Cranial kinesis in palaeognathous birds

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Summary

Cranial kinesis in birds is induced by muscles located caudal on the cranium. These forces are transferred onto the moveable parts of the skull *via* the Pterygoid–Palatinum Complex (PPC). This bony structure therefore plays an essential role in cranial kinesis. In palaeognathous birds the morphology of the PPC is remarkably different from that of neognathous birds and is thought to be related to the specific type of cranial kinesis in palaeognaths known as central rhynchokinesis. We determined whether clear bending zones as found in neognaths are present in the upper bill of paleognaths, and measured bending forces opposing elevation of the upper bill. A static force model was used to calculate the opening forces that can be produced by some of the palaeognathous species. We found that no clear bending zones are present in the upper bill, and bending is expected to occur over the whole length of the upper bill.

Muscle forces are more than sufficient to overcome bending forces and to elevate the upper bill. The resistance against bending by the bony elements alone is very low, which might indicate that bending of bony elements can occur during food handling when muscles are not used to stabilise the upper bill. Model calculations suggest that the large processi basipterygoidei play a role in stabilizing the skull elements, when birds have to resist external opening forces on the upper bill as might occur during tearing leafs from plants. We conclude that the specific morphology of the palaeognathous upper bill and PPC are not designed for active cranial kinesis, but are adapted to resist external forces that might cause unwanted elevation of the upper bill during feeding.

Key words: cranial kinesis, palaeognathae, cranial morphology, adaptation, external force.

Introduction

Cranial kinesis is an important character of the feeding behaviour of birds and, to a lesser extent, of reptiles (Bock, 1964; Iordansky, 1990; Herrel et al., 2000). In birds cranial kinesis is characterised by the ability to move the upper bill or a part thereof relative to the cranium. It is generally accepted that the movement within bony parts of the beak occurs in bending zones, which are clearly recognisable as discrete areas of thin bone (Zusi, 1984). The force for the movement of the upper bill is generated by jaw muscles situated in the caudal part of the orbit and transferred to the bill through a linkage of bony elements in the palate (Bock, 1964; Gussekloo et al., 2001).

Most birds are able to move the upper bill as a whole, a situation known as prokinesis (Fig. 1A; Bock, 1964). In prokinetic birds the bending zone between the skull and the moveable upper bill is situated at the nasal–frontal hinge. Other bending zones are situated on the transition between the palate and the upper bill and between the jugal bar and the upper bill. The prokinetic upper bill itself contains no flexible zones and is rigid. This type of cranial kinesis is considered the most basic form within modern birds (Neognathae; Bock, 1964).

Several other types of cranial kinesis can be distinguished, based on different positions of the bending zones (Fig. 1). After prokinesis the second most common type is the rhynchokinetic configuration (Zusi, 1984). In this type the bending zones are positioned further rostrally, within the upper bill. Therefore only a small portion of the upper bill is moveable, and no flexible zone is present near the nasal–frontal connection. In the rhynchokinetic configuration clear bending zones are present in both the dorsal and ventral bars of the upper bill (Fig. 1B).

In addition to the presence of bending zones, rhynchokinesis has consequences for the rest of the configuration of the skull. To make movement of the rostral part of the upper bill possible, the dorsal and ventral bony bars of the upper beak have to move with respect to each other. The uncoupling of the movement of the two bars is generally achieved by a schizorhinal nostril (Fig. 1B). This type of nostril is characterised by a flexible lateral bar and the attachment of the dorsal part of the lateral bar caudal, instead of rostral to the nasal–frontal articulation (Zusi, 1984).

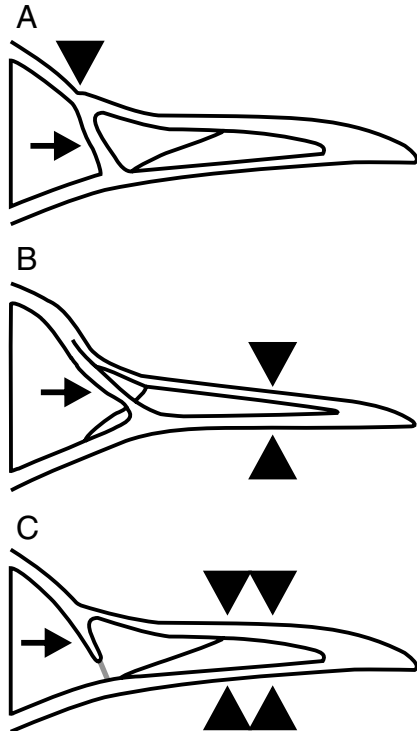Although the main division in types of cranial kinesis is

Fig. 1. Types of cranial kinesis in birds. (A) prokinesis, (B) distal rhynchokinesis and (C) central rhynchokinesis. Skull outlines are given in lateral view. Black triangles indicate the main area of rotation, multiple triangles in a single element indicate the boundaries of an bending zone. The triangle in A indicates the nasal–frontal articulation. Arrows indicate the lateral (nasal) bar of the upper bill, which is incomplete in C. Ligament is shown in grey. (Adapted from Zusi, 1984.)

Fig. 2. Ventral view of the skull of a rhea. A, vomer; B, palatinum; C, rostrum parasphenoidale; D, processus basipterygoideus; E, pterygoid; F, quadrate.

between prokinetic and rhynchokinetic skulls, a number of sub-divisions are recognized within the rhynchokinetic skulls, which are characterized by different positions of the flexible zones in the dorsal and ventral bar (Zusi, 1984). In most of these types of rhynchokinetic skulls a schizorhinal nostril is present, except in central rhynchokinesis in which a holorhinal nostril is found, which has a configuration similar to that of the nostril in the prokinetic morphology. In this type of skulls uncoupling of the dorsal and ventral bar is achieved by a reduction of the lateral bar, resulting in a ligamentous part in the lateral bar of the upper bill (Fig. 1C). Bühler (1981) has described the bending zones in the central rhynchokinetic configuration to be long and located near the center of the upper bill. This description of the bending zones in central rhynchokinesis is endorsed by Zusi (1984), but it is unclear how the position of these bending zones was determined. It is remarkable that this type of rhynchokinesis is described for one avian taxon only: the Palaeognathae. Central rhynchokinesis is therefore also referred to as palaeognathous rhynchokinesis. The conclusion that palaeognathous birds might be rhynchokinetic has been drawn mainly from analyses of skull only. Recently, however, behavioural data showed that bending actually occurs in the upper bill of the Palaeognathae
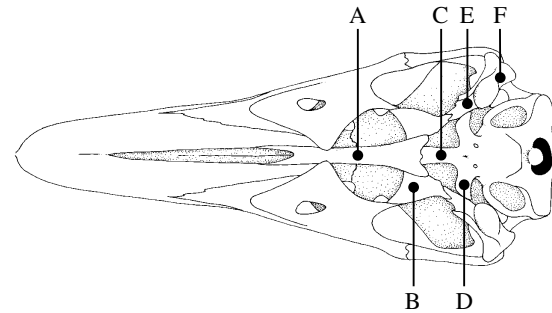
during feeding. The data also showed that bending occurs in a large area, confirming the description of central rhynchokinesis (Gussekloo and Bout, 2005).

The Palaeognathae is one of the taxa of the most basal sub-division within the taxon Aves (Cracraft, 1974; Sibley and Ahlquist, 1990). This basal subdivision divides the taxon Aves into the Palaeognathae and the Neognathae. The Palaeognathae is a small taxon, approximately 60 species, *vs* 8000 species in the Neognathae. Only a few, mainly cranial, morphological characters distinguish the Palaeognathae from the Neognathae (Olson, 1985). The most important character is the presence of the palaeognathous Pterygoid–Palate Complex (PPC, Fig. 2; Gussekloo and Zweers, 1999) also known as the palaeognathous (=dromaeognathous) palate (Huxley, 1867). The PPC consists of the bony elements pterygoid, palatinum and vomer. In Palaeognathae the PPC is rigid and lacks the flexible articulations between elements found in Neognathae (McDowell, 1948; Bock, 1963).

In birds in general the PPC, in combination with the quadrate, has a clear function in the movement of the upper bill. The movement of the upper bill is caused by a forward rotation of the quadrate, which is transferred to the upper bill *via* the PPC (Bock, 1964; Gussekloo et al., 2001). It has always been assumed that the PPC in the Palaeognathae serves the same function, but that a specialised morphology of the PPC is required for effective central rhynchokinesis (Bock, 1963; Hofer, 1954; Simonetta, 1960). Recently it has been shown that the movement patterns of the neognathous and palaeognathous PPC are comparable (Gussekloo et al., 2001). This contradicts the hypothesis that there is a functional relationship between the type of cranial kinesis and the specific morphology of the palaeognathous palate. Without a clear relationship between the morphology of the PPC and central rhynchokinesis the origin of the palaeognathous PPC might be completely different.

Several advantages of a kinetic skull have been suggested (see Zusi, 1993), including higher biting forces (Zweers et al., 1997) and higher closing speeds (Herrel et al., 2000). However, the functional interpretation of cranial kinesis in birds is still problematic and a general explanation might not hold. While for some taxa, such as the Charadriiformes, the type of cranial

kinesis is linked to specific ways of feeding (Zusi, 1984; Kooloos et al., 1989; Zweers and Gerritsen, 1997), cranial kinesis may be an inherent feature of the design of the skull in others (Bout and Zweers, 2001; Herrel et al., 2000). At present the exact role of cranial kinesis in the feeding behaviour of the Palaeognathae is unknown, although it is clear that it does not have the same function as in Charadriiformes, which use rhynchokinesis to catch prey that is buried in the substrate (Gussekloo and Bout, 2005).

Since it seems that there is no direct connection between the palaeognathous PPC and rhynchokinesis, we must consider other options with respect to the origin of the specific morphology of the palaeognathous PPC. When looking at bending in the upper bill there are two options: the upper bill may either bend intentionally by applying muscle force (as in Charadriiformes), or the upper bill can bend as a result of external forces when picking up food items. In living animals these external forces might be counteracted by muscle force, but this will not be noticed when only looking at osteological specimens. In that case a non-rigid configuration may be falsely identified as adapted to induced rhynchokinesis.

To determine whether the skull of the Palaeognathae is truly adapted to induced (active) rhynchokinesis we test whether the morphology of the skulls of the Palaeognathae fits the requirements for effective rhynchokinesis on the basis of a number of characters found in known rhynchokinetic birds, such as Charadriiformes (Zusi, 1984; Gerritsen, 1988). The specific characters of known rhynchokinetic species are: (1) the presence of an uncoupling of the movement of the dorsal and ventral bar, (2) the presence of clear bending zones in both the ventral and dorsal bar of the upper bill, and (3) a configuration of muscles and bony elements in the skull that results in sufficient force output to open the upper bill. The uncoupling of the dorsal and ventral bar in the Palaeognathae is achieved by a ligamentous part in the lateral bar and has been described before (Fig. 1C; Bock, 1963, 1964; Zusi, 1984). Therefore we only address the presence of bending zones and analyses of forces.

To test the alternative hypothesis in which the palaeognathae possess an upper bill morphology that is intrinsically flexible and actively stabilised by muscle force, we analysed the intrinsic resistance against bending during closing of the bill, and the amount of muscle force that can be used to stabilise the upper bill. By comparing the data we determined whether the Palaeognathae are truly rhynchokinetic or that the characters of the upper bill and PPC are the result of other factors, and try to elucidate the possible function of the specific upper bill configuration of the Palaeognathae.

Materials and methods

Three species of palaeognathous birds were used for the analysis: the ostrich *Struthio camelus* L. from Africa, the greater rhea *Rhea americana* (L.) from South America and the emu *Dromaius novaehollandiae* Latham from Australia. Two specimens of both the emu and rhea and three specimens of the ostrich were used. All specimens were heads of adult

deceased birds, which had been stored at a temperature of –20°C and defrosted completely before the experiments. For force measurements on the upper bill (see below) the skin of the cranium was removed to facilitate fixation in the experimental set-up. The integument of the bill and all other parts of the skull were kept intact. After the force measurements the skulls were dissected for the muscle and skull measurements, and for histological processing.

Skull measurements

To test whether flexible zones are present in the upper bill of the palaeognathous birds the thickness of the ventral and dorsal elements was measured. The measurements were performed on both sides of the specimens used for the force measurements. The thickness of both ventral bars and the dorsal bar were measured using a digital calliper rule (Sylvac, Crissier, Switzerland; accuracy 0.01 mm). One ostrich bill was used to make transverse sections, which were stained according to the van Gieson technique (Bradbury and Keith, 1990) and used to measure the thickness of the dorsal and ventral bars more accurately under a dissection microscope using a measuring eyepiece. For comparison, the thickness of the dorsal and ventral bars were measured in a similar way in transverse sections of the bills of the purple sandpiper *Calidris maritima* (Brunnich) and the sanderling *Calidris alba* (Pallas), which have a clear distal rhynchokinetic skull. All thickness measurements were scaled to the head width, measured at the quadrato–jugal articulation, to eliminate potential size differences between individuals.

Intrinsic force measurements of the upper bill

The forces necessary to elevate the upper bill were measured using a force transducer (Aikoh, Osaka, Japan). The head was fixed with screws on each side, and a bar was attached to the skull to prevent dorso-ventral rotation (Fig. 3). The force transducer was attached to the tip of the upper bill. For elevation a small hook was attached to the upper bill and the force transducer was slowly moved upward by a step motor. The force transducer moved with a speed of 5 mm s^{-1} while elevation force and distance were recorded continuously. During the experiments the skull was videotaped from a lateral viewpoint. These recordings were later used to determine the position of maximal bending due to external forces. All experiments were performed at room temperature.

Muscle forces

The jaw muscles acting in feeding behaviour can be divided into five major functional groups: (1) opener of the lower bill (musculus depressor mandibulae), (2) closer of the upper and lower bill acting on the pterygoids and lower jaw (musculus pterygoideus), (3) closers of the lower bill (musculus adductor mandibulae externus complex), (4) closers of the upper and lower bill acting on the quadrates (adductor complex of the quadrate: musculus pseudotemporalis profundus and musculus adductor mandibulae ossis quadrati), and (5) opener/elevator of the upper bill (protractor complex of the quadrate: musculus
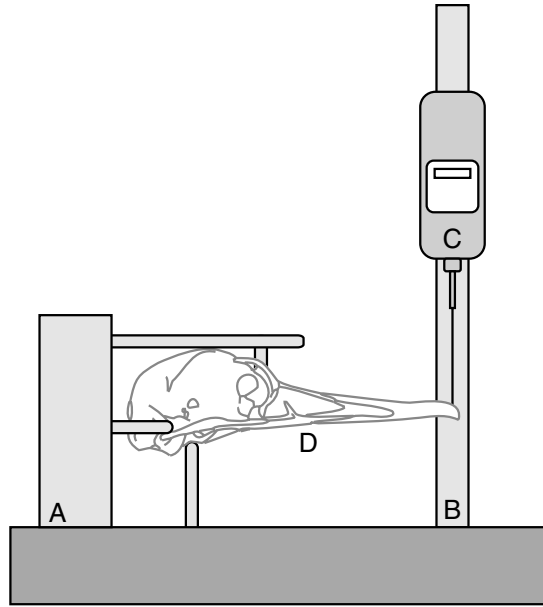
Fig. 3. Experimental set-up in lateral view. A, fixation rods; B, step motor; C, force transducer; D, experimental object.

protractor pterygoideus et quadrati). The lines of action of the different muscles are given in Fig. 4. The jaw muscles of the palaeognathae have a very simple morphology and are all mostly parallel fibred (Webb, 1957; unpublished data). Therefore the maximum contraction force of each muscle can be estimated using the physiological cross section area. Maximal muscle forces were calculated according to the formula: $F_{max}=m/(l\rho)M_c$, where F_{max}=maximal muscle force (N); m=muscle mass (kg); l=mean fibre length (m); ρ=muscle density (1000 kg m^{-3}); M_c=muscle stress constant ($330{\times}10^3$ N m^{-2}; Emerson, 1985). After the force measurements, the specimens were dissected and each muscle was weighed. Fibre lengths were determined using the fibre-dissecting technique of Gaunt and Gans (1990). Maximal muscle forces were estimated from the muscle mass and the mean fibre length of 25 muscle fibres. For each of the muscle complexes, the masses, fibre lengths and maximal forces are given in Table 1.

Model

The estimated maximal muscle forces were used to calculate the opening and closing force that can be exerted on the upper bill, and the maximal biting force. These forces were calculated using an adapted version of a two-dimensional (2D) model of the avian jaw apparatus (Bout and Zweers, 2001) and included the skull represented as a four-bar system, the lower jaw (Fig. 4) and the reaction force at the processus basipterygoideus (Fig. 2). Such a 2D model follows accurately the three-dimensional measured movement of skull elements in several types of avian cranial kinesis (Gussekloo et al., 2001). The bars represented the quadrate, the PPC, the caudal side of the moveable part of the upper bill, and the (stationary)
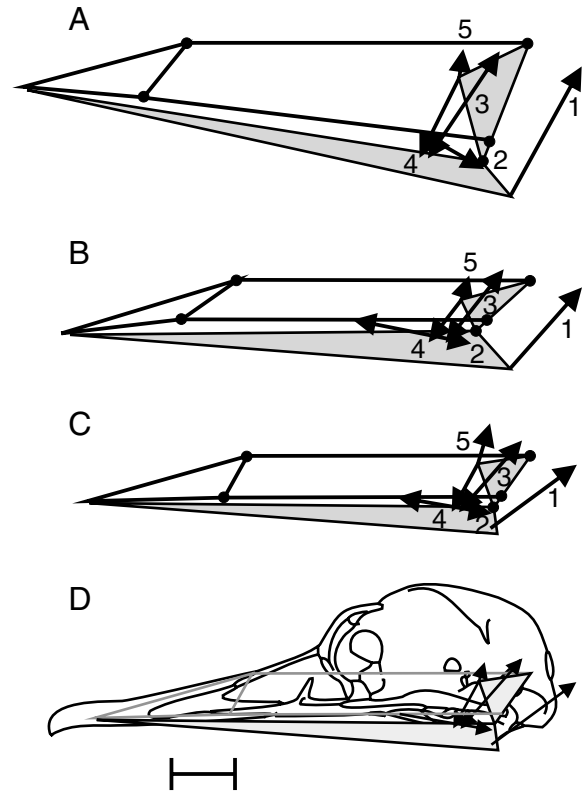

Fig. 4. Schematic representation of the skull of three species of Paleognathae. (A) Ostrich *Struthio camelus*, (B) emu *Dromaius novaehollandiae*, (C) rhea *Rhea americana*. (D) Model of the rhea drawn into a outline of the actual skull, indicating the relationship between the model and the actual skull. Arrows in A–C indicate the line of action and the approximate length of the muscles: 1, musculus depressor mandibulae; 2, musculus pterygoideus; 3, musculus adductor mandibulae externus; 4, adductor muscle complex of the quadrate; 5, musculus protractor pterygoidei et quadrati. Gray areas represent the quadrate and the lower bill. Circles represent rotation points. Scale bar, 2 cm.

skull between the rotation point of the quadrate and the flexible zone in the dorsal bar of the upper bill. The quadrate bar had the length and orientation of the quadrate. The PPC bar had the length and the orientation of the line between the quadrato–jugal articulation and the centre of the bending zone in the ventral bar of the upper bill. The centre of the bending zone was determined from behavioural analyses (Gussekloo and Bout, 2005) in combination with the video recordings from the intrinsic force measurements (see above). The bill-bar is defined by the line between the centres of the bending zones in the ventral and dorsal bar. Finally, the skull is described by the line between the quadrate–skull articulation and the centre of the bending zone in the dorsal bar of the upper bill. The moveable part of the upper bill is represented by a triangle defined by the bill-bar and the bill tip, and moves as a whole with the bill-bar. The position of the rotation points of the model were determined as the centre of the zone of maximal flexion in lateral radiograms of manually elevated upper bills and in video recordings of the force measurement experiments.

Table 1. *Mass, fibre length and maximal muscles forces of the five large muscle complexes in the skull*

	Adductor mandibulae complex	Pterygoid muscles	Depressor mandibulae	Protractor quadratum	Adductor quadratum complex
Struthio (N=3)					
Mass (g)	4.2±0.9 (6)	6.8±0.7 (6)	6.4±0.9 (6)	1.0±0.2 (6)	2.3±0.1 (6)
	2.6±0.2 (6)				
Fibre length (mm)	16.4±4.6 (6)	16.6±4.2 (6)	44.0±11.4 (6)	7.6±2.4 (5)	12.4±4.7 (6)
	14.8±5.3 (6)				
Maximal force (N)	96±48 (6)	147±57 (6)	51.5±15.7 (6)	47±24 (5)	72±36 (6)
	68±31 (6)				
Total max. force (N)	164				
Dromaius (N=2)					
Mass (g)	1.9±0.1 (4)	4.0±0.1 (4)	3.8±0.0 (4)	1.2±0.0 (4)	1.8±0.1 (4)
	1.1±0.0 (4)				
Fibre length (mm)	16.0±1.2 (4)	18.8±0.6 (4)	24.4±0.3 (4)	9.0±0.6 (4)	17.5±0.4 (4)
	12.5±0.5 (4)				
Maximal force (N)	40±3.9 (4)	70±0.5 (4)	51±0.1 (4)	43±3.0 (4)	35±0.5 (4)
	28±0.0 (4)				
Total max. force (N)	68				
Rhea (N=2)					
Mass (g)	2.2±0.2 (4)	3.2±0.4 (4)	2.0±0.2 (4)	0.5±0.3 (2)	0.6±0.4 (4)
	1.4±0.1 (4)				
Fibre length (mm)	9.1±0.3 (4)	8.7±0.9 (4)	28.1±2.8 (4)	5.4±1.2 (4)	5.8±1.2 (4)
	4.8±1.1 (4)				
Maximal force (N)	80±8.5 (4)	123±24 (4)	23.9±4.7 (4)	36±13 (2)	32±15 (4)
	95±25 (4)				
Total max. force (N)	175				

The Adductor mandibulae complex consists of two parts with unequal fibre lengths but with similar lines of action. The total force of these parts is combined as 'Total max. force'.

Values of both mass and fibre lengths are means (number of muscles used).

The lengths of the elements of the four bar system were measured in lateral radiograms. Orientations of muscles were estimated in lateral radiograms from the known position of origo and insertio of the muscles. The lower jaw articulates around the quadrato–mandibular articulation and is in its rest position in all calculations, which is in agreement with the situation when feeding on green plant material, comprising 90% of the natural diet of the rhea (Martella et al., 1996). All forces were calculated assuming static equilibrium.

Several forces were calculated using the model. (1) The opening force of the upper bill (Elev. UB), defined as the force at the bill tip (perpendicular to the long axis of the beak) necessary to balance the maximal force of the upper bill opener muscle (musculus protractor pterygoideus et quadrati). (2) The closing force of the upper bill (Depr. UB), defined as the force at the bill tip (perpendicular to the long axis of the beak) necessary to balance the total muscle force generated by muscles depressing the upper bill only (musculus pseudotemporalis profundus, musculus adductor mandibulae ossis quadrati and musculus pterygoideus). This force was calculated with the bills in rest position but also for an elevation of the upper bill of 10°. (3) The maximal biting (jaw closing) force (Max. close) was calculated as the maximal force acting on a food item of 0 mm (very thin) at the beak tip (closing muscles of upper and lower bill combined). The first calculation is an indication of the amount of muscle force that can be used to intentionally elevate the upper bill, the second is an indication of the muscle force available to counteract external forces that might elevate the upper bill, and the third gives an indication of total biting force. The calculations also included the reaction force of the processus basipterygoideus (Fig. 2). This process is absent in many other species, but has a characteristic morphology in Palaeognathae (McDowell, 1948). It blocks caudal movement of the PPC when the PPC is in its resting position. The combinations of muscle forces required for the maximal jaw forces were found iteratively. Since no left–right asymmetries were found in the natural feeding behaviour (Gussekloo and Bout, 2005), all forces were calculated for a left–right symmetrical muscle force pattern.

Results

Bending zones

Bending zones are only considered effective when they are present caudal to the rostrum maxillae and rostral to the nasal process of the maxillae (Fig. 1). The position of the nasal

process is chosen as the caudal border of the bill. In some species the rostrum parasphenoidale extends beyond the caudal limit of the upper bill, and the most rostral point of the rostrum parasphenoidale is then taken as the most caudal position of an effective bending zone. Outside these borders the bill is unable to bend because both the rostrum maxillae and the rostrum parasphenoidale are very thick and rigid.

In rhynchokinetic birds with known functional bending zones, such as *Calidris*, a clear bending zone can be recognised as an area of low relative thickness in the rostral part of the dorsal and ventral bar (Figs 5, 6). These zones of reduced thickness coincide accurately with the position of the bending zones as determined from behavioural data (Gerritsen, 1988; arrows in Figs 5, 6) indicating a direct link between the slender zones and bending.

In *Rhea* (Fig. 7) and *Struthio* (Fig. 8), the thinnest part in the dorsal bar is located directly caudal to the rostrum maxillae and is relatively small. This position agrees with neither the

bending zones found in the bending experiments of the upper bill (see arrows in Figs 7, 8) nor the location suggested by other authors (Hofer, 1954; Simonetta, 1960; Bock, 1963), nor with the behavioural observations (Gussekloo and Bout, 2005). In *Dromaius* (Fig. 9), the dorsal bar is relatively thick near the rostrum maxillae and becomes thinner to caudal. This suggests that the bar would bend far more caudal than is expected from the observed position of the bending zone. In fact, bending of the caudal part is impossible due to the presence of a thick rostrum parasphenoidale. The position of the thinnest zones in the ventral bars is for all palaeognathous species also situated caudal of, or at the most rostral point of, the rostrum parasphenoidale. This again indicates that these thin zones cannot be bending zones. The difference in position of the areas of low thickness is also remarkable. While in the *Calidris* species thin areas in the dorsal and ventral bar are located at an almost equal distance from the bill tip, such a relationship is absent in the Palaeognathae. In palaeognaths no discrete zone is seen where both the ventral and dorsal bar show locally reduced thickness, indicating that no clear bending zone is present in the upper bills of this taxon.

Intrinsic force measurements upper bill

The forces at the bill tip necessary to elevate the upper bill are relatively small (Fig. 10). Within the physiological
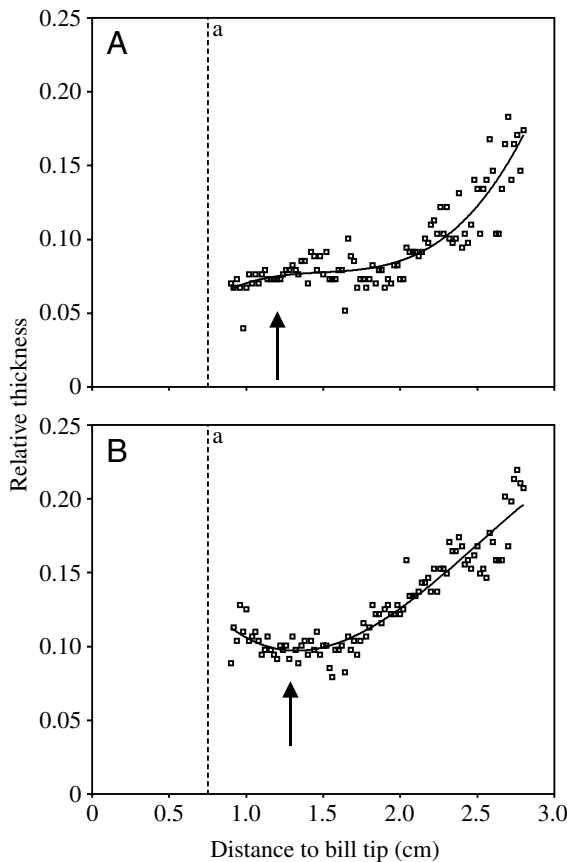
Fig. 5. Bending zones in the upper bill elements of the purple sandpiper *Calidris maratima*. Relative thickness of the dorsal bar (A) and ventral bar (B) *vs* the distance from the bill tip. Lines are Lowess fits indicating average relative thickness. In this and subsequent figures, vertical broken lines where shown indicate morphological characters of the bill: (a) caudal border of the rostrum maxillae, (b) rostral point of the rostrum basisphenoideus, (c) position of the lateral bar (b and c not present in this species). Arrows indicate the position of the bending zones as observed during experimental manipulation of the upper bill or from kinematical analysis.
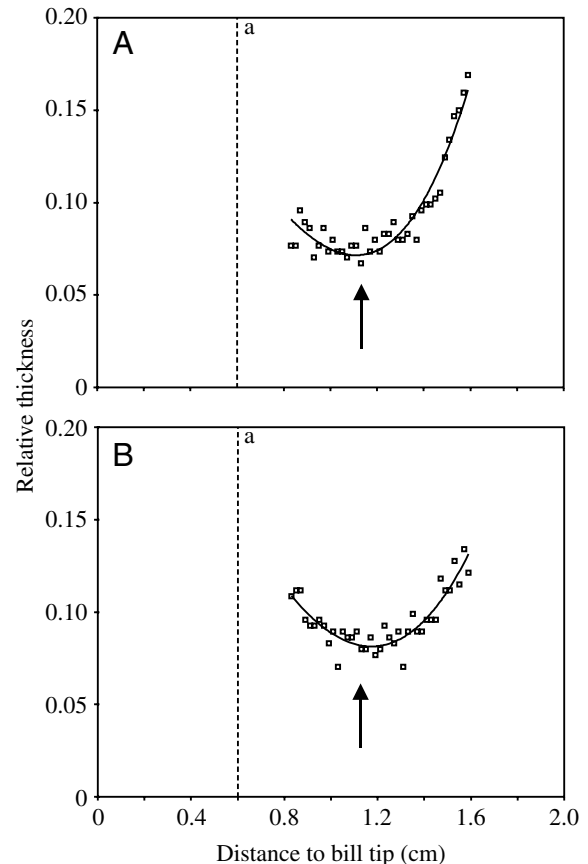
Fig. 6. Bending zones in the upper bill elements of the sanderling *Calidris alba*. See Fig. 5 for details (b and c not present in this species).

elevation range (0–10°; Gussekloo and Bout, 2005) the forces increase almost linearly. The rhea and ostrich show similar resistance to bending. From Fig. 10 it is clear that the upper bill of the emu resists bending more than in the other two species.

When we consider the thickness of the ventral and dorsal bars of the upper bill of the different palaeognathous species (Figs 7, 8, 9), it is clear that the thickness of the dorsal bar is related to the measured bending forces. The emu has on average the thickest dorsal bar (Fig. 9) and the highest resisting forces to elevation (Fig. 10), while the ostrich and rhea have thinner bars, which require lower bending forces.

Opening and closing forces

Maximal opening and closing forces were calculated using a 2D static force model, which uses estimated maximal muscle forces and the coordinates describing the position of muscles and skull elements. The parameters of the four-bar systems are given in Table 2.

For the calculation of the forces the bill tips were considered to be in their rest position, except for depression forces of the upper bill, which were calculated for the rest position and for 10° elevation. The following forces were calculated: (1) the muscle force available for intentionally elevating the upper bill (Elev. UB), (2) the muscle force available for counteracting external forces that might unintentionally elevate the upper bill

Table 2. *Lengths of the elements of the four bar systems*

| | Length (mm) | | | | | |
Species	Skull	Quadrate	PPC	Bill	Angle Q	Angle UB
Struthio	107.0	31.0	111.0	24.0	67	49.5
Dromaius	94.0	19.0	98.0	22.0	43	35.5
Rhea	89.0	16.0	87.0	15.0	55	61.5

For a description of the elements, see text.

Angle Q, angle of the quadrate; Angle UB, angle of the caudal side of the upper bill relative to the skull bar.

(Depr. UB), and the maximal jaw closing force (Max. close). All forces are summarised in Table 3.

The forces available to elevate the upper bill are similar among species. The muscle forces and shape of the four-bar system are also similar, which indicates that all morphologies are equally able to transfer the force of their opener muscle onto the bill tip. Comparison of the opening force with Fig. 10 shows that this muscle force is sufficient for elevation of the upper bill within the physiological range for all species (ignoring the force–length relationships of the muscle and the small change in direction of the muscles as the quadrate swings forward).
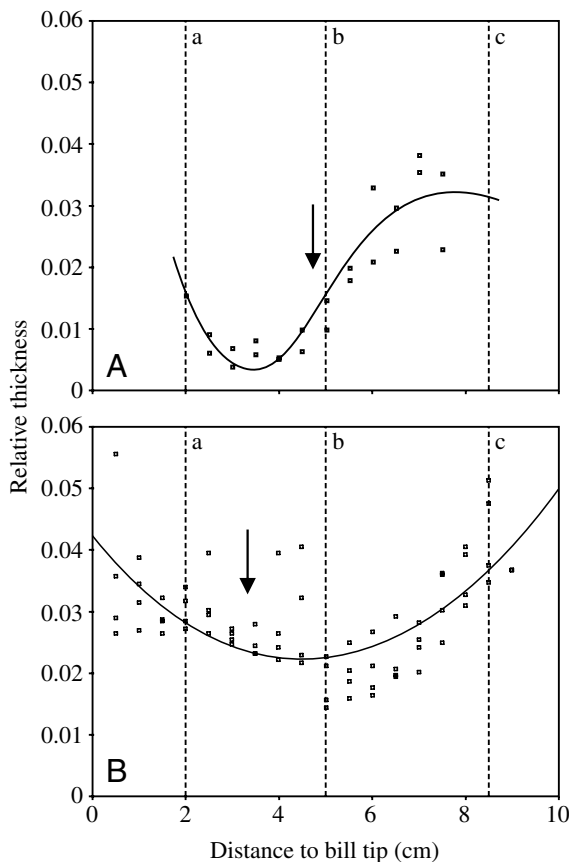

Fig. 7. Bending zones in the upper bill elements of the rhea *Rhea americana*. See Fig. 5 for details.
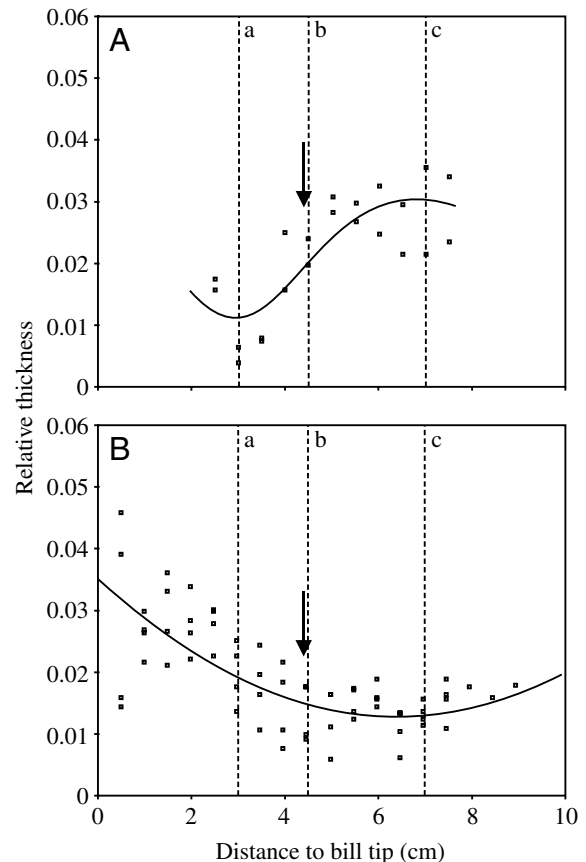

Fig. 8. Bending zones in the upper bill elements of the ostrich *Struthio camelus*. See Fig. 5 for details.

Table 3. *Maximal forces on the bill tip*

		Maximal force (N)		
Species	Elev. UB	Depr. UB (rest)	Depr. UB (elev.)	Max. close
Struthio	19.4	35.6	28.2+3.0=31.2	52.7
Dromaius	30.7	8.6	6.7+4.5=11.2	9.2
Rhea	30.2	24.8	13.9+3.0=16.9	25.8

Values are given for elevation force of the upper bill (Elev. UB), depression force of the upper bill in the rest position [Depr. UB (rest)], depression force with upper bill elevated 10° [Depr. UB (elev.); muscle generated force + passive force upper bill=total force], and the maximal biting force (Max. close).

The calculated depression forces of the upper bill differ among the three species. Both the ostrich and the rhea are capable of producing larger depression forces than the emu. There are no large differences in orientation of the muscles between the species and the low value for the emu is largely explained by its relatively small muscle forces and the acute angle of the quadrate. It must, however, be noted that the emu, which has a relatively low muscle force to counteract external forces, has the highest intrinsic elastic force in the bones to counteract bending (Fig. 10). The comparison of the
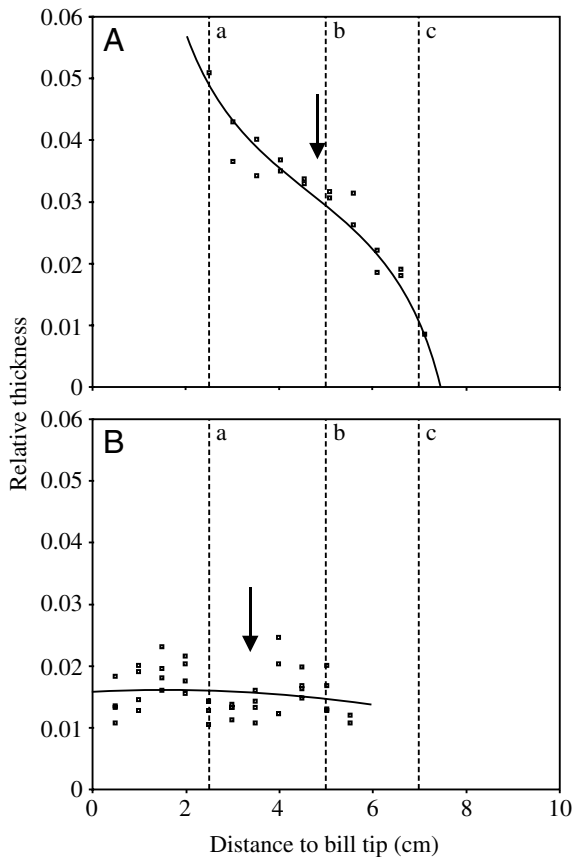
depression forces generated in rest and elevated positions show that these forces decrease when the bill is elevated. This decrease is partly compensated by the increase in elastic force from the kinetic hinge.

Biting forces are relatively low. The ostrich produces the largest biting force, which is explained by its relatively short bill, and therefore relatively small moment arm for the bill tip. The relatively low biting forces of the emu are explained by the relatively small mass of the jaw muscles.

Discussion

Several adaptations in the morphology of the skull of Palaeognathae are expected for them to have a fully functional form of rhynchokinesis. These adaptations have been described for other types of rhynchokinesis in neognathous birds (Zusi, 1984; Gerritsen, 1988), and include firstly the presence of bending zones in the dorsal and ventral bar of the upper bill, and secondly the uncoupling of movement of these elements with respect to each other. The uncoupling of the dorsal and ventral bars in neognathous rhynchokinetic birds is achieved through the schizorhinal nostril, in which the dorsal part of the flexible lateral bar of the upper bill is situated caudal to the frontal–nasal hinge (Fig. 1B). In prokinetic and palaeognathous birds the dorsal part of the rigid lateral bar is situated rostral to the nasal–frontal hinge (Fig. 1A,C). While the lateral bar in neognathous rhynchokinetic birds is a continuous bony connection, this bar is reduced to two small bony protrusions from the ventral and dorsal bars connected by a ligament in palaeognathous birds (Fig. 1C; Bock, 1963, 1964; Zusi, 1984). This condition has probably not evolved from the morphology in neognathous rhynchokinetic birds, since the position of the dorsal part of the lateral bar of the

Fig. 9. Bending zones in the upper bill elements of the emu *Dromaius novaehollandiae*. See Fig. 5 for details.
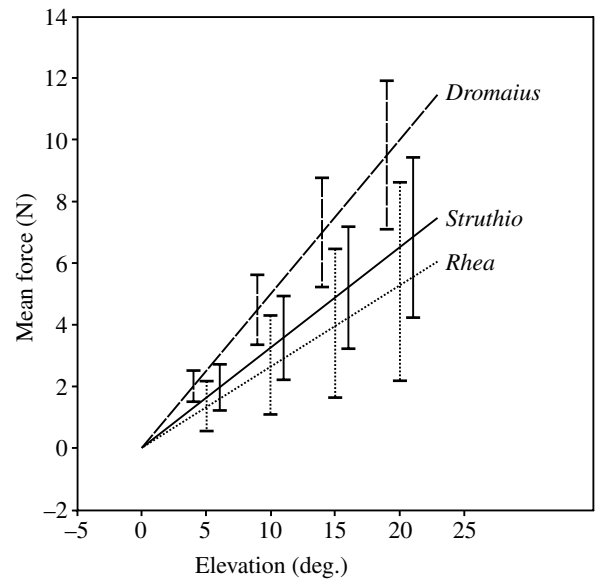

Fig. 10. Reaction force in the upper bill *vs* the elevation angle of the upper bill. Forces were measured in the linear phase and are means ± S.D.

palaeognathous nostril strongly resembles that of prokinetic birds (Zusi, 1984). This difference is an indication that neognathous and palaeognathous rhynchokinesis have evolved independently from each other.

Bending zones are clearly recognisable in both the dorsal and ventral bars of the upper bill in *Calidris* species, which are neognathous rhynchokinetic birds. The position of these bending zones coincides with the bending point determined from behavioural analyses (Gerritsen, 1988). The bending zones in the palaeognathous species are not clear, although the bars are relatively more slender than in *Calidris*. All the palaeognathous species analysed in this study have the thinnest zones in the dorsal bar near the caudal or rostral part of the dorsal bar, outside the effective bending limits of the upper bill. This indicates that no clear bending zone is present in the dorsal bar of the Palaeognathae. Although the thickness curve of the ostrich shows some resemblance to that of the *Calidris* species, note that the slender part is directly behind the rostrum maxillae. This rostrum is very thick and semicircular, which makes this region very rigid and difficult to bend. The ventral bar of the Palaeognathae shows a slight decrease in relative thickness, but this is far less pronounced than in the *Calidris* species. Also the position of the thinnest parts of the ventral bars is situated very caudal in the bill, beyond the most rostral part of the very large rostrum parasphenoidale. This bony element protrudes very far rostrally and becomes a part of the upper bill. It is very rigid and opposes bending in the caudal part of the upper bill. As rostral bending in the upper bill is opposed by the rigid rostrum maxillare, and caudal by the rostrum parashenoidal, the area suitable for bending is very small (Figs 7–9). This indicates that bending in the caudal part of the bill will be very limited, and confirms that bending is absent in the caudal part of the bill, as shown in behavioural analyses (Gussekloo and Bout, 2005).

Another feature of a rhynchokinetic skull is the ability to overcome the elastic forces in the upper bill as a result of bending by muscle force. As shown here, the forces opposing bending in the upper bill of the Palaeognathae are not very high, which means that bending in the upper bill can easily occur as a result of internal or external forces. The calculated muscle forces for upper bill elevation in palaeognaths are large enough to overcome the intrinsic elastic forces opposing elevation, indicating that self-induced elevation of the upper bill (induced kinesis) is possible. However, the elastic forces in the upper bill of the palaeognathous species increase continuously with elevation of the upper bill. This linear increase in resistance seems significantly different from the force reported for (prokinetic) finches (Nuijens and Bout, 1998), where the resistance to upper bill elevation is close to zero over most of the physiological elevation trajectory but then starts to increase exponentially. Since upper bill resistance is very low in prokinetic birds it can be hypothesized that the bill of the palaeognathous species is not optimised for self-induced movement.

On the basis of the findings in this paper, we conclude that the total configuration of the bony elements is not adapted to large bending in the upper bill, even though bending does occur in the upper bill of palaeognathous species (Gussekloo and Bout, 2005). The relatively high resistance of the upper bill compared to prokinetic birds, and the lack of clear bending zones, indicate that the morphology of the Palaeognathae is not 'designed' for elevation of the upper bill. This implies that the function of cranial kinesis in palaeognathous birds is not the same as in neognathous rhynchokinetic birds, such as the Charadriiformes. The bending in the upper bill of palaeognathous species is more likely to be an unwanted effect of the slenderness of the lateral and dorsal bars.

Our findings on jaw closing force also contradict part of the hypothesis of Zweers et al. (1997). They assume that the presence of a moveable palate, in combination with a large pterygoid muscle, results in higher biting forces. Although there are very few data on biting force in birds it is clear that the biting force calculated here for palaeognaths is very low. Even finches with much lower muscle masses are able to produce forces similar to those found in the ostrich (Simms, 1955; van der Meij and Bout, 2000, 2004).

In our analysis we found that the musculus pterygoideus has very little effect on the biting force. Remarkably, this situation is also seen in lizards, where a large pterygoid muscle is also present, but without any large contribution to biting force (Herrel et al., 1999). The main role of the pterygoid muscle in birds that lack a blocking processus basipterygoideus (e.g. finches) is to balance the retraction component of the adductor muscle, which tends to retract the lower bill and quadrate. In these birds the component of the pterygoid muscles that contributes to jaw closing is relatively small.

In the Palaeognathae the retraction component of the lower jaw closers can be balanced by the reaction force on the processus basipterygoideus. This process blocks caudal movement of the pterygoid and blocks depression of the upper bill beyond the resting position.

Additionally, in the palaeognathous morphology part of the pterygoid muscle does not attach to the mandibula but has its origin on the processus basipterygoideus. The function of this part of the muscle is therefore retraction of the PPC only. The combination of these two features can be used to overcome external forces that might act in such a way that they would elevate the upper bill. Such forces are present during grazing in the Palaeognathae. During grazing leaves are pulled forcefully from plants or the ground by a fast ventro–caudally directed, jerky movement of the head and neck. Such a movement generates external forces varying over time that, due to the low intrinsic elastic forces of the bones, might induce unwanted elevation of the upper bill. The processus basipterygoideus acts as a stabilizer for this varying load. The two main muscle complexes, the lower jaw adductors and the pterygoid muscles, can be continuously maximally active and the caudally orientated component of these muscles pulls the pterygoid tight against the processus basipterygoideus. This will stabilise the upper bill and the muscles do not have to adjust their activity to balance the variable external force on the upper bill. Only if the external force exceeds the intrinsic

elastic force of the bones and the force produced by the pterygoid and adductor muscles will it lift the upper bill, and therefore the PPC complex, from the processus basipterygoideus. Note that the palaeognathous species with the stiffest bony configuration also has the weakest muscles and *vice versa*, which seems to indicate a trade-off between rigidity of the bills and jaw muscle force; in other words, a rigid configuration needs less muscle power to stabilise the upper bill, while weak configurations need muscles to stabilise the bill.

It has generally been accepted that the morphology of the palaeognathous PPC is related to rhynchokinesis (Bock, 1963; Hofer, 1954; Simonetta, 1960). Our findings, however, do not support this hypothesis. From the force analysis we conclude that the processus basipterygoideus in combination with the jaw muscles acts as a stabilizing mechanism that helps to resist varying external forces that might otherwise elevate the upper bill. The idea that the large pterygoid muscle in combination with the processus basipterygoideus acts as a stabilising mechanism is also confirmed by the overall configuration of the skull. A large rostrum parasphenoidale is found in combination with an almost completely ossified palate, with very broad bones. In neognathous birds the bones tend to be more slender, especially when no muscles are attached to it. The overall configuration seems to reflect a demand for stabilising of the upper bill and enlarging the amount of bone in the palatal region.

Plausible evolutionary scenarios to explain the morphology of the skull of the Palaeognathae are difficult to postulate. The ancestor of the Palaeognathae was probably a small, flying, species with a kinetic skull and a morphology similar to that of the present day Tinamiformes. A reduction of the lateral aspect of the skull, as observed in the Palaeognathae, can already be observed earlier in evolution with the increased fenestration of the vertebrate skull (Zweers et al., 1997). The ability to fly may have contributed to a further reduction of head weight, e.g. the bony elements of the skull. Although the Palaeognathae became secondary flightless it would still be advantageous to keep the total weight of the skull on top of the long neck as low as possible, especially considering the large increase in size of these species. To reduce weight a further reduction in bony elements may have occurred, mainly in the lateral cranial bars (lateral bar of the upper bill, pre- and postorbital bones). One possible selective force favouring a kinetic upper beak may be that simultaneous movement of the upper and lower jaw increases the speed of opening and closing. This would be advantageous for species feeding on active prey (see Herrel et al., 2000). On the other hand, for tearing of plant material an akinetic upper jaw seems more suited. Forces acting against external loading would not be generated by muscles but by the bony material of the skull. This seems in agreement with the observation that cranial kinesis is strongly reduced in lepidosaurs that use their tongue to catch prey or feed on plant material (Arnold, 1998). When Palaeognathae shifted their diet to a largely herbivorous one, the skull needed reinforcement for the upper bill to resist unwanted bending due to external forces. This was achieved by reinforcement of elements in the ventral aspect of the skull (PPC), and the loss of bending zones. Both skull mass and the fact that part of their diet is still made up of insects and small vertebrates, might contribute to the preservation of cranial kinesis, but without detailed knowledge of the feeding mechanism and external forces acting on the skull it not clear why Palaeognaths do not reinforce the ventral and dorsal bar of the upper beak until it becomes akinetic.

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