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ON THE FLIGHT OF PTERODACTYLS.

BY

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It is perhaps unfortunate, from the point of view of aviators, that the extinct flying reptiles known as "pterodactyls" or "Pterosauria" no longer exist. There can be no doubt that in the case of the more highly evolved members of the group the organisation was more specialised for flight than that of any other animal of which we have knowledge. Other flying animals can walk, run, or swim, besides fly. But in the case of the higher pterodactyls their structure is such that it is difficult to understand how they can have had any other means of progression than flying. With a body little larger than that of a cat they had a span of wing asserted in some cases to have reached 21 feet [6.4 m] or more.[1] These huge wings were so constructed that it was impossible for them to be furled against the body as happens with the wings of birds and bats. Only the outer half of each wing could be bent backwards in the direction of the body (Fig. I). With such partially furled wings it may be asked how they could possibly swim if they ever alighted on the water over which they flew.

That pterodactyls were incapable of progressing as quadrupeds is proved by the fact that, as will be further explained below, the fore limb was incapable of moving in a fore and aft direction at either the shoulder or elbow joints.[2]

If they ever walked on their hind legs they could only have done so with the wings extended, as otherwise the wing tips would have trailed along the ground.

Perhaps the most feasible method of progression for them when on land is that, having alighted on their feet, they fell over on their stomachs and pushed themselves along, after the manner of penguins, by means of their hind legs, perhaps with an occasional slight lift from the wings for surmounting an obstacle.

That they could hang by their hind legs from the boughs of trees, as is the custom with bats, is improbable for various reasons. It is not every bough that could support their weight, which in the larger specimens is supposed to have reached 20lbs []. A bat flies with head first and hind legs stretched out behind. In order to grasp the bough with its feet it has to check speed ahead, which it does by "poise-flapping" at the same time rotating round the transverse axis. As soon as its feet are thus brought forward they grasp the bough and the bat rapidly furling its wings falls over in one direction or another to reach the head downward position. But in view of the large span of its wings the pterodactyl could only attempt "poise-flapping" above the topmost twigs of the tree, which twigs would be quite incapable of supporting its weight. If it chose a bough of sufficient size therefore nearer the trunk it is quite certain it could only have attempted poise flapping with imminent risk of tearing or breaking its wings.

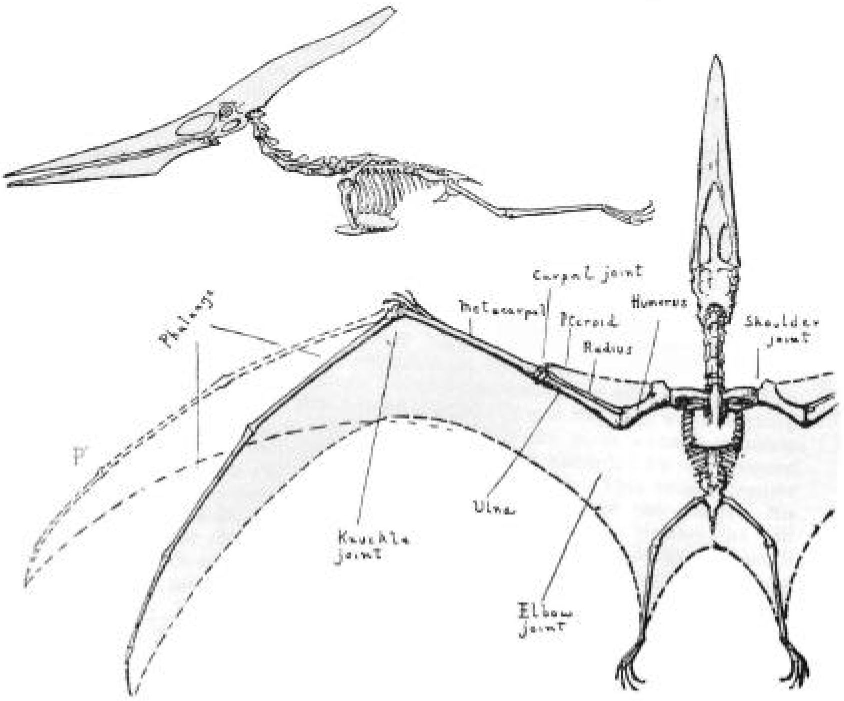

FIG. I. PTERANODON. VIEW FROM BELOW, AND SIDE OF THE BODY WITH WING REMOVED.

On the other hand, there can be no doubt that they were fully adapted for life in the air. Throughout their organisation weight-saving has been carried to an extreme. The hollow air-filled wing bones of vultures were heavy columns compared with the delicate empty tubes that supported the wings of pterodactyls. These tubes were made of hard bone material scarcely thicker than a visiting card. At the extremities the bones were strengthened internally by delicate struts and bands of bone of paper-like thickness. The bones of the hind limb, the vertebrae, and even the phalanges of the wing-finger were hollow and filled with air. Striking illustrations of these facts may be seen in the specimens exhibited in the British Museum (Natural History), South Kensington [Natural History Museum, London].

Remains of the larger pterodactyls are found in some cases in strata of marine origin under circumstances that make it probable that they habitually flew at some such distance as a hundred miles from the nearest land.[3] They seem to have been mainly fish-eating in habit.

In view of the extreme specialisation of the pterodactyls for flight the construction of their wings is a matter of great interest. Owing to the above-described delicacy of the bones the remains met with as fossils are usually so crushed that it is impossible to discover the mode of action of the different joints. Some exceptionally perfect examples of the bones of the pterodactyl Ornithodesmus [Istiodactylus] have recently come into the possession of the British Museum (Natural History). From the study of these and other specimens we are now in a position to describe the movement of which the different joints of the wing were capable. Our account is founded entirely on the Cretaceous forms. The articular surfaces are described from uncrushed specimens in perfect preservation from the English Wealden and Cambridge Greensand. The different specimens agree in the shape, number and arrangement of their articular facets, and further agree exactly with those of similar bones of Pteranodon in the British Museum (Natural History). Ornithodesmus is stated by R. W. Hooley[4] to have had a span of five metres “Allowing for the natural curve.” If the wing bones were placed in contact, end to end, in a straight line, a span of more than five metres would be obtained. But as the bones of the wing were habitually held in a slightly flexed position at the different joints Hooley reduced his estimate to a span of five metres.

As indicated by the name "pterodactyl," the wing is formed by the bones of the arm together with the phalanges of one enormously elongated finger. The structure of the wing was such as to permit movement at the shoulder, elbow, wrist, and knuckle joints (Fig. I). The wing-finger is formed by four phalanges, but these bones were fixed together by bony union in some cases and there is no reason for thinking that movements could occur in any case at the different joints of the finger.

In the case of birds and bats the shoulder joint is a ball and socket joint. Thus the wing can not only be flapped up and down, but it can also be advanced and retired. As has been shown by one of us such advancing and retiring is used by the bird or bat for the purpose of changing the position of the "lift" in relation to the centre of gravity and for thus causing movements round the transverse axis.

But in the case of the later pterodactyls the shoulder joint was a hinge joint that only permitted motion vertically up and down. A wide range of such movement could occur as in the shoulder joint of birds. In that there is absolutely no sign of curvature of the facet of the joint in the anterior posterior direction, we regard it as certain that no advancing or retiring of the wing could occur at the shoulder joint of the large pterodactyls. The flapping up and down at the shoulder joint was in a perfectly vertical direction. Thus, movement at this joint was suitable for high speed flapping flight. Flapping downwards and forwards, which is necessary for slow speed flight of birds, could not be accomplished by movements of the shoulder joint of pterodactyls without further adjustments. It may be noted that there was no possibility of any movement of flexing backwards of the wing against the body as occurs at this joint in birds. That is to say, pterodactyls could not furl their wings against the body by movements at the shoulder joint.

We will now consider the elbow. In the case of birds the elbow is a hinge joint that permits of extending and flexing movements in a horizontal plane. Flexing at this joint is used in furling the wing. In the case of pterodactyls the elbow joint was also a hinge joint. The direction of permissible movement was not horizontal as in birds. It was not vertically up and down as at the shoulder joint of pterodactyls. It was between these two directions. Whereas flapping downwards at the shoulder was vertically downwards, flapping at the elbow was not vertically downwards but in a direction that made an angle, so far as can be judged, of nearly twenty degrees with the vertical.[6] Thus, movement at the elbow joint would five flaps in a downwards and forwards direction. If there was nothing more to be said we might conclude that such flapping downward and forward occurred and was required for slow speed flight, as in the case with birds and bats. But before drawing this conclusion the matter requires discussion.

In the first place birds advance their wings for slow speed flapping flight both to compensate for the travelling backwards of the lift as speed decreases and also in order that the flapping should produce more lift qua [sic] flapping proportionate to the decrease of "pull" with its consequent decrease of life [sic] due to gliding. That a gliding action and consequent lift occurs during flapping flight is shown in "Animal Flight," p. 222. Now the above suggestion as to the method of slow speed flapping in pterodactyls is not excluded on the ground that the suggested method would produce no "rotation up" round the transverse axis. It would be an advantage to the pterodactyl if it could increase lift qua flapping while keeping the ling axis of its body horizontal and therefore in the most suitable position possible for speed ahead. But the above suggestion is excluded on the ground that it takes no account of the backward travel of the lift. This would require to be compensated by an advance of the wings or part of the wings. No advancement is possible at either the shoulder or the elbow joints. Neither, as will be shown below, could there be advancement at the wrist joint lasting through both the up and down strokes. But advancement could be produced, as will be explained in a later paragraph, by increase of extension of the outer part of the wing by movement of the knuckle joint. But if this occurred there would be rotation round the transverse axis and flapping from the shoulder joint would then be downwards and forwards. Hence, the suggested movement at the elbow joint would be superfluous.

In the second place the range of movement at the elbow joint is only about 30 degrees. This is quite sufficient for ordinary flapping flight, whether slow or fast. It would only be sufficient for "half flaps," which in the case of birds only occur in flight under certain infrequent atmospheric conditions.

Thus the first suggested explanation of the movement at the elbow joint having failed we must look for another. Let us first examine more minutely the structure of the joint.

The bones that enter into this joint are the arm bone or humerus, and the boned of the forearm, namely, the radius and ulna. In the human arm the outer end of the radius is not fixed firmly to the outer end of the ulna. The attachment permits of a certain amount of sliding so that the end of the radius can slide round the end of the ulna. This movement is connected with rotation of the hand by movement at the wrist joint. In Pterodactyls the radius had no power of movement of this nature. But the radius could slide in the direction of its long axis through a distance of nearly a quarter of an inch [6 mm] (in Ornithodesmus). The long axis of the two bones the radius and ulna are parallel to each other and remain parallel during this movement. In other words the radius could take up two extreme positions which we may describe as the "inward position" and the "outward position." The elbow, as stated above, is a hinge joint. The surface with which the radius articulated is not of quite regular curvature. The irregularity is such that the radius assumes the "inward position" when the forearm is raised up as far as possible. It assumes the "outward position" when the forearm is directed backwards as far as possible.

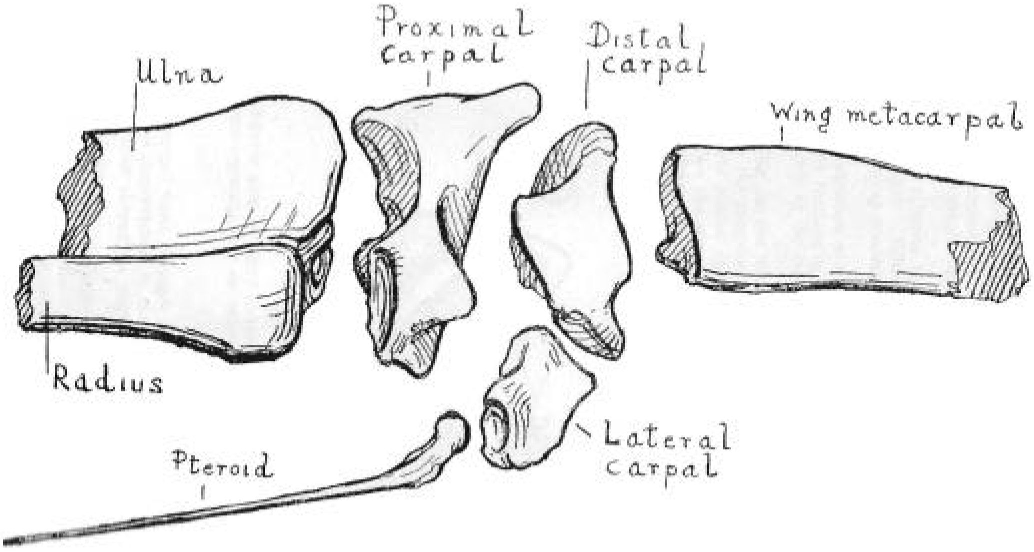

FIG. 2. ORNITHODESMUS. VIEW FROM IN FRONT OF THE LEFT WRIST JOINT WITH BONES DISARTICULATED.

That this in-and-out displacement of the radius actually occurred is proved by the fact that there are two articular surfaces on the radius and ulna where they come into contact with each other near each extremity, which surfaces must obviously have facilitated the movement.

The fact that the radius had this singular power of movement obviously throws no light on the function of the elbow joint. To discover the meaning of the movement it is necessary to consider the effect of the movement of the radius on the bones of the wrist joint.

A front view of the wrist joint with the bones disarticulated for the sake of clearness is shown in Fig. 2. The distal[7] end of the radius is seen lying in front of the distal end of the ulna. On the outer or wing-tip side of the joint is shown the proximal end of the metacarpal of the wing finger. Between these bones are shown the two chief bones of the wrist which are known as the "proximal carpal" and the "distal carpal".

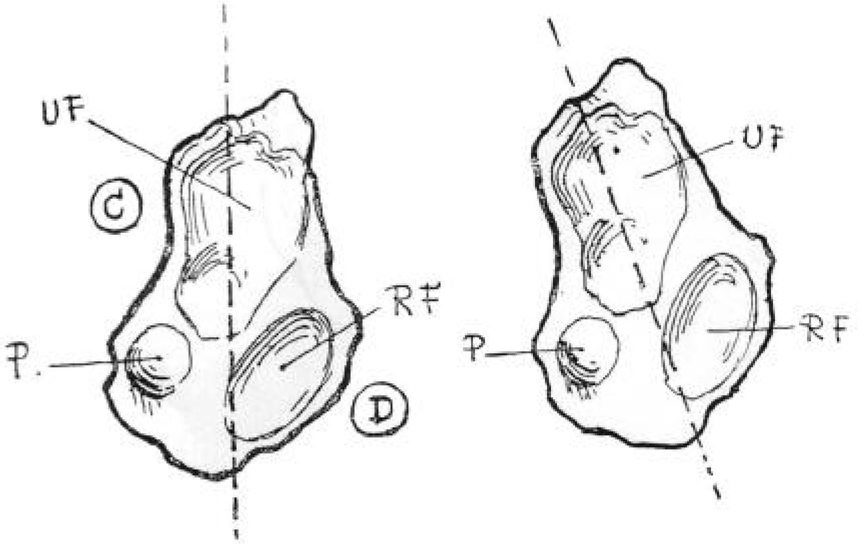

FIG. 3. VIEW FROM THE BODY SIDE OF LEFT PROXIMAL ACRPAL BONE. **A** BEFORE AND **B** AFTER RECEIVING PUSH FROM RADIUS.

We must first consider the movement that occurs on the proximal side that is on the body side of the proximal carpal.

Fig. 3. shows the inner surface of the proximal carpal as seen in end on view from the direction of the body of the animal. At the lower and posterior part of this surface is seen the projection P. This fits into the corresponding depression on the end of the ulna. Thus, the lower side of the end of the ulna was pivoted at this spot. The upper part of the outer end of the ulna rested against the curved surface UF. The outer end of the radius rested against the facet RF.

As stated in the previous paragraph the radius can slide for a short distance in the direction of its own length. When it does this it pushes RF. This push from the radius has the following consequences.

Firstly, there is a slight rotation of the wrist (relative to the ulna) round pivot P. The direction of the rotation is indicated by the two diagrams in Fig. 3. It results in a rotation upwards of the metacarpal bone round its long axis.

Secondly, there is rolling in the direction DC. Before the movement the letter C and the letter D in the diagram may be regarded as having been equidistant from a pair of points placed one on each side of the end of the ulna. After the rolling one point on the ulna is further from D while the other point is nearer to C. This movement is equivalent to a retirement combined with slight depression of the outer part of the wing. In the more perfect specimens of the smaller pterodactyls in the South Kensington Museum the wing bones are seen to be retired at the carpal joint through an angle of between 30° and 40° in the absence of any sign of displacement of the bones. It is probable that in life the bones could only be retired through a slightly smaller angle.

In order to avoid confusion it is advisable to refer to the part of the wing supported by the metacarpal (Fig. I) as the “wing-front.” The term may also be applied to the part of the wing near the carpal joint in gulls. In each of these cases the wing-front probably played a part in the wing adjustments similar to that of the wing of vultures.

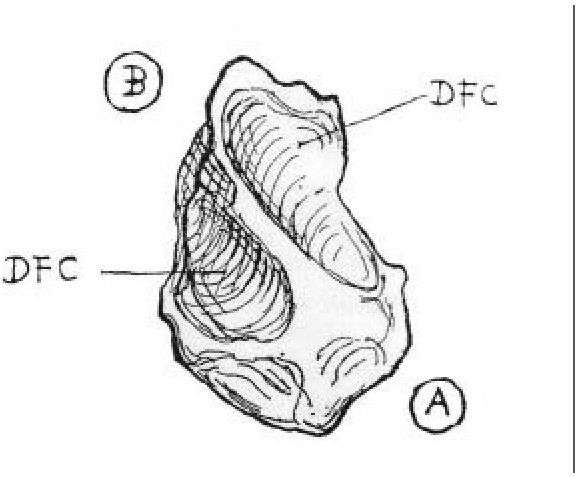

FIG. 4. VIEW FROM WING-TIP SIDE OF LEFT PROXIMAL CARPAL BONE. DFC, DFC, FACETS FOR ARTICULATION OF DISTAL CARPAL BONE.

Now let us consider the movement at the outer surface of the bone we have just been discussing. A view of this surface of the proximal carpal bone is shown in Fig. 4. There are two articular surfaces DFC separated by a ridge. Movement of the outer wing bones at this joint took the form of a rolling movement in the direction BA. The base of these wing bones may be regarded as equidistant from the letters A and B before the movement. After the movement part of the base has approached A and part had receded from B. This rolling movement was of very slight extent. One of the articular surfaces was larger than the other. It is probable that slight sliding occurred on this larger surface. The first of these movements must have slightly retired and markedly depressed the wing-front. The second must have rotated it upwards.

The movements just described were those between the proximal and the distal carpal bones (Fig. 2), the so-called "intercarpal joint."

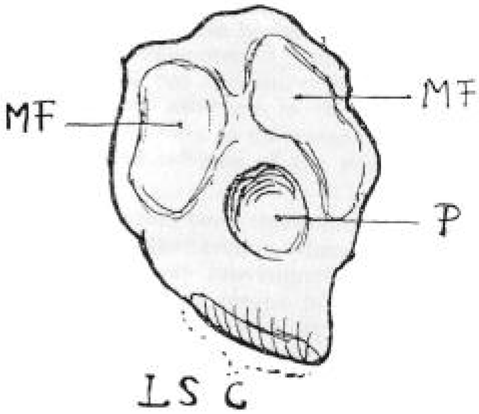

FIG. 5. END-ON VIEW FROM WING-TIP SIDE OF LEFT DISTAL CARPAL BONE. P DEPRESSION FITTING PEG ON BASE OF WING METACARPAL (SHOWN IN FIG. 2). MF, MF, ARTICULAR FACETS FOR ARTICULATION WITH BASE OF WING METACARPAL. LSC ARTICULAR SURFACE OF LATERAL CARPAL.

The movement between the distal carpal and the base of the wing metacarpal was a simple rotation. As indicated in Fig. 5, on the outer surface of the distal carpal there is a depression P which fits a projecting peg on the inner end of the metacarpal. The articular surface of the metacarpal sliding over the facets MF causing rotation of the wing metacarpal round a point P as a pivot. Thus, the wing metacarpal could rotate round its long axis. The permissible movement must have been of very small extent.

One more movement remains to be noticed, namely, that at the knuckle joint K, Fig. I. This was a hinge joint permitting extension and flexion in the horizontal plane. This was the equivalent to advancing and retiring not of the wing-front but of the wing-tip. There is a projection at the base of the wing phalanx which must have served for the attachment of an "extensor" tendon and which may have limited the forward movement of the wing-tip. The fully advanced position of the wing-tip is indicated by the dotted outline P' in fig. 1. This full advancement must have been used for producing "rotation up" round the transverse axis, since at no other part of the wing could movement occur suitable for producing this effect. The probable position assumed in ordinary slow speed gliding flight is indicated by the continuous line P. The wing-tip could be retired till it pointed completely backwards or even could be turned in towards the body of the animal.

The movement of which the different parts of the wing are capable are summarised in the following table:-

Joint		Movement	Remarks
SHOULDER		(1) Downwards	
ELBOW		(2) Downwards and slightly forwards, possibly with slight rotation downwards of wing-front.	Inseparably connected
WRIST	Fore-arm and proximal carpal	(3) Rotation up of wing-front (4) Large retirement (about 30°) of wing-front with slight depression	
	Proximal carpal and distal carpal	(5) Slight retirement with large depression of wing-front (6) Rotation up of wing-front	Inseparably connected
	Distal carpal and wing metacarpal	(7) Rotation up of wing-front	Slight
KNUCKLE		(8) Advancing and retiring or wing-tip	Of wide range

Of these different movements, that at the shoulder joint needs but little discussion. In view of what is now known about the mechanics of flight, it is possible to suppose that movement at this joint was used principally for flapping flight, that high-speed flapping occurred with the wing-tip retired, and that the wing-tips were advanced when flapping at slow speed and when starting or ending a flight.

Movement of the elbow joint need not be separately discussed, as it could only occur in unison with certain movements of the wrist.

As may be seen from the table, the different parts of the wrist joint were capable of no less than five different movements, some of which were inseparably connected. We have to consider whether these movements occurred together or in groups and what was their function.

It is a rule that if the same movement can occur at two positions in a joint it will usually occur at these two positions at the same time and in the same direction. The movements occur in such a way that one reinforces the other. The reason for this fact is that "flexor" and "extensor" tendons are usually inserted not on the bones of a wrist, for example, but pass over it and are inserted on the bones of the hand beyond the wrist. But in the present case movements (3) and (4) are inseparably connected with movement of the elbow (2). Hence if the elbow is kept fixed, movements (5), (6), and (7) might occur independently of (3) and (4).

Movements (3) and (4) occurred with, and no doubt were at least to some extent caused by, movement of the elbow. To understand the probable causation of movements (5) and (6) it is necessary to refer to Fig. 2. On the underside of the joint Pt, known as the "pteroid bone." In the later pterodactyls this is a small tapering split of a bone that has the appearance of having represented the insertion of a tendon.[8] As is indicated in Fig. 2, it was attached to the lateral carpal bone (by a movable joint), and this again was attached to the distal carpal. The position of these bones was such that a pull on this supposed tendon would have caused movements (5) and (6). Of these (6) was a rotation up of the wing-front. It is not necessary to assume that there was a separate tendon with similar function attached to the base of the wing metacarpal to produce movement (7), for as soon as movement (6) had progressed far enough to allow air pressure on the under side of the wing-front, this pressure would of itself cause movement (7).

If we admit that the pteroid bone represents a pteroid tendon, we are obliged to assume that there was another tendon whose pull would reverse the movement caused by the pteroid. We may provisionally refer to this supposed tendon as the "antipteroid." We have no means of deciding whether this tendon was inserted on to the distal carpal or whether running in a curved course over that bone, it was inserted into the base of the wing metacarpal. In the latter case its pull would reverse movements (7) besides (5) and (6). In either case, we are probably safe in regarding movement (7) as merely a continuation of (6), and not requiring separate consideration.

The different movements could have been combined in the following ways:-

A. If the elbow is depressed, then (apart from the effect from the pteroid) there is:-
  (3) Rotation up of wing-front.
  (4) Slight depression of wing front (besides the depression due to forearm movement).
  (4) Large retirement of wing-front.

B. If the elbow remains fixed (and also if it is depressed), the pull from the pteroid causes:-
  (6) Rotation up of wing-front.
  (5) Large depression of wing-front.
  (5) Small retirement of wing-front.

C. If elbow remains fixed, then the pull from the antipteroid tendon causes:-
  (-6), (-7) Rotation down of wing-front.
  (-5) Large elevation of wing-front.
  (-5) Small advancement of wing front.

Of these combinations, it may be noted that C could only occur in the absence of A and B. On the other hand, A and B could occur together or separately.

We appear to be on fairly safe ground concluding that the above is a substantially accurate statement of the facts of the case as to the extraordinary mechanisms of the wrist joint of the pterodactyl. In the case of the human wrist the "flexor" and "extensor" tendons work independently of the rotation and in whatever position of rotation assumed by the joint. The human wrist is a joint adapted for many purposes. In the case of the pterodactyl the "flexor" and "extensor" tendons could only work in connection with and in proportion to rotation of the wrist. It is a joint adapted to one purpose. In view of the high degree to which the movements are inter-related, it is impossible to imagine that any of them are accidental. The movements have been adapted and specialised for one purpose, and we are obliged to conclude that this purpose was flight.

Besides the wrist joint, the whole organisation of the pterodactyl shows that it was fully adapted and specialised for life in the air. But the most extraordinary inference that we are obliged to draw from the structure of the pterodactyl is that the muscle for flapping the wings were extremely weak in comparison with those of birds. The evidence for this fact is the small size of the ridges on the sternum to which these muscles are attached. If the small size of this ridge was the only fact we knew about pterodactyls, we might well conclude that they were land or sea animals that only occasionally rose into the air. But there is no doubt, from other facts, that they were pre-eminently air-frequenting in their habits. Thus the small size of the flapping muscles leads us to suspect, not that they flew worse than birds, but that they flew more scientifically.

The weakness of the flapping muscles makes it highly probable that their habitual mode of flight was by soaring, rather than by flapping. The absence of a wing-tip capable of lifting the wing-front to a large degree, as occurs in the case of vultures and adjutants, indicates that their soaring could not have resembled the slow speed circling of these birds of heavy loading. The retirement of the wing-tip caused the wing of the pterodactyl to have an outline somewhat like that of gulls and albatrosses. The implied suggestion that their flight was like that of an albatross agrees well with the little we are able to infer about their habits.[9]

The weakness of the muscle for flapping the wings renders it highly improbable that they could indulge in "poise-flapping", a form of flight that requires rapid beats of large amplitude. Thus it is improbable that they poised in the air and plunged down suddenly on their prey, as does the pied kingfisher.

The light construction of the wing bones and the weakness of the pectoral muscles renders it improbable that they could indulge in any kind of flight that requires a sudden change in speed. It is not likely that they could dive through the air by "sudden descent," and check speed suddenly in the air in the manner employed by vultures. Neither is it likely that they could plunge into the water as do gulls, in view of the fact that they were unable to furl the wings against the body, and in view of the possible difficulty of rising again from the water in any but the calmest weather.

If their flight was habitually like that of the albatross, and therefore at high speed under certain atmospheric conditions, and if the frailness of their build renders it improbable that they could check speed suddenly, it is probable that they could check speed gradually while in the air and while gliding downwards. Vultures perform this feat (in soarable air) by means of a wing adjustment described by one of us elseware.[10] In view of the high speeds obtained in soaring flight, as compared with the speed obtainable by flapping, it is probable that this power of checking speed is possessed by all soaring animals. Perhaps some of the writs movements of pterodactyls were employed for this purpose.

The complication of the wrist movements of pterodactyls shows strikingly that the study of animal flight is a complicated problem that we can only hope to understand fully when we know more than we do at present of the nature of bird flight and especially of soaring flight.

Our illustrations have been drawn by Mr. G. Howard Short, to whom we are greatly indebted, from specimens preserved in the British Museum (Natural History) at South Kensington.

Footnotes

1. A statement has recently appeared in a semi-popular scientific magazine to the effect that the air of the present day could not support animals of such large span as the pterodactyls, and that consequently the barometric pressure in Cretaceous times must have been about twice as great as it is now. But it may be doubted whether there is so great a difference between birds of the present day and pterodactyls in respect of span as the author of this theory believes. Pelicans reach a span of fifteen feet [4.57 m]. Latham (“General History of Birds,” Vol. X., p. 48, 1824) gives records of the span of albatrosses of 10, 11, 12, and 13 feet. He mentions the “Voyage from England to India in the year 1754, “ by Ives (Edwards), formerly Surgeon of Admiral Watson’s ship and of His Majesty’s Hospital in the East Indies, on p. 5 of which appears :- “An albatrose (sic), a sea fowl, was shot off the Cape of Good Hope, which measured 17½ feet [3.34 m] from wing to wing. A shark also caught and brought on board the Cumberland, with 72 young ones in her belly, each from 6 to 14 inches long.” A gentleman in India gave to one of us a detailed account of his shooting and measuring a bird, stated to be adjutant, with a span of 18 feet [5.4 m]. No reason can be given for believing that the largest existing birds would become incapable of flight were the earth to undergo a great reduction of atmospheric pressure. Large birds of heavy loading, such as the black vulture, can soar as well at a height of two miles above the earth’s surface as at lower levels. At such a height the barometric pressure normally stands about 20 inches [51 cm]. There is reason to believing that pterodactyls were of much lighter loading than the black vulture.
2. A restricted range of fore and aft movement could occur at the wrist joint, but, as will be shown later, this was so connected with movements of rotation as to be singularly ill adapted for purposes of progression.
3. G. F. Eaton, “Osteology of Pteranodon.” (Memoirs of the Connecticut Academy of Arts and Sciences, New Haven, Vol. II., July 1910.)
4. “On the Skeleton of Ornithodesmus latidens, an Ornithosaur from the Wealden Shales of Atherfield (Isle of Wight).” (Quarterly Journal of the Geological Society, Vol. LXIX., June, 1913, No. 274, p. 372.)
5. E. H. Hankin, “Animal Flight,” p. 156. (London : Iliffe & Sons, 1914.)
6. Imagine lines drawn along the greatest diameters of the facets at the two ends of the humerus. When seen in an end-on view of the humerus these two imaginary lines make an angle with each other, which we measured in two cases, and found to be 18° and 19° respectively.
7. The two terms, “distal,” meaning the side furthest from the body or from the centre of the object described, and “proximal,” meaning nearest the body, are in common use in anatomy, and might be found useful in other sciences.
8. The small size of the bone – 9.6 centimetres in a pterodactyl of 15 metres span – renders it unlikely that it supported a prepatagium in the manner suggested by one of us. (“The Development of Animal Flight,” *Aeronautical Journal*, Vol. XVI., p. 28, January, 1912.) In the paper here quoted reasons are given (on aeronautical grounds) for believing that the earlier pterodactyls had four wings, of which the hinder pair were supported by the hind legs. Stromer has recently stated that one of his museum assistants recollects seeing a beautifully preserved specimen of a pterodactyl Rhamphorhynchus in a shop of a dealer some ten years ago, and that this specimen showed a wing membrane supported by the hind legs and passing from the fifth toe of the hind foot to about half way along the tail. This statement appears to deserve further investigation, and if the specimen is still in existence, it would be of great interest for it to be examined and described. Stromer states that the tail fin of Rhamphorhynchus was horizontal, and not vertical, as has hitherto been supposed to be the case. Thus the only instance that has been adduced of the use of a vertical fin by a flying animal turns out to be a myth. (Ernst Stromer, “Bemerkungen zur Rekonstruktion eins Flugsaurier-Skelettes.” Zeitschrift der Deutschen Geologischen Gesellschaft, Vol. 62, 1910, Berlin, footnote on p. 88.)
9. The albatross and certain other of the larger soaring birds resemble pterodactyls more than do other birds in the lightness of the structure of their wing bones. It is probable that the wing membrane of the larger pterodactyls was attached to the hind legs. Hence the pull from this membrane must have tended to draw the legs apart. The muscles that could have opposed this tendency must have been weak, judging from the curiously small size of the pelvis. This weakness of the muscles suggests that the wing membrane was extended across from one hind leg to the other, an arrangement that would diminish the work required from the leg muscles. An analogy for such an arrangement for the hinder part of the volant membrane is given by the vampire bat where there is an interfemoral membrane in the absence of a tail capable of aiding in its support.
10. “Animal Flight,” p. 212.