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## PTERODACTYLS PAST AND PRESENT

BY D. M. S. WATSON, F.R.S.†

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In 1784, Collini the curator of the Grand Ducal Museum of Mannheim described a slab of limestone from Eichstätt in Franconia which contained the complete skeleton of a small animal. He ended his description with a sentence in which he expressed the opinion that it should be possible to determine the mode of life of this animal, by a consideration of the circumstances under which it was buried, in rocks full of marine shells, and of its own structure.

And he concluded it was some kind of fish.

But many years later at almost the same time Cuvier and v. Sömmering discussed its structure, the former rightly holding it to have been a flying reptile, of a kind now extinct, the latter, comparing it with a bat, but giving a most interesting reconstruction of the skeleton as it would have appeared when articulated. Although imperfect this restoration was a very remarkable feat, the first attempt at a procedure now commonly adopted.

Flying animals live a life so difficult in many ways, in the actual flight, in taking off and landing, in feeding and the production and rearing of their young, that they are necessarily highly efficient mechanisms, and their structure must conform to rigid and to a great extent determinable limits.

Thus the pterodactyls give us a unique opportunity of testing our powers of interpreting an animal structure in terms of function, because, owing to the urgent need of economizing weight, we can be sure that very little of the skeleton can be without definite and important functions.

Any investigations of a pterodactyl must begin by an attempt to reconstruct the animal, a process made relatively easy by the perfection of the preservation of such as come from the Solenhofen slate, when not only the bones, but even the impression and some parts of the structure of soft parts may be recognizable.

The most completely known form is *Rhamphorhynchus*, of which admirable accounts, which supplement one another, have been published by Professors Stromer and Broili of Munich.

It is a small animal with a wide shallow chest from which arises a long slender neck having a large head with pointed jaws and long slender teeth so arranged as to be suitable for catching fish. It has large eyes, and by analogy with other pterodactyls, only a rudimentary sense of smell, but a very well developed cerebellum, the part of the brain concerned in the coordination of movements with one another and with the animal's position in space.

There is a long quite stiff tail which has a small horizontal fin at its tip. The fore limbs are very elongated, the first three fingers having relatively large recurved claws, while the fourth is enormously elongated and forms the forward edge of a narrow pointed wing formed by a fold of skin containing a layer of material packed with slender, probably elastic fibres. It is an indication of the perfection of adaptation that the finger bone which forms the leading edge of the wing has exactly the transverse section as the corresponding part of an aeroplane wing.

The hind legs are long, slender, little-muscled structures which stand out at right angles to the body and were involved with the wing. The spreading feet were webbed.

† Deceased 23 July 1973.

All the larger bones are hollow, air filled for lightness as are those of birds. Like some birds also there was a sac between the hind ends of the lower jaw and a tuft of hair-like scales standing up from the top of the head.

It is possible to determine approximately the mass of the animal, and to measure its wing area, and thus to arrive at what is called its 'wing loading', a most important aerodynamical figure.

A *Rhamphorhynchus*, some 60 cm from nose to tail, with a wing spread of 120 cm, had a live mass of about 200 g and a wing loading of  $1.2 \text{ lbf ft}^{-2}$  ( $5.9 \text{ kgf m}^{-2}$ ), figures agreeing well with those for such sea birds as the larger terns.

For some time after their first appearance on this world all pterodactyls resembled *Rhamphorhynchus* in having long tails with a horizontal fin, a device which helps very greatly in giving longitudinal stability, while it handicaps its possessor by preventing any great change in the angle which the wing makes with the direction of flight, and hence changes in the flying speed.

At a time about the middle of the period when pterodactyls lived, tailless forms appeared, and these were the only ones which lived on into Cretaceous times, to become the largest flying animals known, with a wing spread which may even have exceeded twenty feet.

These giant forms are now very well known, the general form and proportions from specimens found in the chalk of Kansas, U.S.A., the details of the articulations of the bones from English specimens from Cambridge and the Isle of Wight.

They were most beautifully constructed. The great bones of the wings, sometimes nearly 60 cm in length and 3 or 4 cm across, are completely hollow, cylinders of bone no thicker than a visiting card, prevented from collapse only by a system of tie-bars, bony rods as thick as a pin passing across the cavity, with their expanded ends continuous with its wall.

The actual articular surfaces fit with the perfection of good machinery, and there is no difficulty in determining by trial what movements were possible. In fact most movements of the wing are so linked together that any closing of the elbow joint automatically brings about movements at the wrist of a complex kind. It seems that the effect of these movements is so to alter the aerodynamical qualities of the wing that the speed through the air necessary to support the animal's weight is reduced, the animal thus changing its course while remaining on an even keel.

It is possible to calculate the force which can be exerted by the wing muscles and the amount of work they can do. Although all that can be said of these figures is that they lie somewhere in a wide range, it seems evident that the force these muscles can exert is not very much greater than that necessary to support the animal's weight, and that they are small in comparison with quick-flying birds like pigeons or ducks.

As the whole design of the wings is that of quick-moving marine birds it is probable that in general pterodactyls soared like albatrosses and had only a slow flapping gait. The great majority of specimens of pterodactyls have been found in marine rocks, and they are common fossils in the Kansas chalk laid down perhaps hundreds of miles from land. It is tempting to see in this habit of life a confirmation of this soaring flight.

It is possible to go somewhat further with the analysis of their structure. If they were essentially soaring creatures it is clear that the energy by which they were moved must have been derived from the vertical component of air currents, as in the identical case of humanly constructed 'gliders'. But this implies that the energy available varies directly as the weight. This energy has to be put to two purposes, in part it is expended in counteracting gravity and in

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part to overcoming the frictional resistance to motion of the creature through the air. This latter figure depends on the nature of the surface of the skin and on the surface area. The remaining fraction is spent in setting up disturbances in the air as a result of inadequate streamlining.

It is possible to calculate the total surface area, and the mass, but the other factors can never be evaluated. There exists a series of tailless pterodactyls of all sizes between that of a sparrow and the great 6 or 7 m span of *Pteranodon*.

In the text-figure I have inserted points representing the weight, and the surface area of a series of forms, picked merely because they were sufficiently perfectly preserved to be restored without too great uncertainty.

These points lie, with very unexpected accuracy, on a curve, of a type which can be paralleled by similar plottings of any family of birds.

But the same animals may be used to form a curve representing the relation of weight to wing loading.

*The manuscript breaks off at this point and the text-figure is missing.*