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BIOMECHANICS OF *PTERANODON*

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[Plates 24 and 25]

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The fossil evidence is re-examined to determine the structure of *Pteranodon ingens*. New measurements include the cross-sections and thickness of the wing bones, the degree and direction of movement of the joints, and the size and position of major tendon and muscle insertions. From this data a reconstruction is made suitable for engineering and aerodynamic analysis. The reconstruction is based largely on Eaton's type specimen, 1175, and has a wing span of 6.95 m. The mass is estimated as 16.6 kg by calculating the volume of each part, making due allowance for the soft parts and cavities.

The engineering design of the wing is considered in some detail. The shape deduced from the angles of the joints agrees well with that required for strength and aerodynamic efficiency. The strength of each part has been compared with the loads on it in gliding flight, showing that the structure is extremely well designed; it is strong enough everywhere, but with little unnecessary weight.

Wind-tunnel experiments on model heads show that the sagittal crest was primarily a weight-saving device; by balancing the aerodynamic loads on the beak, it allows the neck muscles to be reduced, saving much more than its own weight.

The performance of *Pteranodon* as a glider has been calculated, and compared with birds and man-made gliders. With a sinking speed of only 0.42 m/s at a flying speed of 8 m/s, *Pteranodon* is a superb low speed soaring aircraft, able to soar in weak thermals, or hill lift in very light winds. With its low stalling speed, it could also land very gently.

Powered flight is considered, and it is shown that *Pteranodon* is just capable of level flight; but it is clearly primarily a glider.

The environment in which *Pteranodon* lived is determined as far as possible from an analysis of the palaeobotany, palaeozoology and palaeoclimatology of the Cretaceous. The evidence points to a warmer and more uniform climate with lighter winds than today. This agrees well with *Pteranodon's* performance, which is ideally suited to light wind conditions.

The mode of life is considered, showing that *Pteranodon* probably lived on sea cliffs facing the prevailing wind. After landing on the top, it would scrabble forwards (it could neither stand up nor walk) and hang from its hind feet over the edge. From here it could easily launch itself. When flying near the cliff it would soar in the hill lift; when far out at sea it would use the weak thermals generated by convection over the warm sea. Dynamic soaring and slope-soaring over the waves are not possible for such a slow-speed glider.

Some consideration is given to methods of feeding, social organization and defence against predators. Finally it is suggested that extinction could have been due to climatic change, particularly an increase in the average wind speed at the end of the Cretaceous.

1. INTRODUCTION

Palaeontologists assess the mode of life of extinct species from their fossil remains and the sediments that contain them. They make full use of the sciences of zoology and geology and occasionally turn to physics and chemistry. But it is rare indeed for any appeal to be made to engineering.

This is surprising, for every animal is a mechanical structure, required to withstand certain stresses both when stationary and during locomotion. All land animals must stand up against gravity and be able to move about. If the structure of any particular animal is known, then its physical strength and locomotory ability (performance) can be calculated. The limitations found from this will provide useful information about the ecological conditions in which the animal could survive. Conversely if, as in some fossil species, the structure is not well known, engineering considerations can guide the choice between a number of possibilities; the best engineering solution is likely to be the correct one, and certainly if any particular postulated structure is not mechanically feasible it is wrong.

Several workers are now applying engineering considerations to living animals (McNeill Alexander 1968; Pennycuick 1968; Machin 1958). This is nothing new (Galileo 1638) but has been neglected since science has been fragmented into separate disciplines. In this paper a similar approach is taken to an extinct species – the Cretaceous pterosaur *Pteranodon*. A flying animal was chosen because flight is the most structurally demanding type of locomotion and its requirements limit the animal's design to a far greater degree than do the effects of aquatic or terrestrial movement. The genus *Pteranodon* was at the end of an evolutionary sequence and shows extreme specialization for flight. It is also the largest known aerial animal. With increase in size structural requirements become more stringent and economical engineering design is vital. It is essential that a large flying animal be as light as possible, yet it must maintain the required strength and have some safety factor.

Many palaeontologists have realized that *Pteranodon* was primarily a glider (Hankin & Watson 1914; Kuhn 1967; Romer 1966; Bramwell 1971). The estimation of glider performance is well understood (Welch, Welch & Irving 1968; Treiber 1969) – much better than that of powered flight with flapping wings. In view of this it is fortunate that *Pteranodon* was so large because small pterosaurs could be expected to have made more use of flapping flight. The first object of this paper is to estimate the gliding performance and structural strength of *Pteranodon* from a study of its fossil remains. The possibility of powered flight is examined. The aerodynamics are then related to the palaeoecology of *Pteranodon* and various aspects of the mode of life considered. Ultimately one might hope to follow the aerodynamic evolution of all pterosaurs and see how the optimum design achieved by each type relates to its environment and how this optimum shifts as ecological conditions alter.

2. Reconstruction of *Pteranodon ingens*

(*a*) *The wings*

(i) *The fossil evidence*

To understand the functioning of the pterosaur wing skeleton it is necessary to determine three things. These are the dimensions of the individual bones, the thickness of the bony material forming the walls of the wing bones and the degree and direction of movement possible at the articulations.

Pteranodon ingens, from the Upper Cretaceous Niobrara Chalk of Kansas, has been fully described by Eaton (1910). The lengths of the wing bones of our reconstruction are based on his specimen no. 1175, in which part of the wing skeleton is present. The lengths of those bones absent in no. 1175 have been obtained by scaling in proportion from bones of other specimens designated to the same species. Eaton also did this and our wing span of 6.95 m agrees quite closely with his estimate of 6.8 m. Specimens of *Pteranodon* are available in the British Museum (Natural History) in London and the Peabody Museum, Yale University. These were examined for bone lengths, but as in all *Pteranodon* material the fossils are flattened; so to find accurate information on the bone thickness and articulations other evidence was sought.

Many pterosaur fossils very similar in structure (Cope 1872) and age to *Pteranodon* have been collected from the Cambridge Greensand. They were assigned to *Ornithocheirus* and *Ornithostoma* (Seeley 1870), the latter being a synonym of *Pteranodon*. Although the shafts of most of the Greensand bones are missing, the collection, of about 1000 specimens, is very valuable as it contains many undistorted articular ends. This material was used by Hankin & Watson (1914) for their analysis of the joint movements of the wing of *Pteranodon* and we have used it for the same purpose. Working from specimens in the Sedgwick Museum, Cambridge and the British Museum (Natural History), the movements possible at each wing joint were deduced and so gliding and flapping positions for the wings could be found. Knowledge of the degree of articular freedom at each joint also enabled us to understand the use of the wings in locomotion on the land and other wing movements not associated with flight.

Table 1. Dimensions of wing bones

specimen	humerus		radius		ulna		carpals		metacarpals		1st phalanx		2nd phalanx		3rd phalanx		4th phalanx	
	L	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*	*L*	*W*
Eaton																		
1175	**29.0**	**4.7**	—	—	**38.4**	**5.1**	—	**6.3**	—	—	—	—	—	—	—	—	—	—
2239	—	—	—	—	—	—	—	—	57.0	4.4 (5.2)	—	—	—	—	—	—	—	—
2425	**15.5**	—	21.7	—	22.3	—	3.31	—	**36.0**	**2.8** (5.2)	—	—	—	—	—	—	—	—
2452	—	—	32.0	2.3 (2.5)	33.2	3.7 (4.3)	—	—	**58.6**	**4.3** (4.9)	**63.5**	**3.4** (4.2)	**36.4**	**2.0** (3.4)	**30.3**	**1.4** (1.9)	**18.7**	**0.9** (1.2)
2470	—	—	—	—	—	—	—	—	—	—	49.5	2.2 (3.5)	38.0	1.75 (2.8)	26.0	1.0 (1.5)	14.6	0.6 (1.0)
2493	**20.4**	3.5 (5.0)	—	1.5 (1.9)	29.7	3.7 (4.8)	—	—	51.9	3.9 (5.0)	—	—	—	—	—	—	—	—
2562	—	—	—	—	—	—	—	—	42.7	3.9 (6.1)	—	—	—	—	—	—	—	—
2680	—	3.0 (5.0)	—	2.0 (3.3)	—	—	—	—	—	—	—	—	37	1.8 (3.0)	26	1.0 (1.5)	—	—
2689	—	—	—	—	—	—	—	—	—	—	70.3	3.7 (4.1)	—	—	36.0	1.3 (1.4)	—	—
2734	—	—	—	—	—	—	—	—	60.6	4.4 (4.9)	—	—	—	—	—	—	—	—
2738	—	—	—	—	—	—	—	—	—	—	67.0	—	50.0	—	—	—	—	—
2774	—	—	—	—	—	—	—	—	—	—	**47**	**3.1** (5.1)	**36.8**	**2.0** (2.3)	**26.2**	**0.95** (1.5)	—	—
B.M.																		
R 3299	—	—	—	—	—	—	—	—	—	—	43.5	2.3 (4.1)	—	—	—	—	—	—
R 3378 (cast)	16.8	3.1 (5.4)	**24.3**	**1.3** (1.9)	**25.2**	**2.8** (4.3)	4.0	4.7	**39.0**	**2.9** (5.0)	**45.0**	3.3 (5.7)	38.6	1.8 (2.9)	30.0	1.3 (1.7)	16.4	0.7 (1.0)
R 3877	16	2.2 (4.0)	43	0.6 (0.5)	43	1.8 (1.6)	—	—	—	—	—	—	—	2.1	—	—	—	—
R 4358	16.7	—	22.9	—	**22.9**	—	—	—	—	—	54	2.4 (3.5)	43	1.6 (2.3)	**27**	**1.0** (1.5)	**14.6**	0.5 (0.8)
R 4542	—	—	—	—	—	—	—	—	—	—	45.2	2.6 (4.5)	—	—	—	—	—	—
41637	—	—	—	—	—	—	—	—	—	—	40	2.4 (4.7)	—	—	—	—	—	—
K.T.																		
5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	25	2.1 (1.6)	—	—
6	—	—	—	—	33.3	3.6 (4.1)	—	—	—	—	—	—	—	—	—	—	—	—
7	—	—	—	—	—	—	—	—	**54**	**3.8** (5.5)	—	—	—	—	—	—	—	—
values chosen for reconstruction	29.0	4.7	34.7	2.0	38.4	5.1	6.2	6.3	67.1	5.2	77.9	4.5	61.4	3.0	40.0	1.6	24.6	1.0

L, length of each bone (cm) between the central points of its articulations.

W, greatest diameter (cm) of the cross-section at the midpoint of each bone.

The figures in parentheses have been scaled up to the size of the reconstruction. The reconstruction is mainly derived from the measurements that are in bold type.

It is important to know the thickness of the walls of the long, hollow wing bones to calculate the structural strength of the wing. These measurements were taken from a variety of broken wing bones, some belonging to *Pteranodon* itself, although the crushing of these specimens makes them the least reliable source of information. The pterosaur remains from the Chalk of Kent (Wealden) provided the most accurate measurements. These specimens are also in the British Museum.

It may reasonably be argued that the fossil evidence is derived from various individuals belonging to several species. This is inevitable, owing to the fragmentary nature of pterosaur fossils. We have tried to overcome this disadvantage by working on pterosaurs of the same type, using this word in the aerodynamic sense. All the material examined belonged to large, Cretaceous pterosaurs belonging to the Ornithocheiridae. All measurements have been scaled to be analogous with the dimensions of *Pteranodon ingens*. We believe that the information obtained in this way enables a valid reconstruction of the wing to be made.

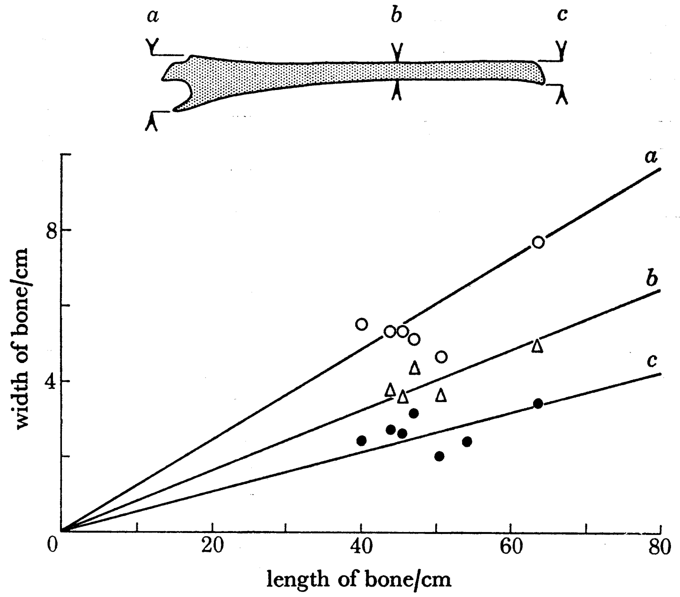


FIGURE 1. Shaft width against length for first phalanges.

(ii) *Bone dimensions*

Table 1 gives the measured dimensions of the bones used to derive the reconstruction. Most of the measurements were taken directly from the original bones, or, where specified, casts, but some of those from Eaton are his own measurements, where given, or measurements taken from his photographs. The final line of the table gives the dimensions of our reconstruction, scaled linearly from those given above in bold type. Linear scaling is justified by figure 1, which shows selected dimensions of the first phalanx plotted against the length of the bone; there is considerable scatter, as one would expect of biological material, but no significant departure from linearity.

(iii) *Bone thickness*

The wing bones of *Pteranodon* are all pneumatic, forming very thin-walled tubes. The bone shaft width and wall thickness were measured in a number of bones in the British Museum, Peabody Museum and the University Museum of Oxford. The thickness seldom exceeds 1 mm in agreement with Eaton (1910), who wrote 'The shafts of the wing bones are of extreme tenuity, fragments from some of the larger specimens having only a thickness of 1 mm.'

The bone thickness measurements are shown in table 2:

Table 2. Measured wall thickness of wing bones

bone	specimen	shaft width/cm		mean wall thickness/mm	$\frac{\text{maximum width}}{\text{wall thickness}}$
		maximum	minimum		
humerus	Eaton 1175	4.7	—	1.0	47
	2493	3.5	—	0.75	47
	2680	3.0	—	0.9	33
	BM R 1935	3.13	2.3	1.3	25
	R 3877	2.2	2.0	0.4	55
radius	Eaton 1175	—	—	1.0	—
	2680	2.0	—	0.7	29
	BM R 3694	0.9	0.9	0.5	18
ulna	Eaton 1175	5.1	—	1.1	46
	BM R 3877	1.8	1.5	0.7	26
	KT 6	3.6	—	0.7	51
metacarpal	Eaton 1175	—	—	0.8	—
	2239	4.4	—	0.8	55
	2310	3.6	—	1.0	36
	2493	3.9	—	0.7	56
	2734	4.4	—	1.0	44
	BM 39417	1.65	0.96	0.5	33
	41638	1.95	1.0	0.58	34
	KT 7	3.8	—	0.8	48
1st phalanx	Eaton 2310	3.5	—	0.6	58
	2470	2.2	—	0.8	28
	2562	3.9	—	1.0	39
	2689	3.7	—	0.8	46
	2834	3.9	—	1.3	30
	BM 41637	2.4	1.95	1.05	23
2nd phalanx	Eaton 2470	1.75	—	0.8	22
	2680	1.8	—	0.9	20
	2774	2.0	—	0.5	40
	BM R 3877	2.1	1.3	0.42	50
	KT 5	2.1	—	0.9	23
3rd phalanx	Eaton 2680	1.0	—	0.75	13
	2689	1.3	—	0.6	22
	2774	0.95	—	0.5	19

Obviously the wall thickness is not just proportional to the shaft width; the shaft width/wall thickness ratio varies from 13 to 58. But for each bony element the ratio is more nearly constant. So the measured ratios for the appropriate bone have been averaged to obtain the wall thickness of the reconstruction. All dimensions of the wing bones of the reconstruction are shown in table 3.

While measuring the thickness of the walls of the wing bones, we observed that when the bone cross-section was oval or subtriangular the bony material tended to be concentrated at the corners. This is shown for two specimens in figure 2. This distribution of bone gives additional strength and stiffness to the hollow cylinder of the wing bone by increasing the moment of inertia of the section.

It is reported (Kozatsiy & Yurbev 1964) that, as in birds, the wing bones of pterosaurs are strengthened by internal struts near the epiphyses. We accept this, as it is obviously necessary for engineering reasons, but we have no suitably broken bones to present personal evidence of it.

Table 3. Dimensions of reconstruction

bone	length/cm	shaft width/cm		wall thickness/mm	maximum width / thickness
		maximum	minimum		
humerus	29.0	4.7	4.0	1	47
radius	34.7	2.0	2.0	1	20
ulna	38.4	5.1	4.6	1.1	46
carpals	6.2	6.3	6.3	1	—
metacarpal	67.1	5.1	2.8	1.3	39
1st phalanx	77.9	4.4	3.6	1.2	37
2nd phalanx	61.4	3.0	1.9	1	30
3rd phalanx	40.0	1.6	1.0	0.9	18
4th phalanx	24.6	1.0	0.7	0.5	20

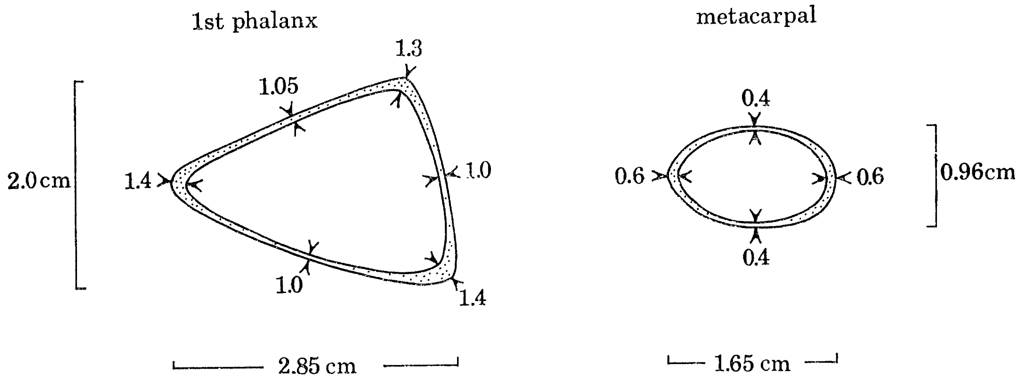


Figure 2. Cross-sections of a first phalanx (B.M. no. 41637) and a metacarpal (B.M. no. 39417) (dimensions in mm unless otherwise indicated).

Table 4. The wing articulations

joint	proximal element	distal element
shoulder	glenoid cavity of scapula/coracoid	humerus
elbow	humerus	radius/ulna
wrist	radius/ulna	proximal carpal
wrist	proximal carpal	distal carpal
wrist	distal carpal	metacarpal
knuckle	metacarpal	1st phalanx
finger	1st phalanx	2nd phalanx
finger	2nd phalanx	3rd phalanx
finger	3rd phalanx	4th phalanx

(iv) *Articulations of the wing*

The pterosaur wing skeleton had the possibility of movement at nine points. These are listed in tables 4 and 5.

The third bone in the wrist is the lateral carpal. This is not part of the wing spar (the skeletal structures actually involved in taking the wing loads), but served to support the pteroid bone which in turn supported the pteroid membrane at the front of the wing. The small wing fingers, digits I, II and III are also not part of the wing spar.

Table 5. Joint movements

The angles given are those between the shaft of each bone and the planes containing the axes (see figure 3), when all proximal bones are in the normal gliding position.

	gliding position/deg				possible movement (deg) of wing bones at fullest extent			
bone	up	down	back	fore	up	down	back	fore
humerus	20	—	19	—	70	25	above lock 65 below lock 17	above lock 0
radius/ulna	3	—	—	8	—	18	—	30
carpals	3	—	—	8	—	—	—	—
wing-metacarpals	3	—	—	25	25	5	35	8
1st phalanx	—	6	—	9	—	2	125	—
2nd phalanx	—	9	—	3	—	—	—	—
3rd phalanx	—	15	2	—	—	—	—	—
4th phalanx	—	22	10	—	—	—	—	—

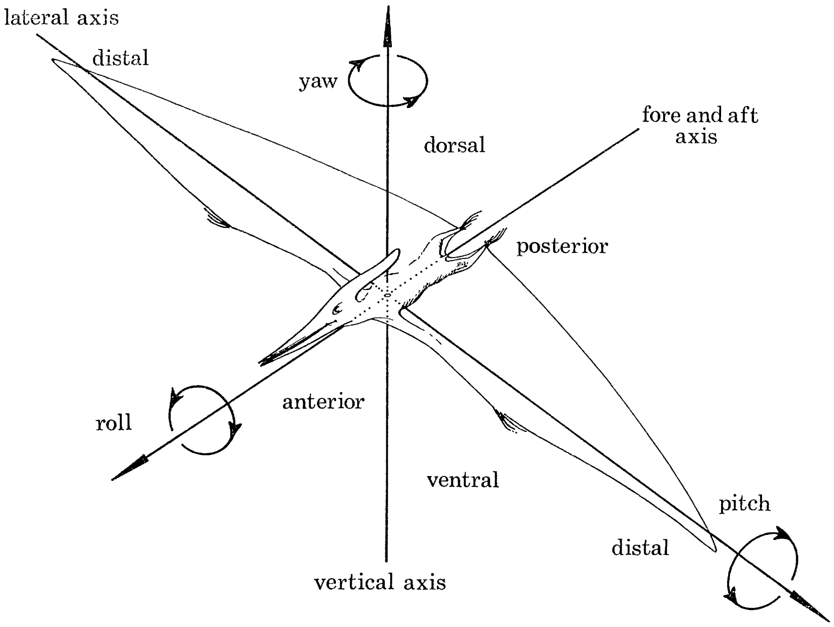


Figure 3. The axes.

All the angles of the wing joints were measured relative to a set of three axes, called, in engineering notation, fore and aft, lateral and vertical (figure 3). The biological terms for these axes are shown in the figure.

The individual drawings of the joints show the bones of the left wing in the gliding position; two views of each joint are shown, the anterior and the dorsal. The angles given are those between the bone shafts and the three axes; the arrows on the axes correspond with those in figure 3. The possible movement at each joint is then described, with all proximal joints held in the normal gliding position. Finally, in figure 23 the whole wing is drawn to scale in the gliding position.

The direction and degree of movement at each joint is obviously related to the requirements of control and of powered flight. But other wing movements must have been made in activities not connected with flight – for example, moving on the ground and grooming. These are discussed in § 5.

Before considering the actual wing joints, it is necessary to determine the position of the pectoral girdle within the body, as this fixes the position of the glenoid cavity into which the wing articulates. It was found from British Museum Specimen no. R 3378 that the girdle is arranged as in figure 4.

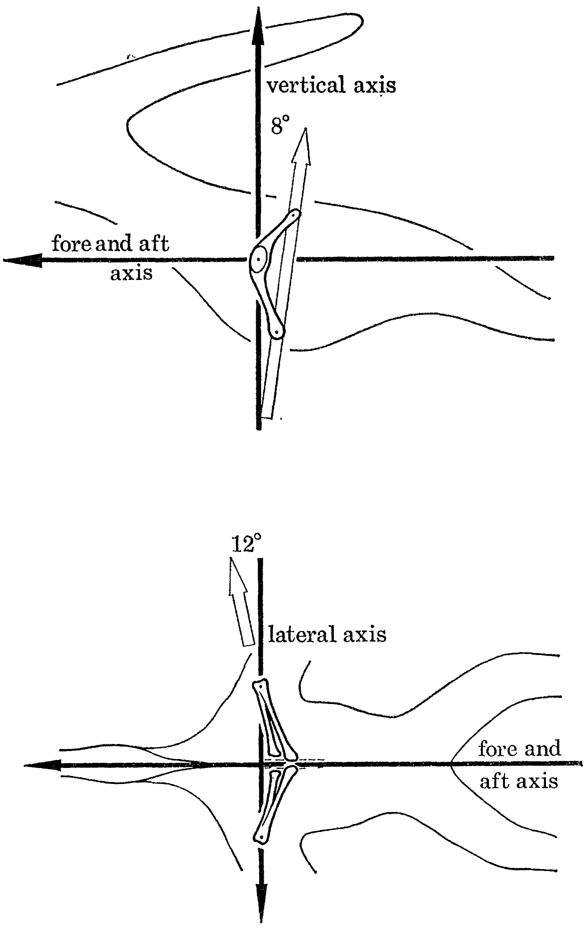


FIGURE 4. Position of pectoral girdle in the body in lateral and dorsal views.

The glenoid cavity itself is made up by the fusion of the scapula and coracoid. Its peculiar shape and the way this fits the head of the humerus is shown in figure 5 – a drawing of Sedgwick Museum specimens nos B 54031 (scapula-coracoid) and B 54061 (articular head of humerus). When the bones are correctly fitted it is seen to be a hinge joint with the line of the hinge parallel to the ridge on the head of the humerus.

The normal gliding position of the humerus was found from the bones in figure 5; as they are incomplete specimens, nos B 54648 (coracoid), B 54081 (humerus), B 54030 (scapula-coracoid) and British Museum *Pteranodon* no. R 3378 were also used to check the angles of articulation and degree of movement possible at the shoulder. The angle at which the humerus is held when gliding is illustrated in figures 6*a* and *b*; 6*a* is a dorsal view and 6*b* an anterior view of the joint.

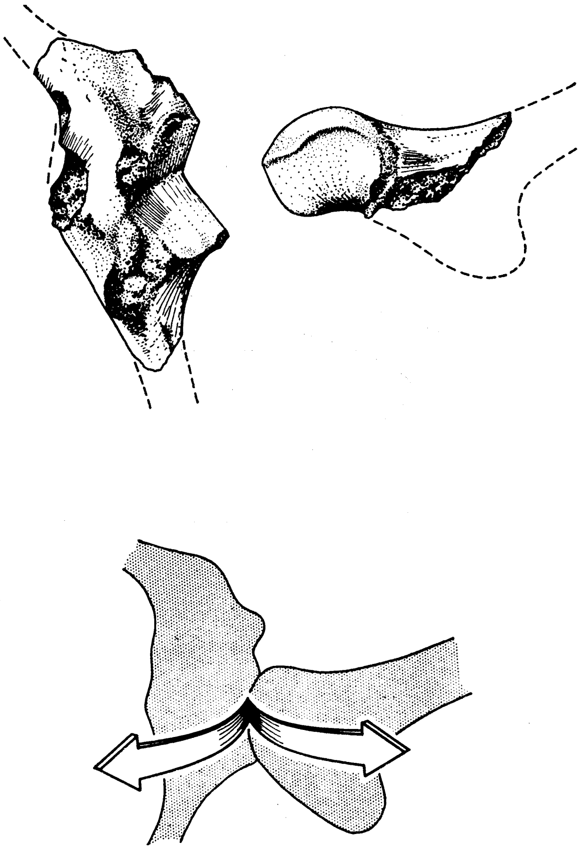


FIGURE 5. The shoulder articulation showing the head of the humerus and the glenoid cavity.

The humerus moved up and down about its hinge during the flapping of the wings. It can move down to an angle of 25° below the horizontal at the lowest point of the downstroke and can be raised to 70° above the horizontal at the highest point of the upstroke. At the bottom of the downstroke the humerus is directed backwards by 17°. As the humerus moves upwards there is one position in which it locks in the glenoid cavity. This is due to the peculiar shape of the cavity which has its upper and lower surfaces set at an angle to each other. When combined with the ridged articular head of the humerus it forms a lock in one position (figure 5). When articulated in this way the humerus is directed upwards at 20° and swept backwards at 19° (figures 6*a*, *b*). We assume that this is the natural gliding position. The lock resists further upward movement of the wing, greatly reducing the muscular effort needed to hold the wings out when gliding. The mechanism of the lock is illustrated in figure 7. As the humerus moves upward, the pivot point shifts from A to the ridge B, increasing the moment arm of the pectoral muscles from *a* to *b*; thus reducing the tension in the pectoral muscles. This arrangement appears to be unique among flying vertebrates. We have examined the shoulder joints of large gliding birds, and they do not have this form, but are round or oval ball-and-socket joints, without any locks. This adaptation in *Pteranodon* was probably due both to its size and to its extreme

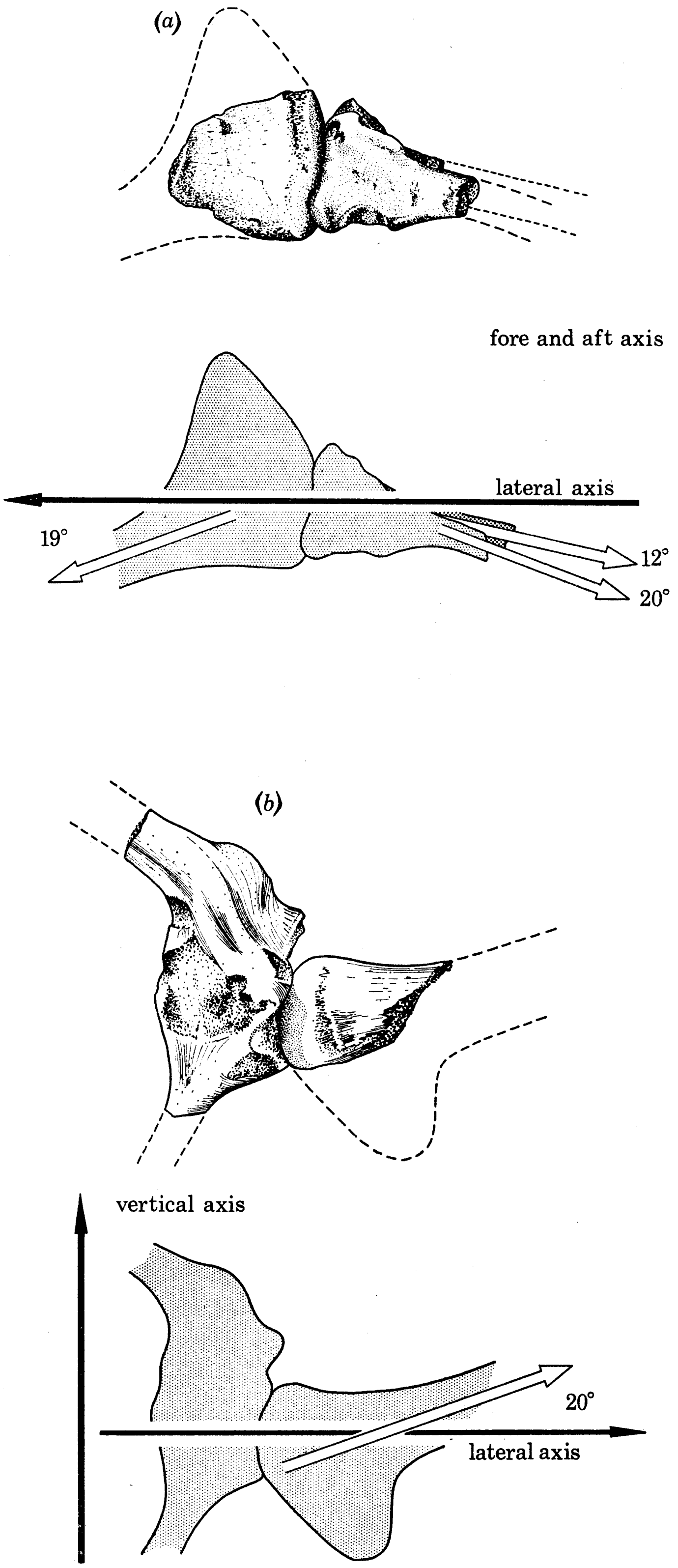


FIGURE 6. (*a*) Dorsal view of the shoulder articulation, showing parts of the pectoral girdle and humerus. (*b*) Anterior view of the shoulder articulation, showing parts of the pectoral girdle and humerus.

specialization for gliding rather than flapping flight. But when the need to flap the wings occurred, the lock could be broken, allowing the humerus to continue on its upstroke. Above the lock the articulating surfaces are spherical, so the joint then behaves as a ball and socket rather than as a hinge. The humerus can then swing backwards by 65° and forwards to 0° (straight out along the lateral axis). It can rotate about its own axis as well as moving up and down; at the top of the upstroke it can twist by 20°.

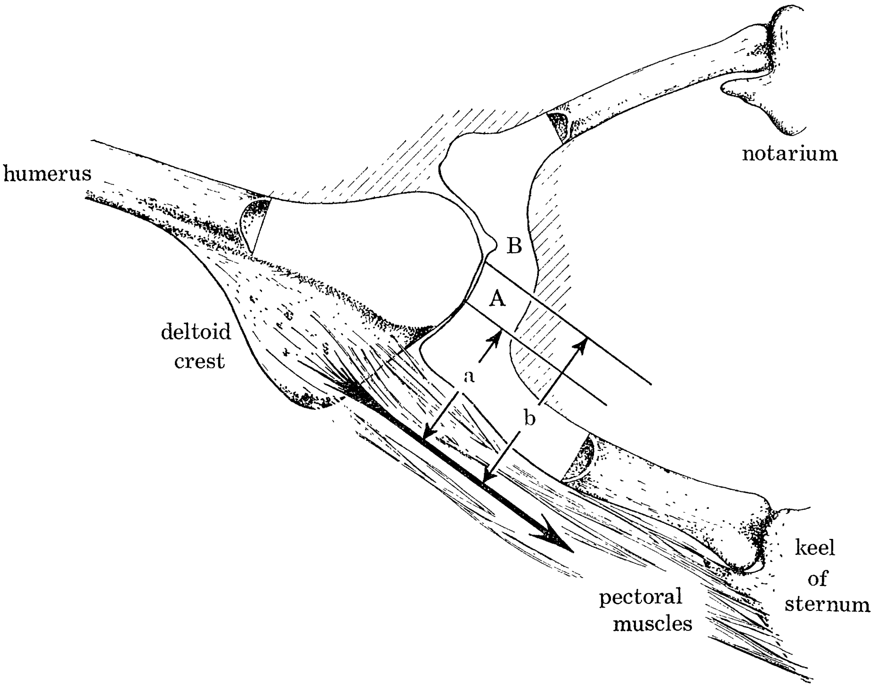


Figure 7. The shoulder joint lock; for explanation see text.

The elbow joint is formed by the articulation of the distal end of the humerus with the proximal ends of the radius and ulna. British Museum specimen no. R 3877, *Ornithodesmus latidens*, shows this joint clearly. The elbow is a hinge, and is shown articulated in the fully extended position in figure 8*a*, *b*. When the bones are alined like this the radius and ulna run forward at 8° to the lateral axis and slightly upward at 3° to the horizontal.

As the elbow is a hinge joint, movement can only occur in one plane. When the joint is flexed the radius and ulna swing forwards and downwards, moving through about 20° in both directions. In the fully flexed position the radius and ulna run forwards at 30° and downwards at 18°. As this action occurs, the radius is pushed by its articulation on the humerus and slides outward along its long axis. This movement of the radius relative to the ulna during the flexing of the elbow was noticed by Hankin & Watson (1914) and mentioned in their work on the pterosaur wing.

The wrist in pterosaurs is made up of three separate articulations. The distal ends of the radius and ulna articulate on the proximal carpal; the proximal carpal rests against the distal carpal; and the distal surface of the distal carpal articulates with the wing-metacarpal. The lateral carpal and the three small metacarpals also originate on the distal carpal, but are not part of the main wing spar. The wrist joint is shown in dorsal and anterior views in figure 9*a*, *b*.

The reconstruction of the wrist is based on *Ornithocheirus* bones from the Cambridge Greensand. Many good examples of these are present in the Sedgwick Museum. The various articulations are best shown by nos B 55057 (ulna), B 54126 (radius), B 54697 (proximal carpal), B 54601 (distal carpal) and B 54652 (wing-metacarpal).

When this series of bones is articulated naturally, the wing-metacarpal runs from the wrist

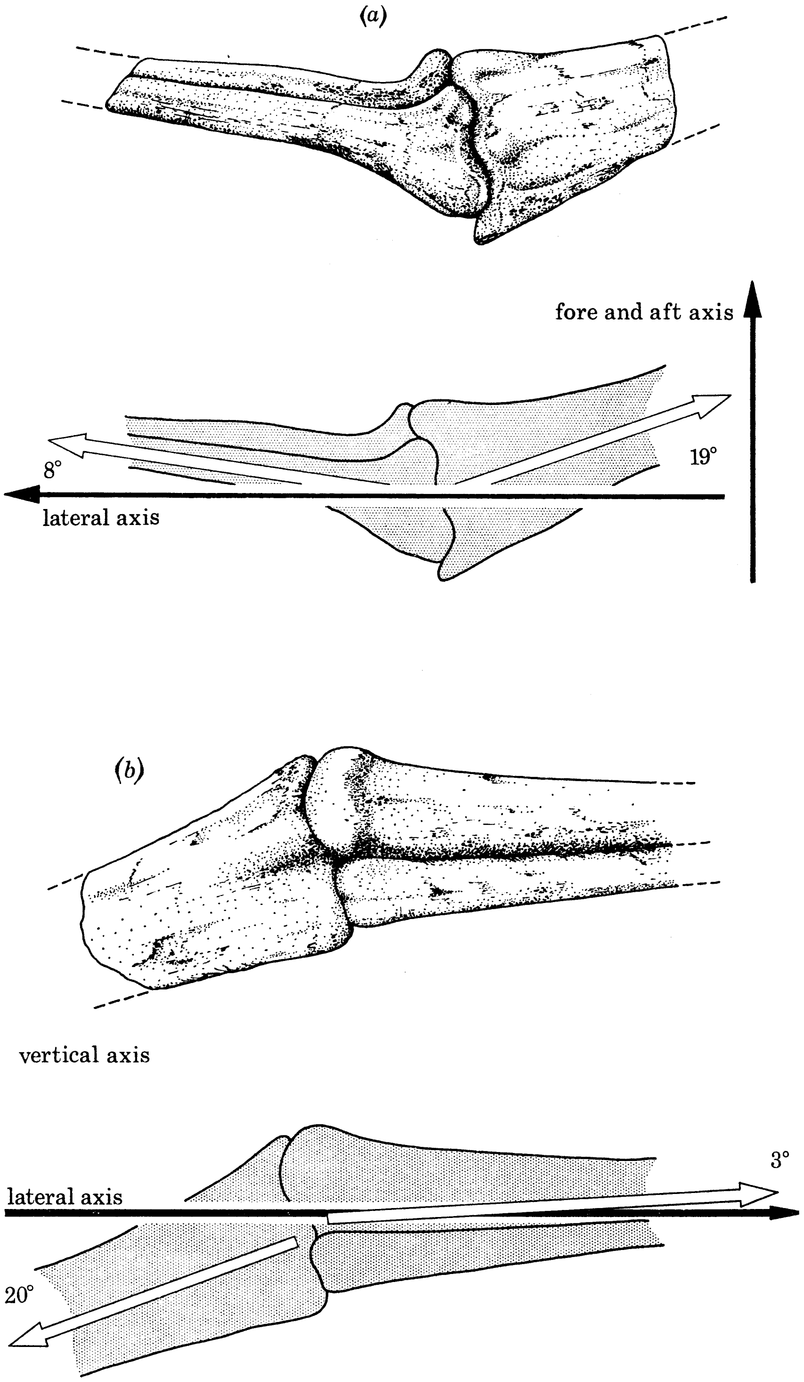


FIGURE 8. (*a*) Dorsal view of the elbow articulation, showing parts of the humerus and radius/ulna. (*b*) Anterior view of the elbow articulation, showing parts of the humerus and radius/ulna.

at an angle of 25° forward and 3° upwards. The articular surfaces of the wrist bones are drawn in figure 10*a*, *b*, *c*.

Figure 10*a* shows the form of the articulation of the distal ends of the radius and ulna with the proximal surface of the proximal carpal. The radius rests in an oval hollow and the ulna articulates via two contacts, inserting into an elongated trough above and a spherical depression

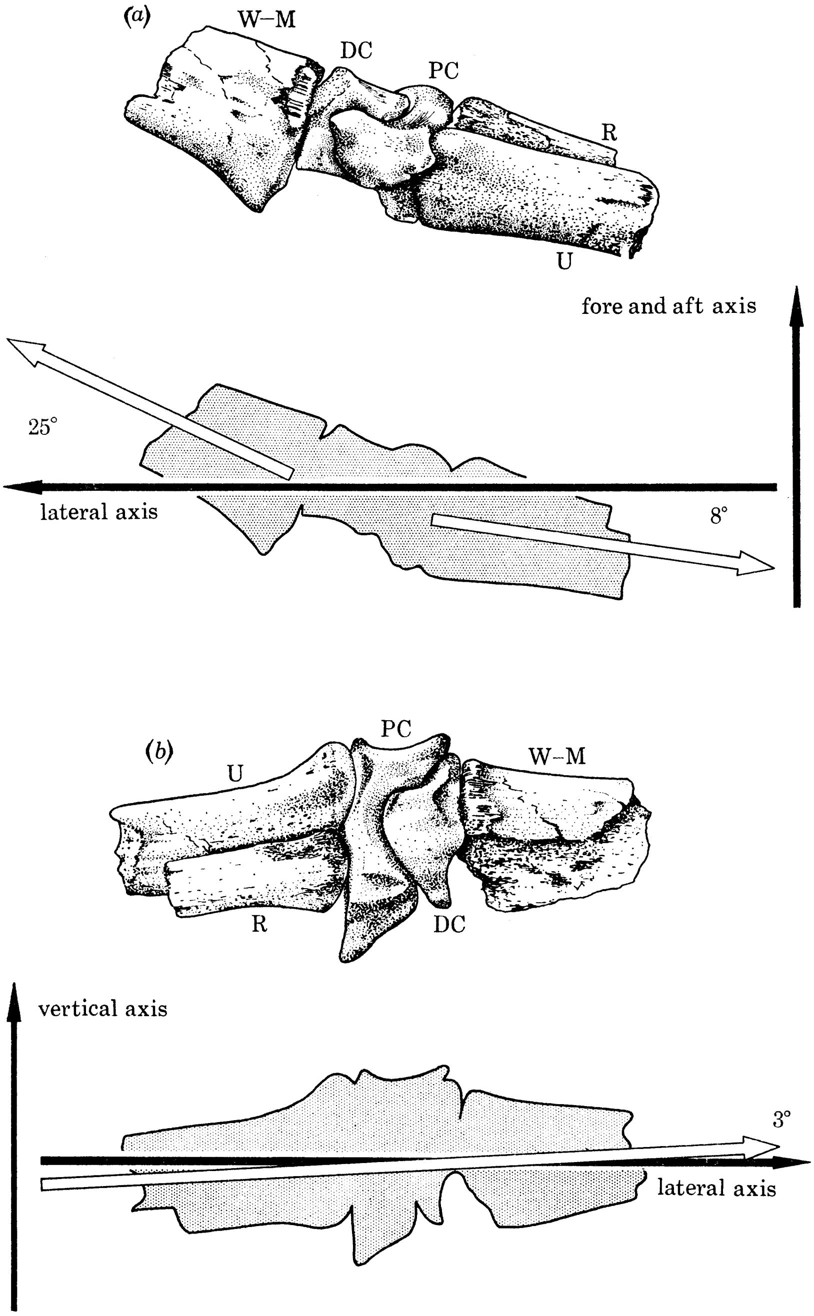


FIGURE 9. (*a*) Dorsal view of the wrist joint with the lateral carpal removed. R, radius; U, ulna; PC, proximal carpal; DC, distal carpal; W-M, wing-metacarpal. (*b*) Anterior view of the wrist joint with the lateral carpal removed. R, radius; U, ulna; PC, proximal carpal; DC, distal carpal; W-M, wing-metacarpal.

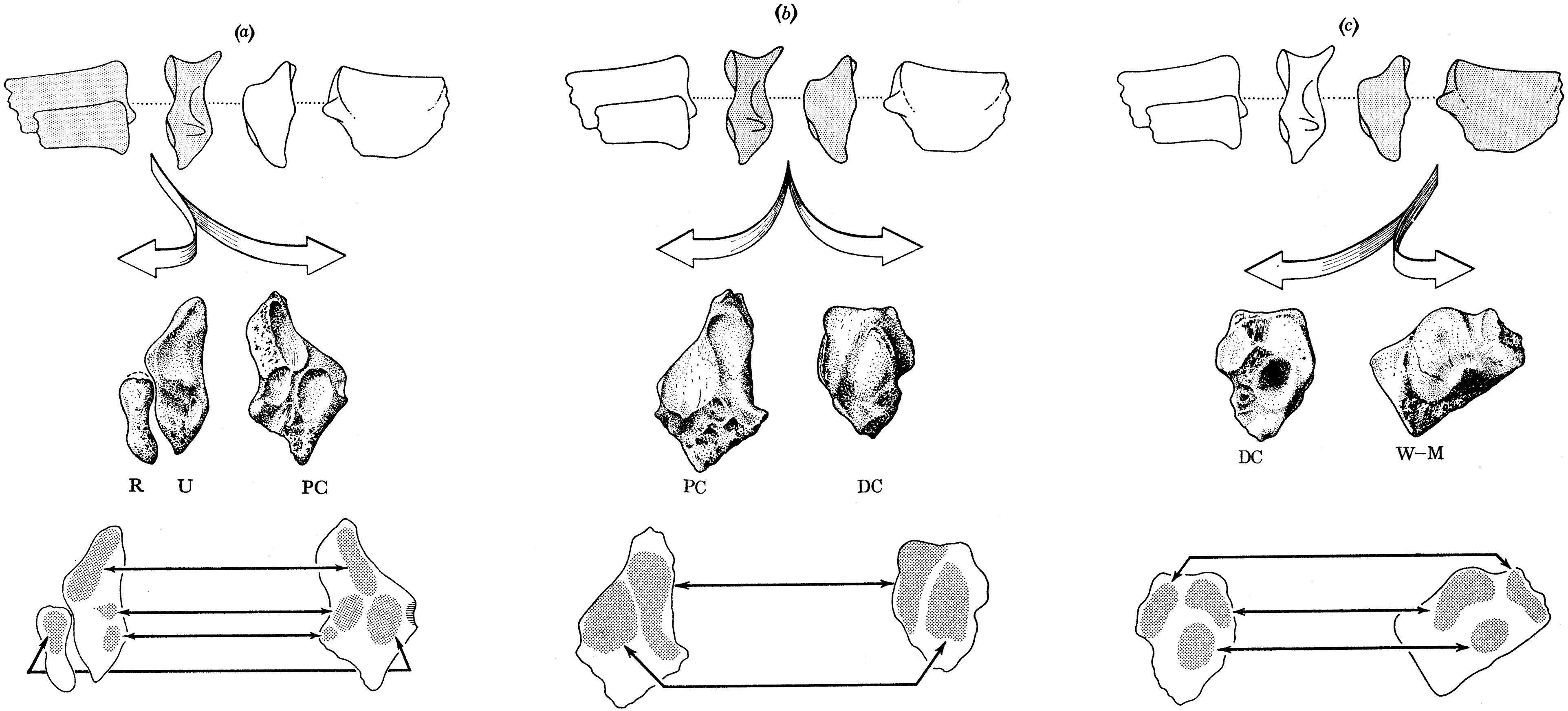


FIGURE 10. (*a*) Articulation between the radius/ulna and proximal carpal. R, radius; U, ulna; PC, proximal carpal. (*b*) Articulation between the proximal carpal and the distal carpal. PC, proximal carpal; DC, distal carpal. (*c*) Articulation between the distal carpal and the wing-metacarpal. DC, distal carpal; W-M, wing-metacarpal.

below. The ulna can pivot on its 'ulna knob' that inserts into this spherical hole in the proximal carpal.

It has been mentioned that when the elbow joint is flexed the radius slides along its axis, relative to the ulna. In doing so, the radius pushes on its articulation with the proximal carpal, causing it to twist and slide, pivoted about the 'ulna knob'. This action had the effect of swinging the wing-metacarpal backwards and upwards. When the movement had occurred to its fullest extent the wing-metacarpal was directed at 25° upwards and 35° backwards (figure 11).

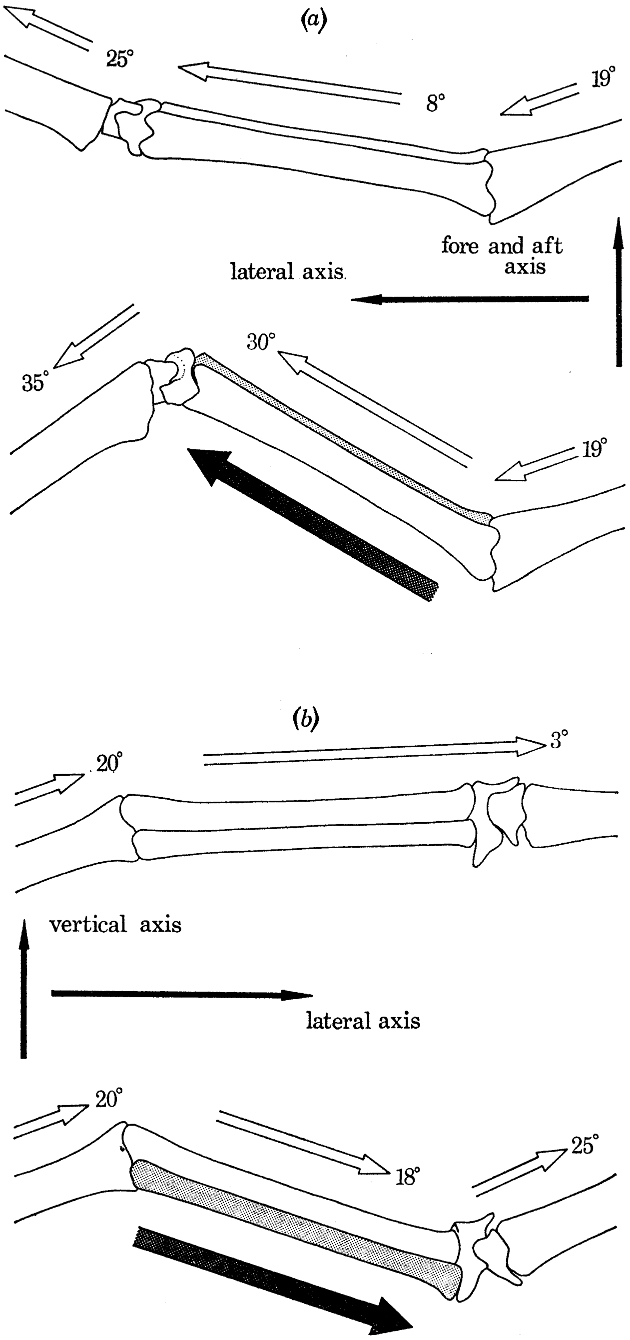


FIGURE 11. (*a*) Diagram showing the flexing of the elbow and its effect on the wrist and wing-metacarpal; dorsal view. (*b*) Diagram showing the flexing of the elbow and its effect on the wrist and wing-metacarpal; anterior view.

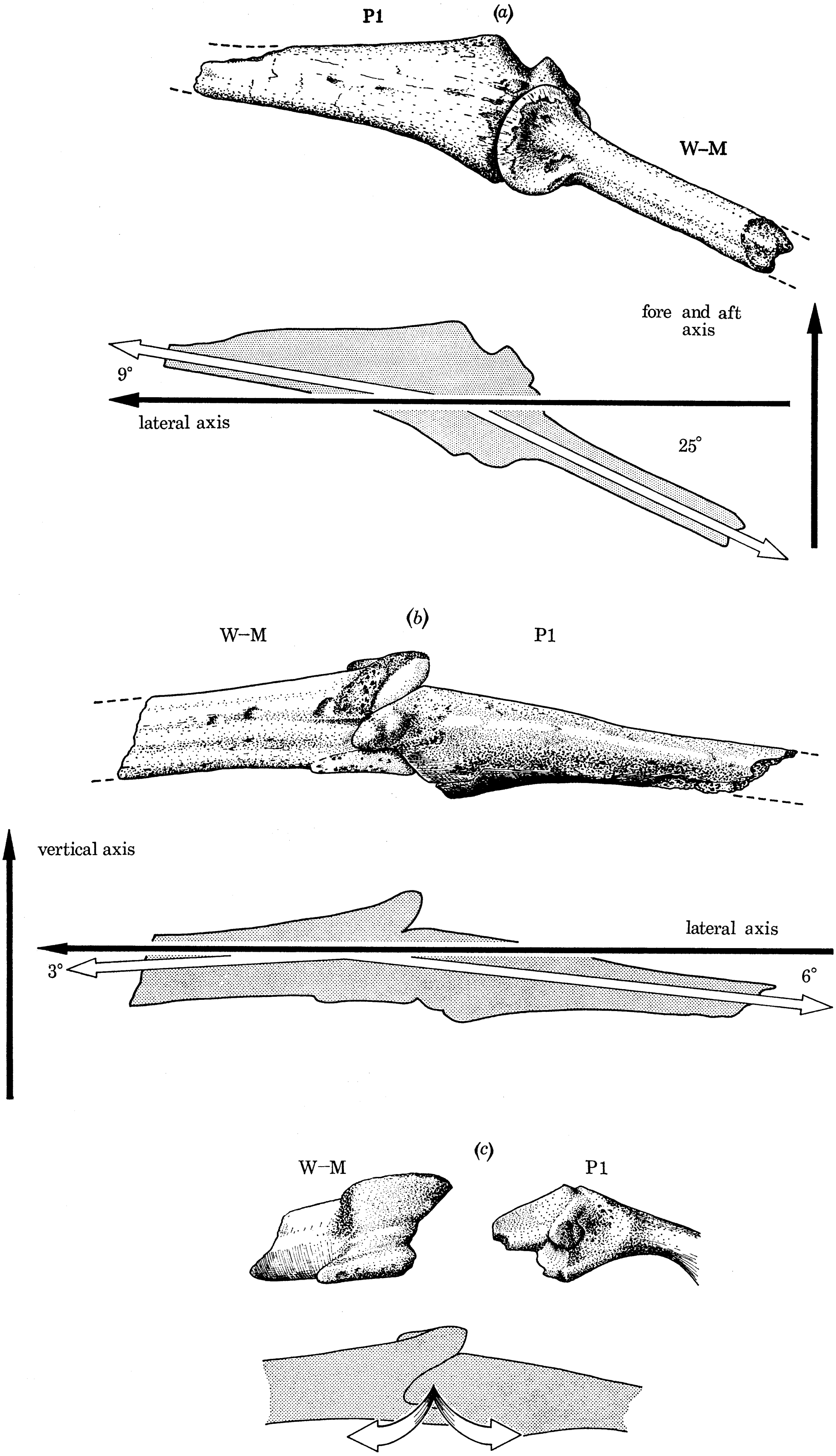


Figure 12. (*a*) Dorsal view of the articulation of the wing-metacarpal with the first phalanx. W-M, wing-metacarpal; P 1, first phalanx. (*b*) Anterior view of the articulation of the wing-metacarpal with the first phalanx. W-M, wing-metacarpal; P 1, first phalanx. (*c*) Drawing showing the pulley like form of the articulation of the wing-metacarpal with the first phalanx. W-M, wing-metacarpal; P 1, first phalanx.

The middle articulation of the wrist, the intercalary joint between the proximal and distal carpals (figure 10*b*) seems to be firmly fixed with no movement possible; the two bones lock together to form a solid block. The outer articulation of the wrist joint is between the distal surface of the distal carpal and the proximal end of the wing-metacarpal (figure 10*c*). A knob protrudes from the wing-metacarpal and inserts into a corresponding hollow in the distal carpal. The wing-metacarpal can twist about this pivot from its normal position, but in one direction only, leading edge downwards, through about 20°. Twisting upwards was prevented by a step-like articulation acting as a 'stop' between the two bones. The effect of the rotation of the metacarpal on the distal carpal was to alter the angle at which it ran from the wrist; when fully rotated the wing-metacarpal is directed at 5° downwards and 8° forwards. Therefore there were two possible movements at the wrist: the movement of the proximal carpal on the ends of the radius and ulna – this was mechanically connected with flexion of the elbow; and the rotation of the wing-metacarpal on the distal carpal – this was an independent action, not necessarily related to any other movement.

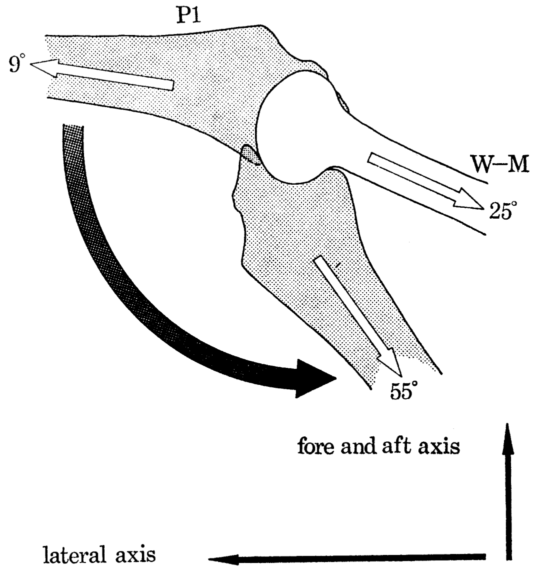


FIGURE 13. Diagram showing the folding back of the first phalanx on the wing-metacarpal. W-M, wing-metacarpal; P 1, first phalanx. This action occurs when the wing is folded.

Working out along the wing, the next joint is the knuckle joint between the distal end of the wing-metacarpal and the proximal end of the first phalanx. Its form is shown clearly by two good specimens from the Sedgwick Museum, nos B 54214 (wing-metacarpal) and B 54656 (first phalanx). This joint is an important one, as it is here that the outer half of the wing could be folded back; the main wing tendon attaches to the first phalanx just beyond the heel of the bone (figure 19), and the three small wing fingers articulate at this point. The joint has a skewed, pulley-like form; it is drawn in figure 12*a*, *b* in dorsal and anterior views; the inner surfaces of the articulation are shown in figure 12*c*.

When the wing-metacarpal and the first phalanx are articulated normally the first phalanx runs downwards at 6° and forwards at 9°. The form of the articulation prevents any further forward swing of the first phalanx, but it can move backwards around the pulley through about 134° to reach a position that folds the wing tip over the animal's back. At the fullest extent of the movement the first phalanx runs inwards towards the body at 55° to the lateral axis and at 2° downwards (figure 13).

The wing finger is made up of the four wing phalanges, but formed one structural unit. The articulations of the phalanges with each other are simple and have a spoon-like form (figure 14*c*). The bones used to study these joints were Sedgwick Museum specimens nos B 54606 (first phalanx), B 54229 (second phalanx), B 54605 (first phalanx) and B 54581 (second

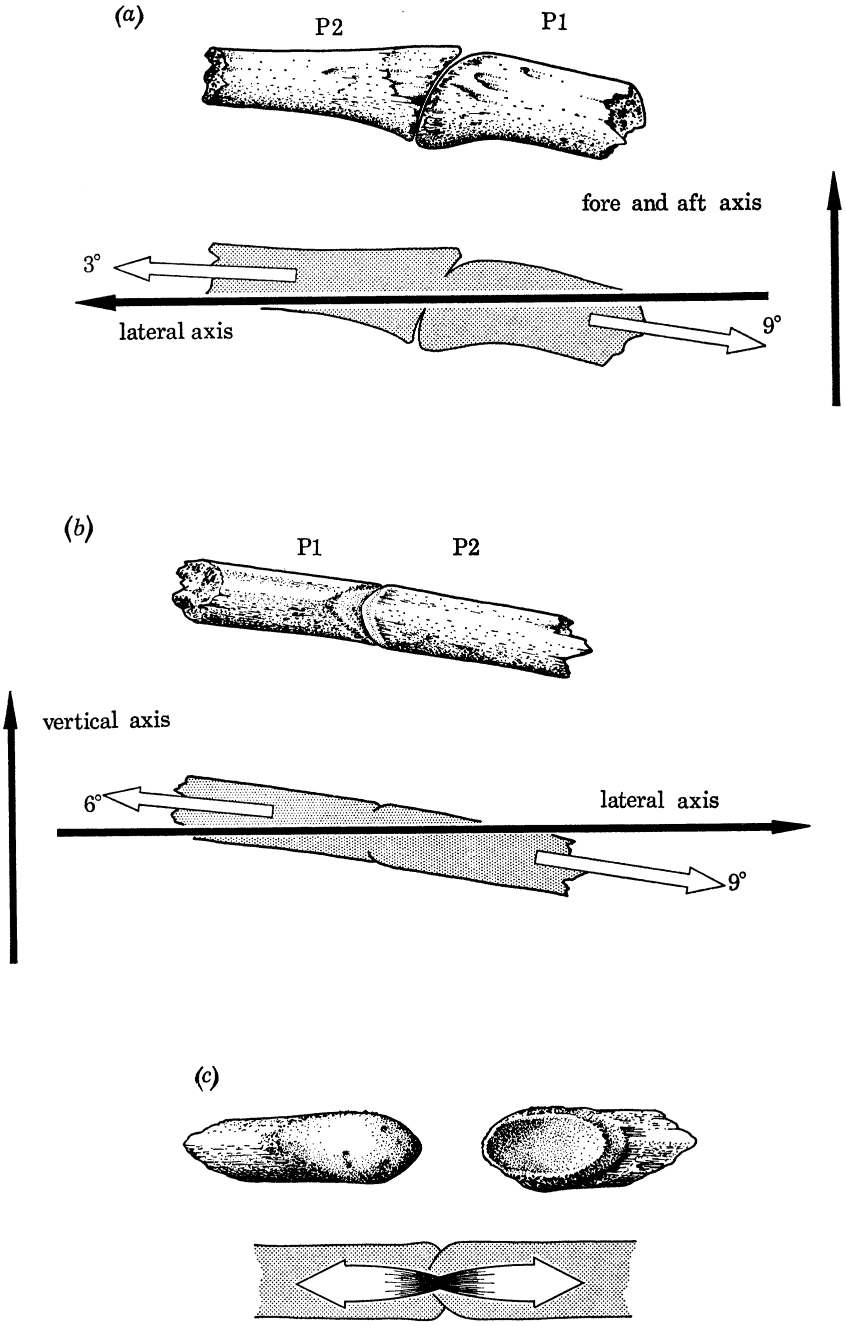


FIGURE 14. (*a*) Dorsal view of the articulation of the first phalanx with the second phalanx. P 1, first phalanx; P 2, second phalanx. (*b*) Anterior view of the articulation of the first phalanx with the second phalanx. P 1, first phalanx; P 2, second phalanx. (*c*) Drawing showing the spoon-shaped articulation that is present in phalanx/phalanx joints.

phalanx). The bones showing the articulations of the second phalanx/third phalanx and third phalanx/fourth phalanx have not been preserved in the Greensand collection; fortunately this does not matter as all the phalanx/phalanx articulations have the same form. The angles at which the phalanges were set relative to each other were obtained from British Museum *Pteranodon* specimen no. R 4534, which is a complete left wing from one animal, and Eaton's photographs of nos 2452, 2774 and 2591.

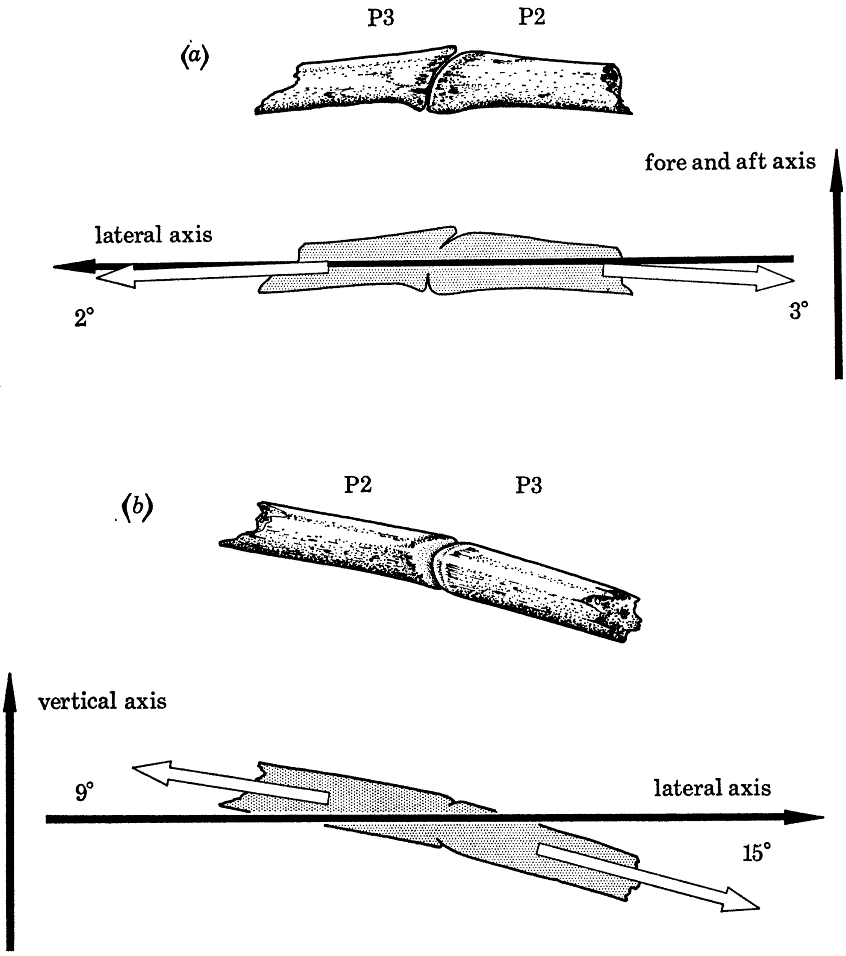


Figure 15. (*a*) Dorsal view of the articulation of the second phalanx with the third phalanx. P 2, second phalanx; P 3, third phalanx. (*b*) Anterior view of the articulation of the second phalanx with the third phalanx. P 2, second phalanx; P 3, third phalanx.

Figure 14*a*, *b* are dorsal and anterior views of the first phalanx/second phalanx articulation. Figure 14*c* shows the form of the articulation. The second phalanx, when articulated naturally, runs forward at 3° and downward at 9°. There appears to be very little movement possible between the wing finger phalanges, and the four bones can be considered as forming one unit for structural and functional purposes. The articulations in dorsal and anterior views of the second phalanx/third phalanx and third phalanx/fourth phalanx are drawn in figure 15*a*, *b* and figure 16*a*, *b*.

Towards its tip the wing bends downwards and sweeps slightly backwards. The third phalanx runs back by 2° and down by 15°; the fourth phalanx back by 10° and down by 22°. The latter bone is the outermost one of the wing and tapers along its length to a point at the wing tip. All the phalanges have a subtriangular cross-section; this is illustrated in figure 2.

Figure 23 shows the whole wing in the gliding position, with the bones at the angles described in this section. The possible movements at each joint are summarized in table 5 and some wing positions are shown in plates 24 and 25. The range of movement given for each joint should not be taken as a precise value as it is derived from fossil material; and variation of a few degrees from the stated figures is likely.

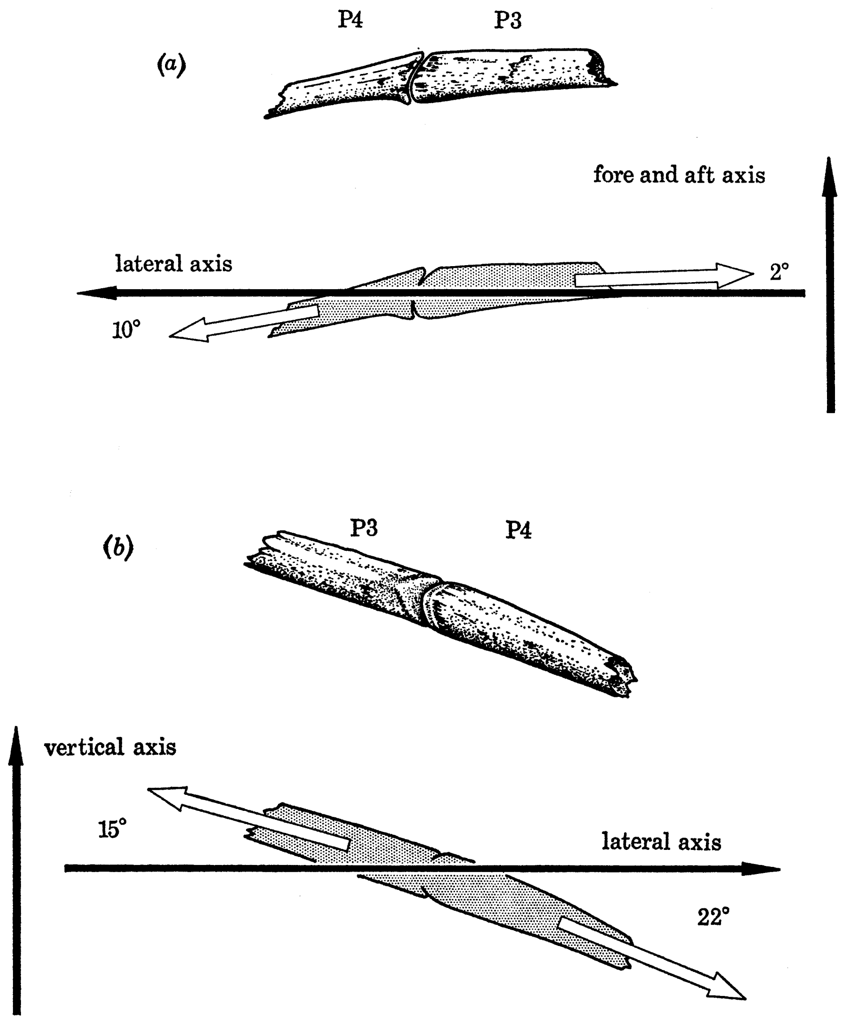


FIGURE 16. (*a*) Dorsal view of the articulation of the third phalanx with the fourth phalanx. P 3, third phalanx; P 4, fourth phalanx. (*b*) Anterior view of the articulation of the third phalanx with the fourth phalanx. P 3, third phalanx; P 4, fourth phalanx.

(v) *Wing muscles and tendons*

During life, each joint of the pterosaur wing must have been served by small muscles for making minor movements and adjustments; these weak muscles leave no actual evidence of their presence as they were not strong enough to need special attachment areas on the bones. But the major muscles and tendons used in flight had to be strong in an animal the size of

Pteranodon; their position and function may be obtained by combining knowledge of the arrangement of vertebrate limb musculature with the physical evidence of their presence that can be seen in the raised attachment areas, ridges and crests on the bones.

The wing of *Pteranodon* was a highly specialized limb, in which the basic vertebrate musculature had been greatly modified; as in all limbs the muscles were derived from a dorsal and a ventral series; they acted to bring about various wing movements.

As this paper is written for engineers as well as for biologists, a brief description of the zoological terms used to describe muscle actions is given before considering the possible muscles present in the wing of *Pteranodon*. The muscle actions are related to the three axes in figure 3. Levator muscles act to pull bones dorsally (up towards the vertical axis) and so raise the wing; depressor muscles pull bones ventrally (down towards the vertical axis) and bring the wing down. Protractors pull the wing forwards (anteriorly, or fore) and retractors pull the wing backwards (posteriorly, or aft). As well as these four basic movements, three other muscle actions commonly occur. A rotator muscle twists a bone about its long axis, a flexor muscle decreases the angle between two bones and an extensor muscle increases the angle between two bones. Muscles may, of course, produce a combination of these movements, pulling a bone forwards and downwards, or upwards and backwards, or act to cause rotation and flexion. Finally, muscles and tendons can only pull on bones, never push; the opposing action is brought about by tension in an antagonistic muscle.

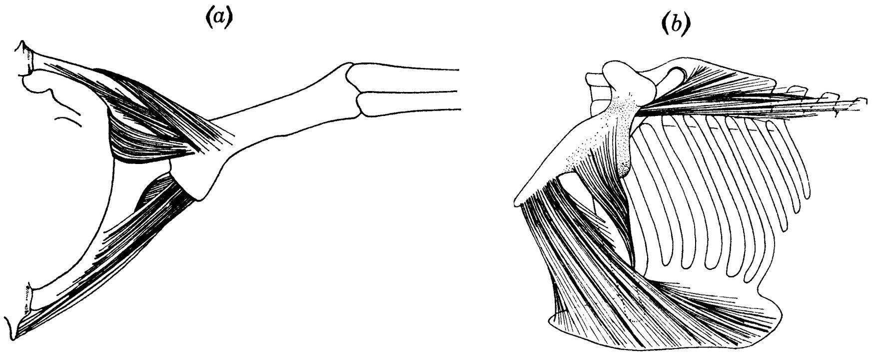


FIGURE 17. (*a*) Anterior view of possible levator and depressor muscles of the humerus. (*b*) Lateral view of possible levator and depressor muscles of the humerus.

The muscle system postulated here is based on that of reptiles and reptilian muscle names are used; but it is likely that *Pteranodon* also had certain muscles unique to itself. An example of this is the pteroid muscle, attached to the pteroid tendon, at the leading edge of the small pteroid wing membrane.

During flight, the forces on the wing acted backwards and upwards, so the main flight loads were resisted by muscles that held the wing down and out. As in other flying animals the levator muscles that raised the wing must have been smaller and weaker than the depressor muscles that held it down; these also brought about the downstroke during flapping flight. The depressor and levator muscles of the reconstruction are illustrated in figure 17, in anterior and lateral views.

Three muscles may have been concerned with raising the wing. These are the subcoracoscapularis, a deep muscle that originates on the inner surface of the girdle and inserts on the head of the humerus; it pulls the humerus upwards. The deltoideus runs from the interior surface of the scapula to the head of the humerus and pulls the humerus up and slightly forwards; but as was mentioned in § 2 (*a*) (iv), the peculiar articulation of the humerus allows little forward travel beneath the shoulder lock and it can only be directed laterally, straight out at 0°, above the lock. Therefore the humerus did not in any position on its upstroke or downstroke actually point forwards. The latissimus dorsi is a superficial muscle with a wide origin over the back and an insertion on the head of the humerus. It pulls upwards and backwards; this is the muscle that would have been responsible for pulling the humerus back to its fullest extent; the 65° backwards angle that was possible for this bone on all upstroke positions above the shoulder lock.

The main depressor muscle, in fact the main flight muscle, the pectoralis, originates on the keeled sternum and inserts on the deltoid crest of the humerus. As figure 17 shows, the deltoid crest was well developed for the insertion of this muscle and directed at the correct angle to receive it. The deltoid crest of *Pteranodon ingens* has an area of 75 cm^2. We do know (§ 2 (*a*) (iv), figure 4) that the unique shoulder joint lock of *Pteranodon* aided the pectoralis in holding the wing down during gliding and enabled this muscle to be smaller than if the mechanism had not evolved; a good example of weight reduction. The second depressor muscle, the coracobrachialis, originates on the posterior surface of the coracoid and runs beneath the pectoralis, to insert on the underside of the deltoid crest and humerus.

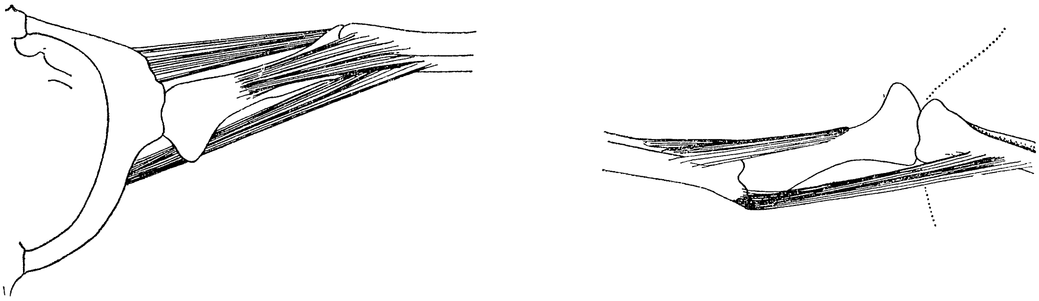


FIGURE 18. Anterior and dorsal views of possible flexor and extensor muscles of elbow.

Flexion and extension of the elbow joint could have been brought about by three muscles; these are illustrated in figure 18 in anterior and dorsal views. The elbow was a hinge joint and so could only move in one plane. It is extended by the action of the triceps muscle, which originates on the humerus and scapula and inserts on the olecranon of the ulna. The triceps is an important muscle in land animals as it extends the elbow and straightens the limb during walking. This is reflected by the well-developed olecranon seen in terrestrial animals; in *Pteranodon* this was not, of course, the case, as the wing was adapted for flight, not walking. The olecranon is comparatively small; flexion of the elbow against the backward and upward forces on the wing that occurred during flight was far more important than the ability to produce strong extension of the elbow joint. Flexion could have been achieved by the action of two muscles. The biceps originates on the coracoid and inserts on the radius and ulna; the brachialis runs from the anterior surface of the humerus to the radius and ulna. Contraction of these muscles would have flexed the elbow, swinging the radius and ulna forwards and downwards. As mentioned in § 2 (*a*) (iv) and shown in figure 11, this action automatically causes the radius to slide along its axis, pressing on the proximal carpal, which in turn pushes the wing-metacarpal backwards and upwards. Thus the two flexor muscles of the elbow could also have acted as indirect retractors and levators of the wing-metacarpal.

The wing was held out during flight by the strong digit extensor muscle and its tendon, running along the front edge of the wing bones from the humerus to the first phalanx (figure 19). Tension in the tendon straightened the wing-metacarpal/first phalanx joint and extended the wing finger. The tendon had to resist upward and backward bending forces in the inner part of the wing and mainly backward forces in the outer part of the wing. Relaxation of the digit extensor muscle allowed the tendon to slacken and the wing finger could then be folded back, as illustrated in figure 13.

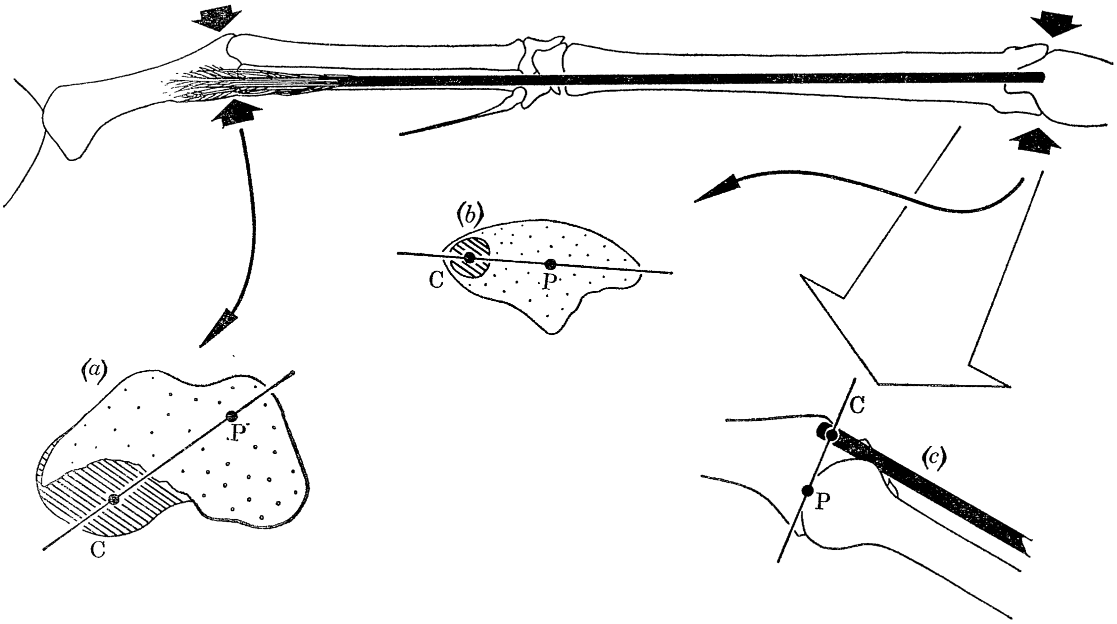


Figure 19. Diagram of anterior view of inner part of the wing spar to show the digit extensor tendon. (*a*) cross-section at origin of digit extensor tendon; (*b*) cross-section at insertion of digit extensor tendon; (*c*) dorsal view of insertion of digit extensor tendon on first phalanx. Moment arm of tendon indicated by distance between black dots, PC.

The arrangement of the digit extensor muscle and tendon in the reconstruction of *P. ingens* is drawn to scale in figure 19. The dimensions and position of the tendon and muscle shown in figure 19 were determined by examination of a number of specimens. The size of the ectipicondyle of the humerus, from which the digit extensor muscle originates, was measured in British Museum specimens nos R 3877 and R 3875 and Sedgwick Museum specimen no. B 54081 (a small, complete humerus). Eaton's photograph of *Pteranodon* no. 2831 was also examined. Scaling up for *P. ingens* gives an ectipicondyle 10 cm long projecting about 0.8 cm from the humerus. The position of the ectipicondyle and the attaching muscle is illustrated in figure 19.

The digit extensor tendon inserts on a well-marked area on the first phalanx, just beyond the heel of the proximal articulation of this bone (figure 19). As the attachment area is in the form of a forwards projection, we have called it the phalangeal tendon projection. Its area was measured in British Museum specimens nos R 3299 and R 4542, and also in the undistorted first phalanx no. B 54656 illustrated in figure 12, and Eaton's nos 2453, 2774 and 2470. The shape of the phalangeal tendon projection is almost circular; scaling gives a diameter of 1.5 cm in *P. ingens*. This value has been taken as the thickness of the digit extensor tendon at its insertion. Another clue to the thickness of the tendon can be found by examining the anterior surface of proximal carpal bones (see figure 9*b*). A groove runs laterally on this bone, situated in a suitable position to direct the tendon in its path along the front of the wing bones. The curvature of this groove is such that it would accommodate a circular tendon about 1.5 cm in diameter in *P. ingens*. This agrees with its width at its insertion; there is obviously no point in having a tendon of variable thickness, as it would break at its thinnest and weakest point however thick it was elsewhere. Figure 19 shows that the tendon insertion on the phalangeal tendon projection lies exactly opposite the pivot of the joint; this is the best position for resisting backward bending of the wing at this joint. Cross-sections of the origin of the digit extensor muscle and the insertion of the tendon on the first phalanx are also shown. It is interesting to see that the muscle originates on the lower anterior surface of the humerus at an angle of 40° below the horizontal. The tendon alters in position relative to the bones as it runs outwards and at its insertion is directly in front of the wing bones. The tendon is thus ideally positioned to resist backwards and upward forces in the inner part of the wing spar and mostly backward force further out. The moment arms about which it works are shown in figure 19 (the moment arm is the distance between the pivot of the joint, point P, and the centre of the muscle and tendon, point C). It is 6 cm at the origin and 4.8 cm at the tendon insertion.

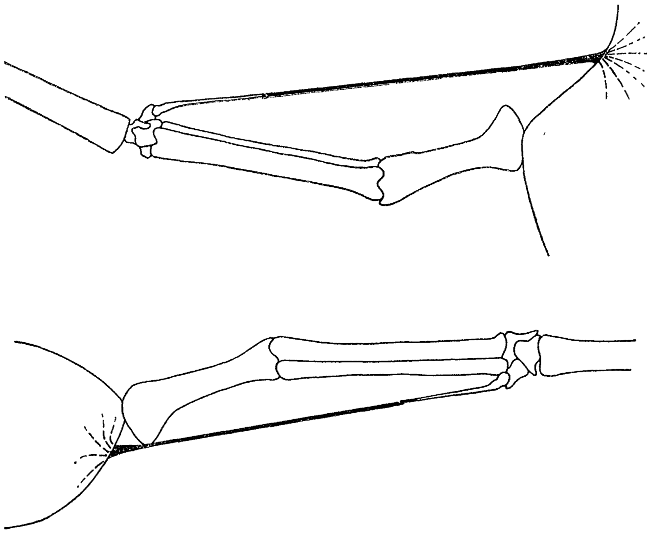


Figure 20. The pteroid bone, tendon and membrane in dorsal and anterior views.

The final muscle system of interest in the wing is that associated with the pteroid membrane (figure 20). This is the small membrane at the front of the wing. It lies in front of the humerus, radius and ulna; the distal part of its leading edge is supported by the pteroid bone which itself arises from the wrist. The pteroid membrane of pterosaurs is analogous to the propatagium of bats and appears to serve the same function – that is, to hold the wing forward during flight by helping to keep the elbow flexed. The action of the membrane is improved in bats by the insertion of a tendon along its leading edge; the muscle associated with this, the occipito-pollicalis (Norberg 1970) inserts at the base of the skull. This is feasible in bats as they have short necks but the system would not be practicable in the long necked *Pteranodon*. The pteroid bone indicates that a leading edge tendon was present in *Pteranodon*. Its associated muscle (designated the pteroid muscle) probably originated on the ventral part of the body in front of the wings, on the ribs, or perhaps on the fore part of the sternum. Such an origin would hold the pteroid membrane curved downwards during gliding, following the curvature of the main membrane.

The pteroid bone is peculiar to pterosaurs and its origin has given rise to much controversy; but its function is fairly obvious – that is, to alter the angle and shape of the pteroid membrane. It articulates via a ball-and-socket joint with the lateral carpal and can rotate freely in a circle. Its movements would have pulled the pteroid membrane up or down, further forwards or backwards. This action may have been associated with wing flapping or perhaps with non-flight activities.

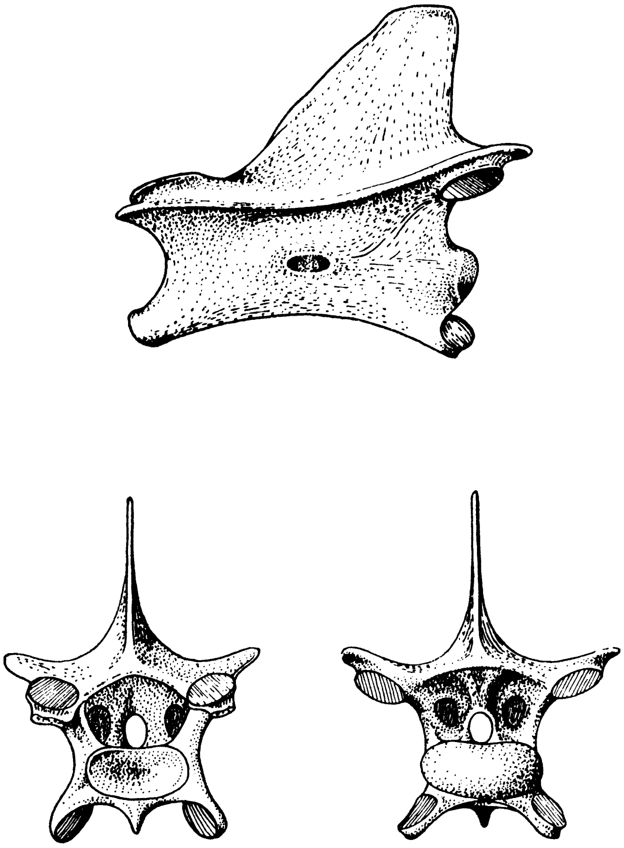


FIGURE 21. The fourth cervical vertebra of *Pteranodon* (after Eaton (1910)).

(*b*) *The head, body and legs*

The form of the skeleton of the head, neck, body and legs of the reconstruction is based on the description given by Eaton (1910), of *Pteranodon ingens*. The dimensions of the reconstruction are given in §2(*c*). Eaton based his description of *P. ingens* on specimen no. 1175, which has most parts of the skeleton preserved; missing parts were based on other specimens assigned to the same species.

The head of *Pteranodon* is characterized by being very large and long. It is flattened laterally. The jaw forms a sharp, pointed beak; but the most striking feature of the head is the enormous bladelike supra-occipital crest, which makes up almost half of the total length of the head. Wind-tunnel experiments to determine the function of this crest are described in §4 (*a*).

As in birds, fusion of the individual skull elements has led to obliteration of the cranial sutures. Although the head is so large, its skeleton is delicate and all the skull bones are pneumatic. The skull articulates with the neck via the occipital condyle, a spherical projection from the base of the skull; it is directed at about 45° downwards and backwards.

The neck skeleton of *Pteranodon ingens* consists of nine cervical vertebrae, the front two being the co-ossified atlas and axis. The cup of the atlas bears the occipital condyle of the skull. The neck vertebrae are large, light and pneumatic. Their general form is shown in figure 21, which shows the fourth cervical in lateral, anterior and posterior views (after Eaton). The sides of the centrum are deeply excavated to reduce weight and also show pneumatic foramina through which air entered the bones. The zygopophyses extend laterally to the full width of the neck, as the distance between them is only a little less than the width of the base of the skull. This fact proved useful in reconstructing the outline of the neck around its skeleton (figure 27).

The nature of the articulation of the neck vertebrae in *Pteranodon* is unique. They are connected at the centrum in the normal manner, the centrum being oval in shape, wider laterally than vertically. But a series of extra articulations has been developed, both on the dorsal and ventral parts of the vertebrae (figure 21). These have been given various names, but will here be termed 'extra-articular facets'. Thus we have anterior dorsal extra-articular facets, anterior ventral extra-articular facets, posterior-dorsal extra-articular facets and posterior ventral extra-articular facets on each vertebrae. Thus the vertebrae are articulated together in five places; at the centrum and in each 'corner' of the vertebrae via the extra-articular facets. This five-point articulation greatly strengthens the joints and also prevents any twist between the vertebrae. Williston (1897*b*) wrote that the special neck articulations of *Pteranodon* limited movement to a vertical plane; but examination of Eaton's photographs and uncrushed cervical vertebrae from the Sedgwick Museum suggests that this is not entirely true; the form and position of the extra-articular facets do seem to completely prevent rotation of vertebrae relative to each other; but allow movement in the vertical plane and also some lateral movement, although less than in the vertical direction. This pattern of flexibility in the neck is an adaptation to flight, partly related to the function of the crest and also to feeding. Its significance is discussed in §§4 and 5.

Of the nine neck vertebrae, only the final two – cervical numbers eight and nine – bear ribs. These are short, strong and ossified to the vertebrae.

The body of *Pteranodon* is relatively small when compared to the wing span. Its skeleton is made up of the pectoral and pelvic girdles, the vertebrae and ribs. The most striking feature is the development of the pectoral region to form a strong and rigid structure to support the wings. The ribs are jointed to allow breathing. The pectoral region is illustrated in figure 22. Eight of the dorsal vertebrae are co-ossified to form the notarium; this is similar to the consolidation of the anterior dorsal vertebrae in birds. The neural spines of the notarial vertebrae have fused to form a plate that bears oval facets for the ends of the scapulae. Well-developed free ribs protrude from the anterior end of the notarium; they could have served for the attachment of the pteroid muscle. The scapula and coracoid are strong bones, fused together laterally to form the glenoid cavity. The ends of the coracoids articulate with the sternum, as do some of the ribs. The sternum in *Pteranodon* was quite well developed and moderately keeled; its form is shown, drawn to scale for *Pteranodon ingens*, in figure 22. The posterior end of the body of *Pteranodon* is small compared with the anterior part. The bones of the pelvic girdle and sacrum are fused; the acetabulum is placed laterally as in bats; it does not appear from the size and position of the legs that *Pteranodon* could ever have stood upright on them in a birdlike way; the wing claws would need to have been rested on the ground to support the animal. The femur articulates laterally, as in bats, and the legs had a large range of movement. The significance of the legs in the life-style of *Pteranodon* will be further discussed in §5.

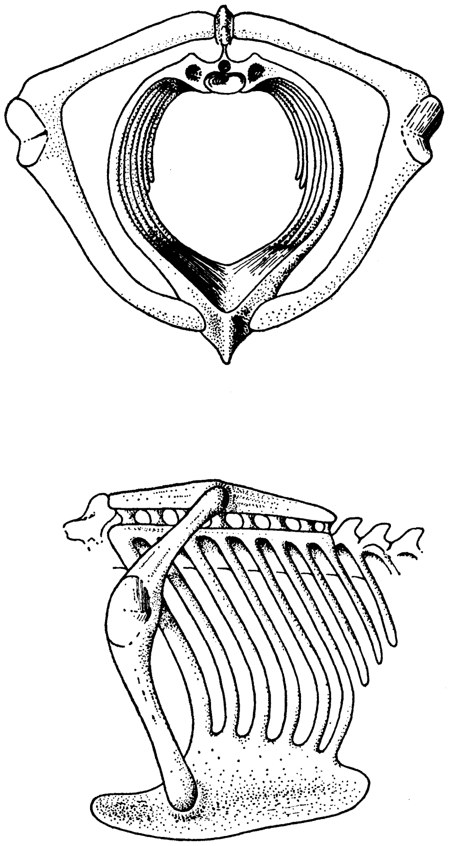


FIGURE 22. Anterior and lateral views of the skeleton of the pectoral region of *Pteranodon*.

(*c*) *Dimensions of* P. ingens

By using the dimensions and the angles of articulation derived in §§2(*a*) and (*b*), the reconstruction of *Pteranodon ingens* has been drawn to scale in the gliding position in figure 23.

A list of various dimensions is given in table 6. The mass derived in §2(*d*) and the wing loading are also included.

(*d*) *Mass estimate for* P. ingens

(i) *Introduction*

Calculating the mass of an extinct animal is not easy and wide variations are found between the estimates of different authors (table 7). The masses have been corrected to a wing span of 6.95 m by assuming that mass is proportional to the cube of the wing span. As early as 1902 Williston worked out the mass of *Pteranodon ingens* as 25 lb (11.3 kg). This was for a specimen with a wing span of 20 ft (6.1 m). It is the lowest estimate made and he wrote that he was 'much impressed by the extreme lightness of structure and small size of the body'. Lucas (1902)

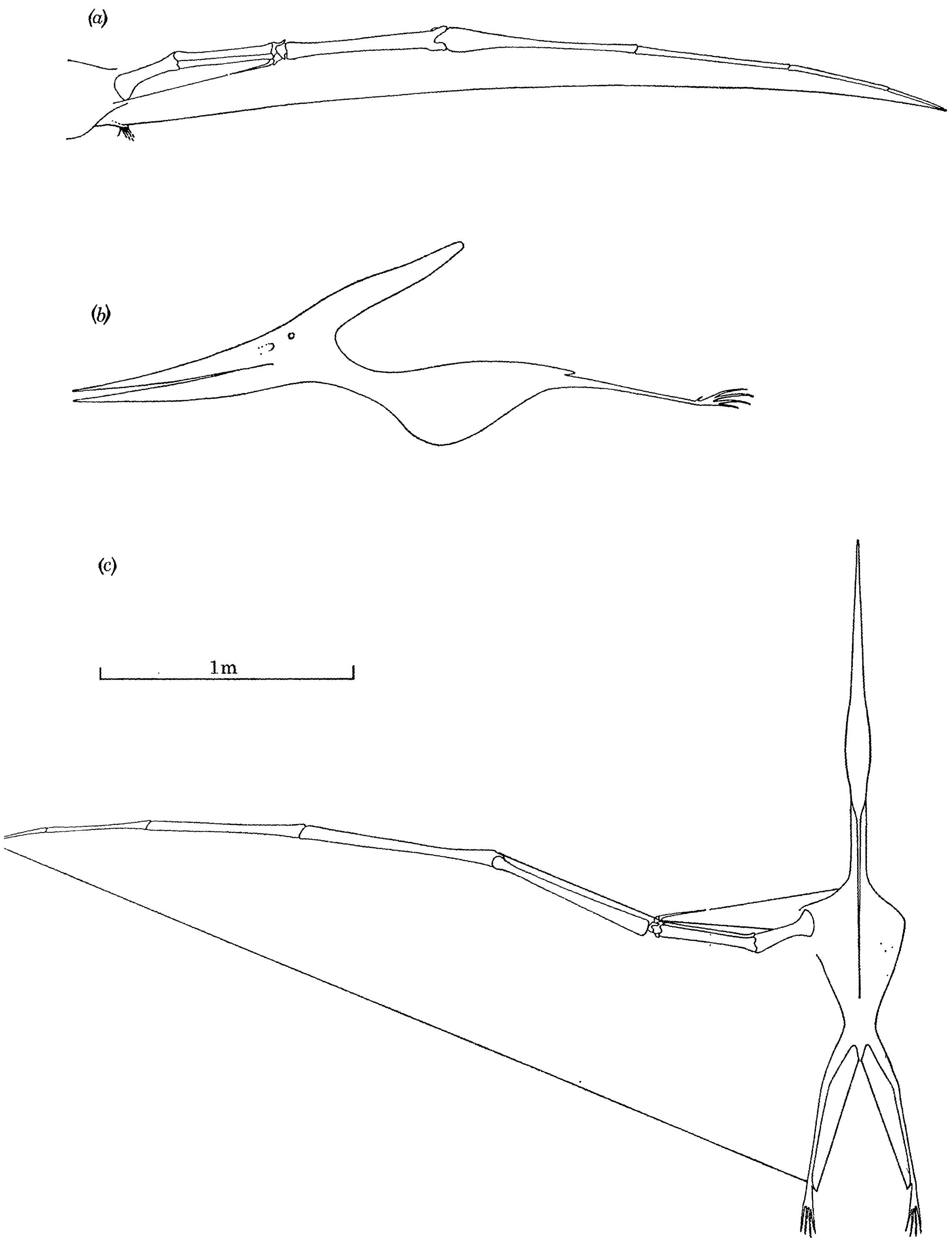


Figure 23. (*a*) Scale drawing of reconstruction of *Pteranodon ingens*, anterior view. (*b*) Scale drawing of reconstruction of *P. ingens*, lateral view. (*c*) Scale drawing of reconstruction of *P. ingens*, dorsal view.

TABLE 6. DIMENSIONS OF *PTERANODON INGENS*

head	cm
total length	179.0
greatest lateral measurement (through occipital condyle)	19.0
greatest dorsal measurement (above jaw articulation)	9.6
dorsal measurement above occipital condyle	6.4
length of mandible	89.0
length of crest blade	68.0
thickness of crest blade	0.3
neck	
total length	35.0
lateral measurement at insertion on head	22.0
lateral measurement at narrowest point	11.0
dorsal measurement of neck	6.4
body	
total length	75.0
greatest lateral measurement (pectoral region)	31.5
greatest dorsal measurement (pectoral region)	37.0
legs	
total length	86.0
length of femur	27.0
length of tibia and tarsals	38.2
length of foot (held slightly curled)	20.8
greatest lateral measurement (at insertion on body)	7.0
greatest dorsal measurement (at insertion on body)	5.0
membrane	
total area of membrane (including pteroid membrane and leg membrane)	4.28 m^2
general information	
total wing span	6.95 m
wing length from glenoid to tip	3.29 m
wing chord at insertion	1.04 m
wing area including middle body section	4.62 m^2
total mass	16.6 kg
wing loading	3.6 kgf/m^2 or 35.25 Pa

realized that such a low mass combined with large size and wing area gives a very low wing loading. He commented that 'with this weight and great spread of wings the creature must have flown as lightly as a butterfly. Even if we increase the estimated weight by 20 %, we still have a creature weighing but 30 lb, so that the body was even more an appendage to the wings than in the frigate bird, and seems to have been just heavy enough to counter-balance the weight of the head and neck and ensure equilibrium.' As we show later in this section, that was indeed the case, the centre of gravity of *Pteranodon* coinciding with the centre of lift of the wings; this must be so for flight to be possible.

A considerably greater estimate of 30 kg was given by Kripp in 1943; but this was for a larger animal of wing span 7.5 m. The mass of *Pteranodon ingens*, with a span of 6.8 m (Eaton

TABLE 7. *PTERANODON* MASS ESTIMATES

author	date	mass/kg	wing span/m	mass/kg (corrected to 6.95 m wing span)
Williston	1902	11.3	6.1	12.9
Kripp	1943	30.0	7.5	27.8
Heptonstall	1971	22.7	6.8	23.2
Bramwell & Whitfield	1970	18.1	8.2	15.7
Present estimate	1973	16.6	6.95	16.6

1910), has been calculated by Heptonstall (1971) as 22.7 kg. He considered this to be an underestimate, rather than an overestimate, of the true mass. We consider that it is in fact an overestimate, but as the basic data on which the calculation is based are not given, we are unable to compare it part by part with our estimate. In earlier papers (Bramwell & Whitfield 1970; Bramwell 1971) we have used a mass of 18.1 kg for *Pteranodon* with a wing spread of 8.2 m. This estimate of mass was made by a less accurate version of the geometrical method used here – for example, we assumed an arbitrary membrane thickness of 1 mm, as at that time we had no bat wing membrane available for measurement. The large wing span was based on Eaton's (1910) suggestion that species of *Pteranodon* attained this size and our own observations of some very large bones from the Cambridge Greensand. It is interesting to note, also, that Arambourg (1959) has described an even larger pterosaur than *Pteranodon*, named *Titanopteryx philadelphiae*, from the Cretaceous of Jordan. But as both Eaton's and Arambourg's very large wing spans are based on fragmentary specimens, we have used the more complete remains of *Pteranodon ingens* to obtain the wing span of 6.95 m used here.

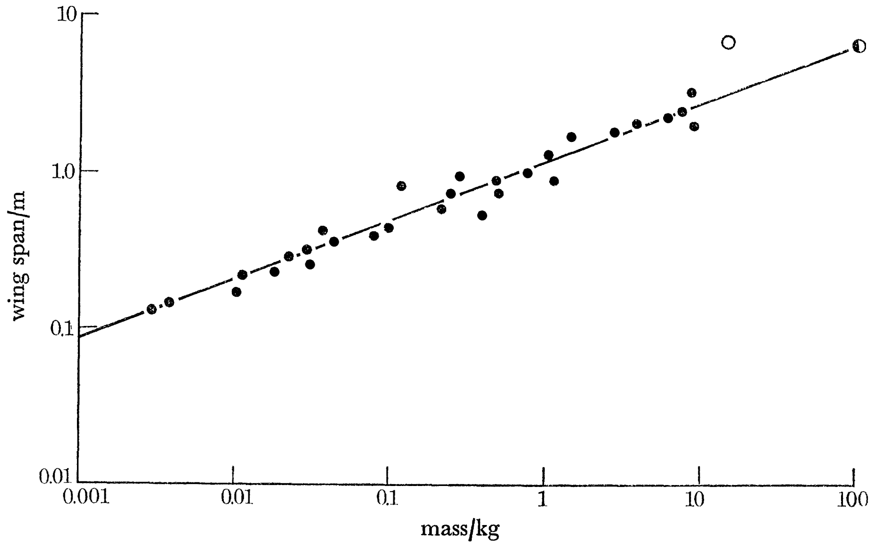


FIGURE 24. Graph of wing span against mass for birds (after Pennycuick (1972*b*)). ●, birds; ○, *Pteranodon*; ◐, bird of the size of *Pteranodon*.

(ii) *Extrapolation from birds*

As the masses and wing spans of living birds can be measured, and there is a simple relation between the two (mass is roughly proportional to the cube of the wing span (Greenewalt 1962)), this can be used to estimate the mass of a theoretical bird with the same wing span as *Pteranodon* (see figure 24).

It can be seen that a bird with a wing span of 6.95 m would weigh 100 kg. But this is only a poor guide to the mass of *P. ingens*. Firstly, *Pteranodon* is not a bird, nor a bat, but a pterosaur, with its own peculiar structure. And secondly one cannot just scale up a bird. If one does, the mass increases as the cube of the wing span, and so does the strength of the wing in bending; but the bending load on the wing increases faster, as the fourth power of the wing span. So extra strength is required, which must be provided either by using more material or by improving the distribution of material. Large birds use the last method, having pneumatic bones with well-placed internal struts to strengthen them, and air sacs to lighten the body. *Pteranodon* took skeletal reduction much farther than any known bird. Many authors have commented on the remarkable thinness of pterosaur bones. Williston (1902) described the wing bones as 'tubes with walls no thicker than blotting paper' while Swinton (1948) said that 'pterosaur bone surface cracks with a characteristic egg-shell type of fracture'. He records that the metacarpal he examined had extremely thin walls – no more than 1 mm thick in a shaft 2.2 cm wide.

As well as reducing the mass of the skeleton more than in birds, pterosaurs like *Pteranodon* also saved weight by the adoption of a primarily gliding mode of life. This allowed reduction of the heavy flight muscles needed for continuous flapping flight. Taking these factors into account, it seems reasonable to expect that *Pteranodon ingens* would have had a lower mass than that found by extrapolation from birds.

(iii) *The geometrical method*

The method used in this paper to find the mass of *P. ingens* is a geometrical one; it involves dividing the animal into sections and finding the mass of each part. The calculations are based on the completed reconstruction described in earlier parts of §2; in table 6 a list of dimensions is given.

Finding the mass by estimating the total volume of *P. ingens* would be relatively easy if the animal were completely solid. This, of course, is not the case, and it is the volume of the actual solid material present that must be found, not the overall volume. How the adjustment for this factor was made is explained as each part of the animal is considered separately. For some portions of the body three estimates have been made – high (maximum mass), low (minimum mass) and normal mass. The high and low extremes of mass for the whole animal have been found by adding all the high and low values respectively, but it does not, of course, follow that they cannot be combined in various ways to give intermediate masses.

TABLE 8. CALCULATION OF THE VOLUME OF SOLID MATERIAL IN THE HEAD OF *PTERANODON INGENS*

part	estimated as	dimensions/cm length	radius	thickness	volume/cm³
beak	hollow cone	85	6.9	0.1	183
skull	hollow cylinder	26	5.7	0.1	90.2
skull contents	sphere	—	5.0	—	525
crest	two flat blades	area 607 cm²		0.025	30.3
throat-sac	area of skin	area 448 cm²		0.1	44.8
				total	873.3

(iv) *The head*

The calculation of the volume of solid material present in the head of *P. ingens* is shown in table 8. The head, although large (total length 179 cm), is mainly hollow and is a light part of the body. It was divided into five sections, as shown in figure 25, and each part was then approximated by a simple geometrical shape. The volume of the beak was calculated by considering it to be a hollow cone with an average wall thickness of 1 mm; the skull was estimated as a hollow cylinder also with a bone thickness of 1 mm. The crest of *P. ingens* is an extremely thin blade, its transverse measurement posterior to the supraoccipital plate being only 3 mm (Eaton 1910). Such a narrow bony blade is unlikely to have a wall thickness as great as 1 mm and we have assumed it to be only 0.25 mm (§4(*a*)).

The posterior parts of the mandibles of *P. ingens* are excavated and it has been suggested that this area housed a throat sac in life. Lucas (1902) commented that 'in the peculiar shape of the lower, back portion of the beak there is a suggestion of the former presence of a small pouch, like that found in cormorants, and this would be in accord with the supposed fish-eating habits of *Ornithostoma* (*Pteranodon*)'. Eaton (1910) described the peculiar spiral-shaped articulations of the mandibles with the quadrates; they cause the posterior ends of the mandibles to move farther apart when the jaw is opened. He found the same specialized type of articulation in the pelican and suggested that its presence in both indicated that *Pteranodon* also had a pelican-like throat sac; this is an extensible area of skin that adjusts to the widening of the gap between the mandibles when the mouth is opened and also serves to catch and carry fish. The volume of the throat sac in *P. ingens* has been obtained from the area of skin needed to form it. In its unstretched state this is about 448 cm^2; its thickness has been assumed to be 1 mm. When stretched the skin naturally would be thinner, but, of course, this does not effect its overall mass. It is of interest to note that the throat sac is large enough to accommodate about 2 kg of fish without much distortion; much more if stretched. As *P. ingens* was such a light animal the amount it was able to carry would have been limited by weight rather than by the extensibility of the throat sac.

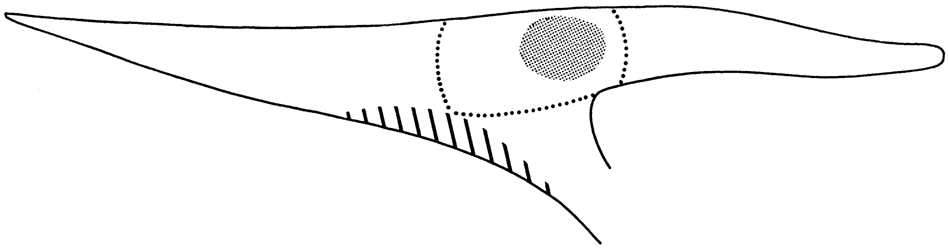


FIGURE 25. Divisions of the head for mass estimate.

The 'skull contents' estimate is for all the solid material within the hollow outer structure of the head. This includes the muscles, brain and sense organs. It does not include the muscles that attach the head to the neck; these have been allowed for in the first section of the neck. No attempt has been made to differentiate between the different parts of the skull contents.

Adding together the volumes of the five parts of the head give a total of 873 cm^3; the skull contents account for over half of this. The whole head is itself about 5 % of the total mass of the animal.

(v) *The neck and body*

The calculation of the volume of solid material in the neck and body of *P. ingens* is shown in table 9. The volume of the neck and body was estimated by dividing these parts into sections, labelled A–S, as shown in figure 26. The neck includes sections A–G and the body is made up by sections H–S. Each section is approximately cylindrical and 5 cm in length, except for S, which is a cone of length 20 cm. The radius of each cylinder was taken as the average radius of that section, as indicated in figure 26. Adding together the sections A–G gives a total volume of 2695 cm^3 for the neck and sections H–S, forming the body, have a volume of 28861 cm^3. But as neither neck nor body are solid, adjustments must be made for the air spaces.

The neck vertebrae of *P. ingens* are very large and hollow; the oesophagus and trachea are air-filled tubes. Sections through the necks of the lizard *Lacerta vivipara* and the goose *Anser*

Table 9. Calculation of the volume of solid material in the neck and body of *Pteranodon ingens*

part†	dimensions/cm		volume if solid/cm^3	high estimate/cm^3	low estimate/cm^3	normal estimate/cm^3
	length	radius				
			NECK			
A	5	6.35	633			
B	5	5.4	458			
C	5	4.8	363			
D	5	4.7	350			
E	5	4.35	297			
F	5	4.35	297			
G	5	4.35	297			
		total	2 695	1 616	539	809
			BODY			
H	5	5.9	556			
I	5	9.0	1 277			
J	5	13.3	2 780			
K	5	16.25	4 140			
L	5	16.7	4 400			
M	5	15.9	4 000			
N	5	14.25	3 220			
O	5	13.38	2 805			
P	5	11.62	2 130			
Q	5	9.87	1 535			
R	5	7.92	988			
S	20	7.0	1 030			
		total	28 861	14 430	5 772	8 658

† Parts A–R estimated as partly hollow cylinder, S as partly hollow cone.

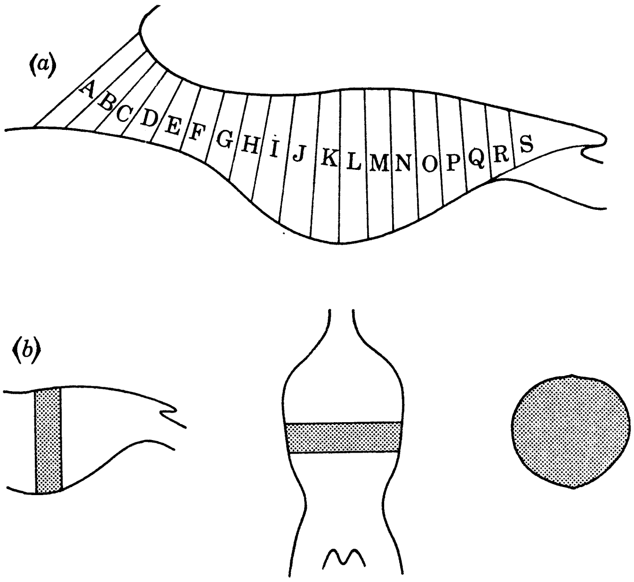


Figure 26. (*a*) Divisions of the neck and body for mass estimate. (*b*) Illustration of one segment of the body used in the mass estimate.

domesticus were examined to determine the size of the air space due to the oesophagus and trachea. In the lizard these accounted for about 40 % of the space and in the goose about 20 %. The cervical vertebrae of the goose occupy the whole width of the neck; this must also be true of *Pteranodon*, since the neck vertebrae are almost as wide as the skull. Figure 27 shows a section through the neck of *P. ingens*, drawn to scale, with the proportion of solid material to space indicated. The vertebra is the fourth cervical and its dimensions are taken from Eaton (1910). The size of the trachea and oesophagus have been estimated by analogy with the goose and lizard.

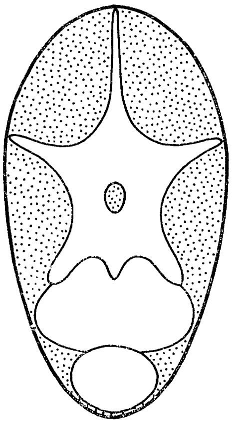


FIGURE 27. Section through the neck at the fourth cervical vertebra. Proportion of solid material to space shown.

This gives an estimate of 30 % solid to 70 % space. In the heavy estimate the neck is calculated as 60 % solid, but this is unlikely, except perhaps in section A. If the size of the oesophagus and trachea are increased or the muscles at the back of the neck decreased, only 20 % of the neck is then solid. This value has been used in the light mass estimate.

The bodies of birds are lightened internally by having hollow spaces. These are the lungs, the air sacs and the hollow bones. It was realized long ago (Seeley 1870) that pterosaurs also had air sacs. Large pneumatic foramina are present in almost all of the bones of *Pteranodon*, leading into the air-sac system. The function of the air sacs in birds is to lighten the body and to help dissipate heat; they are also involved in actual respiratory exchange. No good figures are currently available for the ratio of air space to solid material in the bodies of birds. Some suggestion has been made that air sacs occupy about 20 % of the body; considerably more in lighter, gliding birds. The lungs may be about another 20 % of the total volume: and the skeleton is also air-filled. Because of the lack of a range of measured data, we can only guess at the situation in pterosaurs. As *Pteranodon* had taken weight reduction to an extreme, it presumably would not have neglected the opportunity to lighten the body by all possible means. There is direct evidence for the high degree of pneumaticity of the bones (they had used this method of shedding weight far more than any bird) and also for the reduction of the heavy flight muscles that make up a large proportion (20–40 %) of the weight of a bird's body. If it is assumed that the air-sac system was similarly well developed, it seems reasonable to estimate that the body was only about 30 % solid material. We have taken this figure as the normal value and 20 % solid as the extreme of lightness. The 'heavy' estimate allows for the body to be 50 % solid.

(vi) *The legs*

The calculation of the volume of the legs and feet of *Pteranodon ingens* are shown in table 10. The mass of the feet and legs is fairly easy to find, as they are solid except for the hollow bones. The lengths of the leg bones are known, but the thickness of the flesh that surrounded them during life must be estimated. The bones of the legs and pelvic girdle give some indication of the muscular development. The fruit-bat *Pteropus giganteus* has leg bones with proportions similar to those of *Pteranodon*, and uses them in the same way (§5(*b*)).

Table 10. Calculation of the volume of solid material in the legs and feet of *Pteranodon ingens*

part	estimated as	dimensions/cm length	 radius	volume/cm³	volume of hollow/cm³	volume of solid matter/cm³
upper leg	solid cone with hollow femur	27	3 tapering to 1	451	121	320
lower leg	solid cylinder with hollow tibia	38	1	120	30	90
digits	50% solid cylinders	—	—	—	—	8
					total (one leg)	418

The measurements of *Pteropus* have been used to guide the reconstruction of the external shape of the legs in *Pteranodon*. They are slender with little muscular development beneath the knee. The volume of the upper leg has been calculated as a section of a cone (figure 28*a*) and the lower leg as a cylinder. The feet were considered as individual bones, consisting of 50% solid material. The total volume of solid in both legs is 836 cm³. It is worth noting that although the legs of *Pteranodon* are long (86 cm), they appear small in contrast to the depth of the body and the enormous wings and head.

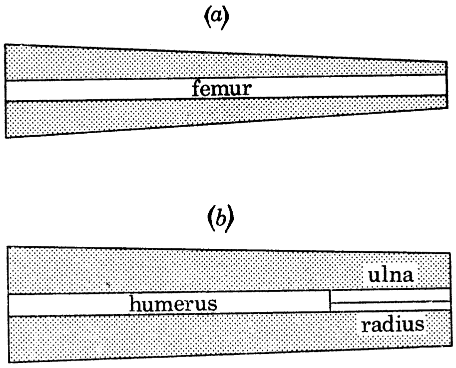


Figure 28. (*a*) Geometric shape of the upper leg used in the mass estimate. (*b*) Geometric shape of the upper arm (wing) used in the mass estimate.

(vii) *The wings*

The wings are made up by the supporting skeleton at the leading edge, the wing tendons and muscles and the actual membrane. Separate estimates have been made for these parts (table 11). The volume of the wing bones was found by calculating them as hollow cylinders with the dimensions derived in §2(*a*)(ii) and (iii). The carpal bones were estimated as hollow blocks. The muscle of the wing spar is all concentrated at the wing root. This muscle was estimated as a section of a solid cone, with an adjustment made for the hollow bones (figure 28*b*). The digit extensor tendon and its muscle were considered as a solid cylinder.

The membrane between the legs (1510 cm^2) was included in the total wing membrane area of 4.28 m^2. It is not possible to know the exact thickness of the membrane. A series of measurements of the membrane thickness of *Pteropus giganteus* were made, with the wing held normally stretched. It was of uniform thickness, except when measured over a blood vessel or muscle.

TABLE 11. CALCULATION OF THE VOLUME OF SOLID MATERIAL IN THE WINGS OF *PTERANODON INGENS*

		dimensions				
part	estimated as	length/cm	radius/cm	thickness/cm	area/cm^2	final volume/cm^3
humerus	hollow cylinder	29	2.35	0.16	—	68.5
radius	hollow cylinder	34.7	1.2	0.13	—	34.0
ulna	hollow cylinder	38.4	2.05	0.09	—	44.5
carpals	hollow blocks	various dimensions		0.1	384	38.4
metacarpal	hollow cylinder	67.1	1.8	0.15	—	114
1st phalanx	hollow cylinder	77.9	1.55	0.15	—	112
2nd phalanx	hollow cylinder	61.4	1.23	0.06	—	28
3rd phalanx	hollow cylinder	40.0	0.675	0.05	—	8.7
4th phalanx	hollow cylinder	24.6	0.45	0.05	—	3.5
small wing fingers	50% hollow cylinders	51	0.4	—	—	12.9
upper arm muscles	section of solid cone with hollow bones	34	5 and 3	—	—	1310
tendon	solid cylinder	117.5	0.85	—	—	267
membrane	area of material	—	—	0.03	21400	650
					total	2691.5
					total for two wings	5383

The membrane is very strong and elastic, yet surprisingly thin, averaging only 0.015 cm thickness. This value was used in the 'light' estimate of *Pteranodon*; twice the thickness in the normal estimate and three times for the 'heavy' calculation. This is obviously an arbitrary choice; but it is unlikely that the wing membrane of *Pteranodon* was very thick, as the wings have a very large area and a thick membrane would have added a lot of mass.

(viii) *The total mass*

The volume of each part has been multiplied by an assumed density of 1000 kg/m^3 to give the masses listed in table 12. Taking a fixed value for the density is an approximation, because different living materials vary somewhat, but we believe the value we have taken, implying a specific gravity of one, is near enough for the error to be negligible in comparison with the other likely errors in any such reconstruction. The individual masses are summed and rounded off to give our estimates of the mass of *Pteranodon ingens*; the average estimate is 16.6 kg, with high and low estimates of 23.8 and 12.8 kg respectively. The difference between estimates comes mainly from variations in body mass and this depends on the relative volume assigned to the air sacs. We consider that this, and the impossibility of knowing the exact membrane thickness, are the greatest sources of possible error in this estimate. It must also be emphasized that the mass is only an average figure, determined for use in the calculations, and that naturally a range of masses is found in any species, varying with age, sex and other factors.

Pteranodon had achieved low mass, yet maintained large size, by the method of internal excavation of material wherever possible. This technique allows a flying animal to exceed the theoretical limit on size that is found from the law that mass increases as the cube of linear dimensions. This law is only true of solid objects or animals.

The wing loading of *Pteranodon ingens*, based on the normal estimate of 16.6 kgf, is 3.6 kgf/m^2 (2.8 kgf/m^2 and 5.15 kgf/m^2 for the low and high estimates). Even if the heavy weight is accepted, the wing loading is still very low compared with that of birds. The gliding birds *Coragyps atratus* (a vulture) and *Diomedea melanophrys* (an albatross) have wing loadings of 8 kgf/m^2 and 16 kgf/m^2 respectively. Man-made gliders, for example the Olympia, must carry the heavy body of the land animal *Homo sapiens* and have a loading of about 20 kgf/m^2.

Table 12. Summary of mass estimate

part	low estimate/kg	normal estimate/kg	high estimate/kg
head	0.873	0.873	0.873
neck	0.539	0.809	1.619
body	5.772	8.658	14.430
legs	0.836	0.836	0.836
wings	4.733	5.383	6.033
total	12.8	16.6	23.8

(ix) *The centre of gravity*

The centre of gravity of a rigid body is the point at which its weight may be assumed to act, or the point at which it must be supported if it is to balance. The position of the centre of gravity can be readily calculated by taking moments about any convenient fixed point of the body. For example, in figure 29, C is the centre of gravity of a body made up of several small components of weights $w_1, w_2, \ldots$. The total weight W is $w_1 + w_2 \ldots$. Taking moments about the convenient point O, we have

$$WX = w_1 x_1 + w_2 x_2 - w_3 x_3,$$

so

$$X = (w_1 x_1 + w_2 x_2 - w_3 x_3)/(w_1 + w_2 + w_3),$$

or more generally

$$(\Sigma\, wx)/(\Sigma\, w).$$

The position of the centre of gravity of an animal depends on the position in which it holds its body. We have calculated the centre of gravity of *Pteranodon ingens* with its body in the natural gliding position (figure 23) assuming that the weight of the membrane was uniformly distributed over its area, and that the air sacs and lungs were uniformly distributed within the body.

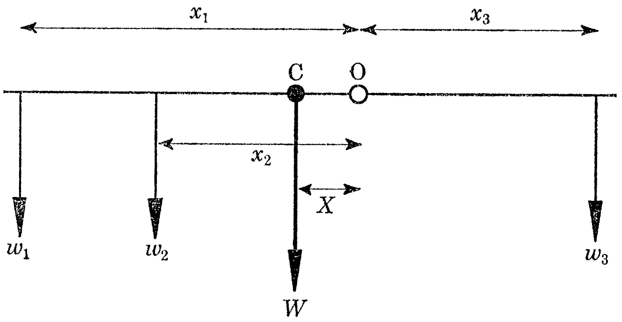


Figure 29. Illustration of method used to determine the centre of gravity of an object. For explanation see text.

The centre of gravity is on the centre line of the animal, 6.3 cm behind the glenoid cavity (figure 30*a*).

The centre of lift of the wing has also been calculated by dividing it up into fore and aft strips and calculating the lift of each. In the absence of detailed wing-section data we have assumed that the centre of lift of each strip lies one third of the way back from the leading edge, the usual position for well-behaved wing sections. The centre of lift of the whole wing is 7.3 cm behind the glenoid cavity. This result is highly satisfactory, for in steady flight the centre of lift and the centre of gravity must coincide. If the centre of gravity lies in front of the centre of lift, the animal will nose dive; if it is behind the centre of lift it will stall. The fact that the calculations show that these two do lie in line indicates that the mass estimate and general arrangement of the animal in its gliding position are consistent.

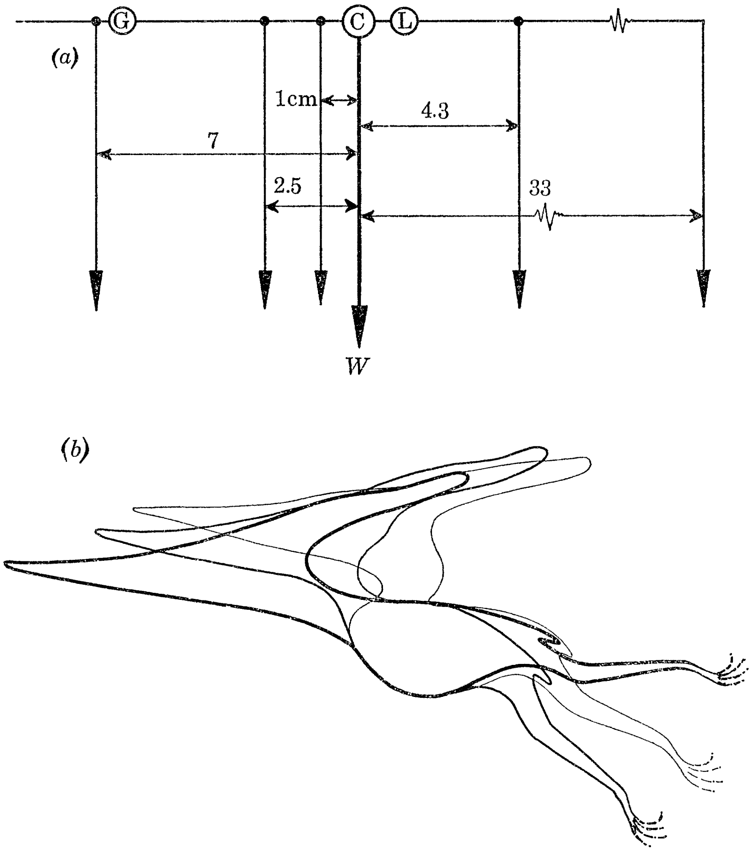


Figure 30. (*a*) Variation of centre of gravity of *Pteranodon* with different actions. G, glenoid cavity; C, centre of gravity; L, centre of lift. (For explanation see text; dimensions in cm.) (*b*) Different positions of *Pteranodon* that alter its centre of gravity in flight.

While gliding, *Pteranodon* would have needed to make movements to alter its centre of gravity, or centre of lift, or both. We have calculated the effect of swinging the head as far forward and as far back as possible, and of lowering the legs (figure 30*b*). If the head was brought forward as indicated the centre of gravity of the animal is moved forward, but the movement is very small, only about 1 cm. Bending the neck and holding the head back in a pelican like manner, as drawn in figure 30, moves the centre of gravity back by 4.3 cm. The neck is articulated to allow this position and it is possible that the head was held like this during normal gliding.

Bringing the legs down to an angle of 45° only moves the centre of gravity forwards by 0.3 cm; but at the same time the curvature of the membrane is greatly altered and this in turn alters the position of the centre of lift.

It was probably simpler for *Pteranodon* to use the head during adjustment, as this does not distort the membrane. On the whole, however, it would be easier to alter the centre of lift by swinging the wing tips backwards and forwards, rather than to alter the centre of gravity by moving parts of the body. In life, a combination of methods was likely to have been used to suit different circumstances.

Finally, it is possible to calculate the effect on the centre of gravity of carrying a heavy load of fish. The fish has been taken to weigh 4 kg – a heavy load for a flying animal weighing only 16.6 kg. If this theoretical fish were held in the feet, with the legs in the normal position, its weight causes the centre of gravity to move back by 33 cm. This is most unlikely to have actually occurred! With the fish stored in the throat sac the centre of gravity moves forward by 7 cm; but with the neck bent and the head held back this heavy fish only upsets the centre of gravity by 2.5 cm, moving it forwards. This shows that the 'head back' position would have been the best one when carrying a very heavy load; it is even better to eat the fish on the spot and get it inside, right over the centre of gravity.

3. Engineering of the wings

(a) *General considerations*

In this section we consider primarily the structural strength of the wing because this is the most critical member of an aircraft. Other parts are mentioned briefly at the end.

The main structural member in the wing is the series of bones of the arm and fourth digit, with their associated muscles and tendons (figure 23). We shall refer to this as the 'wing spar'. The wing spar is clearly designed to resist backward bending all along its length. Near the wing tip the bones are flattened, with their greatest diameter fore and aft, and the phalanges are widened in this direction at the joints. Nearer the wing root, the digit extensor tendon runs in front of the wing-metacarpal and radius/ulna, strongly resisting bending. At its insertion on the first phalanx this tendon is directly ahead of the bone, to resist backward bending, but nearer the root it moves downwards (figure 19), so as to resist upward bending as well. From the wrist inwards, the pteroid membrane and tendon also help to resist backward and upward bending.

The wing membrane is stretched between the wing spar and the body and leg, and is curved upwards by the air pressure. The wing spar follows the same curve, so that the wing incidence does not change significantly along the span, an essential condition for good performance (Short 1914). The engineering problem here is how to provide enough tension in the membrane without exceeding the strength of the wing spar.

All the calculations are for straight and level gliding; manoeuvring and powered flight are considered later.

(b) *The required strength of the wings*

To obtain the best possible performance, the spanwise distribution of lift should be approximately elliptical; for simplicity we assume a constant lift per unit area for each spanwise strip, which is not far from the ideal. The chordwise, or fore-and-aft distribution of lift over each strip depends on the exact shape of the wing section, but typically it is triangular, falling linearly from a maximum pressure of $2W$ Pa at the leading edge to zero at the trailing edge; W is the wing loading, the ratio of the all up weight to the wing area.

This lifting pressure is resisted by tension in the curved membrane; if the curvature is known, the tension can be calculated. For example, consider a parallel strip of membrane of unit width with tension T N along its length and negligible tension perpendicular to this (figure 31). If the pressure is p Pa, then

$$2T \sin \tfrac{1}{2}\mathrm{d}\theta = p\,\mathrm{d}x, \tag{1}$$

or, since $\mathrm{d}\theta$ is small,

$$\mathrm{d}\theta/\mathrm{d}x = p/T. \tag{2}$$

By integrating this expression (numerically if necessary), the shape of a strip of membrane can be found for any tension and load distribution.

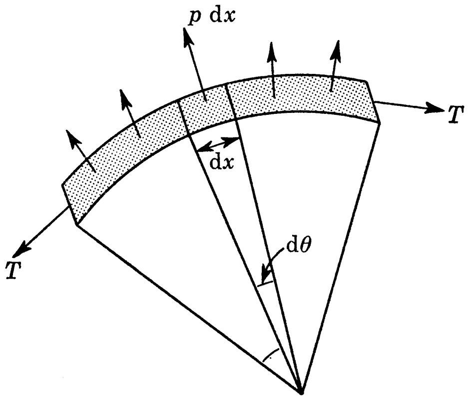


FIGURE 31. Strip of membrane under tension. (For explanation see text.)

The wing is more complex, as the membrane is two-dimensional and can be tensioned in any direction. But there are two simple cases:

(1) The membrane stretched fore and aft between the bone and a strong trailing-edge tendon. This tendon must, of course, be itself in tension, but the membrane itself carries no spanwise tension (figure 32*a*).

(2) The membrane stretched parallel to the trailing edge, from root to tip, with negligible fore-and-aft tension (figure 32*b*). This is the usual method for Bermuda-rig sails, and gives a larger wing area for the same leading edge supports.

Calculations have been made for both methods of tensioning the wing membrane, for the wing shapes given in figure 32*a*, *b*. The results are shown in figure 33 as graphs of backward bending moment at the wing spar against spanwise position, compared with the actual strength of the wing spar at a number of positions. It can be seen that the spar is not strong enough to resist the loads imposed by case 1, which are far more severe than those imposed by case 2. Case 2 allows the use of a straight trailing edge, giving a greater wing area. Also, there is no evidence in the fossil record of the strong trailing-edge tendon necessary for fore-and-aft tensioning, even if the wing spar was strong enough, which the calculations show not to be the case. Thus spanwise tensioning of the membrane is to be preferred both on palaeontological and engineering grounds and all subsequent discussion is based on it.

The actual tension in the membrane is remarkably low, ranging from 420 N/m at the humerus near the shoulder to zero at the trailing edge. This low tension allows the membrane itself to be very thin. The bat *Pteropus giganteus* has a membrane 0.15 mm thick which can take a tension of 1150 N/m; so the assumed membrane thickness for *Pteranodon* of twice this, 0.3 mm thick, can stand 2300 N/m, giving a factor of safety of 5.5.

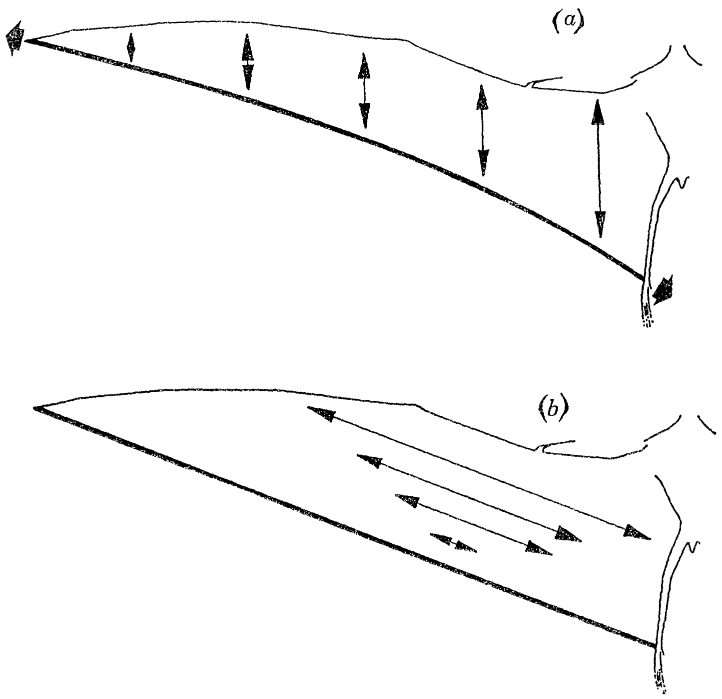


FIGURE 32. (*a*) Case 1: membrane stretched fore and aft between the wing spar and a hypothetical trailing edge tendon. (*b*) Case 2: membrane stretched in spanwise direction from wing root to tip.

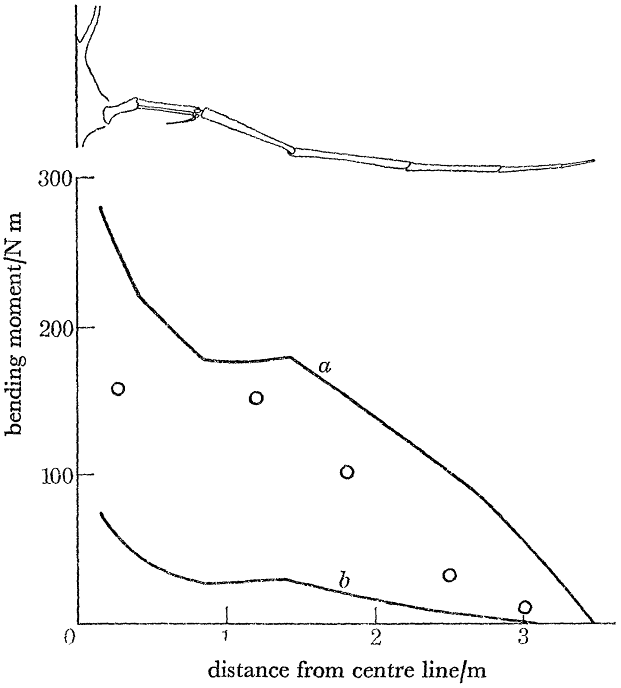


FIGURE 33. Backward bending moments in the wing spar for fore-and-aft and spanwise membrane stretching, compared with the actual strength of the wing spar. ○, actual strength; *a*, fore-and-aft membrane stressing; *b*, spanwise stressing.

The upward bending moment on the leading edge can be calculated from the spanwise distribution of lift. Consider a strip of the wing, of width dx and chord c, a distance x from the centre line (figure 34). The lift of this strip is $Wc\,\mathrm{d}x$, and the moment of this force about a point x_1, from the centre line is $Wc\,\mathrm{d}x\,(x-x_1)$. Integrating from x_1 to the tip, we have the upward bending moment at x_1:

$$\int_{x_1}^{\text{tip}} Wc(x-x_1)\,\mathrm{d}x. \qquad (3)$$

This expression has been calculated and is shown in figure 36*b*. Due allowance has been made in this calculation for the weight of each strip of wing.

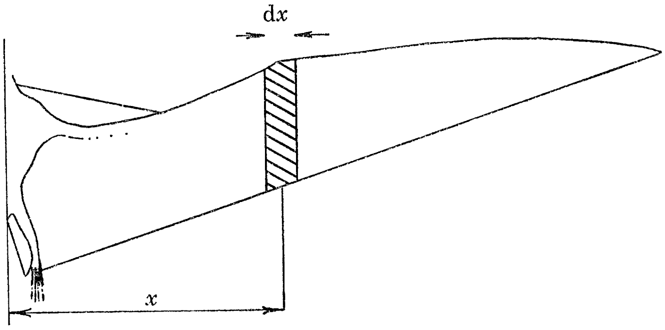


FIGURE 34. Strip of wing dx, distance x from centre line. For explanation see text.

(*c*) *The calculated strength of the wings*

It has been shown in the previous section that the spar of the wing is subjected to upward bending, backward bending and compression along its length. The outer part of the spar consists of the four phalanges, with no extra supporting structure (except that needed to hold the bones together at the joints). Each phalanx is a hollow tube with an approximately elliptical cross-section, whose dimensions are given in table 3.

When such a tube is bent, one side is stretched and the other is compressed. There are two possible modes of failure. The load applied may be too great for the material of the tube, which fails by rupture, usually on the stretched side since most materials are weaker in tension than in compression. Or if the wall of the tube is thin enough, it may buckle locally where it is being compressed, before the load is sufficient to break the material. A wooden pencil will normally fail by rupture, a piece of rubber tubing by local buckling. Currey (1967) considers these mechanisms and shows that a bone will fail by rupture if $D/t < E/(2\sigma_t)$ and by buckling if $D/t > E/2(\sigma_t)$, where t is the thickness of the wall of the tube, D is the mean of internal and external diameters, E is the Young modulus of bone and σ_t is the tensile strength of bone. Taking values from table 12, it is found that the bone will buckle if D/t is greater than 50. All the bones of *P. ingens* (table 3) have D/t less than 50, and so will not buckle, but fail by rupture.

To simplify the calculations, the bone cross-sections have been taken to be elliptical, with constant wall thickness. The bending moment required to bend each bone at its centre has been calculated separately for backward and upward bending. When both loads are applied together, the strength is slightly reduced; in the worst case the reduction factor is $1/\sqrt{2}$. These strength estimates have been used to derive the factors of safety given in table 14.

In the inner part of the wing spar the structure is different. The main backward bending load is carried by the digit extensor tendon in tension and the bones metacarpal, carpals and radius/ulna in compression. The tendon has a diameter of 1.5 cm, estimated from its insertion on the first phalanx. So taking the tensile strength of tendon as 5×10^7 Pa (Elliott 1965), the maximum tension it can stand is 9 kN.

Table 13. The strength of bone and tendon

source of information	material	type of stressing	strength/Pa
McNeill Alexander 1968	compact bone parallel to the osteones	in tension, yield strength	10^8
		in compression, yield strength	1.8×10^8
		Young modulus	10^{10}
Yamada 1970	parallel to the osteones	shear strength	6.4×10^7
	perpendicular to the osteones	shear strength	9.1×10^7
Elliott 1965	tendon	in tension, yield strength	5×10^7

The metacarpal and the ulna will fail by modified Euler buckling (Currey 1967); the failure loads are 2.95 and 10.2 kN respectively. The carpals are so short that strength is no problem, and the radius so weak compared with the ulna that it can be ignored. So the tension in the digit extensor tendon is limited to 2.95 kN by the metacarpal, the weakest of the bones.

The bending moment is the product of the tension in the tendon and the moment arm, this being the distance between the centres of the tendon and bone, which can be found from the sections in figure 35; this is the bending moment in the plane containing tendon and bone, and can be resolved into upward and backward components for comparison with the expected loads. In the calculations it has been assumed that the tension in the digit extensor tendon is just sufficient to hold the wing firmly extended during flight.

From the wrist inwards, the pteroid tendon also contributes to the strength of the wing, resisting both backward and upward bending. There is no fossil evidence for its thickness, so it has been assumed that its strength is just sufficient to balance the backward bending moment at the elbow. This gives a tension of 94 N. With a factor of safety of four, the diameter would have been 0.32 cm. Such a tendon could have been easily attached to the pteroid bone.

Torsion (twisting) loads at the centre of the humerus, ulna and metacarpal have been calculated by the method used by Pennycuick (1967), and compared with the actual strengths of the bone. In the worst case, the humerus, the torsion load is 26 N m, and the ultimate strength of the bone is about 260 N m, giving a factor of safety of 10. This is so high that there was no risk of the bone failing in torsion, and the effect of the torsion load on the bending strength is small.

The loads considered above have been those of straight and (almost) level gliding. When *Pteranodon* turns, or recovers from a dive, the lift has to be increased to provide the acceleration to change the direction of flight. This increases all the loads proportionately to the increase in lift. Typical manoeuvres of birds and aeroplanes require increases of 10 or 20 %, and quite violent manoeuvres are needed to exceed a load factor of 2. The operating limit is usually set about 4, and wings break at load factors around 10. To keep within its safety limits, *Pteranodon* would have had the low load factor of about 1.5. This would allow turns at angles of bank up to 40°, giving a minimum radius of turn of about 9 m. This is a small turning circle for so large an animal and is a natural consequence of the slow-speed gliding.

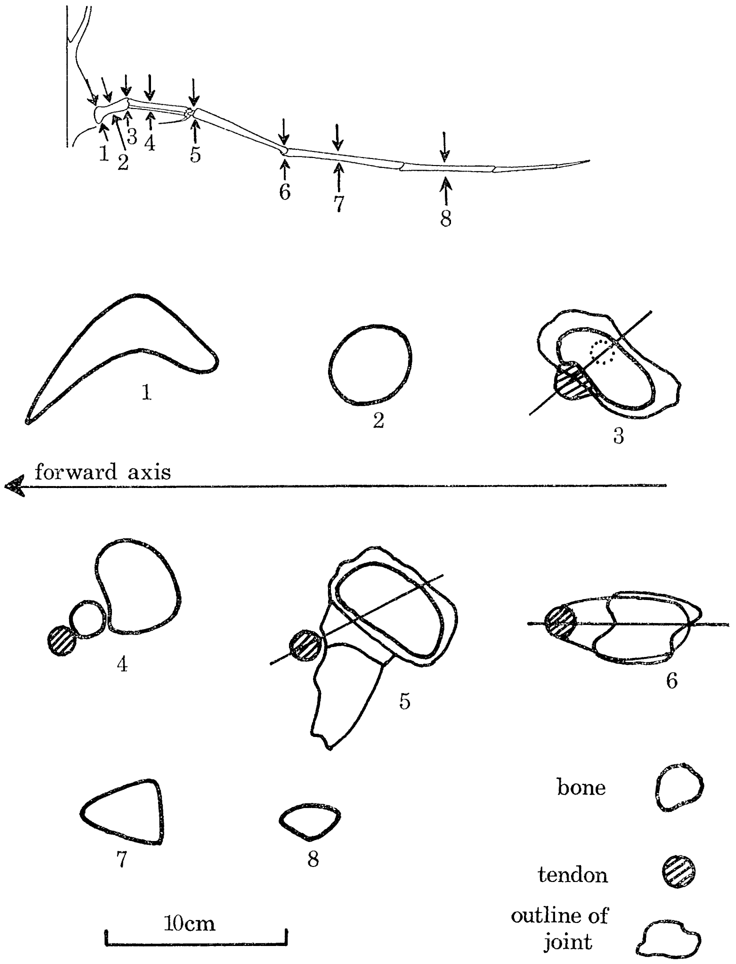


Figure 35. Sections through the wing spar at various positions.

(*d*) *Conclusions*

The stressing of the wing spar is summarized in table 14 and figure 36*a*, *b*. Figure 36*a* shows how the required backward bending moment is resisted by the phalanges alone at the tip, but nearer the body is divided between the digit extensor tendon, the pteroid tendon and the humerus. Figure 36*b* shows how the upward bending moment is divided. Table 14 gives the actual load and the factor of safety of each component at various points in the spar.

The general factor of safety is near 5, a very reasonable figure for a flying animal. *Pteranodon* was certainly strong enough for all its flight activities, despite being so light, because of the extremely good design of the wings. The phalanges are a little stronger than the rest of the spar, probably to resist local damage to the wing tips, which are more vulnerable to injury than the inner parts of the wings. As the phalanges are so light, adding a little extra material for strength purposes incurs very little weight penalty. The ulna is very strong in compression, but this is clearly not the critical load on it. In upward bending, its factor of safety is 6.7. The digit extensor tendon, with a factor of safety of 14, is perhaps too strong, but there is little evidence for its size except for its insertion on the first phalanx. The tendon may have tapered from a 1.5 cm diameter insertion to, say, a 1 cm diameter along most of its length. But there are

TABLE 14. LOADS IN THE WING SPAR

distance from centre line/m	member	backward bending/N m each member	backward bending/N m total	upward bending/N m each member	upward bending/N m total	factor of safety
0.32	humerus	39	53	62	70	2.0^{b}
	pteroid tendon	14		8		
0.44	pteroid tendon	16	42	10	64	
	digit extensor tendon	26		22		14^{t}
	elbow joint	—		32		
0.63	pteroid tendon	26	35	8	55	
	digit extensor tendon	11		18		14^{t}
	ulna	−2		29		6.7^{b}, 30^{c}
0.84	digit extensor tendon	27	27	13	44	14^{t}
	wrist joint	—		31		
1.14	digit extensor tendon	28	28	7	32	14^{t}
	metacarpal	0		25		5.5^{b}, 5.3^{c}
1.44	digit extensor tendon	29	29	0	22	14^{t}
	knuckle joint	—		22		
1.84	1st phalanx	20	20	12	12	7
2.54	2nd phalanx	6	6	3	3	7
3.06	3rd phalanx	1	1	0.5	0.5	11

b, bending; t, tension; c, compression.

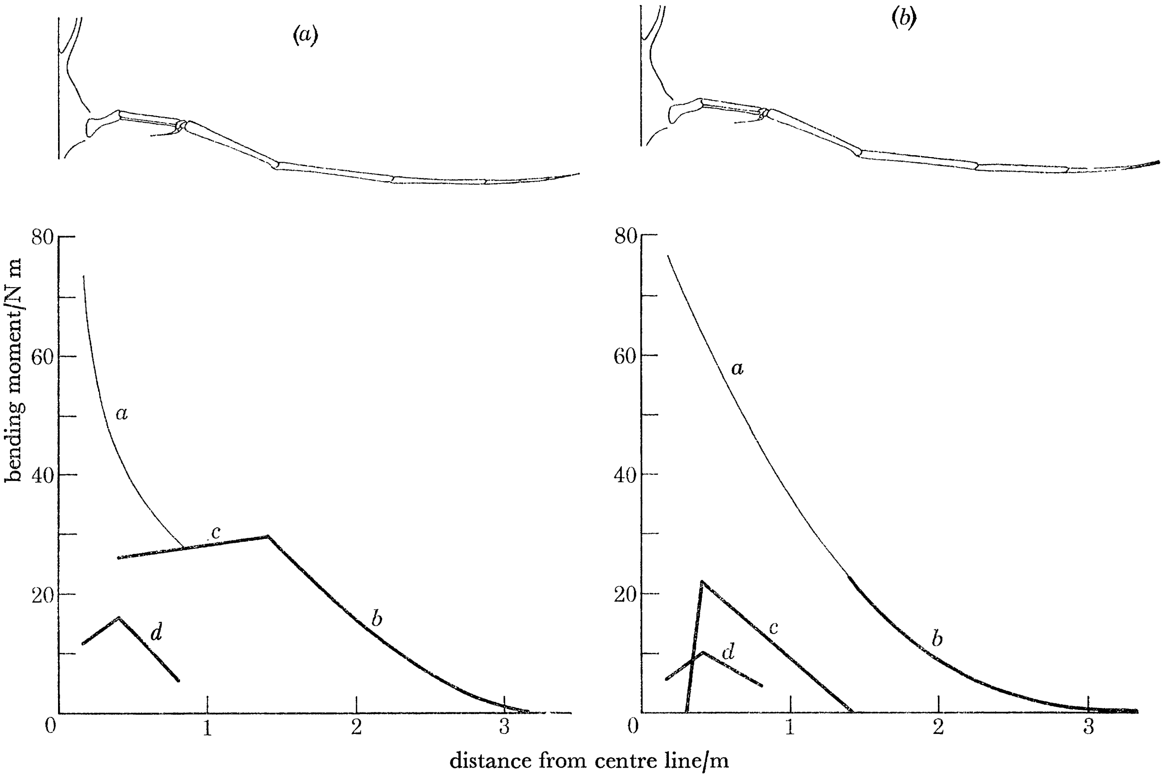


FIGURE 36. (*a*) Backward bending along the wing. (*b*) Upward bending along the wing. *a*, total bending moment; *b*, contribution by phalanges; *c*, contribution by digit extensor tendon; *d*, contribution by pteroid tendon.

other considerations. A strong tendon is stiffer and more resistant to creep, allowing the digit extensor muscle to have been shorter and so lighter.

The weakest element in the wing spar is the humerus, with a factor of safety of only 2. This is unlikely to be due to a dimensional error, as the humerus of no. 1175 is well preserved and the thickness of the bone easy to measure. It is possible that the bone was unusually strong; if so it would be brittle, but this would not matter in a short bone well protected from shock locally. Alternatively, if some of the flight muscles inserted well out along the humerus, the load on the shaft would have been significantly reduced.

The strength of the wing is obviously of critical importance in *Pteranodon*, but it is interesting to consider briefly the other parts of its structure. The body is small and built strongly where necessary, i.e. the pectoral girdle is large and a notarium of fused vertebrae gives extra rigidity to this region. The neck is very long, but it does not have to bear a heavy head. The neck vertebrae are large, so their muscles have a large moment arm. *Pteranodon's* legs look rather weak. We have calculated (using the dimensions of the femur of no. 1175) that the legs would not have been strong enough to take the weight in compression when fully outstretched sideways. They would have broken at 16 kgf. They are just strong enough to take the weight when the leg is bent at the knee and stronger if the legs are directed downwards under the body. But this posture was not possible anatomically, nor is the pelvic girdle posterior to the acetabulum sufficiently developed to take the necessary muscles. Both the design and mechanics of the legs show that they were adapted for taking the tension that occurred in hanging and pulling the body along when walking, rather than for resisting compression as in normal quadruped standing and locomotion.

4. AERODYNAMICS OF *PTERANODON INGENS*

(*a*) *The purpose of the crest*

(i) *Introduction*

When remains of *Pteranodon* were scarce, the existence of an enormously elongated supraoccipital crest was doubted (Williston 1891). Later, with the discovery of more specimens – for example, Eaton's nos 2594 and 2473 – the dimensions of the crest were established and much speculation on its function followed.

In *P. ingens* the crest is a long narrow blade, 68 cm long and 3 mm thick. It is made up of a double layer of bone. To be stable the two layers must have been connected in places by internal struts, but we have no evidence of this. Although the crest is so thin it was strong enough to withstand the aerodynamic force on it.

The aerodynamic load is greatest when the head is turned through 90°, and is broadside on to the airflow. In this position, at the maximum useful flying speed of 14 m/s, the couple at the root of the crest is 3.1 N m. Assuming the bony layers are 0.25 mm thick and 3 mm apart, the couple required to break the crest is 11.2 N m, giving a factor of safety of 3.6.

The function of the crest has led to many suggestions. One common one is that it was a rudder or steering device. Eaton (1910) thought that 'the effect of the crest as a vertical aeroplane cannot be disregarded', although he did not think that this was its main purpose.

Short (1914) described the crest as 'a device for steering to left or right' and this view was echoed by Brown (1943) calling it 'a sort of rudder'. Heptonstall (1971) suggested that the crest doubles the effect of the head as a rudder control.

The idea that the crest evolved as an extra area for the insertion of muscles was put forward by Eaton. He compared *Pteranodon* with the chameleon *Chameleo vulgaris*. This animal has a bony extension of parietals and supraoccipitals for the insertion of extra temporalis muscle, used to close the jaws. Eaton thought that the crest of *Pteranodon* could have served a similar function. However, very powerful jaw muscles would be needed to give a strong bite at the tip of such a long beak.

Even Eaton realized that muscle insertion could not be the whole reason for the evolution of the crest, for he wrote 'it is scarcely imaginable that the temporal muscles of the pterodactyl extended backwards along the entire length of the crest. Its further development may have been dependent upon another totally different function.'

The effect of the crest as an aerodynamic counterpoise to the jaws, rather than a rudder, has been considered by various authors.

Lull (1906) said that 'the crest aided in keeping the head pointed into the wind. This would otherwise not only require great muscular effort but would probably have deflected the creature from its course'. Khozatsiy & Yurbev (1964) simply state that 'the crest appears to function as a counterpoise to the long beak'. Muscles were mentioned again by Heptonstall (1971), who thought 'the function was at least partly to keep the animal's head pointing forward with the minimum effort needed by the neck muscles'.

Finally, the possible ornamental function of the crest has not been overlooked and has been mentioned by several authors, e.g. Seeley (1870) and Short (1914).

It would be wrong to assume that the crest had to have only one function. It could quite well have been used in behaviour, in display for example, and also serve aerodynamic functions, both in the counterpoise sense and in control (see §4 (*b*)). It will always be impossible to know if the crest was of use in the behaviour of *Pteranodon*, but its aerodynamic effect can be investigated by the use of models in a wind tunnel. The next section describes such experiments performed on model heads of *Pteranodon ingens*, with and without crests.

(ii) *Wind-tunnel experiments*

It is important in making wind-tunnel tests to keep the model well clear of the sides of the tunnel, and to operate the model at approximately the same Reynolds number as the animal. The available wind tunnel was a 30 cm × 30 cm open return tunnel, with a maximum wind speed of 40 m/s.

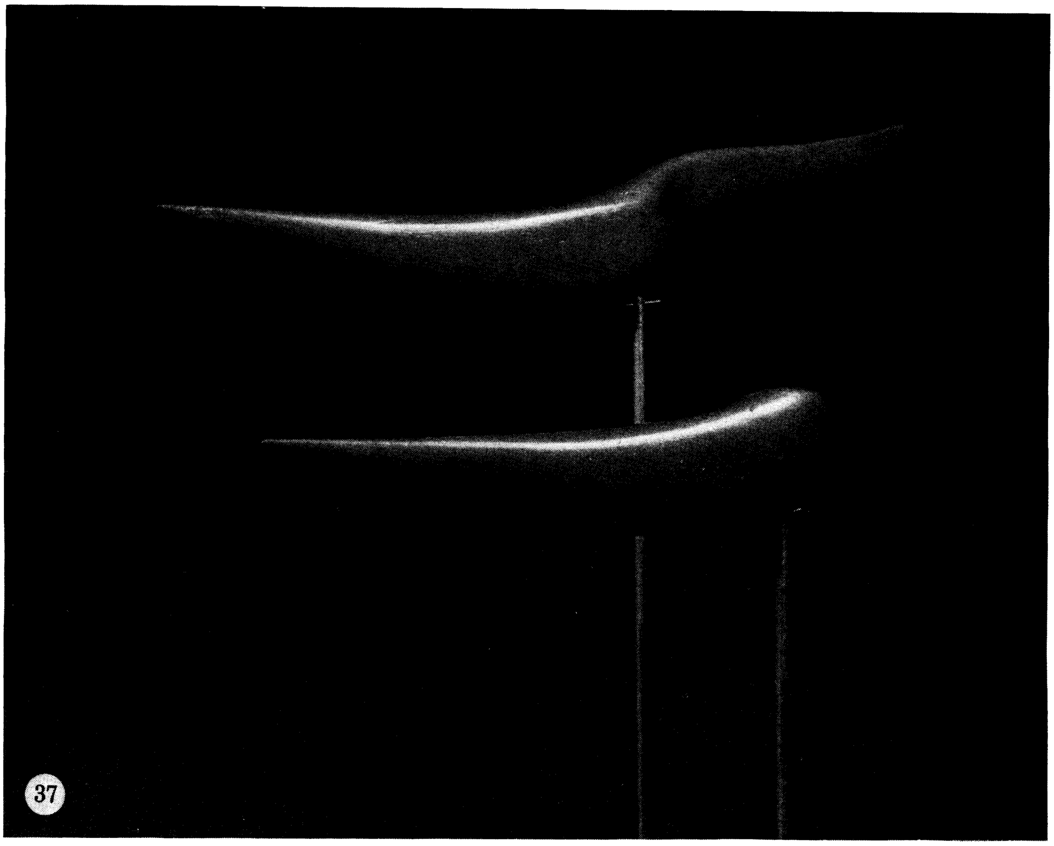
The largest practicable model head for this tunnel was 24.5 cm long, giving a model Reynolds number of 6×10^5. The full-size head at a flying speed of 10 m/s has a Reynolds number of 10^6. These are close enough for the model results to be valid.

Two heads (figure 37, plate 24) were carved from balsa wood, one with crest and one without. The shape was taken from Eaton (1910). They were mounted on shafts through the position of the occipital condyle, so that they were free to rotate laterally. Each head was set at a series of angles, ϕ, and the couple measured by a spring balance.

The wind speed was measured with an aircraft airspeed indicator. The results of the tests, scaled up to the full-size *P. ingens* at a flying speed of 14 m/s, are shown in figure 38.

(iii) *Results and conclusions*

Figure 38 shows that without the crest the couple rises rapidly with increasing angle, to a maximum of 9.6 N m at 55° turn, falling gradually to zero at 180°. The crest has very little



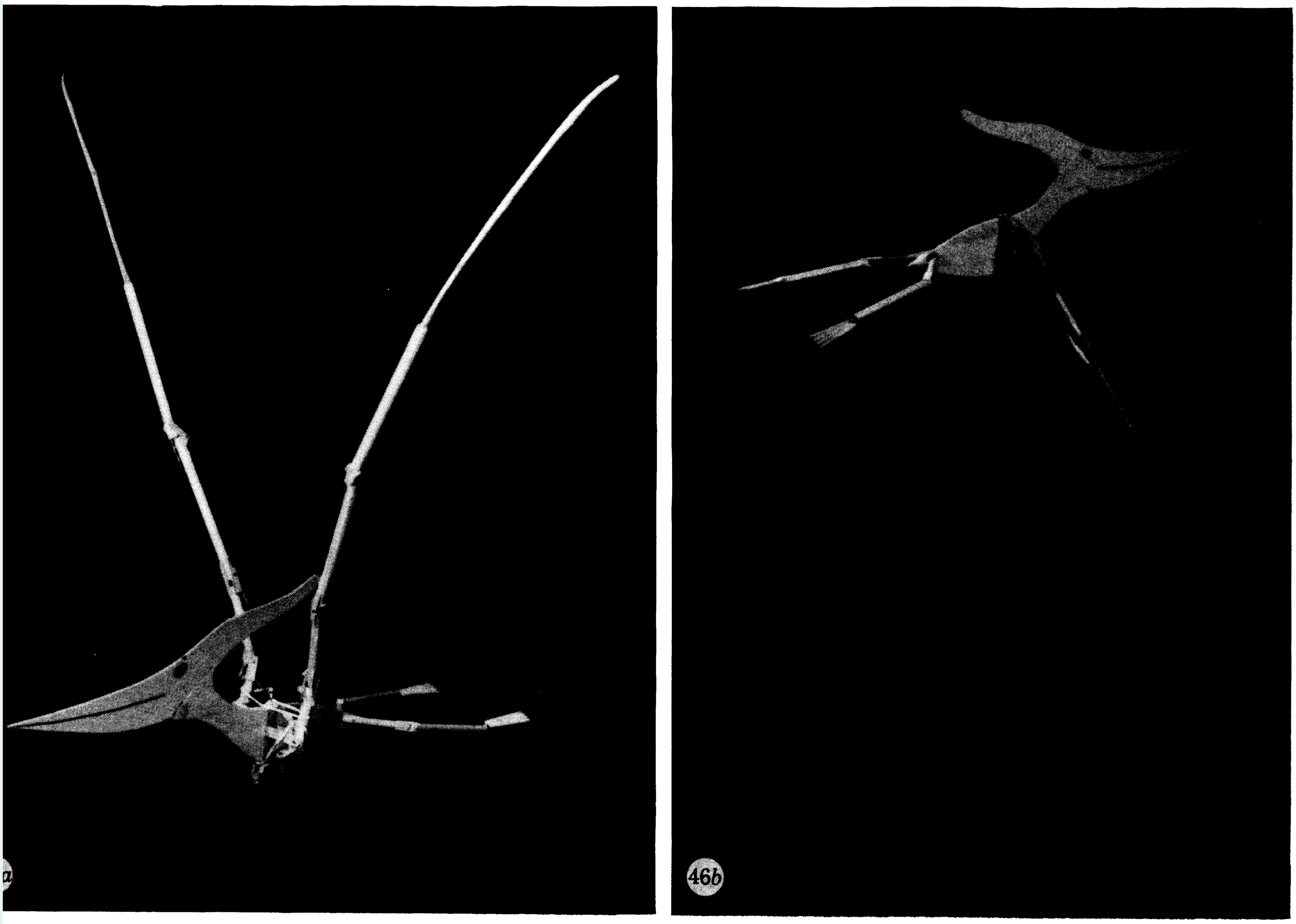


FIGURE 37. The two model heads, with and without crests, used in the wind-tunnel experiments.

FIGURE 46. (*a*) The articulated model with the wings at the top of the upstroke. (*b*) The articulated model with the wings at the bottom of the downstroke.

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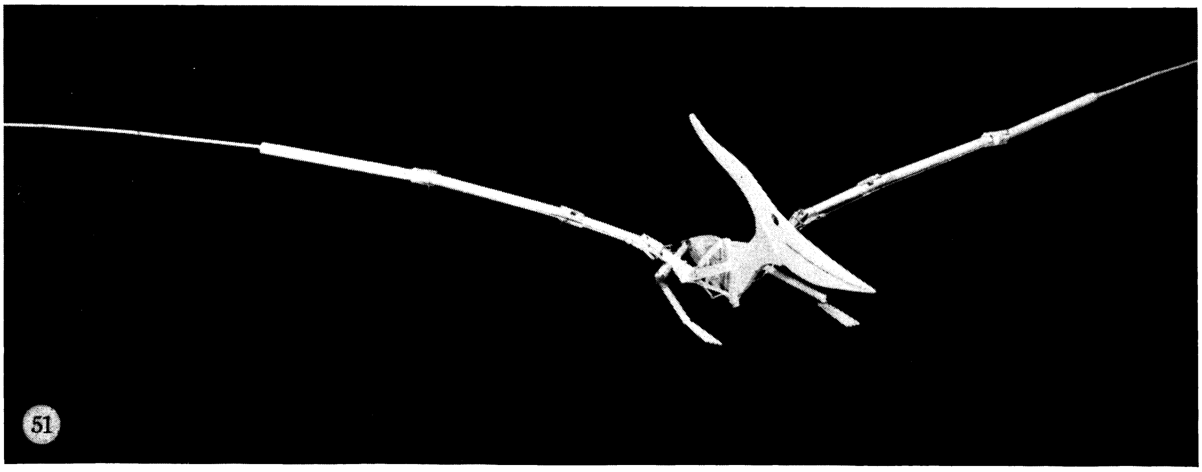

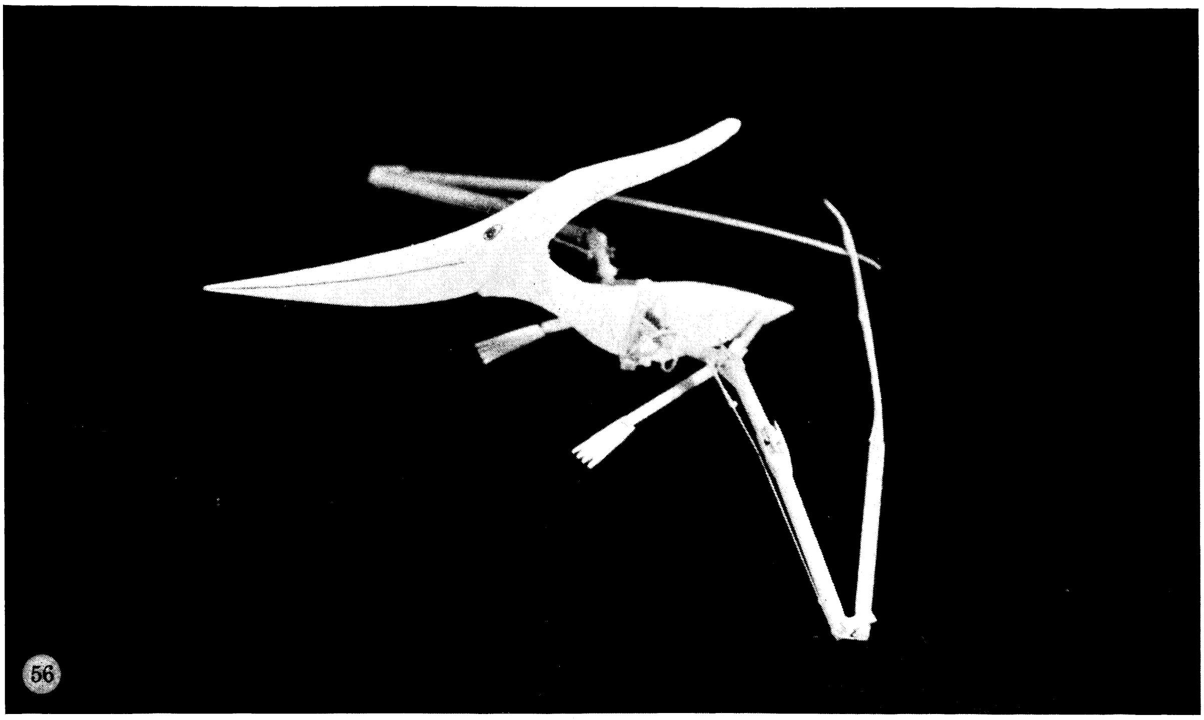

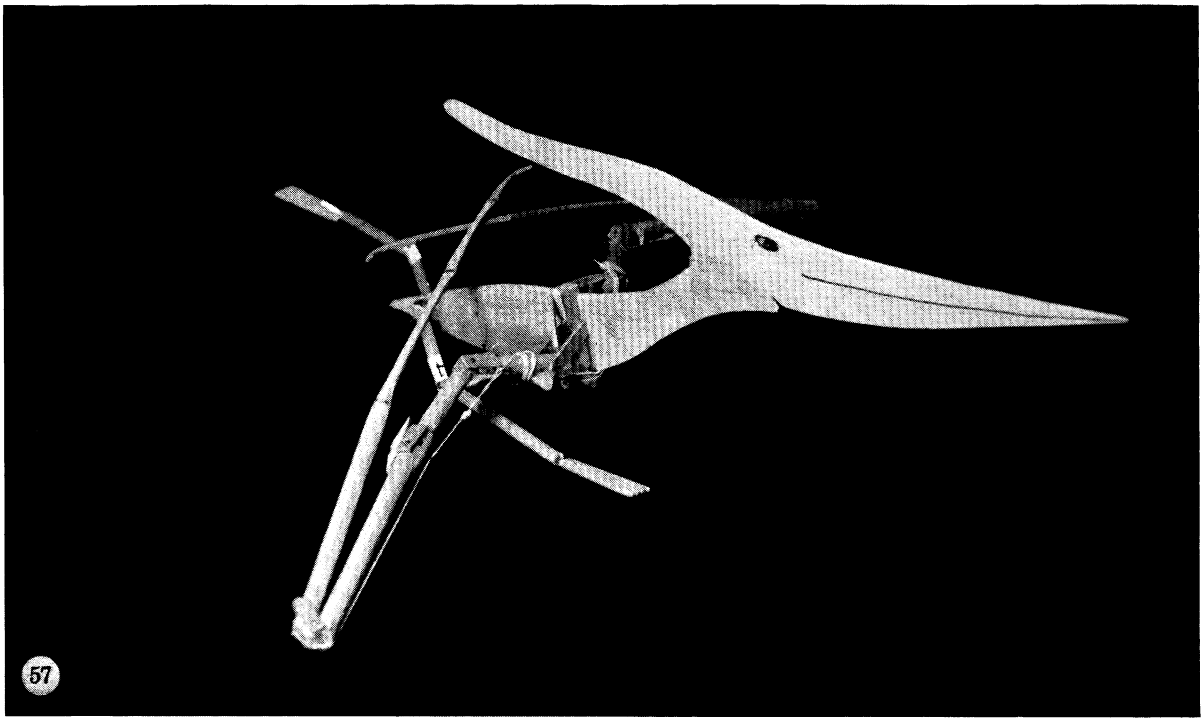

FIGURE 51. Articulated model with wings in position ready to take off from land or water.

FIGURE 56. Articulated model walking. The wings are folded and the weight rested on the body and wing claws. Both legs are forward ready to grip the ground and pull the animal along.

FIGURE 57. Articulated model walking. The wings are folded and the weight rested on the body and wing claws. In this photograph the legs are being used alternately to pull the animal along, rather than both together as in figure 56.

effect at small angles, but beyond 70° it begins to balance the beak and at angles above 100° the couple is very small. This unexpected result suggests that at small angles the crest lies in the turbulent wake behind the head, and is blanketed. At larger angles, it balances the beak, as expected.

The tension that a muscle can exert varies with its extension and its cross-sectional area. McNeill Alexander (1968) gives a graph (figure 39) of the tension of one fibre as a function of length, and quotes the energy released by one contraction by a bush baby jumping as 250 J/kg. Assuming the muscle operates down to 0.4 of its maximum tension, or between 0.7 and 1.42 of its rest length, the maximum tension in the muscle must be 4.5 Pa. This is relatively high.

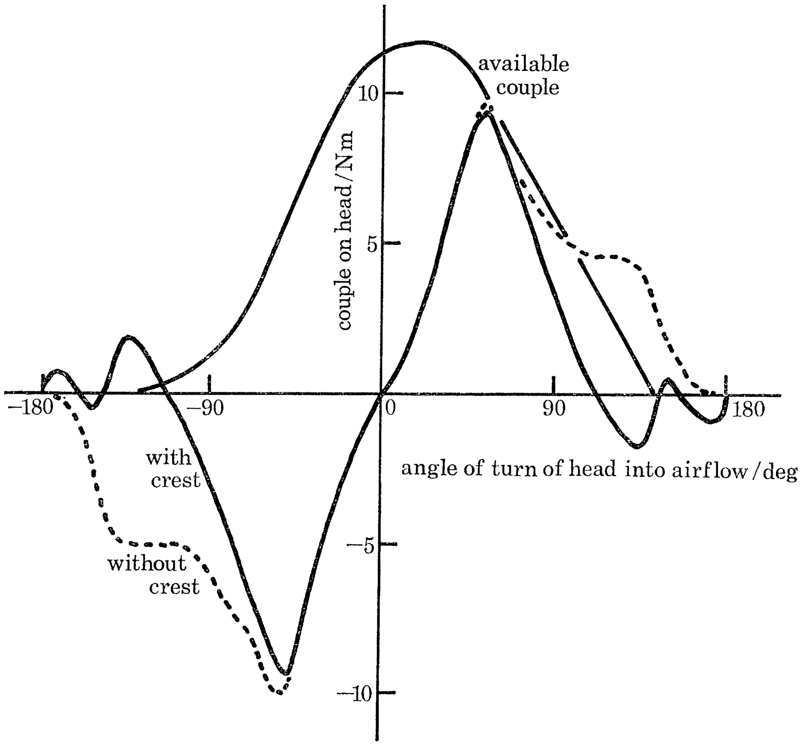

FIGURE 38. Results of the wind-tunnel tests on the model heads of *Pteranodon ingens*, with and without crest

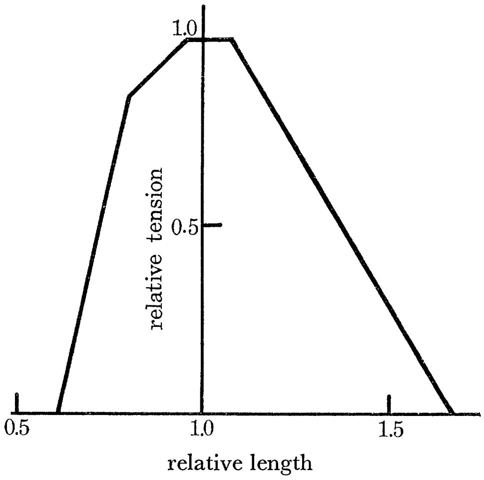

FIGURE 39. Muscle tension against length for one fibre (after McNeill Alexander 1968).

Alexander gives a figure for the energy released by a locust jumping that is half as great as that of the bush baby. Pennycuick & Parker (1966) give figures for pigeon flight muscle that imply a maximum tension of only 1.2 Pa. We have taken the highest value, since *Pteranodon* is so highly evolved that it is likely to have the most efficient muscle possible.

The geometrical arrangement of the neck muscles is also important (figure 40). They must run diagonally round the neck (assumed here to be a cylinder of radius r) from an insertion on the skull to one on a vertebra. As the head turns, both the length and the angle of the muscles alter (figure 41). The available couple is $Tr\cos\theta$, where T is a function of the cross-section and extension of the muscle.

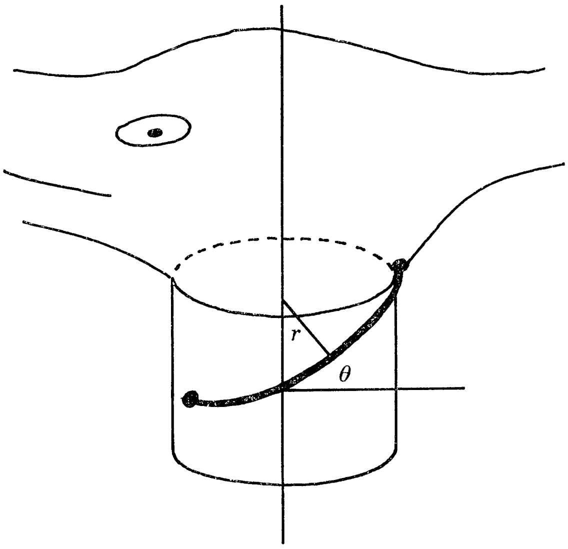

Figure 40. Diagram of the geometric arrangement of the neck muscles of *Pteranodon*.

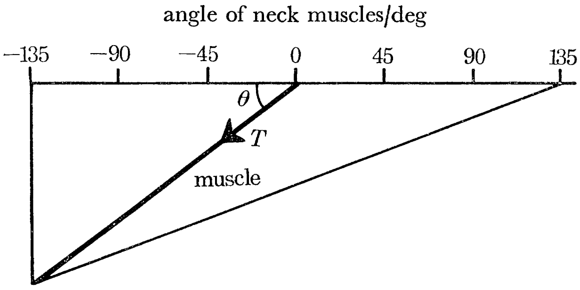

Figure 41. Diagram illustrating the change in length and angle of neck muscles as head turns.

Assuming that the muscles are at 0.95 of their unstretched length when the head is central ($\theta = 0$), that the head can turn through 135° each way, and that almost the full available muscle contraction is used, figure 41 takes the shape shown. The consequent variation of muscle couple with head angle is shown in figure 38. One hundred grams of muscle is just sufficient to resist the loads on the head with the crest at the most difficult angle – about 60°. Without the crest, this muscle is too weak at angles above 100°, and at least twice as much muscle would be needed to hold the head at an angle of 130°. A high value of tension has been used in these calculations. If *Pteranodon* had less-efficient muscles, even more mass of muscle would have been needed. Since there are two neck muscles, the total mass must be 200 g; the crest on the other hand weighs about 30 g. Clearly the crest is lighter than the extra neck muscle that would otherwise have been required.

So the prime function of the crest is mass-saving, by allowing reduction of the neck muscles. The head is also a useful rudder, but the crest contributes little to this as it is so near the centre of gravity. The head, turned through 90°, would also be a good air-brake, contributing drag equal to that of the rest of the animal; about half this extra drag is due to the crest.

(*b*) *Stability and control*

(i) *Stability*

Any flying creature or flying machine has to be capable of steady controlled flight, and of recovering from disturbances due to air movements or intentional manoeuvres. The simplest way of achieving steady flight is to design the aircraft so that it is aerodynamically stable about all three axes (figure 3). Gliders and aeroplanes are made stable in this way. Stability in pitch (about the lateral axis) and yaw (about the vertical axis) are usually provided by horizontal and vertical tail surfaces which act like the feathers of an arrow to keep the aircraft pointing in the direction in which it is going. Stability in roll is given by dihedral – raising the wing tips above the centre section.

Pteranodon has neither dihedral nor tail surfaces so it was almost certainly unstable about all three axes. The slight doubt arises because it is possible to make a tailless aircraft stable by careful choice of wing section or by twisting a swept wing (Weyl 1945). These artifices reduce the performance of the aircraft, and *Pteranodon* is unlikely to have used them. It is normal for highly developed flying creatures to be unstable; most birds have little or no tail, and those with tails can fly without them. The evolutionary trend in birds, insects and pterosaurs seems always to be from stable early forms to unstable later forms (Maynard-Smith 1952).

An unstable aircraft will not fly steadily. Any small departure from its initial path will tend to increase and the aircraft will not return to its path automatically. It is possible to devise an active control system to prevent this by making continual adjustments to maintain steady flight. A human pilot can fly an unstable aircraft, and automatic pilots commonly fly unstable missiles. The process is like balancing a pole on the end of your nose; not very difficult provided one is quick enough. So highly developed animals have developed balance senses and control systems that are good enough and fast enough to overcome their aerodynamic instability. The balance centre, the cerebellum, is highly developed in modern birds, and was as advanced in pterosaurs (Edinger 1941).

There are distinct advantages in achieving stable flight in this way, rather than having an intrinsically stable design. The aerodynamic shape is less constrained, and can be designed to have less weight and less drag. There is no need to carry a heavy tail. It is possible to make all the lifting area generate maximum lift at the same time, giving the lowest possible landing speed; and with no stability to oppose them, the controls are particularly effective. *Pteranodon* would have had all these advantages and would have better performance and more manoeuvrability than a similar creature that was aerodynamically stable.

(ii) *Control*

Control in flight is needed about each axis (figure 3). Control forces can be obtained by using the inertia of suitable members, or by aerodynamic forces on suitable surfaces. Inertial control is seen in many land animals that use their tails rather as a tight-rope walker uses his pole, and would certainly have been a means of pitch control in the Jurassic *Rhamphorhynchus*. But inertial control has the major disadvantage that control forces can only be obtained while the tail is being accelerated; so they are only available for a limited time and cannot be used to balance out steady forces. Moreover, *Pteranodon* had no tail, and could hardly have used its neck as a primary control.

Most flying creatures and man-made aircraft use aerodynamic forces for control. The most powerful control is obtained by having the control surfaces as far as possible from the axis about which rotation is required. Hence, aeroplanes normally have tails for control in pitch and yaw, and movable surfaces (ailerons) near the wing tips for roll. Tailless aircraft are more difficult to design; they usually have ailerons and rudders like ordinary aeroplanes, and use control surfaces near the trailing edge of the wings for control in pitch. An alternative which has been used is to move the centre of gravity of the aircraft relative to its centre of lift. This can, in principle, give control in pitch and roll, and is in fact used in 'hanging gliders' and has also been used in emergency for pitch control of larger aircraft. Birds obtain the same effect by swinging the wings forwards or backwards to move the centre of lift relative to the centre of gravity, and they also use their tails when necessary. *Pteranodon* is a much simpler aircraft than a bird, and has fewer control options available. Its prime control in pitch is probably fore-and-aft movement of the outer wing, pivoting at the knuckle; the inner wing section cannot move much in this direction. A nose-up control couple would be obtained by tightening the digit extensor tendon to swing the wing tip forward, simultaneously moving the foot outwards to avoid increasing the tension in the wing membrane. This control action could be assisted by moving the head back and by bending the knee so as to raise the trailing edge of the wing. The opposite actions would give a nose-down control force.

Control in roll would be obtained by twisting the wing, either by moving one leg down and the other up, or by moving the legs laterally to change the tension in the membrane. Moving the right leg downwards or inwards would cause a roll to the left. In practice both movements would probably be used together.

Control in yaw might be obtained by adjusting the drag of the wings; *Pteranodon* would then yaw towards the wing whose drag was greater. But it is difficult to see how this could be done without simultaneously causing an unwanted roll. Alternatively, the head and crest would make an excellent rudder. Turning the head to the left would provide a large force to make *Pteranodon* yaw to the left.

One other control is needed in efficient gliders – a method of altering the gliding angle. To a small extent this can be done by change of flying speed, but a much more powerful method is to increase the drag. Birds do this by half folding their wings to spoil the shape, but if *Pteranodon* tried this its wings would collapse. Man-made gliders are fitted with spoilers or air brakes on the wings, but *Pteranodon* has no such devices. But if it turned its head through a right angle, the drag of the beak and crest would equal that of the rest of the animal, doubling the rate of sink. The head could be directed forwards again before landing to see the ground easily. This is just what is needed for accurate control of landing.

(*c*) *The gliding performance*

(i) *General considerations*

In still air a glider flies approximately horizontally at a speed v sufficient to generate lift L equal to its weight W (figure 42). Because of aerodynamic losses, its motion is resisted by a force D, the drag, along its line of flight. In order to maintain steady flight, the glider must sink at an angle θ, the gliding angle, such that the resultant of L and D balances the weight W. Since θ is small, we can see at once that

$$L \simeq W$$

and

$$\theta \simeq (v_s/v) \simeq D/L, \tag{4}$$

where v_s is the sinking speed and v is the flying speed of the glider. Both θ and v_s vary with the chosen flying speed v, and the performance of the glider is usually specified by the 'polar' curve – a plot of sinking speed v_s against flying speed v.

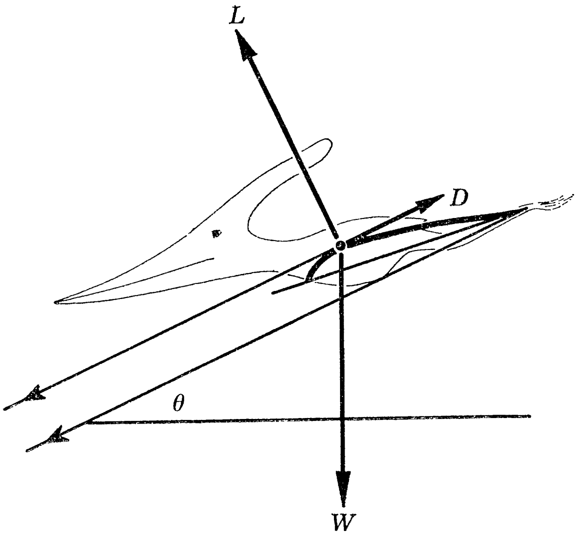

Figure 42. The forces acting on *Pteranodon* in a steady glide. W, weight; L, lift; D, drag.

The lift and drag can be calculated from the standard equations

$$L = C_L \tfrac{1}{2}\rho v^2 S \tag{5}$$

and

$$D = C_D \tfrac{1}{2}\rho v^2 S, \tag{6}$$

where S is the wing area, ρ is the density of the air and C_L and C_D are non-dimensional lift and drag coefficients, which depend on the shape of the glider.

Combining equations (4), (5) and (6) we find

$$v_s/v = C_D/C_L \tag{7}$$

and

$$W = C_L \tfrac{1}{2}\rho v^2 S. \tag{8}$$

The drag of a glider can be considered as the sum of three components (Goodhart 1967).

(1) *Induced drag*, C_{Di}. This component is due to the aerodynamic process which generates the lift, and is strongly dependent on the shape of the wing and the value of the lift coefficient. It can be calculated from the equation

$$C_{Di} = kC_L^2/\pi A, \tag{9}$$

where k is a constant, ideally 1.0 but typically 1.10, and A is the aspect ratio (the ratio of the wing span to the mean chord; the chord of a wing is its width measured parallel to the direction of the airflow).

Induced drag can be minimized by using long narrow wings (high aspect ratio) and operating at low values of lift coefficient, i.e. well above the minimum flying speed.

(2) *Wing profile drag* C_{D_w}. This is due to the pressure distribution and viscous losses round the wing. Like the lift coefficient C_L it depends principally on the shape of the wing section and its angle to the air flow, the angle of incidence, α. Typical published data gives graphs of C_D and C_L against α, or more usefully graphs of C_D against C_L, for each wing section. But C_D and C_L depend also on the Reynolds number at which the wing is operating. The Reynolds number *Re* is a non-dimensional measure of the relative importance of viscous and inertial forces. It is defined as $Re = (\rho/\eta)\, vc$, where η is the viscosity of the air and c the chord of the wing. In air at sea level $Re = 59\,000vc$. The performance of a wing section varies considerably with Reynolds number (figure 44), so it is important to use data for the correct Reynolds number when calculating performance.

(3) *Parasite drag*, C_{D_p}. This is the drag of everything else. With *Pteranodon* the main contributions come from the head, neck and body.

Table 15. The principal parameters of *Pteranodon ingens*

wing span	6.95 m
wing area	4.62 m^2
all up weight	16.6 kgf or 163 N
aspect ratio	10.5
frontal area (head and body)	0.1 m^2

Table 16. Calculation of the gliding performance of *Pteranodon*

			drag coefficients					
lift coefficient, C_L	flying speed m s^{-1}	Reynolds number ($\times 10^5$)	wing profile C_{D_w}	induced C_{D_i}	head and body C_{D_p}	total C_D	lift/drag ratio C_L/C_D	sinking speed m s^{-1}
1.2	6.7	2.6	0.091	0.048	0.005	0.145	8.3	0.81
1.1	7.0	2.7	0.034	0.041	0.005	0.080	13.8	0.51
1.0	7.3	2.8	0.021	0.033	0.005	0.059	16.9	0.44
0.9	7.7	3.0	0.017	0.027	0.005	0.049	18.4	0.42
0.8	8.2	3.2	0.017	0.021	0.005	0.043	18.5	0.45
0.7	8.8	3.4	0.019	0.016	0.005	0.041	17.1	0.51
0.6	9.5	3.7	0.022	0.012	0.005	0.039	15.2	0.62
0.5	10.4	4.1	0.025	0.008	0.005	0.038	13.0	0.80
0.4	11.6	4.6	0.028	0.005	0.005	0.038	10.5	1.11
0.3	13.4	5.3	0.031	0.003	0.005	0.039	7.6	1.76
0.2	16.5	6.4	0.036	0.001	0.005	0.042	4.7	3.45

(ii) *Calculation of performance*

Table 15 shows the principal parameters of our model of *Pteranodon*; and table 16 summarizes the calculations. Choosing a value of C_L, say 1.2, we calculate the flying speed $v = 6.7$ m/s and the mean Reynolds number $Re = 2.6 \times 10^5$. Strictly speaking, the Reynolds number varies along the wing span, but it is sufficiently accurate to take the value corresponding to the mean chord.

We now need wing-section data for the correct wing section at this Reynolds number. Few wing sections have been measured at such a low Reynolds number and few of these look anything like our estimate of *Pteranodon's* section. The nearest is the curved plate, Gottingen 417a, which is compared with *Pteranodon's* wing section in figure 43. It is likely that the two sections will have similar performance, except that the thin trailing edge of *Pteranodon's* section should slightly reduce the drag. This will slightly improve the performance at high speed.

The lift and drag coefficients of Gottingen 417a have been measured by Schmitz (1952) at three low Reynolds numbers (figure 44).

For convenience of interpolation, they were replotted as graphs of C_{D_w} against *Re* for each value of C_L, from which C_{D_w} can be read off for table 16.

FIGURE 43. Wing sections. (*a*) Gottingen 417a; (*b*) *Pteranodon ingens*.

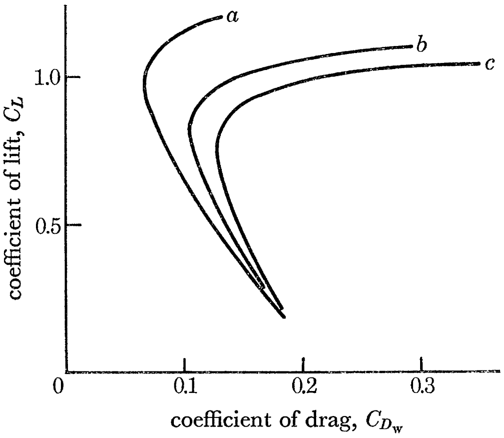

FIGURE 44. Characteristics of the wing section (Gottingen 417a) redrawn from Schmitz (1952). (*a*) *Re* 420000; (*b*) *Re* 168000; (*c*) *Re* 42000.

We now estimate the other components of C_D. C_{D_i} is calculated directly from equation (9) using the typical value 1.10 for k. The most difficult component is C_{D_p}, the drag coefficient of head, neck and body. A reasonable estimate for a streamlined body is 0.05, referred to its frontal area; this becomes 0.001 when referred to the wing area. But there is also the interference drag, due to the airflow round one part upsetting that round the others. To allow for this, we might double the estimate to 0.002. But this seems rather low, because a good modern glider has C_{D_p} of 0.010, which becomes 0.015 for *Pteranodon* when corrected for the different ratios of frontal area to wing area. Supposing that an evolving animal may come rather nearer to the optimum than a man-made machine, we take the intermediate value of 0.005 for C_{D_p}.

We can now add the components to find C_D, and hence the lift/drag ratio and sinking speed. A small computer program was written to facilitate this process. The results are given in table 16 and figure 45. It is immediately apparent that the performance at low speeds depends principally on the induced drag, C_{D_i}, and the profile drag of the wing C_{D_w}, which increases rapidly near the stall. At high speeds the wing profile drag again increases, and is the main cause of the poor high-speed performance. At most speeds the head and body contribute about

10 % of the total drag, so an error in the value assigned to C_{Dp} will not greatly affect the results. But of course the results depend critically on the wing-section data, and there is need for more measurements at these low Reynolds numbers, and for measurements of membrane wings.

A further description of the methods of calculating the performance of gliders is given by Treiber (1969).

(iii) *The performance of* Pteranodon

The polar curve of *Pteranodon* is plotted in figure 45, from which it can be seen that the best flying speed is about 8 m/s, at which the sinking speed is 0.43 m/s and the gliding angle 1 in 18.4. The minimum flying speed, based on a maximum lift coefficient of 1.2 is 6.7 m/s, and the highest useful flying speed is about 14 m/s.

The figure also shows curves for the falcon *Falco jugger* (Tucker & Parrott 1970), the albatross (Schmitz 1952) and a man-made glider, the Ka6CR (Merklein & Zacher 1964). It is immediately apparent that *Pteranodon* is an efficient glider, with a sinking speed about half that of any of the other aircraft. The flying speed is also surprisingly low for a creature of this size. Both these properties may be attributed to *Pteranodon's* very low mass; they are particularly suited to slope and thermal soaring in light winds (see §5 (*b*) (i)).

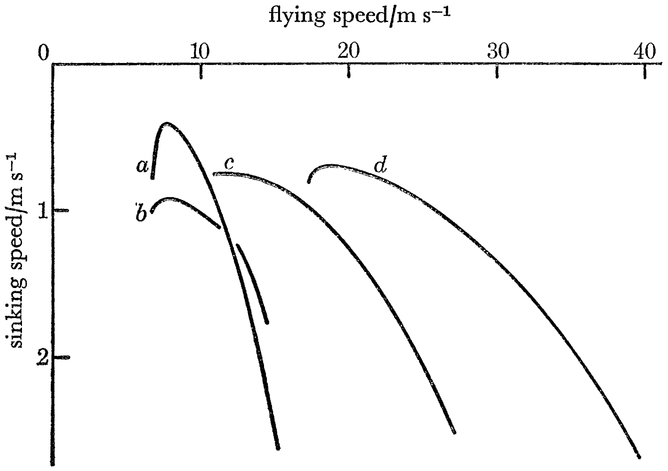

FIGURE 45. Polar curves of (*a*) *Pteranodon*, (*b*) falcon, (*c*) albatross, (*d*) glider Ka6CR.

(*d*) *Powered flight*

Pteranodon is large enough to cast doubt on its ability to fly under power. But it is difficult to see how such a creature could survive without this ability, and the wings are clearly designed to be flapped (figure 46*a*, *b*, plate 24), so it is obviously necessary to investigate the matter.

The power required for level flight is readily calculated from the gliding performance. *Pteranodon's* minimum rate of sink is about 0.42 m/s. Multiplying this by the weight, 16.6 × 9.8 N, gives the rate of loss of energy as 68 W. This power must be supplied by the wing muscles if *Pteranodon* is to fly level.

Suppose the wing muscles weigh 3 kg; this mass of muscle can be conveniently fitted round the reconstruction of the bones of the body and one-fifth of the all-up weight is a typical figure for large birds. Suppose *Pteranodon* flaps its wings through 95°, the full available movement, and that during each stroke the tips move up or down at 45° to the line of flight. Then the time for one complete up and down flap is about 2 s. So each pectoral muscle contracts fully every 2 s. From Pennycuick's & Parker's measurements of the pigeon (1966) the greatest possible energy release in one contraction is 65 J/kg. This is the value for maximum output. Hence the power output of *Pteranodon's* wing muscles is about 98 W. Assuming 80 % efficiency in converting muscular power to thrust, *Pteranodon* has a useful power output of 78 W, compared with a minimum power for flight of 68 W. This is barely sufficient, especially as Pennycuick's & Parker's figure is an upper limit.

In conclusion, it seems that *Pteranodon* was just capable of powered flight, but certainly not of making very steep climbs or hovering. As well as being limited by power output, the strength situation is fairly critical; the loads in flapping are about 50 % more than those in gliding. As the humerus only has a factor of safety of 2, it is obvious that although it is still strong enough to take the loads of flapping the wings, the margin of safety is not high. *Pteranodon* was primarily a glider and had adapted to this mode of flight almost completely, only just retaining the ability to flap the wings when really necessary. This specialization for gliding flight was probably more extreme than in any other pterosaur or bird.

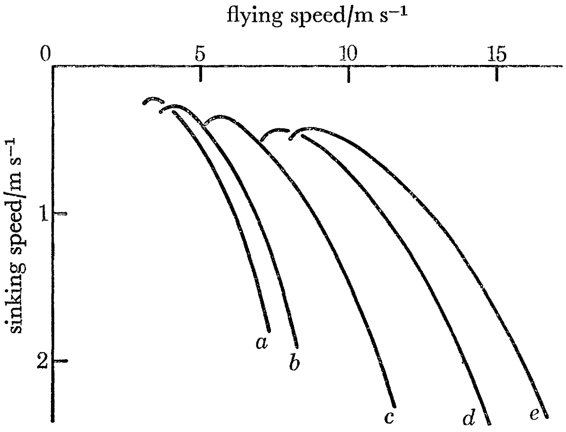

FIGURE 47. The effect of scale on performance. The curves show the computed performance of 'pteranodons' of various wing spans. (*a*) Wing span 1.08 m, mass 0.062 kg; (*b*) wing span 1.74 m, mass 0.26 kg; (*c*) wing span 3.48 m, mass 2.08 kg; (*d*) *Pteranodon* itself: wing span 6.95 m, mass 16.6 kg; (*e*) wing span 9.8 m, mass 47 kg.

(*e*) *Effect of size*

The effect of changing the size of a flying animal is not obvious. It can readily be shown (Pennycuick 1972*b*) that if one enlarges a flying creature without change of shape, then the mass increases in proportion to the cube of the wing span b, but the wing area only increases proportional to b^2. Since the lift coefficient for best performance does not change much, equation (5) shows that the flying speed must be proportional to $b^{\frac{1}{2}}$. So one might expect the animal to glide at the same angle but with increased speed. But the problem is made more complicated because the performance of the wing section depends on the Reynolds number. Having a computer program available, it is easy to calculate the performance of a number of hypothetical pterosaurs, making due allowance for the Reynolds number. Figure 47 shows the result of such a set of calculations for 'scale model' pteranodons.

As expected, the flying speed increases with size, but the gliding angle also improves, due to the increasing Reynolds number. So much so that enlarging *Pteranodon* would not significantly change its sinking speed. It looks as if *Pteranodon* should be made as large as possible.

But there are disadvantages in increasing size. The bending load on the wing spar increases as b^4, while the strength only increases as b^3. So it becomes progressively more difficult to make the wing strong enough. This difficulty is confirmed by the greater engineering refinement of large birds or pterosaurs compared with smaller species. In addition, powered flight becomes more difficult. The wing muscle increases as b^3, but the number of flaps per second must fall, approximately as $b^{-\frac{1}{2}}$. So the power output is proportional to $b^{\frac{5}{2}}$. But the power required for level flight is proportional to $b^{\frac{7}{2}}$. So powered flight becomes progressively more difficult as animals become larger, and there is a fairly well defined upper limit to the size of flying creatures of any particular design. *Pteranodon* is obviously near to this limit for pterosaurs.

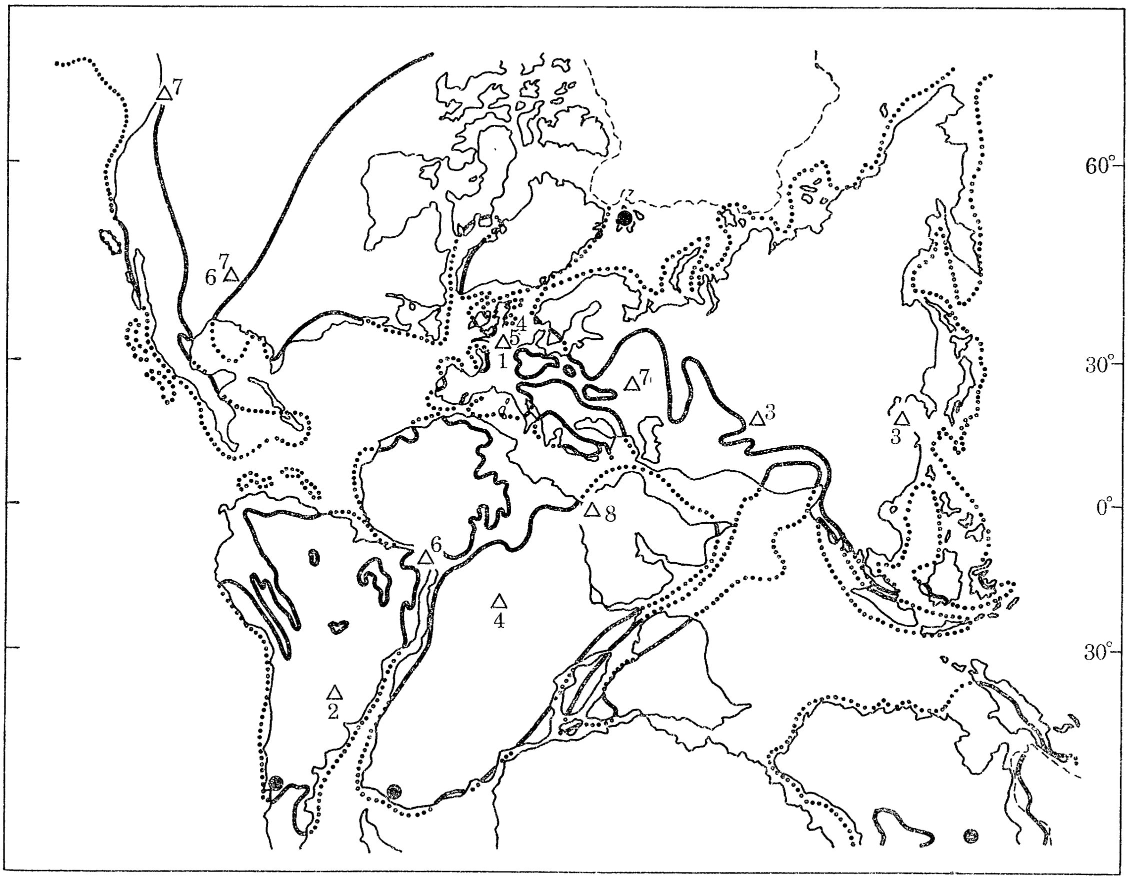

FIGURE 48. Map showing the distribution of Cretaceous pterosaurs. △, pterosaur; ●, northerly and southerly limits of dinosaurs; ▬, land/sea boundary; . . . . ., doubtful land/sea boundary; ——, land/sea boundary at present day.

5. ECOLOGY OF *PTERANODON INGENS*

(*a*) *The environment*

(i) *Distribution of the fossils*

Because of the effect of continental drift, the position of the land during the Cretaceous was not the same as today. The Atlantic Ocean was opening at that time (Allen 1969; Sutton 1968) and Australia had already moved away from the main land mass formed by Eurasia, Africa and South America. A large shallow sea covered most of west and central North America, while the land of Europe was represented by a series of islands. Figure 48 (Briden 1971) shows the positions of the continents during the Cretaceous. Superimposed on this is a map of the actual land distribution (Termier & Termier 1960). The dotted lines are doubtful boundaries between land and sea; the solid lines are more certain.

Places where Cretaceous pterosaurs have been found are marked on the map. These include other genera as well as *Pteranodon*. Ones which appear on the land have all, in fact, been found in marine sediments, throwing doubt on the validity of the land/sea boundaries in these areas. Pterosaurs were present throughout the whole of the Cretaceous from the Neocomian to the Maastrichian. The earliest remains of *Ornithodesmus latidens* (Hooley 1913) (no. 1) show that large, gliding pterosaurs had already evolved by earliest Cretaceous times. *Ornithodesmus latidens* had a wing span of about 5 m and has been found in the Wealden of the Isle of Wight. It lived in the area of the large freshwater Wealden Lake, which was separated from the sea by a barrier of land to the north (Seward 1931).

A new and unusual lower Cretaceous pterosaur has recently been discovered in Argentina, from the Lagarcite formation of San Luis (Bonaparte 1971). This is *Pterodaustro guinazui* (no. 2), represented by a skull and some post-cranial material. The skull has a slender beak armed with numerous short teeth and is peculiar in that the beak is curved upwards to a remarkable degree. Bonaparte suggests that it served for plankton eating.

Another large, gliding, lower Cretaceous pterosaur has been found in China, *Dsungaripterus weii* (no. 3). This species had a 3.5 m wing span and teeth were only retained at the back of the beak (Young 1964). Other fragmentary pterosaurian remains from China have been described by Young. These consist of two ulnae and one second phalanx, all from well-separated localities, suggesting a wide distribution of pterosaurs in that area.

Many species of *Ornithocheirus* (no. 4) are present in the upper Cretaceous of England. Some specimens have been found in the Chalk (Bowerbank 1846) but the majority come from the Cambridge Greensand (Seeley 1870). Well over 1000 broken bones were excavated from localities near Cambridge during the last century. Some of these belonged to very big pterosaurs, perhaps even larger than *Pteranodon*. As well as the many remains assigned to *Ornithocheirus*, the poorly known genus *Criorhynchus* (no. 5) is also present in the Cambridge Greensand (Arthaber 1922). Although so many specimens come from the same area, this is not thought to represent a large colony of pterosaurs living together in one place, but means that the fossils have been concentrated and brought together (Chatwin 1961). The bones show signs of much rolling and abrasion on the sea bed. A metacarpal bone described as being close to the genus *Ornithocheirus* has been found in the Kwanga series (upper Cenomanian–Turonian) of the Belgian Congo (Swinton 1948). The wing span was estimated as about 4.5 m. The Kwanga series was formed by a marine incursion that covered large areas of the Congo basin during the Upper Cretaceous (Haughton 1963).

Several species of *Nyctosaurus* (no. 6) have been found in the Upper Cretaceous Niobrara Chalk of Kansas (Williston 1903). These were highly evolved toothless forms, but smaller than *Pteranodon*, with a 2.5 m wing span. Part of a humerus from the Gramme formation (Maastrichian) of Brazil has been named *Nyctosaurus lamegoi* by Price (1953). As this is said to come from an animal of about 4 m wing span, it is possible that it belonged to *Pteranodon* or *Ornithocheirus* rather than *Nyctosaurus*.

Bones of over 400 individuals belonging to various species of *Pteranodon* (no. 7) have been removed from the Kansas Niobrara Chalk. Most of these are fragmentary, only a few being nearly complete (Eaton 1910). *Pteranodon* remains have also been found in the Upper Cretaceous marine shales of Oregon (Gilmore 1928) and the Senonian Sandstone of the Saratov province in U.S.S.R. (Bogolyubov 1914). This suggests that *Pteranodon* lived over a wide area.

Titanopteryx philadelphia (no. 8) is the largest known pterosaur. It is represented only by one metacarpal bone, but the size of this indicates an animal with a 7 or 8 m wing span (Arambourg 1959). The fossil comes from the phosphates of Jordan, laid down during a marine transgression that occurred in Albian–Turonian times (Daniel 1963).

As pterosaur skeletons are delicate, they are unlikely to be preserved as fossils. The same thing applies to birds. If the fossil record of birds is examined, it is found to contain a high proportion of aquatic species as these are more likely to be fossilized than terrestrial ones. Therefore the fossil record does not represent a typical cross-section of extinct birds. The same may well be true of pterosaurs. Possibly many land-living forms existed of which we have no record, perhaps making use of land thermals in a vulture-like manner. By examining figure 48, it can be seen that Cretaceous pterosaurs had a very wide distribution. Many more specimens must still remain to be discovered in the less-explored parts of the World. Invasion of all the continents would not have been difficult for pterosaurs as they were flying animals. Figure 48 shows that almost all the pterosaur fossils found are in a band within 40° latitude of the Cretaceous equator. It is possible that they either died where they were found, or perhaps drifted on the water before finally sinking and becoming fossilized. Observations on the fate of a dead herring-gull have been made by Schafer (1972). As this bird, like a pterosaur, is light with hollow bones, it did not sink immediately but floated on the surface of the sea for a considerable time. Schafer reports that it floated with the head hanging forward into the water. After 27 days it was still afloat but the legs and sternum had dropped away. On the thirty-eighth day the rest of the animal sank to the sea floor. Twenty-seven days later the body was still held together by ligaments and muscles. The average speed of an ocean current is about 1 m/s. If *Pteranodon* floated for as long as Schafer's herring-gull, the body could be carried 3300 km if caught in a suitable current. It seems likely that drifting like this could have happened as *Pteranodon* was so light and would float easily. Therefore the presence of *Pteranodon* far out to sea need not indicate, as has been suggested (Brown 1943), that it actually flew a long way from the shore.

Pterosaur bones are hollow and air-filled so they are usually crushed flat during fossilization by the weight of sediment above them. The specimens from the Cambridge Greensand are exceptional in not being crushed, although they are broken and abraded. Presumably these bones were broken and became filled in with sediment as they lay on the sea floor, suggesting that they were fossilized in shallow conditions. Turbulence occurs on the sea bed in shallow water, rather than deep quiet water.

(ii) *The Cretaceous climate*

The climatic conditions of the Cretaceous, or any other period of the Earth's history, depend on many factors. These include the positions of the equator and poles, the land distribution and formations, the temperature and flow of water and air and the amount of cloud cover and rainfall. Knowledge of past climates is derived from geological and biological evidence. Rocks indicate the conditions under which they were formed. For example, red beds are produced in hot regions with seasonal rainfall; thick deposits of limestone are laid down in the shallow parts of warm seas (Schwerzbach 1963). As Cretaceous pterosaurs are often found in limestone – for example, the English or Niobrara chalks – it is likely that they lived in these conditions. As well as providing evidence for the temperature at the time of their deposition, the rocks may occasionally indicate other aspects of climate – for example, water currents, wind directions and sometimes rainfall. Physical methods of paleoclimatology include the analysis of the quantity of $^{18}O/^{16}O$ in calcium carbonate, as this ratio depends on the temperature of the water at the time of its formation. Biological evidence for past climates comes from the study of fossil plants and animals. Living species are known to be adapted to particular conditions of warmth or cold, aridity or humidity; related fossil species are presumed to have needed a similar environment.

Several examples of Cretaceous fossil floras have been analysed and show a general uniformity of plant types and hence climate in both hemispheres (Seward 1931). The Wealden formation of England contains a mixture of ferns, cycads, conifers, pines and cypresses, and a similar plant distribution occurred in floras of Japan and South Africa. The lower Cretaceous Kootemai beds of the Rocky Mountains have fossil vegetation resembling that found in beds of the same age in Wyoming, British Columbia and Greenland (Knowlton 1927). At the end of the Lower Cretaceous a period of great change in the floral history of the Earth occurred, with the evolution of the flowering plants. These were soon to dominate the land and largely replace the ferns, cycads and conifers characteristic of the Lower Cretaceous and earlier periods. Upper Cretaceous fossil floras include the newly evolved species, but still show uniformity of pattern over the Earth. Particularly interesting is the Upper Cretaceous Dakota flora found on the land bordering the inland sea of America over which *Pteranodon* flew. This flora stretches north to Alaska, through Kansas and Texas and south to Argentina (Seward 1931). As well as containing some of the earlier ferns, cycads and conifers, a great variety of flowering plants are present, including willows, poplars, oaks, magnolias, hollies, figs and laurels. The Upper Cretaceous fossil plants of Greenland and Alaska indicate the warmth of climate in northerly latitudes. The flora contains mainly flowering plants, including the bread-fruit tree *Artocarpus*, found today only within 20° of the equator. The size of plant leaves and the breadth of the rings of growth in the Greenland flora gives no sign of a physical environment such as we have today in an Arctic land (Seward 1931). The flora of Greenland also suggests that it was a fairly humid area in the Upper Cretaceous; rainfall is also thought to have been abundant in certain other areas, including most of Canada, Alaska, the Alps and Bulgaria, Japan and Mexico (Vakhrameev 1971; Schwerzbach 1963).

The temperature of the Cretaceous seas can be found from the distribution of certain marine organisms. Dilley (1971) has described *Hedbergelle–Heterohelix* foraminiferal associations from the Turonian of northern Alaska and the Senonian of western Canada. These are littoral, tropical genera today and are intolerant of cold-water conditions. Fossil coral reefs also indicate warm water, the optimum temperature for modern reef-building corals being 25–30 °C. They are confined to a band between 30° N and 30° S, but had a far wider latitudinal range during the Cretaceous, ranging up to 54° N in Europe. Animal life on land in the Cretaceous was dominated by large ectothermic reptiles, needing a warm environment for their survival (Colbert 1965); their distribution was world-wide, extending to within 10° of the Cretaceous pole and as far south as the continents penetrated (see figure 48). The presence of pterosaurs themselves cannot necessarily be used to indicate warm climatic conditions, as they were not ectotherms but covered with fur except for the wings (Sharov 1971). The living, non-hibernating Megachiropteran bats are confined to the tropics, but this may only mean that the animals must live in regions where fruit is continually available, not that they are in danger of heat loss through the bare wings. As Cretaceous pterosaurs were mainly piscivorous this restriction would not have applied to them.

There is some limited information on water currents and wind directions in the Cretaceous period. The distribution of foraminifera suggests that a warm current flowed up the west coast of North America and Canada (Dilley 1971). It is interesting that the most northerly *Pteranodon* (no. 7) has been found in this region. There is evidence of a warm Juro-shio and cold Oya-shio and Californian currents (Kobayashi 1963); also, the Gulf Stream is thought to have been already formed, as the warmth-loving rudistic corals lie a few degrees farther north in Europe than elsewhere. Palaeo-wind directions have been studied by Poole (1962), who used geological evidence from the rocks of the southwest United States. These were not Cretaceous, but late Jurassic. At that time the dominant wind direction was northeast. Poole believes that these winds were similar to the northeast trade winds, but that the ancient trade wind belt extended from the equatorial zone to about 43° N, or perhaps that an expanded equatorial belt had displaced the trade winds northwards. The lack of polar ice caps produced higher values of World surface temperature, less zonation of climates and weaker circulation of the atmosphere with slower average wind speeds than today. This situation also broadened the lower latitude wind belts. The difference of air temperature between pole and equator was only 24 °C during the Cretaceous, compared with 48 °C today (Fairbridge 1963). The air temperatures deduced by Fairbridge for a non-glacial period like the Cretaceous, and a summary of Cretaceous water temperatures measured by the $^{18}O/^{16}O$ method applied to belemnites (Nairn 1963), is shown in table 17.

TABLE 17*a*. AIR TEMPERATURES IN CRETACEOUS

latitude/deg	mean sea-level air temperature (Cretaceous)/°C	mean sea-level air temperature (today)/°C
0	31	28
20	29	25
40	23	16
60	14	4
80	9	−16
90	7	−20

TABLE 17*b*. SEA TEMPERATURES IN CRETACEOUS (RANGE OR AVERAGE)

locality	geological horizon	temperature (Cretaceous)/°C	temperature (today)/°C
Crimea	Upper Albian-Cenomanian	19–24	—
Germany and Poland	Albian	24	—
Germany and Poland	Cenomanian	16	—
Germany and Poland	Senonian	20	—
England	Upper Cretaceous	16–23	5–15
Crimea	Campanian	17.6	2–24
Volga and Emba district, U.S.S.R.	Campanian	15–21	—
Tennessee, U.S.A.	Maastrichian	20–27	—

Taking the various lines of evidence into account, the general impression gained of the Cretaceous climate is that it was much warmer than today, with far less contrast in temperature between poles and equator and, consequently, less differentiation of climatic zones. There was a certain amount of variation during the period, particularly in the Upper Cretaceous

(Nairn 1963). The Albian was hot, followed by a decline of average temperature in the Cenomanian; the temperature rose to reach a climax in Santonian times and declined again during the late Maastrichian at the close of the Cretaceous.

(iii) *The Cretaceous fauna*

The animals and plants found associated with Cretaceous pterodactyls are listed in table 18. Because of the bias against preservation of land-living animals, these are mostly aquatic species. Considering the other animals in the environment can give some idea of the possible prey and predators of *Pteranodon* and also which animals would have been in competition with it for the food supply.

Pteranodon was a fish eater. Fossilized stomach contents have been found containing fish scales and bones (Williston 1902); also one specimen has been found 'with the remains of two species of fish and the leg of a Crustacean' in its fossilized throat-sac (Brown 1943). There seems to be no reason why *Pteranodon* should not have eaten invertebrates, but the beak is designed primarily for catching fish (see §5(*c*)). Both cartilaginous and bony fish were present in the Cretaceous seas. The teleosts had undergone radiation to give most of the modern types during the Aptian (Andrews 1967), providing an abundant food supply. Many carnivorous animals were competing with *Pteranodon* for this. Two birds, both piscivorous, have been found: *Hesperornis*, a large diving bird, and *Enionus*, another swimming and diving species. Many marine reptiles also lived off fish, including ichthyosaurs, plesiosaurs, mosasaurs and turtles. The Niobrara chalk contains an abundance of large carnivorous mosasaurs and also many species of flying fish (Williston 1897*a*). Taking to the air, the escape mechanism of the flying fish, was presumably used by them to avoid the mosasaurs.

Pteranodon was a large animal and also skinny, two discouraging features to any potential predator. Possible predators would have included the carnivorous dinosaurs on the land and swimming reptiles in the water. The six genera of mosasaurs in the Niobrara chalk range in size from 5 to 8 m in length and could certainly have eaten a *Pteranodon* providing they could have caught one. Other carnivorous swimming reptiles over a certain size may also have been a hazard. Escape from and defence against predators is discussed more fully in the section on behaviour (§5(*d*)).

(*b*) *The mode of life of* Pteranodon

(i) *Soaring flight*

The performance of *Pteranodon* is characterized by very slow gliding speeds; a low stalling speed and extremely low sink (§4(*c*)(iii)). It is now necessary to try and analyse the way in which *Pteranodon* made use of this performance in the Cretaceous environment. Two things may be suggested immediately; light wind conditions were necessary as *Pteranodon* could not make any progress in a strong wind; and the low sink allowed *Pteranodon* to soar even when very little lift was available.

In still air a glider or gliding animal steadily loses height. The rate of loss depends on the design of the aircraft and the speed at which it is flown. If the animal is to maintain height without flapping it must extract energy from the motion of the air. This process is called soaring and several different techniques are regularly practised by glider pilots (Welch *et al.* 1968).

There are two principal methods of extracting energy from the air. The easiest way is to fly in air which is rising. If the vertical component of the velocity of the air exceeds the sinking speed of the animal through the air, the animal will be carried up, like a man walking slowly

Table 18. Species associated with Cretaceous pterodactyls

pterodactyl	horizon	bird	fish	dinosaur	swimming reptile	invertebrate	plant
Pterodaustro guinazui	Lagarcito formation, Argentina	—	—	—	—	—	gingo, ferns
'Chinese' pterosaurs	Upper Cretaceous, China	—	*Lycoptera*	*Psittacosaurus* also 'a carnivorous dinosaur'	—	insects, crustacea	'plants'
Orni hocheirus	Cambridge Greensand, England	*Enionus baroetti*	many species of fish	*Acanthopholus*, *Iguanodon*, *Trochodon*	*Ichthyosaurus*, *Opthalmosaurus*, plesiosaurs, turtles	many invertebrates	—
Ornithocheirus	Kwanga Series, Belgian Congo	—	*Rhipis moorseli*	—	—	ostracod	—
Nyctosaurus and *Pteranodon*	Niobrara Chalk, Kansas, U.S.A.	*Hesperornis*	*Ptychodus* and many other fish species	—	6 genera of mosasaurs, turtles, *Elasmosaurus*	—	—
Pteranodon oregonensis	Upper Cretaceous, Oregon, U.S.A.	—	—	—	ichthyosaur	ammonite	—
Russian *Pteranodon*	Senonian Sandstone, Saratov Province, U.S.S.R.	—	'sharks'	—	plesiosaurs	—	—
Nyctosaurus lamegoi	Gramme formation, Brazil	—	*Diplomystus*, *Chiromystus*, *Aeriodes*, *Lepidotus* and other species	'a dinosaur'	mosasaur, *Goniopholis*	many gastropods and cephalopods	*Palmo carpon*
Titanopteryx philadelphia	Upper Cretaceous, Jordan	—	—	—	—	*Knemiceras*	—

down the up escalator. When the wind blows against a hill or cliff the air has to rise to pass over it. So there is rising air on the upwind side, providing a reliable area of lift up to perhaps twice the height of the cliff. This is called hill lift and the use of it, by flying backwards and forwards in front of the cliff, is called slope soaring. If *Pteranodon* lived on cliffs facing the prevailing wind, hill lift would always be available for soaring (see figure 49).

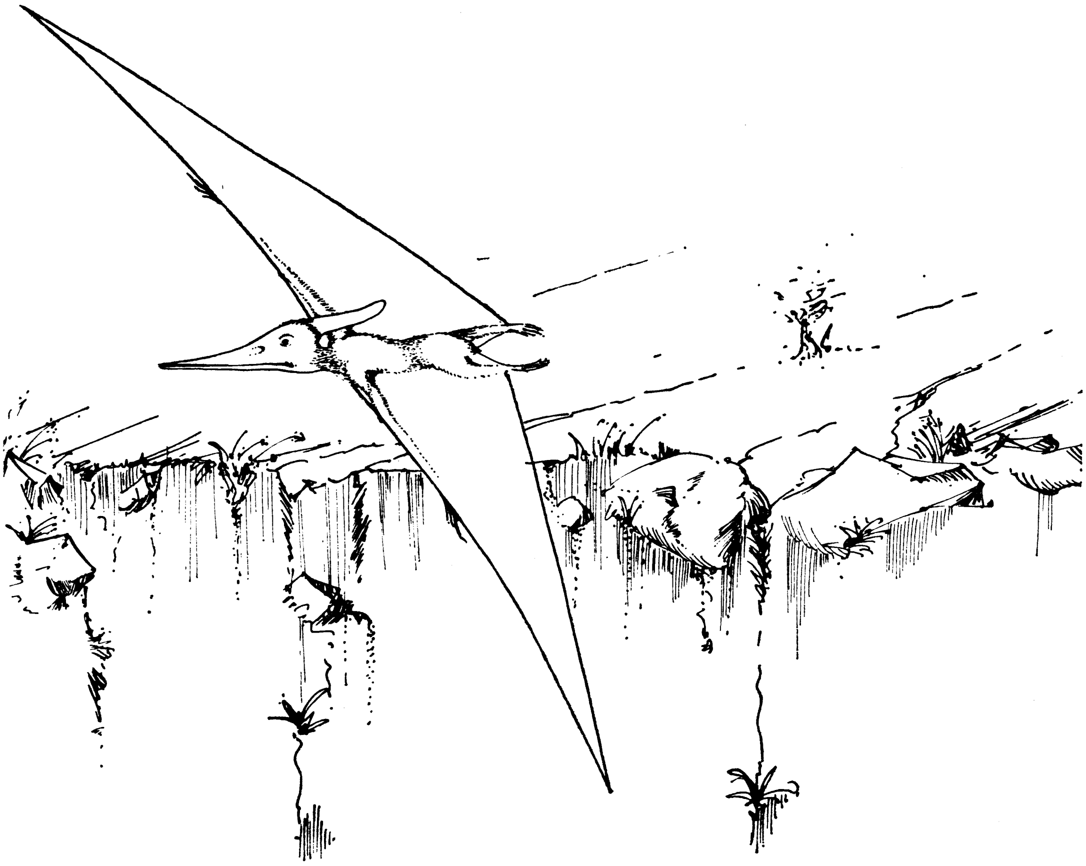

FIGURE 49. *Pteranodon* soaring in the hill lift caused by a cliff.

Slope soaring from oceanic swell is sometimes seen in living birds but appears to have been unsuitable for *Pteranodon*. The average ocean wave has a height of 3–4 m; in storms wave heights of 8 m or more may occur (Barber & Ghey 1969). Wave height in deep water is governed by wind speed and fetch length. It is possible to calculate the lift generated by moving waves from their height, period and fetch (King 1972).

If a light wind is blowing – for example, one of 6 m/s – the waves produced are small and the lift they give is only 0.34 m/s. This is not enough lift to support *Pteranodon*, with a minimum sink of 0.42 m/s. To provide a suitable lift of about 0.5 m/s, waves of 4 m height are required; but such waves are generated by a wind speed of 12 m/s, too high a velocity for *Pteranodon's* slow gliding. So it seems that *Pteranodon* could not have slope-soared waves, because if the wind was light enough to make forward progress, the waves were too small to provide suitable lift; conversely, large waves giving enough lift can only be generated by a wind speed faster than *Pteranodon's* gliding range.

If the air near the ground is warmed, it becomes less dense than the air above it and rises.

Usually the rising air is concentrated in bubbles or columns called thermals whose diameters range from a few metres to a few hundred metres. This lift is used by circling in the thermal to gain height, and then flying straight in the required direction. Thermals are very common over land by day and thermal soaring is used by various bird species (Pennycuick 1972*a*). Convection also takes place at sea when the water is warmer than the air, a common situation in the tropics and during winter in temperate regions. Unlike land thermals, sea thermals increase in strength at night or under cloudy conditions when the air/water temperature differential is greatest. Woodcock (1942) has observed herring-gulls thermal soaring at sea off the East Coast of the U.S.A. and found that they soar when the temperature difference between air and water exceeds 2 °C. *Pteranodon's* sinking speed is half that of a herring-gull, so it could probably have soared with a smaller temperature difference. The mean temperature difference in the tropics is about 1 °C (H.M.S.O. 1967). If this was so in the Cretaceous *Pteranodon* could have soared over the sea on most days. Sea thermals rise straight up in light winds up to 7 m/s but are blown horizontally at higher wind speeds and the convection pattern breaks down. The calm, light wind conditions necessary for the formation of these thermals were far more likely to have occurred during the Cretaceous than today (§5(*a*) (ii)).

The other principal method of soaring at sea is dynamic soaring, extracting energy from the changes in horizontal wind velocity. It is possible to make use of the local variations of wind over waves (Scorer 1958) but these are too irregular for sustained soaring. The wind gradient is more reliable; the air near the sea surface is slowed down by friction, and so the wind increases with height in the first few metres; the change between 1 and 10 m may be as much as a factor of 2.

The albatross (Pennycuick 1972*b*; Jameson 1958) makes use of this by flying upwards into the wind, so it can gain energy from the increasing wind speed at greater heights; then turning and descending down-wind so it can again obtain energy from the decrease in wind as it descends. Detailed analysis (Walkden 1925) shows that the efficiency of this process depends on the gliding angle and on the product $V\mathrm{d}W/\mathrm{d}h$, where V is the flying speed of the bird and $\mathrm{d}W/\mathrm{d}h$ the rate of change of wind speed with height. The albatross, with a gliding angle of about 1 in 18, can climb without loss of airspeed provided that $V\mathrm{d}W/\mathrm{d}h$ is greater than 3.6 m/s^2; since V is about 22 m/s, $\mathrm{d}W/\mathrm{d}h$ must exceed 0.17 (m s^{-1}) m^{-1}, which it frequently does when the wind speed exceeds 5 m/s.

Pteranodon has a similar gliding angle, but its flying speed is only 8 m/s. This means that $\mathrm{d}W/\mathrm{d}h$ must be 0.45 (m s^{-1}) m^{-1} – an unlikely value, especially as *Pteranodon* cannot make headway against strong winds, and so can only fly in winds less than about 7 m/s.

Taking account of the downward section of the flight, which is more favourable, and allowing for the time wasted turning at top and bottom, it would appear that *Pteranodon* might just be able to stay airborne by dynamic soaring in a wind of 7 m/s. But the conditions are so critical, and the margin for manoeuvre so small, that it would inevitably be blown away down-wind. So dynamic soaring, although it might be used occasionally, cannot have been significant in the life of *Pteranodon*.

In summary, the gliding performance of *Pteranodon* fitted it for slope-soaring cliffs but not dynamic soaring. Land thermalling, although possible, would not have helped *Pteranodon* as a fish eater. The slow gliding and low sink of *Pteranodon* were well adapted to the climatic conditions of the Cretaceous, making use of the warm conditions and light winds of that period.

(ii) *Take off and landing*

The mechanism of take off in pterosaurs has never been fully explained (Khozatsiy & Yurbev 1964). The problem must be considered for *Pteranodon* when taking off from both land and water, and in calm and windy conditions.

Birds can stand bipedally, giving them the advantage of holding the wings and the centre of gravity high above the ground. Primitive pterosaurs may have been able to assume this stance, as they have the hind limbs and posterior parts of the body well developed; the Jurassic form, *Nesodactylus hesperius* shows this well, having strong limbs as well as large wings (Colbert 1969). The trend in pterosaur evolution was to reduce the size of the pelvic girdle and legs as the animals adapted to an inverted hanging posture. During this process anatomical changes occurred that made bipedal standing impossible. This is particularly true of *Pteranodon*. The legs are long and evolved to have great freedom of movement with a corresponding lack of strength (Williston 1891). As in the bat, the legs are articulated sideways, enabling the knee to be directed either ventrally or dorsally; Williston (1903) considers that this articulation of the caput femoris in the acetabulum did not allow the femora to be brought parallel to each other without dislocation. Bipedalism is excluded because of the shortening of the post-acetabular part of the pelvis. It was not large enough to have furnished the posterior leg muscles with adequate leverage to hold the animal up (Saint-Seine 1955). Thus, the idea that *Pteranodon* could stand on its rear legs and spring from the ground at take off, as suggested by some early palaeontologists (Dennis 1861), is clearly impossible.

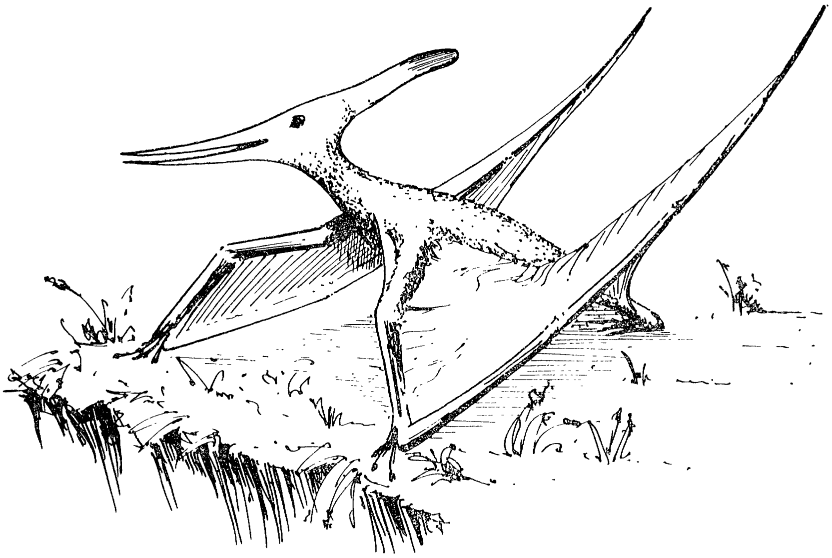

FIGURE 50. *Pteranodon* standing with wings partly folded.

Most birds can take off from their upright position in still air by flapping the wings – for example, pigeons (Pennycuick & Parker 1966). Other birds may need to run to gain air speed to provide the necessary lift. Both these methods were impossible for *Pteranodon*, because it could neither stand bipedally nor run (§5 (*b*) (iii)). When standing on land *Pteranodon* supported itself by the small wing claws at the front and the legs and ventral surface of the body posteriorly (figure 50).

We have observed this kind of quadrupedal stance in the flying fox, *Pteropus giganteus*. It is interesting to note that they can take off from this position in still air and fly upwards at about 60° to the horizontal. We do not fully understand how this is done but it seems unlikely to have occurred in *Pteranodon* because of the power output needed. There would also have been a risk of damaging the wings on the first downstroke. Such a take-off method could conceivably work if the animal was on some raised object on the land, allowing the wings a full flap clear of the ground. When *Pteranodon* has its wings at the top of the upstroke the centre of gravity is high because the weight of the wings is held up. One flap will bring *Pteranodon* up to the position of the centre of gravity, a considerable way above the ground.

As *Pteranodon* could not run to take off, it would have needed a wind speed above the stalling speed of 7 m/s to become airborne from the quadrupedal stance. Take-off could then have been achieved by pointing into the wind and holding out the wings (figure 51, plate 25). This take-off method is seen in albatrosses today, although they stand bipedally while doing it.

The take-off methods so far described were probably not common. The usual method of launching from the land would have occurred from the normal inverted resting position, hanging by the feet from a high object such as a cliff edge or rocky ledges (figure 52).

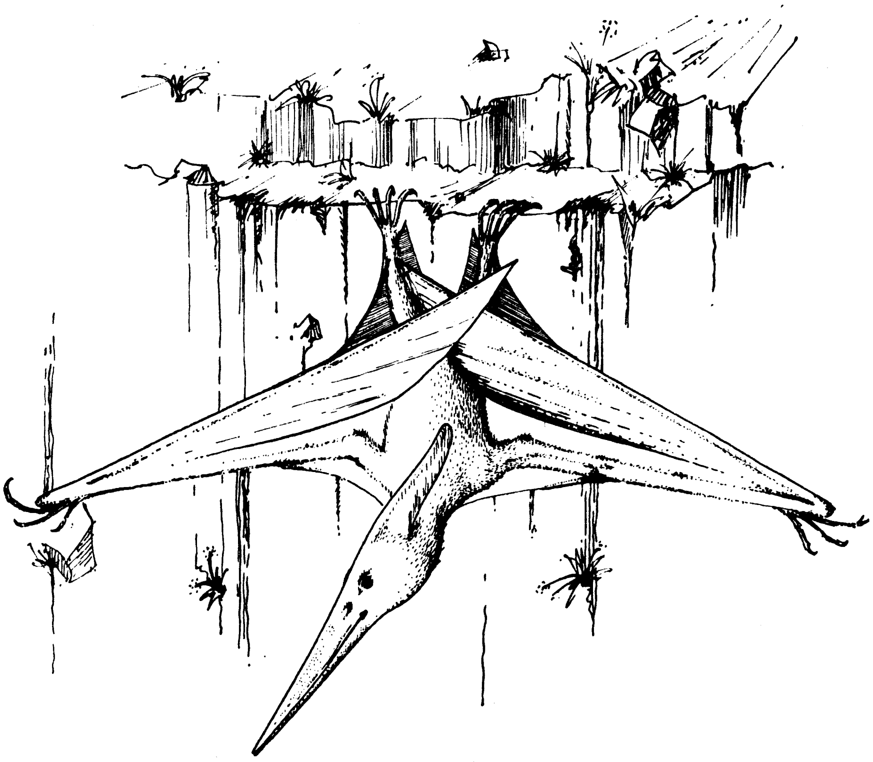

FIGURE 52. *Pteranodon* in normal resting position hanging by the feet.

Pteranodon would only have to spread its wings and let go with its feet to be flying free, launched into the hill lift where the wind blew over the cliff. This method of take-off has been suggested many times in the literature; for example, it is the 'parachuting long leap' of Khozatsiy & Yurbev (1964).

Take-off from a flat water surface in still conditions would present the same problem as take-off from land. Flapping would be necessary to become airborne and the wings would slap the water surface on the downstroke. If waves were present, the situation becomes much easier. The animal could wait until it was on the crest of a wave and either flap its wings or launch itself as a glider if sufficient lift were present (figure 53). This was suggested by Brown (1943), who wrote: 'if they are considered as gliders, the great expanse of wing could easily have lifted their light bodies from the crest of a wave'.

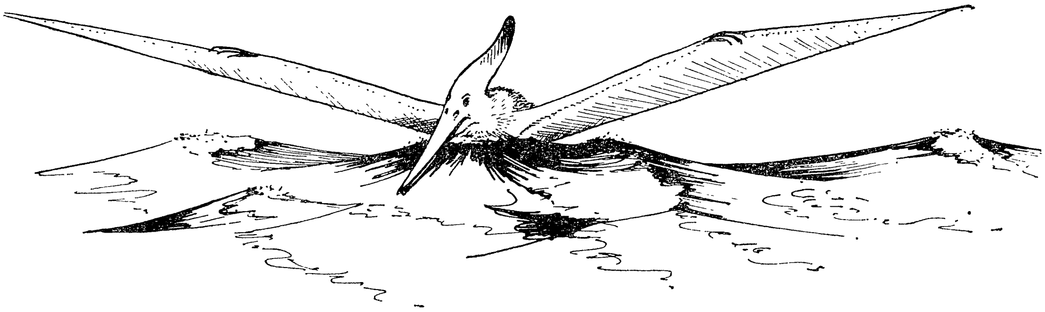

FIGURE 53. *Pteranodon* launching itself from the crest of a wave.

Landing presents fewer problems than take-off. The chief difficulty envisaged by palaeontologists was that in landing *Pteranodon* would have smashed its delicate skeleton (Halstead 1969), but *Pteranodon* landed very slowly. It had a stalling speed only 7 m/s, and since, like birds, it would have landed into wind, the touchdown speed would have been even slower (Bramwell & Whitfield 1970). Ground cover in the Cretaceous consisted of ferns, rather than grass, making a springy surface to land on. The fur, as in *Sordes pilosus*, may have been particularly dense and long on the chest (Sharov 1971), providing further insulation against the shock of landing. *Pteranodon* would probably come in to land on the cliff-top, rather than in a tree, as few trees are either large enough or clear of wing-tearing branches. Before touchdown it would circle and turn to land on the cliff-top into the wind blowing from the sea.

Actual landing would involve a process somewhat like that envisaged by Hankin & Watson (1914), in which *Pteranodon* 'alighted on its feet and then fell over on its stomach'. Except that, as its legs are too weak for this (§3(*d*)), it must have landed directly on its stomach, holding its wings high to avoid damage. After landing the wing tips would be folded over the back, and the animal would scrabble forwards to its comfortable hanging position over the cliff edge.

(iii) *Movement on the ground*

In §2(*a*) the articulations of the wing bones were described and the direction and degree of movement possible at each joint deduced. This information was then used to find the positions of the wings in gliding flight and flapping flight. It can also be used to help understand wing movements not associated with flight – for example, those used in locomotion over the ground or folding the wings when at rest. Photographs of an articulated model demonstrate certain positions in this section. The angles and movements of the 'bones' of this model are those described for *P. ingens* in §2(*a*)(iv).

Wing folding in *Pteranodon* is unlike that of a bird or bat. In these, the humeri can be brought parallel against the body and the wings folded completely. Hankin & Watson (1914) pointed out that this was impossible for *Pteranodon* because the shoulder joint forms a hinge. Our own examination of the articulation confirms this. The wing is, in fact, folded at the wing-metacarpal/first phalanx joint. About 125° movement is possible here, allowing the outer part of the wings to be folded across the back. Figure 57, plate 25, shows that the wing tips clear the back easily in this position, with *Pteranodon* resting the small wing claws on the ground.

If the wing membrane of pterosaurs was as elastic as that of bats, it would not fall into folds running fore and aft when *Pteranodon* brought the wing tips over the back. We have found that the membrane of *Pteropus giganteus* will expand and contract by a factor of three in the spanwise direction before any folding occurs. Further contraction of the membrane then causes first small-scale crinkling and finally overall folding. When the wings of *Pteranodon* are folded the trailing edge of the membrane measures 0.6 of its length when fully stretched in the gliding position. The wing membrane would therefore still be taut along its trailing edge with the wings folded, if its elasticity matched that of living bats. Some spanwise wrinkles in the membrane could be expected when the wings were folded, if the elasticity of the membrane was directional as in bats. Their membrane has great spanwise elasticity, but little fore and aft. *Rhamphorhynchus phyllurus* shows the imprint of the membrane clearly in the rock (Marsh 1882). It appears to be crinkled and folded even though the wings are outstretched. This could not have been the case in life, or flight would not be possible. We have found that *Pteropus* membrane will lose its elasticity and become brittle and crumpled if it dries up. This occurs rapidly after death unless the membrane is kept deep-frozen and protected from desiccation.

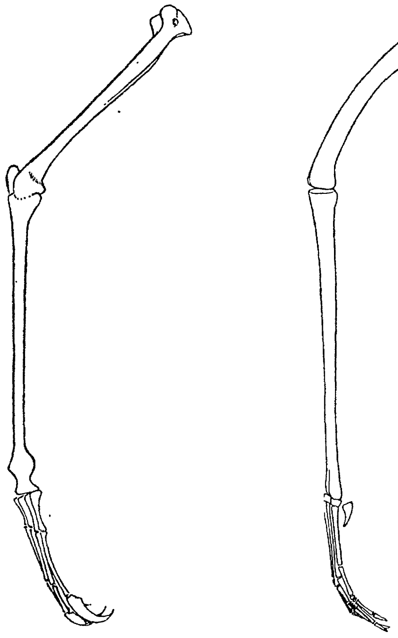
(*a*) (*b*)

FIGURE 54. Drawing of the legs of *Pteropus giganteus* (*a*) and *Pteranodon ingens* (*b*) scaled to same size.

Figure 54 shows the leg skeleton of *Pteranodon ingens* (Williston 1897*b*) compared with that of *Pteropus giganteus*. The overall similarity in design is striking. Articulation of the leg with the pelvic girdle is the same in both. *Pteranodon* has an almost spherical caput femoris forming a ball-and-socket joint. This gave great freedom of movement of the legs; and the posterior position of the acetabulum allows the femur to be directed ventrally or dorsally (Williston 1897*b*).

The same description could be used for the femur and its articulation in the bat. This design serves several purposes. The general mobility of the legs allows the bat to reach any part of its anatomy when grooming with the feet; the lateral articulation of the femur means that the legs can be moved dorsally or ventrally in flight to alter the wing profile; the articulation directs the knee joint sideways, allowing the foot to be rotated to enable the animal to hang either with its front or back to a vertical surface. Both positions are assumed with equal ease. *Pteranodon* would probably have hung with its front towards the cliff, because this is the easiest starting position for take-off. There is no anatomical reason why it should not hang the other way round, but since the inner wings cannot be folded, changing from one hanging position to the other would be very difficult.

The measurements of the legs in *Pteranodon ingens* and *Pteropus giganteus* are shown in table 19, together with the ratios of the femora, tibiae and feet.

Table 19. Leg bone measurements compared for *Pteropus giganteus* and *Pteranodon ingens*

	Pteranodon ingens		*Pteropus giganteus*	
	length/mm	ratio	length/mm	ratio
femur	260	1	62	1
tibia	362	1.39	74	1.19
foot	173	0.67	50	0.81
phalanges only	78	0.3	40	0.65

The measurements of the bones of the longest digit of the foot (no. 3 in both cases) are also given and are illustrated in figure 55.

measurements of bones of 3rd digit

	Pteranodon ingens length/mm	*Pteropus giganteus* length/mm
metatarsal	95	10
1st phalanx	35	12
2nd phalanx	4	15
3rd phalanx	27	13
4th phalanx	12 (claw)	—

The measurements of the bones of the longest digit of the foot (no. 3 in both cases) are also given and illustrated in figure 55. The femora and tibiae are quite similar in relative length, the tibia being slightly longer in *Pteranodon*. The feet in the bat are relatively larger and this is even more pronounced if the phalanges only are considered. The metatarsals are long in *Pteranodon*, accounting for over half of the total foot length. Functionally, the metatarsals are not part of the hook formed by the phalanges (figure 55), but are straight bones parallel with the tibiae when the animal is hanging. They add to the length of the lower segment of the leg rather than act in grasping.

If the actual length of the phalangeal hook is compared in *Pteranodon* and *Pteropus*, the bones measure 78 mm in *Pteranodon* and 40 mm in *Pteropus*. As the total leg length in *Pteranodon* is 4.3 times that of the bat, it is obvious that the phalangeal hook in *Pteranodon* is proportionately small. This can be explained by considering the uses to which a hanging foot is put. It must obviously be strong enough to support the animal's weight, but its actual size is determined by the objects it has to grasp in the environment in everyday life. This would be little different for *Pteranodon* hanging on a rocky cliff surface than for *Pteropus* in a similar posture. A relatively small foot would have allowed *Pteranodon* to use small crevices and ledges for hanging, thus exploiting all resting places in its environment. It is also of more use in manipulation of objects (for example, food) as a small foot can wrap closely round small objects. Finally, a small foot adds less weight.

As *Pteranodon* could not stand bipedally (§5 (*b*) (ii)) it must have supported itself on land by resting the wing claws on the ground, as well as the legs. The legs were positioned wrongly and were not designed to lift the animal clear of the ground, so the ventral surface of *Pteranodon* must also have rested on the surface when standing and walking. We have observed that this is so in *Pteropus* and, for the same reason, the position and weakness of the rear limbs. Locomotion over the ground in *Pteropus* is a dragging of the body over the surface rather than proper walking using four supports. This method of getting about is rarely used except in emergencies.

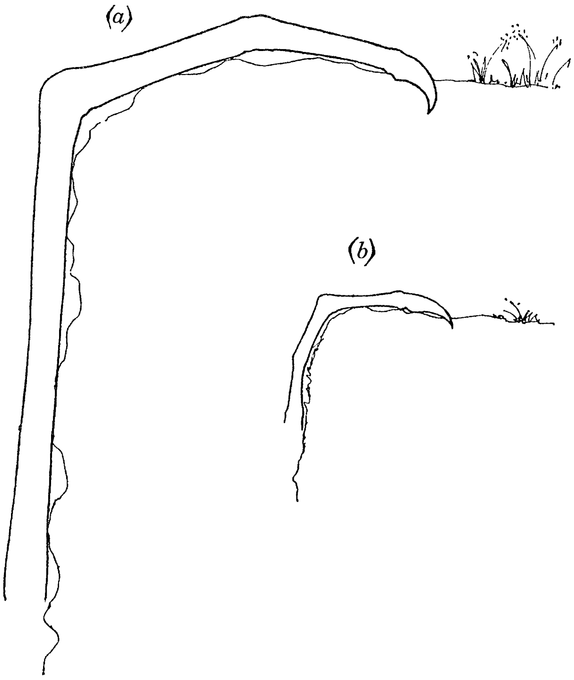

FIGURE 55. The feet of *Pteranodon ingens* (*a*) and *Pteropus giganteus* (*b*) drawn to the same scale.

Movement over the ground is even more difficult for *Pteranodon* because the shoulder joint is a hinge allowing only up and down movement. The lack of forward mobility of the humerus limits the 'stride' of the front limb to only 16 cm.

Pteranodon cannot reach forward and grip with the wing claws to pull itself along so it must have used its feet.

Pteranodon probably slid along on its stomach by reaching forward with the legs, gripping the ground with the feet and pulling itself along. Figures 56 and 57, plate 25, illustrate this. In figure 56 both legs are swung forwards together; alternatively (figure 57) one leg could be swung forwards, followed by the other. These illustrations demonstrate the length and flexibility of the rear limbs. During this crawling the weight is supported by the body and wing claws. The legs give the forward movement by pulling, to which process they were well adapted; hanging is, in fact, a pull (taking the weight in tension). Pushing with the legs occurs in normal quadruped or biped locomotion and suits limbs designed for standing and supporting the weight of the animal in compression.

Movement over the ground was obviously the worst mode of locomotion for *Pteranodon* and probably only occurred over short distances; for example, in scrambling over the cliff to assume the hanging position after landing.

(*c*) *Feeding*

As *Pteranodon* was primarily a glider, its energy demands would not have been as high as those of a continuous flapping flyer. The metabolism of pterodactyls was as advanced as that of other warm-blooded animals (Seeley 1876; Broili 1938; Sharov 1971), and the food requirements would have been similar to those of any homoiotherm of the same mass and size. Food was probably sought daily, rather than at the infrequent intervals often seen in large, living reptiles.

Pteranodon was a fish eater (§5 (*a*) (iii)). The sense involved in finding prey would be sight, rather than smell or hearing. *Pteranodon* had large eyes and the brain was as well developed as that of a bird (Seeley 1869; Edinger 1941). Fishing birds catch prey by various methods. The bird may plunge completely into the water and swim after the fish; or alight on the surface and feed; or fish on the wing while flying.

Pteranodon could not possibly have plunged in to feed, as it was unable to completely fold the wings to assume the necessary streamlined shape. The water must be entered at a high speed and the bird must be fairly dense to stay submerged for this method to be feasible. Neither of these factors apply to *Pteranodon*. Floating on the sea and feeding by plunging the beak into the water could have occurred. Movement of the head and neck alone give a range of 1.2 m. There are certain disadvantages to feeding in this manner. Landing and take-off from the sea would be necessary, while floating *Pteranodon* would have been vulnerable to predators below; fast-swimming fish could not be pursued if *Pteranodon* was stationary on the water surface.

Pteranodon seems to have been best adapted for fishing on the wing. The slow flying speed would have enabled it to glide over the sea at about 8 m/s, just above the stalling speed. If the beak was then plunged into the water and a fish caught, *Pteranodon* could keep on gliding with very little loss of speed. The body would continue forward without check while the neck bent downwards and forwards underneath the animal before the beak was withdrawn (figure 58).

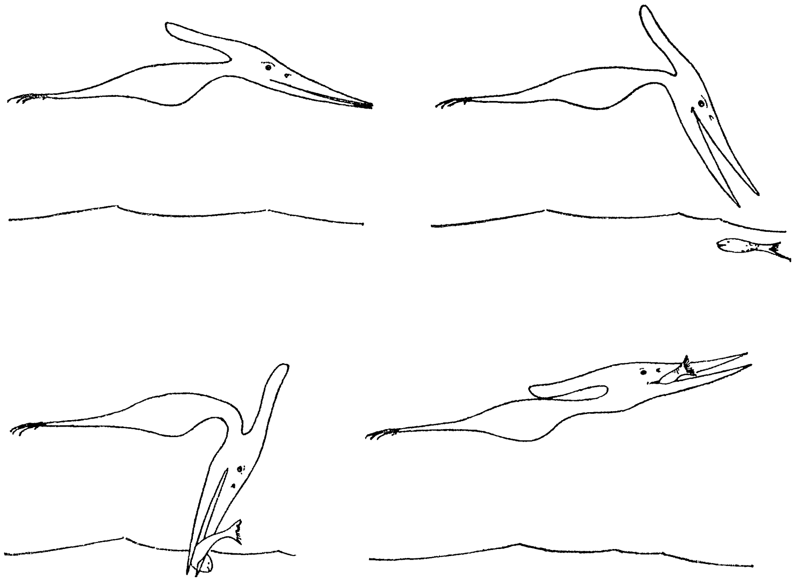

FIGURE 58. Diagram illustrating the method used by *Pteranodon* when fishing on the wing.

The neck bones were adapted to being flexed in this manner (Eaton 1910). Williston (1903) wrote that 'the neck was strong with limited torsion, but with great power and effectiveness in the anterio-posterior direction thus rendering the beak very effective in striking'. The narrow beak gives minimum disturbance and hence has low drag when it enters the water.

As well as the method indicated in figure 58, in which both upper and lower jaw were plunged into the water, the beak could have been used as a scoop, by dropping the lower jaw and using it to catch the fish, which was then passed straight into the throat-sac, but this is unlikely because of the greatly increased drag of the beak used in this way. Moreover the narrow beak would have made it rather easy for a fish to escape, and *Pteranodon* had no fine teeth which are needed for filter-feeding on smaller creatures.

Once the fish was caught it would have been swallowed or stored in the throat-sac. In §2(*d*) it was calculated that a heavy load carried at the tip of the beak or in the feet would upset the centre of gravity of *Pteranodon* and make gliding impossible. Very light loads could be carried like this, but the likely method was to swallow the food or store it in the throat-sac. Neither of these positions of the extra weight would upset the gliding performance to any extent.

(*d*) *Physiology and behaviour*

It has long been suggested that pterosaurs, as active flying animals, were homoiotherms and so could not have been reptiles. Seeley (1876) suggested that they be classified in a separate subclass, the Ornithosauria, to emphasize that their level of organization was as advanced as that of birds or mammals. In 1938 Broili examined *Pterodactylus* and found traces of hair, but it was not until 1971 when Sharov published his account of *Sordes pilosus* that the furry body covering of pterosaurs became accepted. The imprint of the hair of *Sordes pilosus* shows that it was thick and covered the whole animal except for the wings and lower legs. As *Sordes pilosus* is Jurassic it must be presumed that the fur evolved early in pterosaurs and later may have altered to suit different modes of life in various species. *Pteranodon*, as an ocean-going animal, would be best served by dense, short and smooth fur provided with some method of keeping it dry, possibly by the use of oil to repel water and trap air in the fur. The fruit-bat *Pteropus giganteus* has just such a mechanism, the oil being produced by glands in the neck. It is spread over the fur and wings by the feet and mouth. This waterproofing allows the bat to swim if necessary, but is really used to keep the animal dry in heavy tropical rain. The oily surface of the membrane causes the water to form droplets and roll off the wings. It is important that this happened in *Pteranodon* when it was on the water surface, to make take-off easier. It is interesting to note that the legs of *Pteranodon* are flexible and long enough to reach everywhere on its body, except for the wing claws and parts of the wing adjacent to them. These can be reached by the beak, and the beak and feet can be brought in contact by bending the neck. By these movements all parts of the body could be reached when grooming. As the inner part of the wings cannot be folded, the small wing claws could not have helped in grooming, but only in locomotion and hanging.

The colour of *Pteranodon* may have been related to camouflage when feeding. Most ocean flying birds are white, because this cannot be seen easily when viewed from under the water. But it is likely that the wings of *Pteranodon* were dark, rather than light. Some pigment would be necessary for protection against damage by the ultraviolet rays in sunlight.

It is impossible to know if *Pteranodon* was a solitary or social animal. The great accumulation of bones in the Cambridge Greensand were brought to one place after the death of the individuals (Chatwin 1961), so they do not provide evidence of many animals living together. But it seems probable that *Pteranodon* lived in colonies, as suitable hanging places could not have occurred everywhere and where they were available it is likely that they were filled. This could lead to just an aggregate of animals or a true social colony in which the individuals interacted with each other. In such a collection of pteranodons, each one would need a resting space as large as itself with outstretched wings in case take-off became necessary. Ostrom (1971) has recently shown that some dinosaurs were gregarious and moved about in herds, possibly migrating after food. Migration probably did not occur in *Pteranodon*, as the climate of the Cretaceous, and hence the supply of fish, was uniform. The migrating dinosaurs were large herbivorous forms who appear to have roamed in the manner of elephants, consuming the vegetation as they went. Forming a herd in these dinosaurs gave them protection, and social organization could have served the same function in pterosaurs, that of safety from large predators. These would be carnivorous dinosaurs on the land and predaceous swimming reptiles in the water. Escape from land predators would be easy if *Pteranodon* was in the normal hanging position, as it could simply take off. If some warning noise was given – for example, an alarm cry – this could have alerted other animals to the danger. Escape from the quadrupedal position on land would not be easy as *Pteranodon* could not run away and could only take off if suitable wind conditions were prevailing (§5 (*b*) (ii)). Some means of defence would be needed. We have observed that *Pteropus giganteus* uses wing displays to appear large when frightened, but this would not be possible for *Pteranodon* unless hanging, as it could not stand on its back legs to fling the wings out. The most likely method of defence would be striking with the beak at the attacker. Possibly carnivores did not feed on *Pteranodon* if other animals were available, as there would be little solid meat to eat on them except for the flight muscles.

Intraspecific aggression need not necessarily be low in *Pteranodon* because of the risk of damage to the wing membrane. If it had similar elasticity and mechanical properties to that of bats, it would not be easily torn. Occasionally *Pteropus* does damage the wing membrane when two males are competing for territory and dominance. The holes in the wings, which may be quite large, slowly heal as the membrane grows together. Flight is possible even with quite big holes.

Reproduction in *Pteranodon* poses several problems. Whether eggs were laid or young born alive is not known. In either case they must have produced small young as the pelvic opening has been reduced in size as the back parts of the body became smaller in the course of pterosaur evolution. Heavy unborn young would also be a great disadvantage to a gliding animal that had lost weight by all possible means to obtain a low wing-loading. Mating probably occurred in the hanging position, as in bats, as this would have been safer than standing on the land.

As *Pteranodon* was homoiothermic, the eggs or young must have been kept warm. Their small size also indicates that feeding of the young by the adults must have been necessary. Parental care may have been prolonged until the young were able to fly and feed themselves. The young may have hung from the body of the adult, clinging to the fur. It is interesting to note that Sharov (1971) mentions that the fur of *Sordes pilosus* is particularly long on the chest region. Because of the problem of carrying the weight of young pteranodons, it is likely that they were left in the roosting places while the adults hunted for food. Possibly the food was stored in the throat-sac and brought back to feed the offspring. If this was the case, colonial organization would again have been of benefit, as the young would be much more vulnerable as solitary individuals than in a large group with some adults left behind in the colony while others sought food.

(*e*) *Extinction*

Pterosaurs were present until the very end of the Cretaceous, existing right into the Maastrichian. Then, along with dinosaurs and many other reptiles, they became extinct. If the extinction of *Pteranodon* was part of the general Cretaceous extinction, then it cannot yet be explained as none of the many explanations put forward cover all the facts.

If a specific reason for the extinction of *Pteranodon* is sought, then change in climate could easily account for it. *Pteranodon*, with gliding speeds between 7 and 14 m/s was superbly adapted to light wind soaring. If the average wind speed had risen by only 5 m/s this alone would make *Pteranodon's* mode of life impossible. Such a change in wind speed could be brought about by a cooling of the climate giving greater differentiation of temperature between poles and equator, leading to faster overall wind speeds. The birds survived the Cretaceous extinction. It could be significant that they are faster flyers than *Pteranodon*, and would have been able to deal with stronger winds.

Another reason that may be suggested is competition with birds for the food supply and resting places. But birds had always coexisted with *Pteranodon* throughout its history and there is no reason why they should dominate pterosaurs at the end of the Cretaceous. Sometimes it is suggested that birds are better flyers, and that the feathered wing is intrinsically superior. This is not the case; as the calculations of performance show (§4 (*c*)), *Pteranodon* was adapted to be an extremely efficient light-wind soarer, able to stay aloft in conditions that defeat present-day birds. For its particular mode of flight it had no equal, but birds excel in other ways, for example in hovering flight or fast dynamic soaring. Other authors consider that *Pteranodon* had 'outgrown its strength'; for example, Brown (1943) wrote: 'Nature had carried it too far and made her animated flying machines too fragile, and this may have been what spelled their defeat.' But although the bones are remarkably light and thin, they are fully strong enough to withstand the forces acting on them (§3 (*c*)). It is likely that *Pteranodon* became extinct because it was so extremely specialized for a particular mode of flight only suitable in settled, light-wind conditions, but it was certainly designed well in every way to suit its chosen mode of life.

6. ENGINEERING AND PALAEONTOLOGY

We chose to work on *Pteranodon* in this paper as it was the end product of pterosaur evolution and the largest flying animal ever to exist. It was therefore likely to show a high degree of refinement of aerodynamic and structural design, making it a most interesting subject for engineering analysis.

Examination of the fossils allowed the gliding position of the wings to be determined, as well as the movements possible at the articulations of the bones. The leading edge of the wing was found to have a curved shape to prevent twist and loss of efficiency in flight. A geometrical method was used to determine the mass of *Pteranodon ingens* and it was found to be extremely light for its size, weighing only 16.6 kg. The centre of gravity was calculated and shown to be in line with the centre of lift of the wings. Many authors have remarked on the fragility of the bones of *Pteranodon*, and doubted that it was strong enough to be a successful flyer and even suggested that it may have become extinct for this reason. In §3 the strength needed was estimated and the actual strength of the bone tendon system supporting the wing calculated. It was shown that the wings were adequately strong, even though in the course of its evolution

Pteranodon had reduced mass by all possible means, including loss of bone and muscle. The material retained was distributed to give maximum strength combined with lightness.

From the mass and shape the gliding performance was calculated. *Pteranodon* was found to be superbly proficient at slow-speed soaring, with sinking and stalling speeds lower than present-day flying vertebrates. Powered flight was also possible, but not as the usual method of progression. Slow-speed gliding was shown to be well suited to the light-wind conditions of the Cretaceous. Possible functions of the crest were examined and wind-tunnel tests showed that its primary purpose was weight-saving, by reducing the load on the neck muscles.

Various aspects of the mode of life were investigated and a composite picture of the way the animal survived in its environment built up. Certain suggestions were put forward on the behaviour and possible social organization of *Pteranodon*.

The application of engineering to an extinct animal is obviously more difficult than using the same technique on a living one. Parts of a fossil animal are missing, limiting the available information. But much light can be thrown on the way the missing parts must have functioned, as *Pteranodon* was a working flying machine and must have obeyed the laws of mechanics and aerodynamics to have been viable. It was found, in fact, not only to function, but to have been an extremely efficient and successful gliding animal. *Pteranodon* possessed a high degree of beautiful and sophisticated engineering design. We have found it striking that any discrepancy in the results was always due to a mistake in measurements or calculations, rather than an aerodynamic fault in *Pteranodon*, and remeasurement of the fossils or recalculation corrected it.

The interdisciplinary approach used included not only engineering and palaeontology, but other sciences, such as palaeoecology, meteorology and low-speed aerodynamics. It included observations on flying animals, both those made by us and others.

This work would not have been possible without the help of experts in these fields, many of whose names appear in the reference list. We are particularly indebted to our colleagues and students in this department for assistance and discussion, for the loan of the wind tunnel and the housing of our colony of *Pteropus*. We thank the Sedgwick Museum, Cambridge, the University Museum, Oxford, the British Museum (Natural History), London, and the Peabody Museum, Yale, for the pterosaur specimens. Most of the illustrations were drawn by John Smith and the photographs taken by John Simpson. The manuscript was typed by Doreen George. One of us (C. D. B) is indebted to the Science Research Council for a research grant.

While we were writing this paper we were told about the excellent lectures on pterodactyls given by D. M. S. Watson, which we were too young to have heard, and we tried unsuccessfully to obtain the unpublished notes that he was said to have left in Cambridge. Shortly after our paper was completed D. M. S. Watson's notes turned up, but only after two vain searches, among some other material. It is fascinating to see how much progress he had made since Hankin & Watson (1914) and how often his views are similar to our own (see pages 583 and 587). If he had completed his paper he would have anticipated our work by 40 years.

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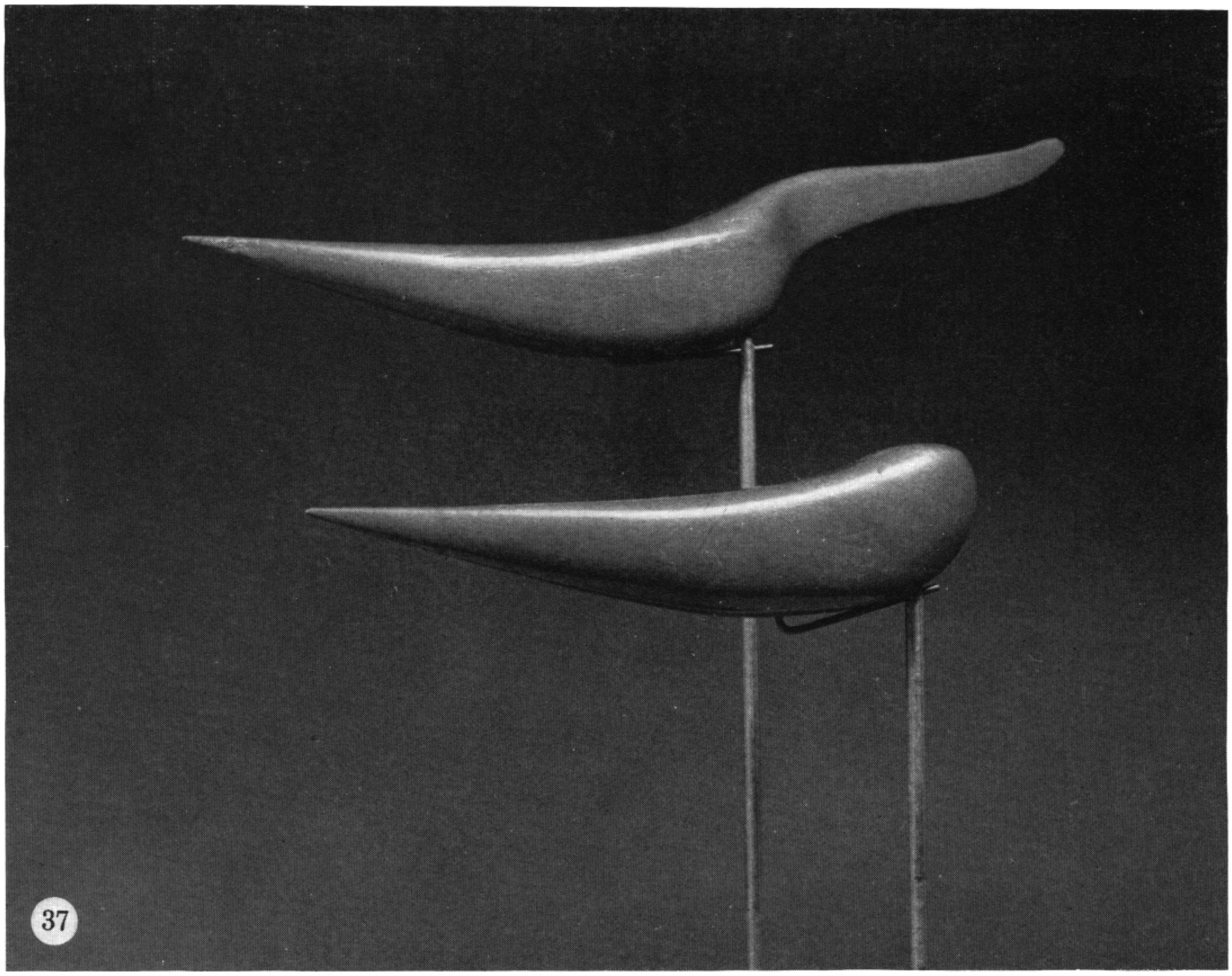
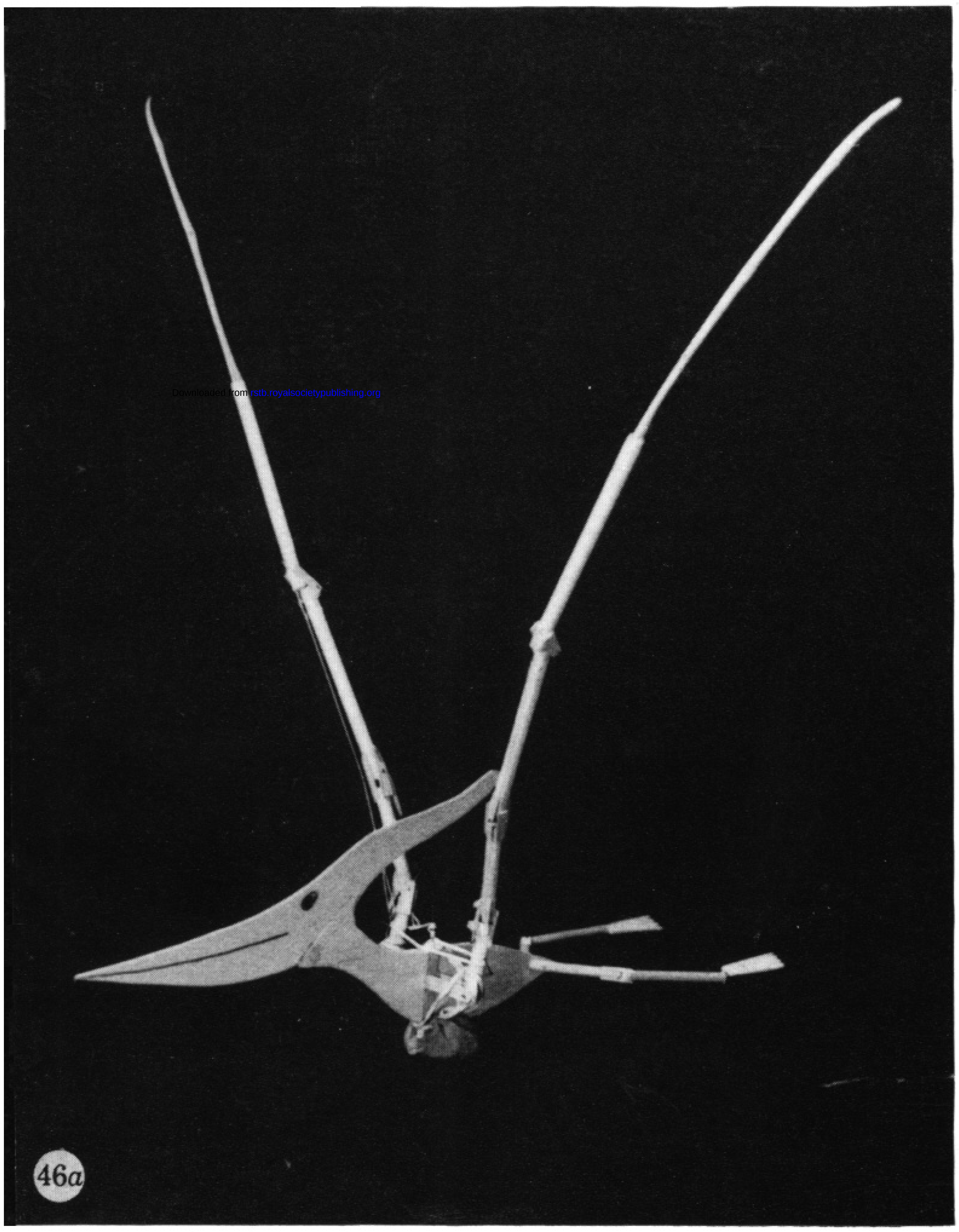




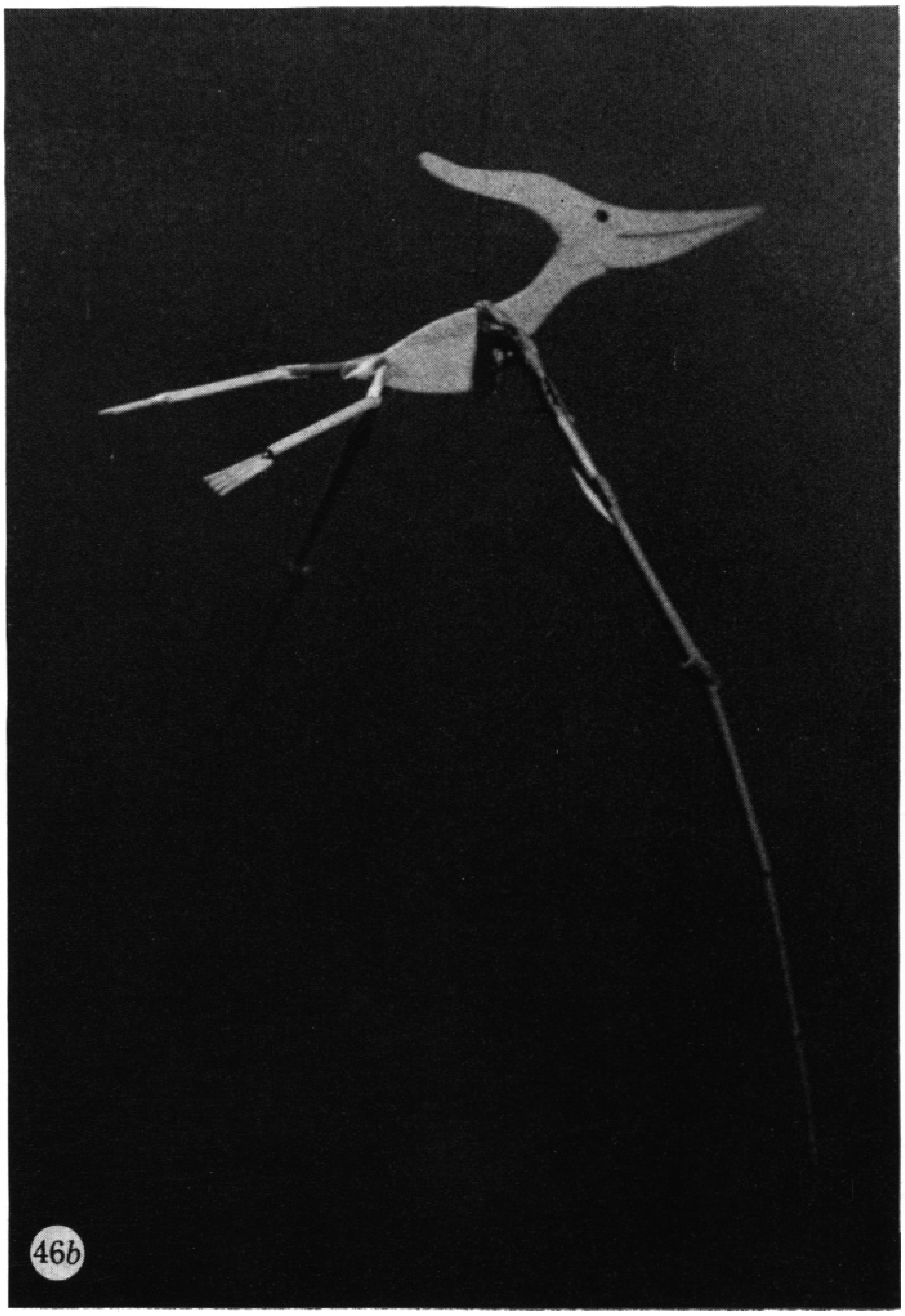
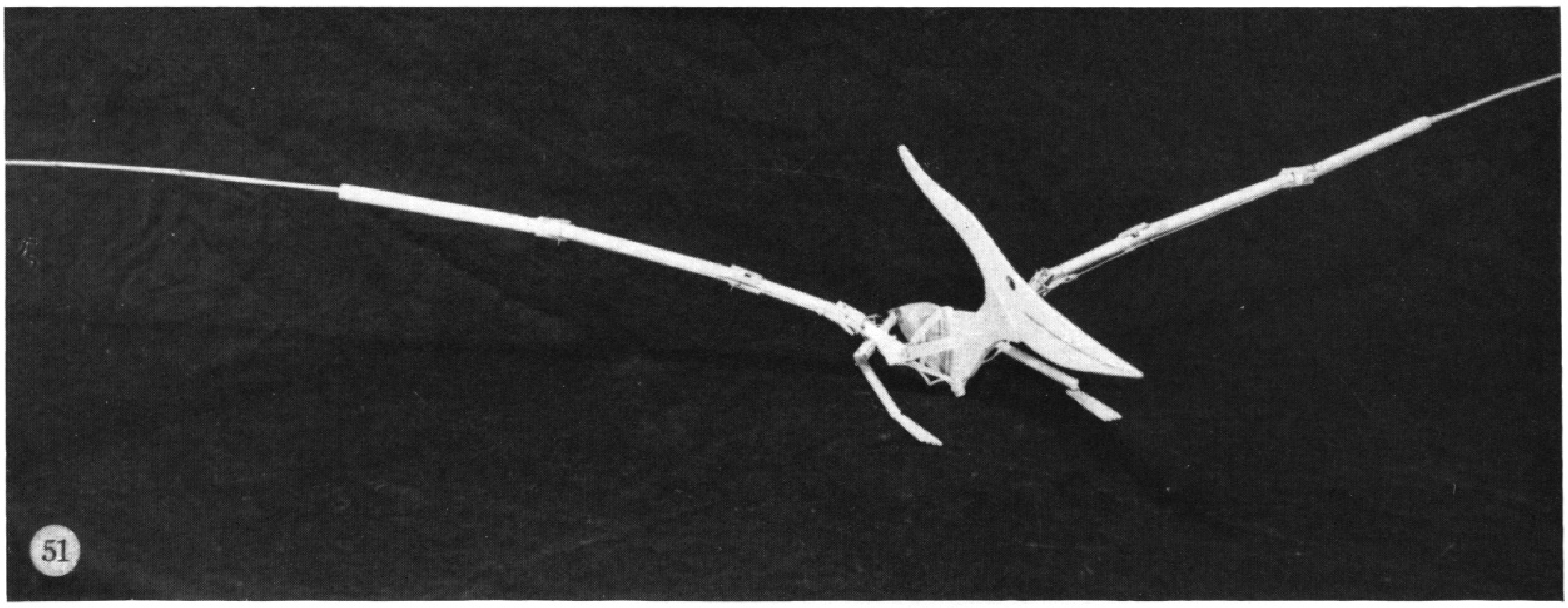


FIGURE 37. The two model heads, with and without crests, used in the wind-tunnel experiments.

FIGURE 46. (*a*) The articulated model with the wings at the top of the upstroke. (*b*) The articulated model with the wings at the bottom of the downstroke.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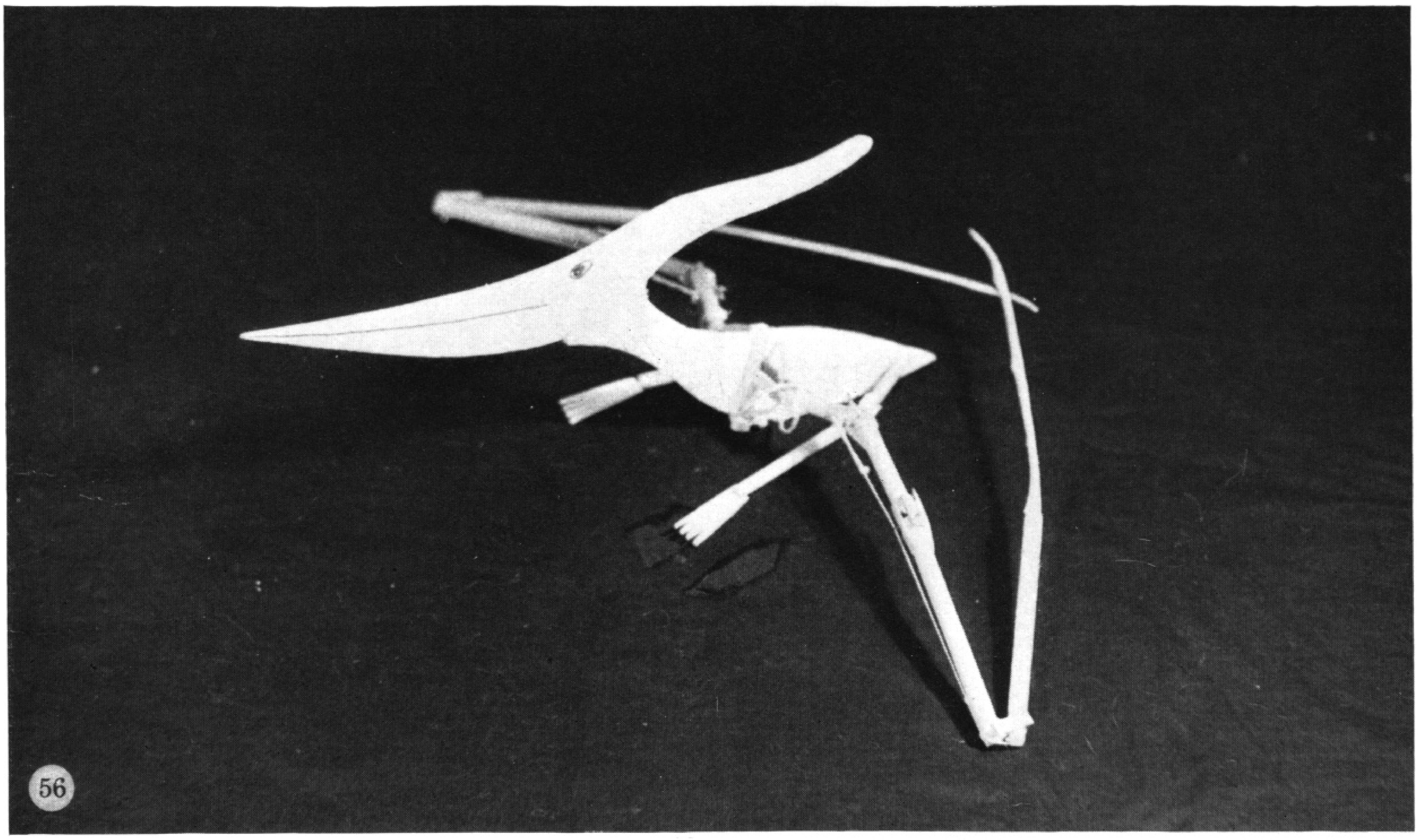
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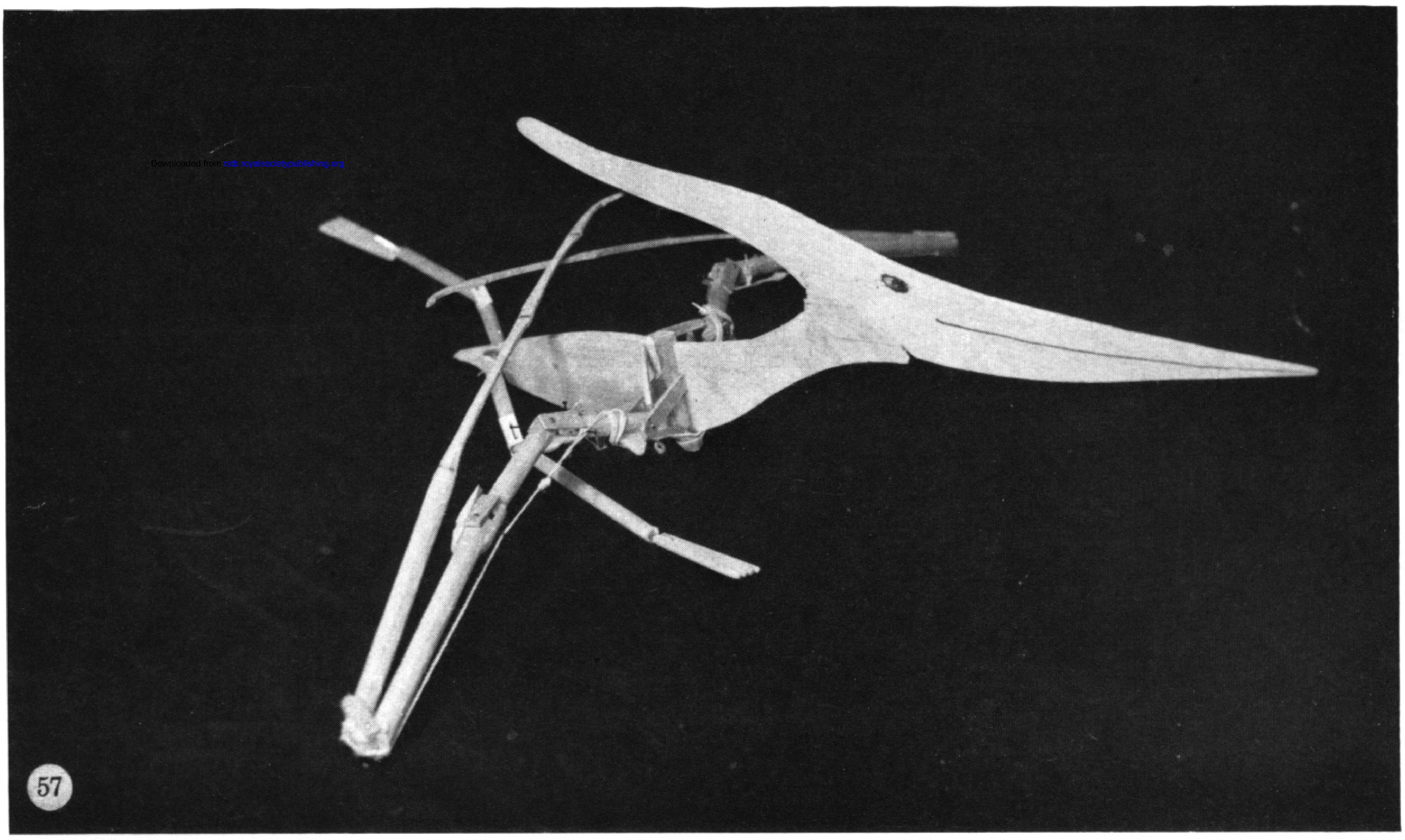
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Figure 51. Articulated model with wings in position ready to take off from land or water.

Figure 56. Articulated model walking. The wings are folded and the weight rested on the body and wing claws. Both legs are forward ready to grip the ground and pull the animal along.

Figure 57. Articulated model walking. The wings are folded and the weight rested on the body and wing claws. In this photograph the legs are being used alternately to pull the animal along, rather than both together as in figure 56.