Vol. 83 No. 1 pp. 25–32 ACTA GEOLOGICA SINICA Feb. 2009

Aerodynamic Characteristics of the Crest with Membrane Attachment on Cretaceous Pterodactyloid *Nyctosaurus*

XING Lida[1,*], WU Jianghao[2,**], LU Yi[2], LÜ Junchang[1] and JI Qiang[1]

1 *Institute of Geology, Chinese Academy of Geological Sciences, Beijing 100037, China*
2 *School of Transportation Science and Engineering, Beijing University of Aeronautics and Astronautics, Beijing 100083, China*

Abstract: The *Nyctosaurus* specimen KJ1 was reconstructed under the hypothesis that there is a membrane attached to the crest; the so-called headsail crest. The aerodynamic forces and moment acting on the headsail crest were analyzed. It was shown that KJ1 might adjust the angle of the headsail crest relative to the air current as one way to generate thrust (one of the aerodynamic forces, used to overcome body drag in forward flight) and that the magnitude of the thrust and moment could vary with the gesture angle and the relative location between the aerodynamic center of the headsail crest and body's center of gravity. Three scenarios were tested for comparison: the crest with membrane attachment, the crest without membrane attachment and the absence of a cranial crest. It was shown that the aerodynamic characteristics (increasing, maintaining and decreasing thrusts and moment) would have almost disappear in flight for the crest without membrane attachment and was non-existent without the cranial crest. It is suggested from aerodynamics evidence alone that *Nyctosaurus* specimen KJ1 had a membrane attached to the crest and used this reconstructed form for auxiliary flight control.

Key words: aerodynamic forces and moment, flight dynamic, *Nyctosaurus*, headsail crest

1 Introduction

Pterosauria (Kaup, 1834) is the first group of vertebrates that overcame gravity to fly in the sky. The notable feature is its elongated digit IV on the forelimb, which consists of three or four long, stout phalanges. The cheiropatagium attached to this finger forms wings that were capable of flight. Pterodactyloidea (Plieninger, 1901; Unwin, 2003) is one form of the Pterosauria, which includes the advanced species, some of which developed strange headsail crests.

The term pterosaurs with exaggerated crest refers to certain Pterodactyloidea which possess exaggerated head crests, a concept not based on taxonomy. These kinds of pterosaurs are distinguished by having their head crests, including parietal crests, premaxillary crests and dentary crests, which account for half of the surface of the skull. Currently the following species of Pterodactyloidea are included: *Pteranodon longiceps* (Marsh, 1876), *Pteranodon sternbergi* (Harksen, 1966) and *Nyctosaurus* sp. (Bennett, 2003) of Ornithocheiroidea (Seeley, 1901; Unwin, 2003); *Tupuxuara longicristanus* (Kellner and Campos, 1988), *Tupuxuara leonardii* (Kellner and Campos, 1994), *Tupuxuara cristata* (Frey et al., 2003b), *Thalassodromeus sethi* (Kellner and Campos, 2002), *Tapejara wellnhoferi* (Kellner, 1989), *Tapejara imperator* (Campos and Kellner, 1997) and *Tapejara navigans* (Frey et al., 2003c) of Azhdarchoidea (Unwin, 1992; Unwin, 2003). For Ornithocheiroidea and Azhdarchoidea, both of these super-orders exhibit this structure, most likely as the result of convergent evolution. However, it is noteworthy that the non-pterodactyloid pterosaur are not included in the taxonomy above, like *Austriadactylus cristatus* (Dalla Vecchia et al., 2002), *Pterorhynchus wellnhoferi* (Czerkas and Ji, 2002) and Raeticodactylus filisurensis (Stecher, 2008).

There have been additional finds of membranous soft tissue attached to the crests of pterosaurs, such as the case of the soft tissue crest of *Tapejara navigans* (Frey et al., 2003c) attached in between the suprapremaxillary spine and the rostral crest. Moreover, evidence of soft tissue was found attached to the elongated parietal spine of *Huaxiapterus benxiensis* (Lü et al., 2007).

The major hypotheses of crest function include: front rudder (Kripp, 1943; Heptonstall, 1971; Stein, 1975),

* Corresponding author. E-mail: *xinglida@gmail.com; **buaawjh@buaa.edu.cn

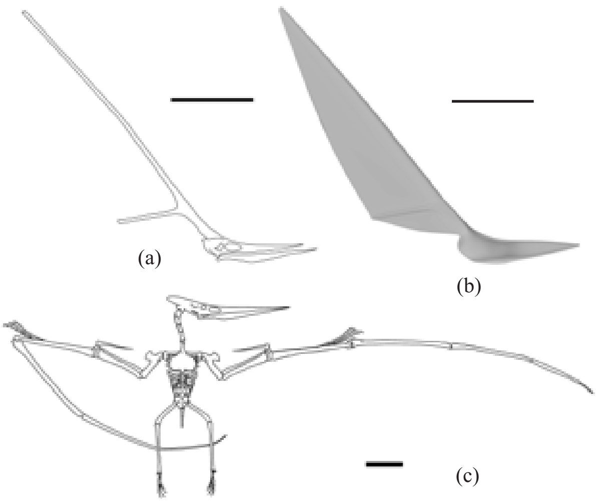

Fig. 1. a: Skull of Nyctosaurus KJ1. Scale bars, 20 cm (Bennett, 2003). b: Restoration of Skull of Nyctosaurus KJ1. Scale bars, 20cm. c: Restoration of skeleton of Nyctosaurus. Scale bars, 10 cm. (Williston, 1902).

aerodynamic counterbalance for skull (Heptonstall, 1971; Bramwell and Whitfield, 1974), airbrake (Bramwell and Whitfield, 1974), intraspecific display (Bennett, 1992, 2003), thermoregulation (Kellner and Campos, 1989) and a sign of sexual maturity (Martill and Naish, 2006). Most of these hypotheses remain in the realm of theoretical speculation and lack specific testable hypotheses. With the aid of new material in recent years, the functions of the exaggerated crest of pterosaurs are discussed from perspectives of flight dynamics and aerodynamics hereunder.

Paleontologists have brought forward their varied viewpoints in the discussion of the flight dynamics of pterosaurs (Heptonstall, 1971; Bramwell, 1971; Frey et al., 2003a; Chatterjee and Templin, 2004; Wilkinson et al., 2005). Based on the structure of the crest of *Nyctosaurus* sp. KJ1 KJ2, Bennett (2003) believes that the two branches have no membrane attached between them and they resemble the horns of cervids. Cunningham and Gerritsen (2003) hypothesized a membrane crest in *Nyctosaurus* sp., after studying aerodynamics and hydrodynamics. They believed the existence of a membrane crest would increase thrust. However, the study only exists as a meeting abstract and no further details were published.

In the present study, first, the geometric data of crest and body weight of *Nyctosaurus* sp. KJ1 according to fossil material were estimated. Second, three scenarios of aerodynamic analyses were tested based on the crest reconstructed of KJ1: the crest with membrane attachment, the crest without membrane attachment and the absence of a cranial crest. Then, the relationship between thrust, moment and the relative location between the aerodynamic center of the headsail crest and the body's center of gravity were explored. Finally, the functions of flight dynamics and aerodynamics of the crest reconstructed with three different scenarios were discussed.

2 Fossil Material

To study the aerodynamics of the pterosaurs with exaggerated crests, we select the most representative genus *Nyctosaurus* sp. (KJ1, KJ2) that has a well-preserved skull with the most exaggerated crest among currently available specimens. This research is based on the pictures provided by Dr. S.C. Bennett.

From the fossil it can be concluded that KJ1 is more completed, and is more favorable for the creation of complete aerodynamic lift surface than KJ2. So the present study is based on KJ1.

Nyctosaurus (Marsh, 1876) is a mid to small sized pterodactyloid, which possesses some typical pterodactyloid features, such as three flight phalanges (Brown, 1986), axe-shaped humerus with triangular ridge, short and broad sternum (width is 1.5 times the length), and a T-shaped neural spine on the middle of the conjoined dorsal vertebrae seen in the cranial view (Williston, 1903; Bennett, 1989, 1994). The preservation condition of *Nyctosaurus* sp. KJ1 differs from that of KJ2. The former has a well-preserved skull though the occipital skeleton is missing. The part preserved in the latter is the opposite. To accurately restore *Nyctosaurus* sp., KJ1 is taken as the object for restoration, and the missing part from KJ2 is reconstructed proportionally.

Both the crests of KJ1 and KJ2 consist of three parts, namely the superior ramus, the posterior ramus and the basal section. This crest bears a strong resemblance to the sail of a windsurfer, which is a triangular sail, supported by an L-type structure made up of a mast and a rail. The crest of KJ1 is 717 mm in greatest dimension and stands at a height of 601 mm above the skull roof, and joins the top of the skull at a 55° angle. The middle of the basal section is 22.6 mm in width. The superior ramus is 620 mm long, and the proximal end is 13.5 mm in width, whereas the distal end is 8.6 mm in width. The posterior ramus formed an angle of 7° with the top of the skull. It is 164 mm long and 9.1 mm wide (Bennett, 2003) (Fig. 1a).

By comparing the average value of the ratio of the humerus, radius, ulna, pteroid and IV metacarpus between KJ1 and KJ2, the scapular, coracoid, pteroid and femur sizes of KJ1 are summarized in Table 1. The other missing parts are sourced from the restoration of *Nyctosaurus gracilis* (Marsh, 1876) made by Williston (1902a, 1902b) (Fig. 1c). The major data are as follows: 244 cm wingspan, 15.3 cm body length, 10.2 cm body diameter, 1.5 cm waist and 2.27 kg weight. The result can be estimated from the scale that KJ1 weighs 1.55 kg with a wingspan of 167 cm. The value results in the study towards the weight of pterosaurs by Witton and Naish (2008) have been grossly underestimated, though it can be used as a reference for this paper. See the analysis of Section 3.2 D for more details.

3 Aerodynamic Analysis

3.1 Methods and assumptions

In this section, the different reconstructed crests of pterosaurs generated aerodynamic forces and moment in forward flight are determined using the methods of aerodynamics (Milne-Thomson, 1966) and flight dynamics theory (Etkin, 1982). Three situations each based on the existing restorations of skulls are taken into consideration herein: first, the crest with membrane attachment (we suppose that a membrane is attached to the crest of *Nyctosaurus* sp. KJ1 and forms an aerodynamic surface like that of a sail (Fig. 1b)); second, the crest without membrane attachment; and third, the absence of a cranial crest. For the first situation, due to the lack of membrane from fossil, it is supposed that membrane is jointed at the superior ramus, posterior ramus and at the top of the basal section. The area of the headsail crest of KJ1 is roughly 550 cm^2 from the fossil (Bennett, 2003). The second situation refers to fossil material in the second part of the paper. In the third situation, KJ1 without cranial crest would be similar to the common *Nyctosaurus* (Williston, 1902a, 1902b).

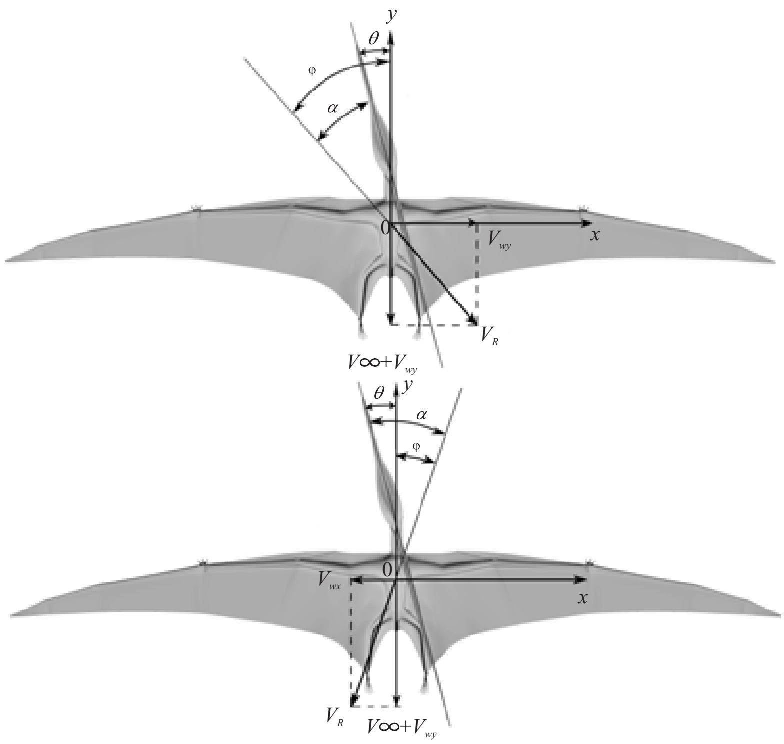

Fig. 2. The coordinate system and the gesture angles.
$\theta \geq 0$, (a) $\varphi \geq 0$, $\alpha \geq 0$; (b) $\varphi \leq 0$, $\alpha \leq 0$.

In order to facilitate the analysis of aerodynamic characteristics, the following assumptions are made: First, according to KJ1, we can estimate that the section of the headsail crest consists of a bone and a membrane and that the camber of airfoil section is zero. That is the headsail crest is rigid and no any distortion is taken into consideration for the convenience of the study even though the patagium of pterosaurs is flexible (Sugimoto, 1998). Second, it is supposed that each of the bones of the crest had a circular cross section. Third, neck muscle and bones of KJ1 can be enough to withstand the crest force and torque. Fourth, the membrane (if existent) is very thin and the distribution of its mass is well-proportioned. Finally, Pterosaurs flew at low-speed, so it is not necessary to consider compressibility of the air (the density of air varies with the flight speed), and the density of air is constant.

So the coordinate system can be defined as following: When KJ1 is balanced in the horizontal plane, *oxyz* is the coordinate system and all of the movements of it are discussed in the *oxy* plane. The origin *o* is the center of gravity, and *y* is the flight direction. Axis *x* is vertical to the *y*-axis, which is shown in Fig. 2. Axis *z* is vertical to the plane *oxy* and the direction outwards is positive. In a coordinate system, if KJ1 flies at the speed V_∞ relative to earth in still air, and the wind speed is V_w relative to earth then the relative speed of KJ1 to the air is

$$V_R = \sqrt{[(V_\infty+V_{wy})^2+V^2_{wx}]}$$

(Fig. 2, because of the benefit in downwind flight, only the flight against the wind is considered, and that is $V_\infty+V_{wy}\geq 0$). Furthermore, there are some angles defined relevant to flight movements: the angle between the axis of symmetry of the body and the headsail crest is θ (the beginning from *y*-axis anti-clockwise is positive, ranges from −90° to 90° due to the structure of the body). The angle between V_R and the axis of symmetry of the body is φ (the beginning from the *y*-axis anti-clockwise is positive, ranges from −90° to 90° against the wind). So the angle of attack between V_R and the axis of symmetry of the headsail crest is $\alpha=\varphi-\theta$ (the beginning from the axis of symmetry of the headsail crest anti-clockwise is positive. Based on aerodynamic theory, lift or normal force (*L*) increases with α from 0 degrees (Milne-Thomson, 1966), but it decreases when α has reached a certain value, namely stalling. For the headsail crest of KJ1 with such a section, the α in stalling is from about 20^o (Wilkinson, 2005). To avoid stalling, the

Table 1 Measurements of *Nyctosaurus sp.* KJ1, KJ2 (mm) (Bennett, 2003, amended)

	KJ1	KJ2	KJ2/ KJ1
Skull	245	316	1.29
Upper jaw	210	270	1.29
Lower jaw	242	299	1.24
Scapula	"43.5"	R54.4; L56.0	–
Coracoid	"37.5"	R48.3; L47.0	–
Humerus	61.8	72.3	1.17
Radius	107	132	1.23
Ulna	107	142	1.28
Pteroid	82.9	121	1.46
Metacarpal IV	202	243	1.20
Wing Phalanx 1	"227.6"	289	–
Wing Phalanx 2	"119.7"	152	–
Wing Phalanx 3	"89"	113	–
Femur	"56.2"	R71.9; L70.9	–
Tibiotarsus	"65.9"	R83.6; L83.8	–

Note: The number inside the quotation mark is the estimated value.

ranges of α from $-20°$ to $20°$ are discussed herein).

3.2 Thrust and angles relevant to flight

If α is not zero, based on aerodynamics (Milne-Thomson, 1966) the speeds and pressures of the surface on two sides of the headsail crest are different (Bernoulli's theorem). Integral surface pressure and friction of airfoil, the total aerodynamic force F_{total} is obtained (Fig. 3). It can be broken down into two components, which are perpendicular to each other: the tangential force D that shares the same direction with $V_{R'}$ and the normal force L that is perpendicular to V_R in the coordinate system (Etkin, 1982). Moreover, the aerodynamic moment would be generated if the aerodynamics center does not overlap the body's center of gravity.

To analyze the force on the headsail crest, the origin is moved to the axis of symmetry of the headsail crest horizontally, as seen in Fig. 4. So the total aerodynamic force is F_{total} (Decomposing L and D or F_{total} directive to ox and oy respectively, thrust (T) and lateral force (F_l) of the headsail crest come out.).

In general, the speed of a pterosaur in flight ranged from 10 m/s to 20 m/s (Bramwell and Whitfield, 1974), and the speed of wind V_w is considered ranging from 0 m/s to 12 m/s. In this paper, the $V_R \approx 20$m/s is taken as the reference speed. As a result, the normal force coefficient C_L and the tangential force coefficient C_D are obtained by non-dimensionalizing L and D, respectively (S=550 cm^2 as the reference area) as followingfollows:

$C_L = 2L/(\rho V_R^2 S)$ (1)

$C_D = 2D/(\rho V_R^2 S)$ (2)

Similarly, we can obtain thrust coefficient C_T, lateral force coefficient C_{F1} and total aerodynamic force coefficient $C_{F\text{total}}$ as following:

$C_T = 2T/(\rho V_R^2 S)$ (3)

$C_{Fl} = 2F_l/(\rho V_R^2 S)$ (4)

$C_{F\text{total}} = F_{total}/(0.5\rho V_R^2 S)$ (5)

where ρ=1.225 kg/m^3, the density of air.

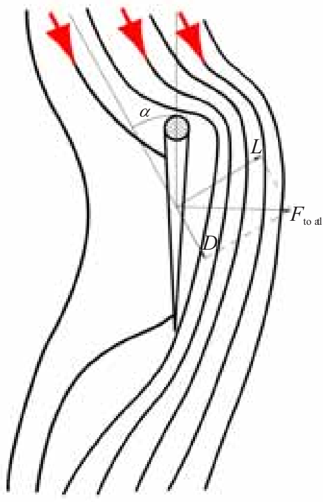

Fig. 3. The sketch of aerodynamics generation due to angle of attack (α) for a symmetric airfoil.

Then, the following formulas can be yielded from the documents (Etkin, 1982):

$C_L = C_{La} \cdot \alpha$ (6)

$C_D = C_{D0} + KC_L^2$ (7)

where the constants are C_{La}=3; C_{D0}=0.01; K=0.05 (C_{La} is the slope of lift line; C_{D0} is the drag coefficient, while lift is zero; $C_{Di}=KC_L^2$ is the induced drag, Etkin, 1982, pp53).

According to Fig. 4, the relationships are listed as followingfollows:

$C_T = C_L \sin(\varphi) - C_D \cos(\varphi)$ (8)

$C_{Fl} = C_L \cos(\varphi) - C_D \sin(\varphi)$ (9)

take equations (6) and (7) to equations (8) and (9),

$C_T = \alpha C_{La} \sin(\varphi) - (C_{D0} + K\alpha^2 C_{L\alpha}^2) \cos(\varphi)$ (10)

$C_{Fl} = \alpha C_{La} \cos(\varphi) - (C_{D0} + K\alpha^2 C_{L\alpha}^2) \sin(\varphi)$ (11)

According to the range of θ, φ and α defined above, the curve group of the thrust coefficient (C_T) versus the angle of attack (α) under different φ and θ is drawn and shown in Fig. 5.

The results can be obtained from Fig. 5 for the crest reconstructed with membrane attachment as following:

(A) In forward flight against the wind, thrust could be generated by the crest with membrane attachment. It might be a positive value to benefit in overcoming body drag in cruising or a negative value to braking. When φ is fixed (wind and flight direction are fixed), only altering θ (making the neck turn right or left) can change the thrust between a positive value and a negative value.

(B) When φ is fixed (wind and flight direction are fixed), C_T keeps growing with α increased. KJ1 can get the maximum C_T by altering α or θ (KJ1 makes its neck turning right or left), which is under a certain speed of wind to get appropriate α to produce thrust by adjusting θ. In Fig. 5, the maximum C_T is about 1.

(C) When C_T and V_w are fixed (in cruising), in order to

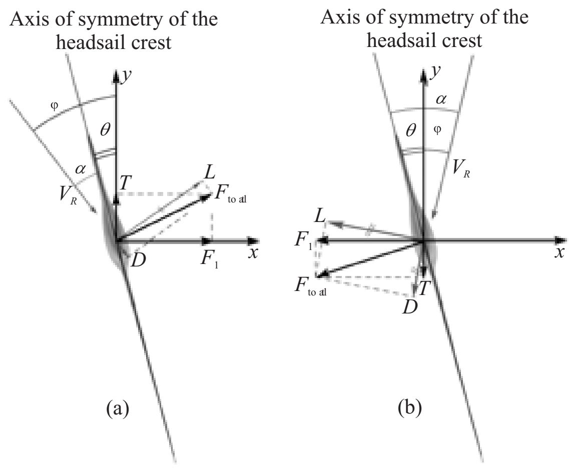

Fig. 4. The loading analysis of KJ1.
$\theta \geq 0$, (a) $\varphi \geq 0$, $\alpha \geq 0$; (b) $\varphi \leq 0$, $\alpha \leq 0$.

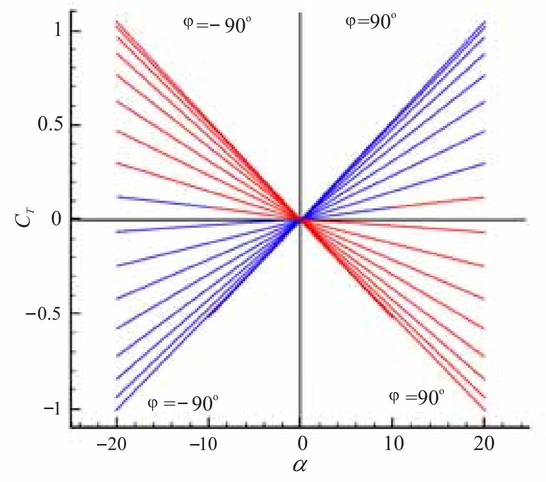

Fig. 5. C_T versus α curve group for the crest reconstructed with membrane attachment.
$-90°\leq\varphi\leq90°$, the interval is 10°, $-20°\leq\alpha\leq20°$, red line: $-90°\leq\theta\leq0°$, the head turns right; blue line: $0°\leq\theta\leq90°$, the head turns left.

minimize θ, KJ1 can change φ (that is the direction of flight). Not only does KJ1 realize θ to the minimum for ensuring forward vision, but it also keeps a reasonable α to produce the thrust needed.

(D) For comparison, with a wing span of 167 cm, the mass of KJ1 being 1.55 kg is a reasonable assumption. From Fig. 5, the maximum of C_T could exceed 1 (for the crest reconstructed of KJ1 with the membrane attachment above, it is estimated that the thrust T_{max} is about 14.15 N), which is considerably large (93%) in relation to the weight of KJ1. Therefore, thrust generated by the crest with membrane attachment could serve as one of the propulsive forces (overcome body drag in forward flight) for KJ1.

In the situation of the crest reconstructed without the membrane attachment (bones only), the aerodynamic forces are obtained (L and D) by the method of Computational Fluid Dynamics (CFD), where the reference area S=102.27 mm^2 is from fossils of the orthographic projection, and the reference velocity $V_R \approx 20$ m/s is the same as the situation of the crest with membrane attachment. The results from CFD are shown in Fig. 6.

Based on Fig. 6 and equation (8), the maximum value of C_T yields 0.096. Similarly, it is estimated that the thrust (T) of the crest reconstructed without the membrane attachment is about 0.24 N (accounting for 1.6% body weight), which is far less than that of the crest reconstructed with the membrane attachment. Therefore, it is impossible that thrust generated by the crest without the membrane attachment could serve as one of the propulsive forces (overcome body drag in forward flight) for KJ1.

3.3 Approach of increasing, maintaining and decreasing thrusts (T) and moment (Mz)

The aerodynamic moment generated by the aerodynamic

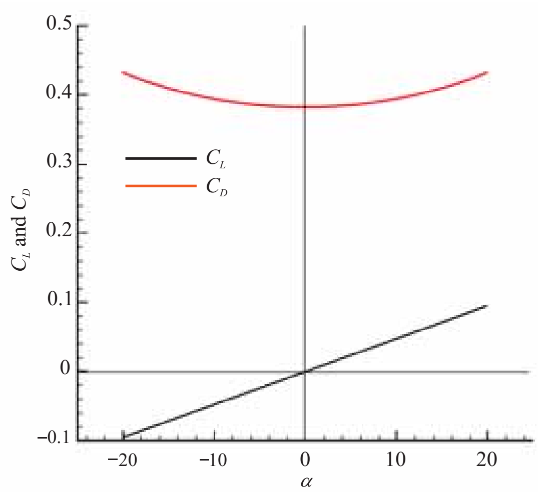

Fig. 6. C_L and C_D vary with α for the crest reconstructed without membrane attachment.

forces surrounding the body's center of gravity should attract attention. Mz is mainly analyzed here (direction of z-axis is positive, it can mainly allow changing the direction of flight in cruising in KJ1). According to the restoration of the crest with or without the membrane attachment, the position of the aerodynamics center can be measured by the method of plane graphing (Raymer, 1999, pp 49), shown in Fig. 7 (for the crest with membrane attachment as an example). The method for measuring the position of the body's center of gravity is referred to as the reference of Bramwell and Whitfield. While flying, KJ1 pitches its head, after which the relative position of the aerodynamics center and the body's center of gravity vary in the following attitude:

First, it is defined that the direction of F_{total} intersected the plane of symmetry of KJ1's body at point A. Then,

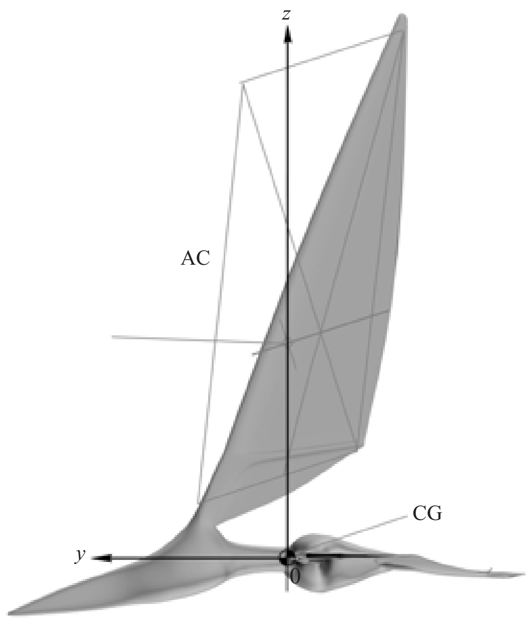

Fig. 7. The sketch of measuring the position of the aerodynamic center (the crest with membrane attachment).

three possible relative locations between point A and the center of gravity are discussed as followings:

(1) When A is on *oz* axis (the body's center of gravity is at point *o*), then Mz=0 regardless of what F_{total} is. In this case, KJ1 needs to constantly adjust the pitch of the head slightly to fit the changing air current (namely the changing of V_R). Meanwhile KJ1 could also gain thrust by keeping θ (or α) and φ in the appropriate magnitude, which would contribute to the flapping wing propulsion (if T>0), and reduce the consumption of energy for a long distance cruise. It is supposed that this situation may be the common strategy during the animal's long distance flying.

(2) When KJ1 pitches its head down, A is located in front of the center of gravity from the view Fig. 8a (namely in the positive direction of *y*-axis). When KJ1 flies in balance, T, φ and θ (or α) keep constant at a certain time. At this time, if the crest is disturbed initiative by itself or passive by the air current to make α increased (or θ decreased), T would be increased (seen in Fig. 5) and Mz would be decreased (seen in Fig. 8a; solid, V_R is from the left side of the head; dotted line, V_R is from the right side of the head). On the contrary, if α is decreased (or θ increased), then T would be decreased and Mz would be increased. This may be the way for KJ1 to make thrust (T) increased (or decreased) and at the same time moment (Mz) decreased (or increased).

(3) When KJ1 raises its head, A is located behind the body's center of gravity from the view Fig. 8b (namely the negative direction of the *y*-axis). Similarly, when KJ1 flies in balance, T, φ and θ (or α) keep constant at a certain time. At this time, if the crest is disturbed initiative by itself or passive by the air current to make α increased (or θ decreased), T would be increased (seen in Fig. 5) and Mz would be increased too (in contrast with the above-mentioned result, seen in Fig. 8b; solid, V_R is from the left side of the head; dotted line, V_R is from the right side of the head). On the contrary, if α is decreased (or θ increased), both T and Mz would be decreased. This may be the way for KJ1 to make thrust (T) and moment (Mz) increased (or decreased) at the same time.

To summarize: KJ1 might be able to control (increasing, maintaining and decreasing) thrust (T) and moment (Mz) with the same or reverse changes by adjusting gesture angle and the pitch of the headsail crest.

3.4 Comparison of three reconstructed crest forms

First, for the purposes of comparison, three possible forms reconstructed with the crest with membrane attachment, without membrane attachment and the absence of cranial crest are named Form1, Form2 and Form3,

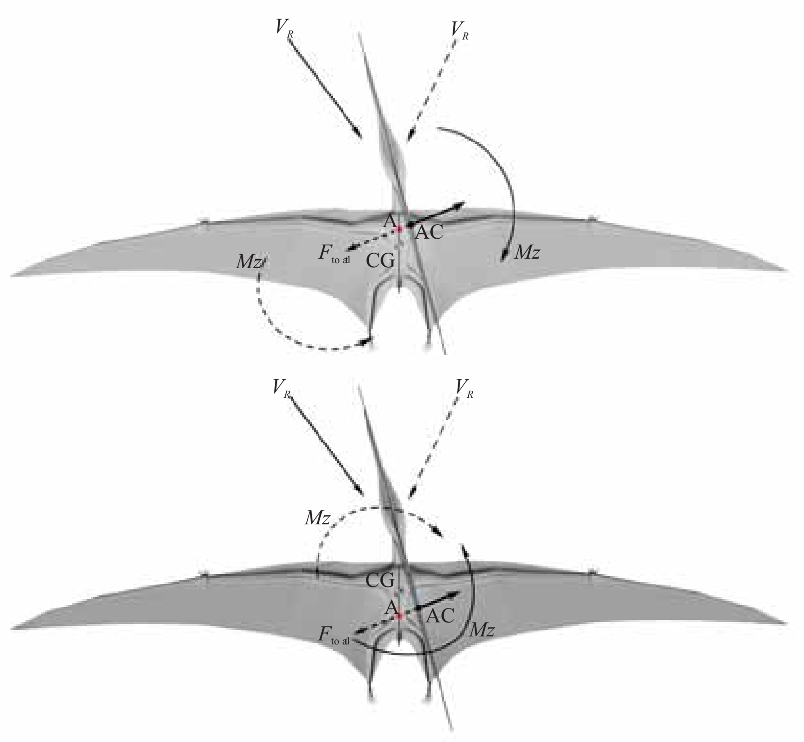

Fig. 8. Aerodynamic force (F_{total}) and momentum (Mz) vary with the relative positions between the aerodynamic center and the center of gravity (solid: V_R is from the left side of the head; dotted line: V_R is from the right side of the head).
a: A is located in front of the body's center of gravity; b: A is located behind the body's center of gravity.

respectively.

According to section 3.2, in forward flight against the wind, Form1 and Form2 could generate thrust, but the magnitude is very different in two forms (for KJ1, thrust ranges from −14.15 N to 14.15 N of Form1 and from −1.08 N to 0.24 N of Form2). Form1 effects on overcoming body drag of KJ1 for auxiliary flight propulsion or braking obviously than Form2. Form3 almost could not generate the thrust in flight.

Based on the section 3.3, thrust (T) and moment (Mz) can be increased, maintained and decreased the same or reversely by adjusting the gesture angle and the pitch of the crest for Form1 and Form2. The effects of T and Mz of Form1 are stronger than that of Form2 because of the different variable ranges of T. It is possible that Form1 can make KJ1 turn right or left and accelerate or decelerate rapidly. Of course, there are no aerodynamic and flight dynamic functions for Form3.

4 Conclusion

Based on the analysis above, we conclude that the huge headsail generates aerodynamic force (thrust, which is almost over 90% of the body weight). By adjusting the angle of the crest in relation to the air current, KJ1 could generate considerable thrust toward the direction of flight, and control the thrust and moment increasing, maintaining and decreasing the same or reversely by changing the gesture angle and the relative position of the aerodynamic center and the body's center of gravity.

Comparison of the aerodynamic and flight dynamic analysis of the crest of KJ1 with membrane attachment, without membrane attachment and the absence of cranial crest, shows that the above aerodynamic characteristics would almost disappear in flight for the crest without membrane attachment and would be non-existent without the cranial crest. In those cases the exaggerated crest of the animal would have few aerodynamic characteristics.

Acknowledgements

The authors thank S.C. Bennett (Fort Hays State University, USA), Margot Gerritsen (Stanford University, USA) and James R. Cunningham (Stanford-National Geographic Pterosaur Replica Project, USA) for their kind help. We thank anonymous reviewers for comments on earlier drafts of this manuscript. We are indebted to David M. Unwin (University of Leicester, UK) and Peter Dodson (University of Pennsylvania, USA) who made critical comments and suggestions on this paper. Thanks for Zhao Chuang who drew the relative 3D pictures and the restorations. Thanks for the assistance of You Hailu, Charles Damien Lu, Jiang Hua and Zhu Wei. This research was supported by the Chinese Ministry of Science and Technology (973 Project, 2006CB701405), China Geological Survey, National Geographic (China Edition) and China Aviation Media Group.

Manuscript received May 19, 2008
accepted Nov. 27, 2008
edited by Jiang Shaoqing

Reference

Bennett, S.C., 1989. A pteranodontid pterosaur from the Early Cretaceous of Peru, with comments on the relationships of Cretaceous pterosaurs. *Journal of Paleontology*, 63: 669–677.

Bennett, S.C., 1992. Sexual dimorphism of *Pteranodon* and other pterosaurs, with comments on cranial crests. *Journal of Vertebrate Paleontology*, 12: 422–434.

Bennett, S.C., 1994. Taxonomy and systematics of the Late Cretaceous pterosaur Pteranodon (Pterosauria, Pterodactyloidea). University of Kansas, *Occasional Papers*, 169, 1–70.

Bennett, S.C., 2003. New crested specimens of the Late Cretaceous *Nyctosaurus*. *Palaontologische Zeitschrift*, 77(1): 61–75.

Bramwell, C.D., 1971. Aerodynamics of *Pteranodon*. *Biological Journal of the Linnean Society*, 3: 313–328.

Bramwell, C.D., and Whitfield, G.R., 1974. Biomechanics of *Pteranodon*. *Philosopical Transactions of the Royal Society, London* (*B*), 267, 503–581.

Brown, G.W., 1986. Reassessment of *Nyctosaurus:* new wings for an old pterosaur. *Nebraska Academy of Sciences, Proceedings*, 47 (Abstract).

Campos, D.A., and Kellner, A.W.A., 1997. Short note on the first occurrence of Tapejaridae in the Crato member (Aptian), Santana Formation, Araripe Basin, Northeast Brazil. *Anais da Academia Brasileira de Ciências*, 69 (1): 83–87.

Chatterjee, S., and Templin, R.J., 2004. Posture, Locomotion, and Paleoecology of Pterosaurs. *Geological Society of America, Special Paper*, 376: 1–64.

Cunningham, J.R., and Gerritsen, M., 2003. American Physical Society, Division of Fluid Dynamics 56th Annual Meeting. Meeting ID: DFD03. (Abstract).

Czerkas, S.A., and Ji, Q., 2002. A new rhamphorhynchoid with a headcrest and complex integumentary structures. In: Czerkas, S.J. (Ed.), *Feathered Dinosaurs and the Origin of Flight*. The Dinosaur Museum, Blanding, Utah, 15–41.

Dalla Vecchia, F.M., Wild, R., Hope, H., and Reitner, J., 2002, A crested rhamphorhynchoid pterosaur from the Late Triassic of Austria. *Journal of Vertebrate Paleontology*, 22(1): 196–199.

Etkin, B., 1982. *Dynamics of Flight-Stability and Control* (2nd Edition). Toronto: John Wiley and Sons, 1–382.

Frey, E., Buchy, MC., Martill, DM., Buffetaut, E., and Mazin, J. M., 2003a. Middle- and bottom-decker Cretaceous pterosaurs: unique designs in active flying vertebrates. *Evolution and Palaeobiology of Pterosaurs, Geological Society Special Publication*, 267–274.

Frey, E., Martill, D.M., and Buchy, M.C., 2003b. A new crested ornithocheirid from the Lower Cretaceous of northeastern Brazil and the unusual death of an unusual pterosaur. In:

Buffetaut, E., and Mazin, J.M. (eds) *Evolution and Palaeobiology of Pterosaurs,* Geological Society, London, Special Publications, 217: 55–63.

Frey, E., Martill, D.M., and Buchy, M.C., 2003c. A new species of tapejarid pterosaur with soft-tissue head crest. *In*: Buffetaut, E. and Mazin, J. M. (eds) *Evolution and Palaeobiology of Pterosaurs,* Geological Society, London, Special Publications, 217: 65–72.

Harksen, J.C., 1966. *Pteranodon sternbergi,* a new fossil pterodactyl from the Niobara Cretaceous of Kansas. *Proceedings of the South Dakota Academy of Sciences*, 45: 74–77.

Heptonstall, W.B., 1971. An analysis of the flight of the Cretaceous pterosaur *Pteranodon ingnes* (Marsh). *Scottish Journal of Geology*, 7: 61–78.

Kaup, J.J., 1834. Versuch einer Eintheilung der Säugethiere in 6 Stämme und der Amphibien in 6 Ordnungen. *Isis, Jena*, 3: 1–315.

Kellner, A.W.A., 1989. A new edentate pterosaur of the Lower Cretaceous from the Araripe Basin, northeast Brazil. *Anais da Academia Brasileira de Ciências*, 61(4): 439–446.

Kellner, A.W.A., and Campos, D.A. 1988. Sobre un novo pterossanro corn crista sagital da Bacia do Araripe, Cretficeo Inferior do Nordeste do Brasil. (Pterosauria, *Tupuxuara,* Cretaceo, Brasil). *Anais da Academia Brasileira de Ciências,* 60: 459–469.

Kellner, A.W.A., and Campos, D.A., 1989. Sobre um novo pterosauro com crista sagittal da Bacia do Araripe, Cretáceo Inferior do nordeste do Brasil. *Anais da Academia Brasileira de Ciências,* 60: 459–469.

Kellner, A.W.A., and Campos, D.A., 1994. A new species of *Tupuxuara* (Pterosauria, Tapejaridae) from the Early Cretaceous of Brazil. *Anais da Academia Brasileira de Ciências*, 66: 467–473.

Kellner, A.W.A., and Campos, D.A., 2002. The function of the cranial crest and jaws of a unique pterosaur from the Early Cretaceous of Brazil. *Science*, 297: 389–392.

Kripp, D., 1943. Ein Lebensbild von *Pteranodon ingens*. *Nova Acta Leopoldina*, 12: 217–286.

Lü Junchang, Gao Yubo, Xing Lida, Li Zhixin and Sun Zhenyuan, 2007. New species of *Huaxiapterus* from the Early Cretaceous of western Liaoning. *Acta Geologica Sinica* (English edition), 81(5): 683–687.

Marsh, O.C., 1876, Notice of a new sub-order of Pterosauria. *American Journal of Science*, 11(3): 507–509.

Martill, D.M., and Naish, D., 2006. Cranial crest development in the azhdarchoid pterosaur *Tupuxuara*, with a review of the genus and tapejarid monophyly. *Palaeontology*, 49: 925–941.

Milne-Thomson, L.M., 1966. *Theoretical Aerodynamics* 4th Edition, Dover, New York: Dover Publications, 1–430.

Plieninger, F., 1901. Beiträge zur Kenntnis der Flugsaurier. *Palaeontologica*, 48: 65–90.

Raymer, D.P., 1999. *Aircraft Design: A Conceptual Approach, 3rd Ed*., AIAA, Washington, USA, 1–745.

Seeley, H.G., 1901. *Dragons of The Air. An Account of Extinct Flying Reptiles.* London: Methuen, 1–239.

Stecher, R., 2008. A new Triassic pterosaur from Switzerland (Central Austroalpine, Grisons), *Raeticodactylus filisurensis* gen. et sp. nov. Swiss Journal of Geosciences 101: 185. doi:10.1007/s00015-008-1252-6. Online

Stein, R.S., 1975. Dynamic analysis of Pteranodon ingens: A reptilian adaptation to flight. *Journal of Palaeontology*, 9: 534–548.

Sugimoto, T., 1998. On flapping characteristics of ancient animals' flexible wings. *Theor. Appl. Mech*., 47: 215–222.

Unwin, D.M., 1992. The phylogeny of the Pterosauria. *Journal of Vertebrate Paleontology*, 12(3) (supplement): 57A.

Unwin, D.M., 2003. On the phylogeny and evolutionary history of pterosaurs. In: Buffetaut, E. and Mazin, J. M. (eds) *Evolution and Palaeobiology of Pterosaurs,* Geological Society, London, Special Publications, 217: 139–190.

Wilkinson, M.T., Unwin, D.M., and Ellington, C.P., 2005. High Lift function of the Pteroid Bone and Forewing of Pterosaurs. *Proceedings of the Royal Society*, doi:10.1098/rspb.2005.3278.

Williston, S.W., 1902a. On the skeleton of *Nyctodactylus*, with restoration. *American Journal of Anatomy*, 1: 297–305.

Williston, S.W., 1902b. On the skull of *Nyctodactylus*, an Upper Cretaceous pterodactyl. *Journal of Geology*, 10: 520–531.

Williston, S.W., 1903. On the osteology of *Nyctosaurus (Nyctodactylus),* with notes on American pterosaurs. *Field Columbian Museum, Geological Series, Publication Series*, 2: 125–163.

Witton, M.P., and Naish, D., 2008. A Reappraisal of Azhdarchid Pterosaur Functional Morphology and Paleoecology. PLoS ONE 3(5): e2271. doi:10.1371/journal.pone.0002271.