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The first Pterosaurians discovered were recognized as flying animals, but were thought to be bats. As soon as their general structure became known, they were classed with the Reptiles, although it was considered possible that their power of flight was due to feathers. Later, their bones were mistaken for those of Birds by various experienced anatomists, and others regarded them as sharing important characters with that group. Some anatomists, however, believed that the fore limbs of Pterodactyles were used for swimming, rather than for flight, and this view has found supporters within the present decade. A single fortunate discovery, made a few years since, has done much to settle the question as to the wings of Pterodactyles, as well as their mode of flight, and it is the aim of the present article to place on record some of the more important facts thus brought to light.

The specimen to be described was found in 1873, near Eichstädt, Bavaria, in the same lithographic slates that have yielded *Archæopteryx*, *Compsognathus*, and so many other Jurassic fossils known to fame. This specimen, which represents a new species of the genus *Rhamphorhynchus*, is in a remarkable state of preservation. The bones of the skeleton are nearly all in position, and those of both wings show very perfect impressions of *volant membranes* still attached to them. Moreover, the extremity of the long tail supported a separate vertical membrane, which was evidently used as a rudder in flight.

These peculiar features are well shown in Plate III, which represents the fossil in the natural size.

The discovery of this unique specimen naturally attracted much attention at the time, and many efforts were made to secure it for European museums. The writer was then at work on the toothless Pterodactyles which he had recently found in the Cretaceous of Kansas, and believing the present specimen important for his investigations, sent a message by cable to a friend in Germany, and purchased it for the museum of Yale College, where it is now deposited.

The Wing Membranes.

A careful examination of this fossil shows that the patagium of the wings was a thin smooth membrane, very similar to that of modern bats. As the wings were partially folded at the time of entombment, the volant membranes were naturally contracted into folds, and the surface was also marked by delicate striæ. At first sight, these striæ might readily be mistaken for a thin coating of hair, but on closer investigation they are seen to be minute wrinkles in the surface of the membranes, the under side of which is exposed. The wing membranes appear to have been attached in front along the entire length of the arm, and out to the end of the elongated wing finger. From this point, the outer margin curved inward and backward, to the hind foot.

The membrane evidently extended from the hind foot to near the base of the tail, but the exact outline of this portion cannot at present be determined. It was probably not far from the position assigned it in the restoration attempted in the cut given below, figure 2. The attachment of the inner margin of the membrane to the body was doubtless similar to that seen in bats and flying squirrels.

In front of the arm, there was likewise a fold of the skin extending probably from near the shoulder to the wrist, as indicated in figure 2. This fold enclosed a peculiar bone (pteroid), the nature and function of which will be discussed below in considering the osteology of this part of the skeleton.

The Caudal Membrane.

The greater portion of the tail of this specimen was free, and without volant attachments. The distal extremity, however, including the last sixteen short vertebræ, supported a vertical membrane, which is shown in Plate III, and also in the woodcut, figure 1. This peculiar caudal appendage was of somewhat greater thickness than the patagial membrane of the wings. It was rhomboid in outline, and its upper and lower

portions were slightly unequal in form and size. The upper part was kept in position by a series of spines, sent off one from near the middle of each vertebral centrum, and thus clearly representing neural spines. The lower half also was strengthened by similar spines, which descended from near the junction of the vertebræ, and hence were homologous with chevron bones. These spines were cartilaginous, and flexible, but sufficiently firm in texture to keep the membrane in an upright position.

1.

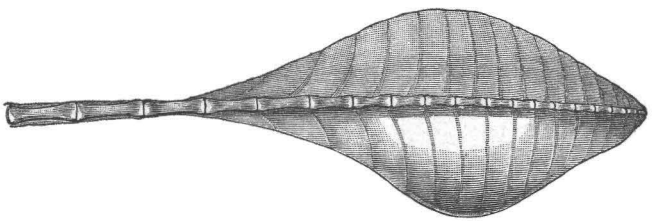

FIGURE 1.—Caudal extremity of *Rhamphorhynchus phyllurus*, Marsh; natural size. Seen from the left side.

THE SCAPULAR ARCH.

The osteology of the scapular arch and wings of Pterodactyles involves many interesting points, some of which have been discussed by anatomists from Cuvier to those of the present day, but with little agreement of opinion. The cause of this diversity of opinion is mainly due to the fact that the specimens examined have been either too small or too imperfect for accurate determination of their more obscure parts. Fortunately, the museum of Yale College has among its specimens of Cretaceous Pterodactyles (some 600 in all), quite a number with the scapular arch and wing-bones nearly perfect, and in position. These specimens were nearly all of gigantic size, having in life a spread of wings from fifteen to twenty feet. They were also destitute of teeth, and belong to the order *Pteranodontia*. Probably their great size induced special modifications of the scapular arch, which is here far more complicated than in any other members of the group.

In the Jurassic Pterodactyles, the scapula is usually bird-like in general form and proportions, the upper or distal extremity being free and compressed. This is the case in the specimen here described. The scapula and coracoid may be coössified, as in the present fossil, or remain more or less separate. No clavicles have yet been found. The sternum here shows no distinct facets for sternal ribs.

In the Cretaceous genus *Pteranodon*, and probably also in some of the other gigantic forms from deposits of this age, the

scapula and coracoid were not only solidly united, but the pectoral arch was further strengthened (1) by the ankylosis of several vertebræ, and (2) by the robust scapulæ articulating on opposite sides of the common neural spine of these vertebræ. This is virtually a repetition of the pelvic arch, on a much larger scale. The sternum also is massive, and shows well marked facets for the sternal ribs. This peculiar method of strengthening the scapular arch has not been observed in any other vertebrates.

The Wing Bones.

The three principal bones of the arm (humerus, radius, and ulna), present such similar characters in all Pterodactyles, that they need not be considered here in detail. It is important, however, to bear in mind that the ulna, although but little larger than the radius, contributes the greater share of direct support to the enormously developed wing finger, which is on the outer or ulnar side of the hand. As this position has been a question of discussion among anatomists, it may be well to state, that the writer bases his opinion upon this point on the results of an examination of the best preserved specimens in European museums, as well as nearly all known in this country. The latter specimens settle the question beyond doubt.

The views expressed by anatomists in regard to the bones of the wrist and hand of Pterodactyles are almost as various as the specimens investigated. Some of the restorations of these parts that have been published from time to time, and repeated in text books, have done much to propagate errors, and little to clear away the serious difficulties in the case. The main facts in regard to the carpus now known may be briefly stated as follows:

In all Pterodactyles, there are two principal carpal bones, placed one above the other. These sometimes show indications of being composite, but their constituent parts have not been satisfactorily determined. On the inner side of the wrist, articulating with the distal carpal, there is a smaller bone which has been called the "lateral carpal." In addition to these three bones, some American Pterodactyles have on the inner side three ossicles, which may be sesamoid bones. Two of these have been seen in a few Jurassic forms in Europe. Beside these, there is often found on the radial side of the wrist, and sometimes attached to it, a long, slender styloid bone, having a rounded articular head on its carpal extremity. This is the so-called "pteroid bone," to which allusion has already been made above. This bone and the "lateral carpal" which supports it are usually placed by anatomists on

the outer or ulnar side, but American specimens prove conclusively that they belong on the radial side.

The nature of the so-called pteroid bone has been much discussed, but without a satisfactory conclusion. After a careful study of many specimens, the writer is disposed to regard it, not as an ossified tendon, but as a part of the first digit, or thumb, which is often considered wanting in Pterodactyles. According to this view, the "lateral carpal" would probably be the metacarpal of the same digit. In favor of this interpretation, it may be said—

(1.) That the position and structure of this appendage of the carpus correspond closely with that of the first digit in some other reptiles, for example, *Iguanodon*.

(2.) The "lateral carpal" unites both with the distal carpal and with the "pteroid" by very free, well-defined articulations.

(3.) In American specimens, the "lateral carpal" stands nearly at right angles to the wrist, and the "pteroid" is much bent near its articular end.

(4.) In no Pterodactyle known is there any remnant of a digit outside the wing finger, where the membrane might be expected to retain it.

(5.) This view would make the wing finger the fifth digit, the same to which the membrane is attached in the hind foot.

Perhaps the strongest objection against this interpretation is the number of phalanges in the respective digits of the hand. These, however, are not constant in the known Pterodactyles, and they vary much in other reptiles which have the digits highly specialized. This subject will be more fully discussed by the writer elsewhere.

According to the above interpretation, there are five digits in the hand of Pterodactyles, although not the five often given in restorations. The first digit, the elements of which have been considered, undoubtedly supported a membrane in front of the arm. The second, third, and fourth are small, and armed with claws. The large wing finger is the fifth, corresponding to the little finger of the human hand.

The metacarpal bones are much elongated in the Pterodactyles with short tails, and quite short in those, like the present specimen, that have the tail long. The metacarpal of the wing finger is always large, and robust, while those of the claw-bearing digits are usually quite slender. In *Pteranodon*, the second metacarpal is a slender thread of bone, throughout most of the length, while the third and fourth are attenuated splint bones, incomplete above.

The phalanges of the three middle digits are quite short, and the terminal ones supported sharp claws. The wing finger has four greatly elongated phalanges, the last being a styloid bone,

without a claw. This digit is well shown in the right wing represented in Plate III, and also in the restoration, given below, in figure 2.

In the restoration here attempted, the writer has endeavored to reproduce (1) the parts actually present or clearly indicated in the specimen described, and (2) those which the former seemed to require to complete the outward form in life. The

2.

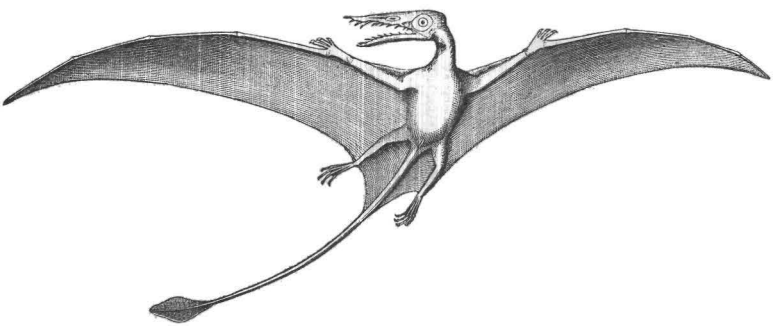

FIGURE 2.—Restoration of *Rhamphorhynchus phyllurus*, Marsh; one seventh natural size.

membrane at the base of the tail may have been somewhat less in extent, and the fold of the skin above the fore-arm either more or less developed than here represented, but the facts now known render the outlines here given more than probable. The hands are represented with the palms forward.

The present species appears to be most nearly related to *Rhamphorhynchus Gemmingi*, von Meyer, from the same geological horizon, and near the same locality. That it is quite distinct, however, is shown, aside from the difference in size, by the complete ankylosis of the scapula and coracoid, and by the fifth digit of the hind foot being well developed, and having three phalanges. In the name *Rhamphorhynchus phyllurus*, here proposed for the species, the latter designation refers to the leaf-shaped caudal appendage, which appears to be one of its most characteristic features.

For the long delay in the description of this important European specimen, the writer can only plead *l'embarras des richesses* nearer home.

Yale College, New Haven, March 14, 1882.

EXPLANATION OF THE PLATE.

Rhamphorhynchus phyllurus, Marsh. Natural size.

The animal lies upon the back, and the under surfaces of the wing membranes are exposed. The caudal membrane is seen from the left side.

F. Bayden, del.

RHAMPHORHYNCHUS PHYLLURUS, Marsh. ½.