Klinghardt, F. (1941) Beobachtungen an Flugsauriern. *Paläontologische Zeitschrift* , **4**, 250-258.

Observations on Pterosaurs

by F. Klinghardt, Berlin, 1941

(with 1 text figure and plates 14-16)

Preliminary Remarks

Interest in pterosaurs has always been great and it has become even greater since BROILI (A *Dorygnathus* with Skin Fossils, *Sitz. Ber. d. Bayr. Akad. d. Wissensch., Jahrg.* 1939, p. 129) was able to prove the presence of hair in these animals. DÖDERLEIN (On *Rhamphorhynchus* etc. On *Anurognathus* etc. A *Pterodactylus* with throat pouch and swimming membrane. *Ebenda* 1929, p. 1-175) gave us information regarding the throat pouch and a large number of particular anatomical points. However, many questions have to be answered and O. KUHN is quite correct when he writes in *The Fossil Reptiles* p. 119: "In the structure of the skull many close analogies with birds can be observed and these certainly merit further investigation." The conclusion that these most specialised of all reptiles were "warm-blooded" would certainly be rather precipitate.

A *Pterodactylus scolopaciceps* preserved in almost natural position Herm. v. Meyer

(Pl. 14, fig. 1 and 2)

(Original in Berlin Geological-Palaeontological Institute and Museum)

Preliminary Remarks: This specimen is very well preserved. In this paper the organs which seem particularly important to the author are emphasised. The specimen was found in the White Jura of Solnhofen.

The Preparation: On the whole, excellent. Above the braincase, level with the occiput, it has unfortunately been scratched; perhaps there are also preparation faults in the neck area, so that the originally present cervical skin was removed accidentally. In the interpretation of the soft parts there are, in this plate, the following problems, which are pointed out by Herr Prof. JANENSCH, Berlin. Below the most superficial layer of many Solnhofen slabs there follows an obviously soft rock layer, which, in its colour, can easily be mistaken for fossils of soft parts. To the above-mentioned scientist, I give sincere thanks for permission to carry out preparation work.

The Cerebral Capsule: In the fore-brain area the bone is rather flaked away, so that the curve of the whole cerebral capsule was originally more regular than it appears on the photograph. The flaking in this area would not have been accidental, since the cerebrum is not in one piece, as has been assumed up to the present, but is broken into several parts (Pl. 16, fig. 1). A comparison of these features in a series of pterosaurs, shows that the brain has caused a remarkable enlargement of the brain case, as can also be observed sometimes in marten-like mammals and otters.

The Cerebellum Area: In this specimen the cerebellum is not so abruptly terminated as in most *Pterodactylus* species considered by the author (Pl. 14, fig. 2). The flaking of the bone seems to coincide with the position of the cerebellum.

The Nasal Aperture: Fossil bones in the apparently triangular and lengthwise extended nasal opening, show that they were in any case a great deal smaller than assumed. *Rhamphorhynchus* and *Pteranodon* have small nasal apertures.

The Curving of the Upper Jaw: This is slight and is seen almost only in the anterior part of the jaw (Pl. 14, fig. 2).

The Temporal Fossa Ventral of the Cerebellum: It has an oval shape and is relatively large.

The Hyoid Bone: It is very thin and long extended. Near to the neck this delicate formation apparently shows a pair of fine points which are perhaps a device acting as a fish trap.

The Postfrontal: In a narrow sense, it is fairly well separated from the cerebral capsule; in its dorsal part it is a truncated triangle; then it is rod-like and is again a truncated triangle in its ventral part. In the framing of the orbital ring, the postfrontal forms a fine ledge, which perhaps served as an attachment place for muscles.

The Lateral Temporal Fossa: For a *Pterodactylus*, it is remarkably large, on the whole oval.

The Jugal: It forms a fork, dorsally directed, lying anterior (nasal) to the eye. Unfortunately, nothing further can be determined in respect of how far the branches originally extended in the direction of the skull. A direct connection with the prefrontal (?lachrymal and prefrontal) is very probable and this view is supported by comparison with other skulls.

The Quadrate and Squamosal: The position of both can be established from the figure; they are obviously closely fused with each other.

The Teeth: It is a question of a small number of tiny teeth.

The Region below (ventral) to the Lateral Temporal Fossa: This is an elevated area which probably does not represent a chance accumulation of lime, but is of an anatomical nature.

The Jaws: The upper jaw, approximately in the middle, displays a shallow, ventrally directed trough, while the lower jaw forms a quite shallow, dorsally running arch.

Flight Membrane Preserved: This shows up so indistinctly that I need give no opinion regarding it.

The Foremost Ribs: Obviously these are more strongly developed than the ribs following. This is a character which PLIENINGER ("*Campylognathus zitteli.* A new pterosaur from the Lias of Swabia" *Palaeontogr.* 1894, p. 209) mentions in the case of this species. The gastral ribs of our specimen are present only as fragments.

The Femur: The left femur is very well preserved. It is longer than the humerus and it can be seen that it curves distinctly to the front (nasal). Its condyle and the outer trochanter are offset by a few millimetres. The binocular magnifying glass shows that both are broad and strongly built. The femur, which is broken off towards the pelvis, shows a sizable cavity with a regular fine groove. The whole structure of the femur indicates vigorous activity, which would have been favourable for swimming.

The Tibia and Fibula: The tibia is much more strongly developed than the fibula. A close fusing of both can be observed for a short distance from the lower (ventral) end of the femur, but a shortening of the tibia (Schienbein) (as in many pterosaurs) is not to be seen. It (the tibia) reaches as far as the lower end of the tibia (*sic*).

Remarks on the Metatarsals: The structure of these bones indicates that they were at any rate very well adapted for swimming.

Some Comparisons: The General Position: If the opinion given above, that our *Pterodactylus* was embedded in an almost natural position, then it is to be expected that occasionally another *Pterodactylus* will be found similarly positioned. In Munich there was a *Pt. scolopaciceps* Herm. v. MEYER from Eichstätt and it lay preserved in an almost identical position. According to an amicable communication from Prof. MAYER FRANZ, Eichstätt, there is still a pterosaur embedded in this way, held in Frankfurt am Main. In his *Palaeobiology* (1912), ABEL illustrates a *Pt. scolopaciceps* which is lying in a somewhat similar position to the present specimen.

Two areas, only a little separate from each other, a dorsally widened club shaped form Pl. 16, fig. 1, 2) and an indistinctly bounded broad trough or hollow (PL. 16, fig. 1, 3) speak in

favour of a special division of work in the frontal brain. This is a feature which up to now, *e.g.* in the toothed birds of the Cretaceous, has not been observed.

A rectangular eminence (Pl.16, fig.1, 4), should at least partly correspond to the mid-brain.

The oval, open area (Pl. 16, fig. 1, 5) seems to derive from the optic lobe.

A *Pterodactylus* cf. *scolopaciceps* Herm. v. MEYER
from the White Jura of Eichstätt
(Pl. 16, fig. 1 and fig. 1, page 250) [Original in the Theological-Philosophical Seminary at Eichstätt (Southern Bavaria)]

Remarks: Although the author has already produced an illustration of this specimen (Remarks on Brains, Skulls, etc., *Palaeont.* No 19, Part 1/2, 1937, p. 165), he feels that he ought to give details concerning the characters of the inner cranial capsule, since it has hardly ever been properly observed.

The whole head, with throat pouch and cervical skin, has been illustrated in the *Z. d. Deutsch. Geolog. Ges.* 1935, Part 1, Pl. 5.

The State of Preservation: The specimen is preserved almost complete, but only the elements which are in particularly fine condition, are given prominence. It is surrounded largely by dendrites, which for the most part interfere with the visibility, but they are actually advantageous in that they make the soft parts stand out more clearly (*e.g.* neck, throat-pouch).

The Crest: It is difficult to distinguish but, with the help of further photographs, enlargements and so on, it can be determined that a low crista is actually present and that it runs in the lengthwise direction of the skull. A crista is very clearly visible in *Pteranodon.*

The Cervical Skin: The skin accompanying the very long neck dorsally, gives an impression of a very strong, presumably muscular formation.

The Throat Pouch: It was detected on a Munich specimen by DÖDERLEIN (1929, p. 68 and 69). Probably throat pouch and also cervical membrane are preserved much more frequently than we realise, but they are obliterated by unsuitable preparation. The throat-pouch is preserved much more completely than it is in DÖDERLEIN's specimen. In both cases it very probably reaches as far as the tip of the lower jaw. These features are very reminiscent of the corresponding structures in the pelican. In both of these examples the greatly lengthened beak, teeth (or horny sheaths), and above all, the throat pouch, are excellently suited for grasping and storing the fish food of these animals.

Cerebral Chamber, in General: The brain cavity seems small in relation to the skull. If we consider, however, that the beak (that of *Pt. longirostris* is still longer) has followed an evolutionary path all of its own (a development which has taken place in certain birds and crocodiles) then we are not at all in a position to decide whether the brain, in relation to the skull, had a great or a small anatomical value.

The Interior of the Braincase: The parts of the braincase lying towards the back of the head are particularly thick walled.

The fine, fissure-like formation above the middle of the eye (Pl. 16, fig. 1, 1) very probably corresponds to the short olfactory lobes.

A horizontally running, broad bulge (Pl. 16, fig. 1, 6) is the wide tent-like form which can be seen in many *Pterodactylus* species. It separates the cerebrum from the cerebellum.

The cavity for the strongly developed cerebellum forms a very broad, irregular trough (Pl. 16, fig. 1, 7).

A short broad tip (Pl. 16, fig. 1, 8) is perhaps to be regarded as the region of the process from the cerebellum to the flocculus.

The author is conscious of the fact that this is just the beginning of an actual clarification.

At the border of the cerebrum and cerebellum, near the framing of the eye, there is a form like the head of a pin, which is clearly separated from its surroundings. A positive interpretation cannot be given.

The Curving of the Jaw: The upper jaw shows a shallow longitudinal trough; probably this would have led to a greater resistance against blows (*e.g.* when it greedily attacked food) and also, to a more efficient closing of its jaws. In many species of *Rhamphorhynchus* the lower jaw is curved to align with the upper jaw. This is certainly no chance character; a slightly curved stick breaks as easily (*sic*) as a straight one.

Fossils of the Hyoid Bone: Perhaps there are still remains of the lengthwise extended hyoid. In any case, the illustrated Berlin *Pterodactylus* (Pl. 14, fig. 1 & 2) shows the delicate hyoid bone, as does a *Pterodactylus* held at Munich.

Observations on *Rh. gemmingi* Herm. v. MEYER

(Pl. 15, fig. 1 & 4)

(Original from Geological Palaeontological Museum, Heidelberg)

Thanks to the co-operation of the Heidelberg Institute, it was possible to further prepare the specimen, which was illustrated from inside, and T. EDINGER's observations "The Brain of the Pterosaurs", *Z. f. Anat. u. Entwicklungsgesch.*, 83, Part 1/3 1927, p. 107) can now be supplemented. At first sight, the greatly developed cerebrum reminds one much more of a mammal than of a reptile. Closer inspection shows a similarity to the structural plan of the bird's brain. After very careful cleaning of the specimen, I observed, under the microscope, a whole network of blood vessels, which unfortunately were run through with fissures. Regarding the fine ledges in the brain pans, I hesitate to give any decisive interpretation; this will have to await the examination of even better preserved specimens. The olfactory lobes seem to be very small.

The cavities for the optic lobes are easier to recognise in the left skull half than in the right. The cerebellum chamber, compared with that of the cerebrum, is very tiny, yet the ratio in different species seems to vary quite substantially. I was unable to proceed with the preparation of the area of the flocculus as far as I should have liked, since this might have led to the endangering of the precious specimen. It can be clearly seen, however, in the one skull half, that it is a question of a spacious cavity, which distinctly bulges caudalwards. Between the flocculus and the lobus opticus there is a constriction. The middle parts of the cerebellum are probably very small.

A comparison with the *Rh. gemmingi* in the Berlin Geological Institute, illustrated on Pl. 14, fig. 1, is an obvious action. The skull capsule of the Berlin specimen is somewhat more shallow than that of the Heidelberg specimen. Common to both are the tiny olfactory lobes. In the Berlin pterosaur the separation region of cerebrum and cerebellum was very probably prepared away.

The author also attempted to draw a parallel with the illustration prepared by E. T. NEWTON ("On the skull, brain and auditory organ of a new species of pterosaur from the Upper Lias near Whitby, Yorkshire". *Philos. Transact. Roy. Soc. of London*, 179, 1888, p. 521, fig. b, London 1889) of the brain of the *Scaphognathus purdoni* from the Upper Lias of Yorkshire.

The egg-shaped half of the cerebrum, the tiny lobi olfactorii, the relatively very large flocculi, remind one of the *Rh. gemmingi* Herm. v. MEYER which is in hand. In the just mentioned illustration by NEWTON, the position of the cerebellum is not quite clear. In the main collection of vertebrates in the Berlin Geological Institute there is a pterosaur with the label "*Pterodactylus* cf. *westmanni* WIMAN. *J. N.* 2, 1865" in which the braincase is well separated from the rest of the skull area. In addition, there is a very good plaster cast of a

Pterodactylus longirostris CUVIER from Solnhofen, in which the position of the cerebrum and the cerebellum can be distinguished. When we consider what the author normally observed in the skulls of European pterosaurs, regarding the current question among brain scientists concerning the mutual effects of brain and skull on each other, we can say:

In many pterosaurs the brain exerts a strong pressure on the skull capsule (cerebrum and cerebellum).

The Throat Pouch: this has already been mentioned in the description of *Pterodactylus* cf. *scolopaciceps* H. v. MEYER.

If we inspect the illustration of *Rh. gemmingi* (Pl. 15, fig. 3) then we shall have to restore the remains of the throat pouch up to the tip of the lower jaw.

The greatest extension of this roomy receptacle is usually in the throat area.

Surely it is no coincidence that the pterosaur *Pteranodon* (illustrated in many textbooks) shows a distinct cut out section in the throat area. Anatomically considered, it is to be expected that there would be a great widening of the pouch at this point.

Pteranodon suevicus QUENSTEDT has, in the anterior part of the lower jaw, a spoon-shaped widening. This probably indicates strongly that the throat pouch, at least in this area, varied a great deal.

Observations on Flight and Swimming Membranes (Pl. 16, fig. 2 & 3)

The Flight Membrane: First of all we may consider the basic investigations by L. DÖDERLEIN, mentioned in the "Preliminary Remarks". Concerning the fibres in the flight membrane I shall still withhold my judgement, since these investigations are not yet completed. To the very friendly cooperation of this scientist, now unfortunately deceased, I am obliged for permission to have his photographic plates reprinted by a particularly experienced photographer. The characters recorded by DÖDERLEIN.(p. 39 *l.c.*) as "puzzling tuft-like forms" are proved to be folds of the somewhat collapsed flight membrane (Pl. 16, fig. 2).

The Swimming Membrane: DÖDERLEIN mentioned a preserved swimming membrane on the right hind foot of *Pt. comoranus* DÖDERLEIN. Unfortunately, in his paper (*l.c.* p. 73, fig. 24), his illustration of the membrane is not at all distinct. With his permission this illustration has been reprocessed and is shown here. Prof. WIMAN, Upsala, questioned the presence of this swimming membrane; it is probably the impression of the skin.

In 1929 *l.c.* DÖDERLEIN pointed out the powerful claws of the pterosaur *Anurognathus*. The figure (Pl. 16, fig. 3) shows claws of *Pt. comoranus* DÖDERLEIN which, in my opinion, would have greatly facilitated the overpowering of its prey.

Summary

1. A pterosaur, embedded in almost natural position, could be prepared anatomically.
2. The skull capsule of *Rh. gemmingi* Herm. v. MEYER permitted me to recognize in its inner regions, an extensive division of work of the cerebrum and probably of the cerebellum also.
3. It was possible to widen our knowledge of the throat pouch and its attachment areas.
4. Flight and swimming membrane of *Rh. gemmingi* H.v.MEYER and of *Pt. comoranus* DÖDERLEIN could be reproduced as a more informative illustration.

Original text received by the Editor on 18/3/1941

Explanation of Plates

Fig. 1. (page 250) *Pterodactylus* cf. *scolopaciceps* Herm. v. MEYER. White Jura from Solnhofen. Original specimen in the Scientific Collection of the Philosophical Theological Seminary in Eichstätt, (Southern Bavaria). The throat pouch is sketched schematically. About natural size.

Plate 14

Fig. 1. (page 258) *Pt. scolopaciceps* Herm. v. MEYER, White Jura, Solnhofen. Original specimen in Berlin in the Geolog.-Palaeont. Museum, Display Collection. Nat. size.

Fig. 2. The greatly magnified skull of the same animal. In the cerebrum, as well as in the cerebellum region, can be seen manifestations of a flaking away of the bone.

Plate 15

Fig. 1. *Rh. gemmingi* Herm. v. MEYER, White Jura, Solnhofen. Original specimen in Berlin in the Geolog.-Palaeont. Museum, Main Collection. A little more than twice nat. size.

Fig. 2. *Pt. comoranus* L. DÖDERLEIN. Throat pouch and cervical skin are visible.

Fig. 3 & 4. *Rh. gemmingi* H. v. MEYER. White Jura, Solnhofen. Original species in the Heidelberg Geolog. Palaeont. Museum. Fig. 4 shows the natural size. Fig. 3 is enlarged by about 1/3.

Plate 16

Fig. 1. *Pt.* cf. *scolopaciceps* H. v.MEYER. White Jura, Eichstätt, Bavaria.

Fig. 2. *Rh. gemmingi* H. v. M. White Jura of Solnhofen. Enlarged by about 1/3. In the left lower corner, folded up membrane.

Fig. 3. *Pt. comoranus* L. DÖDERLEIN. White Jura, Solnhofen. Swimming membrane and claws are distinguishable. For the photographic plates for fig. 2 and 3, I am indebted to Herr. Prof. DÖDERLEIN.

Token of Esteem

The Senkenberg Natural Philosophical Society awarded its Iron Senckenberg Medal to our honorary member Prof. Dr. ERNST STROMER Baron von Reichenbach

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