

THE AERODYNAMICS OF THE BRITISH LATE TRIASSIC KUEHNEOSAURIDAE

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Abstract: The Kuehneosauridae (Late Triassic, Britain, USA) had remarkable adaptations, most notably their elongate mid-dorsal ribs that were presumably covered with a skin membrane in life. These lateral ‘wings’ have always been linked with some form of gliding adaptation, but quantitative studies have been limited. Here, we provide a thorough aerodynamic analysis of both genera of British kuehneosaurids based on theory and on experiments with life-sized models in a wind tunnel. Of the two genera, *Kuehneosuchus*, with elongate ‘wings’, was a glider, and *Kuehneosaurus*, with much shorter ‘wings’, was a parachutist. *Kuehneosuchus* most probably had highly cambered wings and no additional skin membranes on hands or feet, nor did it have a cruropatagium. Lappets on the hyoid apparatus, as seen in *Draco*, were

probably present to enhance pitch control. *Kuehneosuchus* was capable of gliding at angles (θ) between 13 and 16 degrees, at speeds between 7 and 9 m/s, and was probably very manoeuvrable when airborne. *Kuehneosaurus* was capable of parachuting ($\theta > 45$ degrees) at speeds between 10 and 12 m/s. It is unclear whether the British kuehneosaurid material represents two genera, as assumed here, two species of one genus, or sexual dimorphs of a single species, where the gliding *Kuehneosuchus* was the male, which used its gliding and perhaps highly coloured ‘wings’ to display to the parachuting *Kuehneosaurus*.

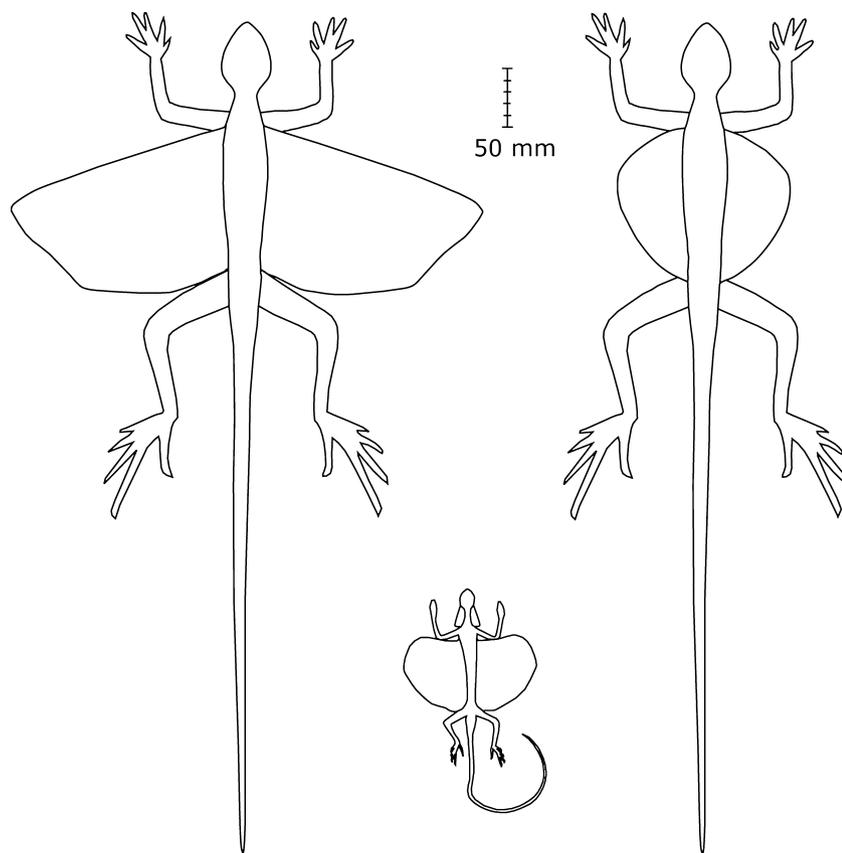
Key words: Kuehneosauridae, Diapsida, Late Triassic, gliding, aerodynamics.

THE Kuehneosauridae are a small clade of Late Triassic amniotes consisting of the genera *Kuehneosaurus* and *Kuehneosuchus* from England, *Icarosaurus* from New Jersey, USA, and the enigmatic *Rhabdopelix* from Pennsylvania, USA (Colbert 1966). Kuehneosaurids were originally (Robinson 1962, 1967; Colbert 1970) classified as lizards proper, within the clades Lepidosauria and Squamata, but they lack crucial lizard characters, and cladistic analyses have placed kuehneosaurids either in a basal position within Neodiapsida (Benton 1985; Müller 2003) or as basal Lepidosauromorpha (Evans (1988, 2003). Kuehneosaurids are modest-sized, lightly built animals with remarkable, extended mid-dorsal ribs that, it is presumed, were covered with a skin membrane that was used as a gliding surface.

Kuehneosaurids were not the first flying vertebrates. The Late Permian Coelurosauravidae (Pettigrew 1979; Evans 1982; Evans and Haubold 1987; Frey *et al.* 1997) also had extended mid-dorsal ribs on which their gliding membrane was supported, but the anatomy of both groups differs, and there is no evidence of a close relationship other than that both groups are members of Diapsida.

The British kuehneosaurids were first described in a short note (Robinson 1962) as two species of a single genus, *Kuehneosaurus*: *K. latus* and *K. latissimus*. The most important distinguishing character is the shape and relative length of the ribs supporting the gliding membrane: *K. latus* has shorter wings than *K. latissimus* (Text-fig. 1). The vertebrae and transverse processes that carry the wing-ribs are also different in both species. The taxonomy was modified after *Icarosaurus* was discovered in the United States (Colbert 1966). *Icarosaurus* was said to be as different from both British kuehneosaurids as *K. latus* is from *K. latissimus* (Robinson 1967; Colbert 1970), so the genus *Kuehneosuchus* was erected for *K. latissimus* (Robinson 1967). Although Evans (2003) suggested that *Kuehneosaurus* and *Kuehneosuchus* might be congeneric, the taxonomy of Robinson (1967) is followed here.

The British kuehneosaurids have never been described in detail, but Robinson (1962) mentioned that she was in the final stage of producing a monograph, the manuscript of which is located in the archive of the Natural History Museum (London). Because the most recent cited



TEXT-FIG. 1. Dorsal view of the outlines of *Kuehneosuchus latissimus* (left) and *Kuehneosaurus latus* (right). Dorsal outline of *Draco melanopogon* (centre) added for comparison.

publication in the manuscript dates from 1978, her unpublished manuscript will be referred to as Robinson (1979).

Despite considerable interest in the aerodynamics of flight of early birds and of pterosaurs, no detailed study has been made of the flying capabilities of the kuehneosaurids. They were recognised from the start as gliders, and their functional similarities with the modern gliding lizard *Draco* were noted in detail (Colbert 1967). Our aim is to determine the aerodynamics of *Kuehneosaurus* and *Kuehneosuchus* by means of experiments with three-dimensional models in a wind tunnel and calculations.

Repository abbreviation. BMNH, the Natural History Museum, London.

GEOLOGICAL BACKGROUND

The fossiliferous fissure fillings of Late Triassic and Early Jurassic age that occur in Carboniferous limestones on both sides of the Bristol Channel are well known (Evans and Kermack 1994; Fraser 1994; Benton and Spencer 1995). The fissures fall into two geographic groups: the quarries of the Bristol-Mendip region of

England to the south-east of the Bristol Channel, and those of the Vale of Glamorgan, South Wales, to the north-west. The western fissure localities in the Vale of Glamorgan are situated on what was once one of the highest limestone plateaux in south-west Britain. During Early Jurassic times this plateau formed an island, known as St Bride's Island (Robinson 1957).

The broad palaeoenvironmental picture of south-west Britain in Late Triassic and Early Jurassic times is one of change from playa lakes and sabkhas to a shallow sea with several small limestone islands (Robinson 1971). Overall there is a consensus that the Bristol-Mendip fissures (except Windsor Hill) are Late Triassic, whereas those of St. Bride's Island are Early Jurassic (Robinson 1971; Whiteside 1986; Fraser 1988), but this difference in age has been questioned by Gill (2004) and Clemens (2007).

Fossils of the British Kuehneosauridae were found mainly at two localities, Emborough quarry near Wells and Batscombe quarry near Cheddar, Somerset, together with isolated bones from Slickstones quarry near Cromhall, in South Gloucestershire (Robinson 1962; Benton and Spencer 1995). *Kuehneosaurus* is the most common fossil from the Emborough fissures, and associated fossils are sphenodontids, archosaurs, and a mammal (Fraser

1994). The major part of the Emborough fissure is a collapsed cavern that formed part of a Triassic underground watercourse system. Before the collapse, laminated clay was deposited in the cavern. Large boulders of Carboniferous limestone, succeeding this clay, represent the fallen roof of the cavern, which collapsed in Late Norian times, creating a depression in the contemporary land surface. This depression became filled with clay deposited by the stream running through it and also red and green silt and pebbles representing surface wash transported during rainstorms. Bones only occur in the red and green silts and not in the laminated clays formed prior to the cavern collapse, which confirms that *Kuehneosaurus* was not a cave dweller but lived on the land surface surrounding the depression (Robinson 1957, 1979).

FLYING AND GLIDING

Aerodynamic principles

Gliding flight is the simplest form of flight, where potential energy is converted into aerodynamic work. When an animal glides, the resultant of the aerodynamic lift and drag forces exactly balances the weight of the animal, so that the animal descends along a fixed path at a constant speed. When parachuting, the fundamental balance of forces is not changed, but a different flow regime applies since the flow over the lifting surfaces becomes separated and stalled. A somewhat arbitrary distinction between gliding and parachuting is made when the gliding angle exceeds 45 degrees, because this corresponds approximately to the transition from an attached to a stalled flow regime. From the animal's point of view, the adoption of one form of flight or another is a matter of combination of flight speed, wing area, and total weight.

Lift varies with the angle of attack (aoa). The relationship is approximately linear until stall is reached, after which further increase of the aoa causes no further increase in lift. The formula for lift (measured in newtons) from an aerofoil is:

$$\text{Lift} = C_L \times 0.5\rho v^2 \times A$$

where C_L is a dimensionless quantity (the lift coefficient), that usually varies between 0 and 1.5. It is primarily a function of the aoa and the shape of the aerofoil: ρ is the density of air (kg/m^3), v is the velocity of the airflow (in m/s), and A is the wing surface area (in m^2).

Lift, like weight, is taken as acting through a central point, termed the centre of pressure (cp). The position of the cp varies with the aoa, and it has a significant effect on stability. The movement of the cp changes the pitching moment of the wing. The pitching moment is calculated as:

$$M = L \times X$$

where L is the lift force and X is the distance from a chosen reference point R to the centre of pressure. Conventionally, R is taken at 25 per cent of the chord (the chord is the mean width of an aerofoil from leading to trailing edge). For the kuehneosaurid models, R lies 144 mm from the tip of the snout.

Drag is the resistance of the air to a body pushing through it. This resistance depends on the streamlining of the body, the roughness of the surface, the density of the air, the velocity of the airflow and the amount of lift produced. Total drag is the result of profile drag, parasite drag and induced drag (drag due to lift). The definitional equation for total drag (in newtons) is similar to the lift expression:

$$\text{Drag}_{\text{total}} = C_d \times 0.5\rho v^2 \times A$$

where C_d is a dimensionless quantity (the drag coefficient). It is (as the lift coefficient) primarily a function of the aoa and the shape of the aerofoil.

The aspect ratio (AR) of an aerofoil is a dimensionless variable that measures the slenderness of the wings. AR is calculated by b^2/A , where b is the span of the wings. High-AR wings reduce induced drag and hence enhance lift relative to drag. They are, therefore, a common feature of gliders. Low-AR wings improve manoeuvrability (Von Mises 1959; Biewener 2003) at the expense of increased induced drag.

The weight of an aircraft relative to the area of its wings (W/A) defines its wing loading. A basic scaling issue emerges when wing loading is considered. The lift needed by a flying or gliding animal must be equal to its body weight and thus to the cube of a linear dimension. But at constant speeds and angle of attack, an aerofoil produces lift in proportion to its area (cf. lift equation) and thus to the square of a linear dimension. Constant wing loading, therefore, requires that shape changes with size: a large glider will need disproportionately large wings. Among animals, larger ones do have relatively larger wings, but this area increase is insufficient to keep wing loading constant (Alexander 1971). This is compensated by increasing flying speed. Larger animals typically fly somewhat faster, but since lift varies with the square of speed, even a small speed increase is significant (Vogel 1994). Biewener (2003) provided wing loading values for non-anatid birds between $16 \text{ N}/\text{m}^2$ (swallow) and $140 \text{ N}/\text{m}^2$ (wandering albatross), and noted that gliding animals also generally operate at lower wing loading than non-gliders.

Under gliding conditions, the ratio of lift to drag (L/D or C_L/C_d) equals $\cot \theta$ (or $\tan^{-1} \theta$), where θ is the gliding angle (Vogel 1994; Biewener 2003). Extant arboreal gliders, like *Draco*, flying lemurs, squirrels and frogs, have

low L/D ratios (two or less), and hence exhibit gliding angles between 25 and 45 degrees (Biewener 2003). The gliding speed (v_g) of an animal can be calculated by substituting lift by the weight of the animal (mass \times g) in the equation for lift:

$$v_g = (2mg/\rho AC_L)^{1/2}$$

For a more comprehensive account of the aerodynamic principles of animal flight, see Vogel (1994) or Biewener (2003).

Draco, a modern analogue

Draco, also called the 'flying dragon', an arboreal agamid lizard from the tropical rainforests of India eastwards to the Philippines (Shine *et al.* 1998; Russell and Dijkstra 2001; McGuire and Dudley 2005), has convergently evolved features similar to the Kuehneosauridae. The most obvious convergences are the elongate dorsal ribs and their origins on the transverse processes of the vertebrae of the mid-dorsal region of the vertebral column. In *Draco* the ribs are covered with a skin membrane and can be folded back along the body, or extended laterally, allowing the animal to use the membranes as a gliding surface (Colbert 1967). Furthermore, the limbs of *Draco* are flattened horizontally, so they may contribute to lift generation and/or drag reduction (McGuire 1998), an observation that may be verified in movies of *Draco* in flight.

Draco is able to control its flight by muscular control of the attitude of the wings, aided especially by movements of the long tail, which is a very important adjunct for flight (Colbert 1967). Evans (1982) emphasised the importance of the tail by pointing out the absence of caudal fracture planes. The long tail in the British kuehneosaurids must have served the same purpose. Other adaptations for aerial locomotion in *Draco* are the canard wings on the hyoid apparatus. These lappets increase surface area, but rather than being simply additional lift surfaces, they are probably more important for flight control (Robinson 1979; McGuire 1998; Russell and Dijkstra 2001), and might have been present in the Kuehneosauridae (Evans 1982).

Draco also possesses cartilage extensions on the distal ends of its long ribs. These recurved costal cartilages, in combination with collagenous strips binding adjacent ribs, create the robust and substantive free lateral margin of the patagium (Russell and Dijkstra 2001), and do not increase the wing area significantly. Interestingly, the distal ends of the ribs of *Kuehneosaurus* and *Kuehneosuchus* have a similar expanded and slightly concave structure at their distal ends and, therefore, probably had cartilage

extensions similar to those of *Draco* (Evans 1982), but again these probably did not increase the wing surface area.

Previous speculations about the Kuehneosauridae

There are few published studies of the aerodynamics of extinct gliding taxa and most have been speculative, but some quantitative studies have been performed recently on *Coelurosauravus* (Frey, *et al.* 1997; Dyke *et al.* 2006), *Sharovipteryx* (Frey, *et al.* 1997; Dyke *et al.* 2006) and *Xianglong* (Li *et al.* 2007).

Colbert (1970) made some comments on the aerodynamics of *Icarosaurus*, but he mostly drew a qualitative comparison with *Draco* and modern birds. The only aerodynamic constant he provided was the wing loading (22.56 N/m²). Robinson (1979) initially attempted to assess the gliding potential of the British kuehneosaurids. She estimated body masses for *Kuehneosuchus* and *Kuehneosaurus* to be between 150 and 250 g on the basis of body masses for *Draco* and other extant lizard taxa. Aspect ratios were found to be 4.0 and 2.0 for *Kuehneosuchus* and *Kuehneosaurus* respectively, and wing loadings were between 50 and 90 N/m² for *Kuehneosuchus* and between 180 and 310 N/m² for *Kuehneosaurus*.

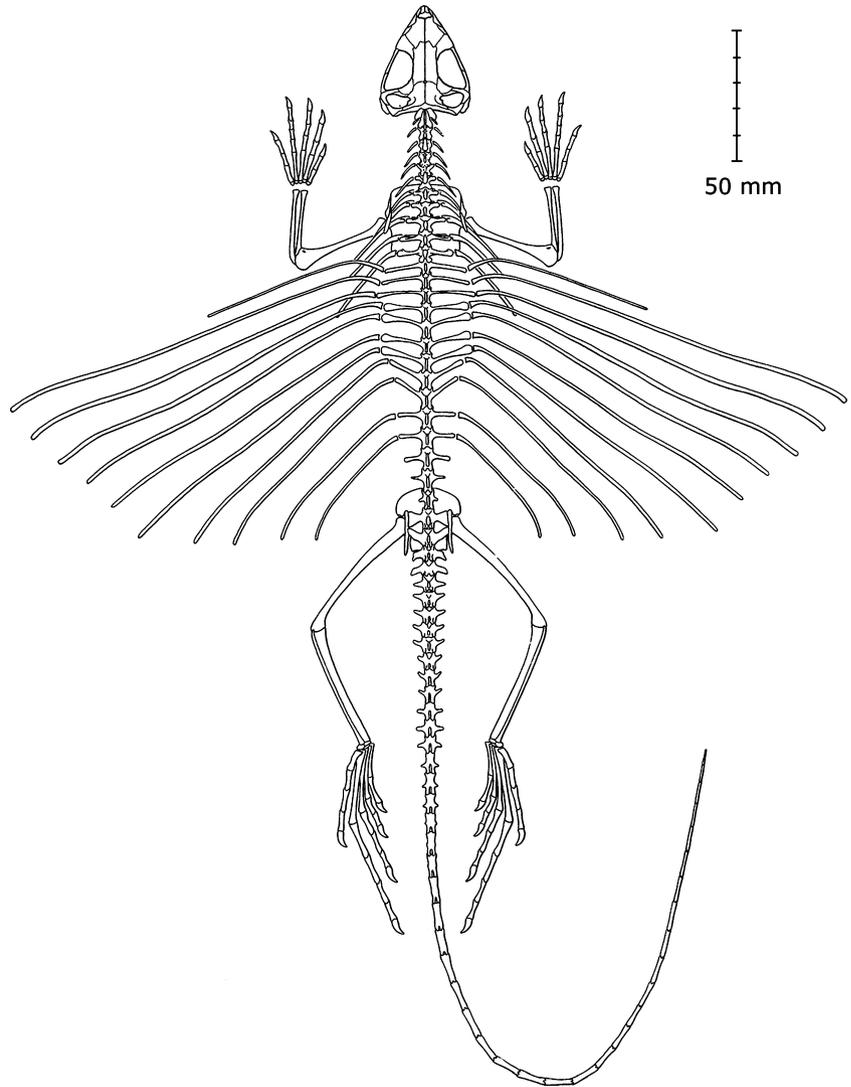
Robinson (1979) also attempted to estimate gliding speeds, assuming maximum C_L between 1.0 and 2.0. Calculations resulted in exceedingly high gliding speeds for *Kuehneosaurus* (between 12.5 and 28 m/s), and acceptable gliding speeds for *Kuehneosuchus* (between 6.0 and 12.5 m/s), so she concluded that *Kuehneosuchus* might have been able to glide but *Kuehneosaurus* probably could not. She suggested that *Kuehneosaurus* might have used its short wings in display and as a means to make fast turns in bipedal runs when evading predators. This startling difference in the postulated behaviour of two such similar animals suggests that there may in fact be a problem with the calculations; we investigate this in our study.

MATERIAL AND METHODS

Fossil specimens

Building a model requires a thorough understanding of the osteology of the animal, so fossil specimens of *Kuehneosaurus* and *Kuehneosuchus* were studied at the Natural History Museum (London). Pamela Robinson had completed a full, formal description of *Kuehneosaurus* and *Kuehneosuchus*, but this remained unpublished at her death. A thorough revision of her work is underway by S. E. Evans, and this will provide a full monographic

TEXT-FIG. 2. Original skeletal reconstruction of *Kuehneosuchus latissimus*, based on Romer (1966), who was given unpublished information by Pamela Robinson.



description of the material. The published reconstructions by Robinson (1962) and Romer (1966) and the unpublished reconstructions (Robinson, 1979) are well supported by the osteological evidence (S. E. Evans, pers. comm. 2007).

Robinson (1962, 1967, 1979) reported that apart from the dorsal vertebrae and ribs, the osteological differences between *Kuehneosaurus* and *Kuehneosuchus* are minute, so a full individual description of each taxon is not necessary. *Kuehneosuchus* is a delicately built animal (Text-fig. 1), with slender limbs, a long tail, and a broad pair of 'wings' supported by elongate ribs that extend laterally and backwards at about 45 degrees to the midline. It differs from *Kuehneosaurus* primarily in the extent of the lateral 'wings' (Text-fig. 2).

The long bones (BMNH R5983, R.6112, R.6189, R.6200) have hollow, thin-walled shafts and coarsely spongy articular ends thinly covered with compact bone.

The flat bones, particularly the coracoids, the larger ribs, and the transverse processes of the mid-dorsal vertebrae, are built from surfaces of compact bone 'no thicker than tissue paper', surrounding a coarsely spongy interior. This makes the bones extremely fragile and light. Although the lightness of the bones may be an adaptation for aerial locomotion, there is no sign that they were pneumatic; there are certainly no openings for air sac extensions from the lungs (Robinson 1979).

The third cervical vertebra (BMNH R.6009, R.6016) has two rib articulations on the centrum, a ventral parapophysis, and a dorsal diapophysis. These articulations supported a very small, double-headed rib. On the fifth cervical vertebra (BMNH R.6015) a third rib articulation develops on the neural arch dorsal to the diapophysis, termed by Robinson (1962) the dorsal diapophysis. The ribs have three heads, and this continues back to the ninth cervical vertebra (BMNH P.L.R.134). The dorsal

diapophysis elongates until, at the seventh vertebra, it is the most prominent rib articulation. At the tenth vertebra (BMNH R.5998), the parapophysis disappears, and the dorsal diapophysis increases further in importance. From this region backwards, both diapophysis and dorsal diapophysis elongate laterally, one remaining vertically below the other, and the space between them is gradually filled in by bone, except at the distal ends.

The anterior dorsal vertebrae have very long, broad, transverse processes that are divided into two portions at their distal ends but, near the mid-dorsal region, the processes become a single undivided structure. By this point, the dorsal vertebrae have become extremely broad, measuring as much across the transverse processes as the width of the back of the skull. The broad, blade-like transverse processes have their edges directed almost vertically, and they are supported on the neural arch by well-developed buttresses. The dorsoventral width of the transverse processes gradually diminishes towards the sacral region until the bones become rod-like. The length of the rod then decreases until it has almost disappeared in the first sacral vertebra. *Kuehneosaurus* differs from *Kuehneosuchus* in minor details of the relative length, breadth, and buttressing of the transverse processes of some of the mid-dorsal vertebrae (Robinson 1962).

In *Kuehneosaurus* the ribs in the anterior dorsal region curve round to the sternal cartilage and support the pectoral girdle. The mid-dorsal vertebrae bear elongate ribs (BMNH R.8172), about two and a half to three times the length of the extensive transverse processes that bear them. These ribs hardly curve, so they extend out almost horizontally, and are nearly perpendicular to the long axis of the body. Their vertical width matches that of the transverse process that bears them, and they are very thin anteroposteriorly, being lath-like structures. Behind the mid-dorsal region the ribs become rod-like to match the transverse processes of the vertebrae, and also shorten towards the sacral region. *Kuehneosaurus* and *Kuehneosuchus* also retain small abdominal ribs (Robinson 1979). The type specimens of *Kuehneosaurus* (BMNH R.8172) and *Kuehneosuchus* (BMNH R.6111) consist of articulated partial skeletons, which illustrate that the 11 pairs of mid-dorsal ribs could be folded back along the body (Robinson 1962), as in *Draco*.

Kuehneosuchus differs from *Kuehneosaurus* in a few main characters of the 11 pairs of mid-dorsal ribs (BMNH R.6111), most prominently their much greater elongation (Text-fig. 3). The first pair of these ribs is about two and a half times the width of the skull, and the second pair more than five times this width, or nearly three times the length of ribs from the same region in *Kuehneosaurus*. The following pairs progressively diminish in length. The distal half of the shaft of the longer ribs is rod-shaped in the posterior pairs, whereas in *Kuehneosau-*

rus they are vertically wide at the distal ends. In all but the first pair there is a moderate ventral curvature of the more distal portion of the shaft.

The first four caudal vertebrae are preserved associated in *Kuehneosaurus* (BMNH R.8172). Based on the large number of dissociated caudals of various intermediate types, Robinson (1979) assumed that, like *Icarosaurus*, the British kuehneosaurids had a long tail. However, there is no definitive evidence for this, so the aerodynamic effect of tail length was investigated.

The models and the wind tunnel

The two-dimensional skeletal reconstruction of *Kuehneosuchus* (Romer 1966) was used as a basis for the model-making. Key measurements (Table 1) were checked on specimens and from Robinson (1979). Modelling plasticine was added to the skeletal templates to make a three-dimensional body outline. The limbs and main body were constructed separately in order to make the limbs articulate. Hands and feet were cut from a 3-mm-thick aluminium sheet and wings were cut from 1-mm-thick aluminium. The wings of *Draco* show little sign of deflection under aerodynamic load, so flexible wings were not manufactured for our models. Rubber moulds were made from the plasticine reconstructions, allowing multiple cast plastic models with different wing types to be made. The plastic body parts were then assembled by drilling holes in the flanges on the limb parts (and hands and feet) and bolting them together. The bolted joints were covered with plasticine and the wings were attached to the trunk with bolts.

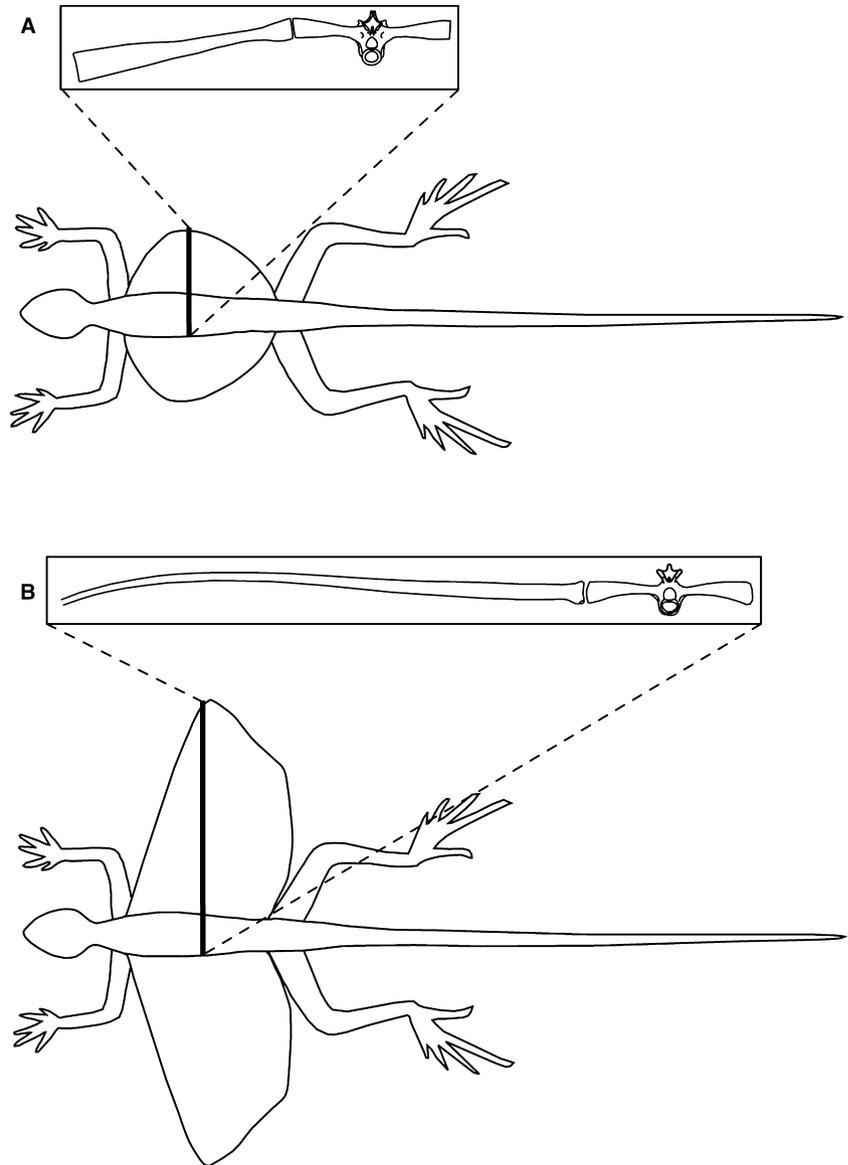
Four life-size models were built (Text-fig. 4), each with differing aerodynamic properties (Table 2): three of *Kuehneosuchus* with wings with different degrees of camber (Text-fig. 5) and one of *Kuehneosaurus*.

The wind tunnel tests were performed in the Department of Engineering at Bristol University. Testing was done with the model inverted in a low turbulence wind tunnel using a three-degrees-of-freedom balance (Text-fig. 6). The angle of attack was varied in steps of 2 degrees between 12 and 25 degrees. Each test was performed at speeds between 10 and 20.5 m/s.

Mass and centre of mass estimates

Accurate mass and centre of mass estimates are essential in order to assess an animal's flight capabilities, and it is essential to get these estimates right. Pough (1973) plotted snout to vent lengths against mass for extant lizards, and these data fall on a smooth curve. Evans (1982) used this snout-vent/weight relationship to extrapolate the

TEXT-FIG. 3. A, mid-dorsal vertebra and rib in anteroposterior view of *Kuehneosaurus latus*, based on BNMH R.8172 and R.6017; length of rib is 48 mm. B, mid-dorsal vertebra and rib in anteroposterior view of *Kuehneosuchus latissimus*, based on BNMH R.6111; length of the incomplete rib is c. 130 mm. Note the difference in overall morphology and extent of the wing-ribs in both species. Redrawn from Robinson (1962).



weight of *Kuehneosuchus*. She estimated the wing loading to be in the range of 157 to 216 N/m², well outside the range of wing loadings for extant non-anatid birds, and so casting doubt on the gliding capability of *Kuehneosuchus*. We obtained similar results when we repeated the calculations. *Kuehneosuchus* has a snout-vent length of 250 mm, which implies a mass of 0.56 kg in Pough's (1973) snout-vent/weight relationship, resulting in a wing loading of 135 N/m².

We think it is unlikely that the kuehneosaurids, with extensive anatomical adaptations to gliding, were too heavy to glide. It is most likely that full account has not been taken of the ways in which flying animals save weight. This can be illustrated with *Draco*. Measurements of mass and snout-vent length of *Draco* do not fall on the curve provided by Pough (1973). *Draco melanopogon*, for

example, measures 77 mm in average snout-vent length (Shine *et al.* 1998), and has an average mass of 3.8 g (McGuire and Dudley 2005). A prediction of the weight of this animal from Pough's (1973) snout-vent/weight relation suggests its mass would be about 15 g, a factor of four higher. If the four times factor is applied to *Kuehneosuchus*, its mass is predicted to be 0.14 kg, not 0.56 kg. Even if the maximum weight of *D. melanopogon* is considered (5.9 g), the factor is 2.66, predicting a mass for *Kuehneosuchus* of 0.21 kg.

We cross-checked the calculated body mass and the weight-saving factors for the kuehneosaurids by Henderson's (1999) mathematical slicing technique. Henderson (pers. comm. 2006) did the calculations using a standard lung volume fraction of 8.75, and determined a mass estimate of 0.40 kg for *Kuehneosuchus* and a cen-

TABLE 1. Key measurements in mm (unless otherwise denoted) of the two British kuehneosaurid genera, based on specimens in the BMNH and on Robinson (1962, 1979).

Measurement	<i>Kuehneosuchus</i>	<i>Kuehneosaurus</i>	Specimen nos.
Length of skull	42	42	Reconstruction in Robinson (1962, 1979)
Maximum width of skull	38	38	Reconstruction in Robinson (1962, 1979)
Length of humerus	39	39	R.5981, R.6111, R.6189, R.6200, P.L.R.95, P.L.R.96, P.L.R.97
Length of radius	26	26	P.L.R.107
Length of ulna	26	26	P.L.R.94
Length of femur	57	57	R.5982, R.5983, R.6112, P.L.R.81, P.L.R.87
Length of tibia	51	51	R.6112
Snout-vent length	250	250	Reconstructions in Robinson (1979)
Total length with original tail	720	720	Reconstructions in Romer (1966) and Robinson (1979)
Total length with short tail	580	580	Measured on model
Wingspan	400	143	Reconstructions in Romer (1966) and Robinson (1979)
Chord	102	100	Reconstructions in Romer (1966) and Robinson (1979)
Wing surface area (cm ²)	406.0	143.0	Reconstructions in Romer (1966) and Robinson (1979)

TABLE 2. The aerodynamic parameters used in the four models, three of *Kuehneosuchus* with wings set at different cambers and one of *Kuehneosaurus latus*.

	Long tail	Short Tail	Stout legs	Thin legs	Limbs tucked	Limbs outstretched	Additional patagia	Ribs
Low camber	X	X	X	X	X	X		
Medium camber	X	X	X	X		X		X
High camber	X	X	X	X		X	X	
<i>K. latus</i>	X	X		X		X		

tre of mass at 242 mm from the tip of the snout of the animal. It should be noted that the model used for these calculations had a rather plump tail, causing the centre of mass to lie well towards the rear end of the animal. In addition, it needs to be repeated that the exact length of the tail of the kuehneosaurs remains equivocal. Therefore, calculations were made for two new models, one with a very slender tail, and one with a shorter tail (total length of the animal, 580 mm). The centre of mass lies respectively at 196 and 195 mm from the tip of the snout, while the mass is estimated to be 0.38 kg for both models.

In summary, we used five body mass estimates for the British kuehneosaurids, namely 0.14, 0.21, 0.38, 0.40, and 0.56 kg, and the location of the centre of mass ranges from 242 to 195 mm from the tip of the snout of the animals.

WIND TUNNEL TESTS AND CALCULATIONS

Aspect ratio and wing loading

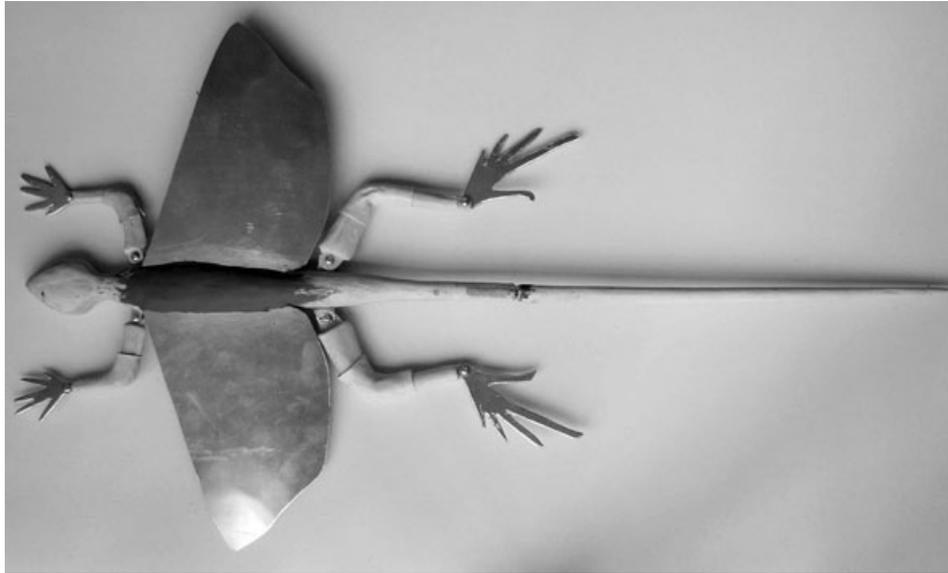
An aspect ratio of 3.94 was calculated for *Kuehneosuchus*, which is slightly lower than that calculated by Robinson

(1979), and 1.43 for *Kuehneosaurus*, which is notably smaller than the figure of 2.00 that she presented. Wing loadings for *Kuehneosuchus* and *Kuehneosaurus* for their respective mass estimates are given in Table 3.

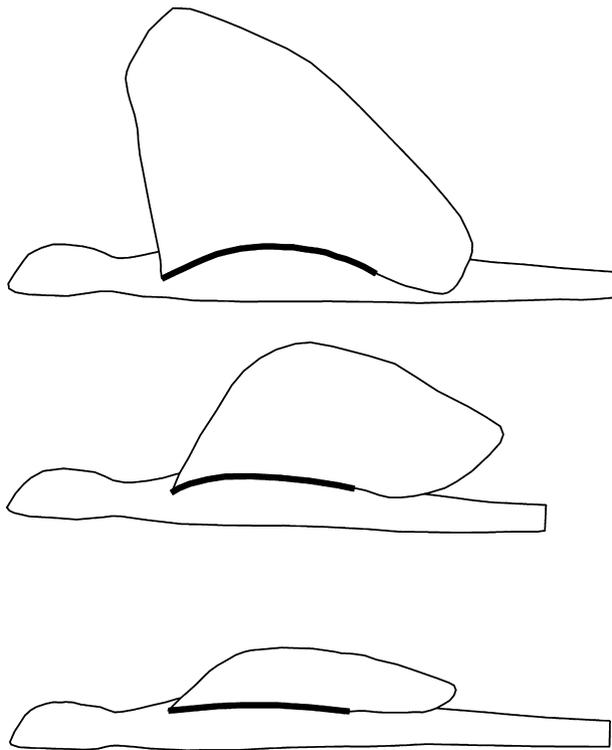
Lift and drag

Tests of the four models were made over a range of wind speeds (10.0, 13.2, 15.3, 16.6, 17.7, 18.7, and 20.5 m/s) and the measured values of lift and drag were converted to non-dimensional lift and drag coefficients. The initial C_L results for the different speeds (Text-fig. 7) collapsed onto the same curve, thus confirming that the results were insensitive to the Reynolds number of the tests. For this reason, it was not necessary to perform all tests at all speeds. The C_d results for different speeds (Text-fig. 8) also collapsed onto the same curve.

Lift coefficients are plotted against drag coefficients at various angles of attack for the different models (Text-fig. 9). The tangent to the curve from the origin gives the maximum lift to drag ratio and the angle of attack at which this occurs. The length of the tail did not have a significant effect on lift or drag coefficients for any of the models.



TEXT-FIG. 4. Top view of a nearly finished model of the original reconstruction of *Kuehneosuchus*, with the limb joints exposed: these were coated with plasticine to reduce drag effects before the model was run in the wind tunnel.



TEXT-FIG. 5. Side view of the different degrees of camber for the *Kuehneosuchus* models: high camber (top), medium camber (middle), and low camber (bottom).

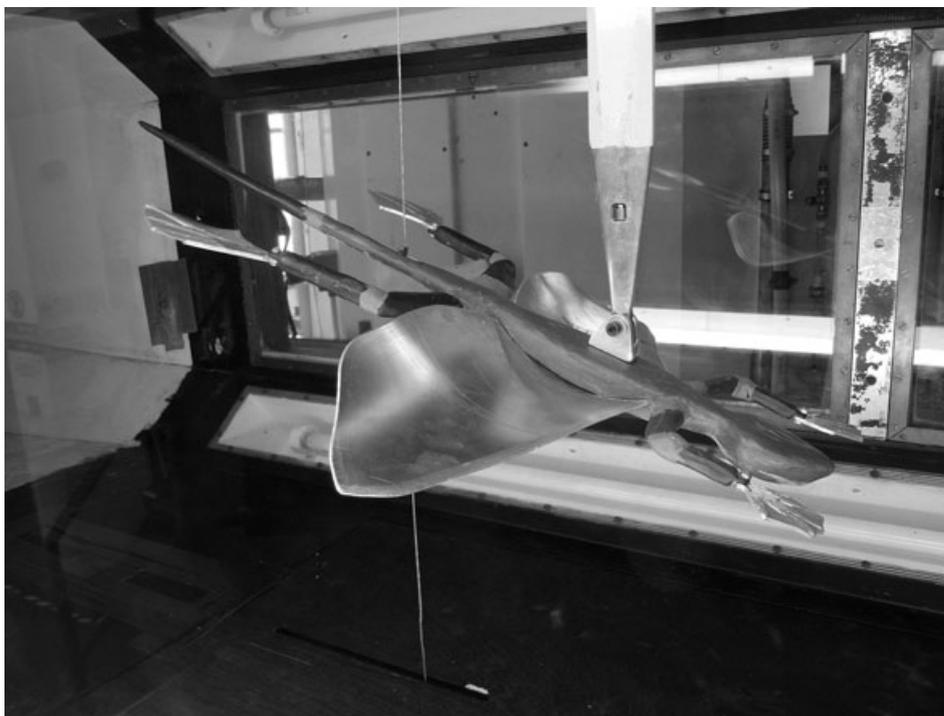
Initially, the ribs were only shaped on the medium camber model. Testing proved that there was no significant effect on lift or drag coefficients, so no correction was needed for the models without ribs.

Adding a cruropatagium and webbed hands and feet lowered the maximum lift coefficients without altering the drag coefficients for an otherwise identical model. This was unexpected. If *Kuehneosuchus* had these additional surfaces, they were probably not used for lift generation. Webbed hands and feet and cruropatagia do not occur in any known *Draco* species. *Draco* possesses extra skin folds on the hyoid apparatus, which can be extended and retracted like canard wings seen in modern fighter aircraft (Evans 1982). However, this device is probably primarily used for pitch control and stability, especially to allow the animal to slow down without losing stability during landing, rather than as an extra lift surface. It is likely that *Kuehneosuchus* had similar structures, allowing it to control its pitch, and force itself to high angles of attack to reach stall.

The position of the limbs did not significantly affect lift or drag coefficients, but presumably, together with the tail, the limbs were used for stability and control. The thickness of the legs only had an effect on the low-camber model, causing higher lift coefficients but no change in drag coefficients. However, because thinner legs did not affect lift or drag coefficients of the medium- and high-camber models, it is presumed that lift increase for the low-camber model is a combined effect of the amount of camber and the thickness of the legs.

Increasing the camber of the wings did not increase maximum lift coefficients significantly, but it did increase the lift to drag ratio. Thus, a higher amount of camber increases gliding performance significantly.

The maximum lift coefficients, which are achieved when stall occurs, could not be reached for *Kuehneo-*



TEXT-FIG. 6. Wind-tunnel set-up of the high-camber model of *Kuehneosuchus*. Note that the model is suspended upside-down and that there is a vertical offset of the attachment structure from the centre of the body.

TABLE 3. Wing loading calculated for the two genera of British kuehneosaurids for five different estimated body masses.

Mass estimate (kg)	Wing loading (N/m ²)	
	<i>Kuehneosuchus</i>	<i>Kuehneosaurus</i>
0.56	135	384
0.40	97	274
0.38	92	261
0.21	51	144
0.14	34	96

saurus. This is because *Kuehneosaurus* stalls at angles of attack greater than 30 degrees, which the wind tunnel set-up did not allow. However, the maximum lift to drag ratio was reached, allowing the gliding angle and gliding speeds for different mass estimates to be calculated.

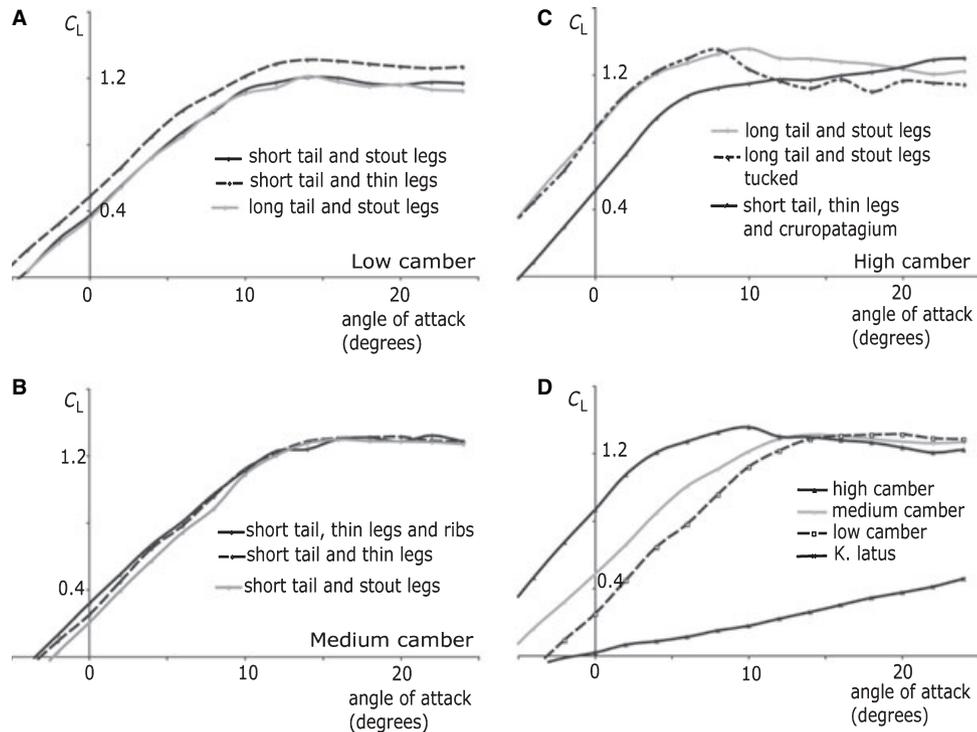
Location of the centre of pressure, stability and aspect ratio

Results for the pitching moment of *Kuehneosuchus* with a long tail showed that the centre of pressure at operational angles of attack (Text-fig. 10) lies between 165 and 170 mm from the tip of the snout for the high-camber model (with and without skin flaps), between 181 and

195 mm for the medium-camber model, and between 173 and 191 mm for the low-camber model.

Original calculations revealed the centre of mass for *Kuehneosuchus* lies at 242 mm from the tip of the snout, suggesting that the animal was unstable during gliding flight. However, the first model had a rather fleshy tail, and moderate changes to the thickness of the tail can significantly alter the location of the centre of mass (Henderson, pers. comm. 2007). Therefore, the centre of mass was also calculated for a second model with a slender tail. For this, the centre of mass lies 196 mm from the tip of the snout of the animal.

As mentioned earlier, the length of the tail did not have any effect on C_L . However, having a shorter tail has implications for the mass and location of the centre of mass. Given the uncertainty about the exact length of the tail, the centre of mass was calculated for a third model with a shorter tail (total length of the animal 580 mm). For this model, the centre of mass lies 195 mm from the tip of the snout. This results in a possible range for the location of the centre of mass from 195 to 242 mm from the tip of the snout of the kuehneosaurs. The centre of pressure lies outside, but very close by the foremost edge of this range. Therefore, it is most likely that the location of the centre of mass of the real animal could be found more towards the foremost edge of the range in question. This means that the animal had an extremely slender tail,



TEXT-FIG. 7. Lift coefficients (C_L) for A–C, *Kuehneosuchus* and D, *Kuehneosuchus* compared with *Kuehneosaurus*. A, low-camber model testing the effect of thin legs and a shorter tail. Thinner legs slightly increase lift coefficients, but the shorter tail has no aerodynamic effect. B, medium-camber model. Here the tests show no significant effect of thinner legs, nor is there any effect of ribs on the lift coefficients. C, high-camber model. Putting the limbs at an alternative angle does not alter lift coefficients. However, the presence of a cruropatagium and webbings on hands and feet significantly lowers the lift coefficients. D, *Kuehneosaurus* compared with three models of *Kuehneosuchus* (all with thin legs and short tail). Note how maximum lift coefficients were reached for all models of *Kuehneosuchus*, but could not be reached for *Kuehneosaurus*.

or a shorter tail than suggested in the original reconstruction. However, with current knowledge it is not possible to determine the exact length of the tail of the British kuehneosaurs.

From the tests it is also clear that hypothetical unpreserved skin flaps (cruropatagium, webbed hand and feet) do not have an impact on the location of the centre of pressure. The centre of pressure of *Kuehneosaurus* only reaches the same location as in *Kuehneosuchus* at an incidence of 16 degrees, suggesting that the animal was only stable when gliding at very high angles of attack, and thus very high angles of decent (35–45 degrees).

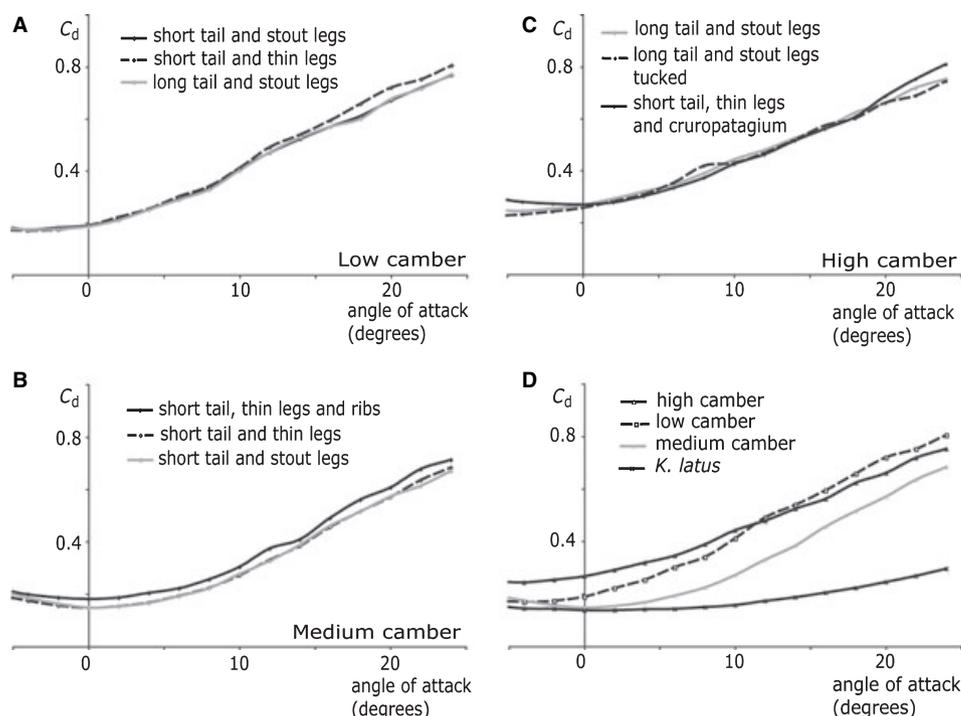
Lift and drag coefficients demonstrate that *Kuehneosuchus* was a reasonably efficient glider. Higher aspect-ratio wings would have improved gliding efficiency, so it is likely that it had relatively low aspect-ratio wings (3.94) to improve its manoeuvrability during gliding flight, and also to avoid a sudden loss of lift at stall speeds. When stall is reached, lift can decrease rapidly, resulting in sudden descent and instability (Von Mises 1959). A lower aspect ratio moderates this effect, reducing the rate of lift decrease and the centre of pressure

movement. The very low aspect ratio of *Kuehneosaurus* (1.43) is similar to modern parachute aspect ratios, suggesting that *Kuehneosaurus* was a parachutist rather than a glider.

Gliding angle and gliding speed

The minimum gliding angles differ substantially between the two genera, in the range 14.0–16.2 degrees for *Kuehneosuchus* and 35.6 degrees for *Kuehneosaurus*. But the values did not vary much among the different models of *Kuehneosuchus*, being 16.2 degrees for the low-camber model, 15.0 degrees for the medium-camber model, 14.0 degrees for the high-camber model with additional patagia and 14.8 degrees for the high-camber model without skin flaps.

Our models show increasing gliding speeds with increasing mass (Tables 4–5), which is to be expected (cf. wing loading). As the British Kuehneosauridae had extremely fragile bones (Robinson 1962), it is likely that they would have glided at the lowest possible speeds. The



TEXT-FIG. 8. Drag coefficients (C_d) for A–C, *Kuehneosuchus* and D, *Kuehneosuchus* compared with *Kuehneosaurus*. A, low-camber model. No effect of the length of the tail or thickness of the legs is observable. B, medium-camber model. The presence of ribs causes a minor increase in drag coefficients, but this is insignificant. C, high-camber model. Putting the legs at an alternative angle, or adding a cruropatagium and webbings has no effect on drag coefficients. D, different models of *Kuehneosuchus* (all with short tail and thin legs) compared with *Kuehneosaurus*.

high-camber model of *Kuehneosuchus*, without any additional membranes, provided the highest lift to drag ratios and lowest gliding speeds for every mass estimate. It is, therefore, likely that *Kuehneosuchus* had highly cambered wings, allowing it to glide at lower speeds. Using the lower mass estimates of 0.14 and 0.21 kg, which are probably most representative of the living animal, it displayed gliding speeds between 6.6 and 8.1 m/s at this lift to drag ratio (Table 4).

Kuehneosaurus exhibits high gliding speeds for every mass estimate (Table 5), and landing at these speeds without sustaining serious injury would have been a problem. Therefore, it is unlikely that *Kuehneosaurus* was a glider, but it may have used its wings for parachuting flight. Drag coefficients of parachutes can reach values of 1.4 (Von Mises 1959), which allows the terminal velocity (v_t) of *Kuehneosaurus* to be calculated for different mass estimates using the expression:

$$v_t = (2mg/\rho AC_d)^{1/2}$$

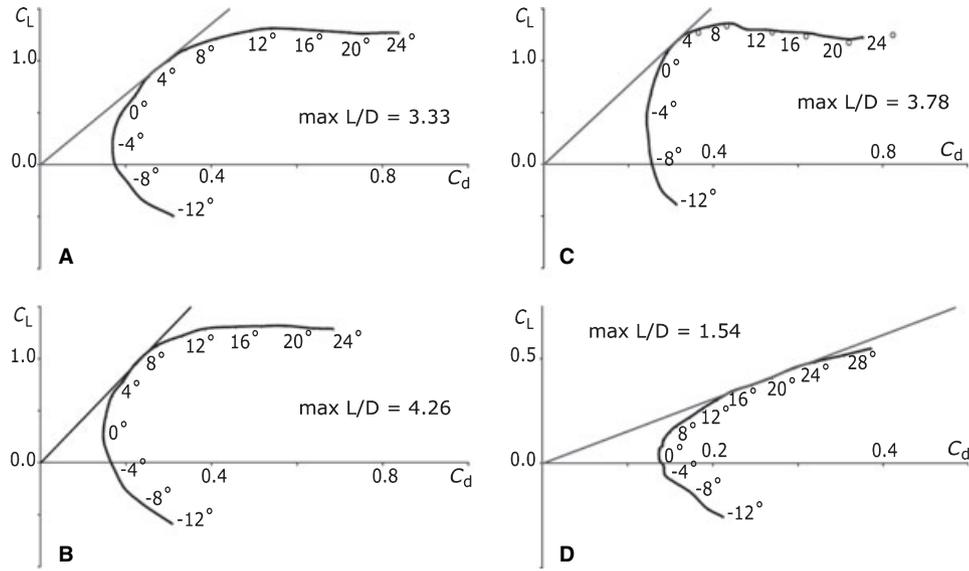
The terminal velocity of *Kuehneosaurus* is 12.6 m/s for a mass estimate of 0.21 kg, and 9.95 m/s for a mass estimate of 0.14 kg. Knowing that human parachutists land at speeds between 5 and 12 m/s (Von Mises 1959), it is likely that *Kuehneosaurus* used its wings for parachuting.

Wing function and behaviour

The confirmation of Robinson's (1979) view that, despite their close skeletal similarities, *Kuehneosuchus* could glide effectively, and *Kuehneosaurus* was not a glider but at best a parachutist, requires explanation. If these were two distinct genera, as Robinson (1979) argued, or even two species, as suggested by Evans (2003), it might seem odd that both could not have been equally effective gliders. Perhaps these were, in fact, sexual dimorphs of a single species, with *Kuehneosuchus* the male and *Kuehneosaurus* the female?

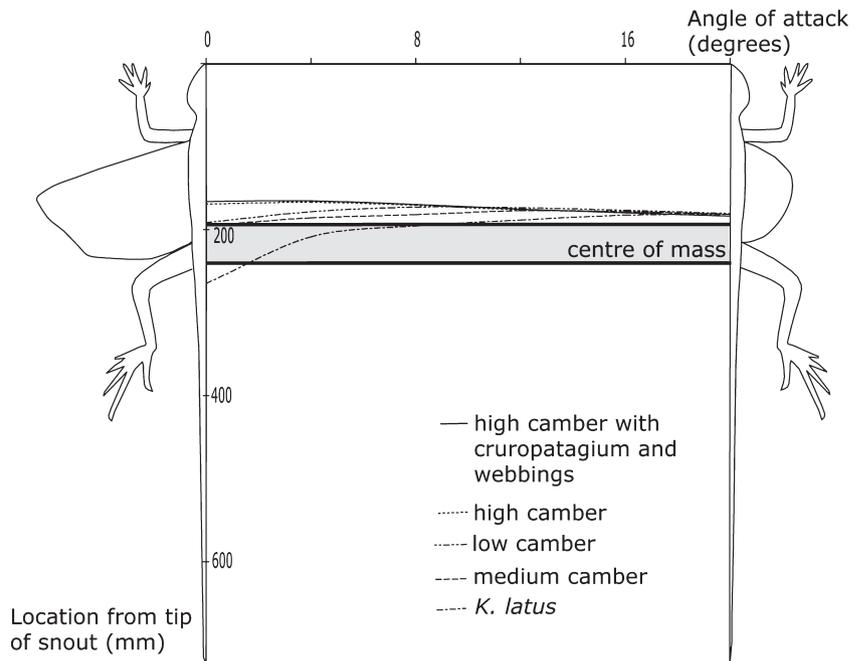
Male *Draco* lizards use their brightly coloured gliding membranes to scare off male rivals, and attract females (McGuire 1998). *Kuehneosuchus* may have had such display features and, apart from using them for display, it could have used them to travel towards females. Females would not have needed extravagant display features, which could explain the smaller wings in *Kuehneosaurus*. The fact that fossils of the two forms do not occur together in the same localities casts some doubt on this hypothesis, but this could be a preservational or sampling artefact.

In support of the sexual display function, Russell and Dijkstra (2001) suggested that the patagium in *Draco*



TEXT-FIG. 9. Lift coefficients (C_L) plotted against drag coefficients (C_d) at various angles of attack for the A, low-camber, B, medium-camber, and C, high-camber models of *Kuehneosuchus*, and for D, *Kuehneosaurus*. Maximum lift to drag ratios (given in every graph) and the angle at which they occur can be found by measuring the slope of the tangent to the curves from the origin.

TEXT-FIG. 10. Location of the centre of pressure along the length axis for four models of *Kuehneosuchus*, and for *Kuehneosaurus*. The centre of mass is located 195–242 mm from the tip of the snout of the kuehneosaurs (grey area). The centre of pressure at operational angles of attack lies outside, but very close by the foremost edge of this range. Therefore, it is most likely that the location of the centre of mass of the real animal could be found more towards the foremost edge of the range in question. This means that the animal had a very slender tail or a shorter tail than suggested in the original reconstruction. Note that the cruropatagium and webbed hands and feet have no influence on the location of the centre of pressure.



evolved from modifications associated with thermoregulation, intraspecific communication, and predator escape. They came to this view because the ‘wings’ have multiple functions in *Draco*, and because there is a diversity of modern lizards other than *Draco* that have small lateral skin flaps that have only a modest aerodynamic function, others that parachute but do not glide, and some with ‘passive’ wings that unfold only when in flight, forms that parachute but do not glide. They believed then that the

aerodynamic function in such modern lizards, and possibly also in ancient gliders, arose as an exaptation, or later co-option, of features that were adapted to thermoregulation, communication, and escape. This model might then support the suggestion of sexual dimorphism in the British Late Triassic kuehneosaurids, or *Kuehneosaurus* could be interpreted as a distinct species or genus on an evolutionary trajectory towards full-scale gliding, as seen in *Kuehneosuchus*.

TABLE 4. Gliding speeds for four models of *Kuehneosuchus* at five different mass estimates.

Mass estimates (kg)	Gliding speed at highest lift/drag (m/s)			
	Low camber	Medium camber	High camber with cruropatagium	High camber
0.56	14.98	14.77	13.71	13.23
0.40	12.66	12.48	11.59	11.19
0.38	12.06	11.88	11.04	10.66
0.21	9.18	9.04	8.40	8.10
0.14	7.49	7.38	6.86	6.62

TABLE 5. Gliding speeds for the *Kuehneosaurus* model at different mass estimates.

Mass estimates (kg)	Gliding speed at max lift/drag (m/s)
0.56	43.55
0.40	36.81
0.38	35.06
0.21	26.67
0.14	21.77

CONCLUSIONS

Kuehneosuchus and *Kuehneosaurus* were capable of aerial locomotion, the former as a glider, the latter as a parachutist. *Kuehneosuchus* probably had highly cambered wings and no additional skin membranes on hands or feet, nor did it have a cruropatagium. Lappets on the hyoid apparatus, as seen in *Draco*, were probably present to enhance pitch control.

Kuehneosuchus was capable of gliding at angles (θ) between 13 and 16 degrees, at speeds between 7 and 9 m/s, and was probably very manoeuvrable when airborne. *Kuehneosaurus* was capable of parachuting ($\theta > 45$ degrees) at speeds between 10 and 12 m/s.

Kuehneosuchus and *Kuehneosaurus* were originally described as congeneric (Robinson 1962) but later revised as two separate genera (Robinson 1967). It is, however, possible they are male and female of the same species, and that sexual display was a major, original function of the 'wings'.

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