

THREE-DIMENSIONAL KINEMATICS OF SKELETAL ELEMENTS IN AVIAN PROKINETIC AND RHYNCHOKINETIC SKULLS DETERMINED BY ROENTGEN STEREOPHOTOGRAMMETRY

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Summary

Several different types of cranial kinesis are present within modern birds, enabling them to move (part of) the upper bill relative to the braincase. This movement of the upper bill results from movement of the quadrate and the pterygoid–palatine complex (PPC). The taxon Palaeognathae is characterised by a very distinct PPC and a special type of cranial kinesis (central kinesis) that is very different from that found in the Neognathae. This has led some authors to hypothesise that there is a functional relationship between the morphology of the PPC and the type of cranial kinesis.

This hypothesis is tested here by analysing the movement pattern of both the upper bill and the PPC in birds with three different types of cranial kinesis: prokinesis, distal rhynchokinesis and central rhynchokinesis. Movement patterns were determined using a Roentgen stereophotogrammetry method, which made it possible to detect very small displacements (0.5 mm) of bony elements in three dimensions, while the jaw muscles and ligaments remained intact.

We found that in all types of kinesis investigated the movements of the quadrate, jugal bars and PPC are similar. Movement of the quadrate is transferred to the upper beak by the jugal bar and the PPC, which moves almost exclusively forwards and backwards, thereby elevating or depressing the upper bill. The differences between the types of kinesis lie only in the position of the point of rotation.

These findings indicate that there is no correlation between the specific morphology of the PPC and the type of cranial kinesis. Several other factors, including the external forces applied during food acquisition, may influence the morphology of the PPC. Differences in PPC morphology therefore appear to be the result of different functional demands acting on the system simultaneously but with different strengths, depending on the species.

Key words: cranial kinesis, bird, kinematics, Roentgen stereophotogrammetry, Neognathae, Palaeognathae.

Introduction

Cranial kinesis in vertebrates is found mainly in birds and reptiles. In birds, especially, cranial kinesis is well developed and found in almost all species (Zusi, 1984). In birds, cranial kinesis always implies the ability to move the upper bill, or a part of it, relative to the braincase. Within birds, three main types of cranial kinesis can be discriminated (Fig. 1; Zusi, 1984): (i) prokinesis, in which the upper bill itself is inflexible and rotates around the nasal–frontal hinge, (ii) amphikinesis, in which the entire bill rotates around the nasal–frontal hinge with additional rotation near the rostrum maxillae, and (iii) rhynchokinesis, in which rotation occurs in flexible bending zones rostral to the nasal–frontal suture, where a clear hinge is absent. Within rhynchokinesis, five different types can be distinguished according to the position of the flexible bending zones (Zusi, 1984).

The movement for cranial kinesis is generated by a complex mechanism in the skull. This mechanism includes the quadrates, pterygoids, palatines, jugal bars and all associated muscles and ligaments. The closely associated pterygoids, palatines and vomer will be referred to as the pterygoid–palatine complex (PPC; Gussekloo and Zweers, 1999). Bock (Bock, 1964) has described the kinematics of the quadrate and PPC in cranial kinesis for a neognathous prokinetic bird as follows: rostro-dorsal rotation of the quadrate results in a rostral movement of the pterygoids, which transfers the movement onto the palatine, vomer, maxilla and premaxilla, resulting in elevation of the upper bill. A caudo-ventral rotation of the quadrate, and a subsequent caudal movement of the pterygoid, palatine, vomer, premaxilla and maxilla, achieves depression of the upper bill.

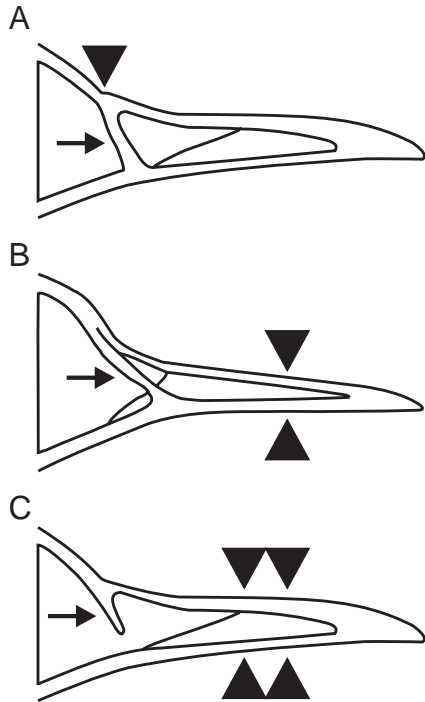


Fig. 1. Types of cranial kinesis in birds. (A) Prokinesis, (B) distal rhynchokinesis, (C) central rhynchokinesis. Skull outlines are given in lateral view. Black triangles indicate the main area of rotation; double triangles in a single element indicate the boundaries of a bending zone. Arrows indicate the lateral (nasal) bar of the upper bill, which is incomplete in C.

Although very little is known about the functional relationship between the type of cranial kinesis and the morphology of the PPC, a relationship has been suggested by several authors on the basis of the morphology of the PPC and the type of cranial kinesis in the taxon Palaeognathae (Hofer, 1954; Simonetta, 1960; Bock, 1963). This taxon consists of the ostrich (*Struthio camelus*), rheas (*Rhea americana* and *Pterocnemia pennata*), the emu (*Dromaius novaehollandiae*), cassowaries (*Casuaris* spp.), kiwis (*Apteryx* spp.) and approximately 50 species of tinamou in the family Tinamidae (Sibley and Monroe, 1990). According to Zusi (Zusi, 1984), only two types of rhynchokinesis are found within the Palaeognathae. Tinamous are thought to have extensive rhynchokinesis, while all the other Palaeognathae are thought to exhibit central rhynchokinesis. In extensive rhynchokinesis, the bending zone extends over the entire region between the rostrum maxillare and the nasal–frontal area, while in central rhynchokinesis a narrow bending zone is present near the centre of the upper bill. This interpretation of the bending zones was based on osteological specimens of the skulls only.

Palaognathae not only show special types of kinesis, but several studies have indicated that the overall morphology of the palaognathous PPC differs markedly from that found in neognathous birds and that it is characteristic for the Palaognathae (McDowell, 1948; Bock, 1963; Gussekloo and Zweers, 1999). The palaognathous PPC is characterised by a

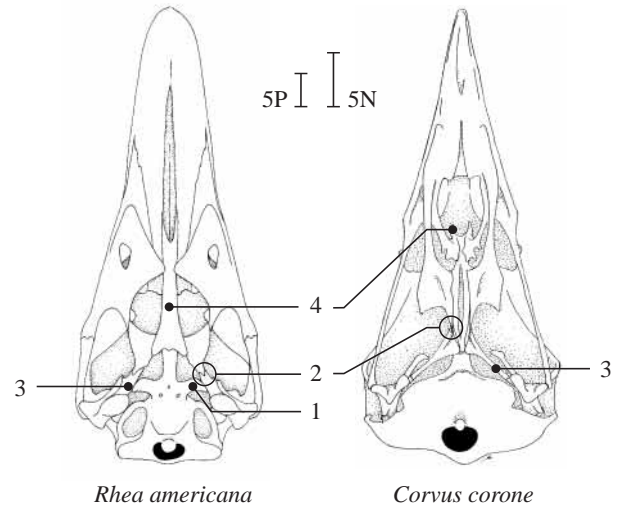


Fig. 2. Differences in the morphology of the pterygoid–palatine complex between a representative of the Neognathae (*Corvus corone*) and the Palaeognathae (*Rhea americana*). Skulls in ventral view. 1, processus basipterygoideus; 2, pterygoid–palatine articulation; 3, pterygoid; 4, vomer. The processi orbitales are not visible in this view. Relative lengths of the processi are indicated for Neognathae (5N) and Palaeognathae (5P). The lateral (nasal) bar is incomplete in palaognathous birds (not shown in this figure, see Fig. 1).

large processus basipterygoideus, relatively short processi orbitales, a broad articulation between the pterygoids and the palatines and relatively broad pterygoids and vomer (Fig. 2). No clear function for this special PPC morphology of the Palaeognathae is known, but a relationship with the special types of kinesis found within the Palaeognathae has been suggested (Hofer, 1954; Simonetta, 1960; Bock, 1963). It is possible that the specific movement pattern associated with a certain type of cranial kinesis would enforce functional demands on the PPC, resulting in a specific morphology of the PPC, or that the morphology of the PPC results in a specific movement pattern that influences the type of cranial kinesis exhibited.

To test this relationship between PPC morphology and cranial kinesis, the kinematics of the bony elements of the PPC was measured in birds with three different kinds of kinesis: prokinesis, distal rhynchokinesis and central rhynchokinesis. Differences in movement patterns could reveal whether specific demands act on the PPC for each type of cranial kinesis, thereby indicating the evolutionary forces that may have shaped the relationship between PPC morphology and cranial kinesis. Prokinesis and distal rhynchokinesis were both investigated in a neognathous species. Since the morphology and the type of kinesis (central rhynchokinesis) are most deviant within the taxon Palaeognathae, three different species from this taxon were examined.

The three-dimensional movement of the PPC elements has never been described experimentally in Neognathae or Palaeognathae. This is mainly because of the very small displacements involved and because the elements are all

situated deep inside the head. To overcome these experimental difficulties, a Roentgen stereophotogrammetry method was developed that made it possible to measure three-dimensional coordinates of markers with an accuracy of 0.12 mm. This gave an accuracy for displacement values of 0.5 mm as a result of the propagated error of both the coordinate measurements and the alignment procedure (Gussekkloo et al., 2000).

Materials and methods

Subjects

The kinematics of three different types of kinesis was analysed. The most common form, prokinesis, is characterised by rotation of the complete upper bill around a nasal–frontal hinge (Fig. 1A). In this analysis, prokinesis was represented by the crow *Corvus corone* L. A qualitative description of the kinesis of this species has been given by Bock (Bock, 1964). Distal rhynchokinesis, in which only the rostral part of the bill rotates (Fig. 1B), is found mainly in the order Charadriiformes. This mechanism was analysed in the red knot *Calidris canutus* (L.). The third type of kinesis, found in the Palaeognathae only, has conventionally been described as central rhynchokinesis. The kinematics of the PPC in this case was determined in three species: the rhea *Rhea americana* (L.), the emu *Dromaius novaehollandiae* Latham and the ostrich *Struthio camelus* L.

For each species, the head of a dead individual was used. The specimens were frozen immediately after death. Before experiments, the specimens were defrosted completely and checked for the absence of *rigor mortis*. The skin and eyes were removed to improve the contrast of the Roentgen images. In each specimen, 20 cobalt spheres with a diameter of 0.8 mm were inserted into the skull (Fig. 3; Table 1). The markers described six subsystems important in the movement of the upper bill and some served as reference markers. To secure their positions, they were attached to bony elements. If necessary, an incision was made in the overlying tissue, and a small hole was drilled into the bone in which the marker was immobilised using alpha-cyanoacrylate adhesive. Large incisions in muscles were closed using a very small amount of the same adhesive. Because of morphological differences, it was not possible to place all the markers in each species, so some markers are missing from some subjects. Some markers were not inserted completely into the bone and were found inside the overlying tissue after the experiment. These markers were not used in the analysis.

Procedures

To determine the displacement of the elements in the skull during kinesis, three-dimensional coordinates of the markers were calculated in two conditions: the resting (closed) position of the bill, and with the upper bill elevated. Stereophotogrammetry methods were used to determine the exact positions of the markers in these two conditions, and a displacement analysis was used to quantify the differences between the two conditions.

Stereophotogrammetry is a method in which three-

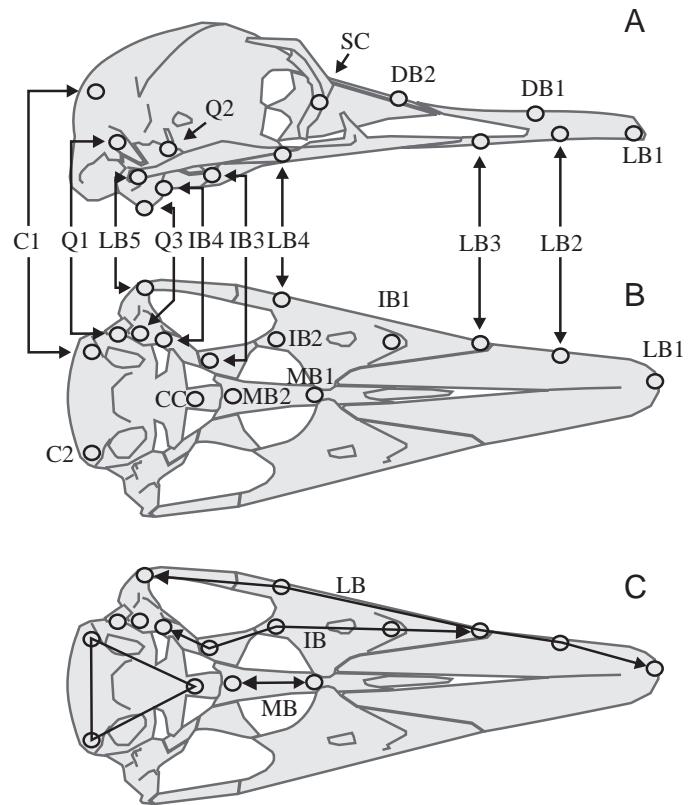


Fig. 3. Distribution of the markers inside the head of the bird. The skull is shown in lateral (A) and ventral (B,C) view. Markers are shown only when their position is visible in the views shown. In C, the division of groups of markers into a number of elements used in the text to describe cranial kinesis is shown: LB, lateral bar; IB, internal bar; MB, medial bar. Letter coding corresponds with the coding in Table 1. In radiograms, all markers are visible unless their projection coincides with that of another marker or the metal support rod.

dimensional coordinates are calculated from multiple two-dimensional projections. Since, in the present study, the markers were embedded in bone, Roentgen imaging was used. A single Roentgen source was used to obtain images of the experimental object in three different directions. Images were taken in sequence, and sufficient differences in projection angle were obtained by rotation of the experimental object while the Roentgen camera remained stationary (1, image from the lateral view; 2, image from the dorsal, rostral end 30° elevated; 3, image from the dorsal, caudal end 30° elevated). This method has been described in detail (Gussekkloo et al., 2000), so only a brief outline of the procedure is given here.

The complete experimental arrangement consisted of a Roentgen source situated above an object frame mounted on a calibration frame. The Roentgen source and the calibration frame were fixed such that they could not move relative to each other or to the environment. The object frame was used to keep the head in position during the analysis and to make elevation of the upper bill possible. The head was attached to the object frame using a small metal rod with a clamp on one end. The

Table 1. *Positions of markers placed in the skulls of the experimental specimens (see also Fig. 1)*

System	Marker	Bony element	Position
Lateral bar	LB1	Os premaxillare	Rostral
	LB2	Os premaxillare	0.25 bill length from tip
	LB3	Os premaxillare	At fusion with palatine
	LB4	Jugal bar	Rostral
	LB5	Jugal bar–quadrate articulation	Lateral
Internal bar	IB1	Os premaxillare	
	IB2	Os palatinum	Processus maxillare
	IB3	Os palatinum	Pars lateralis
	IB4	Os pterygoideum	
Medial bar	MB1	Vomer	Rostral
	MB2	Vomer	Caudal
Dorsal bar	DB1	Dorsal bar of the upper bill	Rostral
	DB2	Dorsal bar of the upper bill	Caudal
Semi-constant	SC	Os ectethmoidale	Lateral
Medial constant	CC	Rostrum parasphenoidale	Caudal/proximal
Lateral constant 1	C1	Cranium	Caudo-lateral
Lateral constant 2	C2	Cranium	Caudo-lateral
Quadrate	Q1	Processus oticum	Central
	Q2	Processus orbitalis	Distal
	Q3	Processus mandibularis	Distal

clamp was inserted into the foramen magnum and tightened around the basioccipital bone. In some cases, the condylus occipitalis had to be removed for proper fixation. Both the length and the vertical position of the metal rod could be adjusted so that the position of the head could be changed. On the rostral side of the head, a second adjustable metal rod was used to fix the bill tips and to elevate the upper bill in the elevated condition. The bill tip was attached to this second metal rod using surgical tape. The upper bill was elevated by moving the second metal bar dorsally within the object frame. This movement was along the specimen's dorsal–ventral axis, and lateral movements were negligible. Before the elevation of the upper bill, the surgical tape was removed to ensure free movement of the bill. After elevation, the bill was again attached to the metal rod. During this procedure, the lower bill was not fixed and could move freely with the movement of the quadrate. In each species, the bill was elevated by approximately 10°, which is the average maximal elevation of the upper bill in birds (Kooloos and Zweers, 1989; Heidweiller and Zweers, 1990; van den Heuvel, 1992; Gussekloo, 2000). However, when the elevation forces required exceeded normal manual force, or if abnormal deformations in morphology occurred, elevation was stopped before it reached 10°. Several

markers were placed inside the object frame to determine the exact position of the frame relative to the camera. The calibration frame was used to determine the position of the Roentgen source relative to the recording film positioned on its base. This was achieved by eight markers situated immediately above the film and four additional markers 6 cm above the film. The exact orientation of these markers was known, and the position of the Roentgen source could be calculated from the projection of these markers onto the film.

The three-dimensional coordinates of the object markers were calculated from the three two-dimensional projections of the object from different positions. The projections of the calibration markers in each view allowed the relative position of the Roentgen source in each radiogram to be determined. The projection of the known coordinates of the object frame were then used to determine the orientation of the object frame relative to the camera. When the orientation of the object frame is known in two directions, three-dimensional coordinates can be calculated. Since the coordinates of the object frame are known, the solution for the three-dimensional coordinates can be optimised, and the optimised solution can be used to calculate the coordinates of the skull markers (for further details, see Gussekloo et al., 2000). In the present study, three radiograms were taken of the experimental object. This is less than the number used previously (Gussekloo et al., 2000), but proved sufficient for the accurate determination of coordinates while reducing the time necessary for analysis.

Displacement analysis (comparison of conditions)

When the marker coordinates are known in both the closed and elevated conditions, changes in the positions of the markers can be determined using a displacement analysis. In this displacement analysis, the marker positions are transformed in such a way that known base markers (those that are known not to change position) have the same coordinates in both conditions. After this transformation, changes in coordinates between conditions were calculated.

First, the base coordinates were tested for stability. The base coordinates in our experiment were markers in the neurocranium and, when less than three were present in the neurocranium, in the ectethmoid bone. The analysis showed that these coordinates were not completely stable and that small movements of the marker in the ectethmoid bone occurred. Since very few completely stable points are present in the highly kinetic bird skull, these positions represented the best possible means of providing a widely distributed base, even if it was not completely stable. Since the base could not always be perfectly aligned, errors in the alignment are included in the standard deviation of the calculated position changes.

Whether a marker has been displaced between conditions depends on the Euclidean distance the marker has shifted between conditions and on the accuracy with which this distance can be calculated. A point is considered stable when the Euclidean distance between the marker in each condition, divided by the propagated standard deviation of this distance,

is smaller than the critical value of the normal distribution ($P < 0.05$).

Differences in coordinates between the closed bill condition and the elevated bill condition were calculated for all markers.

Elements within the skull

In the present analysis, the mechanism of cranial kinesis is divided into a number of elements on the basis of anatomical position. Markers are labelled according to these elements. These elements are the quadrate, the internal bar, the lateral bar, the medial bar and the dorsal bar (Fig. 3; Table 1). The quadrate consists only of the os quadratum. The elements in the internal bar are the pterygoid, palatine and premaxillae. The lateral bar is described by markers along the lateral side of the upper bill and on the jugal bar. The medial bar is described by markers in the vomer, which in Palaeognathae may also transfer forces from the pterygoids to the upper bill. The dorsal bar is the dorsal bar of the upper bill.

It is possible that the externally applied forces required to elevate the upper bill result in deformation of the elements of the PPC or in disarticulation of the joints of the PPC. To test whether such deformations or disarticulations occurred, distances between markers were calculated in both the closed bill and the elevated bill condition. If the distances between markers within a single element, or between markers across an articulation, changed between the two conditions, then deformation must have occurred. The presence of deformation was checked for all elements (quadrate, internal bar, lateral bar, medial bar and dorsal bar) and for the articulations between the quadrate and both the internal and lateral bars. Deformations between conditions were calculated using the same method as for the displacement of the markers.

Rotations in the sagittal plane of both the quadrate and the upper bill were determined from the displacements of the marker. A line through two markers within each of these elements was calculated in both the closed bill and elevated bill conditions. These two lines were projected onto a lateral radiogram of the bird, and the intersection of the lines in combination with morphological characters were used to determine the actual point of rotation of the element. The final rotation of the element was

calculated from this point of rotation and the displacement of the most distal marker in the element.

Results

The displacement data are represented in three dimensions, according to the three perpendicular axes through the skull: the x axis describes the rostro-caudal axis of the skull, the y axis describes the latero-lateral axis and the z axis describes the dorso-ventral axis. Because markers could not be accurately positioned at identical positions in the different skulls, the reference frame was used to define the axes. In addition, since not all the skulls were positioned in exactly the same orientation within the reference frame, position changes rather than absolute coordinates can be compared between species.

The crow (*Corvus corone*)

The elevation of the upper bill of the crow was 6.5° . This rotation angle was calculated from the displacement of the markers in the dorsal bar (DB1 and DB2; Table 2; Fig. 4). Marker DB2 is situated close to the hinge and shows no

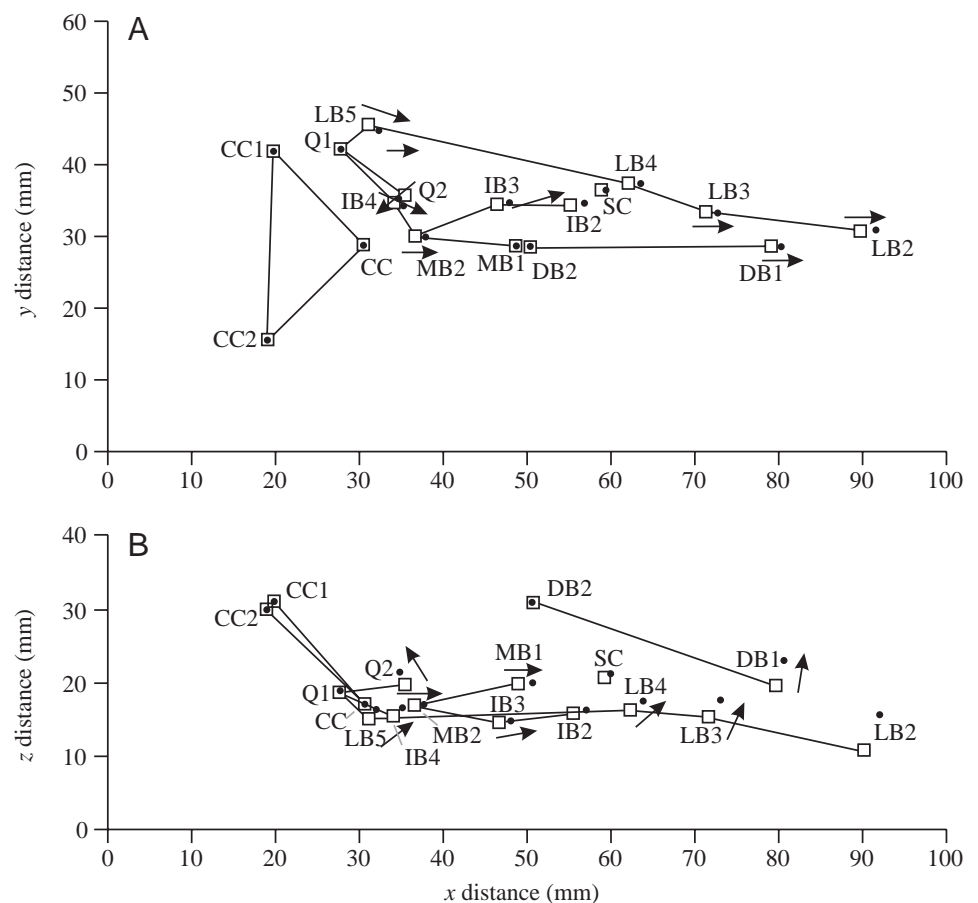


Fig. 4. Marker positions in the crow (*Corvus corone*) in the x,y plane (dorso-ventral view) (A) and the x,z plane (lateral view) (B). Squares indicate the positions of the markers with the bill closed, and filled circles indicate the positions of the markers with the bill elevated. Letter codings correspond with those in Table 1. Lines drawn between marker positions indicate the bony elements present in the skull. Arrows indicate the general direction of displacement.

Table 2. Displacement analysis for the neognathous species

	<i>Corvus corone</i>						<i>Calidris canutus</i>					
	dx (mm)	dy (mm)	dz (mm)	Dist (mm)	s.D. (mm)	Dist/s.D.	dx (mm)	dy (mm)	dz (mm)	Dist (mm)	s.D. (mm)	Dist/s.D.
LB1												
LB2	1.94	-0.04	5.09	5.45	1.46	3.74*	0.61	0.06	2.21	2.29	1.16	1.97*
LB3	1.43	0.03	2.38	2.78	1.09	2.55*	0.54	0.04	0.81	0.98	0.97	1.01
LB4	1.43	0.07	1.04	1.77	0.93	1.91*						
LB5	1.21	-0.42	0.97	1.61	0.56	2.89*	0.26	-0.14	0.24	0.38	0.54	0.69
IB1							0.42	0.10	0.06	0.44	0.56	0.78
IB2	1.54	0.13	0.75	1.72	0.80	2.14*	0.42	0.09	-0.05	0.43	0.48	0.90
IB3	1.60	0.24	0.36	1.66	0.67	2.47*	0.41	0.06	-0.03	0.41	0.44	0.94
IB4	0.84	-0.22	0.81	1.19	0.51	2.34*	0.34	0.04	-0.05	0.35	0.43	0.81
MB1	1.35	0.05	0.26	1.37	0.68	2.02*						
MB2	1.44	-0.05	-0.08	1.44	0.52	2.77*						
DB1	0.69	0	3.45	3.52	1.23	2.86*	0.27	0	1.10	1.13	1.07	1.05
DB2	0	0.09	0.03	0.09	0.70	0.13	0.04	-0.03	-0.05	0.07	0.56	0.13
SC	0.84	0.08	0.54	1.01	0.85	1.18	0.37	0	0	0.37	0.30	1.20
CC	0.01	0	-0.01	0.02	0.31	0.05	0.02	-0.02	-0.02	0.04	0.30	0.13
C1	0	0	0	0	0.35	0	0	0	0	0	0.33	0
C2	0	-0.04	0.01	0.04	0.35	0.12	0	0.01	0	0.01	0.56	0.02
Q1	0.18	-0.09	0.26	0.33	0.49	0.67	-0.02	0.02	-0.04	0.05	0.55	0.09
Q2	-0.73	-0.68	1.82	2.08	0.48	4.35*	-0.25	-0.22	0.23	0.40	0.41	0.98
Q3							0.31	-0.08	0.12	0.35	0.55	0.63

Changes in marker positions between the closed and elevated bill positions in three directions are shown (all in mm): *x*, rostro-caudal; *y*, latero-medial; *z*, dorso-ventral direction. Positive values represent rostral, lateral and dorsal movement, respectively. Although the axes were orientated as given above in each case, the coordinate systems were not orientated identically for each bird.

Dist, displacement (in mm); s.D., standard deviation of the calculated displacement. If the displacement divided by its standard deviation is smaller than the critical value of the normal distribution (1.65, $P < 0.05$), the marker is considered to be stationary.

Significant displacements are indicated by an asterisk.

See Table 1 for explanation of marker letter codings.

significant elevation. Marker DB1, which is situated more rostrally, was elevated by 3.45 mm.

The lateral bar (LB) markers all showed a dorsal and rostral movement, confirming forward movement of the jugal bars and rotation of the upper bill. The same movement, although smaller, was also found in the internal bar (IB). The medial bar (MB) showed rostral movement (1.40 mm) and rotation around the centre of the element, resulting in elevation of the rostral part. The quadrate rotated approximately 10° forwards, resulting in an upward and slightly backward movement of the processus orbitalis (Q2). The cranial markers showed no significant changes in position. No deformations as a result of the external opening forces on the upper bill were observed within elements.

The red knot (Calidris canutus)

The moveable part of the upper bill in the red knot was rotated by approximately 10° during bill elevation. This angle was calculated from the displacements of markers LB2 and LB3 in the lateral bar. The rotation of the quadrate, based on the rotation of the line through markers Q3 and Q1, was estimated to be 9° . Marker LB2 was the only marker that

showed a significant displacement. Although differences in other marker positions were not significant because of the small size of the bird and thus of the displacements, the general pattern of movement was very similar to that of the crow (Table 2). Markers in the lateral bar all showed a rostral and a slightly dorsal movement. The internal bar showed only a rostral movement, and the rostral marker in the dorsal bar, which is close to the bending zone, moved slightly dorsally and rostrally. Although none of these displacements was significant, they probably reflect the true movement pattern since they follow the same pattern as in the other species; displacements resulting only from measuring errors would have been in random directions. There were no significant deformations between and within elements as a result of bill opening.

The rhea (Rhea americana)

The rotation of the upper bill was calculated from the displacements in the dorsal bar (DB1, DB2). The rotation angle was approximately 8° . The quadrate rotated 8° in the rostro-dorsal direction and also rotated slightly medially.

Marker DB2 showed no significant displacement; marker

DB1 was rotated upwards and pulled slightly forwards during opening (Fig. 5; Table 3). Markers in the lateral bar (with the exception of LB5) showed larger displacements in the rostral direction than markers in the dorsal bar. The dorsal displacement of the markers in the lateral bar was very large for the most rostral markers (LB2, LB3), but smaller for the more caudal markers (LB4, LB5). The internal bar showed mainly rostral displacement. The marker in the pterygoid (IB4) was also slightly displaced in the dorsal direction. The cranial markers (C1, C2) showed no significant displacement, and the marker in the ectethmoid bone (SC) showed only slight non-significant displacement in the dorsal direction.

Deformations were found in the lateral bar as a result of the elevation of the upper bill in the rhea. Within the lateral bar, the distance between markers LB3 and LB5 (-1.99 mm), and between markers LB4 and LB5 (-1.67 mm) decreased as a result of upward bending in the lateral bar. No other deformations were observed in either elements or articulations.

The emu (*Dromaius novaehollandiae*)

The rotation of the upper bill by 4° upwards was determined from the displacement of the markers in the dorsal bar. The quadrate was rotated 4° in the rostro-dorsal direction and also showed a large medial displacement of the more distal markers (Q2, Q3).

The markers in the lateral bar showed a displacement pattern similar to that in the rhea, i.e. they moved rostrally and dorsally (Table 3). The rostral movement was almost constant throughout the bar, while the dorsal movement was larger in the more dorsal markers. The internal bar showed mainly rostral movement over a distance similar to that of the lateral bar. Slight dorsal movements were also measured. The same displacement pattern was found in the internal bar and medial bar. In both bars, the rostral markers showed a slightly larger dorsal displacement than the more caudal markers. None of the cranial markers showed any displacement. No significant deformations were found in elements or articulations as a result of the opening of the upper bill.

The ostrich (*Struthio camelus*)

The upper bill of the ostrich was elevated 8° . This angle was calculated from the displacement of the most rostral markers of the

lateral bar (LB1, LB2). The quadrate rotated 5° rostro-dorsally around the processus oticus and also showed medial displacement.

The lateral bar, medial bar and internal bar all show rostral displacement. The more rostral markers also showed a dorsal displacement. None of the cranial markers showed any displacement. No internal deformations within elements or articulations were observed.

Discussion

Avian cranial kinesis is controlled by several bony elements and ligaments, which may constrain movement. Although the movement of the system has been described qualitatively for prokinetic birds (Bock, 1964), actual displacements of only a few elements in the jaw apparatus have been measured previously in two dimensions in a single species (van Gennip and Berkhoudt, 1992). Our study shows for the first time the actual displacement pattern of the bony elements in the skull in three dimensions and confirms that the general displacement pattern described by Bock (Bock,

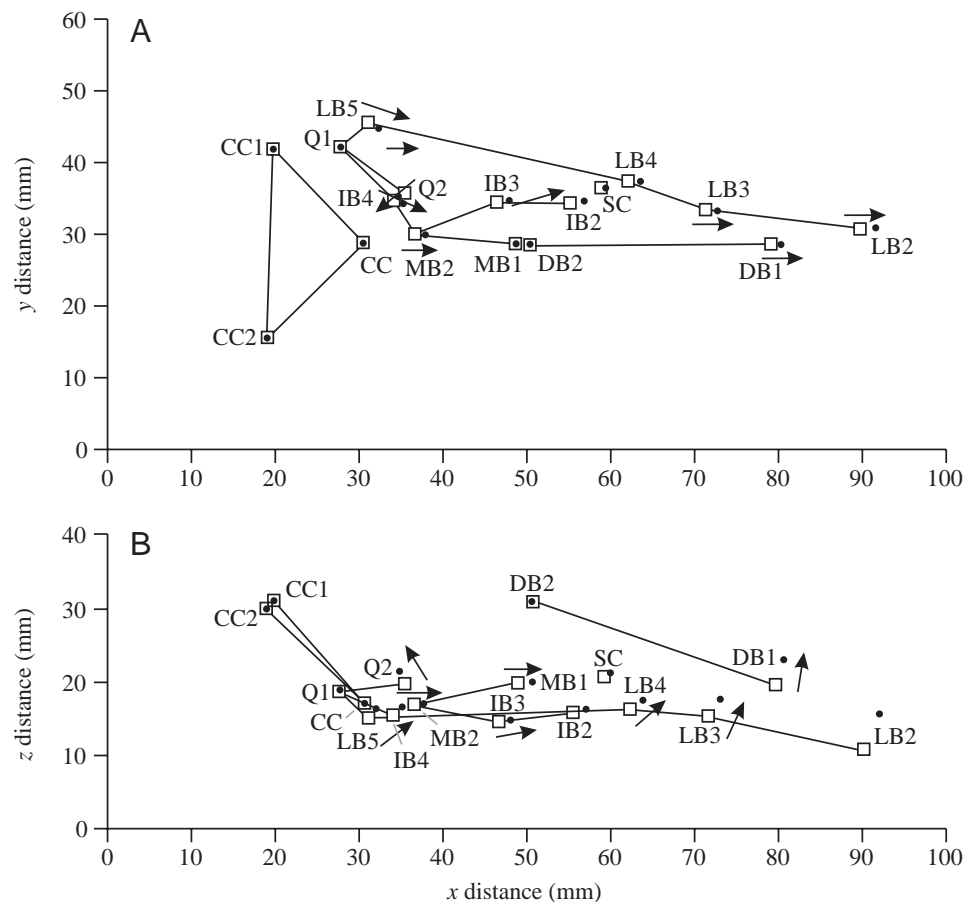


Fig. 5. Marker positions in the rhea (*Rhea americana*) in the x,y plane (dorso-ventral view) (A) and the x,z plane (lateral view) (B). Squares indicate the positions of the markers with the bill closed, and filled circles indicate the positions of the markers with the bill elevated. Letter codings correspond with those in Table 1. Lines drawn between marker positions indicate the bony elements present in the skull. Arrows indicate the general direction of displacement.

Table 3. Displacement analysis for the palaeognathous species

	<i>Rhea americana</i>						<i>Dromaius novaehollandiae</i>						<i>Struthio camelus</i>					
	dx (mm)	dy (mm)	dz (mm)	Dist (mm)	s.D. (mm)	Dist/s.D.	dx (mm)	dy (mm)	dz (mm)	Dist (mm)	s.D. (mm)	Dist/s.D.	dx (mm)	dy (mm)	dz (mm)	Dist (mm)	s.D. (mm)	Dist/s.D.
LB1													3.11	-0.60	9.19	9.72	0.98	9.90*
LB2	3.01	-0.09	10.92	11.32	0.92	12.30*	2.40	-0.48	2.58	3.56	1.32	2.69*	3.00	-0.31	4.84	5.70	0.81	7.00*
LB3	2.79	0.15	2.77	3.94	0.68	5.79*	2.07	-0.39	1.08	2.36	1.02	2.31*	2.49	-0.14	0.54	2.55	0.56	4.57*
LB4	2.15	-0.30	0.23	2.18	0.52	4.19*	1.93	-0.85	0.79	2.25	0.70	3.24*						
LB5	0.44	-0.84	0.35	1.01	0.57	1.77*	1.79	-1.13	0.28	2.13	0.61	3.49*	1.94	-1.13	-0.22	2.26	0.64	3.55*
IB1							2.16	-0.37	0.82	2.34	0.93	2.52*	2.73	-0.04	1.23	2.99	0.65	4.60*
IB2	2.17	-0.44	-0.05	2.21	0.49	4.52*	2.16	-0.58	0.58	2.31	0.72	3.21*	2.65	-0.12	0.45	2.69	0.57	4.69*
IB3							2.11	-0.43	0.36	2.19	0.62	3.52*	2.63	-0.94	0.15	2.80	0.55	5.11*
IB4	2.06	-0.02	0.71	2.18	0.50	4.38*	1.56	-0.88	0.17	1.80	0.53	3.41*	2.70	-1.07	0.11	2.91	0.57	5.09*
MB1							1.97	-0.43	1.33	2.42	1.06	2.28*	2.62	0	0.25	2.63	0.66	3.99*
MB2	2.30	0.13	-0.39	2.33	0.49	4.76*	1.81	-0.18	0.26	1.84	0.63	2.89*						
DB1	1.71	0	8.78	8.95	0.88	10.11*	1.21	0	3.26	3.48	1.32	2.63*						
DB2	-0.78	0.28	-0.04	0.82	0.63	1.31	-0.18	0.07	0.23	0.30	0.97	0.31						
SC	0.47	-0.11	-0.15	0.51	0.32	1.58	0.10	-0.09	0.14	0.19	0.78	0.25	0.25	0.11	-0.19	0.34	0.34	1.00
CC							-0.08	-0.03	0.09	0.12	0.30	0.42						
C1	0	0	0	0	0.39	0	0	0	0	0	0.30	0	0	0	0	0	0.42	0
C2	0	-0.04	0	0.04	0.38	0.11	0	0.09	-0.01	0.09	0.29	0.29	0	-0.06	0	0.06	0.39	0.16
Q1	0.12	-0.26	0.13	0.32	0.50	0.64	-0.15	0.16	-0.04	0.22	0.43	0.51	0.24	-0.33	-0.08	0.42	0.58	0.72
Q2	1.56	-0.28	0.47	1.66	0.50	3.30*	0.15	-1.42	1.22	1.88	0.48	3.93*	0.21	-1.17	1.64	2.03	0.49	4.12*
Q3							1.32	-0.57	-0.05	1.44	0.55	2.64*	2.05	-1.39	0.13	2.48	0.63	3.95*

Changes in marker positions between the closed and elevated bill positions in three directions are shown (all in mm): x, rostro-caudal; y, latero-medial; z, dorso-ventral direction. Positive values represent rostral, lateral and dorsal movement, respectively. Although the axes were orientated as given above in each case, the coordinate systems were not orientated identically for each bird.

Dist, displacement (in mm); s.D., standard deviation of the calculated displacement. If the displacement divided by its standard deviation is smaller than the critical value of the normal distribution (1.65, $P < 0.05$), the marker is considered to be stationary.

Significant displacements are indicated by an asterisk.

See Table 1 for explanation of marker letter codings.

1964) is valid for both prokinetic and rhynchokinetic birds. The elevation of the upper bill in birds is induced by a rostro-caudal rotation of the quadrate. This rotation results in a rostral displacement of both the jugal arch and the PPC. These two bars press against the premaxillae, which results in elevation of either the complete upper bill (for prokinesis and extensive rhynchokinesis) or only the rostral part of the upper bill (for distal rhynchokinesis).

To our knowledge, only one three-dimensional kinematic model of the avian skull has been developed (van Gennip and Berkhoudt, 1992). This model shows that dorso-medial movement of the quadrate may occur in the pigeon (*Columba livia*). In this model, movement of the quadrate is essential to uncouple upper and lower jaw movement, which they assume to be mechanically linked by an unstretchable postorbital ligament. In palaeognathous birds, the postorbital ligament does not insert on the mandible but on the jugal bar (Elzanowski, 1987), while model calculations (R. G. Bout and G. A. Zweers, in preparation) and force measurements (Nuijens and Bout, 1998) show that a blocking action of the postorbital ligament does not exist in a number of birds that do possess this ligament. Our analysis shows that during upper bill rotation the displacement of the quadrate in the lateral/medial plain is very limited. In our experiments, the forces for elevation were applied as pulling forces on the bill instead of pushing forces from the quadrate, and this may have had some effect on the movement pattern of the elements of the skull. Active pulling by the protractor of the quadrate may result in a somewhat larger medial movement of the quadrate. However, the elevations of the upper bill were within the natural range of the birds (Gusseklou, 2000), and no deformations of elements and articulations were found except in the bending zone of the upper bill. This shows that, despite inducing the movement by pulling the upper bill instead of pushing the quadrate, the integrity of the system remained intact and differences in movement due to the method of opening are unlikely. The quadrate does show rotation along its longitudinal axis, which mainly affects the position of the processus orbitalis quadrati. Rotation around this axis will not affect the forward motion of the quadrate. Kinematically, the skull elements behave approximately like a four-bar system moving in one plane (see Hoese and Westneat, 1996).

Although it has been suggested that there must be a relationship between PPC morphology and the special types of kinesis found within the Palaeognathae (Hofer, 1954; Simonetta, 1960; Bock, 1963), the exact nature of such a relationship has never been described. Although we did not attempt to compare species quantitatively for technical reasons (see Results), our kinematic analysis shows that the direction and relative magnitude of the displacements described by Bock (Bock, 1964) are similar for prokinesis and central rhynchokinesis and very probably also for distal rhynchokinesis. Our main conclusion must be, therefore, that the position of the flexible bending zones does not affect the movement mechanism and thus that, from a kinematic point of view, there are no functional differences

between these different types of kinesis. The similarity between the movement patterns for these types of cranial kinesis suggests that the movement of the PPC does not result in different PPC morphology, thus rejecting the hypothesis that there is a relationship between the morphology of the PPC and the type of cranial kinesis.

If the special morphology of the palaeognathous PPC cannot be related to the type of cranial kinesis, other functional demands must have led to the divergence in PPC morphology. Besides the actual movement, the PPC also transfers muscle forces to the bill and external forces from the bill to the head. The transfer of muscle forces in the absence of external forces is dependent on the resistance of the skull elements only. The main factor that might add to the need to transfer large forces is the resistance of the bending zones, which might vary in different types of kinesis. An analysis of the flexible zones has shown that they are very thin in both prokinetic and distal rhynchokinetic birds and require very little force to bend (Nuijens and Bout, 1998; also unpublished data for mallard *Anas platyrhynchos* and pigeon *Columba livia* of R. G. Bout). An analysis of the bending zones in the Palaeognathae showed that they are morphologically less distinct than in neognaths and are not clearly recognisable as thin zones. However, since they are relatively as thin as, or even thinner than, the bending zones of neognaths, no extra force is needed to achieve bending (Gusseklou, 2000). It seems that the strongly reinforced palaeognathous PPC cannot be explained by the resistance of the bending zones alone.

The analysis of the external forces is far more complicated since this includes a large number of factors. The magnitude of external forces on the bill (and the PPC) is highly dependent on the feeding behaviour of the species and on the configuration of the bill and the associated musculature. The general orientation of jaw muscles is similar in neognaths and paleognaths, except for a more medio-lateral orientation of the pterygoid muscles in the latter group. The distribution of jaw muscle mass over the main jaw muscle complexes as a percentage of total jaw muscle mass is also similar in a number of paleognath (ostrich *Struthio camelus*, emu *Dromaius novaehollandiae*, rhea *Rhea americana*; Gussekloo, 2000) and neognath (pigeon *Columba livia*, mallard *Anas platyrhynchos*, a number of finches; unpublished data by R. G. Bout; Classen, 1989; van Gennip, 1988; Nuijens and Zweers, 1997) species: approximately 40% adductor complex, 40% pterygoid complex, 22% depressor muscle and 8% protractor muscle. It is unlikely, therefore, that the differences in PPC morphology are related to basic differences in the muscle forces acting on the system resulting in fundamentally different internal stresses.

Feeding behaviour is very variable among species, and there seems to be no correlation between the type of kinesis and feeding behaviour. An analysis of different types of rhynchokinesis with respect to feeding behaviour (Zusi, 1984) showed no relationship. The only correlation that could be found was that probing birds are distal rhynchokinetic. A

functional explanation for this is that, during probing, birds can reduce the force needed to open the bill by opening a small portion of the bill only (Gerritsen, 1988). In other neognathous birds, all other types of cranial kinesis seem to be compatible with all types of feeding behaviour, suggesting a wide range of force regimes for each type of kinesis. The main factor acting on PPC morphology therefore seems to be linked with the external forces occurring in a specific feeding behaviour and not the type of kinesis.

The main problem with determining the evolutionary forces that may act on the system of cranial kinesis is the fact that the function of cranial kinesis is still unknown. The function of distal rhynchokinesis in probing birds has been postulated to be a reduction in the amount of substratum that has to be moved when opening the bill (Gerritsen, 1988). For other types of kinesis, other functional explanations have been postulated, but none has ever been experimentally proved or refuted. Possible explanations are an improvement in the line of sight (Bock, 1964) or an increase in the rate of closing of the jaws (Herrel et al., 2000). The various morphologies in different groups of birds might result from several functional demands acting in concert, but with different strengths, on the system for cranial kinesis.

In some studies (Zweers et al., 1997; Zweers and Vanden Berge, 1997), the PPC is considered as an element that had a major impact on the early evolution of trophic systems in birds. In this hypothesis, the detachment of the PPC from the cranium was a key innovation that resulted in a wide trophic radiation in birds. Although this argument may be true, these authors also propose that the detachment of the PPC resulted in three different anatomical designs of the PPC: a primary rhynchokinetic (*Hesperornis*), a palaeognathous rhynchokinetic (Palaeognathae) and a prokinetic design. Later in evolution, the latter gave rise to charadriiform rhynchokinesis. Our kinematic analysis of the PPC shows, however, no major differences in the movement pattern of the elements of the PPC in modern birds. Although parallel evolution cannot be excluded, the movement patterns and morphology (McDowell, 1948; Gussekloo and Zweers, 1999) are so similar within modern birds, and so different from that of modern related taxa, such as Reptilia (see Iordansky, 1990), that a polyphyletic origin of the avian kinetic skull is very unlikely.

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