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THE BRAIN OF *PTERODACTYLUS*
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ABSTRACT. The investigation of the neurocranium of a *Pterodactylus elegans* and a comparative review of the figures of other *Pterodactylus* skulls and of the yet undescribed endocranial casts furnished a complete picture of the Pterodactylus brain, except for the base.
The comparis on of the Tithonian *Pterodactylus* brain with the Cretaceous pterodactyloids and the Liassic and Tithonian rhamphorhynchoid brains show that while the form and position of the nervous centers of the olfactory and optic senses and the position of the cerebellum are avian in every Pterosaurian, bird -like of cerebellum and forebrain are achieved only in the later forms of both suborders.

MATERIAL

The *Pterodactylus elegans*, MCZ, No. 1505, was imbedded on its left side in the mud of the Solnhofen Tithonian lagoon. Slab 1503 A represents the petrified stratum into which the corpse sank; it contains most of the skeleton (Plate VI, Fig. 1). Slab 1503 B represents the deposit of the tide after the animal's death; it contains splinters of the bones split by the separation of the two slabs, and the impression of the right side of the skull as far as it rose above the mud surface. The heavier neurocranium had sunk deeper into the mud than did the light beak; consequently, its outline is not impressed in slab B and did not show up on the slab A surface; it was laid open by preparation.

There is no record of when this beautiful, complete skeleton, a gift from Louis Agassiz to the Museum of Comparative Zoology, came to America. It was not in the museum when Maack in 1870 made a list of the vertebrate palaeontological collections, nor is it mentioned in later museum reports. It was, however, painted by the museum draughtsman in October 1873.

The size of the bones is within the limits of variation of *Pterodactylus elegans* as shown in Zittel's table of measurements of three adult and one young specimen and complemented by Broili's measurements. The length of the skull is 35 mm. including an occipital convexity, discovered by the recent preparation, which had not been formerly disclosed in the species; without this eminence, the skull length is that of the type specimen, 34 mm.

As one of the avian characters shared by the Pterosauria is the possession of a tightly fitting braincase, outside views of skulls in many cases convey a picture of the brain portions. This is particularly true of the paper-thin skull of the smaller *Pterodactylus* species, such as *Pterodactylus elegans*.

Yet only one of the many descriptions of *Pterodactylus* skulls makes reference to this intimate skull-brain relation. In a specimen of Pterodactylus elegans, Broili (1925) mentions a hemispherical swelling behind the orbit, erroneously, however, attributing it to a bulging forebrain hemisphere.

Pterodactylus specimens also exist in which the separation of the two imbedding slabs has split the skull in two in the manner which disclosed the Archaeopteryx brain: the calcite druse formed in the endocranium is laid open on the obverse slab, while the inside of the skull part which formed the exposed surface of the endocast is visible on the reverse slab. But these actual Pterodactylus "brains" have been very inadequately utilized for brain research. No more is known at present than that these endocasts have a longitudinal and a transverse furrow. The longitudinal fissure was found by Lorenz Oken; he quite rightly concluded that in the *Pterodactylus* skull an internal crest separated "zwei Hirnhälften wei bei höheren Thieren" [two halves of the brain as in higher animals] (1819: the first palaeoneurological observation!). Hermann von Mayer's own drawing of a *Pterodactylus kochi* (the only figure of a P. endocast disclosing details; see our Text Fig. 1 A) shows that in this specimen are exposed the left and upper sides of the cerebral hemispheres, midbrain lobes and cerebellum; yet Meyer saw only "di e den beiden Hemisphären entsprechenden Wölbungen" [the arches of both hemispheres] (1860, p. 38). The transverse indentation is noted in Döderlein's description of *Pterodactylus cormoranus* [*Pterodactylus kochi*] which incidentally mentions an endocranial cast as a pear shaped swelling somewhat constricted in the middle. Klinghardt confined himself to naming the two parts of the swelling in an endocast of *Pterodactylus scolopaciceps* [*Pterodactylus kochi*], vis., forebrain and cerebellum; the latter designation, however, is incorrect.
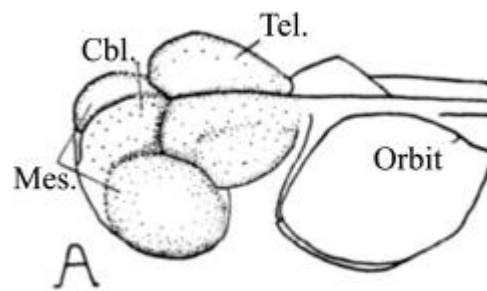

Fig. 1. A: *Pterodactylus kochi* Wagler. Natural endocranial cast: H. v. Mayer's outlines supplemented by shading and lettering. 2x nat size.

Thus, although we are well acquainted with the main features of the brain of several other Pterosauria,[1] the brain is still unknown in Pterodactylus. Yet this is a genus of which many skulls have been described, and three endocranial casts figured. Consequently, the brain characters traced in the almost transparent skull investigated in this paper (Plate I, Fig. 2) could be amply corroborated, and summarized in a brain reconstruction (Text Fig. 2 B)

DESCRIPTION.

In the skull figured here, with a length of 35 mm. and a height of 8 mm., the brain occupied 10 mm. of the length and the entire height. It formed an arc which reached from the occipital foramen in the skull base (concealed in this specimen) to beyond the skull summit. The position of the highest point of the skull vault divided the head in a heavy posterior quarter containing the brain and half the eye, and light anterior three quarters. Only the tapering rostral extremity of the brain extended into the slender bridge between the summits of the orbits.

Olfactory bulbs. As is almost always the case in Solnhofen pterodactyli, the neocranium is crushed by being flattened onto the slab. Through this process, the narrow rostral end of the

brain chamber has been pressed inward, and an anteriorly tapering tube has been disclosed. This tube is about 1 mm. long and less than 1 mm. high at its posterior end. It is the tiny chamber which contains the olfactory bulbs.

Forebrain (Telencephalon). The forebrain-chamber is wedge-shaped. In side-view, it is seen as a rounded triangle in which the front end is an acute angle. The 5 mm.-long forebrain base lies along the upper circumference of the orbit as the descending anterior side of an obtuse angle, the posterior side of which slightly rises but cannot be followed distinctly as far up as the skull roof in the specimen at hand because the posterior part of the forebrain chamber is badly fractured.[2]

Forebrain-length. Yet the hind end of the forebrain has not been arbitrarily drawn in Text Fig. 2 B. It certainly was at the upper anterior side if the triangular area where bone is absent -1, because, in spite of the splintering, the distal part of the osseous border of the gap is so rounded as to give the impression of an original border; 2, because the indentation just above the occipital plane, which may be termed incisura occipitalis superior, is distinctly seen also in the following other *Pterodactylus* specimens:

1. *Pterodactylus elegans*, Winkler, pl. III.
2. *Pterodactylus longicollum*, Mayer 1860, pl. VII, Fig. 2.
3. *Pterodactylus longirostris*, Hofker, pl. I-II.
4. *Pterodactylus meyeri*, Meyer 1860, pl. IV, Fig. 2.
5. *Pterodactylus scolopaciceps*, Wiman, Fig. 12.
6. *Pterodactylus suevicus*, Fraas, pl. XXII.

Of these, the *longirostris* skull is somewhat tilted so as to exhibit, besides the profile, part of the upper surface; it shows that from the incisure forward the lateral outlines of the skull roof diverge, that is the brain case becomes wider anteriorly. In the *longicollum* skull, the incisura is at a point farther caudo-ventrally than the others. This specimen (our Fig. 1 B), however, is split open so as to reveal "das Innere des Schädels" [the inside of the skull] (Mayer 1860, p. 45).
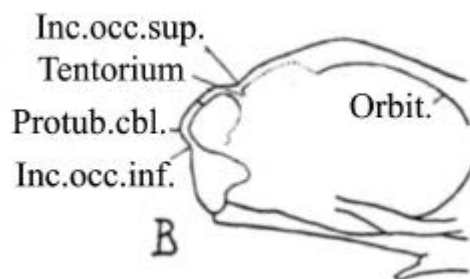

Fig. 1. B: *Pterodactylus longicollum* Meyer. Paramedian saggital section of posterior skull portion; after H. v. Mayer, with added explanation. 2/3 nat. size.

Actually shown is a saggital section through the neocranium – not along the median plane the profile of which is exhibited in the other specimens, but a paramedian (latero-saggital) section. From the incisure, a transverse, almost vertical bony plate is seen (in longitudinal section) to descend into the brain chamber: doubtless the tentorium cerebelli. In the MCZ specimen, there is an almost vertical ridge at some distance below the incisure which, considered alone, would seem accidental; it is, however, situated in the plane which would continue the P. longicollum tentorium in baso-lateral direction, and thus presumably is the bone surface interiorly strutted by this transverse osseous septum.

Furthermore, the incisura occipitalis superior obviously corresponds to the hind end of the forebrain in the *Pterodactylus kochi* endocast, Text Fig. 1 A.

What is seen in the side view as an incisure thus doubtless was a transverse groove across the skull roof, along the line which was interiorly braced by the tentorium. Here the reinforced skull resisted deformation by pressure; the skull figured burst open behind the tentorium. The hind end of the forebrain is now bordered by the triangular gap. This gives the forebrain a maximum length of about 8 mm.

Forebrain height and breadth. Forebrain height increases anterior-posteriorly, in the short rostral tip from about 1 to 1½ mm. The height reaches almost 5 mm. at the caudal orbit border: what may be called the "temporal lobe" is the largest. The occipital part of the forebrain tapers posteriorly.

Forebrain breadth cannot be determined in the specimen at hand which presents the side-view only. For the same reason, the fissure magna cerebri, which separates the cerebral hemispheres, is not visible.

Forebrain-relief. Only the rostral portion of the forebrain chamber is preserved as smooth, undisturbed bone. There follows a convex middle part the surface of which is moulded by the endocranial cast, namely the calcite druse which usually fills the wider hollows in Solnhofen fossils. The posterior portion is crushed onto the slab, and mostly concave.

A horizontal furrow separates the convex portion into an upper and lower half. Its presence can be explained in two ways: geologically and anatomically. The druse probably was not compact but hollow in the more spacious part of the forebrain chamber; due to this, the chamber could be flattened in the posterior section, and it might have been indented in the middle section, by mountain pressure. The position of the dent, however, makes it much more likely that the druse was originally formed with a dent, namely in a chamber with a lateral, longitudinal, low internal crest – which, if it existed, will hardly ever be seen directly in a Solnhofen specimen. – This crest would have corresponded to the osseous crest protruding into the vallecula of the bird forebrain. The horizontal furrow consequently suggests that the *Pterodactylus* forebrain possessed a fissure corresponding to the avian vallecula. The vertical furrow descending from the fissure, furthermore, indicates the presence of a vallecula Sylvii such as separates the frontal and temporal sections of the basal part of the forebrain in birds.

Midbrain (Mesencephalon). It is the sharp caudal and basal delimitation of the *Pterodactylus* forebrain which Döderlein has mentioned as a transverse constriction of the endocast, and which Klinghardt has designated as a tentorium. Actually, this delimitation is composed of two different internal crests (or rather three, since the basal one is bilateral). They appear as ridges on the crushed skull surface because they upheld the bone while the adjoining areas of thin bone were pressed down.

Only the vertical ridge is the tentorium (see above). The ridge basal to the posterior part of the forebrain (Klinghardt's tentorium) is almost horizontal, is continued posteriorly and then basally almost parallel to the occipital outline of the skull, and then turns forward again and thus forms a closed oval. The ovoid pit it encloses is about 3 mm. high and 4.5 mm. long. It cannot be a temporal vacuity since this is very small in *Pterodactylus*. It was indeed originally no concavity, but pressure has transformed, and perhaps somewhat enlarged, a convexity. In other Pterodactylus skulls, this ovoid area bulges conspicuously: it is the protuberance adjoining the posterior side of the orbit, erroneously designated as forebrain by Broili, and as cerebellum by Klinghardt. In Mayer's *Pterodactylus meyeri*, this region is convex on the left side of the skull, but on the right side, as in our specimen, "nur eine nicht knöchern ausgekleidete Grube." [a hollow not covered in bone]. It is interesting to note that Meyer perceived that this was an area moulded by the brain; but, as he could only have a brain of reptilian character in mind, he decided that "als

Gehirndecke liegt sie zu weit hinten und unten" [the cover of the brain lies too far to the back and too far down] (1860, p. 57); He had assumed that it had been shifted downward from somewhere else in the broken skull.
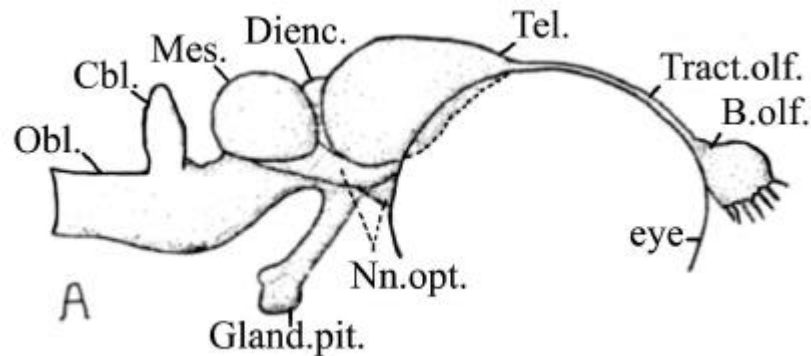

Fig. 2. A: The brain and proximal section through the right eye of a primitive, large eyed , living reptile, *Sphenodon punctatus* Grey. Combined from Gisi, Haller (Handb. vergl. Anat. Wirbelt.) and Sauerbeck (Nova Acta leop. 85). 5/3 nat. size.

The present specimen distinctly shows that the organ enclosed in this original convexity was an ovoid body protruding from the side of the brain stem; its larger axis descending from dorso-posteriorly to ventro-anteriorly. This organ was the right lobe of the midbrain roof.

The rostral extremity of this optic lobe is so close to the orbit that the extracapsular course of the optic, and most important sensory nerve of *Pterodactylus*, was extremely short. A space is designated in Text Fig. 2 B as nervous opticus just to indicate the site of the optic canal; our specimen itself does not reveal any nerve exits. In *Rhamphorhynchus kokeni* [*Rhamphorhynchus longiceps*], MCZ, No. 1886, however, whose neurocranium is split longitudinally, a wide, obliquely transverse canal is revealed at the upper end of the anterior of the optic lobe.

Metencephalon. The knowledge of the lateral site of the midbrain lobes establishes for *Pterodactylus* too the condition, unique in reptiles, that the Pterosaurian cerebellum could develop forward and reached the median posterior border of the forebrain. The upper anterior end of the cerebellum has been described above, as it is coincident with the median posterior border of the forebrain. The tentorium cerebelli, anterior border of the cerebellum chamber, is seen to descend from the incisure occipitalis superior in out Text Fig. 1 B, Meyer's *longicollum* skull section. Behind the incisure, Meyer found the occipital outline protruding so strongly backward that he suggested that the protuberance is due to pressure which deformed the skull. However, there is no break in the outline. Furthermore, this same sickle-shaped protrusion of the dorso-occipital profile can be traced in too many *Pterodactylus* skulls to be anything else but a genuine skull feature.

In the present specimen its upper end is lost. The occipital outline below becomes distinct again in the circumference of a calcite druse which is only partly covered by bone. This druse filled the protuberance shown in Meyer's section. Its lower outline bends forward and forms an angle with the rounded, postero -basal outline of the skull. This establishes another flexure in the occipital profile of the *Pterodactylus* skull which may be termed incisure occipitalis inferior. It is found on or below the level of mid-height of the midbrain lobe. Apart from the specimen described, many pterodactyli show indications of its presence and it is distinctly seen in the following specimens:

1. *Pterodactylus longicollum*, H. v. Meyer 1860, pl. VII, Fig. 2.
2. *Pterodactylus longirostris*, H. v. Meyer 1860, pl. II, Fig. 1.
3. *Pterodactylus longirostris*, Hofker, pl. I-II.
4. *Pterodactylus meyeri*, H. v. Meyer 1860, pl. IV, Fig. 2.
5. *Pterodactylus micronyx*, H. v. Meyer 1862, pl. VIII.
6. *Pterodactylus scolopaciceps*, Wiman, Fig. 12.
7. *Pterodactylus suevicus*, Fraas, pl. XXII.

Specimens number 1, 3, 4, - , 6 and 7 show both upper and lower incisure; the distance between the two, about 3.5 mm. in the present specimen, is in every case just below one-half the distance from the upper incisure to the summit of the orbit (which latter corresponds to the approximate forebrain length).

Although the two incisures have so frequently been figured – even Arthaber's diagrammatical reconstructions of the *Pterodactylus* skull show the protuberance bordered by the incisure, - only two authors have observed this feature. Maybe the other authors assumed, as did Meyer, that the division of the profile into separate curves was due to the crushing of the occiput which they never fail to mention.

It is true that some of the compressed occipita have singular outlines which thus seem disturbed. In some cases, however, it is now obvious that such occipital are not completely uncovered when the two embedding slabs are separated, due to the fact that this heaviest part of the skull is most deeply embedded in the matrix.
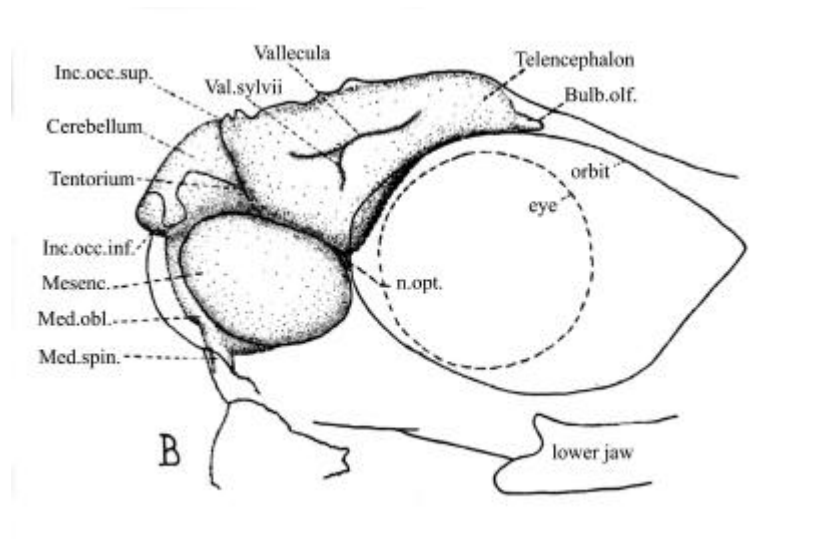

Fig. 2. B: The brain, orbit and eye of *Pterodactylus elegans* Wagner,MCZ, 1505: interpretation of pl. I, Fig. 2; broken lines and stipple shading reconstruction. 6x nat size.

The evidence now accumulated leaves no doubt that there must have existed in every *Pterodactylus* skull a median dorso-caudal protuberance, delimited above and below by transverse furrows which appear as incisures in side views.

Hofker describes it as follows: the supraoccipital ends in a crest which stands out from the back of the skull like a knot. Fraas, who had an excellent preparation which enabled him to see not

only the profile, but also the back view of the skull, perceived this same median outgrowth not as a crest, but as a protuberance vaulted laterally also; and he interpreted it as a tuber cerebellare.

The protuberance indeed contains a chamber – otherwise no calcite druse could have developed here in the MCZ specimen. Text Fig. 2 B shows this chamber, delimited on the skull exterior by two incisures. Thus Fraas' interpretation is right: the protruding part of the occiput contained, and was shaped by, the cerebellum.

It follows that the corpus cerebelli of Pterodactylus was somewhat less than half as long as the forebrain, and its distal side was strongly vaulted.

Since the lateral borders of the corpus cerebelli are rarely parallel but converge rostrally or caudally or are concave, one of the reasons why we believe that the section (Text Fig. 1 B) is paramedian is the smallness of its cerebellum chamber; it appears that the chamber is not cut through its widest, median vault.

Cerebellar giri, if present in *Pterodactylus*, would not be impressed in the skull, as neither avian nor small mammalian skulls are moulded by the cerebellar fissuration.

Doubtless the *Pterodactylus* cerebellum was continued laterally into flocculi, this being the case in other Pterosauria; but they do not show in the specimen investigated, nor can their presence be traced in the figures of other skulls. The smooth curve in which the skull outline is continued below the tuber cerebellar is the right "roundish cheek" (Fraas) formed by the lateral occipital: too thin a structure to have housed the auricular lobes. These lateral wings of the occiput conceal the oblongata chamber, including the foramen magnum. Nor can an atlas be made out in the mass of crystals which are found where the cervical vertebrae must have lain. But from the long established basal position of the foramen magnum on the one hand, and the now known position of the cerebellum, it follows that the medulla oblongata of *Pterodactylus* had a steep dorsoposterior-ventroanterior direction.

<center>COMPARISON.</center>

The braincase in *Pterodactylus*, as in small birds and many Microchiroptera (but not in large birds, large bats and giant Pterosauria), follows the form of the brain in such a degree that the chambers of the individual brain parts are demarcated on the skull exterior. The brain, as in birds, forms an arc around the orbit.

In the small species investigated, the ratio of brain length to skull length is 1:3.5. The well-known reduction of relative brain size with increasing skull length can be observed within the genus; for instance, in a 66 mm.-long *Pterodactylus kochi* skull the braincase: skull length ratio is 1:4.4, in a 115 mm.-long *crassirostris* skull 1:4.8. As regards the rhamphorhynchoids, brain length is only 1/7th of the 190 mm. skull length in *Scaphognathus*, and in *Rhamphorhynchus* the ratio is about 1:2.5 in a 40 mm.-long skull, 1:4 in a 94 mm. skull, 1:5 in 121 and 125 mm.-long skulls.

Olfactory bulbs. The Pterosaurian brain is a graphic illustration of the interdependency between the brain form and the respective development of the sense organs which, in their turn, are correlated with the mode of living. The space assigned to each olfactory bulb, on the summit of the eye-dominated *Pterodactylus* skull, apparently was about 1 cubic mm. The bulb thus probably has about 1/25th the volume of the optic lobe, while in *Sphenodon* – also a large-eyed but otherwise typical reptile – the olfactory bulbs have the same dimensions as the optic lobes (Gisi, p. 87). There were no olfactory tracts; in *Sphenodon*, these may be almost twice as long as the forebrain; but in another large-eyed living reptile, *Chamaeleo*, the tracts are short and the bulbs small. The length of the olfactory bulb compares to forebrain length in Pterodactylus as in the Cretaceous Pteranodon (1:8 - - 2:18): the bird-like reduction of the sense of smell was completed in the early form.

The olfactory bulbs of Malm rhamphorhynchi are unknown. Newton states that in Scaphognathus the bulbs could be traced for about 5 mm. in front of the cerebrum. Such relatively large size of the olfactory centers would not be inconsistent in the oldest pterosaurian, but the present author was unable to verify Newton's observation when investigating the specimen (1927).

Forebrain. The forebrain of *Pterodactylus* was highest where a kind of temporal lobe descended behind the orbit; it was attenuated anteriorly and posteriorly. The maximum height was little more than half the maximum length. The *Pterodactylus* forebrain thus appears to have been a low one, even for a reptile; in birds, the forebrain height is hardly less than the length, which is likewise the case in some reptiles.

There is only one document which indicates the breadth of the chamber which housed the cerebral hemispheres: the detached, and perhaps incomplete skull roof of Meyer's *Pterodactylus kochi,* shown from below in Zittel, Pl. IV, Fig. 1.
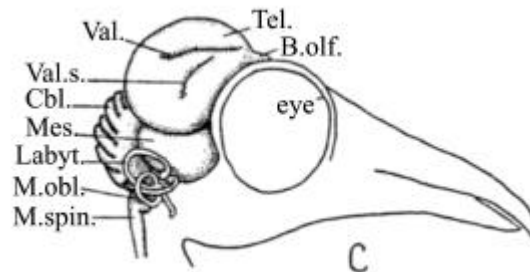

Fig. 2. C: The brain and a section through the right eye of a living bird,
Columba livia Linné. After Krause (from Stresemann, Handb. Zool.)
and Küenzi (forebrain fissures). Nat. size.

Tapering rostrally, the area moulded by the brain is 8 mm. broadest posteriorly, that is, as broad as it is long; but this breadth includes that of the midbrain chambers.

There is, however, a non-anatomical consideration from which it follows that the *Pterodactylus* skull, that is the brain-case, was slender. Although the body may lie on its ventral or dorsal side, all *Pterodactylus* skulls are embedded either on their right or left sides. Yet under the same circumstances some of the *Rhamphorhynchus* skulls were spread out on their lower or upper sides by the embedding mud waves; this will naturally happen only to broad skulls.

It may thus be assumed that the Pterodactylus forebrain was not as wide as long. The forebrain, always the brain part least modelled by function, was not as bird-like as were the other brain parts; for in reptiles, the forebrain breadth is less or equal to, but rarely greater than the length, while in birds the width almost always exceeds the length.

Perhaps the contemporary but more specialized pterodactyloids *Ctenochasma* had a somewhat broader forebrain than *Pterodactylus*. The pair of ovoid cavities in the lower side of the frontals (Broili 1924, Fig. 1) are 8 mm. long and, taken together, 10 mm. broad. However, they may have housed the upper vault of the hemispheres only. That this was so is suggested by the fact that these concavities are rounded in front and do not reach forward into the narrowing bridge between the orbits, into which, in *Pterodactylus*, the anterior extremities of the hemispheres descend towards the olfactory bulbs; these are not impressed in the *Ctenochasma* frontal bone.

The avian forebrain form was achieved by the Pterodactyloidea in the Cretaceous. The forebrain of the *Pteranodon* cast is perhaps laterally incomplete, yet it is as broad as long; in Seeley's Ornithosaurian, forebrain breadth is 21 mm. against 16 mm. in length.

The same phylogenetic development of forebrain form can be followed in Rhamphorhynchoidea. The *Pterodactylus* shape of the forebrain existed in the Lower Jurassic *Scaphognathus*. The chambers housing the broadly kidney-shaped cerebral hemispheres of the Upper Jurassic *Rhamphorhynchus* had lengths and breadths such as 5.5 and 8 mm. (*Rh. Longicaudus*, Meyer 1860, Pl. IX, Fig. 5), 11 and 15 mm. (*Rh. Gemmingi*, ibid. Pl. VII, Fig. 6), 11 18 mm. (*Rh. Gemmingi*, Edinger 1927). The *Rhamphorhynchus* forebrain, with breadth up to 1½ times the length, appears to have had the most bird-like configuration among reptiles.

It seems, however, that the *Pterodactylus* forebrain possessed a decidedly avian character: namely, two fissures. The middle section of the forebrain chamber in our specimen reveals a longitudinal and a transverse furrow of the endocranial cast. These recall the vallecula and vallecula Sylvii, bird brain fissures of variable course which are always reproduced in the skull by corresponding internal crests. The depressions seen in our specimen are in themselves not conclusive evidence of fissuration; but a longitudinal crest found in a *Dorygnathus* skull by Wiman (letter to the writer, see Edinger 1929) already suggested the presence of a vallecula in Pterosauria; and in Newton's description of the *Scaphognathus* forebrain, the words: "below, at about its hinder third, there is a depression or fissure" (p.510) already established the presence of a vallecula Silvii.

Seeley reports that the cerebral surface was smooth in the Cambridge Greensand Ornithosaurian. The *Pteranodon* and *Rhamphorhynchus* brain and braincase specimens do not include the vallecula regions.

Midbrain. In the Rhamphorhynchus preparation which represents only the dorsal brain surface, and in the Pteranodon and Ornithosaurian endocasts which represent the upper halves of the brains, no midbrain lobes could be discerned at all: they must have descended down the sides of the brain as they do in bird ontogeny. Indeed Seeley concluded from an imperfect Cambridge Greensand skull "that in the genus *Ornithocheirus* the optic lobes were developed laterally" (1901, p. 55). Only the *Scaphognathus* endocast includes the midbrain lobes. They are laterally situated. Newton's side view of the cast gives the impression that these lobes reach up to the dorsal brain surface. Newton's text, however, reveals that the cerebellum (which came between the midbrain lobes in the median line) "is almost wholly wanting." Thus it is possible that in *Scaphognathus* the cerebellum rose above the midbrain; but this reached high up.

As regards *Pterodactylus*, the present interpretation of the neocranium as a brain capsule furnishes ample evidence of the site of the midbrain lobes. The lobe chamber is conspicuous and well-delimited, not only in the skull investigated, but in the lateral view of every good *Pterodactylus* skull, just behind the orbit. It clearly shows that the optic lobes of *Pterodactylus* were very large, entirely removed from the dorsal side of the brain, and reached its base. Thus they were avian in character. – Their site makes it appear possible that the little baso-lateral elevation in the *Pteranodon* cast, which I (1927, p. 110) believed to be the insertion of the flocculus, may instead have been the uppermost extremity of the optic lobe. Even if this were so, the *Pteranodon* lobes had descended farther down than those of *Pterodactylus*; this is particularly clear in a comparison of the *Pteranodon* cast with Mayer's *Pterodactylus kochi* cast (our Text Fig. 1 A).

It follows that the optic lobes of all Pterosauria had been shifted from the dorsal site which they occupy in all other reptiles. They probably extended over the whole height of the brain side in the Liassic *Scaphognathus*, they occupy the lower half in the Malm *Pterodactylus*, they are absent in a dorsal view of the Malm *Rhamphorhynchus* brain, and in the Cretaceous *Pteranodon* they are removed to the basal half of the brain or even lower down, as in progressive birds.

Cerebellum. Conditions in *Pterodactylus* show a cerebellum thrust forward above the midbrain to adjoin the forebrain as in birds; obviously, this is one of the characters distinguishing all Pterosauria from the other reptiles.

There is, however, little knowledge of how far the cerebellum reaches caudo-basally; in birds, the cerebellum overlaps the oblongata usually down to the foramen magnum, while in reptiles the oblongata alone, uncovered behind the VIIIth nerve, forms the hind end of the brain. Only the *Scaphognathus* cast shows that in this early Pterosaurian the oblongata extended behind the cerebellum for about one-half the cerebellar length. As the *Pteranodon* cast is taken from the skull roof only, the short portion behind the cerebellum is not a reproduction of the entire cerebellum which extended downwards. The same is true of the *Rhamphorhynchus* specimen described by Edinger 1927; here, as well as in the *Rh. Gemmingi* skull roof interior Mayer 1860 (Pl. VII, Fig. 6), the cerebellar chamber is only 5 mm. long. Side views, however, namely Meyer IX, 1 and X, 1 (*gemmingi*) and the MCZ *kokein* [*Rhamphorhynchus longiceps*] specimen, reveal cerebellum chamber lengths of 10, 10 and 9 mm., respectively; these corresponding to 2/3 of the forebrain length.

The finding of an incisure in the occipital profile of *Pterodactylus* skulls, the incisure occipitalis inferior, now gives evidence of the extent of the cerebellum in *Pterodactylus*. The convexity bordered by two incisures in lateral view is broad and hollow, and obviously corresponds to the tuber cerebellare of birds: it housed the cerebellum. Its presence adds to the non-reptilian characters of *Pterodactylus* the fact that the occiput was not shaped by the attached muscles but by the contained brain. The skull of *Nyctosaurus* (probably a direct descendant of *Pterodactylus*, Williston 1903), which is compressed dorso-ventrally, also has a "posterior flattened prolongation" (Williston 1902, p. 525) which was not a crest but a tuber cerebellare; a small crest runs along its lower side.

The other Pterosaurian occiputs are built so differently from that of *Pterodactylus* that no formation analogous to the cerebellar dome could be traced; but many a protruding occiput suggests at least an interior delimited vaulted cerebellar chamber.

It may be worth noting that not every bird skull has a cerebellar protuberance, and that a study of Fraas' list of birds possessing it (*Ardea* [Heron], *Podiceps* [Grebe], *Pitta* [Pitta]) as well as of the birds mentioned by Marinelli as having a tuber cerebellare particularly well developed (Sphenisciforms [Penguins and Auks], *Colymbus* [Grebe], Anseres [Geese]) reveals that all are birds which catch their food mainly in water…as did *Pterodactylus*!

In all five *Pterodactylus* skulls which show both occipital incisures distinctly, their distance (the length of the cerebellar axis) is somewhat less than the distance from the upper posterior end of the forebrain to its lower anterior end. The Pterodactylus cerebellum was thus just below half of the forebrain length. While there are living reptiles with very small cerebella (see Fig. 2 A), there are others with cerebella 2/3 as long as the forebrain which, however, is not as oblong as in *Pterodactylus*. A short forebrain and a cerebellum 2/3 as long are found in *Scaphognathus* and in *Pteranodon*. Measuring Küenzi's thirty-six side views of bird brains, I found that the length of the cerebellar axis compares to forebrain length as 2:3 only in one-fourth of the cases; the ration is mostly higher, rising to 7:8. As regards length, the Pterosaurian cerebella thus stand at the upper limit of the reptilian and at the lower limit of avian variation.

Better than by its relative length the avian cerebellum is characterized – as contrasting with the reptilian – by its steep instead of horizontal axis, by its reaching forward between the cerebral hemispheres and downward to cover almost the entire oblongata, and by its large flocculi. Both the first characters are shared by all Pterosauria; the third perhaps by *Pteranodon* but not by *Scaphognathus* and *Pterodactylus*; flocculi have been found in the two rhamphorhynchoid brains only, but it is certainly only due to the inadequacy of the material that their presence has not yet been established in the Pterodactyloidea.

Oblongata and brain stem axis. In the specimen investigated, the foramen magnum is not disclosed. The one *Pterodactylus* specimen in which it has been traced, Fraas' *Pterodactylus suevicus* [*Gallodactylus suevicus*], shows that the part of the oblongata not overlapped by the cerebellum was somewhat more than half as long as the latter (7:12 mm.). The proportion must have been similar in Scaphognathus; since while the 4.5 mm. oblongata cast seen behind the cerebellum does not reach the condyle, the actual oblongata was longer. This condition is intermediate between the largely uncovered oblongata of reptiles and the almost entirely overlapping oblongata in birds. The upright direction of the oblongata axis, however, is definitely avian. Steepness of the brain axis anterior to the oblongata is not so rare in reptiles as is commonly believed; but the Pterosauria are the only reptiles with a steep oblongata axis.

There are two osteological factors, both connected with the aerial habits of the pterodactyli, with which the un-reptilian course of the brain axis is correlated. The large-size orbits left no space between them (at their largest circumference) and forced the anterior end of the brain up to the summit of the skull; the basal position of the foramen magnum gave the posterior part of the brain its forward direction. The latter fact, namely the articulation of the head at right angles to the neck, is probably connected with the vaulting of the occiput and the almost avian development of the cerebellum.

Weidenreich has convincingly put forward the thesis that the space for the human brain was procured by the necessity to form a skull which balances on an upright vertebral column. Likewise – cause or effect? – there developed a posterior counterweight to the facial head along with the vertical neck in *Pterodactylus*. Where the cervical vertebrae are found *in situ*, their front line continues the cervical line between midbrain and eyes; that is, the neck directly supports the bulkiest part of the braincase, but not the eyes. An actual equilibrium without muscular effort may really existed in the small pterodactyli. In these, about one-fourth of the skull length lies behind the point of support; but the larger a *Pterodactylus*, the longer the beak, so that the proportion rises to 1/13.

Strong nuchal tendons to hold the head were present in small and in large forms: this is evident from the many specimens in which, after the decay of the neck muscles, tendons pulled the back of the head towards the back and rump. Yet, since we are entitled to regard small size as primitive, as is also the short beak in comparison with the long beak of the large pterodactyli, it seems that the vaulting of the occiput and cerebellum originally did balance the skull at right angles with the neck.

SUMMARY.

The brain of *Pterodactylus* is quite un-reptilian, almost entirely bird-like in form.
Avian were the nervous centers of the olfactory and optic senses. The olfactory bulbs, shifted above the orbits, were as much reduced as in the later Pterodactyloidea. The large optic lobes were situated latero-basally; they were moved even farther downward in Cretaceous forms – in the Rhamphorhynchoidea, similar development can be followed from the Lower to the Upper Jurassic -.
The cerebellum, center of the statotonus, was placed as in birds adjoining the forebrain; but it did not extend as far downwards as in birds though further than in a Liassic rhamphorhynchoid.
The upright direction of the medulla oblongata is avian.
The forebrain seems to have possessed both the fissures of the bird forebrain; but in acquiring avian outlines it was slower to follow the trend towards bird-likeness than the other brain parts. Slender in the Liassic rhamphorhynchoid and the Tithonian *Pterodactylus*, it achieved avian breadth in the Tithonian Rhamphorhynchoidea and in the Cretaceous Pterodactyloidea.
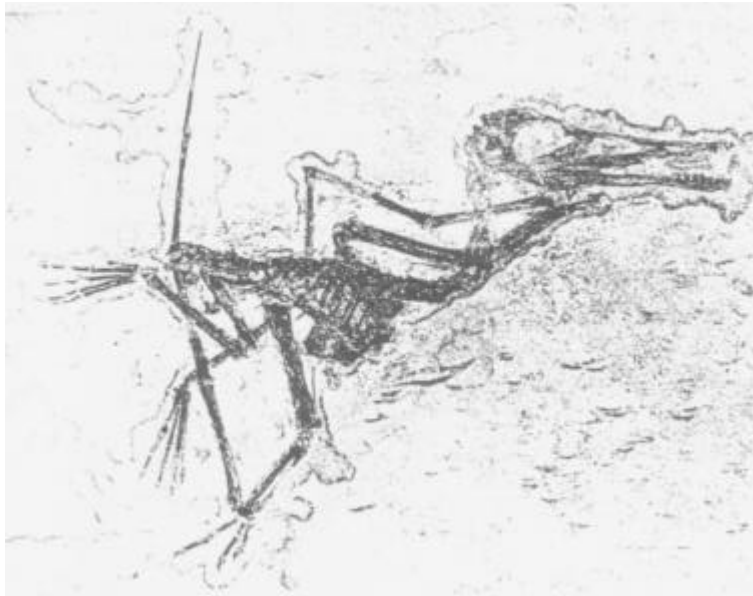The base of Pterosaurian brains remains unknown.

Fig. 1. *Pterodactylus elegans* Wagner. Tithonian, Solnhofen, Bavaria. MCZ. 1503, slab A. Nat size.

Fig.2. The same, neocranium and orbit. 4x nat size.

Footnotes.

1. Rhamphorhynchoidea:
Scaphognathus (Parapsicephalus), Upper Liassic; endocast. Newton 1888, pp. 509-511, Pl. 78, Figs. 6-7.
Rhamphorhynchus, Tithonian; brain case roof interior. Edinger 1927, pp. 106-108, Fig. 2.

Pterodactyloidea:
Ornithosaurian, Upper Cretaceous; endocast. Seeley 1870, pp. 87-88, Pl. 12, Figs. 10-12.
Pteranodon (Ornithostoma), Upper Cretaceous; endocast. Edinger 1927, pp. 108-110, Fig. 3.

2. The shape of the gaps along the skull vault is rather peculiar. Only the largest, at the hind end of the forebrain chamber, is angular and would be expected to arise when pressure flattens, and bursts open, the braincase. Behind this triangular gap, there is a large, rounded one which suggests that bone has been lost since the excavation of the specimen. Anterior to these two, however, there is a sequence of shallow, semicircular breaks in the continuity of the skull outline, as if the head had been bitten: They are fairly equal, with diameters just below 1 mm.

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