassic reptile, obviously adapted for gliding because of the presence of enormously elongated and curved ribs, it became apparent that a comparative study of the modern gliding lizard *Draco* was in order. Various pertinent publications were examined, with the surprising discovery that, until recently, very little attention has been given to the gliding activities of this lizard. In fact, some authors have expressed doubts as to the ability of *Draco* to glide at all. Other authors have, however, given definite proof of gliding ability in this reptile. Two good descriptions are those of Hairston (1957) and Herre (1958), quoted in part below. Dr. John R. Hendrickson of Honolulu, Hawaii, has made excellent observations of the gliding behavior of *Draco*, of which one account, taken from a letter to the present writer, is also quoted

below. Finally, Hans Klingel (1965) set forth the results of some interesting experiments on the method of gliding in *Draco*; parts of his paper are summarized below.

From these reports it is obvious that *Draco* is able to glide and is, indeed, an accomplished glider. In spite of the observations by the several authorities who have described the gliding aptitudes of the oriental "flying dragon," there have been no analyses of its anatomical adaptations for gliding. There are no

<sup>1</sup> Permission to reprint this article is courtesy of the American Museum of Natural History Library, New York, New York. The article was originally published as *American Museum Novitates* No. 2283, 10 March 1967. This and other Museum herpetological publications can be downloaded in full, free of charge, at <http://research.amnh.org/herpetology/pubindex/>.



MARCLUS ING

Lizards in the genus *Draco* are accomplished gliders. The "wings" of this nesting *D. sumatranus* are clearly visible.

## Editor's Remarks

Elsewhere in this issue, an article by Lee Grismer focuses on the “flying” reptiles found in southeastern Asia. To accompany that piece, we chose to include a classic paper on a similar topic by Edwin H. Colbert, whose rich biography is summarized after the article.

This piece was published in 1967, the year that saw the world's first successful human heart transplant. The DNA molecule, today fodder for endless TV whodunits and real-life courtroom dramas, was fully decoded just the year before. Biological exploration of some parts of the world was in full swing, but the main involvement of the United States in Asia stemmed from the ongoing war in Vietnam. By the time that war ended in the early 1970s, over 2.5 million Americans had served and almost 50,000 had died there, but few of them had had the time to engage in scientific research. Our understanding of the biology of the region was extremely poor. Thus, it is not surprising that Edwin Colbert begins his paper by discussing what even amateur herpetologists now take for granted: That lizards of the genus *Draco* have “wings” and can effectively glide between trees. A paleontologist first, Colbert became interested in the issue because of his focus on flight in dinosaurs. This paper provided some of the earliest descriptions of reptilian “flight” and the mechanisms that support it. It is, in many ways, far ahead of its times, bringing a mechanistic, engineering approach that would not become common in herpetology until many years later. This paper is still frequently cited in studies of reptilian gliding in general and the biology of the genus *Draco* in particular.

Parts of Asia remain remote and poorly studied even today. Just a few weeks ago, in early 2006, reports emerged in all the major media of the results of an expedition to a previously unexplored part of Indonesia. Despite the brevity of the visit, the work yielded many new species and biological insights. Just imagine how much less accessible the world was only a few decades ago, before travel became so commonplace.

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In these lizards, elongated ribs on each side support the wing membranes. Historical drawing from *Dover's Animals*.

descriptions of the muscles involved in the control of the wings (the word “wing,” as used herein, designates the gliding membrane of *Draco*), no measurements based on wing shapes and areas and body weights, and no correlative interpretations of relationships between wing areas and body weights. The purpose of the present paper is to correct, in some small way, this deficiency in our knowledge of gliding by *Draco*.

This paper has been inspired not only by curiosity about gliding in *Draco* but also by the evidence gained from the study of the fossil reptile, mentioned above, as well as from closely related fossils found within recent years in the Triassic fissure fillings of the Bristol Channel area of England, that the *Draco* mode of gliding, whereby a wing is formed of a membrane stretched between greatly elongated, free ribs, is geologically probably the oldest attempt at aerial locomotion among the backboneed animals. Reptiles that were able to glide on a rib-supported wing, with the four legs completely free for landing and for running about on the trunks and limbs of trees or on cliffs and rocks, were living in the Northern Hemisphere during late Triassic times some 200 million years ago perhaps 20 million years or more before the first true flying reptiles, the pterosaurs, and 60 million years or more before the first birds. Here we see the first experiment among the vertebrates in aerial locomotion, and as such it is important in the long perspective of aerial locomotion among animals and by man.

### GLIDING FLIGHT OF *DRACO*

Four eyewitness accounts of flight in this lizard are presented [editor's note: two of these have been omitted here]. These descriptions, all by herpetologists, show that its gliding abilities are more extensive and subtle than is generally realized.

"*Draco volans* is an accomplished glider. Ten flights ranged from 4.5 to 12 meters, and averaged 8 meters in length. The distances were doubtless conditioned by the fact that coconut trees are ordinarily planted 8–10 meters apart. Mertens (1930) recorded flights of 15 to 20 meters, and no doubt longer ones are possible, although a habitat in which such flights were necessary would probably be unattractive to the species. In two observations the angle of the glide was estimated. For the first, the estimate was between 200 and 300 degrees from horizontal; for the second, the starting and ending heights were estimated as 6 meters and 3 meters, respectively, and the horizontal distance measured 7.6 meters. Thus, the angle is close to 220 degrees, and is in agreement with the more subjective first estimate. *Draco* would therefore qualify for a gliding animal by the definition of Oliver (1951), who distinguishes 'gliding' from 'parachuting' when the angle is greater than 450 degrees from vertical. The flight appeared rather slow, as though being maintained at close to the stalling point, an observation that agrees with the slight amount of upturn at the end of the glide (see also Schmidt, 1935, on *D. spilopterus*)" (Hairston, 1957, p. 262).

Finally, the recent experiments and observations by Klingel are described. These, seemingly the first carefully controlled experiments, are particularly interesting in that they corroborate the field observations of Hairston, Herre, and Hendrickson.

To measure the distance of flights and their elapsed times, Klingel erected vertical poles, 3.25 and 10 meters high, in an open area, and placed targets, consisting of artificial trees, 20 centimeters wide and 3 meters high, at varying distances from the central poles. According to Klingel: "Usually the animals would immediately run to the top of the pole and within a few minutes would jump off spontaneously." The length of each flight and the height of the landing point on the target were measured. Some of the flights were timed. In some cases the lizards did not fly to the targets, and these targetless flights were also recorded.

In another set of experiments, to determine the control of flight directions, Klingel used a room 4.25 meters square, painted white, and lit by a centrally placed electric bulb. In the middle of one wall was placed a black paper strip, 30 centimeters wide, to serve as a target. The lizards were then thrown upward toward the ceiling, beneath the light, and their flight directions and methods of controlling these directions were observed.

Klingel found that the flight pattern in *Draco* is clearly divisible into three phases. The first phase is the dive flight, in which the lizard launches itself from a tree. In this phase there is a steep downward glide. The kinetic energy developed during the dive flight is then utilized for the second phase of the flight pattern, the glide flight, which can be quite extended. Finally, the third phase of the flight pattern is the ascent flight, or landing phase, in which the trajectory of the lizard rises from the glide flight so that the animal swoops upward as it lands on the target. Klingel recorded flights of as long as 60 meters for animals taking off from a 10-meter pole and flying toward a target. In such flights there was a loss of altitude during the long glide flight of as much as 2 meters, but some of this was recovered during the upward landing. The recovery of altitude at landing was not great, however, because of the slow speed of the glide flight as it reached its end.

### ANATOMY OF THE WING IN DRACO

*Draco* is an oriental lizard of the family Agamidae, ranging from the Philippines, through the East Indies, to Indo-China and portions of India. There are perhaps as many as 14 or 15 species of *Draco*, varying in size from rather small or moderate-sized lizards, with body weights in an adult of 5 or 6 grams, to the relative giant, *Draco maximus*, in which the body weight may be as much as 30 grams.

In these lizards there are five, six, or seven free and elongated ribs on each side, for the support of the wing membranes. Apparently the first of the elongated ribs belong to the eleventh presacral vertebra and thus are situated well behind the pectoral girdle, a position that gives the forelimbs complete freedom of movement. The most posterior of the elongated ribs, whether there be five, six, or seven on a side to support the wing membrane, are likewise at some distance in front of the pelvic girdle, again allowing for freedom of movement of the hind limbs. Each membrane, however, has a free edge, extending from the tip of the last supporting rib to a position just lateral to the cloaca. Thus the posteromedial segments of the membranes are in part beneath the upper segments of the hind legs, but this posterior attachment of the membranes apparently does not limit the movements of the hind limbs when the animal is walking or running.

In a normal resting or walking pose the wings are folded back against the body. But when the animal launches itself into

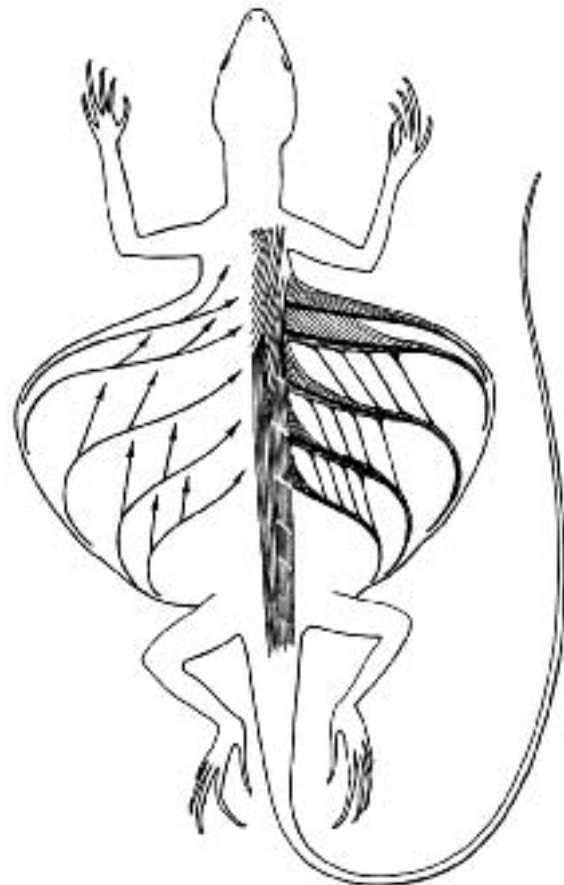


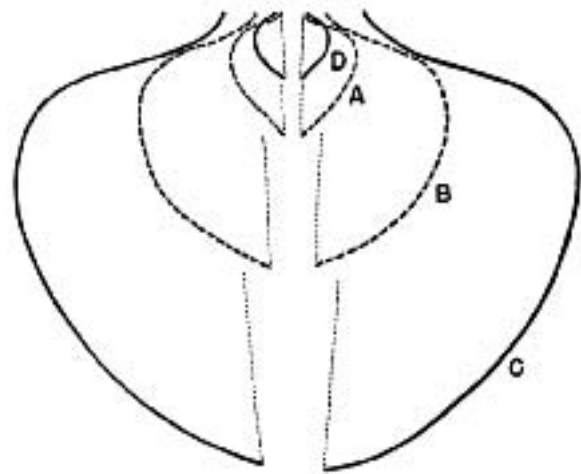
Diagram to show the general arrangement of muscles and ligaments, and their direction of force, in the wing of *Draco*.

a glide, the wings are expanded to their full extent, making a large gliding surface relative to the size and weight of the body.

### WING AREA AND BODY WEIGHT

If wings for gliding are to be truly functional, they must be of such size, as well as of such form, as to permit the animal to glide through the air at a relatively low horizontal angle. As mentioned above, Oliver defined gliding, as distinct from parachuting, as descent at an angle greater than 45 degrees from the vertical (or, conversely, less than 45 degrees from the horizontal). It is obvious from the descriptions of flight in this lizard that the conditions for true gliding are fulfilled. Indeed, it appears that, if there are any air currents, *Draco* is able to take advantage of them and rise through the air during its forward flight. What are the relations of wing areas to body weight that make the rather astonishing flights of *Draco* possible? How are the ratios of wing areas as related to body weight to be compared with the same ratios in birds of similar size? Careful measurements were made of the wing areas in *Draco*, and for each specimen so measured the weight was recorded. Several species of *Draco* were used, but the present discussion is based largely on *Draco whiteheadi*, of which a considerable series, consisting of 54 specimens ranging from small individuals to full adults, was available. A single specimen of *Draco maximus*, kindly lent to the author by Hendrickson, is also included, because it is the giant among these lizards.

From a comparison of the weight of certain preserved lizards with their live weight, as determined in the field, it was established that the weight of the pickled animal should be, on the average, about nine tenths of its live weight. Consequently, the weights of the specimens as preserved were increased by a factor of one-tenth. Each specimen was then placed on a board covered with paper, with the wing on one side stretched to its maximum extent. As can be seen from the figure, in the series of *Draco whiteheadi* the wing area increases more or less directly as body weight increases, but there is a great deal of individual variation in wing area as related to body weight. It thus appears that there is no very crucial weight-wing-area relationship among these animals, which is to say that a lizard may have a wing area of almost a half less than another individual of approximately the same weight, yet presumably is nonetheless able to glide perfectly well. Perhaps many of these animals have wing surface "to spare," i.e., that they have more wing than is absolutely required for their flights.

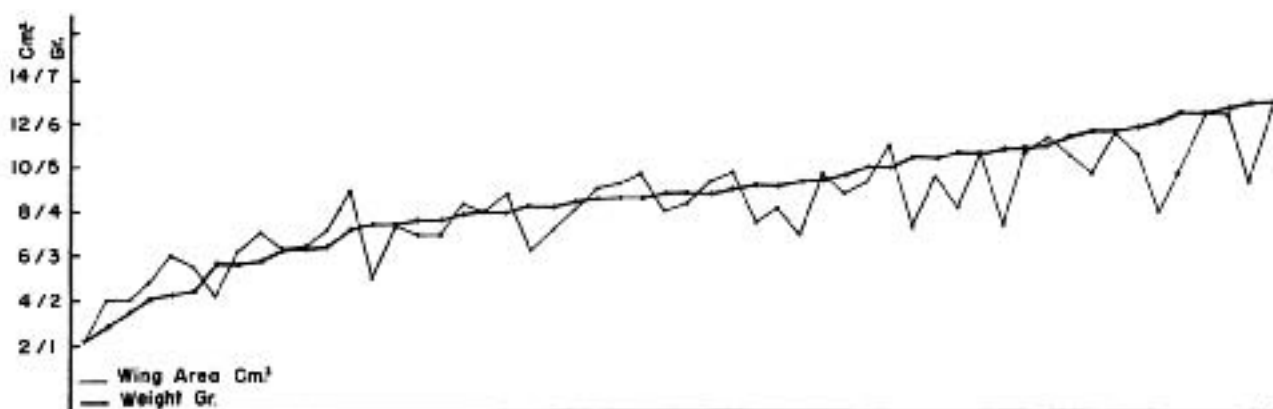


Outlines of the wings. A. *Draco whiteheadi*, A.M.N.H. No. 30905 (smallest individual). B. *Draco whiteheadi*, A.M.N.H. No. 30917 (largest individual). C. *Draco maximus*, John R. Hendrickson No. 5338. D. *Draco* sp., newly hatched, John R. Hendrickson No. 2228. A and B show the comparative wing areas in the smallest and largest individuals available of one species. C shows the wing area of an individual of the largest known species, and D shows that of an individual recently hatched.

A comparison of *Draco* with birds shows that wing loadings in the lizard are similar to those of the large soaring birds (the hawks and vultures) rather than to those of the small birds that approach *Draco* in size. The very low wing loading of *Draco* is probably necessary to offset the relatively inefficient shape of the wing. It is semicircular, as seen from above, not a conventional transversely elongated wing like that in birds or airplanes. Thus in effect it has no well-defined leading or trailing edges. Both of these regions merge into what might be considered as the tip or lateral edge of the wing, this constituting by far the largest part of the border of the flying surface. It seems that the problem of weight and wing area is rather different from that in birds; one might expect solutions to this problem also to be different.

### CONCLUSIONS

This study of *Draco* demonstrates that gliding, so efficiently performed by the several species belonging to the genus, is simply



Weights, in grams, and corresponding wing areas, in square centimeters, of 54 individuals of *Draco whiteheadi*.

effected. The spreading of the flight membrane, which is supported by five, six, or seven elongated ribs, is accomplished by the use of a few muscles, particularly the iliocostalis and the intercostals, while the arching and the stiffening of the ribs are performed by the very long, slender muscle slips that run along the length of each rib. The wings in *Draco*, when expanded, provide a flight surface that is very similar in relative extent, and thus of wing loading, to that in the large soaring birds. Perhaps this similarity is due to the fact that the lizards and the birds in question, though quite dissimilar in size, have similar problems of aerodynamics. The significance of the adaptation for gliding in *Draco* is twofold. First, it represents the one example among modern reptiles for aerial locomotion through considerable distances.

Second, although in itself perhaps comparatively recent in reptilian evolution, it seems to represent the earliest type of aerial locomotion to be adopted by the vertebrates. Recent studies of fossil lacertilians of Triassic age show adaptations for gliding that are remarkably similar to those in *Draco*. Hence it is probable that the first aerial vertebrates were reptiles equipped to glide from tree to tree on expanded membranes supported by elongated ribs, leaving all four limbs free for arboreal and terrestrial locomotion. Apparently such adaptations for flight preceded by several million years the first attempts at true flight, attained by the pterosaurs. Thus, looking at *Draco*, we are, in effect, looking back through some 200 million years, to view the manner in which backboneed animals first took to the air.

## B I O G R A P H I C A L   S K E T C H

### Remembrances of Edwin H. Colbert, Paleontologist

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Photographs courtesy of the author except where indicated.

My grandfather, Edwin Harris (Ned) Colbert, had a long and distinguished career in vertebrate paleontology. Much of this was at the American Museum of Natural History (AMNH) in New York, where he started as a graduate research assistant, and wound up as Chairman of the Department of Fossil Vertebrates. He made good use of the museum's world-class fossil collections and was involved in a number of great fossil discoveries around the world. One of the most significant was the late Triassic Ghost Ranch Quarry of New Mexico, where he recovered multiple skeletons of the early dinosaur *Coelophysis*, a



Ned Colbert in his office at the American Museum of Natural History, ca. 1940s.

discovery that profoundly influenced our understanding of early dinosaur evolution. These global travels also took him on a pioneering trip to Antarctica, where his fossil finds supported emerging plate-tectonic theories. His outstanding publication record includes more than 300 published papers and two textbooks. He also wrote a number of popular books on dinosaurs (including a few targeted at young readers), on plate tectonics, a biography, and two autobiographies. In many ways, his legacy to the field of paleontology was as much a consequence of his efforts at reaching out to the general public, as was his scientific output. Rather than summarize this remarkable career, I here attempt a more intimate portrait using the excavation of *Coelophysis* at Ghost Ranch as a vignette to better understand his life.

When I knew him, my grandfather's research focused on Triassic terrestrial vertebrate faunas from around the world. This research program incorporated newly emerging plate-tectonic theories to explain the distribution of ancient faunas. You can imagine my surprise to find that he wrote a couple of papers on fossil tapirs, a group I now study and one that didn't originate until the Cenozoic! To compound the somewhat inbred feeling that gave me, one of these papers actually reinterprets an earlier tapir-paper by my namesake, great-grandfather William D. Matthew, whose daughter my grandfather had married. Only then did I come to realize the extent of grandfather's work in the middle to late Cenozoic, the study of which was the focus of his Ph.D. dissertation and early career.

My earliest memories of my grandparents predate grandfather's retirement from the AMNH in 1969. My family lived in