Functional significance of the uncinate processes in birds

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Summary

The functional significance of the uncinate processes to the ventilatory mechanics of birds was examined by combining analytical modeling with morphological techniques. A geometric model was derived to determine the function of the uncinate processes and relate their action to morphological differences associated with locomotor specializations. The model demonstrates that uncinates act as levers, which improve the mechanical advantage for the forward rotation of the dorsal ribs and therefore lowering of the sternum during respiration. The length of these processes is functionally important; longer uncinate processes increasing the mechanical advantage of the Mm. appendicocostales muscle during inspiration. Morphological studies of four bird species showed that the uncinate process increased the mechanical advantage by factors of 2–4. Using canonical variate analysis and analysis of variance we then examined the variation in skeletal parameters in birds with different primary modes of locomotion (non-specialists, walking and diving). Birds clustered together in distinct groups, indicating that uncinate length is more similar in birds that have the same functional constraint, i.e. specialization to a locomotor mode. Uncinate processes are short in walking birds, long in diving species and of intermediate length in non-specialist birds. These results demonstrate that differences in the breathing mechanics of birds may be linked to the morphological adaptations of the ribs and rib cage associated with different modes of locomotion.

Introduction

Birds lack the muscular diaphragm of mammals (Brackenbury, 1972) and do not ventilate their lungs by expanding the lung itself, but through the bellows-like movement of air through the air sacs (Brackenbury, 1972; Brackenbury, 1973). Uncinate processes are bony projections that extend from the vertebral ribs of most extant birds (Fig. 1). In 1935, Zimmer postulated that the uncinate processes played some role during inspiration (Zimmer, 1935). Contemporary hypotheses have linked these processes with stiffening or strengthening the rib cage (Kardong, 1988; Walker and Liem, 1994), providing attachment sites for muscles stabilizing the shoulder (Hildebrand, 1982), or serving as an adaptation for flight (Welty and Baptista, 1988). Existing hypotheses on uncinate function appear to have been based on the general morphology of these structures rather than experimental analyses. However, recent electromyographic studies in the giant Canada goose confirmed Zimmer's hypothesis by demonstrating that these processes are integral component of the ventilatory mechanics of birds being involved in both inspiration and expiration (Codd et al., 2005). The processes are associated with fleshy parts of the Mm. intercostales externi, the Mm. appendicocostales that originates from the proximal edge

of the uncinate and inserts onto the following vertebral rib (Shufeldt, 1890). The Mm. appendicocostales is active during inspiration in the giant Canada goose, suggesting the processes facilitate the craniad movement of the ribs, which would in turn move the sternum ventrally (Codd et al., 2005). The base of the uncinate processes serves as a brace for the insertions of the 'finger-like' projections of the M. externus obliquus abdominus that pull the sternum dorsally during expiration (Codd et al., 2005). Given that the processes provide attachment sites for these important respiratory muscles, any change in uncinate morphology may have a significant effect on ventilation. Here we develop a mathematical mechanical model to examine the mechanics of ventilation in birds. This model will then be used to determine the mechanical advantage of the uncinate process system for movements of the ribs and therefore sternum during respiration.

Extant birds are diverse and include species that specialise in running, walking, swimming, flying and diving. As with any animal, morphological alterations in birds are commonly associated with differences in locomotor mode (Tucker, 1993; Patak and Baldwin, 1993; Dyke and Rayner, 2001; Rayner and Couldrick, 2003; Zeffer and Norberg, 2003). Furthermore, variations in uncinate morphology have previously been
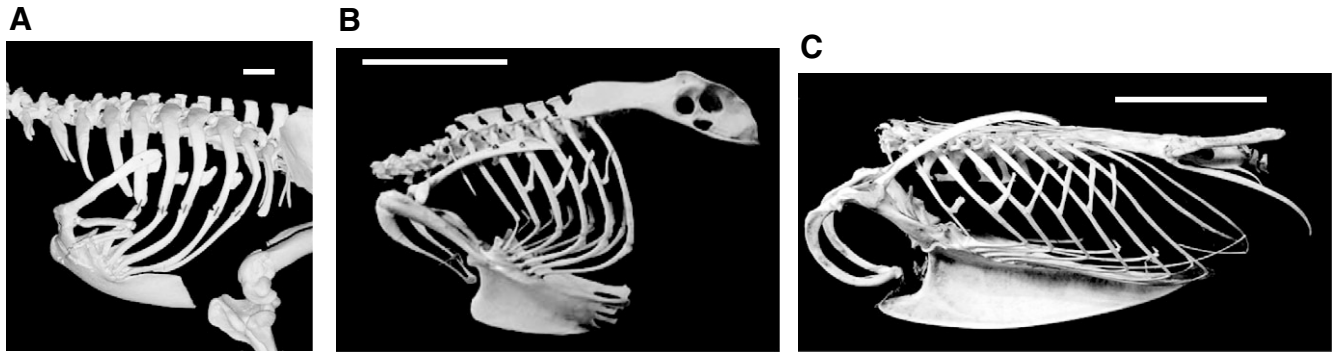
Fig. 1. Representative skeletons showing the morphological differences in the rib cage associated with different forms of locomotion in (A) a walking species, cassowary (*Casuaris casuaris*); (B) a non-specialist, eagle owl (*Bubo bubo*); and (C) a diving species, razorbill (*Alca torda*). Uncinate processes are short in walking species, of intermediate length in non-specialists and long in diving species. In all photographs cranial is to the left; scale bar, 5 cm.

anecdotally linked to differences in locomotor mode, and long uncinate processes noted in diving species (Welty, 1988; Duncker, 1971); however, there has been no further examination or testing of these observations. Here we use morphometric analysis to test the hypothesis that the length of the uncinate processes is predominantly correlated with the locomotor mode of birds. We will then use our mechanical model to examine the functional significance of these differences in uncinate length. In light of our mechanical model, a demonstrable link between the locomotor mode and the length of the uncinate processes will enable us to gain a better understanding of breathing mechanics in Aves.

The geometrical model of uncinate function

At a first approximation, the ribcage of a bird can be considered to be composed of two sets of dorsal and ventral ribs, which are held the same distance apart at the backbone and sternum, and at the same angle. Hence the dorsal and ventral ribs can be regarded as mirror images, which are separated where they join by the same distance as at the backbone and sternum. Therefore two adjacent dorsal ribs can be modeled as the opposite sides of a parallelogram (Fig. 2), running at an angle θ to the backbone and separated from each other by a distance D. Moving such a mechanism is clearly very different from rotating a single bone about a single joint. Any muscle can only alter the angle θ of the ribs to the backbone, and its mechanical advantage is best described by determining how much it changes in length for a given change in the rib angle; the bigger the length change, the more powerful its action and the greater its mechanical advantage.

Consider the effect of a muscle that joins the two ribs, and which is attached to the posterior rib a distance P further from the backbone than it is to the anterior rib (Fig. 2A). The length of the muscle, L, can be readily determined by Pythagoras's theorem:

$$L = x^2 + y^2 = \sqrt{[(D\cos\theta + P)^2 + (D\sin\theta)^2]} . \qquad (1)$$

For the Mm. intercostalis externus, which attaches the same distance down the ribs, P equals zero and the muscle runs
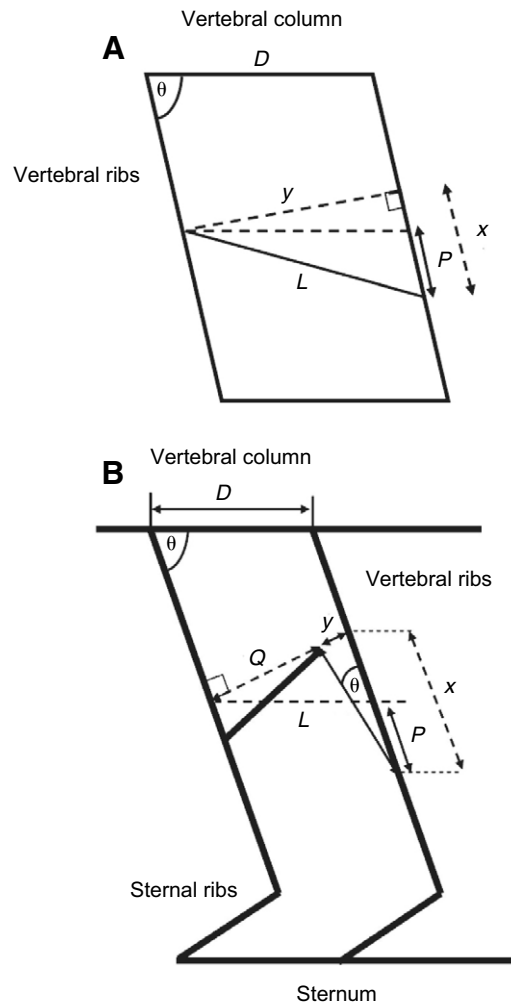

Fig. 2. Geometric model of uncinate function. (A) The situation in birds without an uncinate process. The length of the Mm. appendicocostales, L, changes with the rib angle, θ, depending on the distance down the rib, P, of the posterior attachment. (B) The situation with an uncinate process of perpendicular length Q behind the anterior rib. Cranial is to the left.

approximately parallel to the backbone. Its length is therefore given by the simplified equation:

$$L = \sqrt{[(D\cos\theta)^2 + (D\sin\theta)^2]} = D \ . \tag{2}$$

Whatever the angle of the ribs, the muscle length is constant. It cannot therefore act to move the ribs. The mechanical model supports previous experimental work (Codd et al., 2005), which demonstrated that the Mm. intercostalis externus had no activity related to either inspiration or expiration but was active during contralateral limb support, suggesting it plays a role acting as a brace to stabilise the thorax during locomotion (Codd et al., 2005).

For the appendicocostales muscle, however, for which P is positive, the length of the muscle will vary with the angle of the ribs according to the modified version of Eqn 1.

$$L = \sqrt{[D^2 + P^2 + 2DP\cos\theta)]} \ . \tag{3}$$

The muscle will shorten as θ increases, so the appendicostales muscle will act to swing the ribs forward. Two examples of how the muscle's length will vary with θ are shown in Fig. 3A for $P = 0.5D$ and $P = D$. It can be seen that the length changes more rapidly with θ for larger values of P (the higher the angle of the muscle to the backbone) and at higher values of θ (the higher the angle of the ribs to the backbone). Therefore the mechanical advantage of the muscle will alter with both P and θ. Mechanical advantage (MA) is defined as the relative change in muscle length per unit change in angle and is given by the formula:

$$MA = L_\theta - L_{\theta+1} / L_\theta \ . \tag{4}$$

The mechanical advantage is shown in Fig. 3A. It rises with the rib angle, θ, and is higher for larger values of P.

Effect of the uncinate process

Consider now the same ribcage, but with an uncinate process on the anterior rib that extends back a perpendicular distance, Q, from it, and that has the Mm. appendicocostales attached to its end (Fig. 2B). The length of this muscle is now given by the expression:

$$L = \sqrt{[(D\cos\theta + P)^2 + (D\sin\theta - Q)^2]} \ . \tag{5}$$

The effect of the uncinate process is to increase the length change of the muscle as the ribs are moved, because although as θ rises the reduction in the distance x parallel to the ribs ($D\cos\theta + P$) is unaffected, the increase in the distance perpendicular y to the ribs ($D\sin\theta - Q$) is reduced. Indeed if Q is sufficiently large that the uncinate process extends behind the posterior rib, swinging the ribs forward will actually reduce the perpendicular distance. The effect of uncinate processes of length $Q = 0.5D$ and $Q = D$ on the length of the appendicocostales at different angles are shown in Fig. 3A, and the mechanical advantage at different angles is shown in Fig. 3B. It can be seen that the change in muscle length and the mechanical advantage of the muscle is greatly increased by the uncinate process, giving a good mechanical advantage even at low values of θ. The uncinate acts as a mechanical lever, being most effective when it is longer and, surprisingly, when P is smaller.
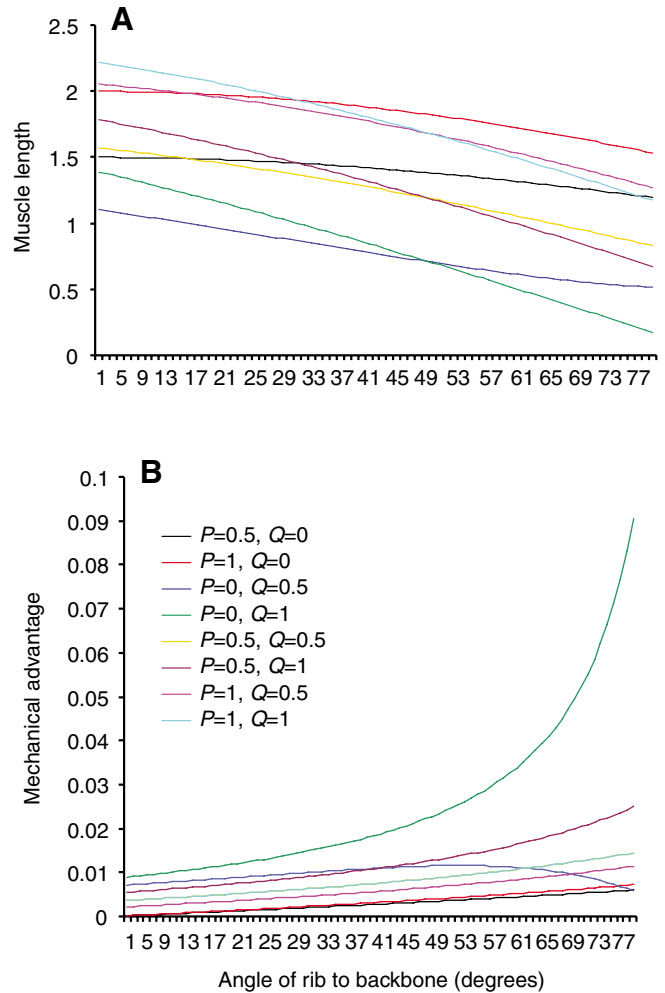

Fig. 3. (A) Changes in length of the Mm. appendicocostales muscle with rib angle, θ, for various relative values of uncinate length, Q, and distance of posterior attachment, P. (B) Changes in mechanical advantage of the Mm. appendicocostales muscle with rib angle, θ, for various relative values of uncinate length, Q, and distance of posterior attachment, P. It can be seen that mechanical advantage increases with θ, and with higher values of Q.

Materials and methods
Mechanical advantage of the Mm. appendicocostales

The uncinate length, Q, the distance between the ribs, D, the distance of the posterior insertion, P, and the rib angle θ of the ribs were measured in four randomly chosen representative bird species: the diving razorbill *Alca torda* L.; the non-specialist locomotors kestrel *Falco tinnunculus* L. and barnacle goose *Branta leucopsis* Bechstein 1803; and the walking red-legged partridge *Alectoris rufa* L.

All lengths were measured on the left hand side of the skeleton using a digital caliper (16EX 150 mm, Product No: 4102400, Mayr GmbH, Berlin, Germany), while the angle was measured using an image analysis system of digital images. Using our mechanical model (Eqn 4), we then calculated the mechanical advantage for each appendicocostales muscle, with and without the uncinate processes.

Skeletal morphology

Data were collected from the skeletons of 100 birds representing examples from all major taxa and orders (see Appendix in supplementary material). To establish if within-species variation in uncinate process length on different ribs was significantly different, the lengths of the processes from ten skeletons of adult barnacle geese *Branta leucopsis* were examined. Birds were then grouped according to specialization to a primary mode of locomotion. (1) Walking, including birds that are either flightless (e.g. cassowary) or incapable of sustained flight (e.g. capercallie); (2) diving, including all birds that actively forage under water by either plunge (e.g. kingfisher) or sustained, deep diving (penguin); and (3) non-specialists, including all other birds flying or swimming that are not facultative diving or walking birds. We collected measurements of the length of the vertebral and sternal ribs, and the length and width of the uncinate processes. Sternal morphology was also examined by measuring the total length and depth of the sternum (height of keel). Correcting for body size is problematic in birds as many species have disproportionably long necks, meaning the traditional snout–vent measurements to scale for size are not feasible. Therefore all data collected were corrected for variations in body size by dividing total length by the length of the vertebral column spanning the thoracic ribs. All data were collected from the left hand side of the skeleton using a Mayr digital caliper (16EX 150 mm, Product No: 4102400, Mayr GmbH).

Statistical analysis

Relationships between the groups were determined using canonical variate analysis (CVA), which maximises the variation between groups relative to the variation within groups (Campbell and Atchley, 1981). Values used in the CVA were: uncinate length and width at base, midpoint and tip; sternal width, length and depth; vertebral and sternal rib length. A one-way ANOVA with a Tukey *post-hoc* test was used to establish if mean uncinate length varies according to mode of locomotion. Within-species uncinate comparison and the ratio of sternal length to depth were analysed using a repeated-measures ANOVA with Bonferroni comparisons. All analyses were completed using the statistical package SPSS (SPSS v.13.0; SPSS Ltd, Chicago, IL, USA).

Results

Mechanical advantage of the Mm. appendicocostales

Measurements on the four bird species were taken and analysed using our mathematical model, with or without the uncinate process. The results of the output from the model are given in Table 1 and Fig. 4. It can be seen that in each species without the uncinate processes the mechanical advantage of the Mm. appendicocostales was low, whereas the presence of uncinate processes improved the mechanical advantage for rib movements by a factor of 2–4. The model therefore demonstrates that uncinate processes act as levers for movements of the ribs (see Table 1, Fig. 4).

Rib cage morphology

Rib number does not always correlate with locomotor mode, although walking species generally tend to have the fewest ribs and the diving species the most. For birds used in this study, 8 had 6 ribs, 43 had 7 ribs, 25 had 8 ribs, 22 had 9 ribs and only 2 had 10 ribs (see Appendix in supplementary material). Our
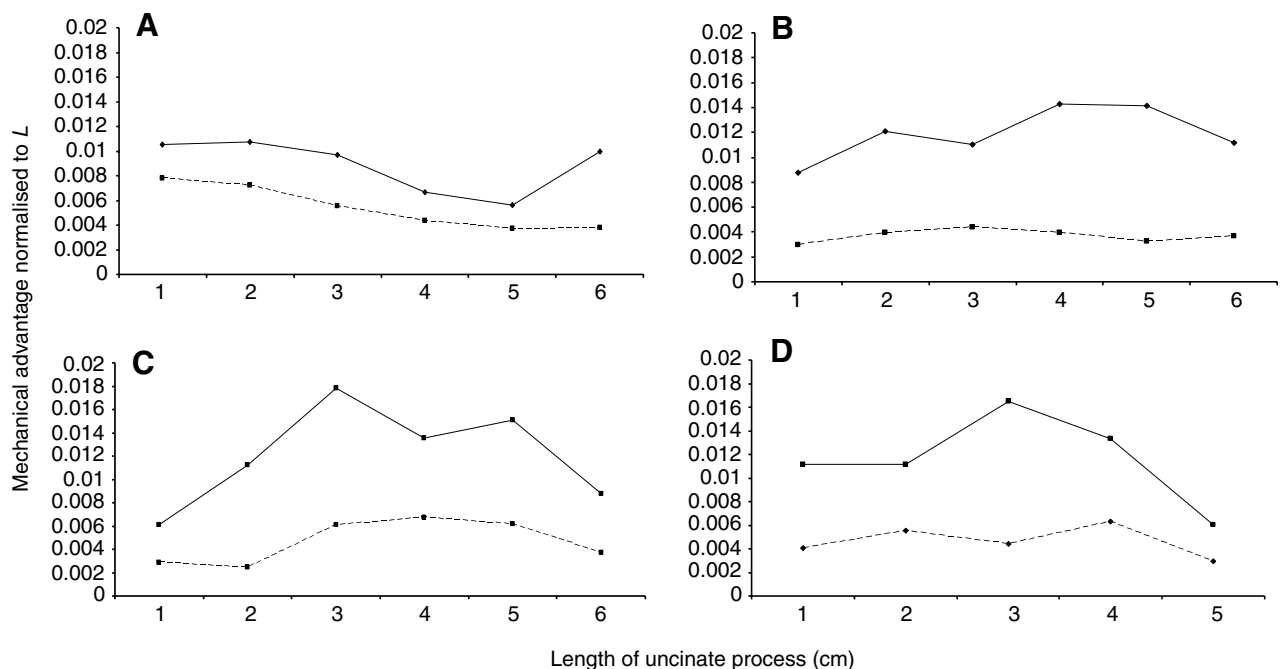

Fig. 4. Mechanical advantage (corrected for muscle length *L*) for representative species calculated with (solid line) and without (broken line) the uncinate processes. (A) A diving bird, the razorbill *Alca torda*; (B,C) non-specialist birds, (B) barnacle goose *Branta leucopsis* and (C) kestrel *Falco tinnunculus*; and a walking bird (D) the red-legged partridge *Alectoris rufa*.

Table 1. *Measurements of the uncinate process on the anterior rib that extends back a perpendicular distance (Q), the distance between the ribs (D), the distance of the posterior insertion (P) and the rib angle (θ) of the ribs in bird species representative of different types of locomotion*

	Barnacle goose	Razorbill	Kestrel	Red-legged partridge
D (mm)	14.9±0.59	7.94±0.44	7.51±1.57	7.6±1.99
P (mm)	4.54±0.43	13.08±1.29	3.79±1.91	3.81±1.13
Q (mm)	7.21±0.43	10.50±1.3	4.50±0.36	3.87±0.50
θ (degrees)	71.19±1.88	64.79±6.77	76.85±3.66	74.26±0.41

Species include the diving razorbill *Alca torda*; the non-specialists kestrel *Falco tinnunculus* and barnacle goose *Branta leucopsis*; and the walking red-legged partridge *Alectoris rufa*.

Values are means ± s.e.m. (*N*=6–10).

correction for body size will tend to make comparisons less different rather than more. The general morphology of the rib cage was similar in all birds examined, as indicated by a within-species comparison of relative uncinate process length (mean ± s.e.m.) for 10 barnacle geese *Branta leucopsis*. Aside from the first rib, sternal ribs connect the vertebral ribs to the sternum and these become increasingly thinner and longer as one moves down the vertebral column. Using one-way ANOVA and Tukey *post-hoc* tests the mean length (± s.e.m.) of the uncinate processes are significantly shorter on the first (0.16±0.02) and last (0.14±0.02) ribs on which they occur. Therefore data from these processes were not used in the canonical analysis. The processes on the remaining ribs are not significantly different in length (rib 2: 0.22±0.03; rib 3: 0.23±0.02; rib 4: 0.22±0.02; rib 5: 0.21±0.03). Therefore the mean length of processes 2–5 was used in all subsequent analyses.
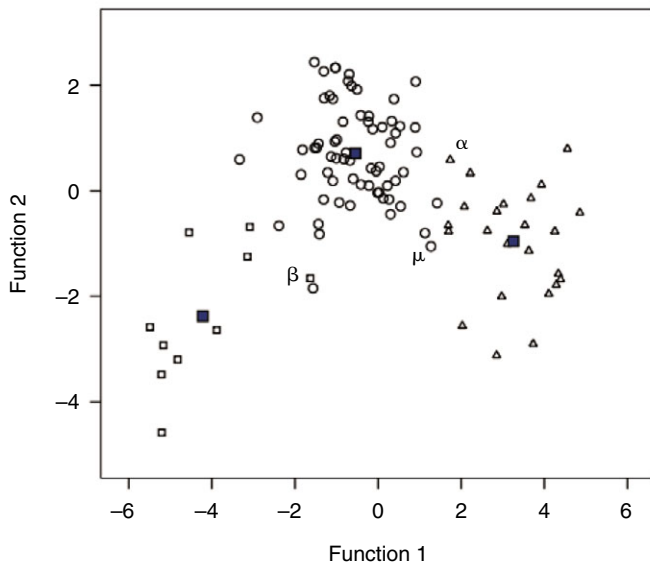

Fig. 5. Canonical variate analysis (CVA) of skeletal morphology in birds. Function 1 against function 2 for walking species (squares, *N*=10); non-specialists (circles, *N*=66); diving birds (triangles, *N*=24). Functions 1 and 2 were primarily functions of relative uncinate length and width and rib length, respectively. Solid black squares represent significantly different group centroids. Letters highlight borderline species of respective groups: the fulmar (α), the green woodpecker (β) and the swallow (μ).

Canonical variate analysis

There was distinct clustering in the data corresponding to locomotor mode and significant differences between group means (Wilks' Lambda=0.82, *P*<0.001, Fig. 5). Some overlap is present, indicating that there are species on the boundary of our classification. Canonical discriminant function 1 accounts for 80.2% of the variation while function 2 accounts for 19.8%. Functions 1 and 2 were primarily functions of relative uncinate length and width and rib length, respectively.

Uncinate morphology

The relative length of the uncinate processes was found to be more similar in birds with the same locomotor mode. They were shortest in the walking (0.11±0.02, *N*=10, *P*<0.01), of intermediate length in non-specialist (0.17±0.01, *N*=66, *P*<0.01) and the longest in diving species (0.23±0.01, *N*=24, *P*<0.01). The processes of the walking birds typically reach about halfway across to the following rib. In non-specialists the processes have a characteristic L-shaped morphology and reach across to the following rib. In diving species the uncinate processes are long, thin and taper towards the end (Fig. 1C), and may overlap the following rib. There is no significant difference between relative uncinate length in the deep (0.21±0.01, *N*=8) and shallow divers (0.19±0.02, *N*=16, *P*=0.32, two-sample *t*-test).

Sternal morphology

The relative ratio of sternal length to depth of walking birds was significantly lower (1.12±0.44, *N*=10, *P*<0.001) than that of non-specialist (2.16±0.07, *N*=66, *P*<0.01) and diving species (2.75±0.20, *N*=24, *P*<0.01).

Discussion

Role of the uncinate process

The mechanical model developed in this paper suggests that the uncinate process acts as a lever, increasing the mechanical advantage of the Mm. appendicocostales, particularly when the ribs are at a low angle to the backbone, helping them rotate the dorsal ribs forwards, pushing the sternum down, and so inflating the lungs. The results of actual mechanical advantage of the four representative species measured, based on the model, confirms this interpretation. In all cases the mechanical advantage increased by a factor of 2–4 compared with what it would have been had an uncinate process not been present, though the effect was least pronounced in the diving species, the razorbill.

These results can help shed light on the two main findings of the morphometric study: first that the anterior and posterior uncinates are shorter than the intermediate ones; and second that the uncinates and sternum of diving birds were relatively longer than those of walking birds, with non-specialist birds having uncinates and sternum of intermediate length. The sternum in birds is the site of attachment for the large flight muscle, the pectoralis and supracoracoideus (Duncker, 1971). The pectoralis can account for up to 35% of the body mass of some birds (Dial et al., 1988). This large muscle mass, together with the abdominal viscera, must be moved up and down during breathing (Brainerd, 1999). The importance of movements of the sternum is highlighted by the entrainment of wing beat with sternal movements (Jenkins et al., 1998) and the fact that birds can suffocate if movements of the sternum are restricted (Ludders et al., 2001). The uncinate processes also act as a brace for the insertion of the M. obliquus externus, which pulls the sternum dorsally to effect expiration (Codd et al., 2005), meaning there is a functional link between sternal and uncinate morphology and the breathing mechanics in birds. The sternum of walking birds is reduced and this group has the shortest length processes, while the elongated sternum of diving birds correlates with the longest length processes. Differences in uncinate morphology may translate into anatomical differences in the associated musculature such as the Mm. appendicocostales and M. obliquus externus, meaning that different patterns of muscle activity facilitate breathing; this, however, remains to be determined.

The Mm. appendicocostales attaches to the proximal edge of the process, meaning that the total length of the process is the most significant characteristic in uncinate morphology. The width of the process along its length may contribute to the overall strength. However, the process is rigidly fixed from above to the rib it extends from by a strong triangular aponeurotic membrane that is attached from the anterior edge of the process along its entire length (Shufeldt, 1890). This ligament provides a strong anchorage for the lever action on the ribs and may negate any thickening of the process itself. Aside from the walking birds, the uncinate processes are also typically thin and taper towards the tip of the process. Alterations in uncinate length may also have implications for the area available for muscle insertion, given the role of the processes during expiration, as thickening of the base would increase the area for attachment for the insertion of the M. obliquus externus (Codd et al., 2005). In all birds examined the anterior and posterior uncinates are siginficantly shorter than the remaining processes. Aside from the diving species, the mechanical advantage for the anterior and posterior processes is also correspondingly lower, suggesting these processes and their associated muscles probably have little function in moving the ribcage during breathing.

Determination of locomotor modes

The locomotor modes used in the morphometric study are broadly defined into walking, diving and non-specialist birds. Although within each group there remain potentially significant differences between the birds, i.e. foot and wing propelled divers, these modes can be considered to be representative as there are broad mechanical differences between specialization for running *versus* diving and/or non-specialists (all other birds). Swimming birds were not categorized as a separate grouping as there are no birds that swim but do not fly. The results of the CVA analysis indicate that there are species that overlap or are near the border of the locomotor groups. These species represent birds that have intermediate morphology; for example, the fulmar (Fig. 5α), which is classed as a diving species, is a strong flyer, which may explain why it borders the non-specialist group. The green woodpecker (Fig. 5β), which clusters close to the walking species, can be considered an atypical bird as it has pronounced broadening of the vertebral ribs as an adaptation to head banging (Kirby, 1980). Swallows (Fig. 5μ) have highly streamlined bodies, which may explain why they cluster close to the diving species.

Contrast in uncinate morphology between diving and walking species

Longer processes have previously been assumed to play a role in preventing collapse of the rib cage by counteracting the increased pressure with increased depth during dives (Welty, 1988). However, aside from the penguins (*Aptendytes patagonicus*, *Spheniscus demersus* and *S. humbolti*) and auks (*Pinguinis impennis*, *Alca torda* and *Alle alle*), the vast majority of diving birds investigated in this study do not dive to depths likely to encounter large increases in pressure. Species from diverse groups such as the kingfisher (*Alcedo atthis*), the white throated dipper (*Cinclus cinclus)*, the gulls (*Larus argentatus* and *L. canus*), the ducks (*Clangula hyemalis* and *Mergus merganser*) and the terns (*Sterna paradisaea* and *S. hirundo*) have nominal diving depths of less than 10 m; i.e. approximately 1 atmosphere of pressure (Jones and Furilla, 1987). Despite this, there is no significant difference between uncinate length in the deep and shallow divers; all diving birds have significantly longer uncinates than the non-specialist and walking birds (see Appendix in supplementary material). Any muscle pulling on the uncinate processes will facilitate movement of the associated rib rather than prevent it. Furthermore, given that the uncinate processes are not found on every rib, it seems unlikely that they are essential in stiffening the body cavity against increased pressure. The caudally located thin and long ribs, i.e. those that would need the most stiffening as pressure increased on the rib cage, lack uncinates (Fig. 1C). Diving birds have a streamlined body form, long ribs and sternum, to reduce resistance on entry to the water. In diving birds the greater relative length of the uncinate processes is probably related to the greater length of the sternum and the lower angle of the ribs to the backbone and sternum (Fig. 1C). As indicated by our model, without an uncinate process the mechanical advantage of the Mm. appendicocostales in lowering the sternum is low, while the force needed to lower the sternum against the large pectoralis muscle in these species would be extremely high. Interestingly, in the razorbill the effectiveness of the uncinate process at increasing the mechanical advantage was actually rather low. This is probably due to the large angle between the ribs and the vertebral column in this species, which may make the uncinate less important, but it contrasts strongly with the low angle seen in its relative the guillemot (J.R.C., unpublished observations). During surfacing both penguins (Wilson et al., 2003) and tufted ducks (Parkes et al., 2002)

maximise gas exchange by increasing breathing frequency. The increased mechanical advantage of longer uncinates may be especially important upon resurfacing when inspiration occurs against the pressure of water against the body. In walking birds, in contrast, the sternum is relatively small (Fig. 1A) and the ribs are at a large angle to the backbone and sternum (Fig. 2A). Even without an uncinate process the appendicocostales muscle could have a reasonable mechanical advantage, and little force needs to be exerted against the tiny pectoralis muscle. In any case the dorsal and ventral ribs tend towards being parallel, meaning that rotating the dorsal rib forward would have little effect in increasing the volume of the chest cavity.

Conclusion

The morphology of the rib cage and the length of the uncinate processes varies with locomotor mode. The reduction in uncinate length found in the walking species suggests that they may play a reduced role during breathing in these species, meaning muscles such as the Mm. intercostalis externi may play a significant role during inspiration in walking birds; this, however, remains to be determined. The elongation of the ribs, rib cage and sternum associated with streamlining in diving species suggests that differences may also exist in their breathing mechanics. Given the increased length of the processes in diving birds, the insertion of the Mm. appendicocostales towards the end of the tip of the processes may further improve the mechanical advantage for moving the elongated ribs during breathing. Future work may improve our understanding of anatomical differences in musculature associated with variations in uncinate morphology. Alternative functions of the uncinate processes remain to be determined; for example, the role of the uncinate processes in stabilizing the scapula during retraction of the wing has not been examined here. Additionally the 'finger-like' projections of the M. obliquus externus abdominus insert onto the base of the processes, and in the opposite manner the M. serratus superficialis originates at the top of the processes and inserts on the ventral margin of the scapula (Vanden Berge and Zweers, 1993), suggesting that they may act antagonistically. Variations in uncinate morphology seem likely to relate to differences in the muscles involved in breathing or in the pattern of muscle activity. Respiration in Aves is complex, with a great many axial muscles reported to be involved (Fedde, 1987). This research suggests that there may be fundamental differences in the breathing mechanics of different birds, driven in part by the morphological differences of the rib cage and sternum associated with skeletal adaptations to locomotion.

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