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Adaptations for Gliding in the Lizard *Draco*

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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 (e.g., Pope in Schmidt, 1927; Gray, 1953) 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 "fly-

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ing dragon," there have been no analyses of its anatomical adaptations for gliding. There are no descriptions of the muscles involved in the control of the wings,¹ 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 backboned 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.

ACKNOWLEDGMENTS

I wish to express my gratitude to various persons who have assisted me in this study. To Dr. John R. Hendrickson, Vice-Chancellor, Institute for Student Interchange, Center for Cultural and Technical Interchange between East and West, Honolulu, Hawaii, I am particularly indebted for information about *Draco*, including those passages from his letters quoted in this paper. Also to Dr. Hendrickson I am grateful for field

¹ The word "wing," as used herein, designates the gliding membrane of *Draco*. There is precedent for this usage (Hairston, 1957). Some authors have used other terms, such as "wing-membrane" (Taylor, 1922) and, the equivalent in German, "Flughaut" (Hennig, 1936) as well as "wing-membrane and patagium" (Malcolm A. Smith, 1935). Tweedie in 1956 used the term "wings." In an aerodynamic sense the large expanded membranes supported by elongated ribs so characteristic of *Draco* are wings, so I call them "wings," even though in vertebrate zoology it is commonly the practice to restrict the term "wing" to the specialization of a forelimb. The word "wing" is short and simple and, in the case of *Draco*, describes nicely the shape and function of the gliding membrane. Such usage does not imply any homology with the wings in other flying or gliding vertebrates.

photographs of *Draco*, one of which is reproduced here as figure 1, as well as for the loan of specimens for study, including an individual of *Draco maximus*. To Dr. Charles M. Bogert, Chairman of the Department of Herpetology of the American Museum of Natural History, I am indebted for the opportunity to study several series of *Draco*, including the particularly valuable sample of *Draco whiteheadi*, consisting of 54 individuals, collected by Clifford Pope on the island of Hainan, China. I wish to express my appreciation to Prof. Walter J. Bock of Columbia University for valued help on the anatomy of the wing of *Draco*. My particular thanks are extended to Prof. Bruno A. Boley, and especially to Prof. Morton B. Friedman, both of Columbia University, for advice on problems of aerodynamics with reference to this lizard. The drawings illustrating this paper were made by Mr. Michael Insinna.

GLIDING FLIGHT OF *DRACO*

Four eyewitness accounts of flight in this lizard are presented. 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 20° and 30° 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 22°, 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 45° 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).

Herre (1958) mentioned the fact that for many years he had observed *Draco* throughout the South Pacific and the Philippines and added (p. 338): "No one who ever saw the activities of *Draco* in the field could ever have the slightest doubt about their gliding ability." He then (p. 339) described an incident that occurred on the campus of the College

of Agriculture, Laguna Province, Luzon. "I left the house soon after 8 A.M. and struck across an open grassy area. As I approached a young coco palm a flying lizard took off from it at a height of between 7 and 8 feet . . .

"There was a good breeze blowing, just about right for a pleasant cruise in a sailing canoe. Evidently the lizard took full advantage of the air currents, just as good gliders do everywhere, whether turkey buzzards, albatross, human gliders, or *Draco*. When the lizard had gone more than half way toward its objective . . . the path of flight was deflected . . . but upward instead of downward. As a result of this, plus the terminal upturn that always comes at the end of a flight, the lizard landed at a height somewhat more than 10 feet above the ground. The length of the flight was about 70 feet."

A letter from Hendrickson is next quoted: "The animal is so thoroughly adapted for aerial locomotion that flights are a normal part of territorial behavior and pursuit by the dominant party continues during the period in the air. I have on several occasions seen hot pursuit involving zigzag maneuvers while airborne, and on one occasion I observed the pursued individual convert an extremely high banking turn into what I could only call a 'slow roll,' the animal's wings going from vertical orientation at the top of the bank into an upside down, horizontal orientation and on over to complete the roll. I never observed actual contact between individuals in the air.

"During crude experiments to determine the maximum angle of glide over long distances, I caused individuals to glide from a tall vantage point out across a broad, flat grass lawn. Desiring to have the animals fly straight at a slow motion camera, I discovered that I could control the direction of their flight by planting a leafy bough immediately behind the camera. Most of the time, individuals would glide directly toward the target bough from as much as 50 feet away. Toward the end of extreme, flat glides, I was always amused by a reaction of the animal which reminded me of a small boy trying to see how far he could coast on a bicycle—at the extreme point, the animals would begin to 'pump' with the forepart of the body as if to push themselves just a bit further."

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



FIG. 1. *Draco*, with the wings extended in display. From a photograph by Dr. John R. Hendrickson.

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 at an average angle of about 45 degrees, with extremes ranging from about 30 degrees to 60 degrees. During this part of the flight the wings make an obtuse angle of about 160 degrees, and the tail is inclined up at an angle of about 60 degrees to the axis of the body. 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. The glide flight of animals not directed toward a target was relatively steep, on the order of 30 degrees, but that of animals flying toward a target was frequently almost horizontal. During the glide flight the body axis and the tail form a straight line. 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. In this portion of the flight, the tail is again directed up, as in the dive flight.

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.

In the test of flight directions, Klingel found that *Draco* has a remarkable ability to steer itself toward a selected target. When the lizards were thrown upward, they rotated their tails rapidly to gain a stable position in the air, a fact that had also been noted by Hendrickson. Then, from their apogee position, they were able to steer themselves by positioning the wings and the tail at various angles and curving the body. Klingel remarked, "In open areas as well as during experiments we frequently observed spiral and curving flights with a diameter of less than 1.50 meters" (Klingel, 1965; translated).

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

Since, as indicated above, there seems to be no account in the literature describing the mechanism whereby the wings of *Draco* are expanded for gliding, a dissection was made of *Draco whiteheadi*, in order to clarify this point. As shown in figure 3, control of the wings in *Draco* is accomplished by enlargement and specialization of the iliocostalis and intercostal muscles. Strong slips of the intercostal muscles connect the proximal portions of the elongated ribs, parallel to, beneath, and lateral to the longissimus dorsi. In addition these muscle slips, in their posterolateral position, curve out to extend along the anterior border of each rib. The proximal part of the iliocostalis muscle, which pulls the first rib forward, is large and extends far anteriorly beneath the trapezius and the longissimus dorsi, as well as beneath the scapula, to its insertion on the anterior ribs and vertebrae. Since the attachment for this muscle extends well into the neck region, the muscle consequently is very long, a requisite to allow a degree of contraction sufficient to pull the ribs into place. A similar, though not so extensive, development of intercostal muscles is seen on the second elongated rib. The contrast in musculature between these first two elongated ribs and the three or four posterior ribs of the wing, in which the extension of muscle slips along the ribs is comparatively slight and somewhat restricted, is marked. These latter are pulled forward in part by several thin ligaments between the ribs. In brief, the first elongated rib is pulled forward by strong muscles, as is the second rib to a lesser degree. In addition, ligaments from the first

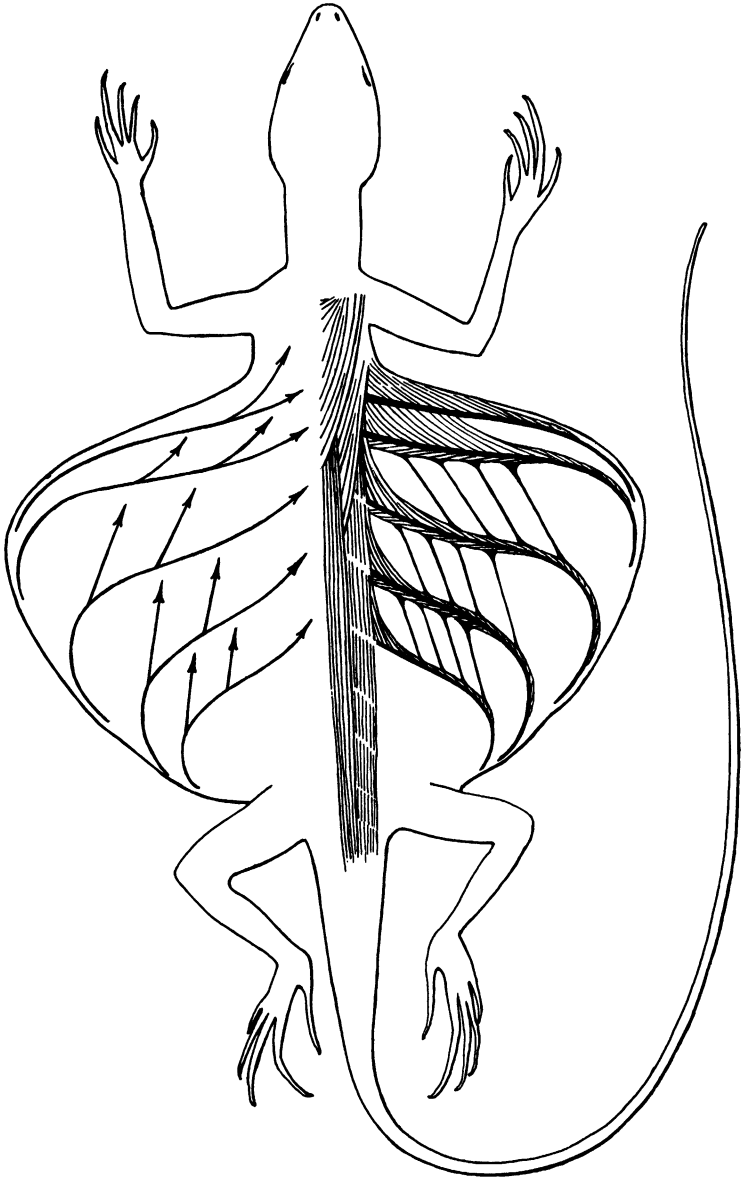


FIG. 2. Diagram to show the general arrangement of muscles and ligaments, and their directions of force, in the wing of *Draco*.

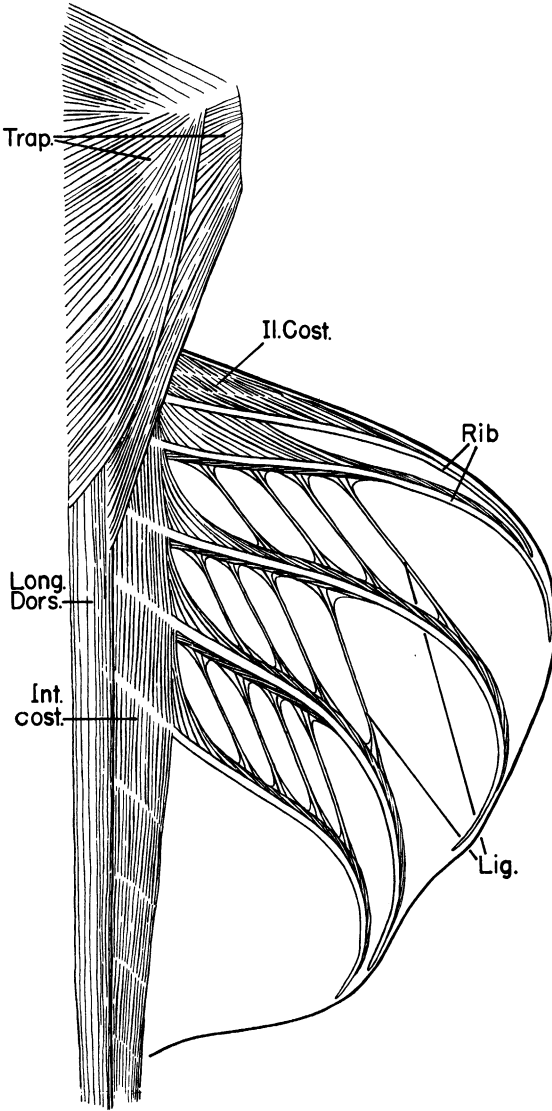


FIG. 3. Anatomy of the wing in *Draco whiteheadi*. Note the strong muscles for pulling forward the first two elongated ribs, and also that the outer ligaments to the third, fourth, and fifth elongated ribs are more or less in alignment with the outermost curve of each rib. The number of ligaments medial to each lateral-most ligament is not definitely determined.

Key: Il. Cost., iliocostalis muscles; Int. cost., intercostal muscles; Lig., ligaments between the ribs; Long. Dors., longissimus dorsi muscle; Rib, ribs; Trap., trapezius muscle.

to the second rib help to pull this latter rib forward, and, in a like manner, ligaments from the second to the third rib, from the third to the fourth, and so on, complete the forward extension of the ribs, with a consequent stretching of the wing membrane. When the tension on the wing is released by a relaxation of the strong muscles attached to the first rib and to the one behind it, the wing is folded back, probably mainly by the action of the wide slips of the intercostal muscles and the inherent elasticity of the bones.

The actions of muscles and ligaments, inferentially described above, provide a simple mechanism for spreading a wing, the wing in turn being a simple structure. It seems probable, however, that the wings in *Draco* are not, in spite of their simplicity, static structures (mere planes formed by the forward extension of the ribs). The ribs in this lizard are quite flexible, and apparently they are subject to a certain amount of bending, caused by the action of the muscular slips, attenuated though they may be, that extend along each rib. At the same time it seems probable that these muscles can, by varying degrees of tension, augmented by the connections between the muscles and ribs, fix the ribs rather rigidly at different curvatures. Consequently the extended wings are not flat planes but curved surfaces, ventrally concave and dorsally convex, which give them a greater aerodynamic lift than could be achieved with flat planes. This form of the wings, which can be seen in some photographs of *Draco* with the membranes extended, together with the ratio of wing areas to body weight, explains the remarkable gliding ability of *Draco*. Moreover, as is evident from the descriptions of flight, especially the account given by Hendrickson, *Draco* has considerable control over its flight. Such control is envisaged as being managed by changes in wing curvatures, brought about by varied muscular tensions, combined with the action of the long, whiplike tail. The result is directed, efficient gliding, which is what would be expected if this adaptation were to have had true significance in the survival of the genus over a considerable period of geologic time.

WING AREA AND BODY WEIGHT

If wings for gliding are to be truly functional, they must be of such size, as well 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° 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

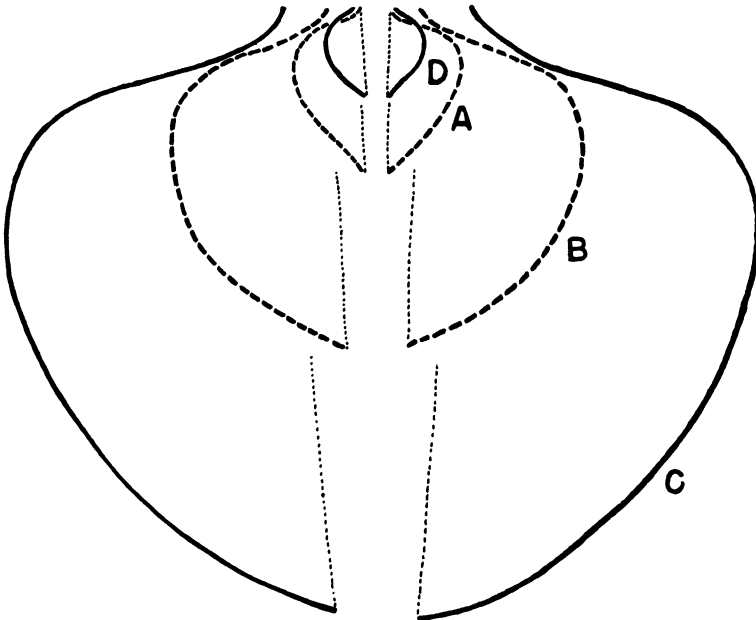


FIG. 4. Outlines of the wings. A. *Draco whiteheadi*, A.M.N.H. No. 30905 (smallest individual). B. *Draco whiteheadi*, A.M.N.H. No. 30917 (largest individual). C. *Draco maximus*, John R. Hendrickson No. 5338. D. *Draco* sp., newly hatched, John R. Hendrickson No. 2228. A and B show the comparative wing 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. All $\times 1$.

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

TABLE 1
Draco whiteheadi

Specimen	Weight in Grams	Total Wing Area in Square Centimeters	Wing Area in Square Centimeters per Gram	Wing Loading in Grams per Square Centimeter
A.M.N.H. No. 30900	2.8	6.10	2.18	0.46
A.M.N.H. No. 30901	2.9	7.04	2.42	0.41
A.M.N.H. No. 30902	3.1	6.14	1.97	0.51
A.M.N.H. No. 30904	4.5	9.68	2.15	0.465
A.M.N.H. No. 30905	1.0	2.42	2.42	0.41
A.M.N.H. No. 30906	5.2	7.24	1.39	0.72
A.M.N.H. No. 30907	5.2	9.46	1.82	0.55
A.M.N.H. No. 30908	2.8	4.18	1.49	0.67
A.M.N.H. No. 30909	5.0	9.36	1.87	0.535
A.M.N.H. No. 30911	3.8	6.90	1.81	0.55
A.M.N.H. No. 30912	3.7	7.36	1.99	0.50
A.M.N.H. No. 30913	5.4	7.30	1.35	0.74
A.M.N.H. No. 30914	5.4	10.60	1.97	0.56
A.M.N.H. No. 30915	5.5	11.28	2.03	0.49
A.M.N.H. No. 30916	4.2	8.10	1.92	0.52
A.M.N.H. No. 30917	6.4	12.44	1.95	0.51
A.M.N.H. No. 30918	4.0	8.78	2.20	0.455
A.M.N.H. No. 30919	4.1	7.24	1.77	0.565
A.M.N.H. No. 30920	3.2	6.16	1.92	0.52
A.M.N.H. No. 30921	5.3	8.10	1.53	0.65
A.M.N.H. No. 30922	4.4	8.22	1.87	0.535
A.M.N.H. No. 30923	3.2	7.06	2.20	0.455
A.M.N.H. No. 30924	4.3	9.04	2.10	0.48
A.M.N.H. No. 30925	4.7	9.62	2.04	0.49
A.M.N.H. No. 30926	4.6	7.44	1.62	0.62
A.M.N.H. No. 30927	1.3	3.90	3.00	0.33
A.M.N.H. No. 30928	2.0	4.74	2.37	0.42
A.M.N.H. No. 30929	1.7	3.92	2.30	0.435
A.M.N.H. No. 30930	6.2	9.82	1.63	0.61
A.M.N.H. No. 30931	4.1	6.22	1.52	0.66
A.M.N.H. No. 30932	6.3	12.32	1.96	0.51
A.M.N.H. No. 30933	3.7	4.94	1.33	0.75
A.M.N.H. No. 30934	4.7	6.94	1.47	0.68
A.M.N.H. No. 30935	5.3	10.50	1.98	0.505
A.M.N.H. No. 30936	5.8	11.42	1.97	0.51
A.M.N.H. No. 30938	5.0	10.96	2.20	0.455
A.M.N.H. No. 30939	6.4	9.32	1.46	0.685
A.M.N.H. No. 30940	6.2	12.34	1.99	0.50
A.M.N.H. No. 30941	5.9	10.52	1.79	0.56
A.M.N.H. No. 30942	3.9	8.24	2.11	0.47
A.M.N.H. No. 30943	4.4	7.98	1.81	0.55

TABLE 1—(Continued)

Specimen	Weight in Grams	Total Wing Area in Square Centimeters	Wing Area in Square Centimeters per Gram	Wing Loading in Grams per Square Centimeter
A.M.N.H. No. 30945	4.0	7.94	1.98	0.505
A.M.N.H. No. 30946	5.7	10.52	1.85	0.54
A.M.N.H. No. 30947	2.2	5.50	2.50	0.40
A.M.N.H. No. 30948	3.6	8.84	2.45	0.41
A.M.N.H. No. 30949	4.3	9.72	2.26	0.44
A.M.N.H. No. 30950	5.8	9.66	1.67	0.60
A.M.N.H. No. 30951	2.1	5.98	2.85	0.35
A.M.N.H. No. 30952	4.6	8.04	1.77	0.565
A.M.N.H. No. 30953	6.0	7.88	1.31	0.76
A.M.N.H. No. 30954	3.8	6.94	1.83	0.55
A.M.N.H. No. 30955	4.3	9.24	2.14	0.47
A.M.N.H. No. 30956	4.4	9.16	2.08	0.48
A.M.N.H. No. 30958	4.8	8.78	1.83	0.55

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. A tracing was made of the wing outline, and its junction with the body was noted. The width of the body at the anterior and posterior wing junctions was determined, and the opposite wing was then drawn by reversing the wing outline already executed. Some of the wing patterns thus obtained are shown in figure 4. For the determination of wing areas, one wing was measured, and the resulting figure was doubled.

As can be seen from figure 5, in the series of *Draco whiteheadi* the wing area increases more or less directly as body weight increases. But as this figure and table 1 show, there is a great deal of individual variation in wing area as related to body weight. Thus, for example, two animals, one with a body weight of 6.0 grams and the other with a weight of 6.2 grams, a difference of 3 per cent, show wing areas of 7.88 and 12.34 square centimeters, respectively, a difference of 36 per cent, the larger wing area taken as 100. Or, again, of two animals with weights of 3.6 and 3.7 grams, a difference of 3 per cent, the wing area of the heavier animal, which is 4.94 square centimeters, is only 56 per cent of that of the lighter animal with a wing area of 8.84 square centimeters, a difference of 44 per cent. It thus appears that there is no very crucial weight-

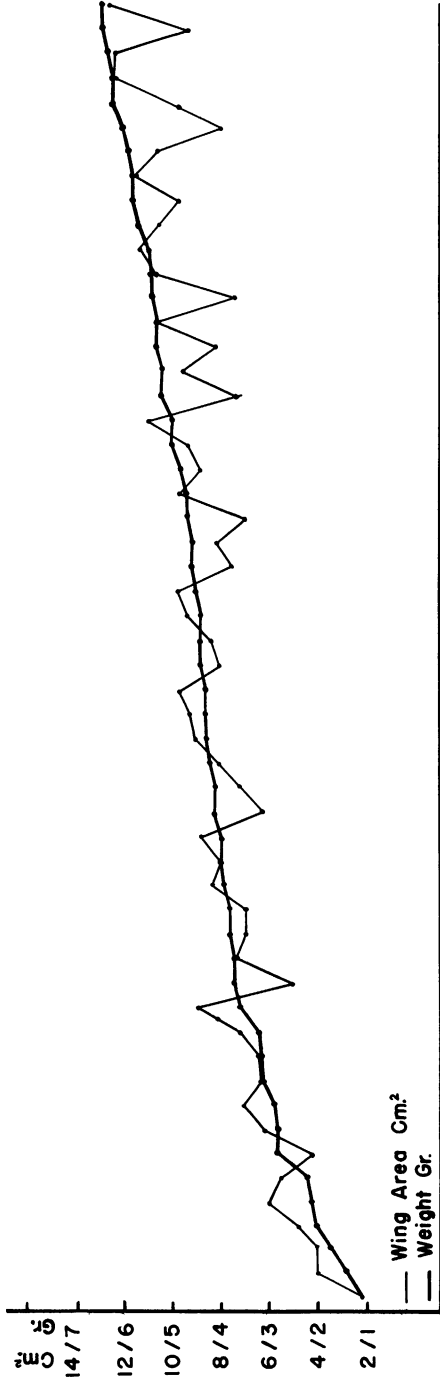


FIG. 5. Weights, in grams, and corresponding wing areas, in square centimeters, of 54 individuals of *Draco whiteheadi*.

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.

A measure of the gliding efficiency of a winged object is its rate of descent during a glide; lower descent rate means more efficient gliding. It is well known from aerodynamics that the rate of descent is proportional to the square root of the ratio of the weight of the object to its total wing area. This ratio is known as the wing loading. A low wing loading means a flat glide path and consequently a small decrease in height of the path during glide. The square-root dependence indicates that small variations in wing loading will have very slight effect on the efficiency. Even a doubling of the wing loading will increase the rate of descent by only about 40 per cent.

As can be seen from table 1, the wing loading in *Draco whiteheadi* ranges from

$$\frac{1}{1.31} = 0.76 \frac{\text{gr.}}{\text{cm.}^2}$$

to

$$\frac{1}{3.00} = 0.33 \frac{\text{gr.}}{\text{cm.}^2}$$

the larger figure indicating, of course, less wing area per weight than the smaller figure. As pointed out above, this range of wing loading indicates a maximum variation of gliding efficiency of about 40 per cent. Most of the specimens, however, have wing loadings much closer together, and the average variation in efficiency is nearer 20 per cent, which might be expected.

An interesting aspect of the measurements of *Draco whiteheadi* is that the smaller individuals in general show a lower wing loading than do larger individuals. Thus lizards with body weights of 2 grams or less show ratios of

$$\frac{1}{3.0} = 0.33 \frac{\text{gr.}}{\text{cm.}^2}$$

to

$$\frac{1}{2.3} = 0.43 \frac{\text{gr.}}{\text{cm.}^2}$$

Various authors, notably Poole (1938), Storer (1948), and Greenewalt

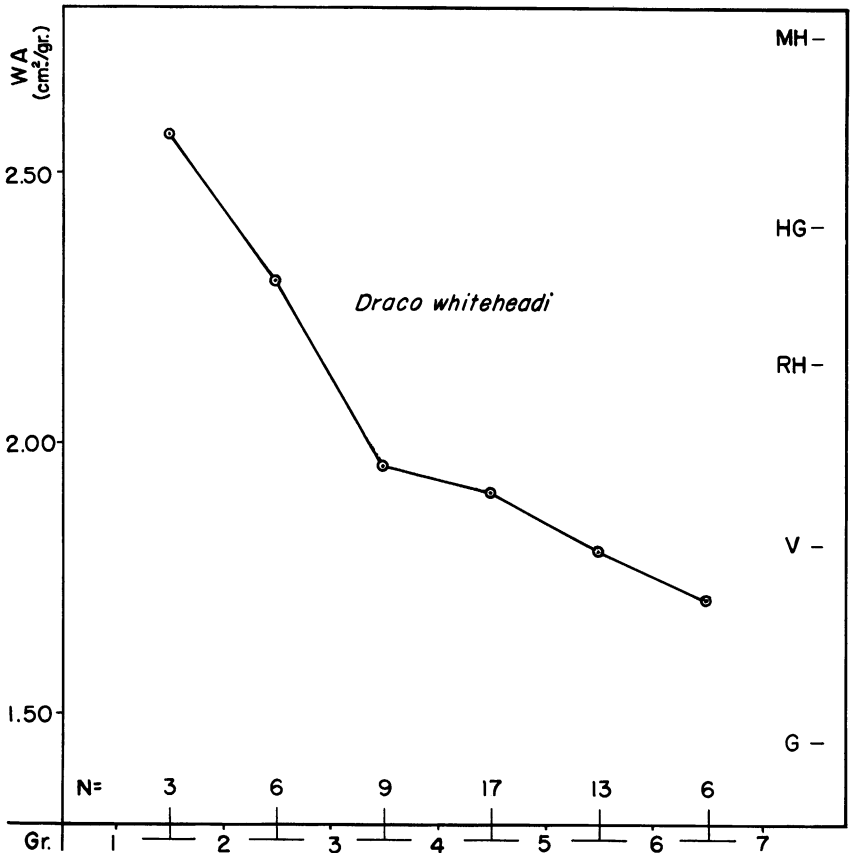


FIG. 6. Average wing areas (WA), in square centimeters per gram, of 54 individuals of *Draco whiteheadi*, arranged in classes of 1 gram each. *N*, number of individuals in each class. On the right are the wing areas, in square centimeters per gram, of some soaring birds (data from Poole, 1938): G, goshawk (*Astur atricapillus*); HG, herring gull (*Larus argentatus*); MH, marsh hawk (*Circus hudsonius*); RH, red-tailed hawk (*Buteo borealis*); V, turkey vulture (*Cathartes aura*).

(1962), have shown that this relationship holds in birds, i.e., the smaller the bird, the smaller the wing loading in comparison with that of similar birds (Storer, 1948, p. 75). A partial explanation is that the efficiency of a wing in general also depends on the proportion of the wing that is near the wing tips where the air flow is disturbed by eddies. For a smaller bird, proportionately more of the wing is so situated and consequently is less efficient. Hence a lower wing loading is required to produce an adequate over-all efficiency. Such a relationship seems to obtain in *Draco*.

TABLE 2
Draco whiteheadi

Weight Class in Grams	Number of Specimens	Average Wing Area in Square Centimeters per Gram	Average Wing Loading in Grams per Square Centimeter
1.0-1.9	3	2.57	0.39
2.0-2.9	6	2.30	0.435
3.0-3.9	9	1.96	0.51
4.0-4.9	17	1.91	0.52
5.0-5.9	13	1.80	0.57
6.0-6.9	6	1.71	0.585

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 small birds have ratios from about

$$\frac{1}{4} = 0.25 \frac{\text{gr.}}{\text{cm.}^2}$$

to

$$\frac{1}{8} = 0.125 \frac{\text{gr.}}{\text{cm.}^2}$$

and more, as contrasted with ratios of

$$\frac{1}{1.81} = 0.55 \frac{\text{gr.}}{\text{cm.}^2}$$

for the vulture, for example, and

$$\frac{1}{2.11} = 0.47 \frac{\text{gr.}}{\text{cm.}^2}$$

TABLE 3
COMPARISON OF SPECIMENS OF *Draco* FROM THE
JOHN R. HENDRICKSON COLLECTION

	<i>Draco maximus</i> No. 5338	<i>Draco</i> sp., Newly Hatched No. 2228
Weight in grams	28.8	0.33
Wing area in square centimeters	43.06	0.66
Wing area in square centimeters per gram	1.49	2.00
Wing loading in grams per square centimeter	0.67	0.50

for the red-tailed hawk. Perhaps similarities here reflect similar problems of gliding and soaring. Among the smaller birds with high ratios, gliding or soaring is rare; these birds fly by rapid wing movements. Possibly, therefore, there is a low wing ratio in *Draco*, even though it is a small animal, because it is strictly a glider.

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 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 backboned animals first took to the air.

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