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## ON A SKELETON OF *PTERODACTYLUS ANTIQUUS* FROM THE LITHOGRAPHIC SHALES OF BAVARIA, WITH RE- MAINS OF SKIN AND MUSCULATURE

BY OTHENIO ABEL<sup>1</sup>

I. During my stay in New York in the spring of 1925, I had opportunity to study a remarkably well-preserved skeleton of *Pterodactylus antiquus* (Sömmering, 1812) in the American Museum of Natural History. I take pleasure in expressing my cordial thanks for this privilege to my honored friends, Henry Fairfield Osborn and W. D. Matthew.

II. LOCALITY.—The skeleton (Fig. 1) comes unquestionably from the lithographic shales (shaly limestone) of the Altmühl region in Bavaria. To judge from the preservation it is probably from one of the Solnhofen quarries, perhaps at Mörnsheim. For information in regard to the localities of the fossil remains which have been obtained from the Jurassic (Tithonian) shaly limestones of Bavaria, see Johann Walthfer, 1904 (Die Fauna der Solnhofener Platten-Kalke, bionomisch betrachtet. Festschrift für Ernst Haeckel, Jena, 1904).

The specimen is catalogued under the number 1942 in the American Museum collections and was purchased through Ward's Natural Science Establishment, Rochester, in 1922.

III. PRESERVATION.—This specimen may well be one of the most complete and best preserved pterodactyl skeletons ever obtained from the lithographic shales of Bavaria. Not only are all skeletal parts present, but very considerable portions of the skin as well as traces of the muscles are preserved.

The two plates, obverse and reverse, are seven millimeters thick. To increase the strength and security of the specimen each of them has been cemented to a somewhat thicker plate by the previous owner, probably soon after the discovery of the specimen; the reddish cement is visible around the borders of both pieces.

The structure of the matrix in which the fossil is imbedded is unusually fine and close-grained, to which is partly due the preservation of skin and musculature and the exceptional perfection of the bony

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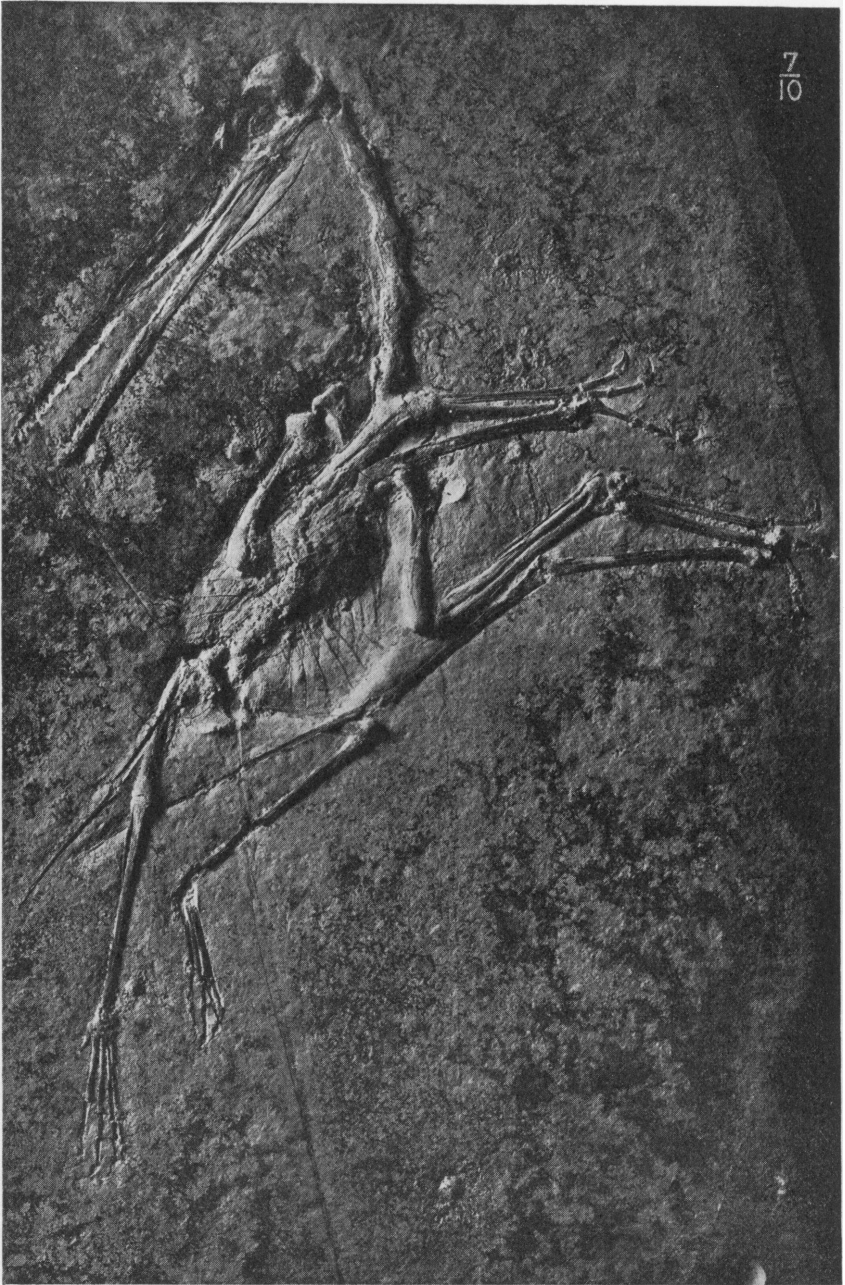


Fig. 1. *Pterodactylus antiquus* Sömmering, from the lithographic shales of the Altmühl region in Bavaria.

Obverse plate. X $\frac{1}{10}$ . Original in the American Museum of Natural History, New York (No. 1942).

parts. The color of the matrix is a pale yellowish gray; on this pale gray background are scattered many smaller or larger rusty-yellow, irregularly shaped flakes, besides numerous black, very finely branching dendrites, which, however, all lie outside the limits of the skeleton.

Obverse and reverse were clearly broken apart throughout their length when the fossil was first discovered and laid open in the quarry. The line of breakage runs along the anterior end of the beak, through the middle of the pelvic region, and crosses the third phalanx of the left wing-finger as well as the left lower leg. On account of this break the pelvic region is somewhat shattered, and the head of the right femur destroyed, the only damages that the specimen has suffered.

On the obverse, which represents the upper side of the sedimentary stratum in the lagoon, on which the in-drifted carcass rested, numerous specimens of *Saccocoma* are scattered, the bodies and arms beautifully preserved. The best of the *Saccocoma* lies above the right humerus, another under the anterior end of the lower jaw. Others of the kernel-shaped bodies of this little crinoid of plankton habitat, which appears to have lived in vast numbers in the open seas [of the Jurassic period] and is the most abundant fossil of the shaly limestone of Bavaria, may be seen above the right metacarpus and the proximal phalanx of the right wing-finger, above the lower end of the right lower jaw, in the neighborhood of the cranial portion of the skull, etc.

The bones are of a clear reddish-brown to golden-brown color; the areas where the brown color is overlaid by white show the portions where the skeletal remains are covered by muscle remains or skin.

At the articular ends of some of the bones, in particular the smaller phalanges, etc., some crystalline calcite has formed which could be partly removed by careful preparation under a six-power binocular microscope.

The muscle traces, visible especially clearly on the anterior side of the right femur, form, as well as the remains of skin, a more or less thin tegumentary layer, particularly well shown in the abdominal region, the under side and left side of the vestigial tail, also along the wing-finger.

In the splitting of the plate that led to the discovery of the fossil, a part of the lower jaw was split in two so that the anterior end of the muzzle with the intermaxillary is separated from the rest of the skull which lies on the obverse and is imbedded in the reverse or cover plate. The crowns of the right upper teeth, however, remain bedded in the obverse. Also some parts of the lower jaw and teeth are in the cover-plate, and in addition a part of the third phalanx of the right wing-finger, parts of the phalanges of the hind foot and the lateral process of

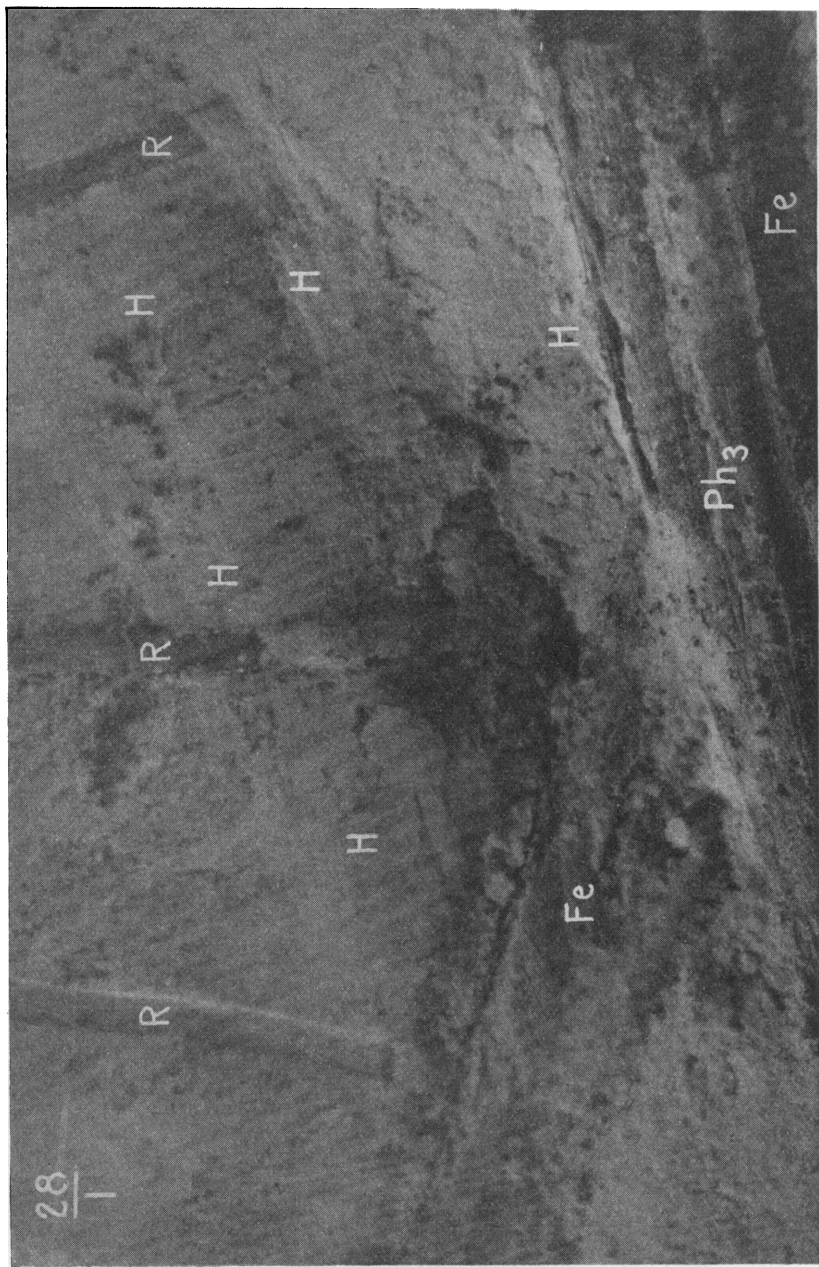


Fig. 2. Portion of the left ventral side of the same specimen, seen from below.

Obverse plate. X28.

R = Ribs.

Ph<sub>3</sub> = Phalanx 3 of the left wing-finger.

Fe = Left femur.

H = Remains of skin, with fine striations, in some parts overlying one another.

the left humerus, all as a result of the splitting of the obverse and reverse plates.

IV. POSITION OF THE ANIMAL ON THE OBLVERSE PLATE.—The skeleton lies on its back, presenting the ventral side upward. The skull has fallen over on its right side so that the left side is presented. The neck vertebræ lie with the ventral side up, likewise the shoulder girdle, which, however, is mostly covered by the overlying anterior end of the left side of the body.

The right fore limb, in consequence of this displacement toward the left, shows the anterior and external sides of the humerus and the external side of all other elements of this extremity. The fingers lie in normal relations to the metacarpus, that is to say, in divergent position, the claws of the phalanges directed toward the cranium.

The right wing-finger is folded backward against the elbow articulation; the distal end of the first phalanx lies close to the lower side of the ulna, and the three more distal phalanges continue on backward in a nearly straight line; the second phalanx of the right wing-finger occupies the space between the ulna and the calcified stomach contents, while the right side of the body lies so that the delicate abdominal ribs are visible beneath it. The third phalanx of the right wing-finger crosses the right femur, while the sharp-pointed fourth phalanx lies in line with the axis of the femur.

The left fore limb is seen from the inner side, and shows in the arrangement of the digits and position of the claws the same characteristics as the right. Here also the first phalanx of the wing-finger is folded against the lower side of the forearm, and the articulation between the first and second phalanges of the wing-finger lies a little beyond the middle of the ulna. This leaves a small triangular area whose sides are formed by the lower half of the ulna, the whole length of the wing-finger metacarpal, and its first phalanx. As the latter is 39 mm. long, the fourth metacarpal only 29 mm., the articulation between first and second phalanges of the wing-finger cannot in consequence correspond with the carpal joint when the wing-finger is folded against the lower side of the forearm. There is no doubt, however, of the W-shaped bending of the wing-finger, as observed by me in 1912 (*Grundzüge der Palæobiologie der Wirbelthiere*, p. 322).

The W-shaped bending of the wing-finger, which was questioned by G. A. Arthaber (1919), although it is shown in many previously known specimens of various species of pterodactyls, shows well in this specimen if we compare the axial positions of the second and third wing-finger

phalanges with one another. Likewise this specimen shows very clearly that in the pterodactylids in opposition to the rhamphorhynchids, the phalanges of the wing-finger must have stood at an angle to each other even during flight.

The proximal end of the third phalanx of the left wing-finger lies transversely over the distal end of the left femur, whilst the fourth phalanx is pushed under the proximal end of the right lower leg bones. This position appears to me specially noteworthy because it throws some light upon the position of the folded wing in a resting pose.

The wings, when the animal was in a resting position, that is to say, hanging to a branch with the body underneath and the feet clinging, would appear to have lain close to the ventral surface and must have rested with their tips between the hind legs.

The series of abdominal ribs<sup>1</sup> is finely preserved. Beneath them the thoracic ribs are in large part visible, but a part of the thoracic arch is hidden by the fossilized contents of the abdominal cavity.

The pelvic girdle presents its ventral side to the observer, but as noted above, is considerably shattered by the splitting of the block.

The posterior extremities are admirably preserved. The right limb is stretched out nearly straight and the anterior surfaces of the bone presented; the dorsal aspect of the right foot is seen, and the plantar aspect of the left, so that in both cases the fifth digit lies outward, the first digit inward.

The fifth digit consists of a short metatarsal and a short proximal phalanx whose distal end is rounded off. The fourth and third digits show in the number and relative length of the phalanges exactly the same relations as described by G. F. Eaton in *Pteranodon*: between the first and the fourth phalanges of the fourth digit lie two separate small phalanges, whilst in the third digit a single small phalanx is interposed between first and third. The phalangeal formula of the hind foot, which may also be clearly distinguished on the left pes, is for digits I-V, 2-3-4-5-1.

The tail is completely preserved and lies close to the inner side of the right femur.

It may also be noted that beneath the lower jaw a pair of long, slender hyoid bones is to be observed, as has already been described by Hermann von Meyer (*Fauna der Vorwelt*, 1860) on different species of pterodactyls. Moreover, both of the sclerotic rings can be seen beauti-

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<sup>1</sup>As the term "ventral ribs" is used morphologically for other structures, the term "gastral ribs" may be used for these structures which are present also in many other reptiles.

fully preserved, the left from the outer side and the underneath one from the inner side. The sclerotic ring consists of extremely thin, delicate, bony plates which overlap after the manner of fish scales. The inner circle of the sclerotic ring has a diameter of about 5 millimeters.

A remarkable feature in the specimen before me, which is not observed in other pterodactyls in good preservation, is the notably broad interosseous space between the metacarpal of the wing-finger and the three metacarpals of the free claw-bearing digits. The feature is present to an equal degree in either fore limb. It is hardly possible to determine with safety whether or not this condition is of any physiological significance. Normally, in the pterodactyls, the metacarpals of the clawed digits lie close to the fourth metacarpal (wing-finger), but this specimen furnishes an exception.

The shortening and general reduction of the intermediate phalanges in the third and fourth digits are, to all appearances, correlated with the hanging-climbing adaptation, as is also the elongation of the thigh and lower leg comparable to the analogous conditions in the extremities of the tree sloths.

V. REMAINS OF SKIN AND MUSCULATURE.—Although the present specimen is noteworthy on account of the excellent and complete preservation of all parts of the skeleton, it is especially remarkable in the preservation of parts of the skin. Remains of the skin are preserved in the first place on both sides of the abdomen, where they lie as a very delicate white layer with fine parallel striations (about 8 striæ to the millimeter) over the gastral (abdominal) ribs. Along the wing-fingers, especially clearly along the left one, the skin is preserved almost to the tip of the terminal phalanx, and here the striæ run parallel to the wing-finger axis. The relation of this striated white layer in the region of the third phalanx of the left wing-finger shows that it represents not the muscular fibres but the skin. Where the elbow articulation of the left fore limb lies next to the thorax, and where the left wing-finger lies with its second phalanx close to the abdominal wall, so that the angulation between the second and third wing-finger phalanges follows the curvature of the abdominal surface, several white striated skin surfaces can be observed lying one over another and with varying directions in the fine striation. This area corresponds to the region in which the wing is folded and lies against the abdominal wall, so that several successive layers of membrane would lie one over another (Fig. 3). The skin parts stretched between the left humerus, radius, and tensor-bone, and representing the propatagium, are somewhat less clearly visible. There is,

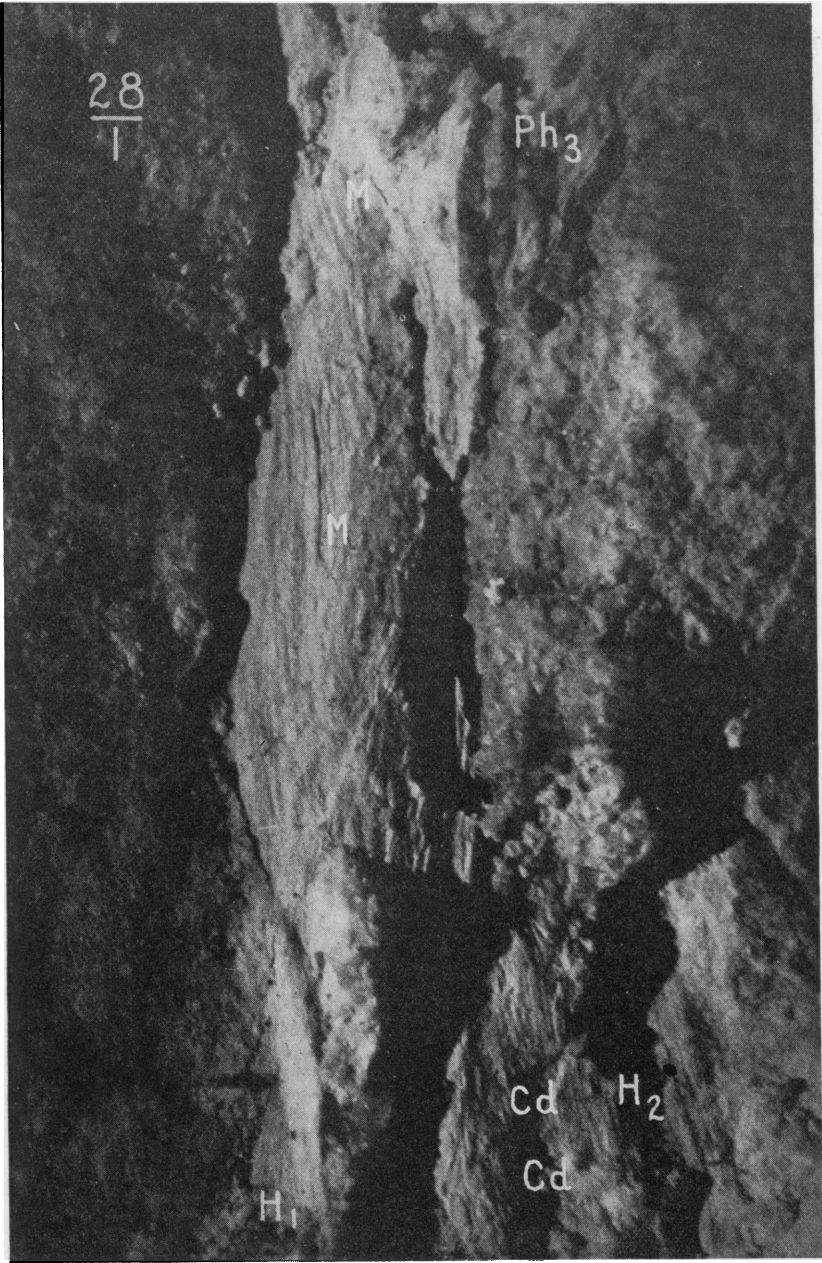


Fig. 3. The same specimen.

X28. Anterior view of the proximal end of the right femur. A small fragment of the third phalanx of the right wing-finger remains, otherwise only the impression of the bone, which is seen on the reverse plate. To the right of the femur, the lower side of the tail is visible; below and at the right side of it (that is, on the left side of the tail) are the remains of the uropatagium.

M = Traces of muscle (M. pubo-ischiotibialis).

Ph<sub>3</sub> = Fragment of the third phalanx of the right wing-finger.

Cd = Caudal vertebrae, covered with skin and remnants of muscle.

H<sub>1</sub> = Skin of the right wing-finger.

H<sub>2</sub> = Remains of the uropatagium.



however, no possible doubt that the similar delicately striated layer found at the anterior side of the proximal part of the humerus, is to be looked upon as the remains of a propatagium, whose existence has previously been assumed as certainly indicated by the presence of a tensor-bone. Parts of the finely striated layers in this area may, however, be muscle (*M. triceps*).

I have expressed the opinion on several previous occasions that the pterosaurs must have possessed a throat sac. It is of particular interest, therefore, that the outlines of this organ, as well as the course of the anterior neck line, can be observed in the specimen before me. The anterior end of the throat sac, whose outlines can be clearly distinguished in the photograph (Fig. 1), is close to the anterior ends of the two elongated hyoid bones, and is likewise well outlined by the limits of the moderately light gray portion of the matrix free from the dendritic coloration of the surrounding rock. In some places, especially below the posterior part of the hyoids, one can see by close study of the surface viewed obliquely a delicate parallel striation upon the remains of the throat sac, corresponding in direction here to the longitudinal axis of the hyoids. The parts preserved at the anterior side of the neck show, on the other hand, a more granular, rough structure without recognizable traces of striation.

Of especial importance is the extension of the skin-traces in the region of the uropatagium. This is, so far as may be judged from the distinctly outlined margin of the skin impression on each side of the rudimentary tail, very weakly developed, and limited to a small fold of skin on each side of the tail, so that only the uppermost part of the inner side of the femur can have served to stretch the uropatagium.

An important observation can be made in the proximal region of the right femur. The right wing-finger lies, as above described, directly over the right femur. Here one sees the skin of the wing-finger in very good preservation and can determine that the longitudinal skin striations which extend along the wing-finger, here follow the third wing-finger phalanx. Beneath this skin layer is visible a portion which likewise consists of a white layer with striæ, but the striæ lie here in somewhat wider spacing and their structure appears coarser. The elongation of this portion follows the axial line of the right femur. From the circumstance that on the uppermost part of the femoral region certain small parts of this lower striated layer are broken away, it may be perceived that we have here to do, not with a part of the skin, but with remains of the upper leg muscles, perhaps a remnant of the *M. pubo-ischiotibialis* (Fig. 3).

Besides the above-described remains of skin and musculature, there are also scattered remains of skin to be seen in various other areas, but for the most part not permitting of positive identification.

VI. DRIFTING OF THE CARCASS INTO THE SOLNHOFEN LAGOON.—The opinion has been repeatedly expressed that the flying saurians whose skeletons are found in the lithographic shales were accustomed to hunt in the lagoons when they were laid dry at certain times by the ebbing of the water, and the attempt has even been made to interpret certain tracks (*Kouphichnium lithographicum* Oppel) as the footprints of these animals, a quite untenable theory. All specimens of flying saurians yet secured from the lithographic shales of Bavaria drifted into the lagoons as corpses. Many of them were in a condition of far advanced decay when they were buried; others were flung by the waves into the lagoon shortly after their death, laid dry, and quickly thereafter<sup>1</sup> covered by a protecting layer of mud now turned into stone. That is what has happened to the specimen before us; a little time after its death it drifted into the lagoon and was covered over by a coating of fine calcareous sediment so rapidly that the usual process of decay was arrested.

VII. REMARKS UPON THE BODY-POSITION OF *PTERODACTYLUS* DURING REST OR SLOW-CLIMBING MOVEMENTS.—I have on several occasions in the past few years attempted to show that the earlier restorations which represented the pterodactyls as adapted to stand or walk on terra firma were all erroneous. Seeley's reconstructions in his well-known book 'Dragons of the Air' (London, 1901) give always the impression of being caricatures. The same is the case if photographs of the modern fruit bats (*Pteropus*) taken in their usual hanging or climbing poses are turned upside down in the position that Seeley gave to his pterodactyls. If, however, we take Seeley's pterodactyl reconstruction and turn it around 180° as I represented it in 1919, a very reasonable looking picture results of the body position of a pterodactyl climbing upside down or hanging at rest.<sup>1</sup>

The study of the present pterodactyl specimen in the American Museum has strengthened my conviction that my interpretation of the body position of pterodactyls in climbing or hanging at rest is correct. I must, however, advance certain modifications in the position of the animal, which I have attempted to express in figure 4. These altera-

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<sup>1</sup>Abel, O., 1922, Lebensbilder aus der Tierwelt der Vorzeit, Jena.

<sup>1</sup>Abel, O., 1919, Neue Rekonstruktionen der flugsauriergattungen *Pterodactylus* und *Rhamphorhynchus*, Die Naturwissenschaften, VII Jahrg., 37 Heft, p. 661, Berlin, September 12, 1921, Die Methoden der paläobiologische Forschung, Handb. d. biolog. Arbeitsmethoden, Abt. X, pp. 270-279, Wien u. Leipzig; 1925, Geschichte u. Methode der Rekonstruktion vorzeitlicher Wirbeltiere, Jena, pp. 91-117.

tions affect the position of the head, the angulation between the hand and forearm, the bending of the wing-finger, and the position of the hind leg.

VIII. SYSTEMATIC POSITION.—There can be no question that this specimen belongs to that group of pterodactyls in which the dentition of the skull is limited to the premaxillæ, while the maxillæ are toothless.

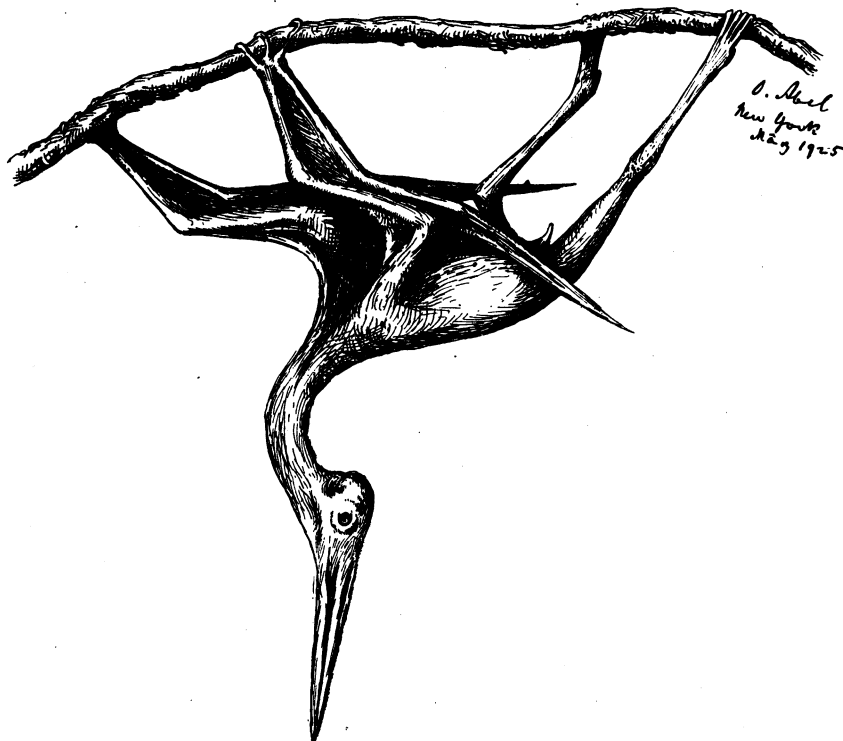


Fig. 4. Reconstruction of *Pterodactylus antiquus* Sömmering, in climbing pose.

This is the group principally known through the species *Pterodactylus suevicus* Quenstedt and *P. antiquus* (Sömmering (= *P. longicollis* Cuvier), while in the group represented by *P. kochi* Wagler and *P. longicollum* H. von Meyer, the maxilla is also provided with teeth. The view that *P. antiquus* might represent a young form of *P. longicollum* may be considered as excluded, but on the other hand it is very probable that many of the pterodactyls now assigned to the systematic group of

*minores* may turn out, when carefully studied, to be really the young of certain species of the *mediæ* and *majores* groups, as J. Hofker has suggested.<sup>1</sup>

The species is commonly known under the name "*Pterodactylus longirostris* Cuvier." This name, however, must give way on grounds of priority to that of *P. antiquus* Sömmering, as Sömmering's name was proposed as early as the year 1812.

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<sup>1</sup>Hofker, J., 1922, 'Beschrijving van een exemplaar van *Pterodactylus longirostris* Cuvier,' Koninkl. Akad. van Wetensch, Amsterdam; Verslag van de gewone Vergaderingen, etc., 29 November, p. 349. [Hofker also expresses here the opinion that *P. antiquus* (= *P. longirostris*) was "een jong exemplaar van *P. longicollis*," a view which is not probable (see above).]