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A *Pterodactylus* with Remains of Flight Membrane.

by F. Broili (with 3 plates).

Read at the Conference on 7th February 1925.

The State Collection for Palaeontology and Historical Geology in Munich recently acquired a *Pterodactylus* from the lithographic schist of the Upper Jura; the specimen was found in Winterberg near Eichstätt, the same region which gave us *Archaeopteryx* and several other pterosaurs, including the splendid fossil of *Rhamphorhynchus gemmingi* with its flight membrane preserved.

Due to the lack of skill of the finder, the so-called "membrane", to which in the freeing from the surface of the bed, most of the bones were still attached, was broken up and destroyed, so that to a great extent only the negative of the skeleton is held. This shows the observer its posterior side and was probably embedded soon after death. The two wings lie folded up, the right with its tip turned downwards, the left preserved incomplete beside the body. The first of the cervical vertebrae are bent backwards, so that the skull, showing its left side, lies in the same direction as the posterior cervical vertebrae; the two hind limbs are strongly bent in towards the body.

As far as the condition of our specimen allows a comparison, it agrees for the most part with the original specimen of *Pterodactylus elegans* WAGNER in the Munich Collection, therefore all that is required instead of a more detailed description, are a few supplementary remarks.

On the part of the skull lying to the rear of the eyes, which, as is frequently the case, is also badly deranged, there is especially noticeable a swollen hemispherical section which can clearly be attributed to the frontal bone on the left, which covers one hemisphere of the brain. Some separate parts of the ossified sclerotic ring are still preserved. This ring lies within the orbital aperture, which is obviously greatly enlarged by the pressure. The aperture is 3mm long and 6mm high. Here it is apparently a question of a uniform bone ring, as H. v. MEYER describes it in *Pt. scolopaciceps* 1) (see footnote on p. 24). This observation is

contrary to ZITTEL's statement referring to the Augsburg specimen; he says that there is visible in the orbital aperture a small part of the sclerotic ring which is composed of small plates 2) (see p. 24). As far as the teeth are concerned, all that can be seen are a few of them as vague impressions. These seem to indicate that the teeth are larger than the teeth of *Pt. elegans*, but in view of the poor state of preservation, I should not attach much importance to this indication, especially since the teeth in our specimen, just as in *Pt. elegans*, are confined to the foremost quarter of the jaw, while in *Pt. kochi*, which might possibly come into ones mind – ZITTEL (*l.c.* p. 30) has already pointed out in detail the difference between the two dentitions – they occupy more than half of the jaw.

Owing to the preservation condition, the number of the cervical vertebrae cannot be definitely decided; of the other vertebrae 14 can be counted.

The two 10mm long coracoids show as impressions and are fairly well preserved. They form the anterior edge of the trunk, they are slightly curved and join each other median at an acute angle. Below the coracoidea can be seen the remains of a sternum, apparently shield-shaped, above which a few ribs have slid. The right scapula also shows as an impression and is about 7mm long.

Between the ribs, whose proximal ends are nowhere conserved, there appears to the left in the anterior section of the trunk below the sternum, a brownish coloured surface marked with pale spots; this is probably the remains of the body skin. On the left outer corner of this part lie two mid sections of gastral ribs which join at an angle and are thickened at the join.

It may be pointed out in this connection, contrary to v. ARTHABER 1) (see p. 25), according to whom the gastral ribs of the pterodactyls lack the angular middle piece, that such a part is also present in other forms of the genus, namely in *Pt. antiquus*, *Pt. longirostris*, *Pt. medius*, *Pt. rhamphastinus* and finally in ZITTEL's original, the one referred to by ARTHABER, namely *Pt. kochi* (ZITTEL, *Paläontographica* XIII; fig. 1). Also DÖDERLEIN illustrates this same middle piece in the splendid specimen of *Pt. spectabilis*, belonging to Prof. BENECKE, in the Strasburg Collection (DÖDERLEIN in STEINMANN: *Elemente der Paläontologie* 1890, p. 648, 796).

The lateral bones of the gastral ribs on the right side are surprisingly long, especially the middle bones which are also noteworthy in that their distal ends show slight knot-like swellings.

The number of the phalanges on the hind foot cannot be determined exactly; the shortened stump-like metatarsus of the fifth toe shows up indistinctly as an imprint, as do the remains of an atrophied phalanx.

The following shows the lengths which were obtainable:

Length of the (somewhat distorted) skull	37 mm
Length of the upper arm	14.5 mm
Length of the lower arm	19.5 mm
Length of the metacarpus	16 mm
Length of the 1st flight finger phalanx	18 mm
Length of the 2nd flight finger phalanx	18 mm
Length of the 3rd and 4th flight finger phalanx (no definite boundary between the two)	28 mm
Length of the upper leg	12.5 mm
Length of the lower leg	17 mm
Length of the trunk	about 30 mm

A comparison of these measurements with those given by ZITTEL in *Pt. elegans*, shows that in most of the skeletal elements there is a satisfactory agreement; certain differences such as the greater length of the skull and the lesser length of the body in our specimen could be attributed to the distortion of the skull or to the incomplete preservation of the trunk.

However, what makes our find so interesting is the fact that for the first time in a specimen in our collection of the *Pterodactylus* genus, it displays well preserved parts of the flight membrane.

As already mentioned above, the right wing lies folded up near the body with its tip pointing to the rear. Between the 1st and 2nd phalanx can be seen that insignificant bend, rightly pointed out by DÖDERLEIN 1) (see p. 26) and a corresponding similar bend between lower arm and metacarpus. A further bend is visible between the 2nd and 3rd flight finger phalanx. The space between the lower arm and the 2nd phalanx, which is very near to it, is occupied by flight membrane whose first distinct remains are visible above that nick between the 1st and 2nd phalanx; below the articulation between upper arm and lower arm this membrane can be followed as far as the trunk where it runs along the body as far as below the third and starting at the uppermost of those already mentioned gastral ribs. A further portion

of flight membrane fills the acute angle between upper leg and lower leg and a third part shows up in the crook between upper and lower arm.

The left wing is also folded, but it is preserved much less completely than the right wing. Only the first flight finger is held more or less complete. The impression of another one runs from the body over the knee of the upper and lower leg; the distal end of the 4th finger would seem to lie at an approximate distance of 6mm from the left tarsus in a very fine impression 4.5mm long, and its lower tip including a slight bone remnant is present.

Because of the unfavourable preservation of this flight finger, the displacement of the remains of the patagium held, which is no longer in its original position, can also be explained. Therefore a part of the flight membrane lies directly below, *i.e.* dorsal of the distal section of the first phalanx, and apparently continues into the larger flight membrane parts lying in their normal position. These membranes can be followed along the lower arm as far as below the lower arm upper arm articulation. A further portion of the patagium shows up in the metacarpus lower arm bend and finally another part is seen, just as on the right side, inside the bend of the upper and lower arm.

Consequently, quite considerable sections of the flight membrane are preserved and all of these have a characteristic colour of their own. While the bone fossils, as is usual in the lithographic schist, have a dark yellow ochre colour, the membrane is brown, and dark brown fine streak systems clearly stand out from a pale ground colour. These systems of streaks are the same feature that ZITTEL (*l.c.* p. 7) first observes on the splendid flight membrane of *Rh. gemmingi* and they were again thoroughly investigated recently by DÖDERLEIN (*l.c.* p. 150) on the same specimen. These streaks which I, in agreement with ZITTEL and DÖDERLEIN, regard as stiff elastic fibres, are in our *Pterodactylus* – certainly it is one of the most delicately formed of the pterosaurs – much finer than those from that *Rhamphorhynchus*. They are, as in the *Rhamphorhynchus* specimen, separated from one another by fine spaces, having about the same breadth as the fibres themselves, and in various places are even somewhat broader. In this way the fibres, as they were so well described by DÖDERLEIN, remind one of the surface of a metal worker's file. At the flight membrane, below the second right phalanx, the streaks attain an average length of almost 5mm. This find provides a very good support for DÖDERLEIN's view (*l.c.* p. 152 & 153) that in *Pterodactylus*, apart from the bend of the first and second flight finger phalanges, which is also mentioned above, a stronger bending of the phalanges and an associated transverse folding of the flight finger patagium is ruled out. In the

resting position therefore the finger wing of *Pterodactylus*, just like that of *Rhamphorhynchus*, apart from that bend between the 1st and 2nd phalanx, must remain stretched out.

The nature and characteristics of the lengthwise fibres on the various parts of the flight membrane of *Rhamphorhynchus* were shown by DÖDERLEIN in an illustration which could not be improved upon. All I can do is to refer to a character on that flight membrane of *Rh. gemmingi* already mentioned explicitly by ZITTEL (*l.c.* p. 7): "some individual streaks seem to be rather thicker than the others, and since these others are at the same time distinguished by a rusty brown colour, they give the impression of being ossified tendons". Actually, several of the streaks, and particularly those which lie on the crests of the rougher longitudinal folds and which run over the patagium more or less parallel to the flight fingers, give that impression. But examination with the binocular lens makes it quite clear that this picture is conjured up by the merging of the normal lengthwise fibres running closer together thus producing the impression of lengthwise folds. Only sporadically over short stretches does there seem here to be a direct fusing, especially in the region of the flight membrane at the elbow articulation, where that brown colouration of the fold ridges is especially pronounced; but here also it would simply be a question of the coming together of the normal lengthwise fibres.

Examination of the flight membrane impressions of our *Pterodactylus* leads us to the following observation on the right wing. Below, anterior of the proximal articulation of the 2nd phalanx with the first, thus at that frequently mentioned bend or kink, the lengthwise fibres form first of all an acute angle with the 2nd phalanx. This stretch then joins up with a fairly (about 3mm) broad system of fibres which at first run parallel to the phalanx but finally turn towards it; this zone is then cut off by some darker coloured fibres which form an acute angle with the zone. The fibres lie closer together and lie on top of one another. These extend as far as the lower arm, and the acute angle between the fibres and the lower arm is then combined with a line of fibres running parallel to the lower arm. The part following this flight membrane region, approximately as far as the beginning of the elbow articulation, is preserved only in the form of more or less incomplete shreds on which the fibres, for the most part, run in the same direction as the 2nd flight finger phalanx or as the lower arm. In the elbow articulation area there follows a better preserved section; below the flight finger lies a system of fibres parallel to this finger and then a very narrow band of fibres from the system form an acute angle and this latter band comes to an end at a dark coloured ?thicker fibre which is interrupted several times in its course; from this fibre now stretches a broad line of fibres

extending to the trunk at an acute angle; after about 7mm the fibres become indistinct and there follows a short space which permits no definite observation; then close to the trunk, fibres are again visible but these are shorter and lie closer together than the stretch lying nearer to the flight finger; at times they lie on top of one another. To begin with, they were tending towards the trunk but they soon change direction and run more or less parallel to it. The distal knot-like thickened ends of two lateral bars from the gastral ribs seem to be inserted into this system of fibres. Near to the lower of these bars this line of shorter fibres bends outwards knee-like in a right angle – a direct curving of the fibres themselves could not be observed with certainty, – below the right angle and forming a 45° angle with it, a new system of fibres, again more or less parallel to one another, and also longer fibres, turns on to the upper leg.

The flight membrane part between upper and lower leg shows a fibre system running obliquely to the two bones. At the part of the left patagium which remains and is away from its natural position, separate lines of fibres are nevertheless able to keep clearly separate from one other.

Consequently, the nature of the flight membrane of *Pt. elegans* was the same as that of *Rh. gemmingi*. Let into the membrane were stiff yet elastic fibres which according to their position within the flight membrane were arranged in suitable sizes and in correspondingly different systems or lines. In a state of rest a partial curving (see below) of some of these fibre systems could occur, also along a fold corresponding to them, and in separate folds such as there are at the elbow articulation and in the region of the ulna between ulna and 1st phalanx; a transverse folding of the fibres at the finger part was ruled out; however, in flight, the fibre lines must join together smoothly to form a uniform, very elastic surface. Therefore when the flight membrane was stretched out, the flight finger formed a more or less straight continuation of the lower arm and as DÖDERLEIN (*l.c.* p. 153) emphasised "the fibres originating from lower arm and metacarpus continue in a straight line into the fibres of the finger wing; in the resting state, the fibres standing rather steeply on the ulna must form a very acute angle with those of the finger wing". The arrangement of the fibres in separate stretches in the folded flight membrane of *Rh. gemmingi*, which, shows hardly any displacement – in contrast to our *Pt. elegans*, which already gives evidence of a strong post mortal change, – is visible only at certain places and in various folds, especially near the ulna and the elbow joint. Naturally here also the individual fibres run much closer together, as they do below the flight finger members where the spaces between the fibres are considerably

greater, and in the same ulna elbow joint area various fibres show a very strong bow shaped curve, thus proving how very elastic they are and consequently how elastic the whole flight membrane must have been.

The find is also of great interest because it shows several features which are not to be observed even in any specimen belonging to the genus *Rhamphorhynchus* with traces of flight membranes preserved. Firstly, as explained above, it shows the distinct connection of the flight membrane with the trunk and the upper arm, as well as between this and the lower arm. These features have for some time normally been assumed and also illustrated in most of the modern reconstructions of *Pterodactylus*. Then there can be confirmed on both left and right, clear traces of flight membrane running from the span bone area – on the left seems to lie the distal end of this bone, on the right there is the impression of a part of it – visible more or less distinctly, as far as the proximal part of the humerus. Finally, on the right side above the humerus and the coracoid, as well as near the first cervical vertebrae, can be seen traces of flight membrane.

Consequently our find, as regards the extent of the flight membrane in *Pterodactylus*, is identical in the main with ABEL's 1) (see p. 31) specimen in the various areas shown on his reconstruction.

I have, as a follow-up on this find, once again checked over the Munich Collection material for traces of flight membrane in *Pterodactylus*, but could confirm only irregular confused traces of fibres below the span bone of an individual of *Pt. elegans*, ZITTEL's original: *Palaeontographica* 29th Vol., 4th fig., 2nd (main slab), as described by DÖDERLEIN also in his *Anurognathus*. In addition, in 1874 WINKLER 2) (see p. 31) in the same species (according to ZITTEL *l.c.* p. 76 it is not a question of a young specimen of *Pt. kochi* but of *Pt. elegans*) described a flight membrane but without giving a detailed description of it. Accordingly, up to now, only flight membranes of *Pt. elegans* are known.

While I was observing the various runs of fibres, there was a peculiar feature which I shall briefly point out: in the belly region, the fibres run more or less parallel to the body, whereas the fibres stretching from the arm to the body, as shown above, form an angle with the body. In this way this seems to be intended as a compensation for the very strong traction produced on the body when the wings are unfolded and during flight. Possibly also, there is a connection with this in the characteristic feature in the other local *Pterodactylus* material, a feature which is not observed in other reptile groups, namely that the distal ends of the surprisingly long lateral bones of two gastral ribs are thickened knot-like; and along those

of the ventral region there seem to be embedded streaks of fibre. These fibres were presumably intended, with the help of their thickening, to provide a special firmness to those in the ventral region. At the same time it is to be observed that the largest knots are seen on the lower of the two bones. This bone is situated exactly at the place where the lateral stretch of fibres bends outwards and where the system of fibres heading for the upper leg is situated.

Herr Prof. Dr. L. DÖDERLEIN was kind enough to prepare the photographic enlargement of the flight membrane. I should like to convey to him at this stage my very sincere thanks.

All illustrations are without any retouching.

Translated by A. C. Benton, March, 1998.