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### 5. Remarks on the Reconstruction of a Pterosaur Skeleton.

by Herr Ernst Stromer with one text plate.

Page 85. Munich, 24th. January, 1910.

(Footnotes all listed at end)

When we disregard the reconstructions of the pterosaurs made by SEELEY<sup>1)</sup>, which are to a large extent a subject of amusement, the only skeletal reconstruction of a pterosaur prepared recently is by WILLISTON<sup>2)</sup>, of the Upper Cretaceous *Nyctodactylus*. PLIENINGER, who frequently studied the group in detail<sup>3)</sup>, and was able to investigate so many splendid skeletons, unfortunately had not at the same time attempted a reconstruction, although he had felt obliged to provide the readers of his papers, and, above all, himself, with the answers to many important questions.

For my textbook on palaeozoology, in spite of my lack of specialist knowledge, I felt compelled to attempt a reconstruction sketch based on the specimens held in Munich and also on what is contained in the literature. For this purpose I chose the particularly instructive fossil of *Rhamphorhynchus gemmingi* H. v. M., which is represented by many skeletons, at times wonderfully complete. For the proportions I based my drawing on an illustration by H. v. MEYER<sup>4)</sup>. I had the animal sketched in half natural size, viewed from belly side and with the wings half folded up, so that the wings, the girdle and the gastral ribs show as clearly as possible. The position of the pterosaur illustrated here, in one third natural size, would not therefore be a natural position, but that of a specimen prepared for exhibition purposes. The drawing which Fräulein E. KISSLING prepared with my guidance in the local zoological institute gave us very great difficulty, although the only organs I permitted to be reproduced are those actually held as fossils. In this task, I believe I have found out many things of interest and I should like to put them on record briefly in this paper.

The only noteworthy point concerning the skull is that I allowed the alteration of the teeth, which were directed surprisingly slanting to the front, but the beak-like processes on the

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<sup>1)</sup> *Dragons of the Air*. London 1901.

<sup>2)</sup> *Amer. Journ. Anat.*, Vol. 1, S. 297ff., 1902.

<sup>3)</sup> *Paläontogr.*, Bd 41, 1894, Bd 48, 1901 and Bd 53, 1907.

<sup>4)</sup> *Fauna der Vorwelt*. Reptilien aus dem lithographischen Schiefer, Frankfurt am M. 1860, Pl. IX, Fig. 1.

tips of the jaws, observed by H. v. MEYER<sup>1)</sup>, I did not dare to have illustrated, because I was not certain of their original form.

In order to indicate the mobility of the neck with its seven vertebrae, it was shown rather twisted and curved; in addition, the first three broad pectoral ribs are depicted as ending free, but the remaining four, with calcified or ossified sternocostalia, as in the birds, are attached to the very broad and only slightly curved breastbone; this corresponds not only to PLIENINGER's statements regarding *Campylognathus zitteli* (1907, p. 222, fig. 1) but also to H. v. MEYER's excellent drawings (*l.c.* Pl. X, fig. 1). The characteristics of the gastral ribs and the posterior ribs became quite clear to me when I compared them with those on a very well-prepared *Sphenodon* skeleton, even if our form is different from that of the Rhynchocephalia, because of the crocodilelike attachment of the ribs to the transverse processes of the vertebrae, by the small number (6) of gastral ribs and apparently also by the lack of processus uncinati. Each gastral rib consists of a bent, obtuse-angled middle piece and at each side a piece lying laterally; the ribs, however, would not have joined on in this way, as PLIENINGER (*loc. cit.* p. 222) found in *Campylognathus*, but as in *Sphenodon*, since according to H. v. MEYER's Pl. IX & X, exactly the same type of indented cartilaginous and perhaps somewhat calcified sternocostalia of the posterior ribs are present, as in *Sphenodon*. Moreover the posterior edge of the breastbone is scarcely a natural edge; it may still have been cartilaginous, and, as in *Sphenodon*, may have extended below the first gastral ribs. However, as I could not find it anywhere, it was omitted from the drawing<sup>2)</sup>.

The best basis for the two ventral lumbar vertebrae, which seem very narrow, and for the four sacral vertebrae, was an original by ZITTEL<sup>3)</sup>. For the length of the tail I was guided by H. v. MEYER's Pl. IX, fig. 1 and the excellent specimen from the American National Museum<sup>1)</sup>.

Contrary to several reconstruction pictures showing the tail curved, it was actually quite stiff; I feel that, judging by its preservation position, it was at the most bent, but never strongly curved and, in addition, the wrapping of ossified tendons obviously gave it a special stiffening. The caudal steering sail was illustrated first by MARSH<sup>2)</sup>, in his *Rh. phyllurus*,

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<sup>1)</sup> *loc. cit.*, Pl. X, fig. 1.

<sup>2)</sup> The pectoral ribs are too strongly curved and the gastral ribs are not shown thin enough; also the anterior sternocostalia, which certainly run essentially dorsoventral, are not shortened according to perspective and the posterior indented ones are shown more slanting to the lengthwise axis of the body than they should be in reality. These organs should be identifiable as clearly as possible in the figure.

<sup>3)</sup> *Paläontogr.*, Vol. XXIX, 1882, Vol. III, fig. 2.

<sup>1)</sup> *Proc. U. St. Nation. Mus.*, Vol. XXX, Washington 1906.

<sup>2)</sup> *Amer. Journ. Sci.*, Vol. XXIII, 1882, Plate III.

which besides, is so different in its proportions from specimens of *Rh. gemmingi* (= *münsteri*) of approximately equal size that I am not convinced of a specific identity. MARSH has the sail placed vertically, since the delicate processes which stretch it out, according to him, should rise up, on the one hand, in the middle of the vertebrae as dorsal spinal processes and on the other hand, between them as ventral processes of the chevrons. Now, disregarding the fact that I could not observe chevrons anywhere in *Rhamphorhynchus* I was also not in a position to establish the vertebral boundaries definitely in a still undescribed specimen of the local collection which showed membrane and its delicate supports so very clearly. I also found the supports in some cases in opposition so that they could actually have been transverse processes. In agreement with MARSH's opinion, the fact is that, in the specimens in the American National Museum, which are displaying a lateral view, the surface of the caudal sail can be seen, and always the two halves are a little asymmetrical. In the local specimen, however, the membrane lies horizontally and this is backed up also by a technical flight consideration. A vertical rudder was actually superfluous since a slight additional flap of one of the large wings would certainly have resulted in a turning of the animal to right or left, whereas a horizontal caudal sail could have performed very well as a height regulator, especially since it would have been acting on a long lever arm and lay so remarkably far behind the animal's centre of gravity.

The girdle was the greatest problem. At the front, in *Nyctodactylus*, WILLISTON (*l.c.*) placed the coracoidea and with it also the scapulae, and these were firmly connected together to form a moderately acute angle; they are slanting, thus nearly at a right angle to the vertebral column, and TORNQUIST<sup>3)</sup>, in his criticism of the usual *Diplodocus* reconstruction, quite rightly states that in reptiles this position is the normal one. WILLISTON<sup>1)</sup>, however, mentions that in *Nyctodactylus* the sternal facets for the coracoidea are directed upwards and outwards and in our animal laterally directed coracoidea would stand out too far over the thoracic cage and also the long cristospina of the sternum would rise up towards the head without purpose.

However, above all, not only is the form of the scapulae bird-like but in a great number of *Pterodactylus* and *Rhamphorhynchus* skeletons, particularly well in the *Pt. spectabilis* skeleton H. v. M.<sup>2)</sup>, it can be established with certainty that it was placed, as in the birds, at a sharply acute angle to the vertebral column and that the coracoidea were directed slanting to

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<sup>3)</sup> *Sitz.-Ber. Gesellsch. naturf. Freunde*, Berlin, 1909, pages 198, 199.

<sup>1)</sup> *Field Columbian Mus.*, Publ. Nr. 78, *Geol. Ser.*, Vol. II, Nr. 3, Chicago 1903, p. 139, Pl. 42, Fig. 1.

<sup>2)</sup> *Paläontogr.*, Vol. X, Pl. 1, 1861.

the front, above and a little outwards. Also FÜRBRINGER<sup>3)</sup>, stated that this position was normal, but yet he accepted WILLISTON's illustration because the coracoidea were credited by WILLISTON with great mobility. There is no doubt that, in sharp contrast to the flying birds, the medial coracoid end is not wide and is not attached firmly to the sternal anterior border – it also lacks a furcula and a high crista sterni – but movements of the coracoidea, which here are assumed to be in a completely transverse slanting position, could hardly be carried out in the case of a good flyer. The shoulder girdle in our animal has even, because of a similar life style, likewise maintained a bird-like position. The same applies to the position of the head, which certainly differs from that of most reptiles.

The free forelimb, corresponding to the local originals, is represented in complete or semi-resting position, but not laid laterally of the body; therefore the flight membrane appears more or less folded up<sup>4)</sup>. In any case, even if the membrane became wider in a tensioned state, it was still relatively narrow and it certainly reached as far as the side of the body, but probably not as far as the hind feet, nor quite as far as the tail. Even when the membrane is very well preserved, no trace of it can be found on the hind feet or tail<sup>5)</sup>. On the other hand, I feel it is quite possible, that anteriorly, on the arm of the so-called span bone outwards, which PLIENINGER 1907, p. 301 ff.) quite rightly interpreted as metacarpal of the first finger, a membrane stretched out to the base of the neck.

The claw fingers were probably used by the animal for hanging during sleep, when it most likely concealed its head between its wings. The strong processus lateralis and medialis of the humerus and also the very large sternal plate and its long spina, which runs out to the rear in a low keel, provided strong muscles with numerous attachment points; in addition, the form of the wings, and what we can observe from the fossils of the animal, are all in favour of a good flying ability. We may conclude by the fact that we find its fossils in marine beds, that the animal lived well on the beaches as a fish catcher and flew out over the surface of the sea.

As far as the pelvic girdle is concerned, I searched in vain in PLIENINGER for exact information on the character of the symphysis of the ischia and on the reason for the roundish hole which usually appears in it below the hip articulation. This I found, not only in several

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<sup>3)</sup> *Jenaer Zeitschr.*, Vol. 34, 1900, page 360.

<sup>4)</sup> The left flight finger is turned slightly around its longitudinal axis so as to show the articulation of the metacarpal and its first phalanx; at this point an olecranon-like process prevented a hyperextension.

<sup>5)</sup> About 10 years ago, according to information from LOOS, (the local collection supervisor), the late natural history dealer, KOHL, possessed a splendid specimen of *Rhamphorhynchus*, which showed a flight skin stretching from the pelvic region to the middle of the tail. Since the whereabouts of the fossil was not known, I cannot decide whether or not, in this specimen, the ossified caudal tendons only, were squashed flat, so as to give a false interpretation, as is the case in the local original of *Rhamphorhynchus longimanus* WAGNER.

local specimens of *Pterodactylus*, but also in the *Rhamphorhynchus* illustrated by ZITTEL (*Paläontogr.* 1882, Pl. III, fig 2), and in WILLISTON (*l.c.* 1903, Pl. 40) and also in *Nyctodactylus*.

In the crocodiles, the ischium, I agree, along with the ilium, surround an aperture in the acetabulum, but a foramen of this nature in our animal, to my knowledge, is never found; on the other hand, in reptiles there is often in the pubis a foramen obturatorium, or the combined pubis and ischium enclose a foramen ischiopubicum, which often replaces the foramen obturatorium. The occurrence of this opening seems to me to contradict completely PLIENINGER's opinion that we are dealing with an ischium only and favours SEELEY's<sup>1)</sup> view that pubis and ischium in this case, are intimately fused together. The general form of both approximately resembles the form of those pelvic bones of *Champsosaurus*, a relative of *Sphenodon*<sup>2)</sup>; these are not fused but are simply lying directly alongside each other and the bar or belt-shaped bones anterior of these are thus to be interpreted as prepubes<sup>1)</sup>. They certainly form, *e.g.* in the ZITTEL original already mentioned, a symphysis which is still preserved; the pelvis itself, however, surprisingly enough, apart from the original of the *Campylognathus zitteli* (PLIENINGER 1894, p. 214, fig. 5) is almost always found badly squashed laterally and that is not in favour of a closer fitting median connection. WILLISTON, and at one time SEELEY (*l.c.* 1891), nevertheless assumed an ischial symphysis, but WILLISTON<sup>2)</sup>, stressed his uncertainty because the pelvic opening in *Nyctodactylus* was also far too narrow to allow eggs, or even more so, for the passage of living young. I therefore believe that between the two ischiopubica, and more often in reptiles, there was a median cartilaginous strip. I did not have this sketched and I did not assume for it too great a breadth, so that in the figure the foramina ischiopubica and the ilia might be clearly seen; this ilia was lengthened to the front and rear and was firmly connected to the vertebral column.

Their formation, that of the hind legs also and above all the weak claw form, does not indicate that the pterosaurs were originally climbing animals who, to begin with, used their wings as parachutes, but as FÜRBRINGER (*l.c.* 1900, p. 664) stated, they were at one time, walking or running creatures, which, like birds and many of the dinosaurs, had a semi-erect gait. However, it would be too involved for me to enlarge on the probable acquisition of the

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<sup>1)</sup> *Ann. Mag. natur. hist.*, Ser. 6, Vol. VII, p. 237ff., London 1891.

<sup>2)</sup> Barnum Brown in *Mem. Amer. Mus. natur. hist.*, Vol. IX, 1905, Pl. 4, Fig. 3, 4.

<sup>1)</sup> V. HUENE (*Anat. Anz.*, Vol. 33, p. 402ff., Jena 1908), by studying the muscle attachment places in the crocodile, attempted to suggest the probability that those bones, usually regarded as pubes, (which PLIENINGER compared with those of the pterosaurs in a similar position), may be prepubes, while the pubes on the other hand, could be rudimentary.

<sup>2)</sup> *Amer. Journ. Anat.*, *loc. cit.*, 1902, page 300.

power of flight, this having been dealt with, and published a few years ago, by DÖDERLEIN, v. BRANCA and v. NOPCSA.

Finally, as far as the hind legs are concerned, I had them drawn in the reptilian position, with the toes stretched out straight, as they are normally held. However, I must remark that the short fifth toe is almost always found to be bent in the fossil, *e.g.* in ZITTEL's frequently referred to original, and that, contrary to PLIENINGER's (*l.c.* 1907, p. 310) assertion, had more than two phalanges<sup>3)</sup>.

To conclude, I might still emphasise that my reconstruction merely represents an attempt to depict the reality and that I therefore present it and my reasons for having the reconstruction sketched, for the judgement of my fellow scientists, since I feel that it is necessary to clarify finally the questions regarding the structure of this extremely interesting pterosaur.

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

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<sup>3)</sup> The lengths of the 4th. and 5th. metatarsals in the figure are unfortunately shown rather too large, also the lengths of the 3rd. and 4th. toe phalanges are not quite correct.