CHAPTER 6

CRANIAL KINESIS IN PALAEOGNATHOUS BIRDS

Summary

In palaeognathous birds the morphology of the Pterygoid-Palatinum Complex (PPC) is remarkably different from the PPC of neognathous birds. Palaeognathae are also believed to possess a specific type of cranial kinesis known as central rhynchokinesis. We experimentally determined bending forces opposing elevation of the upper bill and used a mathematical model to calculate the opening forces that can be produced by the Palaeognathae. It was found that muscle forces are more than sufficient to overcome bending forces and to elevate the upper bill. The large pterygoid-muscles contribute only slightly to the total biting force, but may resist external opening forces on the upper bill. No clear bending zones are present in the upper bill, and if bending occurs it will be over the total length of the upper bill. We conclude that the palaeognathous upper bill and PPC are designed to resist external forces that elevate the upper bill.

Introduction

Cranial kinesis is an important character of the feeding behaviour of birds and, to a lesser extent, of reptiles. In birds cranial kinesis is characterised by the ability to move the upper bill or a part thereof. Most birds are able to move the whole upper bill, a situation known as prokinesis (Bock, 1964). The bending zone between the skull and 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 as a whole contains no flexible zones and is rigid. This type of cranial kinesis is considered the most basic form within modern birds (Bock, 1964). Several other types of cranial kinesis can be distinguished, based on different positions of the bending zones. The second most common type is the rhynchokinetic configuration. In this type the bending zones are positioned further rostrally within the upper bill. This means that in these species only a small portion of the upper bill is moveable and bending zones are present in both the dorsal and ventral bars. Rhynchokinesis also has consequences for the rest of the configuration of the skull. To make the movement of the rostral part of the upper bill possible, the movements of the dorsal and ventral bars have to be uncoupled. This uncoupling is achieved by a schizorhinal nostril (Fig. 1.3), which means that the dorsal attachment of the lateral bar, connecting the dorsal and ventral bar, is positioned caudal to the nasal-frontal hinge (Zusi, 1984). Although the main division in types of cranial kinesis is between prokinetic and rhynchokinetic skulls, a number of sub-divisions is recognised within the rhynchokinetic type, which are characterised by different positions of the flexible zones (Zusi, 1984). In the proximal rhynchokinetic type the bending zones are just rostral to the nasal-frontal area, in central rhynchokinesis the bending zones are positioned in the middle of the upper bill, and in distal rhynchokinesis the bending zones are just caudal of the rostrum maxillae. One subtype, double rhynchokinesis, has two bending zones and is a combination of proximal and distal rhynchokinesis. Finally, extensive rhynchokinesis is characterised by a flexible zone that extends over almost the entire bill. In all these types a schizorhinal nostril is present, except in central or palaeognathous rhynchokinesis. In the latter subtype uncoupling of the dorsal and ventral bar is achieved by a gap in the lateral bar of the upper bill. It is remarkable that this type of rhynchokinesis is found in one avian taxon only: the Palaeognathae.

The Palaeognathae is one of the taxa of the most basal sub-division within the taxon Aves (Cracraft, 1974; Sibley & Ahlquist, 1990). This basal subdivision divides the taxon Aves into the Palaeognathae and the Neognathae. The Palaeognathae is a small taxon, approximately 60 species, versus 8000 species of 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; Gussekloo & Zweers, 1999), which consists of the pterygoid, palate and the vomer. In Palaeognathae the PPC is rigid and lacks the flexible articulations between elements found in Neognathae (McDowell, 1948; Bock 1963). In neognathous birds this complex, in combination with the quadrate, has a clear function in the movement of the upper bill. The movement of the



Figure 6.1. Experimental set-up in lateral view. A. Fixation rods, B. Step motor, C. Force transducer, D. Experimental object.

upper bill is caused by a rotation of the quadrate, which is transferred to the upper bill via the PPC (Bock, 1964). It has always been assumed that the PPC in the Palaeognathae serves the same function, and that central rhynchokinesis is related to the special morphology of the PPC (Bock, 1963; Hofer, 1954; Simonetta, 1960).

In this paper we test whether the skulls of the Palaeognathae are rhynchokinetic on the basis of a number of morphological characters typical for rhynchokinesis and which are present in other rhynchokinetic birds, such as Charadriiformes (Zusi, 1984; Chapter 3). These characters are the presence of a uncoupling of the dorsal and ventral bar, and the presence of clear bending zones in both the ventral and dorsal bar of the upper bill. We also tested whether sufficient muscle forces are for rhynchokinetic movement of the upper bill. Earlier analyses of cranial kinesis of the

Palaeognathae have been done by manipulating osteological specimens and were mainly qualitative (Bock, 1963; Hofer, 1954; Simonetta, 1960). In this study we try to quantify both the presence and location of bending zones.

Materials and Methods

Three species of palaeognathous birds were used for the analysis: the Ostrich (*Struthio camelus*) from Africa, The Greater Rhea (*Rhea americana*) from South- America and the Emu (*Dromaius novaehollandiae*) from Australia. Two specimens of both the Emu and Rhea and three specimens of the Ostrich were used. All specimens were heads of deceased birds, which had been stored at a temperature of -20 °C. Before the experiments the skin was removed to facilitate fixation in the experimental set-up (see below). All other parts of the skull were kept intact.

The forces necessary to elevate and depress the upper bill were determined in an experimental set-up (Fig. 6.1) in which the upper bill was depressed or elevated and reaction forces were measured using a force-transducer (Aikoh). The head was fixed with screws on each side, and a bar was attached to the skull to prevent dorso-ventral rotation. 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. For

depression a blunt bar was used to push against the upper bill while the force-transducer moved downward. The force-transducer moved with a speed of 5 mm/sec while forces and elevation were recorded continuously. All experiments were performed at room temperature.

The specimens were then dissected and of each muscle the weight and mean fibre length was determined. Fibre-lengths were determined using the fibre-dissecting technique of Gaunt & Gans (1990). An estimate of maximal muscle forces was made from the physiological cross section of the muscle according to the formula:

$$F_{\max} = \frac{m}{l \cdot \rho} \cdot M_c$$

with: F_{max} = maximal muscle force (N); m = muscle mass (kg); I = mean fibre length (m); ρ = muscle density (1000 kg.m⁻³); M_c = muscle stress constant (330x10³ N.m⁻²; Hildebrand *et al.*, 1985).

The estimated maximal muscle forces were used to calculate the force that can be asserted on the upper bill, and the maximal biting force. These forces were calculated with twodimensional models, in which the skull is represented as a four-bar system. The bars represented the guadrate, the PPC, the caudal side of the moveable part of the upper bill, and the stationary skull between the rotation point of the quadrate and the flexible zone in the dorsal bar of the upper bill. The guadrate bar had the length and orientation of the guadrate. The PPC bar had the length and the orientation of the line between the ventral part of the quadrate bar and the centre of the bending zone in the ventral bar of the upper bill. The PPC bar describes roughly the orientation of the PPC. The Bill bar is defined by the line between the centres of the bending zones in the ventral and dorsal bar. Finally the stationary skull bar is described by the line between the dorsal end of the guadrate bar and the centre of the bending zone in the dorsal bar of the upper bill. The moveable part of the upper bill is added to the Bill bar. This part is defined by both ends of the bill bar and the bill tip and moves as a whole with the Bill bar. All articulations included in the model are considered to be rotation points without friction or other opposing forces and one degree of freedom (rotation). The position of the flexible zones in the upper bill was measured in lateral radiograms and in video-recordings of the force measurement experiments. The lower jaw articulates around the ventral point of the quadrate and is in its rest position in all calculations. All forces were calculated under the assumption of static equilibrium. 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. Schematic drawings of the models used for the different species are given in figures 6.2.

A number of forces were calculated using the models. The elevation force on the upper bill, defined as the necessary force on the upper bill tip to balance the maximal force of the elevator muscle of the upper bill (*Musculus protractor pterygoideus et quadrati*), was calculated and compared to measured elevation forces. The contribution of the adductor muscles to biting forces of the lower jaw was calculated at the lower bill tip as the necessary force to cancel the maximal force of the *Musculus adductor externus* complex. Finally total biting forces were

calculated for a food-item of 10 mm at the bill tip. This was done using an adapted version of the model of the avian jaw apparatus of Bout (*in prep.*) and included the four-bar system, the lower jaw and the reaction force at the *Processus basipterygoideus*. This processus is only found in Palaeognathae (McDowell, 1948) and blocks in the rest position and in combination with the *Processus zygomaticus* caudal movement of the PPC. For the calculation of the maximal biting force the upper bill elevation was varied between 0 and 10 degrees and maximum forces of the *Musculus adductor mandibulae externus, Musculus pterygoideus* and Adductor muscles on the quadrate were used.



Figure 6.2. Schematic representation of the skull of three species of Paleognathae. A. Ostrich (Struthio camelus), B. Emu (Dromaius novaehollandiae), C. Rhea (Rhea americana). Arrows indicate the line of action and the 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.

Table 6.1. Mass, Fibre length and Maximal muscles forces from the 5 most important muscle complexes in the skull. The Adductor mandibulae complex consists of two parts with unequal fibre-lengths, but with similar work-lines. The total force of these parts is combined as 'Total Max. Force'. Mean values of both mass and fibre lengths are given.

Struthio	Adductor Mandibulae	Pterygoid	Depressor Mandibulae	Protractor Quadratum	Adductor Quadratum
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	Adductor Mandibulae	Pterygoid	Depressor Mandibulae	Protractor Quadratum	Adductor Quadratum
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)
	$28\pm0.0\;(4)$				
Total Max. Force (N)	68				

Rhea	Adductor Mandibulae	Pterygoid	Depressor Mandibulae	Protractor Quadratum	Adductor Quadratum
Mass (g)	2.2 ± 0.2 (4) 1.4 ± 0.1 (4)	3.2 ± 0.4 (4)	2.0 ± 0.2 (4)	0.5 ± 0.3 (2)	0.6 ± 0.4 (4)
Fibre Length (mm)	9.1 ± 0.3 (4) 4.8 ± 1.1 (4)	8.7 ± 0.9 (4)	28.1 ± 2.8 (4)	5.4 ± 1.2 (4)	5.8 ± 1.2 (4)
Maximal Force (N)	80 ± 8.5 (4) 95 ± 25 (4)	123 ± 24 (4)	23.9 ± 4.7 (4)	36 ± 13 (2)	32 ± 15 (4)
Total Max. Force (N)	175				

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 the specimens used for the force measurements and some additional osteological specimens. The thickness of both ventral bars and the dorsal bar were measured using a digital calliper rule (Sylvac, accuracy 0.01 mm). One Ostrich bill was used to make transverse sections. The sections were stained according to the van Giesson method (Brodal *et al.*, 1978) and used to measure the thickness of the dorsal and ventral bars more accurately under a dissection microscope. 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*) and the Sanderling (*Calidris alba*), which have a distal rhynchokinetic skull. All

thickness measurements were scaled to the head-width, measured at the quadrato-jugal articulation, to eliminate size effects. In the analysis bending zones were only considered effective when they were present caudal to the *Rostrum maxillae* and rostral to the nasal process of the maxillae. In some species the *Rostrum parasphenoidale* extents beyond the caudal limit of the upper bill. In these cases the most rostral point of the *Rostrum parasphenoidale* is taken as the caudal border for the 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. The position of the nasal process is chosen as the caudal border of the bill.

Table 6.2. Lengths of the elements of the four bar systems. For description of the elements see text. Angle Q and Angle B indicate the angle of the quadrate and of the caudal side of the upper bill relative to the skull bar.

Species	Skull	Quadrate	PPC	Bill	Angle Q.	Angle B.
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

Results

Muscle Forces

The cranial muscles acting in feeding behaviour can be divided into 5 major functional groups. These groups are: 1) closer of the lower bill (*Musculus adductor mandibulae externus* complex), 2) closer of the upper bill (*Musculus pterygoideus* complex), 3) closer of both upper and lower bill (adductor complex of the quadrate), 4) opener of the lower bill (*Musculus depressor mandibulae* complex), and 5) opener of the upper bill (protractor complex of the quadrate). The lines of action of the different muscles are given in figures 6.2. For each of these complexes the

Table 6.3. Maximal forces (N) on the bill tip as a result of muscle action. Values are given for elevation force of the upper bill, depression force of the upper bill, elevation force of the lower bill, and the force for simultaneous closing of the upper and lower bill. Column Max. elev. indicate the maximal elevation angle that can be obtained with these forces. >> indicate no limitation to rotation within the boundaries of the measured opposing forces.

Species	Elev. UB (N)	Max. Elev. UB	Depr. UB (N)	Lower bill (N)	Max. Force (N)
Struthio	11.7	56	61.0	24.4	24.6
Dromaius	15.0	>>	19.5	6.2	8.2
Rhea	11.2	38	39.3	12.6	14.6



Figure 6.3. Reaction force in the upper bill versus the elevation angle of the upper bill. Forces were measured in the linear phase.

weights, fibre-lengths and maximal forces are given in table 6.1. The adductor complex consisted of two parts with different fibre lengths but a similar line of action. The forces of these two parts were combined for the final analysis.

Forces in the skull

The forces at the bill tip necessary to elevate the upper bill are relatively small (Fig. 6.3). Forces of 3 N will result in an elevation of the upper bill of more than 10 degrees. From the graph it is clear that the upper bill of *Dromaius* resists bending more than in the other two species. *Rhea* and *Struthio* show similar resistance to bending. Within the elevation range measured (0-15 degrees) the forces increase almost linearly.

The parameters of the four-bar systems are given in table 6.2. The main muscle responsible for the elevation of the upper bill is the *Musculus protractor pterygoideus et quadrati*. Depression of the upper bill from an elevated situation is achieved by the action of the *Musculus pterygoideus* and the adductor muscles attached to quadrate (Bühler, 1981). For the calculation of the forces on the bill tips of the subsystems the bills were considered to be in their rest position. The calculated forces on the bill tip as a result of the contraction of the *Musculus protractor pterygoideus et quadrati*, the simultaneously contraction of the *Musculus*

pterygoideus and the adductors on the quadrate, and finally the *Musculus adductor externus* are given in table 6.3.

The forces on the bill tip as a result of the protraction of *Musculus protractor pterygoideus et quadrati* are comparable between species. The muscle forces and shape of the four-bar system are similar which indicates that all mechanisms are equally able to transfer the force of this muscle onto the bill tip. As can be seen in figure 6.5 this muscle force is sufficient for an elevation of the upper bill of approximately 30 degrees for all species (ignoring the force-length relationships of the muscle and the small change in direction of the muscles as the quadrate



Figure 6.4. Bending zones in the upper bill elements of the Rhea (Rhea americana). Relative thickness of the dorsal bar (A) and ventral bar (B) vs. the distance from the bill tip. Lines are Lowess fits indicating relative thickness. average Vertical dashed lines indicate morphological characters of the bill: a) caudal border of the Rostrum maxillae, b) rostral of the Rostrum point basisphenoideus, c) position of the lateral bar. Arrows indicate the position of the bending zones as observed during experimental manipulation of the upper bill.



Figure 6.5. Bending zones in the upper bill elements of the Emu (Dromaius novaehollandiae). See figure 6.4 for details.

swings forward). The muscle forces resulting in a depression of the upper bill are larger than the elevation forces for all species. However, depression of the upper bill from rest position is prevented by the presence of the Processus basipterygoideus. Note that the large pterygoid muscles are also able to oppose external forces that would result in the elevation of the upper bill. Such external forces might act on the upper bill during grazing or when leaves are pulled from plants by a fast backward movement of the head and neck.

Large differences are found in the forces on the bill tip as a result of the closing muscles of the upper bill. The Ostrich is capable of producing a much larger force than the other two species. Since there are no large differences in orientation of the muscles, this is the effect of the higher mass of both the pterygoid and the adductor quadratum muscles in the Ostrich. The difference between the Rhea and the Emu can also be explained by the difference in muscle mass.

The differences in the forces on the bill tip produced by the *Musculus adductor mandibulae externus* are the result of differences in muscle mass, position of the muscles on the lower bill and the length of the bill. The high muscle mass of the Rhea does not result in the highest force output

on the bill tip because the muscle attaches relatively close to the point of rotation in combination with a relatively long bill. The Ostrich has relatively the shortest bill, and therefore the most efficient force transfer. All forces on the bill tip produced by the *Musculus adductor externus* complex are however relatively small compared to those produced by the closing muscles of the upper bill.

The model including all head elements (Bout, *in prep.*) also showed that elevation of the upper bill had very little effect on the biting force. The force produced by the *Musculus*

pterygoideus had also very little effect on the total biting force. Finally the contribution to the biting force of the *Musculus adductor mandibulae externus* is approximately twice as high as the contribution of the adductor muscles on the quadrate.

Bending Zones

When we consider the thickness of the ventral and dorsal bars of the upper bill of the different palaeognathous species (Fig. 6.4 - 6.6), it is clear that the thickness of the dorsal bar is related to the measured bending forces. The Emu with the highest resisting forces to elevation (Fig. 6.3) has a very thick dorsal bar and a very stable overall configuration (Fig. 6.5), while the Ostrich and Rhea have thinner bars (Figs. 6.4 & 6.6), which require lower bending forces (Fig. 6.3). In rhynchokinetic birds with known functional bending zones, such as Calidris, a clear bending zone can be recognised from the relative thickness of the bones (Fig. 6.7 & 6.8). These bending zones, characterised by a reduction of the thickness of the bones, coincide accurately with the position of the bending zones as determined from behavioural data. In Palaeognathae such zones of reduced thickness were not found, indicating that no clear bending zones are present in the upper bills of this taxon. Remarkable are also the differences in the morphology of the dorsal and ventral bars in the



Figure 6.6. Bending zones in the upper bill elements of the Ostrich (Struthio camelus). See figure 6.4 for details.

Palaeognathae. While in the *Calidris* species the dorsal bar follows the same pattern as the ventral bar with a clear bending zone, such a bending zone in the dorsal bar is absent in the Palaeognathae. Thinner regions can be found in the ventral bar, but these do not represent bending zones. In *Struthio* and *Rhea* the thinnest part in the dorsal bar is located directly caudal to the *Rostrum maxillae* and is relatively small. This position does not coincide with the bending zones found in kinematic analyses (Chapter 5 & 7) nor with the location suggested by other



Figure 6.7. Bending zones in the upper bill elements of the Purple sandpiper (Calidris maratima). See figure 6.4 for details.

authors (Hofer, 1954; Simonetta, 1960; Bock, 1963) In *Dromaius* the dorsal bar is relatively thick near the *Rostrum maxillae* and becomes thinner to caudal. This suggests that the bar would bend far more caudally than is expected from kinematic analyses. In fact bending at this point is impossible due to the presence of a thick *Rostrum parasphenoidale*.

Discussion

number of adaptations in the А morphology of the skull of Palaeognathae are expected if they would have a fully functional form of rhynchokinesis. These adaptations have been described for other types of rhynchokinesis in neognathous birds (Zusi, 1984; Chapter 3). These adaptations first of all include the uncoupling of the dorsal and ventral bar of the upper bill, and the presence of bending zones in these elements. The uncoupling of the dorsal and ventral bar in neognathous rhynchokinetic birds is achieved through the schizorhinal nostril, which is not present in palaeognathous birds. The lateral bar in prokinetic birds is a rigid bony bar and in neognathous rhynchokinetic birds a flexible, but still bony, bar. In Palaeognathous birds this bar is reduced to two small bony protrusions from the ventral and dorsal bar connected by a ligament. This

condition has probably not evolved from the morphology in neognathous rhynchokinetic birds, since the overall configuration of the palaeognathous nostril strongly resembles that of prokinetic birds (Zusi, 1984).

The second adaptation, the presence of bending zones in the upper bill is less clear in the Palaeognathae. In *Calidris* species, neognathous rhynchokinetic birds, bending zones are clearly recognisable in both the dorsal and ventral bar. The position of these bending zones

coincides with the bending point found in behavioural analyses (Gerritsen, 1988). In the dorsal bars of the bills of Palaeognathae no slender areas. indicating bending zones, can be found, 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 can be found in the morphology of the Palaeognathae. Although the thicknesscurve of the Ostrich shows some resemblance to that of the Calidris species it has to be noted that the slender part is directly behind the Rostrum maxillae. This Rostrum is very thick, rigid and semicircular, which makes bending in this region very unlikely. A behavioural analysis of the feeding of the Rhea has shown that limited bending in the upper bill occurs over the full length of the upper bill during feeding (Chapter 7). The ventral bar of the Palaeognathae shows a slight decrease in relative thickness, but this is far less pronounced than in the Calidris species. The thinnest parts of the ventral bars are positioned very caudally in the bill, far beyond the most rostral part of the Rostrum parasphenoidale. Since no



Figure 6.8. Bending zones in the upper bill elements of the Sanderling (Calidris alba). See figure 6.4 for details.

bending can occur in the rigid *Rostrum parasphenoidale* it is very unlikely that bending does occur along this part in the ventral bar.

Another condition for a rhynchokinetic skull is the ability to move the upper bill and to overcome the reaction forces from bending. As is shown here, the bending forces in the upper bill of the Palaeognathae are relatively small (max 0.5 N/degree elevation). The available muscle forces are large enough to overcome the forces opposing elevation. The lack of clear

bending zones indicates that the morphology of the Palaeognathae is not 'designed' for extreme elevation of the upper bill and agrees with earlier findings that the bill bends slightly, but over its full length. Due to the large *Musculus pterygoideus* complex, the forces that can be used to resist elevation of the upper bill by external forces are larger (Table 6.3). From a functional point of view these findings contradict the idea that the palaeognathous skull is rhynchokinetic.

It has generally been accepted that the palaeognathous PPC is related to rhynchokinetic feeding behaviour (Bock, 1963; Hofer, 1954; Simonetta, 1960). Our findings, however, show no evidence for this hypothesis. In the force analysis we found that the pterygoid muscles have a large component acting on the upper bill, which is stabilised by the presence of the *Processus basipterygoideus*. The strong *Musculus pterygoideus* can pull the PPC against the *Processus basipterygoideus*. By doing so, it is possible to resist strong external forces that might 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 to enlarge the amount of bone in the palatal region.

Our findings 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. In our analysis we found that the *Musculus pterygoideus* has very little effect on the biting force and that elevation of the upper bill also has a very small contribution to the biting force. The function of the *Musculus pterygoideus* in birds that lack a blocking *Processus basipterygoideus* is to balance the retraction component of the adductor muscle, which tends to retract the lower bill and quadrate. In the Palaeognathae this retraction component is balanced by the *Processus basipterygoideus*. It is therefore very unlikely that additional biting force has resulted in the special palaeognathous configuration of the PPC.

Two different evolutionary pathways can be postulated to explain the morphology of the skull of the Palaeognathae. The first is based on the large increase in size of the species of the Palaeognathae. The ancestor of the Palaeognathae was a small species with an akinetic skull. With the increase in size of the birds the total weight of the skull decreased to reduce the weight on top of the neck. A reduction in bony elements already occurred during the transition from the ancestral reptilian skull to the present avian skull. The main reduction occurred in the lateral bars, which disappeared (Zweers *et al.*, 1997). When the Palaeognathae, after reduction of the lateral bars, started to increase in size the skull needed an alternative method of reinforcement of the upper bill to resist unwanted bending due to external forces.

Prevention of large bending may be necessary to protect the upper bill itself and to ensure sufficient biting force, but may also prevent damage to other structures such as the olfactory organs. These are well developed in the Palaeognathae but have never been noticed as a significant feature. Within the large nasal cavity well-developed lamina are present, supporting the olfactory epithelium. In all Palaeognathae, including the Tinamidae, these cartilageous, or

sometimes even bony, lamina are found and at least the Kiwi is known to have a well-developed sense of smell. It is possible that the morphology of the palaeognathous skull has evolved as a lightweight protective measure for the nasal cavity. When large bending occurs in the upper bill, the lamina in the nasal cavity may be damaged. The damage from this movement can be avoided by a stabilising the upper bill or by reducing the local displacement. The stabilising basipterygoid process that opposes depression of the upper bill, the strong pterygoid muscles that opposes elevation of the upper bill, and the absence of bending zones, protect the nasal cavity from movement damage. The evolutionary pathway in this case has either followed the same route of reduction of lateral bars as mentioned above, or the ancestral type had a rhynchokinetic skull. It has to be pointed out, however, that in both cases the bifurcation of the palaeognathous birds and the neognathous birds must have occurred early in evolution, since the long and broad vomer is still present. A reappearance of a long vomer from a situation as found in the neognathous birds where it is almost missing would be highly unlikely. We therefore have to conclude that the cranial characters of the Palaeognathae have evolved early in avian evolution and are not the direct result of a specific type of cranial kinesis.

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