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A REPTILIAN ADAPTATION TO FLIGHT

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Reprinted from JOURNAL OF PALEONTOLOGY
Vol. 49, No. 3, May 1975
pp. 534-548

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DYNAMIC ANALYSIS OF *PTERANODON INGENS*: A REPTILIAN ADAPTATION TO FLIGHT

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ABSTRACT—Wind tunnel modeling and biomechanical analysis of the flight dynamics of the Cretaceous pterosaur *Pteranodon ingens* indicates that the reptile was adequately suited to soaring and gliding flight, which is the traditional interpretation, but was primarily adapted to slow, flapping flight, and long flight endurance. Wind tunnel data suggest a weight for the adult species of ~ 15 kgm, a stall speed (minimum velocity for level flight) of ~ 4.5 meters/sec, a maximum speed of ~ 15 m/sec, and muscular output of ~ 0.1 hp. A wing-beat cycle of 1 stroke/sec would have allowed unassisted takeoff. The supraoccipital crest probably functioned as an attachment structure for a vertical membrane which had an instrumental role in turning and feeding. The reptile's long, narrow jaws are interpreted as an adaptation for minimum induced drag during underwater immersion when feeding. *P. ingens*, the largest animal ever to fly, possessed an economical and efficient skeletal structure, attained maneuverability due to dynamic instability, and employed a unique system of propulsive flight; these factors are integral to its successful adaptation to the uncompromising airborne existence.

INTRODUCTION

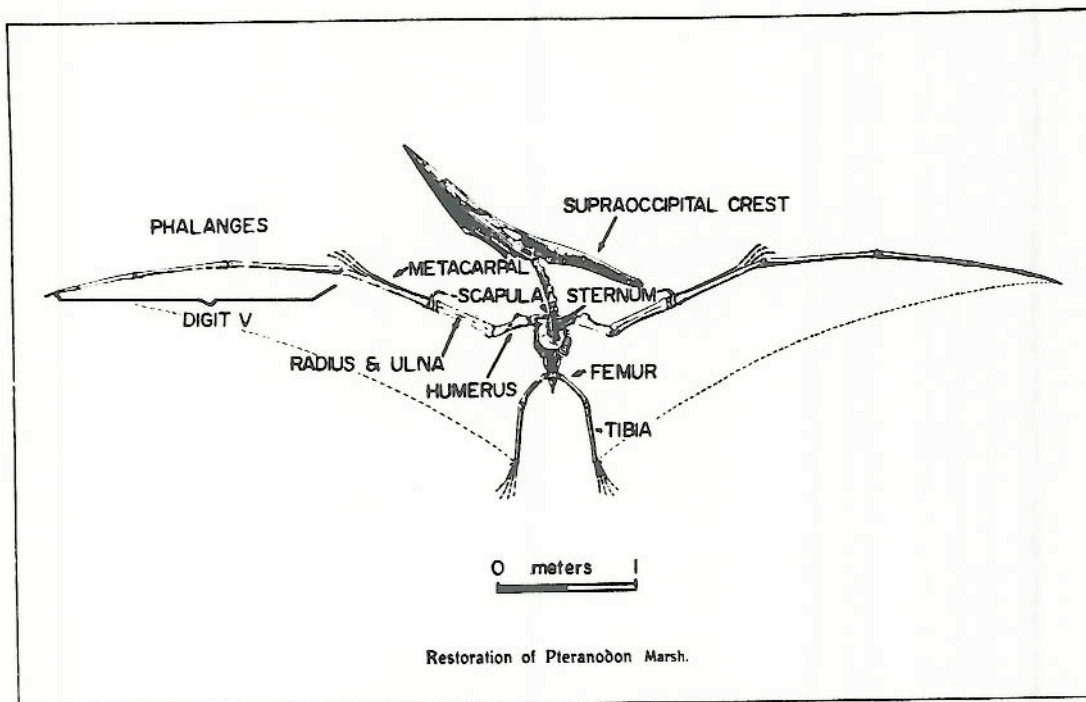
UNLIKE the Phoenix, the pterosaur will never again arise from its ashes. Yet one hundred and fifty million years aloft testifies to an enduring form. *Pteranodon ingens* (Text-fig. 1) emerged as one of the last species in the evolution of flying reptiles. The thinnest walled bones of any vertebrate ever, coupled with the greatest weight and wing span of any flying creature ever, remain remarkable structural distinctions.

At the turn of the century, when *Pteranodon* remains were first unearthed, scientists thought that these reptiles might provide answers to the secrets of the flight of heavy bodies. O. C. Marsh, S. W. Williston, G. H. Short, E. H. Hankin, D. M. Watson, and such aerodynamic pioneers as S. P. Langley had difficulty imagining how *Pteranodon* could have mastered the air; indeed, they doubted if man would ever attain his goal of sustained flight. They reasoned that since *Pteranodon* appeared to be solely a soaring animal, man would be limited to fixed-wing flight. Simulating flapping flight had failed and offered little hope for improvement. In 1903 man achieved his goal of sustained flight, so that by 1914 attention toward the giant reptile dwindled, leaving the life and locomotion of *Pteranodon* largely a mystery. The purpose of this study was to obtain an accurate and quantitative model of *P. ingens*' flight mode through a program of wind tunnel testing. This data provides the basis for further re-

construction of the reptile's habitat and adaptations.

SYMBOLS AND DIMENSIONS

- AR—Aspect Ratio, (wing span or length from root to tip)² ÷ (wing area).
C. E.—Center of Effort, the point of origin for the vector sum of all forces generated on the animal.
C. G.—Center of Gravity, the center of mass for the animal.
C_{fr}—Coefficient of Surface Friction, a function of surface roughness.
C_D—Coefficient of Drag, resulting from the aerodynamic resistance of the wings to movement through the air.
C_L—Coefficient of Lift, force generated by the wings, perpendicular to the relative air direction.
C_T—Coefficient of Total Force, the vector sum of the lift and drag components of force generated on the wings.
L/D—Lift to Drag ratio.
Re—Reynolds Number, a ratio of the inertial to viscous forces acting in a fluid (air).
V—Velocity of the animal relative to the air direction and velocity.
α°—angle of incidence, the angle between the relative air direction and the wing cord.
β°—angle of the longitudinal body axis, the angle between the body axis and the direction of flight.



TEXT-FIG. 1—The Marsh, Eaton, Langley, Lucas, Matthew, and Bramwell restoration. Note small size of body relative to wing span.

WIND TUNNEL MODELING

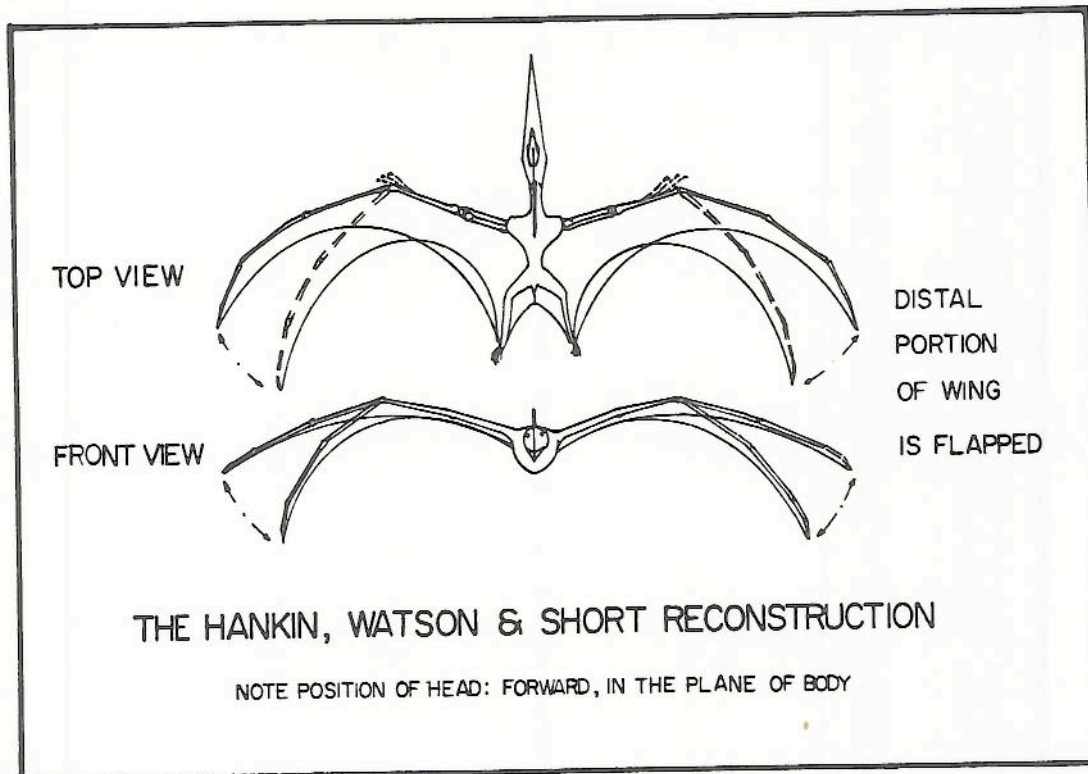
Two prevalent wing bone restorations, Marsh, Eaton, Lucas (1910) and Bramwell (1971) (Text-fig. 1) and Hankin, Watson, and Short (1914) (Text-fig. 2), were tested with varied general and localized membrane tension, leading edge form and profile, trailing edge profile, and wind velocity (flight speed).

The wing bones were constructed of semi-rigid metal rods shaped identically to the bones of the *P. ingens* as described by Eaton (1910). Surgical rubber, with a thickness of 1 mm, was used to simulate the wing membrane. The scaling parameters in wind tunnel modeling which determine the nature of the flow over the model surface take precedence over all others. These factors are contained in a relation called a Reynolds number, which is an index of friction drag which incorporates the length of the surface in the flow, the fluid velocity, viscosity and density. If *P. ingens* flew above the transitional Re range, between 6×10^5 and 5×10^6 , smooth and straight laminar flow would not be maintained, giving way to small gyrations in the turbulent regime. This would decrease the efficiency of the wings, requiring increased muscular output to maintain performance. Studies indicate

that all animals fly in the laminar regime most of the time (Hertol, 1966). Assuming wing surface smoothness (Cfr, coefficient of surface friction) similar to a bat or bird, *P. ingens* would have to have flown slower than ~ 15 m/sec to maintain efficient flight. Tests were thus conducted in the sub-transitional laminar regime, at 1×10^5 .

Wing performance is calculated in a non-dimensional coefficient of total force (C_T) that has a lift component which acts perpendicular to the air flow (C_L) and a drag component which acts parallel to the flow (C_D). In a comparison of wind tunnel tests using clay bird models with actual birds in flight, Raspel (1960) found that wind tunnel inaccuracies occur below a C_L of 0.8, which is sufficiently below the performance range of the wings tested in this study.

Although there is no direct evidence that the wing membrane on *P. ingens* was attached to the femur and tibia, it is assumed here, as in all past interpretations, since without leg attachment, 1) there would be no angle of incidence control, the acute angle formed by the wind direction and wing, in cross-section (birds rotate the entire wing at the scapula), 2) the extremely high AR, Aspect Ratio, in



TEXT-FIG. 2—Hankin and Watson (1914), and Short (1914) suggested this departure from the traditional reconstruction.

this case length/width of wing, ($AR = 20-25$) would make camber control (the wing's shape, in cross-section), extremely difficult to maintain, 3) there would be $\sim 50\%$ less wing area, doubling the wing loading and bending stress on the spar.

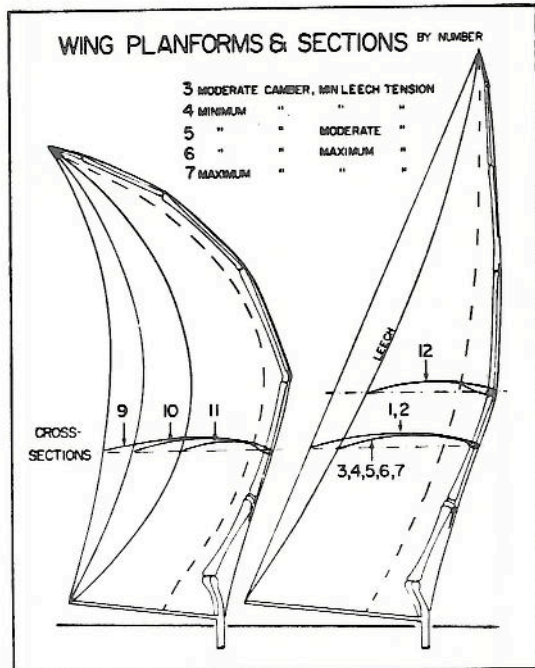
Three distinct flight modes were considered in this study: gliding, dynamic and static soaring, and propulsive flight (flapping). In gravitational gliding, a horizontal flight path is not maintained, the rate of sink (altitude loss) corresponding to the ratio of lift to drag (L/D). For example, at $L/D = 10$, one meter altitude loss would accompany every 10 meters flown. In dynamic soaring, the animal remains level through a horizontal wind component. Although the flyer cannot remain airborne indefinitely in a horizontal air current, it can do so if it is able to fly from one air mass to another (Gray, 1968). In static soaring, the flyer maintains or gains altitude through the extraction of energy from air movement which has a vertical component, such as a thermal. Finally, flapping flight is accomplished by a wing beat cycle, where the wings move faster than the flyer, producing

lift on the down (forward) stroke, and thrust during the up (back) stroke.

WIND TUNNEL RESULTS

Gliding.—Gliding demands a low sink speed (meters of altitude loss/second) for maximum flight duration and distance. This requirement is met by a high L/D ratio. To maintain the L/D over the full expanse of the wings, rigidity and uniformity of the wing form becomes critical. Wing 5 (Text-figs. 3, 4, 5) is superior with a L/D max = 21, while its maximum total thrust, C_T , is also high at 3.0.

Soaring.—In addition to high L/D , soaring requires high lift, C_L , to extract the maximum altitude gain from a vertical air current or air density interface. Wing 4 (Text-figs. 3, 4, 5) appears best suited for this compromise between L/D (= 8.0) and C_L (= 3.8). The maintenance of L/D max over a broad angle of incidence is advantageous in avoiding stalls, the sudden loss of speed and altitude, during soaring maneuvers. By comparison, a contemporary soaring bird may have an L/D max ≈ 35 (Hertol, 1966), while modern soaring plans have L/D s $\approx 35-50$ (Conway, 1969)

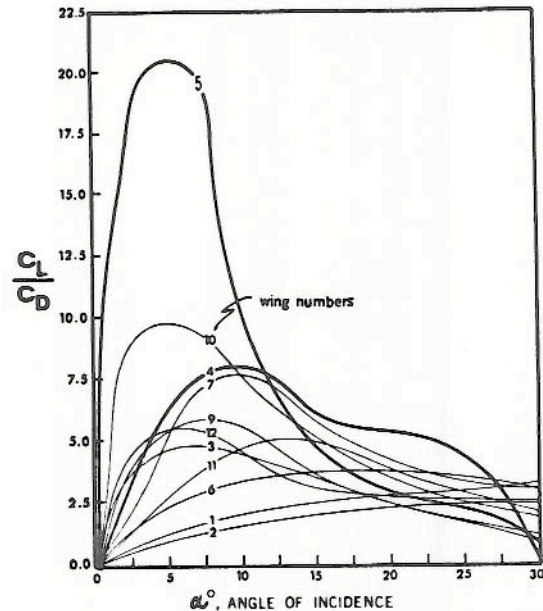


TEXT-FIG. 3—Key to wind tunnel 1:9 scale models. Wing numbers 3-7 represent expanded tests carried out to establish the criteria for optimum performance, with varied leech (trailing edge) tension.

These values neglect drag due to the animal body which would further reduce the L/D by raising C_D .

Flapping.—In flapping flight, forward force is accomplished through the backstroke, so that a low sink speed, and hence high L/D, are not required. Total force, C_T , becomes the criterion for efficient flapping. Wing 4 is also superior under these requirements, with C_T max = 4.2, C_L max = 3.8, and C_D max = 1.9.

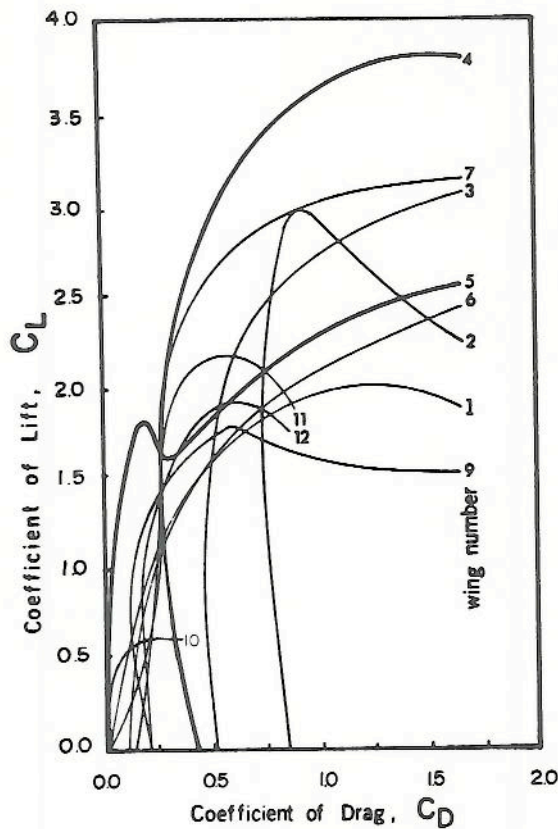
Camber Control.—Wings 4 and 5 are thus selected as the most efficient adaptations for the three flight modes. It is important to note that the only difference between these wings, which both conform to the Marsh, Lucas, Eaton, and Bramwell reconstruction (Text-fig. 1), is in the tension along the wing's trailing edge. The tension was controlled on the wind tunnel models by a wire which ran along the trailing edge in a thin membrane sleeve. With maximum tension imposed, *P. ingens* could flatten and stiffen the wing for gliding. In soaring, increased camber due to the easing of tension would increase the lift generating properties of the wing.



TEXT-FIG. 4—Lift/Drag ratios as a function of angle of incidence.

This effective but simple method for controlling the wing shape suggests that *P. ingens* did not require complex control musculature throughout the wing membrane. Aerodynamic resistance, and hence increased drag, caused by trailing edge tendons would be minimal due to their posterior position on the wings. This solution to wing control would not, however, be unique in flight. Bat wings are also controlled by elastic fibres along the wing's trailing edge, (Vaughan, 1970 a, b). These are supplemented by the stress applied by the bat's hind limbs, which would appear equally likely for *P. ingens*.

Soaring Efficiency.—Further morphological comparison of *P. ingens* to bats reveals important structural differences. In bats, digits III through V extend posteriorly along the wing, bracing the membrane and reducing its tendency to stretch under pressure. No such skeletal control existed for *P. ingens*. Stretch leads to the development of twist, where angle of incidence increases distally out to the wing tips (Text-fig. 6). In wind tunnel tests where wind velocity was varied from 3 m/sec to 45 m/sec, results indicated that performance optimized within a specific velocity range. Examination of the wing during tests showed that above this optimal range, the wing twisted beyond 5° from base to tip, causing a deterioration in performance.



TEXT-FIG. 5—Lift vs. Drag. Note that while wing 10 has a high L/D ratio, its total force, C_T , is low.

The optimum angle of incidence could not be maintained along the full expanse of the wing. Stretch would also cause the position of maximum camber to shift posteriorly on the wing (Marchaj, 1964), reducing the critical L/D ratio. Bramwell and Whitfield (1971) suggest that the skin fibers would be aligned parallel to the wing bones, since an anterior-posterior stretched membrane would exert greater force on the metacarpal and phalanges, increasing the likelihood of buckling. Non-uniform stretch caused by the unidirectional alignment would also contribute to twist and loss of camber control. These three factors are responsible for the reduction in efficiency due to twist. In both soaring birds and soaring planes, $\sim 3^\circ$ of twist forms the maximum allowable limit (Conway, 1969).

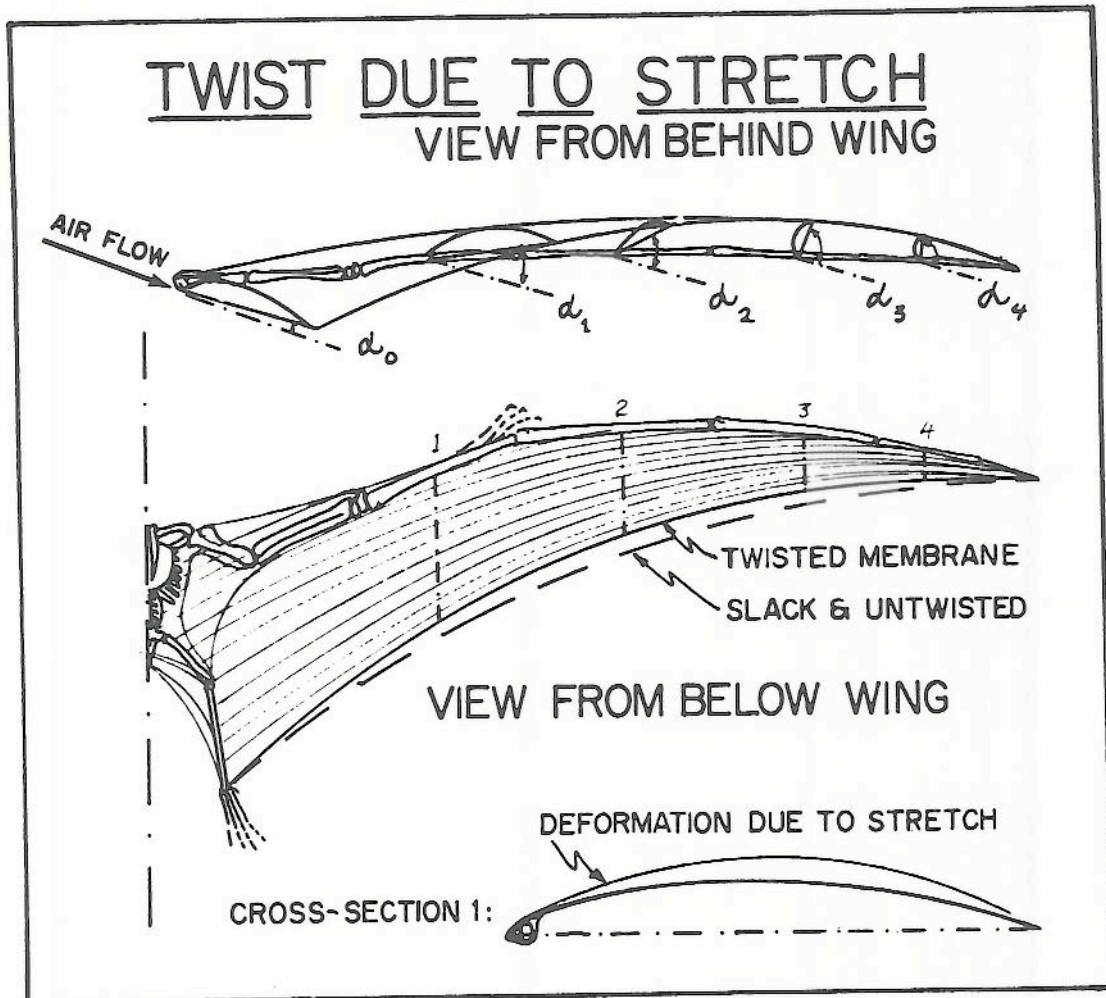
In discussing soaring animals, Gray (1968) states that elbow and wrist joints must remain fixed and rigid to maintain a constant camber and angle of incidence. Hankin and Watson

(1914) performed a taxonomic study of *P. ingens*' wing bones, and concluded that not only did the bones rotate, but that flexion at the ulna and humerus joint was inseparably linked to the rotation of the phalanges (Text-fig. 1). It would appear that *P. ingens* was not primarily adapted to the requirements of soaring or gliding flight, which demand rigidity, and has been the interpretation of all students of *Pteranodon* flight (Langley, 1901; Lucas, 1901; Seeley, 1901; Hankin and Watson, 1914; Matthews, 1920; Gray, 1968; Bramwell and Whitfield, 1971) and that flexion of the elbow may have played an instrumental role in flight.

Flapping Efficiency.—In flapping flight, the wings are in motion relative to the animal. On the upstroke, where the wings move forward of the center of gravity (or mass), C_G , of the animal, the wings experience a greater airspeed than the animal's body. In addition, the airspeed increases toward the wing tips, since they move the greatest distance through the arc inscribed by the wing during the wing-beat cycle. Since the wind direction results from the combined effects of the true air current direction and speed, and the direction and speed at which the flyer moves through the current, the angle of incidence will decrease distally. Thus twist, rather than being detrimental as in gliding and soaring, becomes obligatory in flapping. The same criterion exists for propellers, fans, and bird wings during flapping; in each case, the blade or wing twists distally. Whereas a bird must mechanically twist its wing, this occurs automatically in *P. ingens*. In bats, the proximal wing segment is braced by the humerus and radius, distally by digit V, and posteriorly by the hind feet and elastic fibers in the wing's trailing edge. This proximal region contributes lift, with a high angle of incidence and low L/D, whereas the distal region is flexible and twists, for a low angle of incidence and high L/D, producing the required forward thrust (Vaughan, 1970b).

Wind tunnel tests showed that absolutely no flexion was tolerable at the metacarpal joints while in flight, in order to maintain membrane tension and uniformity. Even a 2° flexion at the knuckle (metacarpal and 1st phalanx) would collapse the membrane, causing a total loss of lift. Thus, the wings could not be swept back for high speed flight.

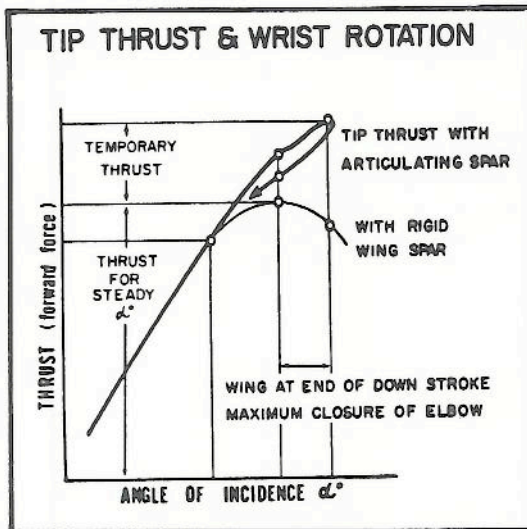
Intrinsic to past arguments against a flapping habitat for *P. ingens* has been the absence of a large sternum. Additionally, since flight



TEXT-FIG. 6.—Twist results in increasing angle of incidence distally along the wing, deteriorating performance. Membrane fiber alignment is represented by parallel lines. Deformation causes the maximum camber to shift posteriorly, reducing Lift/Drag ratio.

musculature in birds varies between 15–35% of the animals' weight, it was felt that this would bring *P. ingens*' total weight up to an exceedingly heavy 20–25 kgms (Langley, 1901). In bats, however, which exhibit many more skeletal similarities to Pterosaurs than do birds, the flight muscles comprise only 6–10% of the total weight (Vaughan, 1970). Vaughan finds that in bats, since the kinetic energy required for each wing stroke is reduced by decreasing the weight of the wing distally, metabolic economy is achieved by transferring the burden of wing control from centrally located muscles out through long, slender tendons along the wing bones. Weight is thus concentrated near the center of gravity. In

addition, four muscles, rather than two as in birds, serve as adductors for the important downstroke. Bats also lack a large sternum and deep chest, for only one out of the four adductors originates on the sternum. Thus neither the absence of a large sternum, nor the weight of propulsive flight musculature preclude flapping for *P. ingens*. Short (1914) had discarded the possibility of flapping flight due to the limitations in movement of *P. ingens*' wing bones. However, if the 140° motion allowable at the humerus-scapula joint in the vertical plane was accompanied by the 30° maximum flexion of the ulna-humerus joint, a complete wing-beat cycle can be reconstructed:



TEXT-FIG. 7—Suggested aerodynamic effect of the proposed tip thrust, revised from Marchaj (1964).

Downstroke—

- Shoulder: Down 140°
- Elbow: Down and forward 30° (maximum capability)
- Carpus: Rotation forward, adding camber.

Upstroke—

- Shoulder: Up 140°
- Elbow: Up and aft 30°
- Carpus: Rotation aft, streamlining, flattening wing.

Aerodynamic consideration of the flapping sequence leads to an additional possible flight adaptation: The phalanges, and to a lesser degree, the long metacarpal may have been flexible. The effect would have been to whip the distal portion of the wing, allowing a longer forward stroke than limited by the elbow joint, and would have increased the wing tip speed. This would offer an important reason for *P. ingens*' tremendous wing span and high aspect ratio; with increased wing span, greater wing tip deflection may have been possible without buckling the wing finger (digit V). This wing tip deflection would be very similar to the flexibility observed in bat wing tips (Vaughan, 1970b), and accomplishes the same function as the wrist flick of a pigeon (Brown, 1967).

Marchaj (1964) found in laboratory tests that if angle of incidence is increased abruptly, the character of the wing surface flow is altered if this quick change in angle of

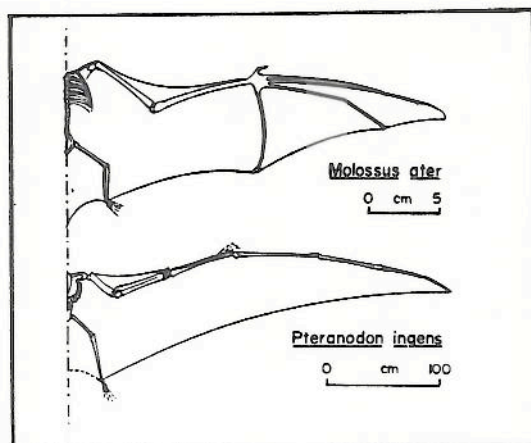
incidence occurs near C_L max. For a short time after angle of incidence has been increased (to a value which normally would have some separated flow), the flow adheres smoothly to the wing surface, with a corresponding increase in thrust (Text-fig. 7). The inseparably connected movements of the elbow closing and wrist flexion induces this increased angle of incidence, and suggests the possibility of a greater C_L max obtained in flapping flight than indicated by the wind tunnel tests. However, the C_L max of *P. ingens* is greater than twice the value Raspet (1960) determined for the Laughing Gull and Black Buzzard in flight.

Arguments which state that *P. ingens* could not have withstood the wing loadings associated with flapping flight (Short, 1914) which are higher than for soaring do not apply if limited flexibility occurs on the wing. Extreme bending posteriorly in the horizontal plane is limited by an unavoidable reduction in trailing edge tension, which would collapse the airfoil and reduce the load. Extreme bending in the vertical plane acts to reduce the vertical component of the lifting force, transferring it to compressive loads, and relieving tensile bending stress on the wing bone. Thus, if wing loading became excessive, the wing would have deformed, reducing the lift and high loading, forestalling buckling.

Another possibility in *P. ingens*' propulsive flight mode which is not available to birds (except in the lone case of the hummingbird) involves gaining lift on the back (up) stroke. Since the angle of incidence of the wing can be controlled by the leg, simply raising the leg during the backstroke would allow the generation of lift. In wind tunnel tests of wing 5 with reversed flow, a L/D of 2 was produced with the wrist rotated forward as in the downstroke, and a L/D of 3 with the wrist rotated as expected for the upstroke. The results indicate that it would have been possible for the reptile to gain increased lift per wing-beat cycle, without reducing propulsive force. Whether this maneuver occurred depends on the stability problems associated with raising and lowering the hind limbs, which would presumably require large dorsal recovery muscles.

FLIGHT SPEED

The stall speed, below which an animal can no longer maintain level flight, can be calculated from wing 5's C_L max (3.85), the approximate area of the wings and body section



TEXT-FIG. 8—Long flight endurance, high wing loading, and high aspect ratio characterize the Molossidae (free-tailed bats). Morphologic similarities to the wing of *P. ingens* in planform and skeletal structure are evident.

between them, S , (5.6 m^2), the density of air, ρ , and estimated *P. ingens* weight values, W , utilizing Gray's (1968) relation:

$$W = \frac{1}{2} C_L S \rho V^2$$

WEIGHT

(lbs):	25	30	35	40	45	50	55	60
(kgms):	11.3	13.5	15.9	18.2	20.4	22.7	25	27.2

SPEED

(m/s):	4.1	4.4	4.9	5.2	5.5	5.7	6.1	6.4
(mph):	9	10	11	11.5	12	13	13.5	14

These stall speeds are 30% less than Bramwell and Whitfield's (1971) figure (7 m/sec for 15.9 kgm) based on theoretical predictions, and suggests that landing and take-off speeds would be less than previously determined, reducing the difficulties associated with these maneuvers. The transition into turbulent flow, considered previously in this paper, combined with *P. ingens*' inability to reef or in any way reduce its wing area, suggest a maximum speed of $\sim 15 \text{ m/s}$.

ESTIMATION OF WEIGHT

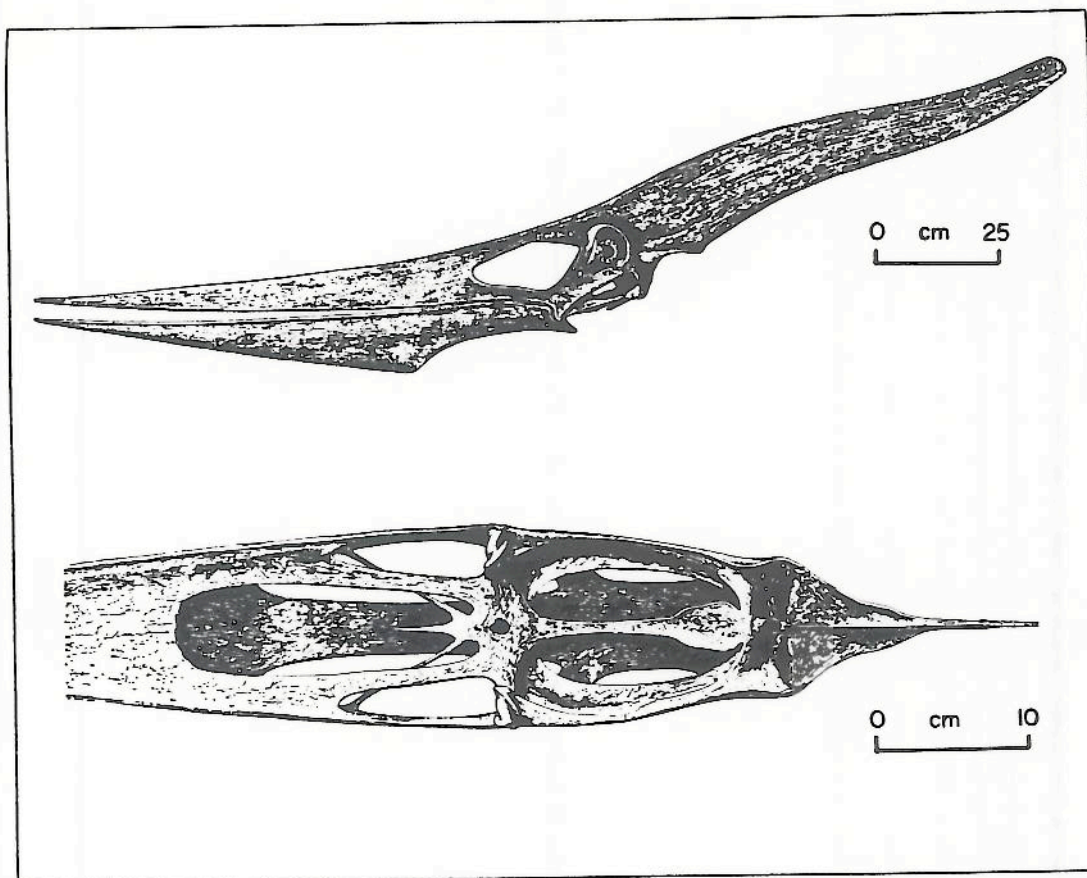
The striking skeletal similarities between the free-tailed bats (Molossidae) and *P. ingens* (Text-fig. 8) suggests similar adaptations to the flapping flight mode. Of particular interest are their high AR wings (aspect ratio; (wing span)²/wing area). These wings are capable of developing very high lift, while tending to minimize drag. Vaughan (1970b) considers the long, narrow wings to be an

adaptation for flight endurance, with a consequent sacrifice in maneuverability. Finds of fish teeth in *P. ingens*' jaws suggest that the reptile might have maintained an oceanic habitat, where long flight endurance is stressed (Miller, 1971). Similarities in structure and habitat may imply similar wing loadings (weight/wing area). *Eumops perotis* (Molossidae), similar in its flight characteristics and morphology to *Molossus ater*, has a wing loading of 0.266 gm/cm^2 and an AR of 10. With the same wing loading, wing area of $56,000 \text{ cm}^2$, and an AR of 9, *P. ingens* would have weighed 15 kgm (33 lbs.). Bramwell and Whitfield (1971) suggested 15.9 kgm (35 lbs.) by combining separate estimations of bone, muscle, and membrane weight.

TAKE-OFF

Instrumental to the take-off process is the animal's ability to raise its wings and shift them forward of their normal flight position. The center of effort, C. E., moves forward of the center of gravity, C. G., and an upward pitching moment develops which counterbalances the nose-down pitching moment of the highly cambered wings (Raspel, 1960). This might have been accomplished in *P. ingens* by moving its large head (Text-fig. 9) posteriorly, the head situated above the C. E., causing the C. E. to be positioned anterior to the C. G. In birds and bats, the wings are raised so that immediately upon lift-off, the body will swing forward, increasing the angle of incidence for a climbing orientation. *P. ingens* was extremely limited in its take-off capabilities, for the plane of its wings could not be raised without angling each wing up, resulting in a loss of lift, nor could the wings be raised to a great degree because the membrane was rooted to the hind limbs.

In order to initiate flight without the aid of a breeze or updraft, *P. ingens* would have to attain its stall speed ($\sim 4.5 \text{ m/sec}$ for 15 kgms total weight) along its wings. A running take-off would have caused difficulties since the angle of incidence was controlled by each leg's position, a different direction of force being produced on each wing simultaneously, varying with every step. By alternately raising and lowering each wing, *P. ingens* may have been able to overcome the problem, but this method would have been awkward and complex, and it is doubtful if the necessary speed could be reached with such apparently weak leg bones (Williston, 1891).



TEXT-FIG. 9—Eaton's (1910) drawing of the skull of *Pteranodon ingens*. Upper. As seen from the left side. Note large lightening holes anterior to the eyes (external nares, antorbital fenestra). Lower. The palatal view. Note the spiraling upper jaw hinges, and internal trussing for maximum strength/weight ratio.

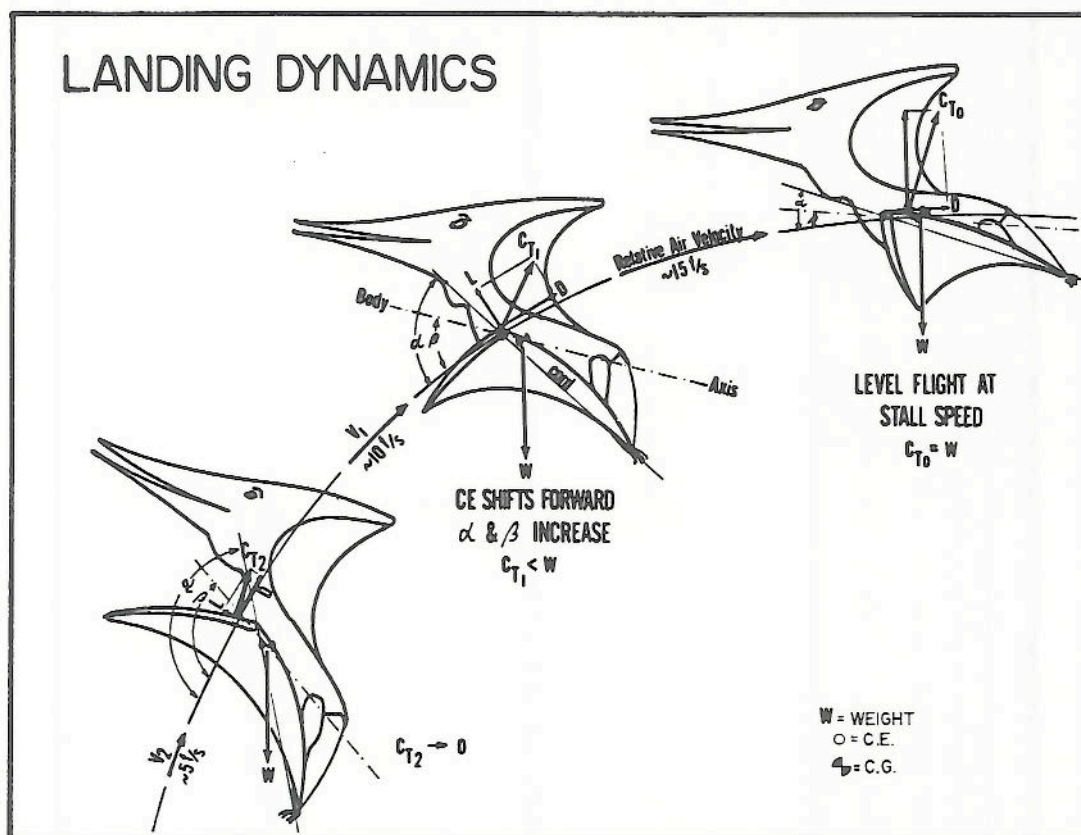
Bramwell (1970) suggests that *P. ingens* could have simply raised its wings while facing a breeze equal in velocity to *P. ingens*' stall speed, and it would become airborne. However, the boundary layer of the ground (the dissipation of wind velocity due to ground friction and interaction) generally extends above the 1 meter height of *P. ingens*, causing turbulence and a velocity reduction which would limit this assistance to take-off (Marchaj, 1964). As has been suggested by Langley (1901) the reptile could easily have fallen forward off a cliff or precipice utilizing an air current up-draft, but this would preclude take-off on a windless day, from a sheltered beach, inland lagoon or tidal flat.

For *P. ingens* weighing between 14 and 15 kgm, with a wing span of 7.5 m, and a wing-beat cycle of one stroke-per-second, a tip speed of 12 m/s could be maintained. The distal por-

tions of the wings would be well above stall speed, enough so that an average 6 m/s could be attained, allowing for lift-off. From these calculations, then, a wing-beat cycle of one stroke per second would have been necessary for unassisted takeoff.

LANDING

Examination of *P. ingens*' landing posture supplies strong evidence for bipedalism: if the reptile were to land on all fours, it would have had to retract the wing finger at the knuckle, which would collapse the wings, the animal impacting the ground without any lift. It is essential that the wing remained at its maximum angle of incidence for greatest C_T throughout the landing maneuver. At a weight of 15 kgm, deceleration and altitude loss ensues following a drop below ~ 4.5 m/sec air



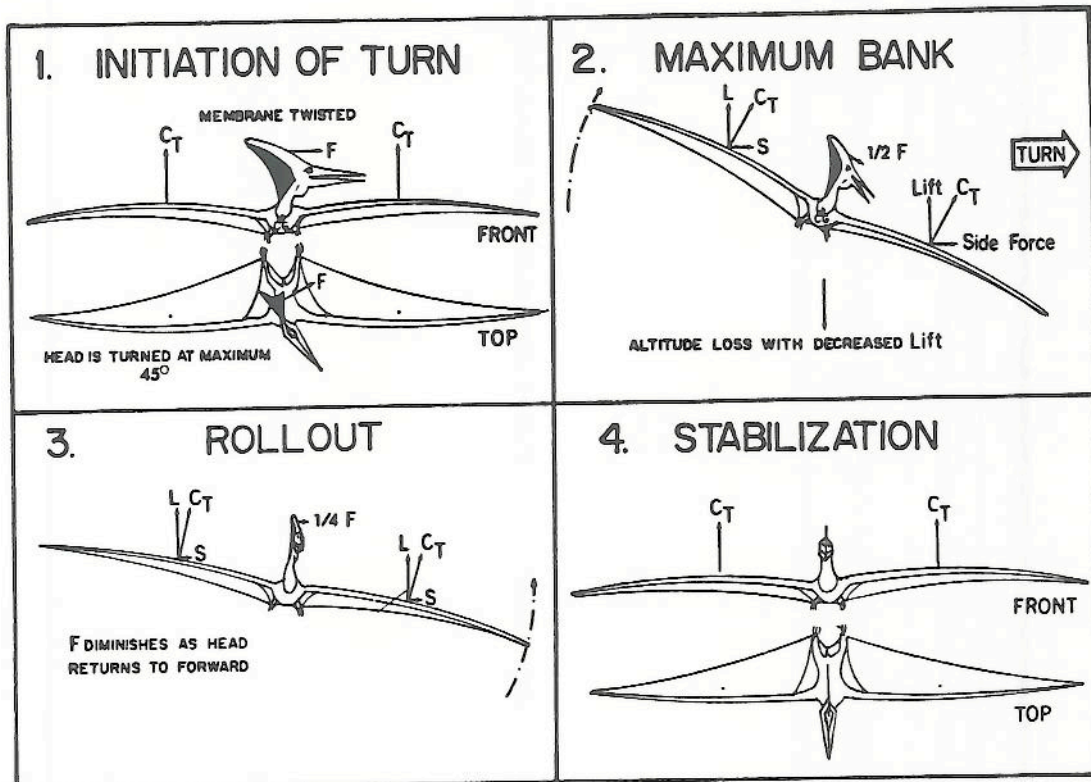
TEXT-FIG. 10—Suggested sequence for the landing maneuver, with increasing α and β , decreasing forward velocity and total force, C_T , and shifting Center of Effort, C. E. (for a body weight = 15 kgm).

speed (Text-fig. 10). How did *P. ingens*' hind limbs absorb the load upon landing? The slender femur and tibia might be expected to fracture with the compressive loads encountered (Williston, 1891). However, if stress was absorbed by the femur pivoting outward in response to the load, the tibia could remain vertical. Elastic fibers suspended between the femurs could have acted as a shock absorber, as in bats (Vaughan, 1970b). The landing stance, with legs spread, would also ease membrane tension so that upon touch-down, the wings' membranes would slacken, arresting lift and keeping the animal from being blown over by any prevailing wind. The lowering of the legs into the landing stance simultaneously increases the angle of incidence and C_T which accomplishes automatically what birds must do mechanically.

THE SKULL AND CREST

A most striking and unusual feature of *P. ingens* is the immense skull, with its supra-

occipital crest (Text-fig. 9). The function of the two meter long, approximately three millimeter thick crest has been the subject of much discussion in the past. O. C. Marsh (1910) considered it to be a steering aid, while Short (1914) felt its purpose could have been merely ornamental; Eaton (1910) attributed it to muscle attachment area for the jaw closing muscles. Bramwell and Whitfield (1971) conducted a wind tunnel experiment to test the hypothesis first proposed by Matthew (1920) that the purpose of the crest was to reduce the size and weight of the neck musculature by counterbalancing lateral torque developed about the neck when the head was turned. However, the proposed counterbalancing effect would necessitate maximization of C_D and not C_L , for the crest would be acting solely as a drag device in Bramwell's reconstruction. Therefore, the most efficient planform for the crest would have an AR of 1, for optimum pressure distribution. But the crest has an AR of 0.26 (since span is measured perpendicular to the



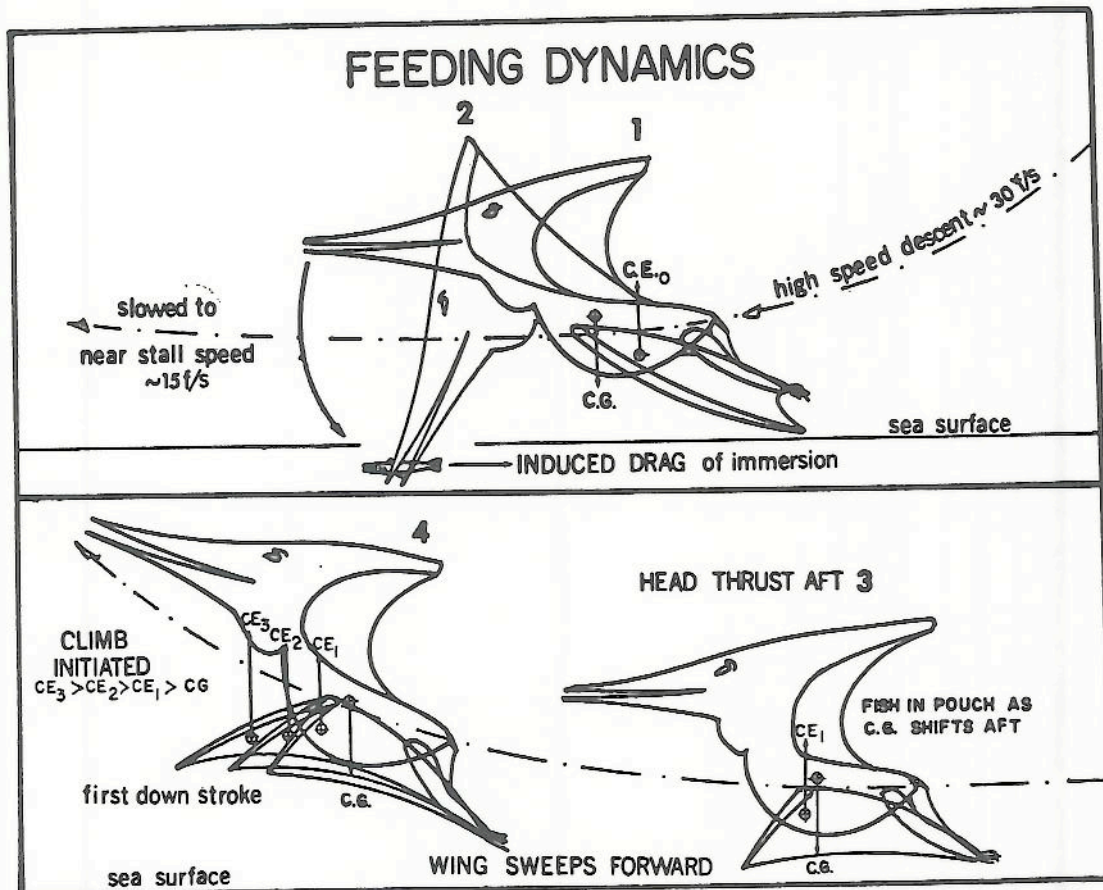
TEXT-FIG. 11—Suggested turning sequence, demonstrating the effect of the crest and twisted membrane in initiating a bank which enables the turn. The altitude loss is proportional to the reduction lift during the turn.

air flow), which would suggest that it is extremely inefficient as an airfoil of this kind. The low AR of the crest would contribute to increased tensile bending on the 3 mm thick bone while adding only a small amount of drag. Their test also indicates that the crest has no balancing effect until the head is turned past 90°. However, at this angle, turbulence generated along the two meter length of the head would seriously disrupt the animal's balance, lateral stability, and speed.

Dynamic analysis of the past restorations of *P. ingens* (Text-figs. 1 and 2) show that the skull has been placed too far forward of the center of effort, causing the C. G. to occur in front of the C. E. The C. E. must be in balance with the C. G. for level flight, and the weight should be concentrated in the center as much as possible to dampen pitch. The large skull had a profound effect on both weight position and concentration. In Eaton's osteology of *P. ingens* (1910), he commented that the atlas and axis should connect with the skull at a right angle, yet in all restorations

this angle is acute. It seems that the restorers endeavored to place the head in the horizontal plane of the body, which resulted in a streamlined appearance which is common on fast flying birds. However, since other evidence presented here indicates that *P. ingens* was not a fast flying creature, streamlining of its body would be relatively unimportant (a slow bird, such as the pelican, is not streamlined).

In a bird, the head is essentially fused to its body, due to the compression of its neck, and turning the head does not produce an aerodynamic force of any magnitude (Gray, 1968). However, if the head is turned on the present restoration of *P. ingens*, a strong moment is produced due to the anterior position of the head relative to the C. G., which would immediately upset the balance of the flying creature. Eaton (1910) had also mentioned the possibility of a membrane suspended between the supraoccipital crest and back. Aerodynamic considerations which follow suggest that such a membrane would have been instrumental to turning and feeding.



TEXT-FIG. 12—Suggested sequence for the feeding maneuver. As the sea becomes rougher, longer jaws provide a tremendous advantage in avoiding wing clipping by waves. Pouch keeps the added weight of the fish near the C. G.

Turning.—There are two aerodynamic requirements associated with turning: They are, (1) the development of a side force to overcome forward inertia, exerted perpendicular to both the lifting force and the longitudinal body axis of the flyer, and (2) the ability to position the body axis into the turn, reducing drag and slip. Birds accomplish both of these functions through the tail, which twists, causing the animal to roll on its body axis and bank. The tail also pivots to one side, repositioning and streamlining the body during the turn. The use of the tail incurs very little increased drag yet sacrifices some maneuverability, due to its posterior position.

Due to *P. ingens*' great wing span, there would be more limitations on its maneuverability than for a bird. Thus, a responsive turning system becomes a more important adaptive advantage for the reptile. With *P.*

ingens' head positioned above its body, the reptile would simply have to turn its head in the direction it desired to fly, and both turning requirements would automatically be fulfilled. This is because the membrane would twist, developing its greatest side force at the top of the crest. The lever arm effect of the side force would increase the ability to roll the reptile about its body axis, and the rudder vane effect of the membrane would position the body axis, into the turn (Text-fig. 11). Since the crest was located above the C. G., no adverse yaw or nose-down pitching moments would have developed. The membrane also would aid in the suppression of yaw during straight flight; this is critical due to *P. ingens*' short body and long wing span. The lever arm effect of the membrane means that very little force would have been required to effect a turn.

When the crest is considered with its at-

tached membrane, the AR of the total airfoil (crest and membrane) would be ~ 1.1 , which should ensure its efficiency as a lift (rather than drag) producing steering device. Unlike Bramwell's reconstruction (1971), the crest's function as interpreted here is to develop C_L max, while developing only a minimum amount of drag, and thus causing only slight loss of speed. This analysis demonstrates the functional purpose of having the crest raised, relative to the jaws; the area of maximum force on the crest is above the skull's wind turbulence shadow.

Feeding.—The elastic membrane would have acted to restrict the movement of the head. If the head were turned at an angle of 90° or greater in any direction, as Bramwell and Whitfield (1971) have pointed out, the neck muscles would be at their weakest, causing difficulties in repositioning the head. This circumstance would be prevented by the presence of the membrane.

An essential and uninvestigated adaptation of *P. ingens* is its feeding habits. As its feet had no opposable digit, probably had little muscular strength (Williston, 1891), and could not have reached the jaws in flight without collapsing the wing, the reptile must have fished with its jaws. However, this interpretation introduces three severe problems: First, the induced drag caused by even a momentary immersion of the jaws into the water would drastically reduce the reptile's forward progress. Secondly, the added weight of the fish, held in the jaws forward of the C. G., would make the essential shift of the C. G. behind the C. E. more difficult, which *P. ingens* must do to arise from the water surface. Third, the induced drag of the immersion might push the head under the body.

The membrane is at maximum tension as the head is extended forward and down. Upon immersion, tension on the membrane would spring the head up with adequate force to thrust the head aft of the C. G., enabling stabilization and the climb. *P. ingens* had to shift the fish sufficiently aft to maintain the C. G./C. E. balance. Eaton (1910) noted that opening the jaws of the animal caused a widening of the lower jaw posteriorly, as is the case for a pelican, allowing the fish to slide posteriorly, whereupon a pouch immediately anterior to the neck would keep the fish weight sufficiently close to the C. G. (Text-figs. 9 and 12). The pouch has been absent on all previous reconstructions, although Eaton (1910) had suggested it.

Evolution of the Skull.—From the early Jurassic to the late Cretaceous, the Pterosaur shows a gradual change from short parabolically shaped of the early *Dimorphodon* and *Scaphognathus*, to the long and narrow jaws accompanied by a supraoccipital crest on the later *Pteranodon* species. This analysis suggests that the change was the result of a transition from small, terrestrially feeding forms to larger, tailless species, where the minimization of the induced drag when feeding on the water, and the need for low altitude maneuverability took precedence over low form drag supplied by the earlier skulls.

THE POWER FOR FLIGHT

The dynamic analysis presented here indicates that *P. ingens* could not rely entirely on soaring for its locomotion as has been previously suggested. Limitations due to twist, camber placement, and planform preclude excellent soaring performance. With the development of C_L max at L/D between 8 and 10 and estimated speeds between 4.5–15 m/s, the reptile's predicted soaring performance falls short of today's soaring birds with L/D ratios of ~ 35 , and speeds above 30 m/sec (Brown, 1963). *P. ingens* was, however, structurally and aerodynamically suited for efficient, although slow, propulsive flight. But could a reptilian muscle generate the power output needed for flapping flight?

In an effort to answer this question, an attempt is made to establish the range of *P. ingens*' possible horsepower and muscle efficiency.

$$\text{Power} = \frac{C_D}{C_L} \times \text{Weight} \times \text{Velocity} \quad (\text{Gray, 1968})$$

From this equation, the power produced by *P. ingens* flying near its stall speed, for a weight of 15 kgms:

$$\frac{1}{4} \times 15,000 \times 450 = 843,750 \text{ cm/gm/sec} \approx 0.1 \text{ horsepower (hp)}$$

From his studies of present animals, both capable and incapable of flight, Wilkie (1959) determined that the minimum power required for flight, in horsepower is:

$$\text{hp} = 2.33 \times 10^{-3} W^{1.167}$$

The minimum required power for *P. ingens* would thus be 0.07 hp. From these methods,

then, *P. ingens* may have had 30% greater power than needed for flight, when near its stall speed.

FLIGHT STABILITY

A gliding animal is defined as stable if, when it is disturbed from its course, the forces acting upon it tend to restore it to that course without active muscular contractions in the animal. In stable flapping flight, the forces acting on the animal tend to restore it to its course without any modification to the flapping cycle (Smith, 1952). Stability requires a reflex response of the wings to a change in the environmental conditions which affect flight. However, maneuverability depends on the ability of an airborne creature to actively change its line of flight by altering the position or motion of its wings relative to the air (Brown, 1963). Therefore high stability and high maneuverability are mutually incompatible.

For both bats and birds, a lifting surface posterior to the center of effort, a uropatagium or tail respectively, has, as its primary function, stability (Vaughan, 1970a, b; Gray, 1968). *P. ingens*, however, was not only tailless, but lacked sufficient area (relative to its wing surface) between its hand limbs for a large and efficient uropatagium. A stable flying creature is also severely limited in size due to its higher stall speeds, which mean less control over its landing speed (Smith, 1952). As a tail adds weight without providing any appreciable lift, it would have deterred from *P. ingens'* flying ability. But its loss would cause a reduction of stability, which must be met by increased muscular and cognitive control. Smith, (1952) has found that an animal can only lose its stability if it has a highly evolved sensory and nervous system. This suggests that *P. ingens* was a highly evolved, maneuverable and unstable flyer.

CONCLUSION

Pteranodon ingens occupied a unique position in the evolutionary pageant. Flight imposes stringent demands upon the structural integrity and muscular capability of an animal. Moreover, the exigencies of life on the wing are manifest as the animal increases in size. Only through the evolution of the most efficient possible structure and propulsive flight mechanism could a Pterosaur have attained the greatest weight and wingspan of any creature to fly. The requirements of take-off, feeding, turning, and landing take precedence over all other morphological parameters. Only in such

a rare case as this can the principles of functional morphology be quantitatively and exclusively applied to a species; *P. ingens* could not afford to be inefficient. For this reason, wind tunnel and biomechanical data can be offered as a criteria for paleo-reconstruction. The animal envisioned in this paper represents the most efficient solution to the problems of an airborne habitat consistent with its fossil record.

The successful exploitation of a niche which has never again been filled does not imply specialization of form or function. Rather, it attests to a tenuous and extraordinary balance of the rigorous requirements of large animal flight. An animal of long flight endurance, a slow but highly maneuverable flapping species emerges: the product of one hundred and fifty million years of reptilian adaptation to flight.

ACKNOWLEDGMENTS

I would like to thank the following people who have offered advice, assistance and criticism: John Imbrie, who provided research funds, William L. Balsam, James W. Head, and Jan A. Tullis, from the Department of Geological Sciences at Brown University; T. F. Morse, Donald Avery, and Paul Paslay, from the Division of Engineering at Brown University; John H. Ostrom, Peabody Museum of Natural History; Douglas A. Lawson, who reviewed this paper; Craig J. Mathais, for computer consultation; Sharon Lack and Robert Schwarz for encouragement.

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MANUSCRIPT RECEIVED DECEMBER 11, 1973

REVISED MANUSCRIPT RECEIVED AUGUST 2, 1974