CHAPTER 5

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

Summary

Several different types of cranial kinesis are present within modern birds. These types are characterised by the position of the rotation point. The Pterygoid-Palatinum Complex (PPC) plays an important role in the transfer of movement from the quadrate to the upper bill. The taxon Palaeognathae is characterised by a very distinct PPC morphology, which is very different from that of Neognathae, and a special type of kinesis (central rhynchokinesis). We investigated whether kinematics of the PPC differs in different types of cranial kinesis, which might indicate specific selective forces that explain the morphology of the Palaeognathous PPC. We found that in all investigated types of kinesis (prokinesis, distal rhynchokinesis, central rhynchokinesis) the movement pattern is similar and no differences in functional demands on the PPC, as a result of different types of kinesis, could be determined. In all types of kinesis the PPC moves almost exclusively forward and backward thereby elevating or depressing the upper bill. We therefore conclude that the difference in PPC morphology must be the result of other selective forces than those acting on the movement and that all types of cranial kinesis have probably evolved from a single kinetic ancestor.

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Introduction

Cranial kinesis can be found in a limited number of vertebrate groups such as reptiles and birds. Especially in birds, cranial kinesis is well developed and found in almost all species. In birds cranial kinesis always implies the ability to move the upper bill, or a part thereof, relative to the braincase. Within birds three main types of cranial kinesis have been described (Zusi, 1984): 1) Prokinesis, in which the upper bill itself is inflexible and rotates around the nasal-frontal hinge, 2) Amphikinesis, in which the entire bill rotates around the nasal-frontal hinge with additional rotation near the rostrum maxillae, 3) Rhynchokinesis, in which rotation occurs rostral to the nasal-frontal hinge and a clear hinge is absent. Rotation takes place around flexible zones in the bones of the upper bill.

Within rhynchokinesis a subdivision is made on the basis of the position of the bending zones (Zusi, 1984). Five different types can be distinguished (Zusi, 1984): 1) double rhynchokinesis in which two bending zones are present, one near the nasal-frontal area and a second near the rostrum maxillae, 2) Distal rhynchokinesis in which a single bending zone near the rostrum maxillae is present, 3) Proximal rhynchokinesis in which a single bending zone near the nasal-frontal area is present, 4) Central or Palaeognathous rhynchokinesis in which a single bending zone is present near in the central area of the upper bill, and 5) Extensive rhynchokinesis in which the bending zone extends over the complete area between rostrum maxillare and nasal-frontal area.

A complex mechanism of bony elements, muscles and ligaments generates the movement of the upper bill. This complex includes the quadrates, pterygoids, palates, jugal bars and all associated muscles and ligaments. The closely associated pterygoid and palate will be referred to as the Pterygoid-Palate Complex (PPC; Gussekloo & Zweers, 1999). The role of the quadrate and PPC has been described for a prokinetic bird (Bock, 1964). In this description movement of the quadrate is considered to induce the movement of the upper bill. Rostro-dorsal rotation of this element results in a rostral movement of the pterygoids, which transfer the rostral movement onto the palate, vomer, maxilla and premaxilla resulting in an elevation of the upper bill. Depression of the upper bill could be achieved by a caudo-ventral rotation of the quadrate and a subsequent caudal movement of pterygoid, palate, vomer, premaxilla and maxilla.

Very little is known about the cranial kinesis of the Palaeognathae. This group consists of the Ostrich (*Struthio camelus*), Rheas (*Rhea spec*. and *Pterocnemia spec*.), the Emu (*Dromaius novaehollandiae*), Cassowaries (*Casuarius spec*.), Kiwis (*Apteryx spec*.) and the approximately fifty species in the family Tinamidae (Tinamous; Sibley & Monroe, 1990). According to Zusi (1984) two types of rhynchokinesis can be found only within the Palaeognathae. Tinamous are thought to have extensive rhynchokinesis while all the other Palaeognathae are thought to be central rhynchokinetic. This interpretation was based on osteological specimens of the skulls.

In addition to these special types of rhynchokinesis the species of the Palaeognathae also possess a remarkable PPC, different from that found in neognathous birds (McDowell, 1948; Bock, 1963; Gussekloo & Zweers, 1999). Although several authors have studied the system (Hofer, 1954; Simonetta, 1960; Bock, 1963) no clear function of the special PPC morphology of

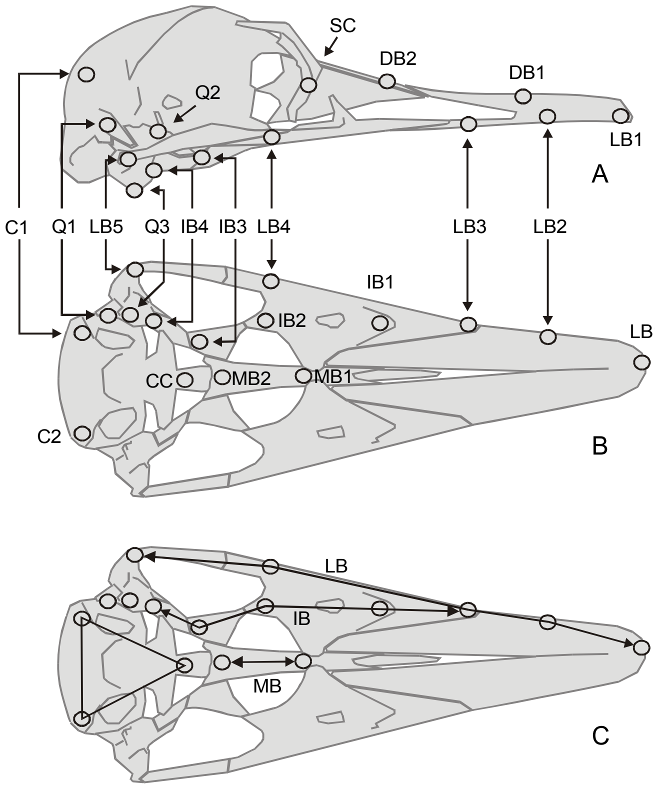

Figure 5.1. Distribution of the markers inside the experimental object. The skull is projected in lateral (A) and ventral view (B), and bars in ventral view (C). Markers are only shown when their position is visible in the views shown. Letter coding correspond with the coding in table 5.1. In radiograms all markers are visible, unless their projection coincides with the projection of another marker or metal rod. LB=Lateral Bar, IB=Internal Bar and MB=Medial Bar.

the Palaeognathae has ever been identified. It is possible that the function of the PPC in Palaeognathae is completely different from that of the prokinetic neognathous birds, for example the reinforcement of the skull (see Gussekloo & Zweers, 1999). The description of the movement of the PPC elements has never been tested experimentally. Differences in types of kinesis or morphology of the PPC maybe associated with differences in the kinematics of these elements. To test whether the PPC serves the same kinematic function independent of the type of kinesis, the displacement of bony elements of the PPC was measured in birds with three different kinds of kinesis. These types are prokinesis, distal rhynchokinesis as one of the most common forms of rhynchokinesis and finally central or palaeognathous kinesis because of its special morphology. Displacement will be measured in three dimensions using a roentgen-stereophotogrammetry technique (Gussekloo *et al.*, 2000).

Table 5.1. Markers placed in the skulls of the experimental specimen. Positions of markers are also given in figure 5.1.

System	Marker	Bony element	Position
Lateral Bar	LB1	*Os premaxillare*	Rostral
	LB2	*Os premaxillare*	¼ bill length from tip
	LB3	*Os premaxillare*	At fusion with Palate
	LB4	Jugal bar	Rostral
	LB5	Jugal bar-quadrate articulation	Lateral
Internal Bar	IB1	*Os premaxillare*	
	IB2	*Os palatinum*	Proc. 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 paraspenoidale*	Caudal/Proximal
Lateral Constant 1	C1	*Cranium*	Caudo-lateral
Lateral Constant 2	C2	*Cranium*	Caudo-lateral
Quadrate	Q1	*Proc. oticum*	Central
	Q2	*Proc. orbitalis*	Distal
	Q3	*Proc. mandibularis*	Distal

Materials and Methods

The Species

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. In this analysis prokinesis was represented by the Crow (*Corvus corone*). A qualitative description of the kinesis of this species has already been given by Bock (1964). The type of kinesis in which only the rostral part of the bill rotates (distal rhynchokinesis) is mainly found in the order Charadriiformes. This mechanism was analysed in the Red Knot (*Calidris canutus*). The third type of kinesis, found in Palaeognathae only, has conventionally been described as central rhynchokinesis. The kinematics of the PPC was determined in three species of the

Palaeognathae: the Ostrich (*Struthio camelus*), the Emu (*Dromaius novaehollandiae*) and the Rhea (*Rhea americana*).

Of each species a skull of a deceased individual was used. The skin and eyes were removed from all specimens to improve the contrast of roentgen-images. In each specimen 20 cobalt spheres with a diameter of 0.8 mm (1/32 inch) were placed (Fig. 5.1, Table 5.1). The markers (object markers) described 7 sub-systems important in the movement of the upper bill and some served as reference markers. To secure the position of the markers 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. Due to morphological differences it was not possible to place 20 markers in each species, therefore some markers are missing in some species. Some markers were not inserted into the bone completely, and were found inside the overlying tissue after the experiment. These markers were not used in the analysis. An overview of the markers that were used in each species can be found in tables 5.2 to 5.6.

The Procedure

To determine kinematics of the elements in the skull during kinesis three-dimensional co-ordinates of the markers were calculated in two conditions. These conditions represent the rest position of the bill (‘Closed Bill”), and the condition in which the upper bill is elevated (‘Elevated Bill’). Stereophotogrammetry methods were used to determine the exact position of the markers in both conditions, and a displacement analysis was used to quantify the differences between the two conditions.

Stereophotogrammetry is a method in which three-dimensional co-ordinates are calculated from multiple two-dimensional projections. Since in this study the markers are 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 made 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 lateral; 2.image from dorsal, rostral end 30 degrees elevated; 3. image from dorsal, caudal end 30 degrees elevated). This method was described in detail by Gussekloo *et al*. (2000), therefore only a brief outline of the procedure is given here.

The complete experimental set-up is shown in figure 4.2. It consisted of a roentgen-source, an object frame and a calibration frame. The roentgen-source in combination with the calibration-frame is called ‘the camera’. Elements of the camera are stationary and do not change position relative to each other or relative to the environment. The object frame (Fig. 4.4) was used to fix the heads 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 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 rod could be adjusted so that the position of the head could be changed. On the rostral side of the head a second metal rod, of which the length and vertical position could also be changed, 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 with surgical tape. The specimens were analysed with the upper bill in rest position and with the upper bill elevated. The upper bill was elevated by moving the second metal bar dorsally within the object frame. The amplitude of the elevation was as large as possible without applying excessive force. Some markers were placed inside the object frame to determine the exact position of the frame relative to the camera.

The calibration frame (Fig. 4.3) was used to determine the position of the roentgen-source relative to the film. This was achieved by eight markers situated right above the film and four additional ones at 6 cm above the film. The exact orientation of these markers was known and from the projection of these markers on the film the position of the roentgen-source could be calculated.

The three-dimensional co-ordinates of the object markers are calculated from three two-dimensional projections of the object from different positions. Based on the projection of the calibration-markers it is possible to determine the relative position of the roentgen-source in each radiogram. The projection of the known co-ordinates of the object frame can then be 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 co-ordinates can be calculated. Since the co-ordinates of the object-frame are known, the solution for the three-dimensional co-ordinates can be optimised. The parameters of the optimised solution are used to calculate the co-ordinates of the other markers (for further detail see Gussekloo *et al.*, 2000). As described above three radiograms were taken of the experimental object. This number is less than used by Gussekloo *et al.* (2000), but still sufficient for accurate determination of co-ordinates and reduced the amount of time necessary for the analysis.

Displacement Analysis (comparison of conditions)

When the co-ordinates of markers are known in both the ‘Closed’ and ’Elevated’ condition the changes in the position of the markers have to be determined. This is done using a displacement analysis. In a displacement analysis the markers of both the ‘Closed’ and ‘Elevated’ condition are transformed in such way that known stable markers (or base) are at the same co-ordinates. After this transformation the change in co-ordinates between conditions can be calculated.

First the base was tested for stability. The base in our experiment consisted of markers in the neurocranium and, when less than three were present, in the ectethmoid bone. The analysis showed that the chosen base was not completely stable and that small dislocations of the marker in the ectethmoid bone had occurred. Although the base was not completely stable, it was used anyhow, since in the highly kinetic bird skull very few completely stable points are present.

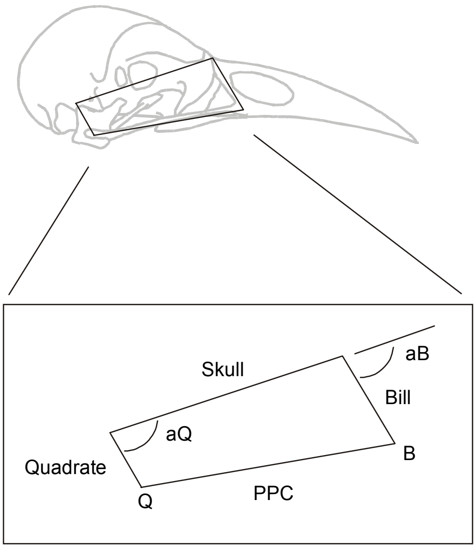

Figure 5.2. Terminology of the four-bar system. The four elements are called ‘skull’ (connection between the two rotation points in the skull), the quadrate, the PPC and the bill (lateral bar, or connection between the dorsal and ventral Zona flexoria maxillare). Q is the articulation point between the quadrate and the PPC, B is the connection point between the PPC and the ‘Bill’-bar. aQ and aB are the angles of the ‘Quadrate’-bar and the ‘Bill’-bar with the skull.

Whether a marker has been displaced between conditions depends on the Euclidean distance the marker has shifted between conditions and the accuracy of this distance. 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 co-ordinates between the ‘Closed bill’ condition and the ‘Elevated bill’ condition were calculated for all markers. These differences indicate the displacement of markers.

Elements within the skull

For this analysis the inducing mechanism for cranial kinesis is divided into a number of elements, based on 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. 5.1). The quadrate consists only of the *Os quadratum*. The elements in the Internal Bar are the pterygoid, palate and premaxillae. The Lateral Bar is defined by markers along the lateral side of the upper bill and on the jugal bar. The Medial Bar is defined by markers in the *Vomer*, which in Palaeognathae might also transfer forces from the pterygoids onto the upper bill. The Dorsal Bar is the dorsal bar of the upper bill.

It is possible that the externally applied forces to elevate the upper bill result in a deformation of the elements of the PPC, or in a dis-articulation of the joints of the PPC. To test whether deformations or dis-articulations have occurred, distances between markers were calculated in both the ‘Closed Bill’ and the ‘Elevated Bill’ condition. If distances between markers within a single element, or between markers across an articulation, have changed between the two conditions, a deformation has occurred. Deformations were tested 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 Bar. Deformations between conditions were calculated using the same method as for the displacement of the markers.

From the displacement of markers the rotation in the sagittal plane of both the quadrate and the upper bill were determined. Through two markers within each of these elements a line was calculated in both the 'Closed Bill' and 'Elevated Bill' condition. These two lines were projected on a lateral radiogram of the bird, and the intersection of the lines in combination with morphological characters was used to determine the actual point of rotation of the element. From this point of rotation and the displacement of the most distal marker in the element, the final rotation of the element was calculated.

Determination of bending zones

The position of the ventral bending zones in the palaeognathous birds and to a lesser extend in *Calidris* cannot be easily determined from morphological characteristics in radiograms. Therefore the position of these bending zones was calculated by using a four-bar system. The mechanism for the elevation of the upper bill has been described as a four-bar system by Hoese & Westneat (1996). The bars represent the stationary cranium, the quadrate, the PPC, and the caudal side of the upper bill. In a rhynchokinetic skull this last bar is the shortest distance between the flexible zones (*Zonae flexoriae maxillares*) in both dorsal and ventral bar. The lengths of the quadrate and skull bar (see fig. 5.2) and the angle between these bars were measured from radiograms in the rest position. The length of the PPC and the bar formed by the caudal bar of the upper bill were unknown, but kept constant for the 'Closed Bill' and 'Elevated Bill' conditions. For different lengths of the two unknown bars and the measured rotation of the quadrate, the rotation of the upper bill was calculated and the difference with the measured rotation of the upper bill was minimised. The lengths of the elements of the four-bar systems were chosen within he range of the actual morphology. When these four-bar systems were determined the displacement of rotation points were calculated and compared to the measured displacements of markers near the rotation points of the four-bar systems.

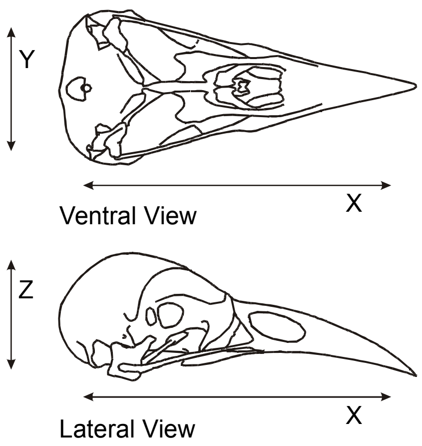

Figure 5.3. Orientation of the axis shown on the skull of the crow (Corvus corone). The X-axis describes the rostral-caudal axis, the Y-axis the lateral-lateral axis, and the Z-axis the dorsal-ventral axis.

Results

The displacement data are represented in three dimensions. The dimensions are according to three 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 the dorso-ventral axis (Fig. 5.3).

The Crow (Corvus corone, Table 5.2, Fig. 5.4)

The elevation of the upper bill of the Crow is 6.5 degrees. This rotation angle was based on the values of displacement of the markers in the Dorsal Bar. Marker DB2 is situated closely to the hinge and shows no significant elevation. The DB1 marker, which is situated more rostrally, is elevated 3.45 mm.

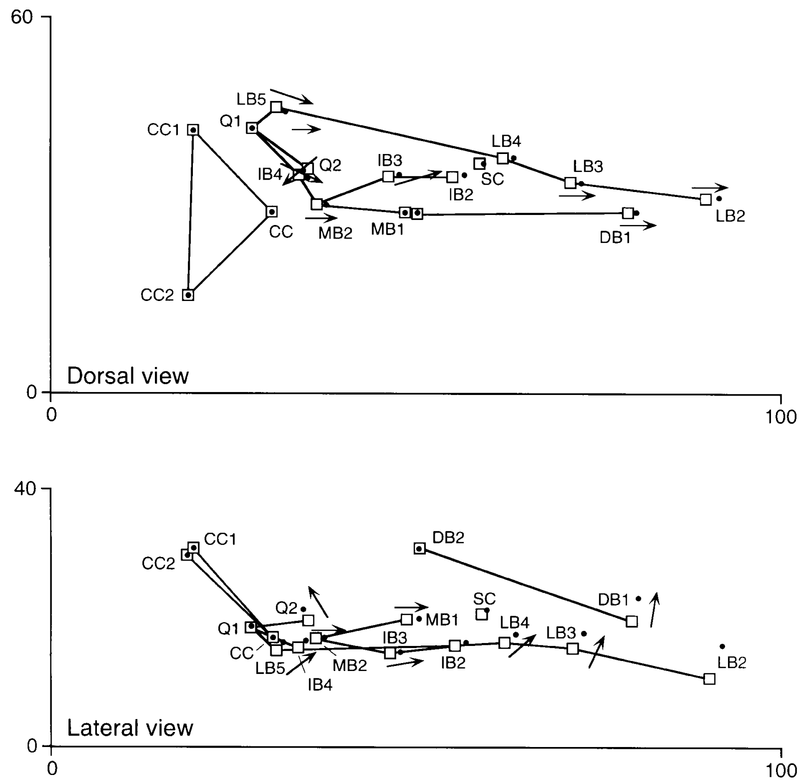

Figure 5.4. Corvus corone. Distribution and relocation of the markers in the X_Z plane (lateral view) and the X-Y plane (dorsal-ventral view). Squares indicate the position of markers in the 'Closed Bill' condition, dots indicate the position of the markers in the 'Elevated Bill' condition. Letter coding corresponds with the numbers in table 5.1. Drawn lines are schematic indicators of bony elements present in the skull. Distances on the axes are given in millimeters. Arrows indicate the general displacement pattern.

The Lateral Bar markers all show a dorsal and rostral movement which agrees with a forward movement of the jugal bars and a rotation of the upper bill. This movement, although smaller, is also found in the Internal Bar. The Medial Bar shows forward movement and a rotation around the centre of the element, which results in an elevation of the rostral part. Besides the rotation, the Medial Bar also showed a rostral movement of 1.40 mm. The quadrate rotates forward, which results in an upward and slightly backward movement of the *Processus orbitalis* (Q2). The distance between the articulation and marker Q1 was measured in the radiograms (2 mm). This distance and the displacement of marker Q1 were used to calculate the angle around which the quadrate had rotated. This rotation angle was estimated at 10

Table 5.2. Displacement analysis for Corvus corone. Change of marker positions in the experimental object in three directions (all in mm): dX: in rostro-caudal direction, dY: in latero-medial direction, dZ: in dorso-ventral direction. Column s.d. gives the standard deviation of the calculated displacement in mm. When the distance of relocation between the two conditions divided by its standard deviation is smaller than the critical value of the normal distribution (1.65, p<0.05) the marker is considered stationary. Movements are expressed as: No (N) if the marker has remained stable and Yes (Y) if the marker has moved.

Element	dX	dY	dZ	Dist 3D	s.d.	Dist/s.d.	Moved
LB1							
LB2	1.94	-0.04	5.09	5.45	1.46	3.74	Y
LB3	1.43	0.03	2.38	2.78	1.09	2.55	Y
LB4	1.43	0.07	1.04	1.77	0.93	1.91	Y
LB5	1.21	-0.42	0.97	1.61	0.56	2.89	Y
IB1							
IB2	1.54	0.13	0.75	1.72	0.80	2.14	Y
IB3	1.60	0.24	0.36	1.66	0.67	2.47	Y
IB4	0.84	-0.22	0.81	1.19	0.51	2.34	Y
MB1	1.35	0.05	0.26	1.37	0.68	2.02	Y
MB2	1.44	-0.05	-0.08	1.44	0.52	2.77	Y
DB1	0.69	0.00	3.45	3.52	1.23	2.86	Y
DB2	0.00	0.09	0.03	0.09	0.70	0.13	N
SC	0.84	0.08	0.54	1.01	0.85	1.18	N
CC	0.01	0.00	-0.01	0.02	0.31	0.05	N
C1	0.00	0.00	0.00	0.00	0.35	0.00	N
C2	0.00	-0.04	-0.01	0.04	0.35	0.12	N
Q1	0.18	-0.09	0.26	0.33	0.49	0.67	N
Q2	-0.73	-0.68	1.82	2.08	0.48	4.35	Y
Q3							

degrees not including inward rotation. The cranial markers showed no change in position, which indicated no movement in these elements. Similarly, no deformations as a result of the external opening forces on the upper bill were observed within elements.

The Red Knot (Calidris canutus, Table 5.3, Fig. 5.5)

The rotation of the moveable part of the upper bill in the Red Knot was approximately 10 degrees. This angle was calculated from the displacement of markers LB2 and LB3 in the

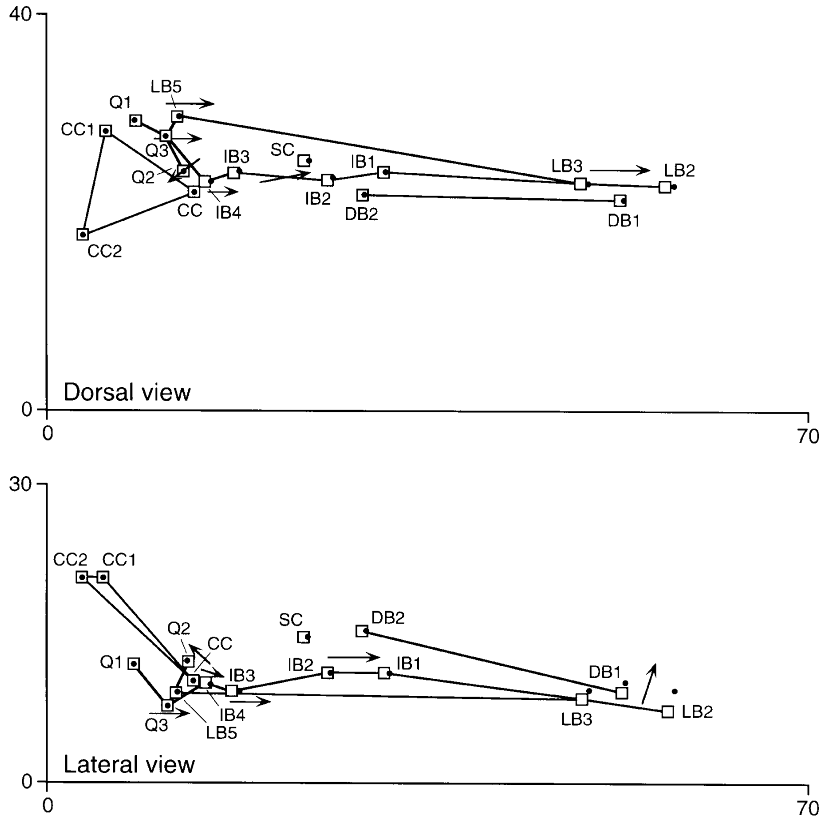

Figure 5.5. Calidris canutus. Distribution and relocation of the markers in the X_Z plane (lateral view) and the X-Y plane (dorsal-ventral view). Squares indicate the position of markers in the 'Closed Bill' condition, dots indicate the position of the markers in the 'Elevated Bill' condition. Letter coding corresponds with the numbers in table 5.1. Drawn lines are schematic indicators of bony elements present in the skull. Distances on the axes are given in millimeters. Arrows indicate the general displacement pattern.

Table 5.3. Displacement analysis for Calidris canutus. Change of visible points in the experimental object in three directions (all in mm): dX: in rostro-caudal direction, dY: in latero-medial direction, dZ: in dorso-ventral direction. Column s.d. gives the standard deviation of the calculated displacement in mm. When the distance of relocation between the two conditions divided by its standard deviation is smaller than the critical value of the normal distribution (1.65, p<0.05) the marker is considered stationary. Movements are expressed as: No (N) if the marker has remained stable and Yes (Y) if the marker has moved.

Element	dX	dY	dZ	Dist 3D	s.d.	Dist/s.d.	Moved
LB1							
LB2	0.61	0.06	2.21	2.29	1.16	1.97	Y
LB3	0.54	0.04	0.81	0.98	0.97	1.01	N
LB4							
LB5	0.26	-0.14	0.24	0.38	0.54	0.69	N
IB1	0.42	0.10	0.06	0.44	0.56	0.78	N
IB2	0.42	0.09	-0.05	0.43	0.48	0.90	N
IB3	0.41	0.06	-0.03	0.41	0.44	0.94	N
IB4	0.34	0.04	-0.05	0.35	0.43	0.81	N
MB1							
MB2							
DB1	0.27	0.00	1.10	1.13	1.07	1.05	N
DB2	0.04	-0.03	-0.05	0.07	0.56	0.13	N
SC	0.37	0.00	0.00	0.37	0.30	1.20	N
CC	0.02	-0.02	-0.02	0.04	0.30	0.13	N
C1	0.00	0.00	0.00	0.00	0.33	0.00	N
C2	0.00	0.01	0.00	0.01	0.56	0.02	N
Q1	-0.02	0.02	-0.04	0.05	0.55	0.09	N
Q2	-0.25	-0.22	0.23	0.40	0.41	0.98	N
Q3	0.31	-0.08	0.12	0.35	0.55	0.63	N

Lateral Bar. The rotation of the quadrate, based on the rotation of the line through markers Q3 and Q1 is estimated to be 9 degrees. Marker LB2 is the only marker that has moved significantly. Although differences in other markers are not significant, due to the small size of the bird and thus of the displacements, the pattern of movement is very similar to that of the crow. Markers in the Lateral Bar all show a rostral and a slightly dorsal movement. The Internal Bar shows only a rostral movement and the rostral marker in the Dorsal Bar moves slightly dorsally and rostrally. There were no significant changes in distances between and within elements when conditions were compared.

The Rhea (Rhea americana, Table 5.4, Fig. 5.6)

The rotation of the upper bill was calculated from the displacements in the Dorsal Bar (DB1, DB2). The rotation angle was approximately 8 degrees. The quadrate rotated 8 degrees in rostro-dorsal direction and also rotated slightly to medial.

Marker DB2 showed no displacement, Marker DB1 was rotated upward and pulled slightly forward during opening. Markers in the Lateral Bar showed larger displacement in the rostral direction than the markers in the Dorsal Bar. The dorsal displacement of the markers in the

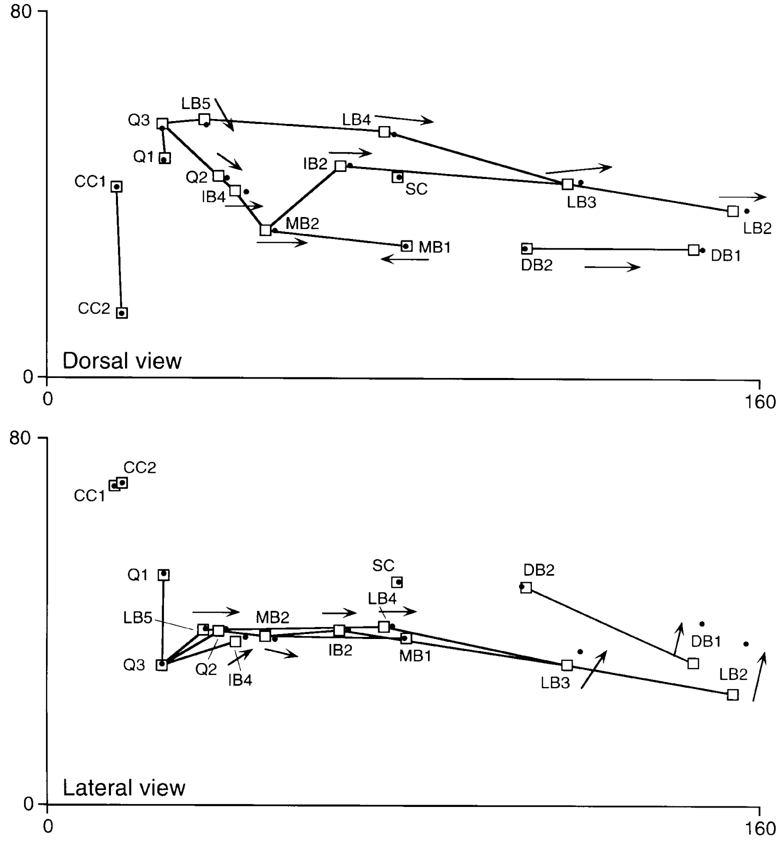

Figure 5.6. Rhea americana. Distribution and relocation of the markers in the X-Z plane (Lateral View) and the X-Y plane (Dorso-Ventral view). Squares indicate the position of markers in the 'Closed Bill' condition, dots indicate the position of markers in the 'Elevated Bill' condition. Letter codings correspond with the numbers in table 5.1. Drawn lines are schematic indicators of bony elements present in the skull. Distances on the axes are given in millimeters. Arrows indicate the general displacement pattern.

Table 5.4. Displacement analysis for Rhea americana. Change of visible points in the experimental object in three directions (all in mm): dX: in rostro-caudal direction, dY: in latero-medial direction, dZ: in dorso-ventral direction. Column s.d. gives the standard deviation of the calculated displacement in mm. When the distance of relocation between the two conditions divided by its standard deviation is smaller than the critical value of the normal distribution (1.65, p<0.05) the marker is considered stationary. Movements are expressed as: No (N) if the marker has remained stable and Yes (Y) if the marker has moved.

Element	dX	dY	dZ	Dist 3D	s.d.	Dist/s.d.	Moved
LB1							
LB2	3.01	-0.09	10.92	11.32	0.92	12.30	Y
LB3	2.79	0.15	2.77	3.94	0.68	5.79	Y
LB4	2.15	-0.30	0.23	2.18	0.52	4.19	Y
LB5	0.44	-0.84	0.35	1.01	0.57	1.77	Y
IB1							
IB2	2.17	-0.44	-0.05	2.21	0.49	4.52	Y
IB3							
IB4	2.06	-0.02	0.71	2.18	0.50	4.38	Y
MB1							
MB2	2.30	0.13	-0.39	2.33	0.49	4.76	Y
DB1	1.71	0.00	8.78	8.95	0.88	10.11	Y
DB2	-0.78	0.28	-0.04	0.82	0.63	1.31	N
SC	0.47	-0.11	-0.15	0.51	0.32	1.58	N
CC							
C1	0.00	0.00	0.00	0.00	0.39	0.00	N
C2	0.00	-0.04	0.00	0.04	0.38	0.11	N
Q1	0.12	-0.26	0.13	0.32	0.50	0.64	N
Q2	1.56	-0.28	0.47	1.66	0.50	3.30	Y
Q3							

Lateral Bar was very large for the most rostral markers, but smaller for the more caudal markers. The Internal Bar showed mainly rostral displacement. The marker in the pterygoid (IB4) was also slightly displaced in dorsal direction. The cranial markers (C1, C2) showed no displacement at all and the marker in the ectethmoid bone (SC) only slight non-significant displacement in the dorsal direction.

Deformations were found in the Lateral Bar as 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 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, Table 5.5, Fig. 5.7)

The rotation of the upper bill was determined from the displacement of the markers in the Dorsal Bar. The upper bill was rotated 4 degrees upward. The Quadrate was rotated 4 degrees in the rostro-dorsal direction and showed also a large medial displacement of the more distal markers (Q2, Q3).

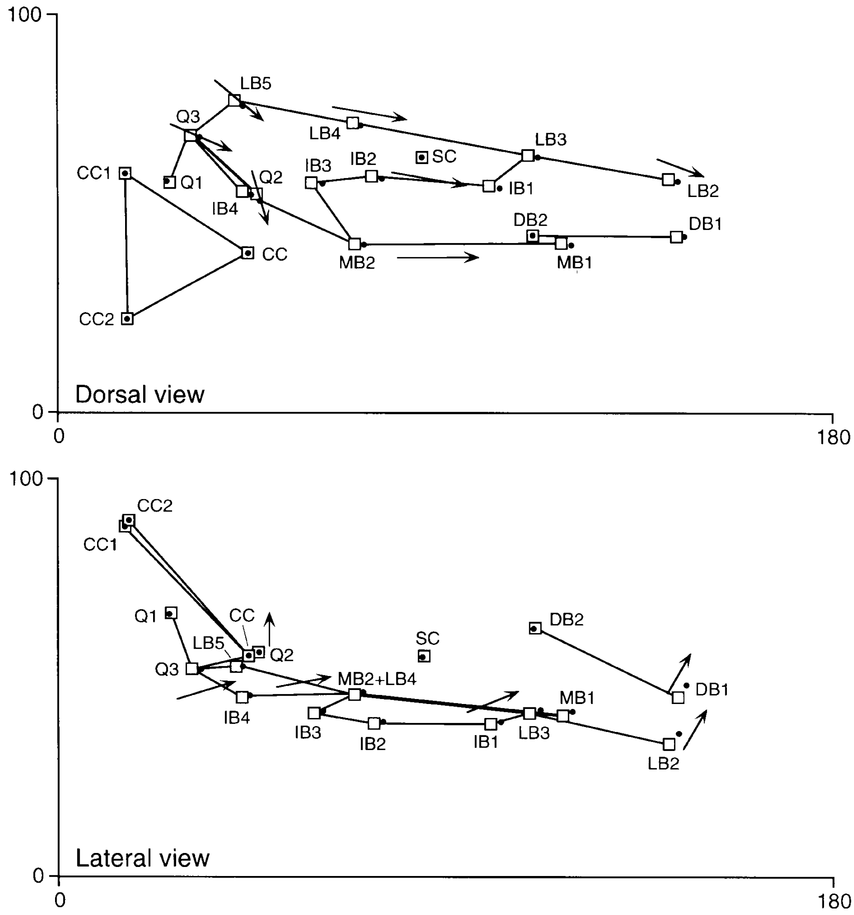

Figure 5.7. Dromaius novaehollandiae. Distribution and relocation of the markers in the X-Z plane (Lateral view) and the X-Y plane (Dorso-Ventral view). Squares indicate the position of markers in the 'Closed Bill' condition, dots indicate the position of markers in the 'Elevated Bill' condition. Letter coding correspond with the letters in table 5.1 Drawn lines are schematically indicators of bony elements present in the skull. Distances on the axes are given in millimeters. Arrows indicate the general displacement pattern.

Table 5.5. Displacement analysis for Dromaius novaehollandia. Change of visible points in the experimental object in three directions (all in mm): dX: in rostro-caudal direction, dY: in latero-medial direction, dZ: in dorso-ventral direction. Column s.d. gives the standard deviation of the calculated displacement in mm. When the distance of relocation between the two conditions divided by its standard deviation is smaller than the critical value of the normal distribution (1.65, p<0.05) the marker is considered stationary. Movements are expressed as: No (N) if the marker has remained stable and Yes (Y) if the marker has moved.

Element	dX	dY	dZ	Dist 3D	s.d.	Dist/s.d.	Moved
LB1							
LB2	2.40	-0.48	2.58	3.56	1.32	2.69	Y
LB3	2.07	-0.39	1.08	2.36	1.02	2.31	Y
LB4	1.93	-0.85	0.79	2.25	0.70	3.24	Y
LB5	1.79	-1.13	0.28	2.13	0.61	3.49	Y
IB1	2.16	-0.37	0.82	2.34	0.93	2.52	Y
IB2	2.16	-0.58	0.58	2.31	0.72	3.21	Y
IB3	2.11	-0.43	0.36	2.19	0.62	3.52	Y
IB4	1.56	-0.88	0.17	1.80	0.53	3.41	Y
MB1	1.97	-0.43	1.33	2.42	1.06	2.28	Y
MB2	1.81	-0.18	0.26	1.84	0.63	2.89	Y
DB1	1.21	0.00	3.26	3.48	1.32	2.63	Y
DB2	-0.18	0.07	0.23	0.30	0.97	0.31	N
SC	0.10	-0.09	0.14	0.19	0.78	0.25	N
CC	-0.08	-0.03	0.09	0.12	0.30	0.42	N
C1	0.00	0.00	0.00	0.00	0.30	0.00	N
C2	0.00	0.09	-0.01	0.09	0.29	0.29	N
Q1	-0.15	0.16	-0.04	0.22	0.43	0.51	N
Q2	0.15	-1.42	1.22	1.88	0.48	3.93	Y
Q3	1.32	-0.57	-0.05	1.44	0.55	2.64	Y

The markers in the Lateral Bar showed a similar displacement pattern as in the Rhea. The markers of the Lateral Bar moved rostral and dorsal. The rostral movement is almost constant throughout the bar while the dorsal movement is 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 but these were very small. The same displacement pattern was also 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, Table 5.6, Fig. 5.8)

The upper bill of the Ostrich was elevated 8 degrees. This angle was calculated from the displacement of the most rostral markers of the Lateral Bar (LB1, LB2). The quadrate rotated 5 degrees rostro-dorsal around the Processus oticus and showed a medial rotation also.

The Lateral Bar, Medial Bar and Internal Bar all show a 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.

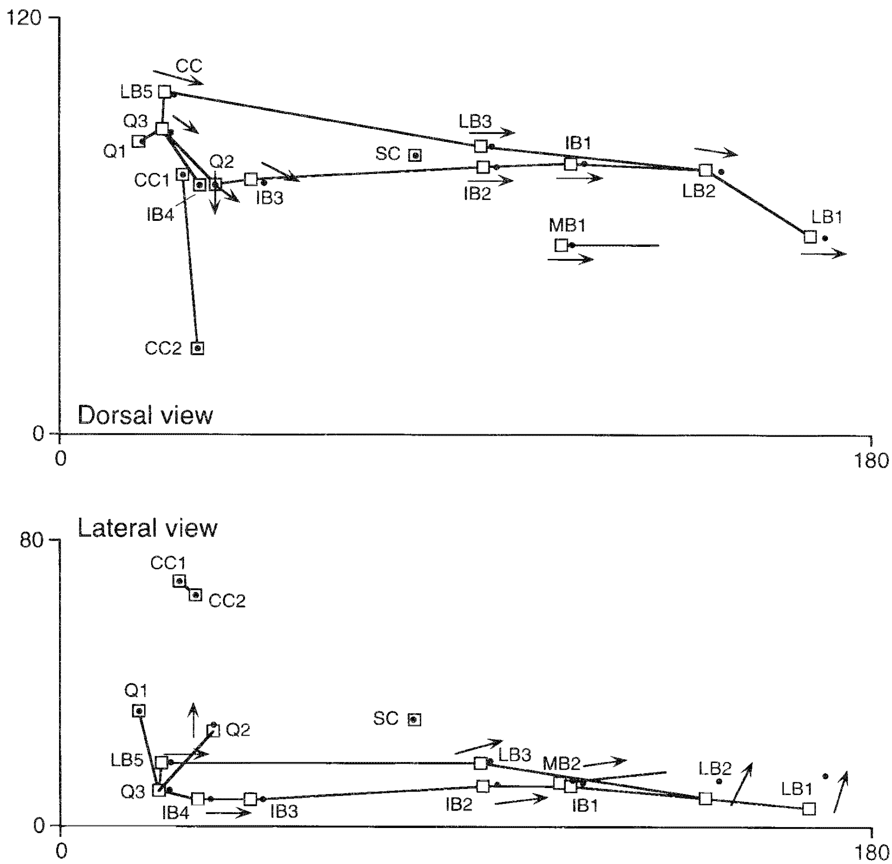

Figure 5.8. Struthio camelus. Distribution and relocation of the markers in the X-Z plane (Lateral view) and the X-Y plane (Dorso-Ventral view). Squares indicate the position of markers in the 'Closed Bill' condition, dots indicate the position of markers in the 'Elevated Bill' condition. Letter coding correspond with letters in table 5.1. Drawn lines are schematical indicators of bony elements present in the skull. Distances on the axes are giver in millimeters. Arrows indicate the general displacement pattern.

Table 5.6. Displacement analysis for Struthio camelus. Change of visible points in the experimental object in three directions (all in mm): dX: in rostro-caudal direction, dY: in latero-medial direction, dZ: in dorso-ventral direction. Column s.d. gives the standard deviation of the calculated displacement in mm. When the distance of relocation between the two conditions divided by its standard deviation is smaller than the critical value of the normal distribution (1.65, p<0.05) the marker is considered stationary. Movements are expressed as: No (N) if the marker has remained stable and Yes (Y) if the marker has moved.

Element	dX	dY	dZ	Dist 3D	s.d.	Dist/s.d.	Moved
LB1	3.11	-0.60	9.19	9.72	0.98	9.90	Y
LB2	3.00	-0.31	4.84	5.70	0.81	7.00	Y
LB3	2.49	-0.14	0.54	2.55	0.56	4.57	Y
LB4							
LB5	1.94	-1.13	-0.22	2.26	0.64	3.55	Y
IB1	2.73	-0.04	1.23	2.99	0.65	4.60	Y
IB2	2.65	-0.12	0.45	2.69	0.57	4.69	Y
IB3	2.63	-0.94	0.15	2.80	0.55	5.11	Y
IB4	2.70	-1.07	0.11	2.91	0.57	5.09	Y
MB1	2.62	0.00	0.25	2.63	0.66	3.99	Y
MB2							
DB1							
DB2							
SC	0.25	0.11	-0.19	0.34	0.34	1.00	N
CC							
C1	0.00	0.00	0.00	0.00	0.42	0.00	N
C2	0.00	-0.06	0.00	0.06	0.39	0.16	N
Q1	0.24	-0.33	-0.08	0.42	0.58	0.72	N
Q2	0.21	-1.17	1.64	2.03	0.49	4.12	Y
Q3	2.05	-1.39	0.13	2.48	0.63	3.95	Y

The Four-Bar systems

For all skulls a two-dimensional four-bar system was determined that describes the rotation of the Quadrate and Upper Bill, as well as the displacement of the markers. These four-bar systems were used to determine the position of the flexible ventral zones in the upper bill. The lengths of the elements for each species are described in table 5.7 and schematically represented in figure 5.9. Estimated and calculated displacements of markers are given in table 5.8. For all species the calculated displacements are very similar to the displacements measured using the stereo-photogrammetry method. This indicates that the four-bar systems

Table 5.7. Estimated four-bar systems describing the skull (Fig. 5.9). Skull: the stationary part of the four bar system, Quadrate the length of the quadrate, PPC: the length of the PPC and Bill the distance between the rotation points in the dorsal and ventral bar of the upper bill. Ang. Q is the angle between the 'Skull'- bar and the Quadrate, Ang. B. the angle between the Skull-bar and the Bill-bar. The dAng. Q and dAng. B represent the change of the Quadrate Angle and Bill Angle between the closed and opened condition.

Species	Skull	Quadrate	PPC	Bill	Ang. Q.	Ang. B.	dAng. Q	dAng. B.
Corvus	31.5	10.0	29.0	13.0	68	86	10	6.5
Calidris	46.0	5.0	40.0	3.0	32	126	9	10
Rhea	89.0	16.0	87.0	15.0	55	61.5	8	8
Dromaius	94.0	19.0	98.0	22.0	43	35.5	4	4
Struthio	107.0	31.0	111.0	24.0	67	49.5	5	8

provide a good description of the displacement in the skull after elevation of the upper bill. The position of the flexible zones in the ventral bars of the upper bill were estimated to be at the following positions from the bill tip: *Struthio*: 36 mm, *Rhea*: 47 mm, *Dromaius*: 37 mm, *Calidris*: 12 mm.

Discussion

Avian cranial kinesis is controlled by several bony elements. Although the system has been described qualitatively for prokinetic birds (Bock, 1964) the actual displacements of the elements in the jaw apparatus have only been measured in two dimensions in a single species (van Gennip & Berkhoudt, 1992). Our three-dimensional analysis of displacement patterns of the bony elements in the skull shows that the general displacement pattern is indeed valid for both prokinetic and rhynchokinetic birds. The elevation of the upper bill in birds is initiated by a rostro-caudal rotation of the quadrate. This rotation results in a rostral displacement of both the jugal arc and the PPC. These two bars press against the premaxilla, which results in elevation of either the complete upper bill (prokinesis and extensive rhynchokinesis), or only the rostral

Table 5.8. Calculated and measured displacement of markers closest to the moveable connections of the four-bar systems. Markers indicate the marker used, dXZ M the measured displacement in the XZ-plain, dXZ C the calculated displacement in the XZ-plain.

Species	Caudal Marker	dXZ M	dXZ C	Rostral Marker	dXZ M	dXZ C
Corvus	IB4	0.9	1.2	SC	0.9	0.9
Calidris	IB4	0.3	0.8	LB3	1.0	0.5
Rhea	IB4	2.2	2.2	LB4	2.2	2.1
Dromaius	IB4	1.6	1.3	LB3	2.3	1.5
Struthio	IB4	2.7	2.7	IB1	3.0	3.3

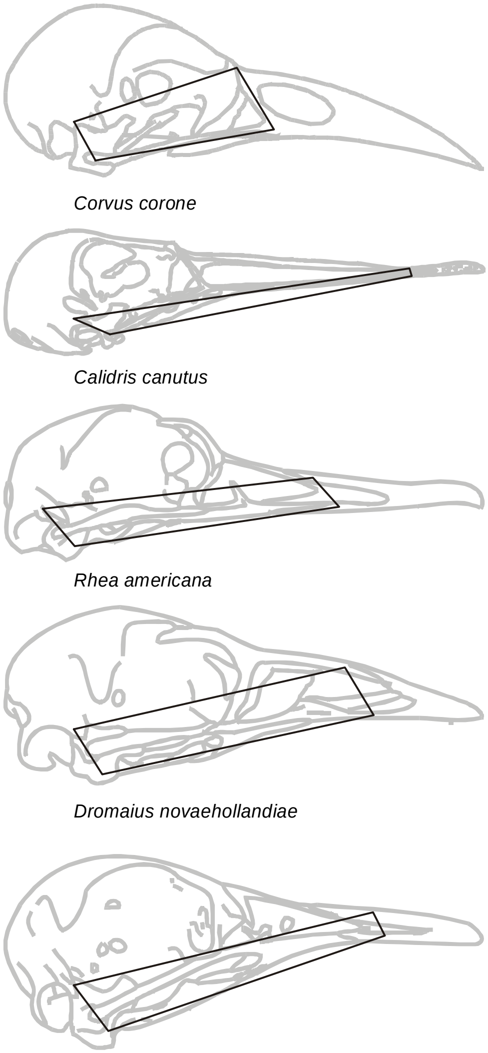

Figure 5.9. Four bar systems projected onto the skulls in lateral view. Different skulls are not drawn to scale.

part of the upper bill (distal rhynchokinesis).

Our kinematic analysis shows that these displacement patterns are valid for all types of cranial kinesis. This indicates that no differences in the PPC are to be expected on the basis of the type of cranial kinesis alone. This is in contrast with several hypotheses about the origin of the palaeognathous PPC. The palaeognathous PPC is always linked to the central kinesis found in these birds (Bock, 1963; Hofer, 1954; Simonetta, 1960). An analysis of *Calidris*, a bird with a distal rhynchokinetic bill used for probing, shows that the PPC is very similar to that of prokinetic birds. The adaptations found in this species are mainly due to the functional demands of probing behaviour and not due to the type of cranial kinesis (Gerritsen, 1988; Chapter 3). The present analysis confirms that the type of cranial kinesis does not pose specific functional demands on the PPC.

The main difference between the various types of cranial kinesis is the position of the rotation points in the upper bill (see Zusi, 1984). The prokinetic crow has a very clear rotation point of the upper bill at the nasal-frontal hinge. All other birds in this study have bending zones instead of a true rotation point. The position of these bending zones can be determined based on a comparison of elevated and non-elevated skulls. In *Calidris* these bending zones can also be morphologically identified from the thickness of the bars. In the Palaeognathae, however, there seems to be no clear morphological characters that indicate the position of these bending zones. In *Calidris* our predicted bending point coincides with the thinnest part in the elements of the upper bill (Gerritsen, 1988; see also chapters 3 and 6).

The four-bar systems show that the movement of the PPC and the upper bill can be predicted with a two dimensional model. Very few three-dimensional models have been developed. The three-dimensional model of van Gennip & Berkhoudt (1992) shows that lateral/medial movement of the quadrate is of great importance in the Pigeon. During grasps, pigeons open both jaws, but during intra-oral transport only the mandible is depressed. The medial quadrate movement uncouples upper and lower jaw movement, which they assume to be linked by the postorbital ligament. Our analysis shows that during upper bill rotation the displacement of the quadrate in the lateral/medial plain is, except for the crow, very limited. However, the quadrate does show rotation along its longitudinal axis, which mainly effects the position of the *Processus orbitalis quadrati*. A rotation around this axis will not affect the forward motion of the quadrate.

In recent papers (Zweers *et al.*, 1997; Zweers & Vanden Berge, 1997b) the PPC is considered one of the elements that had a major impact on the early evolution of trophic systems in birds. In their hypothesis the detachment of the PPC from the cranium was a key-innovation, which resulted in a wide trophic radiation in birds. Although this argument in itself might proof to be true, they 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 the 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, both the movement patterns and morphology (McDowell, 1948; Gussekloo & Zweers, 1999) are so similar within modern birds, compared to other modern (reptilian) taxa, that a polyphyletic origin of the avian kinetic skull is very unlikely. Based on the movement patterns we conclude that all kinetic types described in this study must have evolved from a single kinetic ancestor.

Acknowledgements

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