Uni Bonn

RHEINISCHE FRIEDRICH-WILHELMS-UNIVERSITÄT

THE UNCINATE PROCESSES IN BIRDS AND THEIR IMPLICATIONS FOR THE BREATHING MECHANICS OF MANIRAPTORAN DINOSAURS

Dissertation

zur

Erlangung des Doktorgrades (Dr. rer. nat)

der

Mathematisch-Naturwissenshaftlichen Fakultät

der

Rheinischen Friedrich-Wilhelms-Universität Bonn

vorgelegt von

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Dunstable (UK)

Bonn 2004

Angefertigt mit Genehmigung der Mathematisch-Naturwissenshaftichen Fakultät der Rheinischen Friedrich-Wilhelms-Universität Bonn

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Tag der Promotion: October 13th 2004

I’m patient of this plan
As humble as I can
I’ll wait another day
Before I turn away
I’m coming through the door
But they’re expecting more
Of an interesting man
Sometimes I think I can

Jack White

TABLE OF CONTENTS

CHAPTER 1
GENERAL INTRODUCTION
UNCINATE PROCESSES

CHAPTER 2
MORPHOLOGY OF THE UNCINATE PROCESSES IN BIRDS: PHYLOGENETIC APPROACHES

CHAPTER 3
THE MECHANICS OF BREATHING IN BIRDS: RESPIRATORY MUSCULATURE AND X-RAY CINEMATOGRAPHY

CHAPTER 4

ELECTROMYOGRAPHY OF THREE RESPIRATORY MUSCLE GROUPS IN THE GIANT CANADA GOOSE (*BRANTA CANADENSIS MAXIMUS*)

CHAPTER 5

UNCINATE PROCESSES AND THEIR IMPLICATIONS FOR THE BREATHING MECHANICS OF MANIRAPTORAN DINOSAURS

CHAPTER 6

GENERAL DISCUSSION

APPENDIXES:

LIST OF FIGURES

LIST OF TABLES

DECLARATION

This thesis contains no material which has been accepted for the award of any degree or diploma in any university and, to the best of my knowledge, contains no material previously published or written by another person, except where due reference is made in the text. The author consents to this thesis being made available for photocopying and loan.

Hiermit versichere ich, daß ich die Dissertation, abgesehen von der angegebenen Hilfsmittlen, persönlich, selbstständig und ohne unerlaubte Hilfe angefertigt habe.

Signed

Jonathan R. Codd

Bonn, July 2004

ACKNOWLEDGEMENTS

I would first like to thank my supervisor Steve Perry for his invaluable assistance, advice and friendship over the years. I have always enjoyed our many conversations during my time in Bonn from science to philosophy and back again. I would also like to thank Martin Sander and Bernhard Misof for their contributions to this project and for teaching a physiologist about palaeontology and phylogenetics. This project would not have been possible without the many collaborators here in Germany and around the world who I have been fortunate to have the opportunity to meet and work with and I would like to thank them; The American Museum of Natural History: Dr Mark Norell & Carl Mehling; Tyrrell Museum: Dr Phil Currie & Dr Jim Gardner; Mongolian Academy of Sciences: Dr Rinchen Barsbold & Khishigjav Tsogtbaatar; Harvard University: Leon Claessens & Prof Farish Jenkins; Jena University; Prof Gerhard Zumbusch; Bonn University: Dr Martin Sander; Koenig Museum: Dr Bernhard Misof & Dr Renate van den Elzen. The electromyography work was conducted in collaboration with Dr David Carrier and Dr Dona Boggs at the University of Utah. I would especially like to thank Dave, Colleen and Barbara for their hospitality and for making my stay in Utah so enjoyable.

This work was supported by the Deutsche Forschungsgemeinschaft through the Graduiertenkolleg ‘Evolution und Biodiversität in Raum und Zeit’. I would like to thank our Speaker Prof. Dr. K.P. Sauer for his constant support of my project and research throughout my PhD. I would also like to thank all the other students in Bonn who made life much more interesting and made an ‘Auslander’ feel at home in Germany: Anna-Lisa, Carmen, Carsten, Crista, Dagmar, Elke, Jean-Luc, Jörg, Lars, Lexa, Martin, Monica, Nadia, both Oli’s and Conny’s, Roland, Ruth and Torsten. I would also like to thank Wilfried, Klaus and Marion for their help during the last few years.

Lastly I would like to thank my own and newly extended families for their long distance support and of course my beautiful Anne for her love, encouragement and endless patience in trying to get me to understand formatting.

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1. **Codd, J.R.,** Daniels, C.B. and Orgeig, S (2000) Thermal cycling of the pulmonary surfactant system in small heterothermic mammals. **Life in the Cold** proceedings volume (Springer – Verlag)

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2. **Codd, J.R.,** Sanderson, K.J. and Clark, B. (1999). Drinking behaviour of the common bent wing bat, *Miniopterus schreibersii,* in Bat Cave Naracoorte. ***Bat. Res. News***. 40:9-10.

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11. **Codd, J.R**., Boggs, D.F., Perry, S.F. and Carrier, D.R. (2004) Electromyography of three respiratory muscle groups in the Giant Canada goose (*Branta Canadensis maximus*). ***J. Exp. Biol.*** (to be submitted).
12. **Codd, J.R.,** Sander. P.M. and Perry, S.F. (2004). Uncinate processes and their implications for the breathing mechanics of maniraptoran dinosaurs. ***Paleobiol***. (to be submitted).

INVITED PRESENTATIONS

1. **Codd, J.R**., Slocombe, N.C., Wood, P.G., Orgeig, S. and Daniels, C.B. (1999), Alterations in the surfactant system in response to diurnal fluctuations in activity and body temperature of the bat Chalinolobus gouldii. Fifth International Congress of Comparative Physiology and Biochemistry, Calgary, Alberta, Canada, August 23rd-28th.

2. **Codd, J.R.,** Wood, P.G., Orgeig, S. and Daniels, C.B. (1999) Alterations in the Surfactant System in Response to Diurnal Fluctuations in Activity and Body Temperature of the Heterothermic Bat *Chalinolobus gouldii.* Australian and New Zealand Society for Comparative Physiologists and Biochemists, UNE, Armidale, December 3rd-5th.
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5. **Codd, J.R.** & Perry, S.F. (2003) Functional Morphology of the Uncinate Processes in Birds and Dinosaurs, Bonn University Symposium ‘Graduiertenkolleg: Evolution und Biodiversität in Raum und Zeit’, Bonn University, Germany.
6. **Codd, J.R.** (2004). Uncinate Processes in Maniraptoran Dinosaurs: Homology or Homoplasy? Bonn University Symposium Graduiertenkolleg: Evolution und Biodiversität in Raum und Zeit’, Bonn University, Germany.
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CHAPTER 1

GENERAL INTRODUCTION

UNCINATE PROCESSES

1.1 THE AVIAN RIB CAGE AND UNCINATE PROCESSES

1.1.1 General Morphology of the Rib Cage in Birds

The thoracic region of the avian trunk is composed of between 3-10 vertebrae (Duncker, 1971). Avian rib cages have vertebral and sternal ribs connected by kinetic joints. The sternal ribs articulate ventrally along the sides of the sternum and dorsally form an acute angle with the vertebral ribs. The vertebral ribs have twin articulations, the capitulum articulates on the diapophysis of the vertebral column and the dorsomedially projecting tuberculum, on the parapophysis of the processus transversus, dorsal and posterior to the articulation point of the capitulum. The anatomical arrangement of the twin articulations means each rib moves in a fixed plane defined by the angle of articulation of the two heads. Cranial movement of the ribs results in dorsoventral and transverse expansion of the body cavity (Brackenbury, 1973).

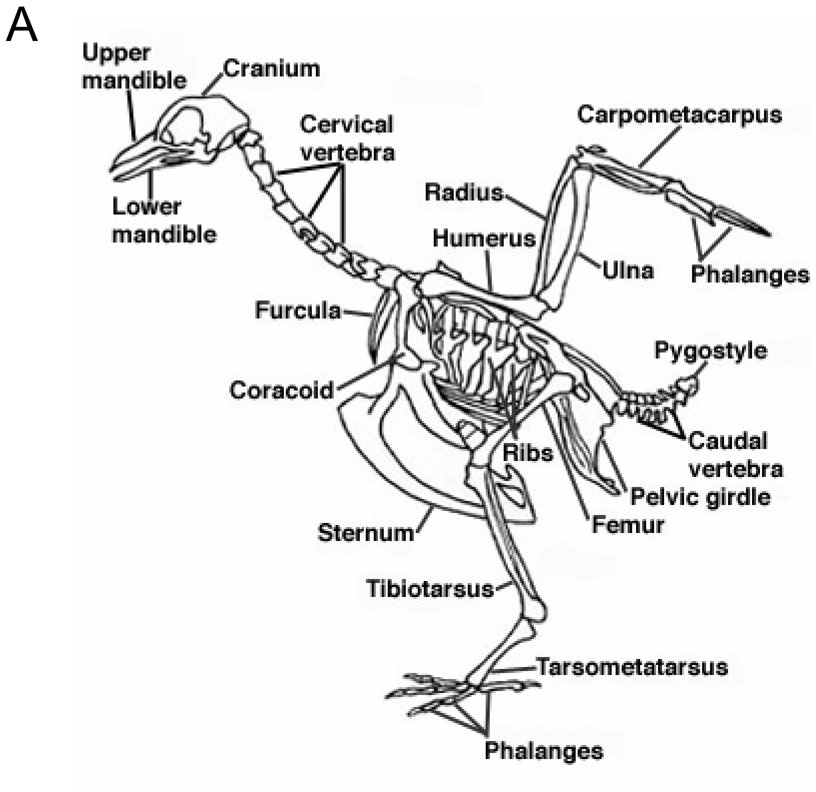
1.1.2 What are Uncinate Processes?

Uncinate processes are ossified projections (Figure 1a & b) that extend posteriorly from the proximal surface of the vertebral ribs in all extant birds except the Emu (*Dromaius novaehollandiae*) and the Screamers (Anhimidae) (Bellairs & Jenkin, 1960). The term ‘uncinate’ (Lat. uncinatus, hook) describes its general morphology. Once thought to be unique to birds, similar structures of uncertain homology, to which the term ‘uncinate process’ is also applied, occur in some early amphibians (Kent & Miller 1996), some crocodylia (Romer, 1956), some theropod dinosaurs (Paul, 2002) and in *Sphenodon* sp (Romer, 1956).

1.1.3 Function of the Uncinate Processes

Despite recent interest in uncinate processes (Paul, 2002), there are few tested hypothesis to explain their function. Hypotheses that do exist fall into one of three main categories: that uncinate processes are an adaptation for flight (Welty, 1988), they serve as an attachment site for respiratory muscles and the muscles of the shoulder (Romer, 1956; Romer, 1977; Hildebrand, 1982) or that they provide mechanical support for and strengthen the ribs and rib cage (Libbie et al., 1942; Kardong, 1988; Walker, 1994; Liem et

Figure 1: A) Skeleton of a typical bird - showing details of the skull, cervical vertebrae, humerus, radius, ulna, carpometacarpus, phalanges, pygostyle, caudal vertebra, pelvic girdle, femur, ribs, tarsometatarsus, tibiotarsus, sternum, coracoid and furcula. B) close up of thorax region of typical bird showing details of the clavicle, scapula, synsacrum, pygostyle, uncinate processes, sternal ribs, sternum, interclavicle and procoracoid.


A
Upper mandible
Cranium
Cervical vertebra
Carpometacarpus
Lower mandible
Radius
Humerus
Ulna
Phalanges
Furcula
Pygostyle
Coracoid
Ribs
Caudal vertebra
Pelvic girdle
Sternum
Femur
Tibiotarsus
Tarsometatarsus
Phalanges

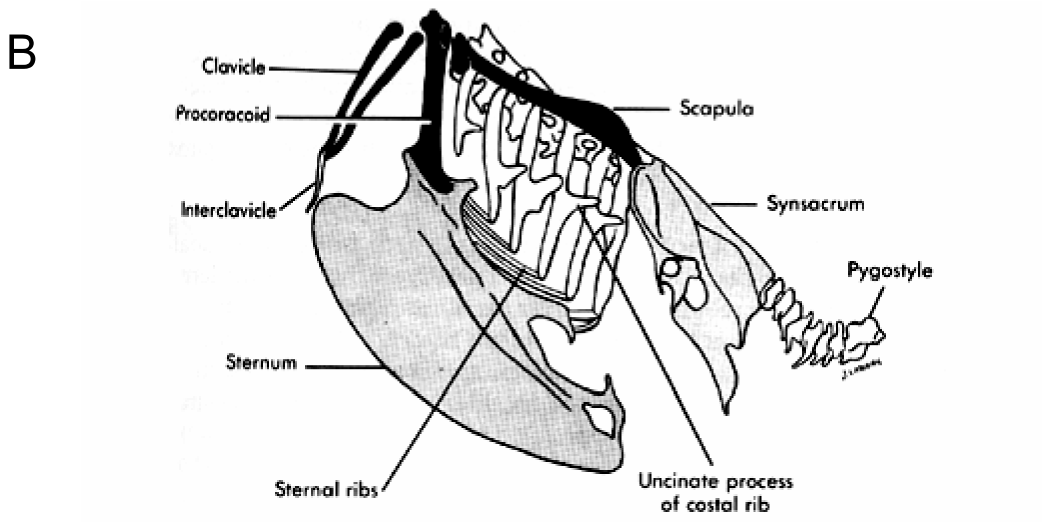
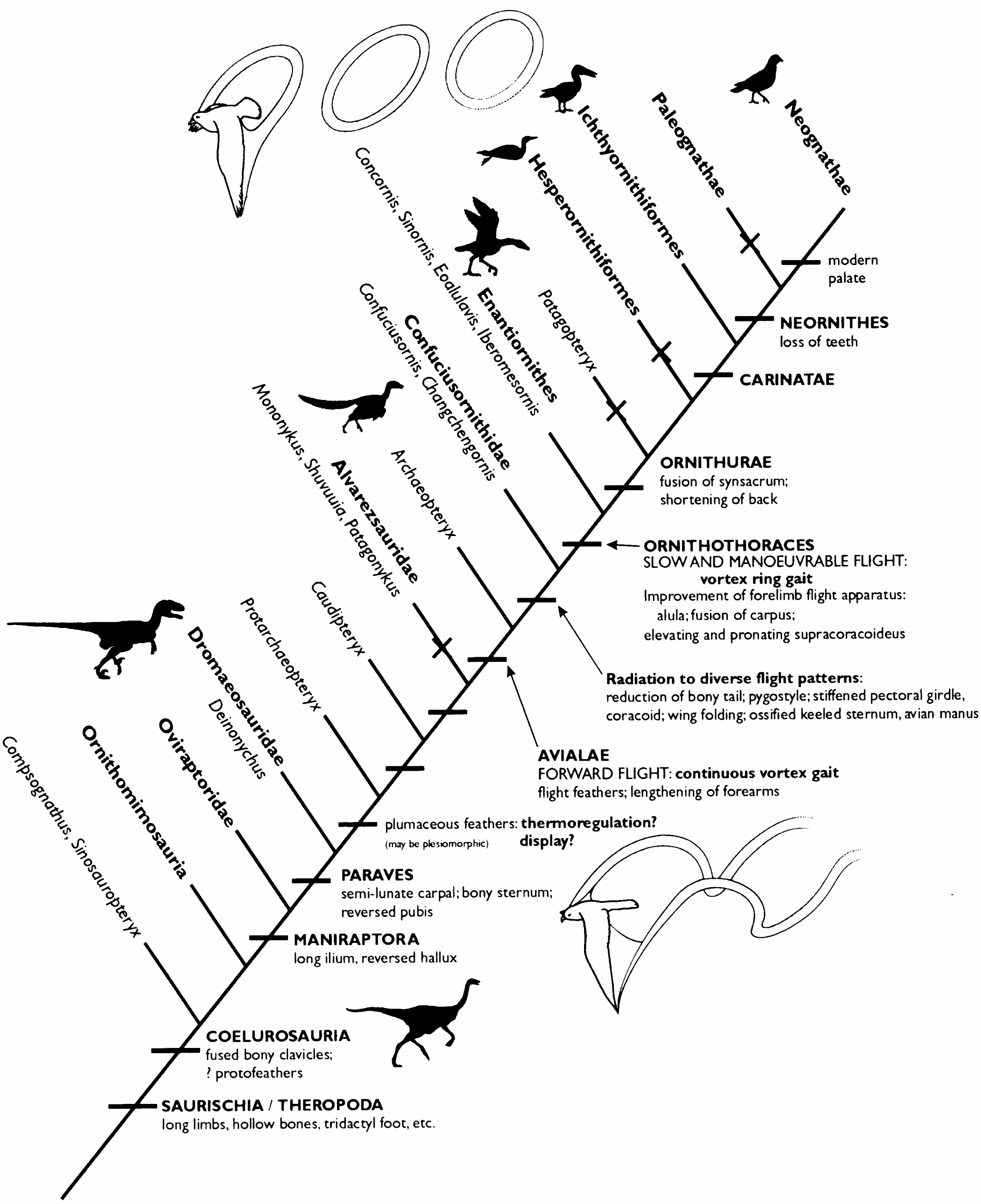

B
Clavicle
Procoracoid
Scapula
Interclavicle
Synsacrum
Pygostyle
Sternum
Sternal ribs
Uncinate process of costal rib

Figure 2: Consensus phylogeny of birds and related theropod dinosaurs (Rayner 2001). This is not intended to depict a formal phylogeny but rather to present the sequence in the acquisition of characters related to flight. Features such as hollow bones, proto-feathers, bony clavicles, a long ilium, reversed pubis, plumaceous feathers and flight feathers are all found in the theropod ancestors of modern birds.


Neognathae
Paleognathae
Ichthyornithiformes
Hesperornithiformes
Patagopteryx
Concornis, Sinornis, Eoalulavis, Iberomesornis
Enantiornithes
Confuciusornithidae
Confuciusornis, Changchengornis
Archaeopteryx
Alvarezsauridae
Mononykus, Shuvuuia, Patagonykus
Caudipteryx
Protarchaeopteryx
Dromaeosauridae
Deinonychus
Oviraptoridae
Ornithomimosauria
Compsognathus, Sinosauropteryx
modern palate
NEORNITHES
loss of teeth
CARINATAE
ORNITHURAE
fusion of synsacrum; shortening of back
ORNITHOTHORACES
SLOW AND MANOEUVRABLE FLIGHT:
vortex ring gait
Improvement of forelimb flight apparatus:
alula; fusion of carpus;
elevating and pronating supracoracoideus
Radiation to diverse flight patterns:
reduction of bony tail; pygostyle; stiffened pectoral girdle, coracoid; wing folding; ossified keeled sternum, avian manus
AVIALAE
FORWARD FLIGHT: continuous vortex gait
flight feathers; lengthening of forearms
plumaceous feathers: thermoregulation?
(may be plesiomorphic)
display?
PARAVES
semi-lunate carpal; bony sternum; reversed pubis
MANIRAPTORA
long ilium, reversed hallux
COELUROSAURIA
fused bony clavicles;
? protofeathers
SAURISCHIA / THEROPODA
long limbs, hollow bones, tridactyl foot, etc.

al., 2001). It has even been suggested that without uncinates the rib cage of birds would collapse as a result of the forces associated with flying (Sereno, 1997). Uncinate processes have also been linked to endothermy and the evolution of the air-sac system in extant birds (Hou et al., 1996).

Existing hypotheses on uncinate function appear to be based on the general anatomy of the thorax. The hypothesis that the uncinates are a prerequisite for flight, or components of an air-sac system, is refuted by the existence of the Screamers (Anhimidae). The Screamers are widespread in the wetlands of South America and consist of at least four species all of which lack uncinates but are capable of powered flight, walking and swimming (Del Hoyo et al., 1992). As for their importance as sites of attachment for respiratory or locomotor muscles, these functions are not necessarily mutually exclusive, and definitive experiments have yet to be conducted to test hypothesis regarding breathing and locomotion in birds. Furthermore electromyographic studies into the respiratory musculature of the chicken (Kadono et al., 1963) failed to investigate the uncinate musculature at all.

The only experimentally tested hypothesis into uncinate function (Zimmer, 1935) is based on a two-dimensional model reconstruction. Zimmer (1935) concluded that uncinate processes facilitated the movement of the ribs forward, which he interpreted as aiding inspiration. Although the ribs are restricted to movements in a single plane, intercostal, abdominal and uncinate musculature could all exert significant influence in other planes to guide rib movement. In addition, as the angle of articulation differs from rib to rib a two-dimensional model is inadequate. The one unpublished attempt at a 3-dimensional model reconstruction of uncinate function (Schmitz, 2000 unpublished), was based on an inadequate coordination system. Despite methodological shortcomings, the uncinates were reported to stabilise the capitulum and to play some role in inspiration.

1.1.4 WHY ARE UNCINATE PROCESSES IMPORTANT?

Osteological characters, such as the uncinate processes, are important as they are preserved in the fossil record and present an opportunity to functional interpret extinct animals using modern analogs. Duncker (1971) and Welty (1988) both mention anecdotally that the uncinate processes of diving species such as Guillemots, Loons and Penguins are longer than those seen in other species of bird. The length of the uncinate processes has been postulated to be proportional to the effectiveness of the appendicocostalis muscle to move the ribs (Fedde, 1987). If the uncinate process do act as a lever arm on the ribs, differences in morphology, such as length, width or thickness of the uncinate process, may have important functional correlations.

1.1.5 UNCINATE PROCESSES AND MANIRAPTORAN DINOSAURS

The evidence that birds are surviving maniraptoran dinosaurs is now overwhelming (Dingus & Rowe, 1998). Characters previously thought to be unique to birds, such as hollow bones, proto-feathers, clavicles, long ilium, reversed pubis, plumaceous feathers, and flight feathers (Figure 2) are all found in theropod ancestors (Morell, 1997). Ossified uncinate processes are also reported in some maniraptoran dinosaurs; *Deinonychus* (Ostrom (1969), Velociraptine specimens (Barsbold, 1983, Norell & Makovicky, 1999), *Microraptor* (Xu et al., 2000), *Bambiraptor* (Burnham, 2000), the Oviraptorids (Clark et al., 1999). Interestingly they are absent in *Archaeopteryx* which is more closely related to modern birds (Paul, 2002).

As the homology is not completely understood, the occurrence of uncinate processes in maniraptoran dinosaurs does not imply that uncinates are a plesiomorphic character for Archosaurs. A systematic analysis of the uncinate processes in dinosaurs has not been carried out, possibly because these are small structures easily overlooked during excavation of large fossils. However, reports of uncinates are increasing with little discussion as to what their function in maniraptoran dinosaurs may have been. As birds are the sister group of some maniraptoran dinosaurs, the dromaeosaurs, a functional analysis of the breathing mechanics and function of the uncinate processes in maniraptoran dinosaurs can be viewed against a background of the evolutionary transition from some dinosaurs to birds.

1.2 OVERVIEW AND THESIS AIMS

Existing hypotheses on uncinate function are inadequate. Before importance can be attributed to their possible function(s) in maniraptoran dinosaurs a more complete understanding of their function in extant birds is required. The overall aim of this dissertation is to increase our understanding of the mechanics of breathing in birds, the function of the uncinate process and provide insights into the breathing mechanics of maniraptoran dinosaurs.

The following specific aims are addressed:

1. To study the morphology of the uncinate processes in extant birds from a wide range of species and from birds with different locomotor modes (walking, swimming, flying and diving).
2. To examine the biomechanics of rib movements in birds using x-ray cinematography techniques.
3. To describe the musculature associated with the uncinate processes.
4. To examine the activity and function of the thoracic musculature, including that of the uncinate processes, using electromyographic techniques.
5. To re-examine the uncinate processes in selected maniraptoran dinosaurs, in light of and with view to the application of the information gained from the extant birds.

CHAPTER 2

MORPHOLOGY OF THE UNCINATE PROCESSES IN BIRDS:

PHYLOGENETIC APPROACHES

2.1 INTRODUCTION

There are almost 10000 species of birds (Welty, 1988), occupying all major biogeographic habitats. Extant birds vary in size from hummingbirds weighing around 3 grams, to Ostriches weighing 80 kilograms and standing over 2.5 metres tall. Birds represent one of only three vertebrate lineages, bats and pterosaurs being the others, that have evolved the ability to sustain powered flight. The evolution of flight has allowed birds to become one of the most successful vertebrate lineages and its members include species with diverse locomotor modes; walking/wading, running, flying, swimming and diving.

Despite occupying a wide variety of habitats and the associated anatomical adaptations, the general body architecture of all birds is similar. Morphological specialisations in wing morphology are associated with different types of flight, be it gliding, soaring or powered flight (Kardong, 1988); morphological differences in the leg bones are associated with wading or running birds (Liem et al., 2001) and diving birds show specialisations which include compression and lengthening of the rib cage (Welty, 1988). Because extant birds are diverse and widespread, they are an excellent group for comparative studies into functional morphology (Mindell, 1997).

2.1.1 PHYLOGENETIC RELATIONSHIPS OF EXTANT BIRDS

A detailed understanding of phylogenetic relationships is crucial to understanding the evolution of morphological and behavioural differences amongst birds. However, owing in part to the rapid radiation of modern birds (Mindell, 1997), our understanding of the precise phylogenetic relationships amongst existing bird species remains unresolved (Cracraft, 1981; Cracraft, 1988; Hedges & Sibley, 1994; Sibley, 1994; Feduccia, 1996; Mindell, 1997; Poe & Chubb, 2003).

There are two methodological approaches to generating phylogenies, those created using morphological characters and those based on molecular techniques. Morphological characters include among others skeletal parameters, while molecular techniques focus on the information in molecular sequences. One of the major problems with generating avian phylogenies based on morphological characters is that they have many polytomies. This is due to the fact that there are few recognised derived morphological characters which unite avian orders. The only comprehensive phylogeny that exists which is based on molecular data, DNA-DNA hybridisation, is that of Sibley & Ahlquist, (1990). The sensitivity of

DNA-DNA hybridization declines rapidly as the organisms become more diverged, meaning the method is best suited to the characterization of closely related strains, species and genera (Mindell, 1997). While research is currently continuing in an attempt to resolve some of the problems associated with the DNA-DNA hybridisation approach and in the development of improved molecular methods, such as mitochondrial DNA markers (Mindell, 1997), the Sibley and Ahlquist tree represents the best currently available for phylogenetic comparisons in birds (Frappell et al., 2001).

2.1.2 INDEPENDENT CONTRAST ANALYSIS

Species comparisons are often made to test hypotheses on evolutionary patterns. Shared phylogenetic history means that species are not completely independent with regard to their statistical treatment. Therefore the use of standard statistic tests is inappropriate. Nested ANOVA and regression analysis have been purported to offer a solution, however it remains unclear as to how well these methods take phylogenetic relatedness into account (Harvey & Pagel, 1991).

Felsenstein (1985) suggested that while species are not significantly independent, the differences between them are. Relationships between taxa are defined in terms of common ancestral species. Two species are said to be more closely related to each other than to a third species if they share a more recent common ancestor than either of them does with the third species. The two taxa which are the most closely related to each other are referred to as sister groups. Sister group comparisons are a form of independent contrast analysis which generates dependent data and as such hypotheses must be analysed using non-parametric tests of significance. When certain assumptions such as normal distribution are not satisfied non-parametric tests must be used to detect population differences.

2.1.3 PHYLOGENY AND THE UNCINATE PROCESSES IN BIRDS

Anecdotal evidence suggests that the uncinate processes are different in different birds. For example, Welty (1988) and Duncker (1971) have both described longer uncinate processes in diving species. If uncinate processes differ amongst birds it is important to establish if there is a functional reason for this or if it may be explained by the close phylogenetic relationship of taxa. Sister group comparison aims to minimise the differences between groups by choosing sister taxa that are closely related to each other. If two avian species are closely related (and if the morphology of the uncinate processes varies with phylogeny) then one would expect these sister taxa to have uncinate morphology that is more similar to each other than that of taxa which are more distantly related. However, if uncinate morphology varies functionally then the length of the uncinate processes should be more similar in birds with the same functional constraints, regardless of phylogenetic relatedness.

Here I will test the hypothesis that the length of the uncinate process is correlated with the locomotor mode (walking, swimming, flying or diving) rather than with phylogeny. Should it be possible to refute the null hypothesis of phylogenetic determination of uncinate morphology, a link between the anatomy of uncinate processes and the mode of locomotion will enable us to gain insight into the function of avian uncinate processes from their structure alone.

2.2 MATERIALS AND METHODS

2.2.1 WITHIN SPECIES VARIATION

To establish if within species skeletal variation was significantly different, the length of the uncinate processes from twelve skeletons of adult common sparrows, *Passer domesticus,* was investigated for variation between males and females, within individual and between different specimens.

2.2.2 MORPHOLOGY OF THE UNCINATE PROCESSES IN BIRDS

A morphological analysis was undertaken of 88 extant bird skeletons (Table 1) representing all major taxa and across all locomotor modes (running/walking, swimming, flying and diving). Birds were assigned to different locomotor groups using The Handbook to the Birds of the World, Volumes 1-9 (Del Hoyo et al., 1992). Classification of birds into locomotor mode groups is based on specialisation to a locomotor mode. There are some birds which fly and dive, for example, but flying birds that dive would be classified as diving birds whereas birds that fly but do not dive would be classified as flying bird. For the purpose of this analysis running and walking groups were combined in the walking subgroup and birds that dive using their wings and those that dive using their feet were grouped into the diving category. Sternal morphology was examined in all birds by comparing the length, depth and width of the sternum at the respective longest, widest and deepest points.

Skeletons were chosen to ensure that examples of both closely and distantly related birds with different locomotor modes were included. All data were collected from the left-hand side of the skeletons, with the assumption that the rib cage is bilaterally symmetrical. Data collected are summarised in Table 1. Data were collected using a Mayr Digital Calliper (16EX 150mm, Product No: 4102400, Mayr GmbH). Measured specimens were from the Ornithology Department of the Research Institute and Museum Alexander Koenig (Bonn, Germany). Additional specimens were from the collections at the Department of Ornithology of the American Museum of Natural History (New York, U.S.A.).

2.2.3 INDEPENDENT CONTRAST ANALYSIS: SISTER GROUP COMPARISONS

For phylogenetically independent sister group comparisons, phylogenetic relationships (Figure 3) were obtained from Sibley and Ahlquist (1990). A species whose phylogenetic position was unavailable was included taxonomically within a genus on the basis of the classification scheme of Sibley and Monroe (1990). If the phylogenetic place position of the genus was unavailable it was then placed in the position of the closest one in the classification scheme (Frappell et al., 2001).

Paraphyletic groups (see Figures 7E, 9E and 10E) were included in the sister group analysis as the number of independent occurrences of swimming as a locomotor mode is low. However, avian phylogeny is not completely resolved and the exact phylogenetic relationships are not completely understood. For sister group comparisons I have restricted the analysis to the total length of the uncinate process, defined as the straight-line distance along the uncinate process from its tip to its base on the vertebral rib. Within the different sister taxa there are still potentially major differences between the birds. For example there are walking birds that can (pheasants) and cannot (ostriches) fly, diving birds that can (pelicans) and cannot (penguins) fly, birds that dive using their feet (diving duck) and those that dive using their wings for propulsion (penguins). To account for these possible sources of error data, sister group comparisons were analysed with and without each of these subgroups. Standard methods for correcting for body size, such as dividing by snout-vent length, are problematic in birds because neck lengths vary drastically among species.

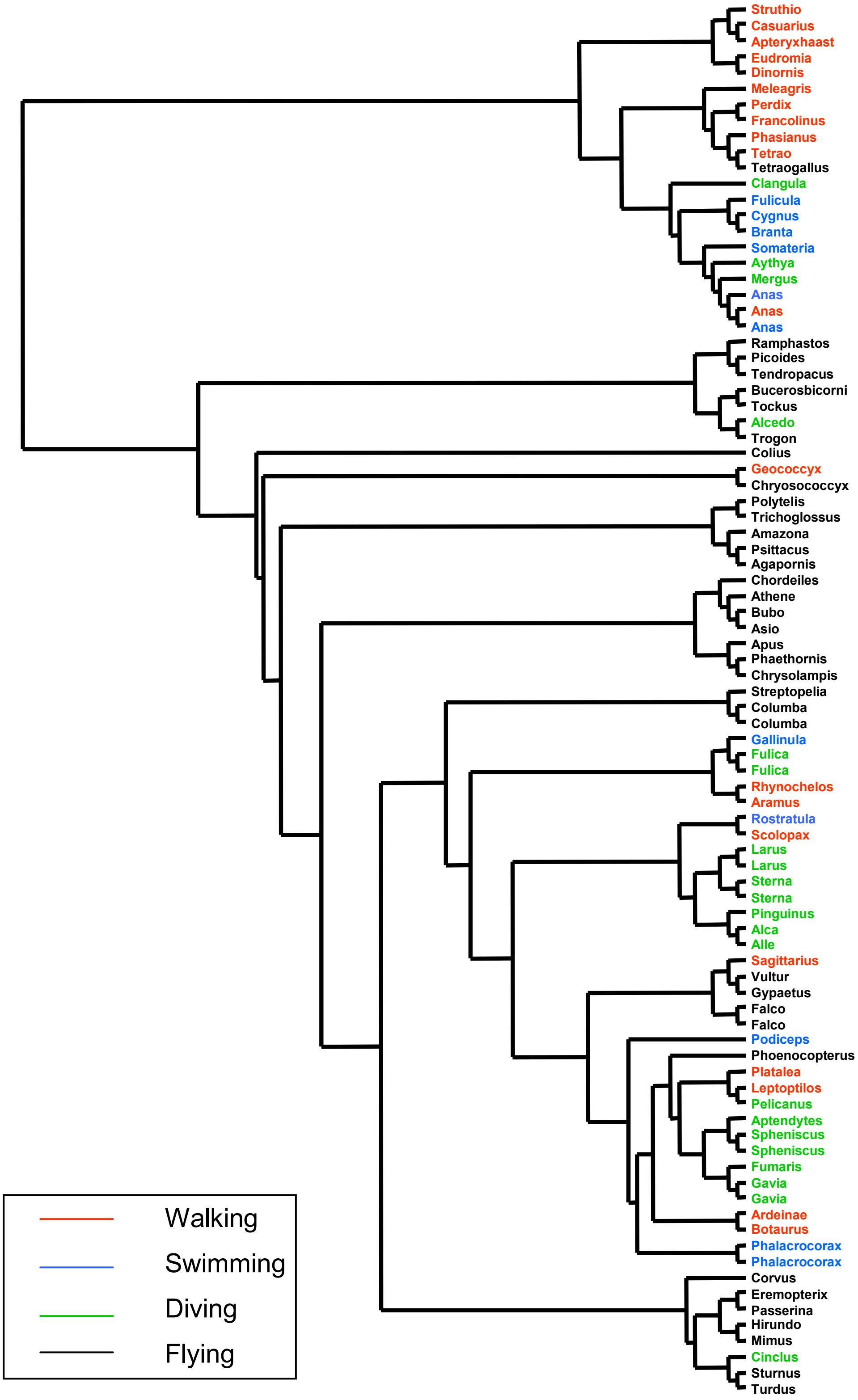
Table 1: Order, family, genera, species, common name, locomotor mode, uncinate length, sternum length, width and depth of the bird species examined in this study. Uncinate length is corrected for body size by dividing by the length of the vertebral column from the beginning of the rib cage. Institutional abbreviations: MK – Museum Koenig, AMNH – American Museum of Natural History.

Order	Family	Genera	Species	Common Name	Locomotor Mode	Uncinate Length	Sternum Length (mm)	Sternum Width (mm)	Sternum Depth (mm)	Vertebral Length (mm)	Collection
Struthioniformes	Stuthionidae	Struthio	camelus	Ostrich	walking	0.0780	207.37	218.45	21.1	426.62	MK
Casuariiformes	Casuariidae	Casuarius	casuaris	Casorwary	walking	0.0854	208.07	125.37	32.7	333.05	MK
Apterigiformes	Apterygidae	Apteryx	haasti	Kiwi	walking	0.2629	30.13	46.3	3.46	104.26	MK
Tinamiformes	Tinamidae	Eudromia	elegans	Tinamu	walking	0.1859	20.26	83.98	1.54	53.07	MK
Tinamiformes	Dinothornidae	Dinornis	maximus	Moa	walking	0.0803	98.22	122.82	6.44	587.7	MK
Galliformes	Phasianidae	Meleagris	gallopavo	Wild Turkey	walking	0.1343	40.33	26.76	48.91	58.23	MK
Galliformes	Phasianidae	Perdix	perdix	Californian Quail	walking	0.1497	48.23	20.09	37.08	40.39	MK
Galliformes	Phasianidae	Francolinus	pondicerianus	Grey Francolin	walking	0.1575	42.49	16.11	27.95	28.95	MK
Galliformes	Phasianidae	Phasianus	polyplectron	Pheasant	walking	0.1571	70.32	21	37.73	46.46	MK
Galliformes	Phasianidae	Tetrao	urogallus	Capercaillie	walking	0.1667	104.77	39.67	58.97	65.99	MK
Galliformes	Phasianidae	Tetraogallus	himalayensis	Himalayan Snowcock	flying	0.2143	74.31	36.87	59.58	61.12	MK
Anseriformes	Mergidae	Clangula	hyemalis	Long Tailed Duck	diving	0.3798	98.85	41.72	25.21	50.62	MK
Anseriformes	Tadornidae	Fulicula	tadorna	Rudy Duck	swimming	0.1581	103.53	48.16	30.77	89.67	MK
Anseriformes	Anseridae	Cygnus	atratus	Black Swan	swimming	0.1231	191.51	76.21	63.84	164.4	MK
Anseriformes	Anseridae	Branta	leucopsis	Barnacle Goose	swimming	0.1276	122.14	52.49	46.48	88.92	MK
Anseriformes	Anatidae	Somateria	mollosima	Common Eider	swimming	0.1666	102.34	57.84	34.62	92.82	MK
Anseriformes	Anatidae	Aythya	fuligula	Tufted Duck	diving	0.2741	63.72	36.49	21.31	50.98	MK
Anseriformes	Anatidae	Mergus	merganser	Common Merganser	diving	0.2519	116.25	53.11	21.82	93.18	MK
Anseriformes	Anatidae	Anas	acuta	Pintail	swimming	0.1488	94.98	39.1	25.69	84.32	MK
Anseriformes	Anatidae	Anas	albifrons	White Fronted Goose	walking	0.1390	125.99	56.79	48.39	97.96	MK
Anseriformes	Anatidae	Anas	clypeata	Northern Shoveler	swimming	0.1636	88.06	41.09	27.64	76.11	MK
Piciformes	Ramphastidae	Ramphastos	tucanos	Tucan	flying	0.2116	44.51	21.3	15.23	51.69	MK
Piciformes	Picidae	Picoides	viridis	Great Spotted Woodpecker	flying	0.2124	39.56	15.89	17.54	36.23	MK
Piciformes	Picidae	Tendropacus	major	Woodpecker	flying	0.2303	42.78	17.72	19.87	41.32	MK
Coraciiformes	Bucerotidae	Buceros	bicornis	Great Hornbill	flying	0.2176	106.07	53.32	42.71	122.22	MK
Coraciiformes	Bucerotidae	Tockus	nasutus	African Grey Hornbill	flying	0.2348	36.79	19.72	15.21	40.83	MK
Coraciiformes	Bucerotidae	Alcedo	atthis	Common Kingfisher	diving	0.2689	25.94	12.17	10.03	17.68	MK
Trogoniformes	Trogonidae	Trogon	viridis	White Tailed Trogon	flying	0.2533	27.33	18.89	14.86	22.15	MK
Colliiformes	Colliidae	Colius	colius	White Backed Mouse Bird	flying	0.2387	24.82	12.18	8.95	23.43	MK
Cuciliformes	Cucilidae	Geococcyx	californicus	Roadrunner	walking	0.1353	32.28	23.13	11.45	48.49	AMNH
Cuculiformes	Cululidae	Chryosococcyx	caprius	Diederik Cuckoo	flying	0.1969	14.84	8.79	8.19	20.16	MK

Psittaciformes	Psittacidae	Polytelis	swainsonii	Superb Parrot	flying	0.2078	45.61	18.42	21.12	32.08	MK
Psittaciformes	Lorridae	Trichoglossus	haematodus	Rainbow Lorikeet	flying	0.2068	45.16	17.59	23.83	37.57	MK
Psittaciformes	Psittacidae	Amazona	aestiva	Blue Fronted Amazon	flying	0.2433	64.91	26.17	28.42	51.75	MK
Psittaciformes	Psittacidae	Psittacus	erithacus	Grey Parrot	flying	0.1731	65.98	27.83	26.74	55.51	MK
Psittaciformes	Psittacidae	Agapornis	roseicollis	Lovebird	flying	0.2265	32.15	14.27	14.21	21.02	MK
Strigiformes	Caprimulgidae	Chordeiles	acutipennis	Lesser Nigh Hawk	flying	0.2309	22.89	14.1	13.61	18.29	MK
Strigiformes	Bubonidae	Athene	noctua	Little Owl	flying	0.2246	27.25	18.53	10.94	29.96	MK
Strigiformes	Bubonidae	Bubo	bubo	Eagle Owl	flying	0.2146	78.23	45.14	38.83	80.45	MK
Strigiformes	Bubonidae	Asio	otus	Long Eared Owl	flying	0.2294	53.87	38.74	33	67.93	MK
Caprimulgiformes	Apodidae	Apus	apus	Common Swift	flying	0.2476	26.2	9.79	15.65	18.28	MK
Caprimulgiformes	Trochilidae	Phaethornis	yaruqui	Hummingbird	flying	0.1757	14.86	5.24	10.55	11.24	MK
Caprimulgiformes	Trochilidae	Chrysolampis	mosquitus	Ruby Topaz Hummingbird	flying	0.2171	15.3	4.16	10.63	9.94	MK
Columbiformes	Columbidae	Streptopelia	decaocto	Collared Dove	flying	0.2196	52.12	21.17	27.56	35.15	MK
Columbiformes	Columbidae	Columba	bollei	Bolle's Pigeon	flying	0.2210	58.15	27.35	31.12	38.77	MK
Columbiformes	Columbidae	Columba	cayenensis	Common Pigeon	flying	0.2201	58.16	24.7	31.57	42.44	MK
Gruiformes	Rallidae	Gallinula	chloropus	Moorhen	swimming	0.1653	40.6	15.64	16.8	55.41	MK
Gruiformes	Rallidae	Fulica	americana	American Coot	diving	0.3035	46.92	23.37	21.73	54.49	MK
Gruiformes	Fulicidae	Fulica	atra	Common Coot	diving	0.2744	57.92	23.58	24.43	65.87	MK
Gruiformes	Rynochetidae	Rhynochelos	jubatos	Kagu	walking	0.1058	66.24	27.34	12.07	50.71	AMNH
Gruiformes	Balearicidae	Aramus	guarana	Limpkin	walking	0.1086	72.24	26.69	26.36	85.26	AMNH
Charadiformes	Rostratulidae	Rostratula	semicollaris	Sth American Painted Snipe	swimming	0.2201	58.16	24.7	31.57	42.44	AMNH
Charadiiformes	Scolopacidae	Scolopax	rusticola	Woodcock	walking	0.1523	58.43	24.08	30.72	42.61	MK
Charadiiformes	Laridae	Larus	argentatus	Italian Gull	diving	0.3701	67.05	40.83	36.66	53.24	MK
Charadiiformes	Laridae	Larus	canus	Common Gull	diving	0.3002	50.73	28.81	27.4	43.06	MK
Charadiiformes	Sternidae	Sterna	hirundo	Common Tern	diving	0.2781	34.43	16.98	20.61	33.77	MK
Charadiiformes	Sternidae	Sterna	paradisaea	Artic Tern	diving	0.2813	32.82	16.63	18.75	33.13	MK
Charadiiformes	Alcidae	Pinguinus	impennis	Great Auk	diving	0.2724	115.09	39.03	39.77	81.54	MK
Charadiiformes	Alcidae	Alca	torda	Razorbill	diving	0.2180	99.04	34.29	33.06	73.67	MK
Charadiiformes	Alcidae	Alle	alle	Little Auk	diving	0.2806	56.64	20	22.9	39.49	MK
Falconiformes	Sagittaridae	Sagittarius	serpentines	Secretary Bird	walking	0.1326	103.07	49.23	50.98	100.54	AMNH
Falconiformes	Cathartidae	Vultur	gryphus	Condor	flying	0.2362	127.97	72.18	69.97	152.83	MK
Falconiformes	Cathartidae	Gypaetus	barbatus	Bearded Vulture	flying	0.3499	111.8	87.66	55.7	108.85	MK
Falconiformes	Falconidae	Falco	biarmicus	Lanner Falcon	flying	0.2142	73.7	33.88	38.28	75.12	MK
Falconiformes	Falconidae	Falco	islandicus	Gyr Falcon	flying	0.2578	81.22	47.69	34.21	77.69	MK

Podicipediformes	Podicipedidae	Podiceps	cristatus	Crested Grebe	swimming	0.2287	61.69	38.5	26.15	67.96	MK
Phoenicopteriformes	Phenocopteridae	Phoenocopterus	rubus	Flamingo	walking	0.2045	109.76	57.06	64.6	139.03	MK
Ciconiiformes	Palataleidae	Platalea	leucorodia	Spoonbill	walking	0.1135	83.69	46.43	38.41	101.67	MK
Ciconiiformes	Ciconiidae	Leptoptilos	crumeniferus	Marabu	walking	0.0389	87.89	79.97	109.68	163.83	MK
Pelicaniformes	Pelicanidae	Pelicanus	rufescens	Pelican	diving	0.2929	86.4	85.05	158.85	106.65	MK
Spheniciformes	Spheniscidae	Aptendytes	patagonicus	Penguin	diving	0.2277	229.86	106.95	62.55	185.31	MK
Spheniciformes	Spheniscidae	Spheniscus	demersus	Black Footed Penguin	diving	0.2770	119.83	66.4	44.36	101.93	AMNH
Spheniciformes	Spheniscidae	Spheniscus	humboldti	Humbolts Penguin	diving	0.2388	119.42	36.83	40.47	93.21	AMNH
Procellariformes	Procellaridae	Fumaris	glacialis	Petrel	diving	0.2633	45.8	42.39	32.33	68.73	MK
Gaviiformes	Gaviidae	Gavia	artica	Black Throated Diver	diving	0.2818	152.97	58.84	31.25	83.84	AMNH
Gaviiformes	Gaviidae	Gavia	stellata	Loon	diving	0.2708	140.82	56.18	30.78	81.61	MK
Ciconiiformes	Ardeidae	Ardeinae	alba	Heron	walking	0.1486	88.29	50.05	50.96	90.91	MK
Circoniformes	Ardeidae	Botaurus	stellaris	Great Bittern	walking	0.0405	69.34	31.07	29.56	104.15	MK
Pelicaniformes	Phalacrocacidae	Phalacrocorax	graculus	Cormorant	swimming	0.2311	75.03	51.82	27.99	90.27	MK
Pelicaniformes	Phalacrocacidae	Phalacrocorax	bougainvillii	Shag	swimming	0.2237	98.41	56.42	34.2	92.9	MK
Passeriformes	Corvidae	Corvus	corax	Common Raven	flying	0.2849	69.79	41.68	30.04	60.04	MK
Passeriformes	Alaudidae	Eremopterix	leucotis	Black Crowned Sparrow Lark	flying	0.3170	9.84	7.63	4.2	11.93	MK
Passeriformes	Passeridae	Passerina	domestica	Common Sparrow	flying	0.2584	18.49	11.37	9.76	19.65	MK
Passeriformes	Hirundinidae	Hirundo	rustica	Barn Swallow	flying	0.2571	15.71	9.75	6.71	13.69	MK
Passeriformes	Mimidae	Mimus	polyglottos	Mockingbird	flying	0.2463	12.79	6.82	6.01	11.37	MK
Passeriformes	Cinclidae	Cinclus	cinclus	White Throated Dipper	diving	0.2756	25.53	14.61	10.36	23.77	MK
Passeriformes	Sturnidae	Sturnus	vulgaris	European Starling	flying	0.2629	29.7	15.5	13.08	25.32	MK
Passeriformes	Muscicapidae	Turdus	merula	Blackbird	flying	0.3142	29.24	16.04	14.15	27.25	MK

Figure 3: Phylogeny of birds used in this study using DNA-DNA hybridisation, modified from Sibley & Ahlquist (1990). Colours correspond to the locomotor mode of the bird: Orange – walking birds, Blue – swimming birds, Green – diving birds and Black – flying birds.


Struthio
Casuarius
Apteryxhaast
Eudromia
Dinornis
Meleagris
Perdix
Francolinus
Phasianus
Tetrao
Tetraogallus
Clangula
Fulicula
Cygnus
Branta
Somateria
Aythya
Mergus
Anas
Anas
Anas
Ramphastos
Picoides
Tendropacus
Bucerosbicorni
Tockus
Alcedo
Trogon
Colius
Geococcyx
Chryosococcyx
Polytelis
Trichoglossus
Amazona
Psittacus
Agapornis
Chordeiles
Athene
Bubo
Asio
Apus
Phaethornis
Chrysolampis
Streptopelia
Columba
Columba
Gallinula
Fulica
Fulica
Rhynochelos
Aramus
Rostratula
Scolopax
Larus
Larus
Sterna
Sterna
Pinguinus
Alca
Alle
Sagittarius
Vultur
Gypaetus
Falco
Falco
Podiceps
Phoenocopterus
Platalea
Leptoptilos
Pelicanus
Aptendytes
Spheniscus
Spheniscus
Fumaris
Gavia
Gavia
Ardeinae
Botaurus
Phalacrocorax
Phalacrocorax
Corvus
Eremopterix
Passerina
Hirundo
Mimus
Cinclus
Sturnus
Turdus
Walking
Swimming
Diving
Flying

Therefore, to correct for body size uncinate length was divided by the total length of the vertebral column from the beginning of the rib cage to the end of the synsacrum.

2.2.4 STATISTICAL ANALYSES

Data for within-species comparisons of the body-size normalised length of the uncinate processes in *P. domesticus* were analysed using Wilcoxon Ranked Sum tests and two-tailed probabilities were tested for between rib comparisons on individual birds. Analysis of variance (ANOVA) was used for comparisons between birds. Sternal morphology was analysed using two sample t-tests on log transformed data. For sister group comparisons Wilcoxon Ranked Sum analyses were used and two-tailed probabilities were tested throughout. All data are corrected for body size and presented as mean±SE. Full statistical analysis can be found in Appendix 1.

2.3 RESULTS

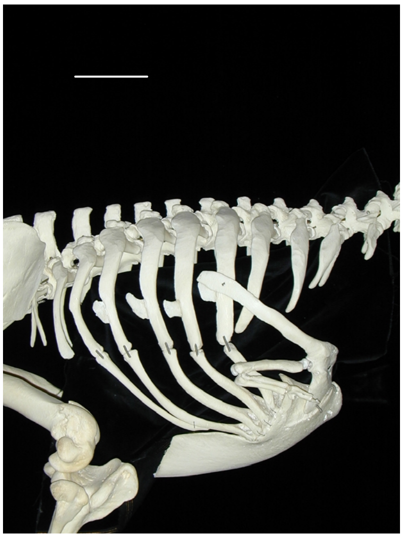
The number of ribs, for the birds in this study, varied from 6 to 10. Rib number does not always correlate with locomotor mode, although walking species generally tend to have the fewest ribs and the diving species the most. Morphological data were collected on a total of 88 skeletons representing 29 Orders and 53 Families (Table 1). Representative skeletons of rib cage and uncinate morphology for the birds from walking, swimming, flying and diving locomotor modes are shown in Figure 4 (in all figures cranial is to the right).

2.3.1 WITHIN SPECIES VARIATION IN UNCINATE LENGTH

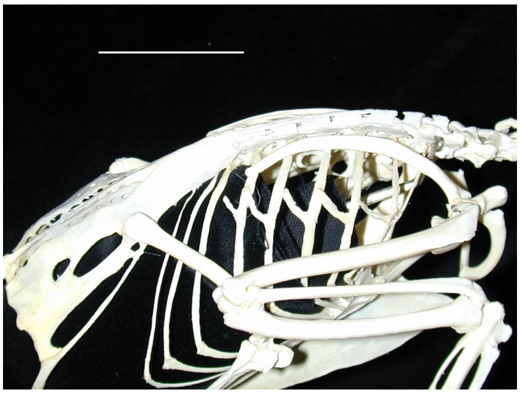
The common sparrow, *P. domesticus* has 7 pairs of ribs. Uncinate processes are present on ribs 1-6. While rib number and length vary from species to species, the general rib cage morphology of the sparrow, Figure 5, can be considered representative of the rib cage morphology seen in all species and locomotor modes used in this study. The first rib is usually reduced in length and thickness compared with the other ribs, and is not attached by sternal rib to sternum. There was no significant difference between male and female birds, once corrections for body size were applied; therefore data from male and female birds was pooled. There was no significant difference between the lengths of the uncinate processes on the second through fifth ribs. However, the uncinate processes on the first rib

Figure 4: Representative skeletons showing the different morphology of the uncinate processes in A) walking bird – Cassowary (*Casuaris casuaris*), B) swimming bird - Pintail (*Anas acuta*), C) flying bird – Eagle Owl (*Bubo bubo*) and D) diving bird - Razorbill (*Alca torda*). Uncinate processes are shortest in the walking birds, of intermediate length in the flying and swimming birds and are long in the diving birds. Scale bars 5cm.

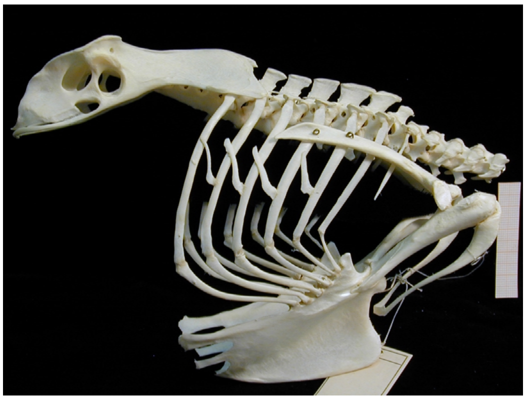
A



B

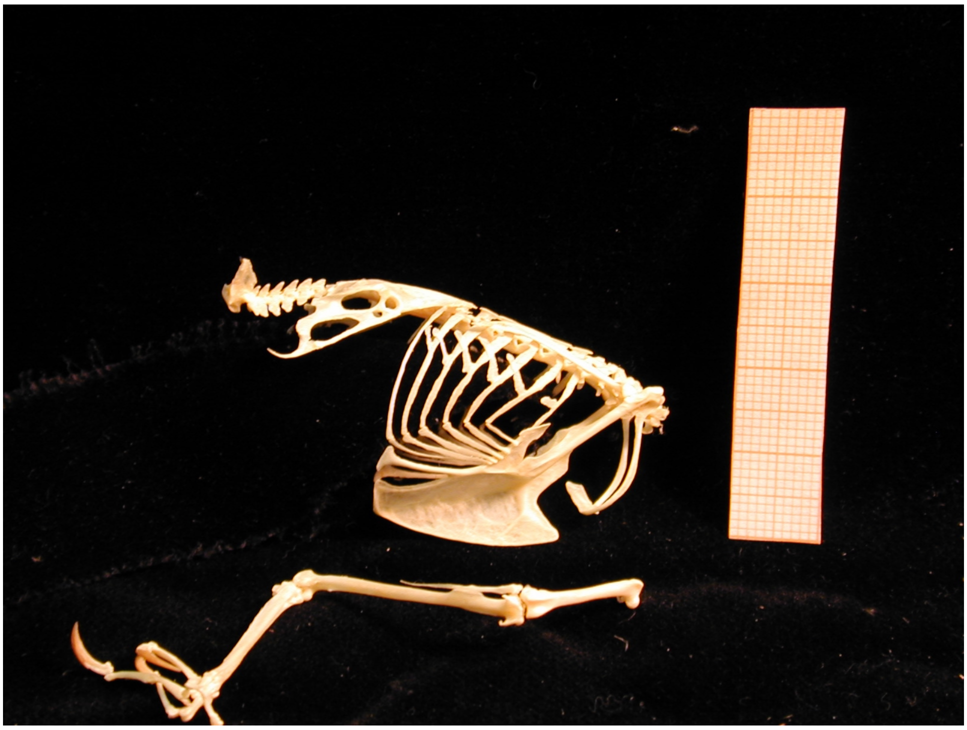


C



D

Figure 5: Representative skeleton of the common sparrow, *Passer domesticus*, demonstrating the different morphology of the uncinate processes as you move caudally along the rib cage. The uncinate processes on the first and last ribs are reduced in length. The uncinate processes on the second to the fifth ribs are uniform in length and similar in morphology. Scale bar 5cm.



(0.12±0.02, n=12, p=0.012) and last rib (0.17±0.02, n=12, p=0.01) were significantly shorter than the uncinate processes on the other ribs (0.28±0.006, n=12). Aside from the first rib, sternal ribs connect the vertebral ribs to the sternum and these become increasingly thinner and longer as one moves caudally. Therefore, data from the first and last ribs with uncinate processes were disregarded and sister group comparisons were made using the average length of the uncinate processes on the remaining ribs, corrected for body size.

2.3.2 SISTER GROUP COMPARISON OF UNCINATE LENGTH

Sister groups were chosen using the phylogenetic relationships of Sibley and Ahlquist (1990). All possible sister group comparisons of different locomotor modes were included in the analysis to ensure the data set were unbiased. Sister groups were compared from flying and diving birds (Figure 6), swimming and diving birds (Figure 7), walking and diving birds (Figure 8), walking and flying birds (Figure 9) and walking and swimming birds (Figure 10). There were too few sister groups comparisons to enable comparison between flying and swimming birds (Figure 11). Full statistical analysis can be found in Appendix 1, data are summarised in Table 1.

2.3.2.1 Walking Birds

All data were included for analysis as there was no significant effect of including or excluding the walking birds that could and could not fly (Table 2). The length of the uncinate processes was significantly shorter in the walking birds when compared to the flying and diving birds (0.13±0.01, Figures 4 and 12). The uncinate processes in walking birds spanned less than half the distance to the following rib and were stout and broad at the base. The first and last uncinate processes are shorter and less tapered than the uncinates in the central region of the rib cage. The flightless ratites lack a keeled sternum altogether. In the other walking birds the sternum is significantly shorter than in the diving, flying and swimming birds and significantly narrower than in the diving and flying birds. The sternum is also significantly shallower than in the flying birds (Table 3).

The kiwi, *Apteryx haasti*, has uncinate processes (Figure 13) that are much longer (0.26) than those found in other walking birds (0.13) being of a length more commonly found in the flying birds (0.24). Kiwi uncinate processes are also very broad at the base

Figure 6: Phylogeny of birds used in this study using DNA-DNA hybridisation, modified from Sibley & Ahlquist (1990). Arrows indicate the five sister group comparisons for the flying and diving birds, A – E. Colours correspond to the locomotor modes of the bird: Orange – walking birds, Blue – swimming birds, Green – diving birds and Black – flying birds.

Sister Group Comparisons for Flying & Diving Birds

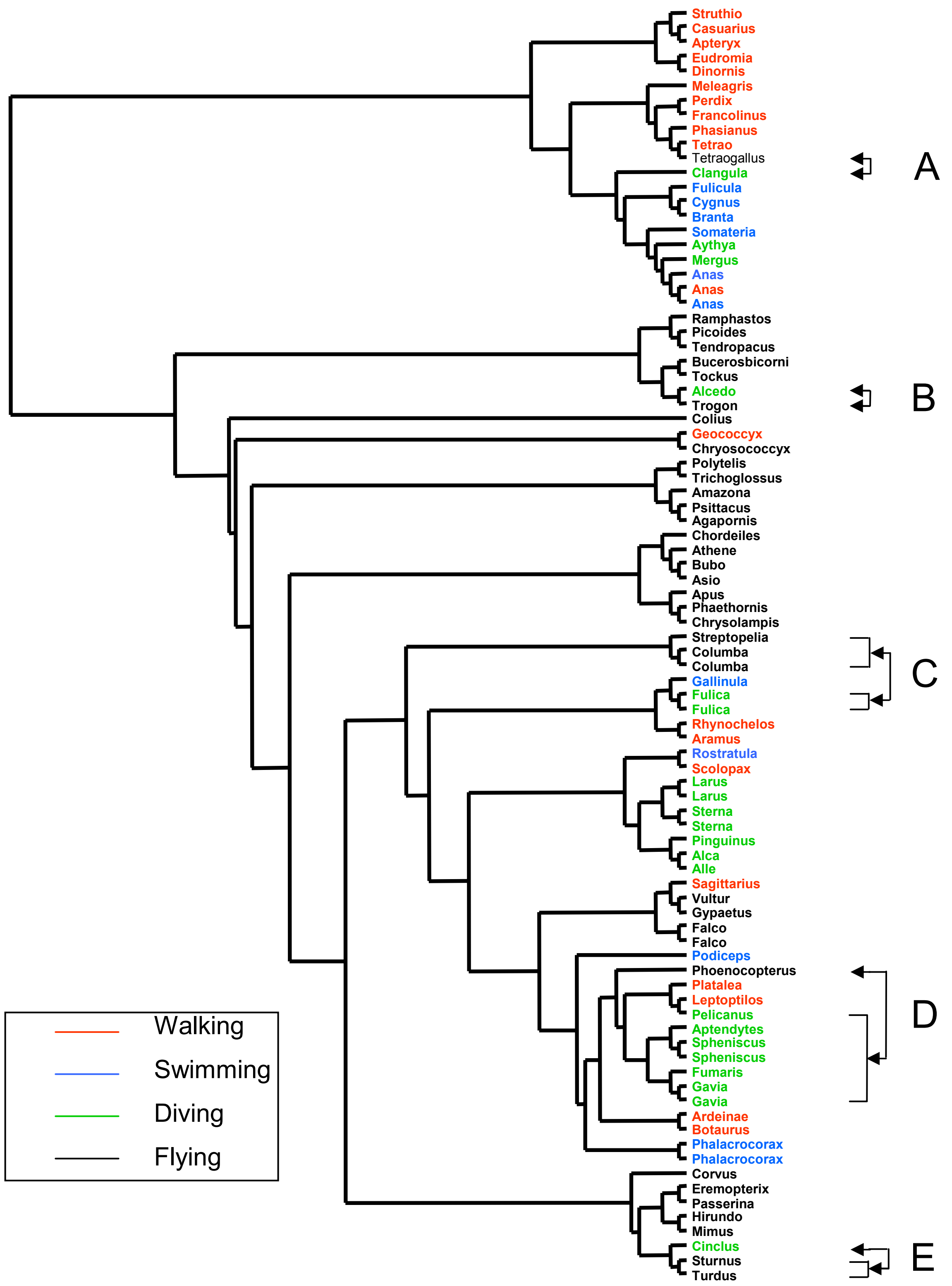


Figure 7: Phylogeny of birds used in this study, using DNA-DNA hybridisation, modified from Sibley & Ahlquist (1990). Arrows indicate the five sister group comparisons for swimming and diving birds, A – E. Colours correspond to the locomotor modes of the bird: Orange – walking birds, Blue – swimming birds, Green – diving birds and Black – flying birds.

Sister Group Comparisons for Swimming & Diving Birds

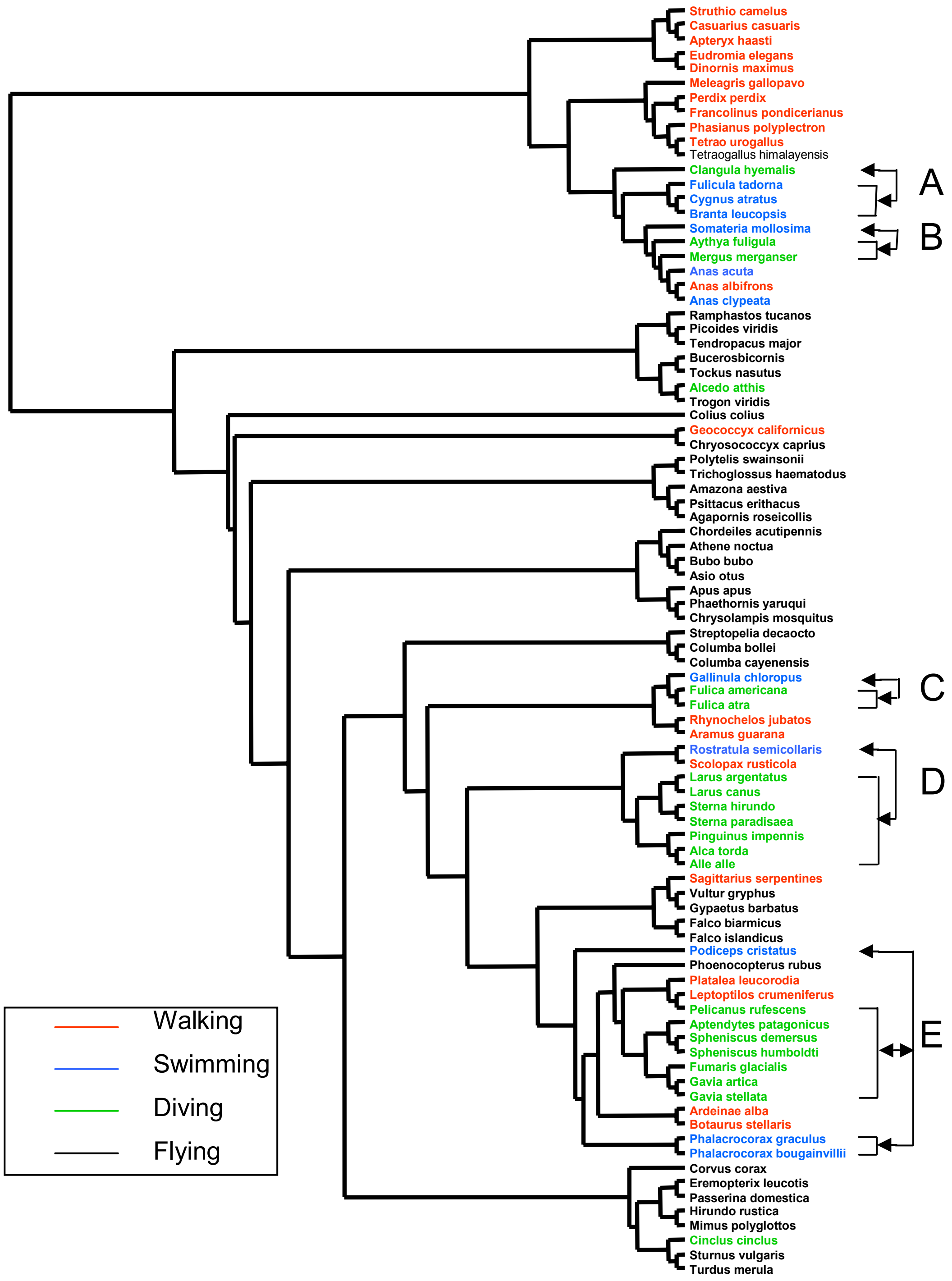


Figure 8: Phylogeny of birds used in this study, using DNA-DNA hybridisation, modified from Sibley & Ahlquist (1990). Arrows indicate the seven sister group comparisons for walking and diving birds, A – G. Colours correspond to the locomotor modes of the bird: Orange – walking birds, Blue – swimming birds, Green – diving birds and Black – flying birds.

Sister Group Comparisons for Walking & Diving Birds

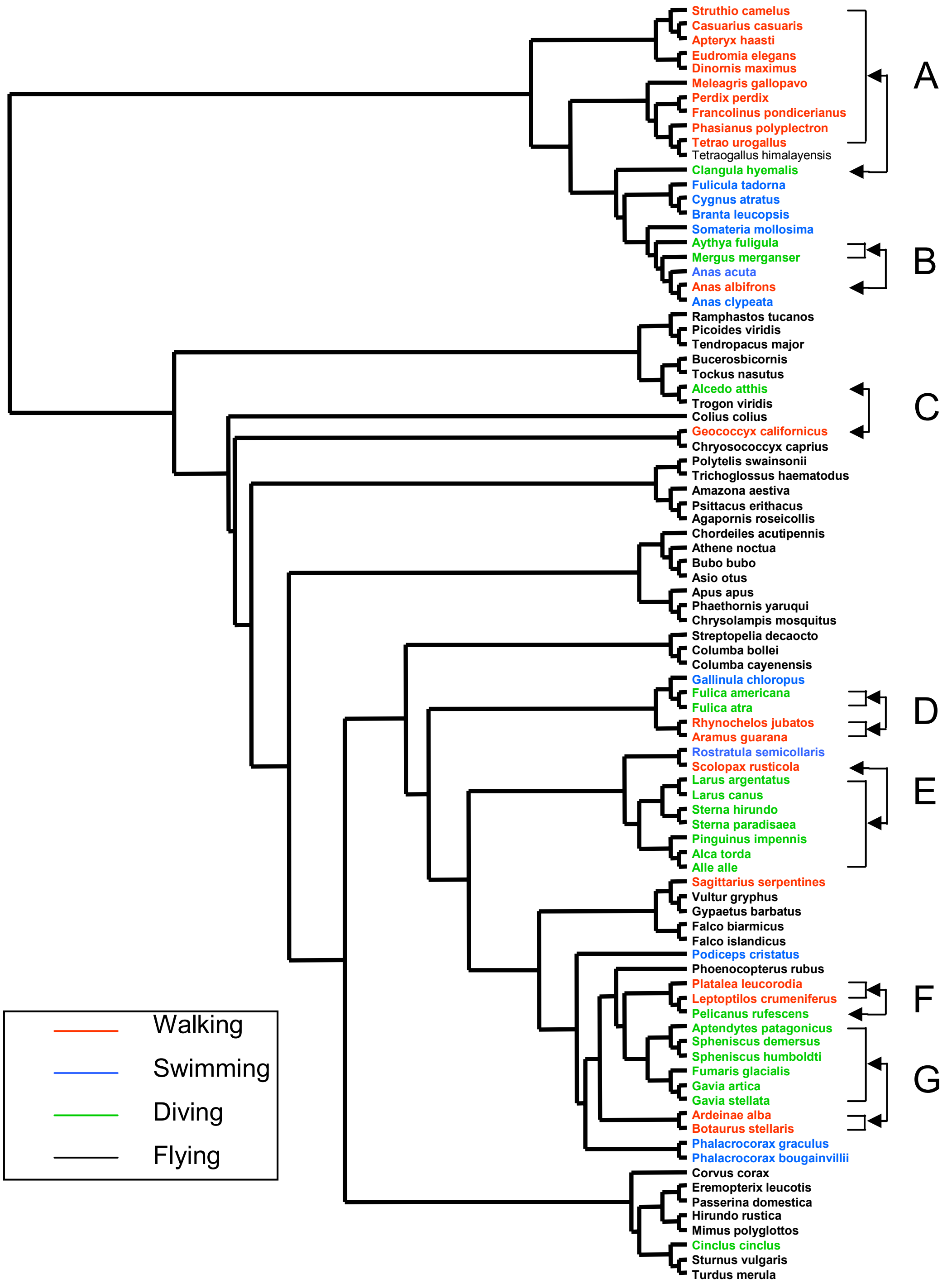


Figure 9: Phylogeny of birds used in this study, using DNA-DNA hybridisation, modified from Sibley & Ahlquist (1990). Arrows indicate the six sister group comparisons for walking and flying birds, A – F. Colours correspond to the locomotor modes of the bird: Orange – walking birds, Blue – swimming birds, Green – diving birds and Black – flying birds.

Sister Group Comparisons for Walking & Flying Birds

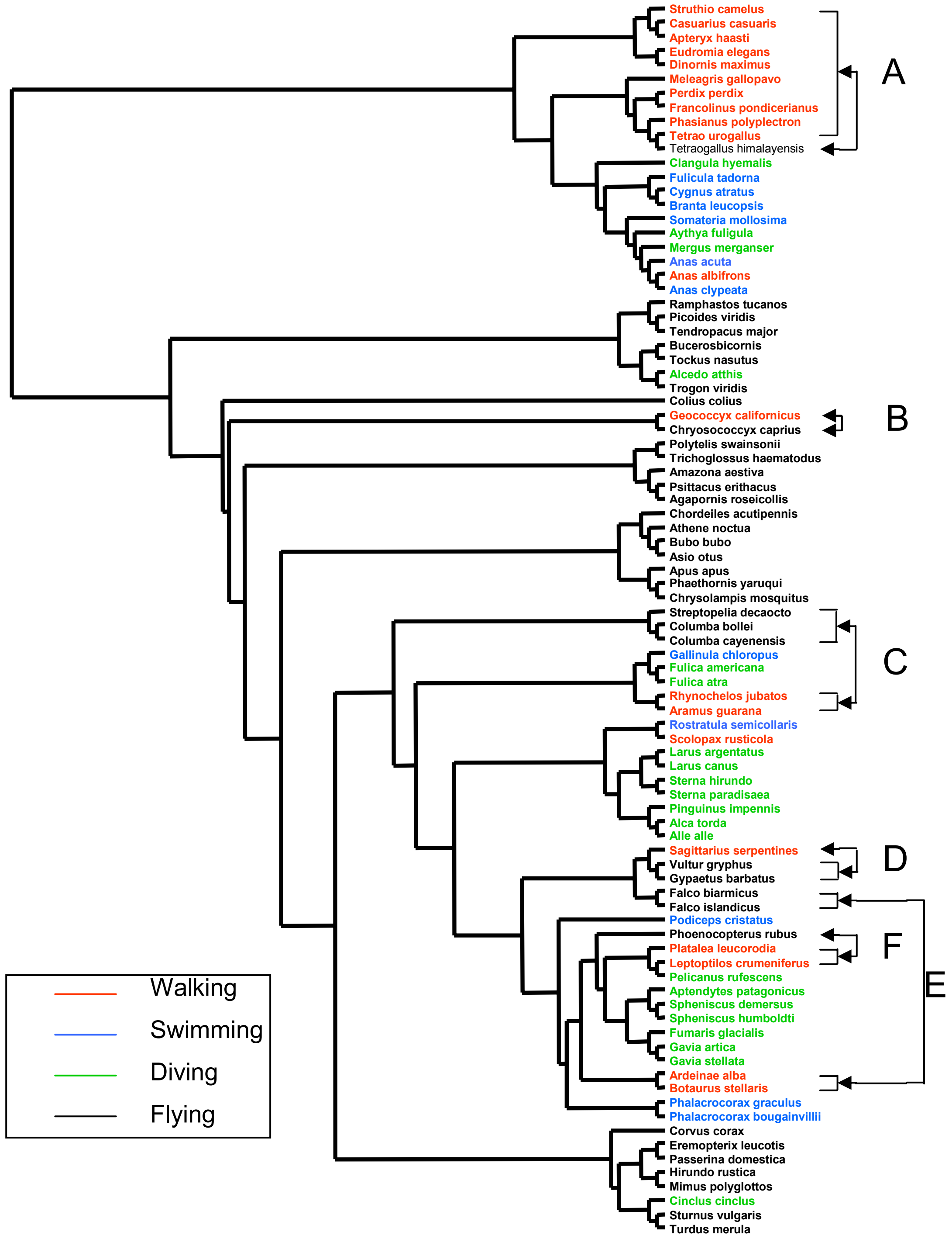


Figure 10: Phylogeny of birds used in this study, using DNA-DNA hybridisation, modified from Sibley & Ahlquist (1990). Arrows indicate the five sister group comparisons for walking and swimming birds, A – E. Colours correspond to the locomotor modes of the bird: Orange – walking birds, Blue – swimming birds, Green – diving birds and Black – flying birds.

Sister Group Comparisons for Walking & Swimming Birds

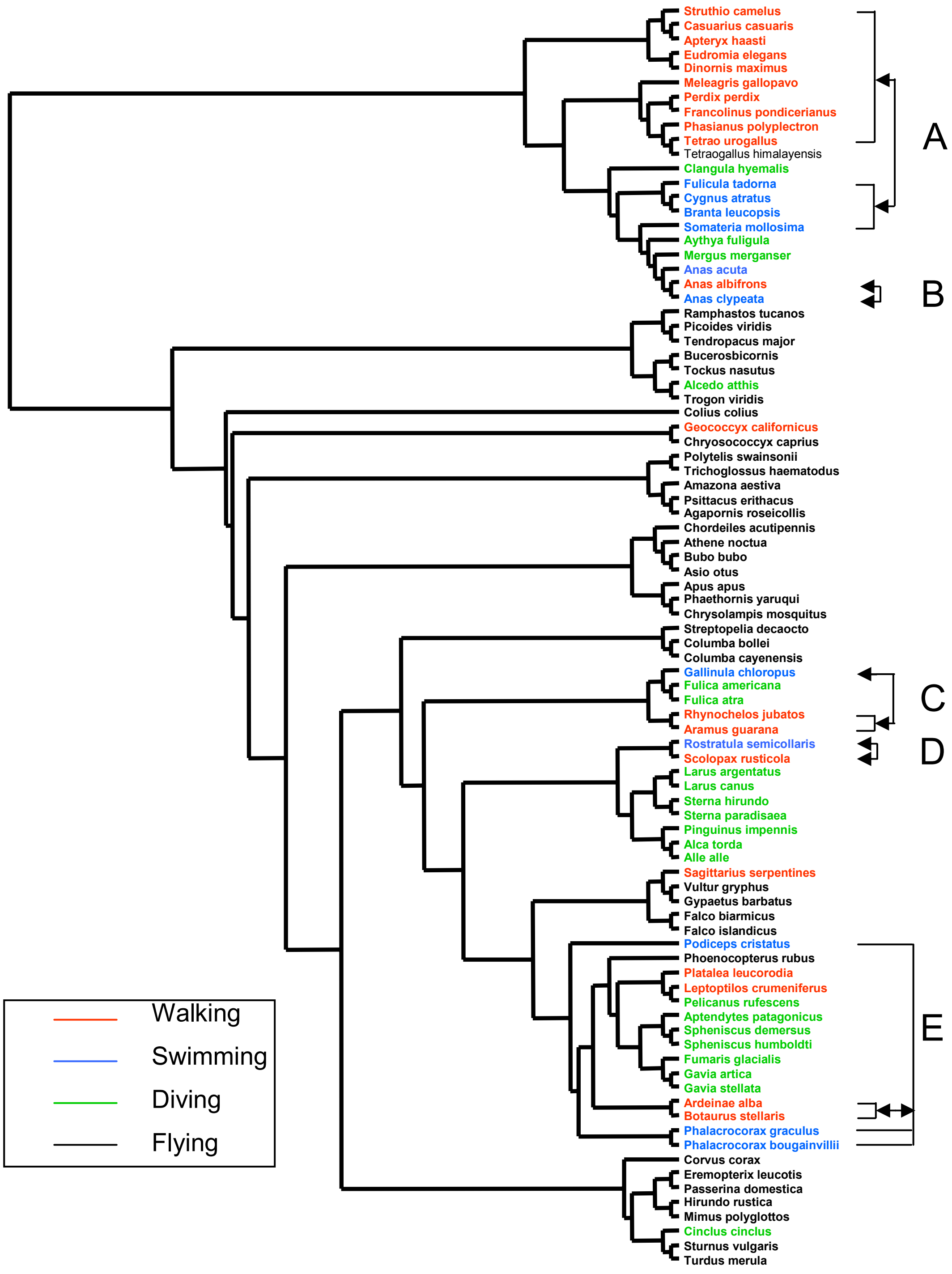


Figure 11: Phylogeny of birds used in this study, using DNA-DNA hybridisation, modified from Sibley & Ahlquist (1990). Arrows indicate the sister group comparisons for flying and swimming birds, A – C. There were too few sister group comparisons to enable a comparison between the uncinate length of the flying and swimming birds. Colours correspond to the locomotor modes of the bird: Orange – walking birds, Blue – swimming birds, Green – diving birds and Black – flying birds.

Sister Group Comparisons for Flying & Swimming Birds

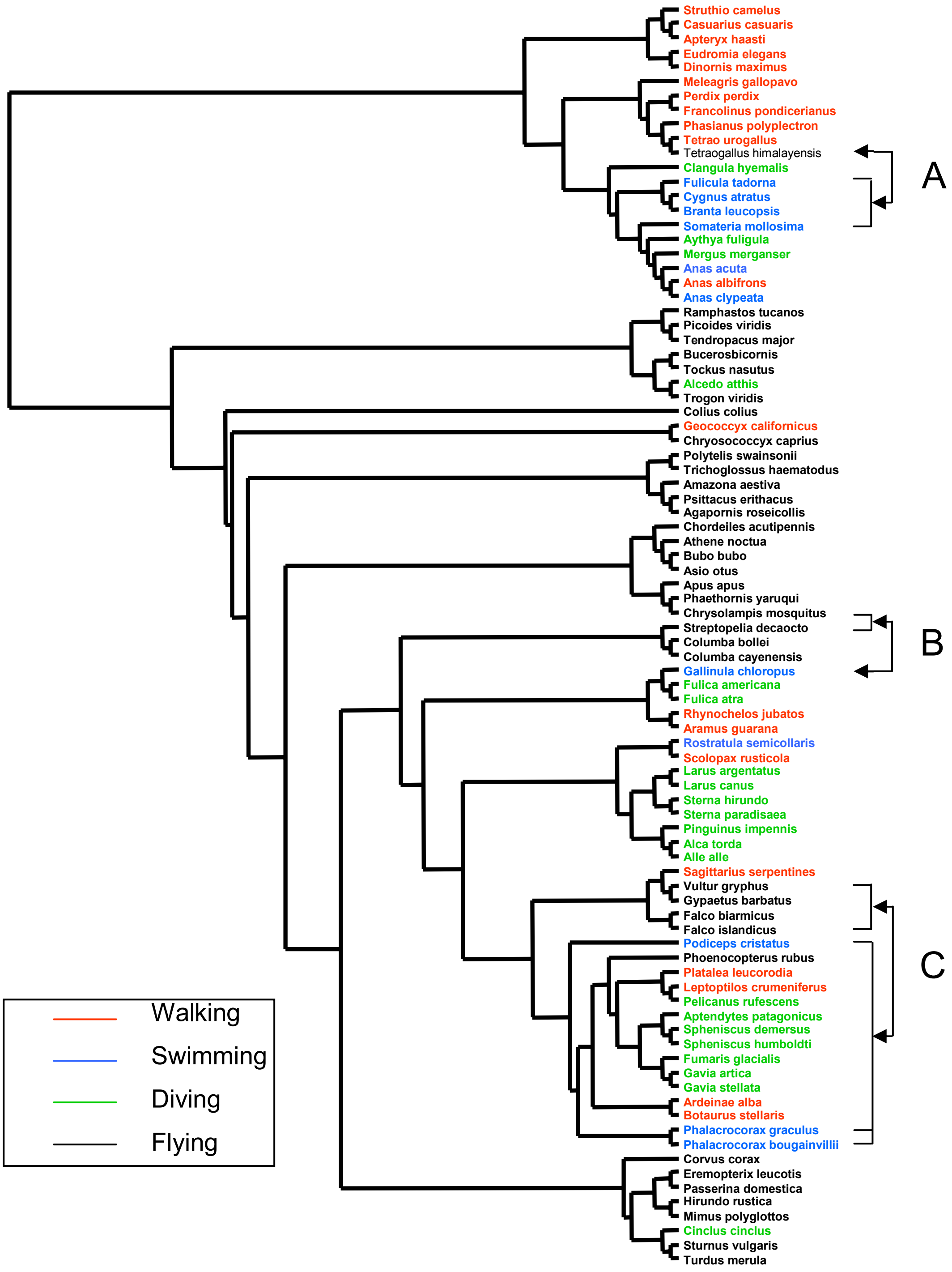


Table 2: Sister group comparisons of the differences within the locomotor modes used in this study. To investigate the possible effect of the potentially significant differences in birds within each locomotor mode, sister group comparisons were analysed for diving birds that do and do not fly and those that dive with their feet and using their wings. Walking birds that do and don't fly were also examined for each comparison. No significant difference was found within each locomotor mode, therefore all data were pooled in subsequent analysis.

Sister Group Comparison	n	p-values
all walking vs all diving	7	0.018
walking but not flying vs diving but not flying	7	0.018
walking but not flying vs diving not with feet	6	0.028
all walking vs all flying	6	0.028
walking and flying vs all flying	6	0.028
all walking vs all swimming	5	0.08
all swimming vs walking and flying	5	0.08
all flying vs all diving	5	0.08
all swimming vs all diving	5	0.04
all swimming vs diving but not flying	5	0.04

Table 3: Comparison of sternal length, width and depth between diving, flying, swimming and walking birds. Data are presented as mean±SE, two-tailed t-tests of significance, significant set at $p<0.05$, NS – not significant $p>0.05$.

Sternum	Locomotor Mode Comparison (mean±SE)		p-value
	Diving	Flying	
Length	1.24±0.07	1.15±0.05	NS
Width	0.6±0.03	0.57±0.02	NS
Depth	0.52±0.05	0.56±0.05	NS
	Diving	Swimming	
Length	1.24±0.07	1.09±0.06	NS
Width	0.6±0.03	0.53±0.03	NS
Depth	0.52±0.05	0.4±0.04	0.04
	Diving	Walking	
Length	1.24±0.07	0.87±0.09	0.001
Width	0.6±0.03	0.52±0.06	0.03
Depth	0.52±0.05	0.46±0.07	NS
	Flying	Swimming	
Length	1.15±0.05	1.09±0.06	NS
Width	0.57±0.02	0.53±0.03	NS
Depth	0.56±0.05	0.4±0.04	NS
	Swimming	Walking	
Length	1.09±0.06	0.87±0.09	0.04
Width	0.53±0.03	0.52±0.06	NS
Depth	0.4±0.04	0.46±0.07	NS
	Flying	Walking	
Length	1.15±0.05	0.87±0.09	0.0004
Width	0.57±0.02	0.52±0.06	0.02
Depth	0.56±0.05	0.46±0.07	0.003

Figure 12: Summary figure showing the mean length of the uncinate process (Mean±SE) versus the locomotor mode. Orange – walking birds, Blue – swimming birds, Black – flying birds and Green – diving birds. The uncinate processes are short in the walking birds, intermediate in the swimming and flying birds and the longest in the diving birds. Symbols indicate significant difference: *** p-value<0.02, ** p-value<0.03, * p-value<0.05, ns – not significant.

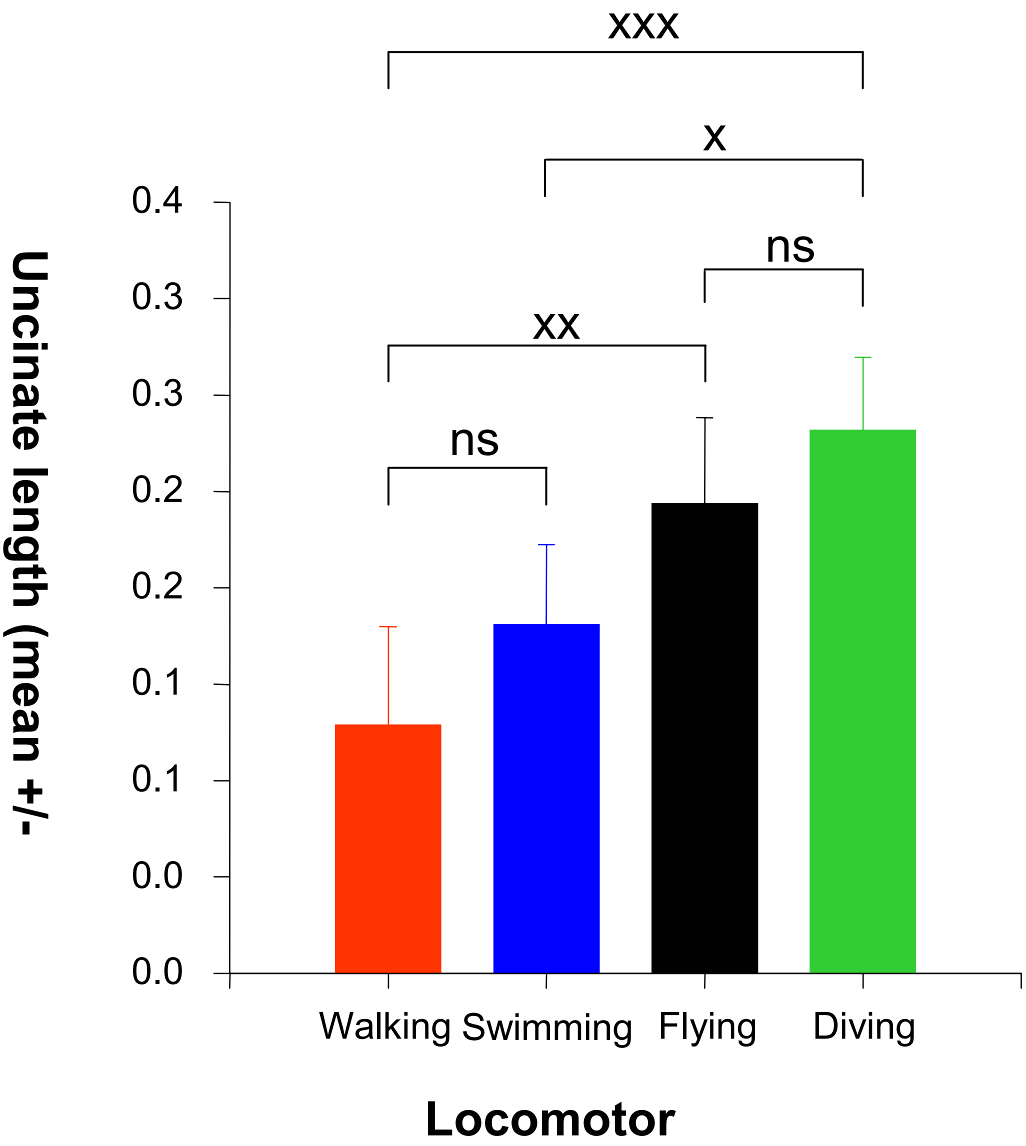

xxx
x
ns
xx
ns
0.4
0.3
0.3
0.2
0.2
0.1
0.1
0.0
0.0
Uncinate length (mean +/-
Walking
Swimming
Flying
Diving
Locomotor

Figure 13: Skeleton of the Kiwi (*Apteryx haasti*) demonstrating the broad and extended ribs. The uncinate processes are longer than those typically found in walking birds and have a broad triangular base. Scale bar 10cm.

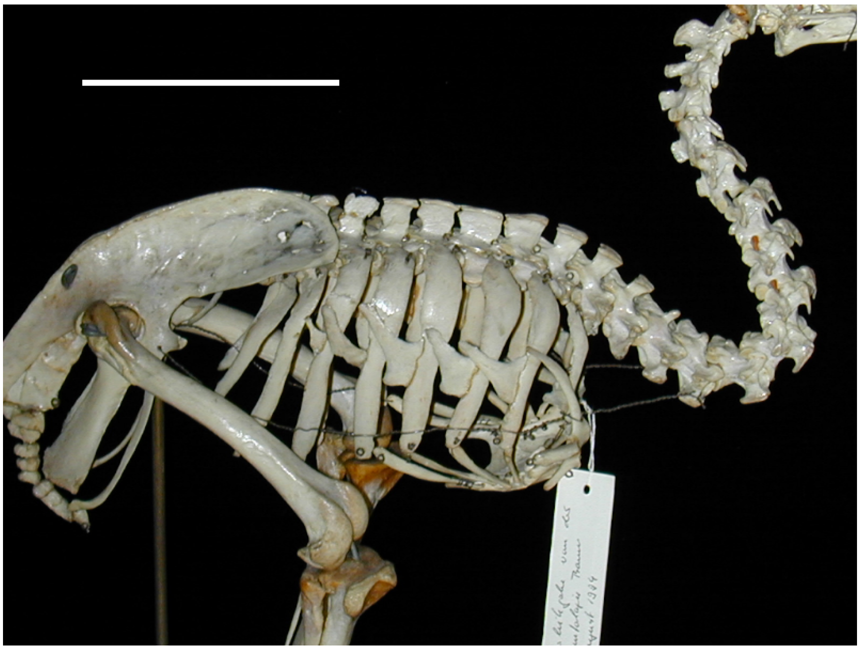
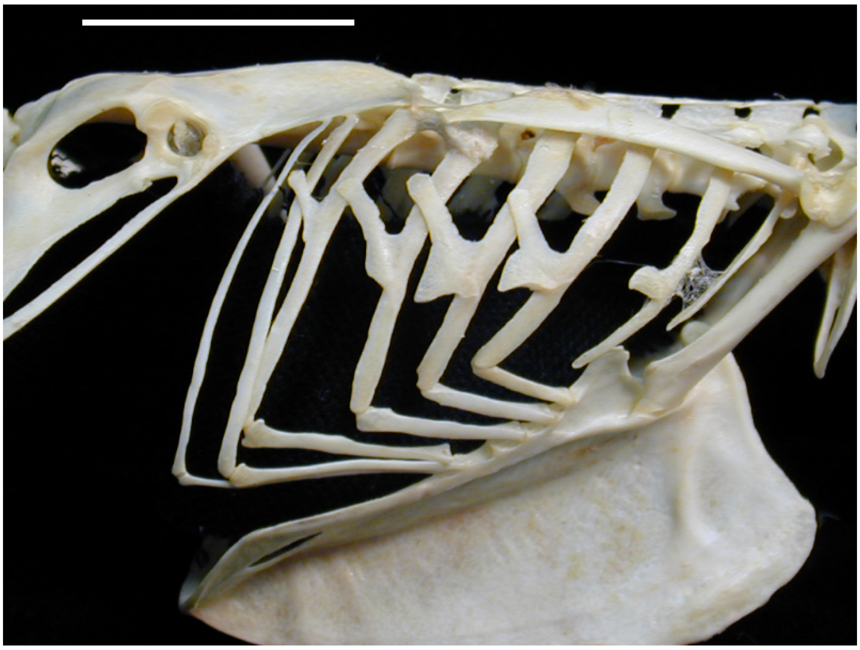


Figure 14: Representative skeleton from the Psittaciformes; the Lorikeet (*Trichoglossus haematodus*) demonstrating the triangular projections extending from the posterior surface of the uncinate processes, scale bar 3cm.



and extend across to overlap the following rib. The ribs also differed in overall morphology being extended, flattened and broad.

2.3.2.2 Swimming Birds

The sternum of swimming birds was significantly longer than the walking birds and significantly shallower than in the diving birds (Table 3). The rib cage is extended so that most, but not all, of the body cavity is enclosed by the rib cage. The sternal ribs in swimming birds are longer and thinner than those found in the walking or flying birds. Uncinate processes are not found on all ribs (Figure 4). The uncinate processes in the swimming birds were intermediate in length and significantly shorter than in the diving birds (0.18±0.01, Figures 4 and 12). The uncinates reach to the edge of the following vertebral rib and are uniform in thickness along the length of the process.

2.3.2.3 Flying Birds

Flying birds comprised the largest group of birds examined in this study. The sternum of flying birds is significantly longer, wider and deeper than that of the walking birds (Table 3). The rib cage itself is more compact and does not span the entire body as seen in the swimming and diving birds. The uncinate processes have a characteristic L-shaped morphology where they attach to the vertebral ribs and are uniform in thickness along the length of the process. They are intermediate in length (0.24±0.01, Figures 4 and 12) and significantly longer than those of walking birds. Within the flying birds, the woodpeckers (not illustrated), *Picoides viridis* and *Tendropacus major*, have a pronounced broadening of the first and second vertebral ribs. The parrots (Psittaciformes) all have triangular projections extending from the posterior edge of the uncinate processes (Figure 14); the function of these projections is currently unknown.

2.3.2.4 Diving Birds

There was no significant effect for either including or excluding birds that locomote under water using their feet and those that use their wings (Table 2). Therefore, data were pooled in the subsequent analysis. Diving birds have a long and wide sternum, almost all of the abdominal cavity in enclosed by skeletal elements. The sternum is parallel to the vertebral column. The uncinate processes are significantly longer than in the walking birds and the sternum is deeper than that of the swimming birds (Table 3). The ribs are long and thin and the rib cage is extended so that the entire body cavity is enclosed. Uncinate processes are found on the ribs corresponding to the sternum. The uncinate processes spanned across to the edge of the second following rib. The uncinate processes are thin and taper towards the tip and were significantly longer than those found in either the swimming or walking birds (0.28±0.01mm, Figures 4 and 12).

2.4 DISCUSSION

Uncinate processes are reported to act as a lever arm for rib movement (Zimmer, 1935). Therefore, uncinate length is likely to be an important factor in terms of their function. The longer the uncinate the greater the mechanical advantage would be to move the rib about its fulcrum at the articulation on the vertebral column. A longer uncinate would also provide a larger area for muscle attachment, which would enable the application of larger forces on the other hand, muscle attachment at the end of the uncinate process would also increase any lever advantage.

2.4.1 WITHIN-SPECIES VARIATION

Uncinate length is not significantly different between or within birds of the same species as demonstrated for the Common Sparrow (*P. domesticus*). Conservation of skeletal proportions is common in bats, the other extant flying vertebrates, with little variation in wing bone length and leg length within a species (Reardon & Flavel, 1987). There was also no difference between uncinate length between male and female birds, the male birds being proportionately larger.

2.4.2 FUNCTIONAL SIGNIFICANCE OF THE UNCINATE PROCESSES

Sister group comparisons indicate that uncinate length in not dependent on phylogeny and correlates instead with the mode of locomotion in birds. The uncinate processes are longest in diving birds, of intermediate length in swimming and flying birds, and shortest in the walking birds. Perhaps due to the difficulties in quantifying stiffening, there are no tested hypotheses to support the role of uncinates in strengthening the trunk. Despite this uncinate processes are frequently reported to be involved in acting as a brace to strengthen the rib cage (Libbie et al., 1942; Kardong, 1988; Walker, 1994; Liem et al., 2001). The uncinate processes sit on top of the following rib but are not attached to it, thereby limiting their ability to act as a brace. Furthermore, as the ribs move it is likely that rather than bracing them, the uncinates would slide across the following rib surface. The processes are fragile structures in some species that are attached by fibroelastic tissue to the vertebral ribs, allowing lateral deflection. If their primary function were to provide stability, one would expect them to be much more stable. A more likely hypothesis is that the uncinates are directly involved in moving the ribs and rib cage rather than in preventing movement.

The uncinate processes of the first and last ribs are reduced in size, length and (presumably) function compared to those on remaining ribs. The sternum in birds, allows the attachment of large flight muscles, the pectoralis and the supracoracoideus (Duncker, 1977). The pectoralis muscle alone accounts for up to 35% of the total body mass of some birds (Dial et al., 1988). This large mass of muscle together with the abdominal viscera must be moved up and down during breathing (Brainerd, 1999). The location of the uncinates, in direct correlation (dorsoventrally) to the deepest portion of the sternum and their absence from ribs which are not directly over the sternum, suggests their function may have more to do with moving this large mass of muscle than with any putative strengthening or stiffening function. If the uncinate processes are involved in moving the sternum and associated flight muscles, this would account for the reduction in uncinate length seen in the walking species. Due to the decreased importance of the flight muscles in walking birds, the sternum is also reduced. The extreme case is seen in the flightless running birds, such as the ratites, which lack a keeled sternum altogether and have very short uncinates.

Both in the kiwi (*A. haasti*) and the woodpeckers (*P. viridis* and *T. major)* strengthening the rib cage is important. Kiwi birds lay the largest eggs of all birds, which can weigh up to 25% of the females body weight (Gould, 1992). Woodpeckers on the other hand are known for their head-pounding foraging (Kirby, 1980). The kiwi does have uncinates longer than other walking birds but they fall into the normal range of the flying or swimming birds, as do those of the woodpeckers'. However, both species show divergent rib structure. In the kiwi the ribs are broad, flattened and may overlap. It is this overlapping of the ribs, rather than the bracing of the uncinates, that allows the ribs to lock together when additional thorax stability is required, such as during egg laying (Gould, 1992). Woodpeckers exhibit a pronounced broadening of the first and second vertebral ribs where they articulate with the sternal rib. The last cervical rib is also broadened, as are the vertebral attachments of these ribs, which function to stabilise the neck against repeated impacts (Kirby, 1980). Rib expansion and broadening is also seen in some anteaters (*Cyclopes didactylus, Tamandua tetradactyla and Myrmeccophaga tridactyla*) and some primates; the golden and common poto (*Artocebus calabarensis, Periodicticus potto*) and the slender loris (*Loris tardigradus*). The stouter ribs are associated with a thickening of intercostal musculature and these adaptations are associated with extension or dorsiflexion of the vertebral column, and provide additional thorax stability needed for digging and climbing (Jenkins, 1970).

The thorax of birds is already stiffened as the thoracic vertebrae are capable of only small movements. The lumbar vertebrae are also fused to form the synsacrum while the terminal vertebrae fuse to form the pygostyle (Kardong, 1988). These adaptations stiffen the vertebral column and establish a firm, stable axis during flight. If the rib cage does need strengthening this is likely to be achieved by a widening and broadening of the ribs themselves and a thickening of the associated musculature as we see in the kiwi and woodpeckers rather than by altering the length of the uncinate processes.

2.4.3 FUNCTION OF THE UNCINATE PROCESSES IN DIVING BIRDS

The diving birds have a deep sternum, are strong fliers (penguins ‘fly’ underwater) and have significantly longer uncinate processes than the other groups examined in this study. Longer uncinates are assumed to counteract high pressure during dives (Welty, 1988). Aside from the penguins (*Aptendytes patagonicus, Spheniscus demersus* & *Speheniscus humbolti*), the vast majority of 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 Auks (*Pinguinis impennis, Alca torda* & *Alle alle*), the White Throated Dipper (*Cinclus cinclus),* the Gulls (*Larus argentatus* & *Larus canus*), the Ducks (*Clangula hyemalis* & *Mergus merganser*) and the Terns (*Sterna paradisaea* & *Sterna hirundo*) have nominal diving depths of less than 10m; i.e. approximately 1 atmosphere of pressure (Jones & Furilla, 1987). Despite this there is no difference in uncinate length between the deep and shallow divers: all diving birds have significantly longer uncinates than the swimming and walking birds.

If the uncinates stiffened the body cavity against increased pressure then one would also expect to find them on every rib. However, as one moves caudally along the rib cage, the thinnest and longest ribs (i.e. those which would need the most stiffening as pressure increased) lack uncinates. At the point of entry into the water, there is likely to be some increase in pressure on the body cavity. This is likely to be minimised by the elongation of the ribs and sternum as a consequence of streamlining the rib cage and body (Welty, 1988). Streamlining and the subsequent elongation of the sternum cause the centre of mass to move caudally. The increased length of uncinates may be a direct result of the lengthening of the ribs and the subsequent need for a longer lever arm to move them during breathing. The uncinate processes may also play some role in maintaining the integrity of the body shape for streamlining during diving. Furthermore, the increased mechanical advantage of longer uncinates may be important during inspiration in diving birds upon resurfacing which must be done against gravity and the pressure of water against the body (Duncker, 1971). Birds' breath-hold during diving therefore an increase in uncinate length may facilitate rapid inspiration upon resurfacing.

2.4.4 CONCLUSIONS

The length of the uncinate processes in extant birds does not vary phylogenetically but rather with the locomotor mode of the birds. The rib cage of birds needs to be flexible for breathing, irrespective of whether the bird is walking, flying, swimming or resting. The only birds in which it is desirable to maintain a fixed rib cage shape is in streamlined diving birds. Any muscle pulling on the uncinate processes will facilitate movement of the associated rib rather than prevent it. While further experiments are required before any stiffening function of the uncinate processes can be completely ruled out, the location of the uncinates on the rib cage and the correlation between uncinate length and sternal morphology suggest that they play a significant role in movement of the ribs and sternum during breathing. A detailed examination of the breathing mechanics of birds and the associated musculature is required to establish how the uncinate processes are involved during respiration.

CHAPTER 3

THE MECHANICS OF BREATHING IN BIRDS:

RESPIRATORY MUSCULATURE AND X-RAY CINERADIOGRAPHY

3.1 INTRODUCTION

The avian respiratory system consists of paired lungs firmly fixed to the dorsal wall of the thoracic cavity. Gas exchange takes place in small air capillaries that branch from the parabronchi; which in turn connect with the secondary bronchus and finally with the anterior part of the trachea. The parabronchi and connecting tubes form the lung. The parabronchi receive their air from the secondary bronchi that originate in the posterior bronchus. Most birds have nine air sacs connected to the lungs. The anterior air-sac group includes the unpaired interclavicular sac, and the paired cervical and anterior thoracic air sacs. The thoracic air sacs are surrounded by bone and are not involved in breathing. The posterior group consists of the paired posterior and abdominal air sacs (Kardong, 1988). Birds ventilate their lungs by filling and emptying the air sacs, which act like bellows to provide the tidal air flow (Scheid & Piiper, 1989).

The paleopulmo is present in all birds and makes up the entire lung of emus (Withers, 1992) and penguins (Duncker, 1971). In most other birds a second neopulmo lung originates as an additional complex of parabronchi leading from the lateral side of the main bronchus and dorsobronchi to connect with the posterior air sacs. The neopulmo lung is most extensively developed in galliform and passeriform birds where it can comprise up to 25% of the total lung volume (Withers, 1992). Air flow in the paleopulmo is unidirectional and in the neopulmo it is bidirectional, but in both cases the gas-exchange model is crosscurrent exchange. This system allows oxygenated blood to leave the lung with a greater PO_2 than that of the expired air. On inhalation air enters the trachea with some passing through the paleopulmo, filling the lung and the anterior air-sac group and the rest going through the neopulmo into the posterior air sacs. Upon exhalation the air from the posterior air sacs flows through the neopulmo again, then into the paleopulmo and is exhaled together with the air from the anterior air sacs. As the air sacs are not usually completely filled and emptied with each breath and the volume of the lungs is not negligible, it takes a nitrogen molecule an average of two breaths to complete the entire circuit (Bretz & Schmidt-Nielsen, 1972; Perry, 2003).

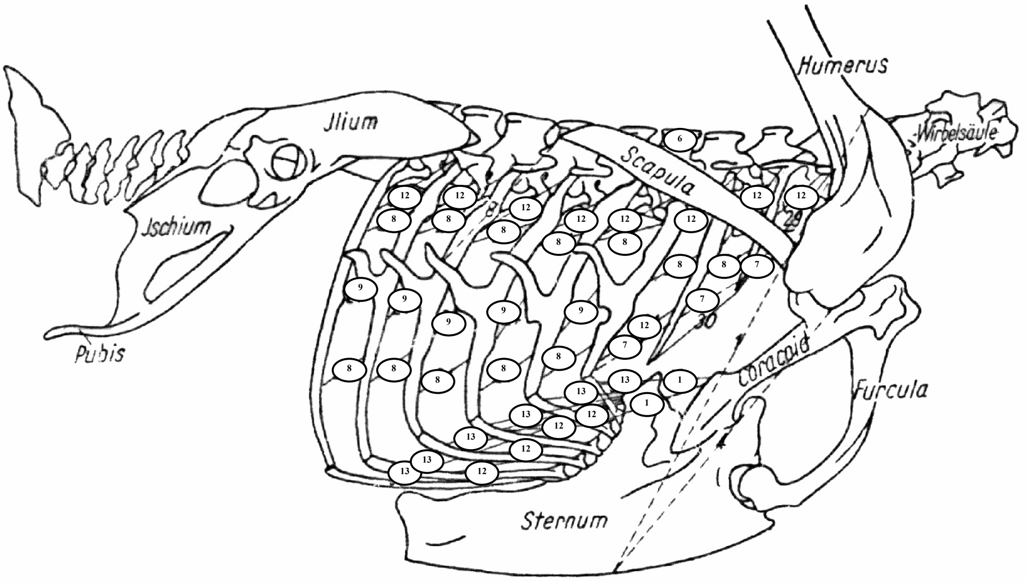
3.1.1 RESPIRATORY MUSCULATURE

The respiratory muscles of birds unlike those of mammals are constantly active as both inspiration and expiration are active processes (Kardong, 1988). There are two distinguishable functional sets of respiratory muscles, inspiratory and expiratory (Baumel et al., 1990). The principle breathing muscles (Figure 15, Table 4) are involved in all respiratory acts, including quiet breathing, and have the most influence on altering the volume of the thoracic cavity. Accessory breathing muscles (by definition) (Figure 15, Table 4) are not active during quiet breathing but are recruited to help out the principle respiratory muscles during laboured breathing (Fedde, 1987). The external intercostal, the appendicocostalis, levatores costarum, interappendiculares, costocoracoideus, costosternalis and scalenus muscles are principle breathing muscles and are responsible for the inspiratory motion of the rib cage (Fedde, 1987). Expiratory movements are caused by the internal intercostal, the rectus abdominus, the internal and external obliques, and transverse abdominal muscles (De Wet, et al., 1967; Duncker, 1971). In physiological preparations the inspiratory muscles become active a few milliseconds before the initiation of inspiratory movements of the sternum and their activity continues until after the beginning of expiration. The expiratory muscles are also active before the expiratory movements of the sternum have begun (Fedde, 1987).

3.1.2 MECHANICS OF BREATHING IN BIRDS

Birds lack the muscular diaphragm pump of mammals, breathing instead by rocking their sternum in a scissor like motion with the fulcrum at the sternal-coracoid joint (Figure 16). The bellows-like filling and emptying of the air sacs is facilitated by coupled costal movements (Schmidt-Nielsen, 1997). Restricting the movement of the sternum and rib cage can be fatal when holding or restraining birds (Ludders, 2001). The sternum is the origin of the two largest flight muscles, the pectoralis and sternocoracoideus, both of which insert on the humerus (Boggs, 1997). The importance of moving this large muscle mass is reinforced by the coupling of locomotor and ventilatory cycles. The cost of respiration during locomotion is reduced by coupling footfall with breathing in running guinea fowl (*Numida meleagris*) (Nassar et al., 2001) and by coordinating wing beat and breathing in flying birds (Boggs, 1997; Boggs et al., 1997a; Boggs et al., 1997b; Funk et al., 1993). Coupling ensures that wing beat or footfall are synchronous with the downward displacement of the sternum which increases thorax volume during inspiration, and expiration occurs with the power stroke of flying and upwards rebounding of the sternum which reduces thorax volume.

Figure 15: Muscles of the avian thorax (modified from Zimmer, 1935). 1) Sternocoracoid, 2) External oblique, 3) Quadratus lumborum, 4) Internal oblique, 5) Transverse analis, 6) Rhombiodeus profundus, 7) Internal intercostal, 8) External intercostal, 9) Appendicocostalis, 10) Rectus abdominal, 11) Transverse abdominal, 12) Levatores costarum, 13) Internal intercostal, 14) Ilio-costales. The external intercostal (No 8), appendicocostalis (No 9) and external oblique (No 2) muscles were investigated using EMG techniques in this dissertation.


Humerus
Jlium
Wirbelsäule
Scapula
Jschium
Pubis
Coracoid
Furcula
Sternum
29
30
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1

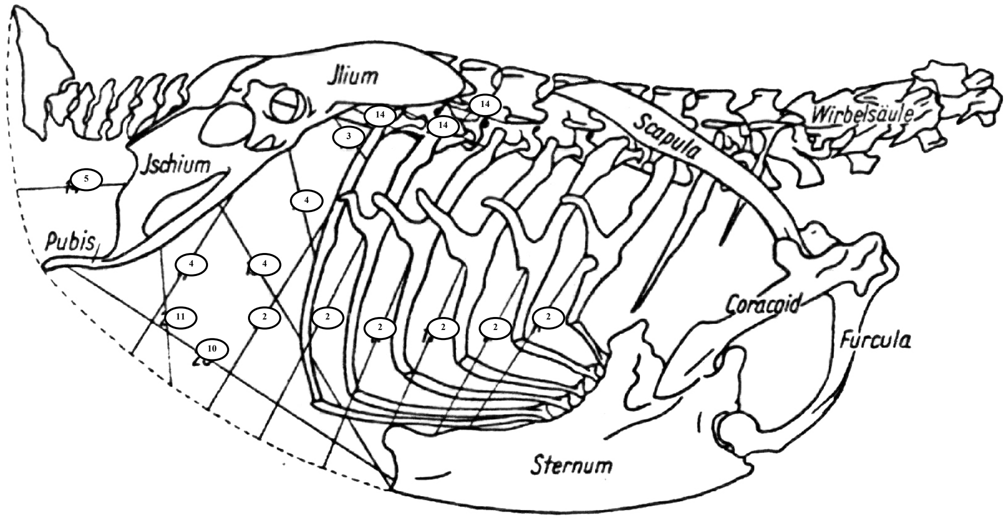

Jlium
Wirbelsäule
Scapula
Jschium
Pubis
Coracoid
Furcula
Sternum
14
3
5
4
2
11
10

Table 4: The origin, insertion and action of the muscles of the avian respiratory system: A) Principle respiratory muscles and B) Accessory respiratory muscles. The principle respiratory muscles are involved in quiet breathing, whereas the accessory breathing muscles can be recruited into assisting breathing when the work of breathing is increased. Modified from Fedde (1987).

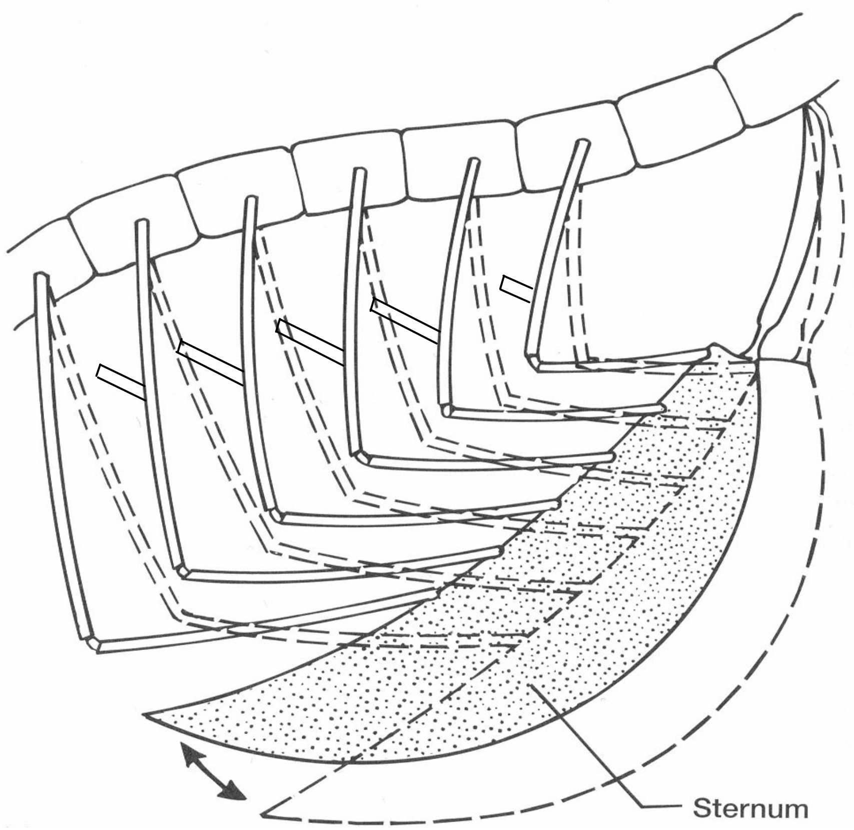
A

Principle Respiratory Muscles	Origin	Insertion	Action
External Intercostal	Posterior border of rib	Anterior distal border of ribs	Contracts thoracic cavity
Appendicocostalis	Posterior border of rib	Posterior border of uncinate process	Draws ribs forward
Internal Intercostal	Posterior distal border of ribs	Anterior proximal border of ribs	Expands thoracic cavity
Internal Oblique	Ventral border of Pubis	Caudal border of last vertebral rib	Supports body wall
External Oblique	Posterior ribs and fascia posterior to ribs	Fascia of ventral abdominal midline	Supports body wall
Transverse Abdominal	Pubis and ilium	Fascia of ventral abdominal midline	Supports body wall
Rectus Abdominus	Last sternal rib and sternum	Pubis	Supports abdominal wall
Costosternalis	Caudal surface of craniolateralis process	Distal tip of second rib	Expands thoracic cavity
Scalenes	Transverse process of 11th and 12th vertebrae	Medial surface of scapula	Draw scapula ventromedially
Levatores Costarum	Transverse process of thoracic vertebrae	Anterior surface and uncinate process of rib	Elevates ribs
Trapezius	Unclear	Unclear	Retracts shoulder

B

Accessory Respiratory Muscles	Origin	Insertion	Action
Serratus Posterior	Between 3rd and 4th ribs below uncinate process	Distal third of medial surface of scapula	Draws scapula ventrally
Serratus Anterior	Between 2nd and 3rd ribs below uncinate process	Ventromedial surface of scapula	Draws scapula ventrally
Rhomboideus	Spines of thoracic vertebrae	Entire vertebral border of scapula	Draws scapula medially
Sternocoracoideus	Sternum and ventral costal processes	Medial border of procoracoid	Draws ribs forward
Latisimus Dorsi	Spines of last and first thoracic vertebrae	Posterior humerus	Draws humerus medially

Figure 16: Mechanics of breathing in a standing bird. The solid lines represent the position of the sternum at the end of expiration; the sternum moves dorsally and the ribs move caudally. The dotted lines represent the position of the sternum at the end of inspiration; the sternum moves ventrally and the ribs move cranially.


Sternum

The uncinate processes on the vertebral ribs are attached to the following caudal rib by the appendicocostalis muscle (Table 4). Based on a 2-dimensional model Zimmer (1935) concluded that contractions of the muscles attached to the uncinate processes move the ribs forward and aids inspiration. Uncinate length correlates with the locomotor mode in extant birds and their location on the vertebral ribs and suggests they may be functionally linked to movements of the ribs and sternum (Chapter 2). Restricting the ventral excursions of the sternum may alter the breathing mechanics of birds and place different demands on the inspiratory and expiratory muscles (Baumel et al., 1990).

3.1.3 X-RAY CINEMATOGRAPHY

X-ray cinematography is a non-invasive technique which allows visualisation of the movements of the internal skeleton. The surgical implantation of carbide steel markers or wire can be used to quantify bone kinematics (Jenkins et al., 1988). X-ray cinematography previously has been used in birds to examine the function of the furcula (Jenkins et al., 1988) and movements of the pelvis during flight (Gatesy and Dial, 1993).

Here I will describe the breathing mechanics of the tinamu (*Eudromia elegans*) and guinea fowl (*Numida meleagris*) using x-ray cinematography, during free-standing breathing and when the sternal movement is restricted by resting on the sternum. The purpose of this current study was not to quantify precise rib movements, but rather it was to describe the breathing mechanics and associated movements of the ribs and the rib cage when sternal rocking is restricted. Establishing the mechanics of how birds breathe without moving the sternum will be used to generate hypotheses on the implications of different postures on the action of respiratory musculature and the function of the uncinate processes.

3.2 MATERIALS AND METHODS

3.2.1 X-RAY CINEMATOGRAPHY

X-ray cinematography experiments were conducted at the Museum of Comparative Zoology, Harvard University, U.S.A using a Siemens cineradiographic apparatus 70mV, 200-220mA (grid controlled tube with 0.06mm focal spot, 27.94cm Sirecon image intensification system) coupled with an Eclair GV 16 high speed cine camera. X-ray footage was taken of a single tinamu (*E. elegans*) and a guinea fowl (*N. meleagris*) in both the dorsoventral and lateral view during quiet free-standing breathing and whilst resting on their sternum.

3.3 RESULTS

Video files from the x-ray cinematography analysis are in the attached CD Appendix. Lateral and dorsoventral free standing breathing footage for *N. meleagris* in the files named: Nm_Standing.avi and Nm_SternumResting.avi, while lateral and dorsoventral footage of *E. elegans* free standing and resting on the sternum can be found under filenames: Ee_Standing.avi and Ee_SternumResting.avi.

3.3.1 MECHANICS OF BREATHING WHEN STANDING

Free standing *E. elegans* and *N. meleagris* breathe by sternal rocking (Appendix 2). During inspiration the thoracic ribs move cranially, causing the sternal ribs to move in a ventral and lateral plane. The sternum moves ventrally and the thoracic cavity expands. The subsequent drop in pressure, allows expansion of the posterior and anterior air sacs. During expiration the vertebral ribs move in a dorsal and caudal plane, retracting the sternal ribs. The sternum rocks dorsally which reduces the volume of the thoracic cavity and hence the volume of the anterior and posterior air sacs.

3.3.2 MECHANICS OF BREATHING WHEN RESTING ON THE STERNUM

When sternal movements are restricted, *E. elegans* and *N. meleagris* breathe by lateral flaring of the rib cage (Appendix 2). To increase the volume of the thoracic cavity, the vertebral ribs move cranially and laterally. This cranial movement of the vertebral ribs, and subsequent flexing about the kinetic joint, results in a lateral movement of the dorsal part of the sternal ribs and expansion of the rib cage. After flaring the vertebral ribs move caudally and medially, retracting the sternal ribs and returning them to their original position. With each lateral movement of the rib cage there is a synchronous upwards movement of the pelvis.

3.4 DISCUSSION

The extent of air-sac development is variable in extant birds (Duncker, 1971). However all birds must ventilate the air sacs to breathe regardless of posture or locomotor mode. Free-standing birds breathe by moving the sternum up and down, which requires movement of the large flight muscles and the viscera with each breath. There is a marked change in the breathing mechanics when sternal movements are restricted, whereby expansion of the thorax is achieved by lateral flaring of the rib cage.

Pelvic aspiration has been suggested as a means by which birds resting on their sternum may ventilate their air sacs (Carrier and Farmer, 2000b). The epaxial Longissimus dorsi muscle in the pigeon (*Columba livia*) is consistently active during inspiration and functions to elevate the pelvis (Baumel et al., 1990). Subsequent depression of the pelvis was attributed to the infrapubic abdominal muscles, caudofemoralis, pubocaudalis externus, pubo caudalis internus and the transverses cloacae, which are active during expiration (Baumel et al., 1990; Kadono et al., 1963). Furthermore, cineradiographic footage of flying black-billed magpies (*Pica pica*) showed some rotation of the synsacrum during downstroke which could contribute to abdominal expansion, (Boggs et al., 1997a). The correlation between the activity of the longissimus dorsi, levator caudae and depressor caudae muscles (Gatesy and Dial, 1993) and the ventilatory cycle (Boggs et al., 1997a) suggests pelvic aspiration may also play some role in ventilation during flight.

The results of this study suggest that movements of the ribs are also important in ventilating the air sacs in the absence of sternal rocking. Lateral flaring of the rib cage in conjunction with pelvic aspiration may effectively replace the dorsoventral movements of the sternum to facilitate the filling and emptying of the anterior and posterior air sacs. As the ribs flare outwards and the pelvis is elevated the resulting expansion of the thoracic and abdominal cavities would lower pressure and cause inspiratory air to flow into the anterior and posterior air sacs. The retraction of the ribs inwards and the downward movement of the pelvis would reduce the volume of the thoracic and abdominal cavities and facilitate expiration. The activity of the external and internal intercostal muscles may be important in lateral rib movements. The uncinate processes are located on the vertebral ribs and may act as a lever arm to move the ribs and sternum (Chapter 2). The mechanical advantage provided by the uncinate processes may be especially important when sternal movements are restricted and increased lateral movements of the ribs are required. The activity of the large abdominal muscles involved in moving the sternum such as the external oblique may be compromised when the bird is resting on the sternum.

While the physiological significance of breathing during resting on the sternum remains to be determined, it may be energetically cheaper to breathe by flaring the rib cage and pelvic aspiration than by sternal rocking which involves movement of the entire flight musculature and viscera up and down with each breath.

3.4.1 HYPOTHESES GENERATED

The following hypotheses have been generated and will be examined in Chapter 4.

1. The uncinate processes and associated appendicocostalis musculature may facilitate inspiratory rib movements during normal breathing and when movements of the sternum are restricted.
2. As the appendicocostalis musculature is located in a superficial position and rests on the ribs rather than occupying a medial position, they may also facilitate the lateral flaring of the ribs and rib cage
3. Inspiratory muscle activity of the rib musculature may increase when sternal movements are restricted and the bird is breathing by lateral rib flaring.
4. Resting on the sternum may decrease the activity of the abdominal expiratory muscles involved in sternal movements.

CHAPTER 4

ELECTROMYOGRAPHY OF THREE RESPIRATORY MUSCLE GROUPS IN THE GIANT CANADA GOOSE (*BRANTA CANADENSIS MAXIMUS*)

4.1 INTRODUCTION

The anatomical arrangement of the respiratory muscles in birds has been traditionally used to characterise their function (Sibson, 1846; Zimmer, 1935). The attribution of function based on fibre architecture is however complex and often flawed (Gans, 1965). The use of integrated action potential recordings, electromyography (EMG), allows direct correlations to be made between muscle activity and function. There are few EMG studies on the activity of the respiratory muscles in birds. Furthermore, although sternal movements are known to be an integral part of the breathing mechanics in birds (Brainerd, 1999), EMG experiments have always been performed on anaesthetised birds in a supine or restrained body position, using needle electrodes (Zimmer, 1935; Kadono, 1963; Fedde, 1964). Body positioning is known to alter respiratory movements due to the effect of gravity on the large muscle mass attached to the sternum (Zimmer, 1935) and the level of anaesthesia has a marked effect on muscle activity by depressing neuronal discharges (Fedde et al., 1964). When placed in the supine position, tidal volume is reduced by up to half and the vertical displacement of the sternum is almost doubled with the higher respiratory frequency and larger end-expiratory carbon dioxide concentrations (Fedde, 1987). Against the background of these methodological shortcomings, the external intercostal muscles of the 2nd, 3rd and 4th intercostal spaces are reported to be inspiratory and those in the 5th and 6th intercostal space are expiratory. The serratus dorsalis, scalenus, transverses thoracis, levatores costarum and costi-sternalis muscles are also reported to be inspiratory. All abdominal muscles, the external oblique and internus, rectus abdominus and the transverses abdominus, have an expiratory function (Kadono et al., 1963; Fedde et al., 1964; Zimmer, 1935).

The uncinate processes on the vertebral ribs and associated muscle (Mm appendicocostales) may act as a lever arm for rib movement and, based on a 2-dimensional model reconstruction, are thought to be contribute to inspiration (Zimmer, 1935). Alternatively uncinate processes are hypothesised to be an adaptation for flight (Welty, 1962), a site for the attachment of respiratory and shoulder muscles (Hildebrand, 1982) or to mechanically strengthen the rib cage (Kardong, 1988). However these hypotheses remain untested. Perhaps, because the appendicocostalis muscle is often included within the external intercostal musculature (Baumel, 1962; George & Berger, 1966), EMG has not been individually performed on this muscle (Fedde et al., 1964; Kadono et al., 1963).

X-ray cinematography of the tinamu (*Eudromia elegans*) and the guinea fowl (*Nunmida meleagris*) confirms the importance of sternal rocking to the mechanics of breathing in these birds. When movement of the sternum is restricted, the birds alter the way they breathe from sternal pumping to lateral rib flaring (Chapter 3). Restricting sternal movements may compromise the activity of the abdominal muscles involved with moving the sternum. The switch to breathing by lateral rib flaring may have implications for the activity of the intercostal and uncinate musculature involved in rib movements. Functional anatomy alone is inadequate in completely elucidating the function of the respiratory muscles in birds. Furthermore, previous EMG experiments have been conducted under inappropriate conditions and have failed to address the possible importance of integrating ventilation with locomotion.

4.1.1 LOCOMOTION AND VENTILATION

The integration of locomotion and breathing is important in understanding the evolution of tetrapod body design. The ancestors of the tetrapods ventilated their lungs by buccal pumping using derived brachial and hypobranchial muscles, and the hypaxial musculature evolved as locomotor muscles in fish long before it became associated with lung ventilation (Carrier, 1996). The hypaxial muscles have been shown to retain locomotor function in salamanders (Bennett et al., 2001; Carrier, 1993), lizards (Ritter, 1996), dogs (Carrier, 1996; Fife et al., 2004) and in birds (Boggs, 1997; Nassar et al., 2001). The inability of some lizards to breathe whilst running (Carrier, 1987) and the coupling of locomotor and respiratory cycles in mammals and birds (Bramble and Carrier, 1983; Nassar et al., 2001) reinforce the conflicting demands placed on the respiratory muscles by locomotion and breathing. Running guinea fowl couple at a frequency of two breaths to every stride (Nassar et al., 2001), and in flying birds a wide variety of coupling patterns are seen ranging from one to five breaths per stride (Boggs, 1997). Coupling of ventilatory and locomotor rhythms appears to be functionally linked to sustained locomotion and may reduce the locomotor and ventilatory conflict for the muscle involved (Deban and Carrier, 2002).

Here, I will investigate the function of three reported respiratory muscle groups: the external intercostal, appendicocostalis and external oblique, in un-anaesthetised and unrestrained Giant Canada Geese (*B. canadensis maximus*). Muscle activity was examined during normal quiet breathing in standing animals, and when sternal movement was restricted during spontaneous resting on the sternum. Muscle activity was also examined during moderate speed treadmill running. All experiments were conducted using patch or sew-through electrodes.

4.2 MATERIALS AND METHODS

Avian respiratory musculature is thin and fragile. To enable accurate recordings and direct comparisons of muscle activity in different postures, it is crucial that the electrodes do not move. The use of patch or sew through electrodes (Loeb & Gans, 1986) avoids problems caused by cross talk (picking up signals from other muscle layers) and electrode movement when recording from thin muscles (Carrier, 1993). Electromyograms were recorded in five Giant Canada Geese (*Branta canadensis maximus*) during sitting, standing and treadmill running at moderate speed ($0.87 ms^{-1}$). The body mass of the five birds was 3.56±0.05kg (mean±SE). Birds were obtained from a licensed hobby farm breeder and housed at the animal holding facilities at the University of Utah. Birds were fasted for 12 hours prior to all surgery, water was available *ad libitum*. All surgery was performed using aseptic techniques. Heart rate and body temperature were monitored throughout surgery. Feathers were plucked from the surgical sites the day before electrode implantation surgery to minimise the total length of time under anaesthesia, the plucked region was treated with Betadine® antiseptic.

Electrodes were surgically implanted in the external intercostal, appendicocostalis and external oblique muscles and the interclavicular air sac was cannulated. Following a one-day recovery period after surgery, data were collected for 2-3 days. Post operative analgesia (Flumeglumine, 0.5mg/kg) and antibiotics (Baytril, 2.5mg/kg) were given once a day for four days. Following completion of experiments, reversal surgeries were performed to remove electrodes and air sac catheters. After a recovery period of 7-10 days the geese were adopted as pets. All procedures conform to the guidelines of the University of Utah Institutional Animal Care and Use Committee.

4.2.1 ELECTRODE AND AIR SAC CATHETER IMPLANTATION

Birds were anaesthetised using Isoflurane (USP 99.9% Isoflurane/mL) inhalation anaesthetic (2-5%), intubated with paediatric endotracheal tubes and maintained on a ventilator (flow rate 3L/min, tidal volume 100mL) for the duration of all surgeries. It is crucial to breathe for the bird during surgery, using a 'push-pull' ventilator, to avoid any complications caused by the fatigue of the respiratory muscles (Ludders, 2001).

Two incisions were made through the skin above the sites for electrodes placement. Sew-through (appendicocostalis, external oblique) or patch (external intercostal) electrodes were attached to the respective muscles. Electrodes were made from 0.3mm diameter multi-stranded, Teflon-coated stainless steel wire (Cooner Wire Inc, Part No: AS 631). Following deflection of the serratus muscle, three sites in the external intercostal and appendicocostalis musculature, (anterior: the space between the 3rd & 4th ribs, middle: the space between the 5th & 6th ribs and posterior: the space between the 6th & 7th ribs) and three sites directly below these intercostal spaces in the external oblique muscle were examined in all birds. For patch electrodes wire was sewn through 5mm square patches of Silastic sheeting (Dow Corning). Exposed wire sections, about 1mm long and 1mm apart, were parallel to each other, and arranged at 90° to muscle fibre orientation. For sew-through electrodes, an overhand knot was tied in the wire and 1mm of insulation was exposed, separated by 1-2mm. Two 5mm square buttons of Silastic sheeting were used to hold the electrode in place, electrodes were sewn directly into the muscle parallel to muscle fibres.

Electrode wires were tunnelled subcutaneously to the midline of the back and fixed to a Velcro platform, attached to a Velcro collar secured around the front of the bird. The collar was fashioned so as not to restrict sternal movements. Electromyographic signals were passed through separate connecting shielded wires (Cooner Wire Inc), filtered above 1000 and below 100Hz, and amplified 1000 times with Grass P511 AC amplifiers. Signals were then analysed using LabVIEW software sampled at 4000Hz on an Apple Macintosh Computer. Locomotion was monitored during treadmill running using a high-speed camera (Peak Performance Technologies Inc). The locomotor cycle was monitored using an accelerometer (Microtron, 7290A-10) attached to the Velcro platform on the bird's back. Video images were synchronised with locomotor events using an LED and synchronisation circuit.

Inspiration and expiration were monitored using an air-sac catheter. The interclavicular air sac was cannulated using PE 200 Polyethylene tubing (Intramedic Clay Adams Brand, internal diameter 1.4mm, external diameter 1.9mm) with side holes, held in place by cyanocrylic glue and sutures. Silastic tubing was tunnelled subcutaneously, exiting and sutured in place on the back of the bird, next to the electrode platform.

Miniaturised differential pressure transducers (Endevco, 8507C-2) were used to record pressure changes in the interclavicular air sac.

4.2.2 ELECTROMYOGRAPHY ANALYSIS

Ensemble averages (Banzett et al., 1992a, b) were used to analyse EMG bursting activity during sitting, standing and locomotion. To analyse the effect of sitting or standing on EMG activity, samples were analysed relative to ventilation (20 breaths). For the locomotion analysis samples were analysed relative to ventilation (20 breaths) or stride (20 strides). A breath is defined as the time from the beginning of expiratory airflow to the end of inspiratory airflow (Figure 17). A stride is defined as the time from peak contralateral limb support to the next peak contralateral limb support (Figure 18). Both coupled (ventilation and breathing locked in phase, Figure 18) and uncoupled (ventilation and breathing out of phase, Figure 19) stride averages were analysed during locomotion. The distinction between coupled and uncoupled locomotion was based on visual examination of EMG activity traces. EMG activity was also examined in threat (hissing) responses when standing (Figure 20) and during locomotion (Figure 21).

EMG traces were analysed using a custom built LabVIEW program (Deban and Carrier, 2002). Data from uncoupled averages were sampled equally from uncoupled breathing trials relative to breath or stride to ensure unbiased data collection from the sampling window (Deban and Carrier, 2002). Drifting of EMG activity does not occur in coupled traces. Data were normalised to a percentage maximum to enable average ensemble averages to be calculated. By generating ensemble EMG traces relative to breath and stride we are able to determine if the pattern of muscle activity corresponds with inspiration, expiration or footfall.

4.2.3 INTERPRETATION OF ENSEMBLE AVERAGE TRACES

If a muscle is ventilatory one would expect EMG activity to correspond to either inspiratory or expiratory airflow and not to stride average, assuming the animal is not coupled. However if the muscle is locomotor its activity will correspond with either contralateral or ipsilateral footfall in uncoupled strides. If the muscle has both a ventilatory and locomotor function bursting will occur in both averages. Using a combination of quiet breathing when either sitting and/or standing and breathing activity during or following locomotion, muscles can be assigned to the following groups: Group 1) locomotor function: EMG bursting in uncoupled stride averages but no EMG bursting when standing or sitting or in uncoupled breath average, indicating the muscle only has a locomotor function. Group 2) primarily locomotor function: EMG bursting is seen during either sitting or standing and in the coupled and uncoupled stride averages, while no bursting is seen in the uncoupled breath averages, this would indicate that although the muscle is active during breathing it has a locomotor function that overrides its ventilatory function. Group 3) dual ventilatory and locomotor function: EMG bursting during either sitting or standing and in both coupled and uncoupled averages. This would indicate that the muscle is only active during locomotion when it can contribute to both ventilation and locomotion. Group 4) ventilatory function: EMG bursting in either sitting or standing average but not in the coupled or uncoupled stride averages, this would indicate the muscle is only active when it can contribute to breathing and has no locomotor effect.

A quantitative comparison of coupled versus uncoupled breathing can tell us whether a muscle is primarily ventilatory or locomotor (Deban and Carrier, 2002; Farley and Koshland, 2000). Calculating the coefficient of determination (r^2) tells us how much variation there is in the uncoupled averages. A high value for r^2 indicates the ensemble averages are similar and uncoupling the breathing has no effect on the muscle activity. A low r^2 indicates that the ensemble averages are affected by coupling or there is no bursting activity when analysed by stride.

4.2.4 STATISTICAL ANALYSIS

Due to differences in electrode placement in different muscles and the location, depth and orientation of the electrode in a given muscle, statistical comparisons can only be made for electrodes for one day and not between electrodes or even on the same electrode on different days (Loeb & Gans, 1986). To compare the integrated area for sitting, standing, coupled and uncoupled locomotion two-sample t-tests were performed on $\log_{10}$ transformed data. All data are presented as mean±SE.

4.3 RESULTS

B. canadensis maximus demonstrate different patterns of muscle activity when sitting, standing and during coupled and uncoupled locomotion. There was no difference in the activity pattern of the muscles in or corresponding to the anterior, middle or posterior intercostal spaces during sitting and standing or during coupled and uncoupled locomotion. Therefore, representative results from one goose (Goose A) will be presented from the middle intercostal space during sitting and standing and during coupled and uncoupled locomotion. Complete results and statistical comparisons of the ensemble average EMG activity in the anterior, middle and posterior regions for the external intercostal, appendicocostalis and external oblique muscles during sitting, standing, and for coupled and uncoupled locomotion relative to breath and stride can be found in appendixes 2 and 3.

4.3.1 EXTERNAL INTERCOSTAL

The bursting activity of the external intercostal muscle is consistent with locomotor function (Figure 17, 18, 19). In the ensemble averages from all geese the external intercostal muscle demonstrated no ventilatory bursting activity during sitting (Figure 22a), standing (Figure 22b), or during the large inspirations and expirations associated with treat (hissing) displays (Figure 20, 21). In all geese during coupled and uncoupled locomotion (relative to stride) there is significantly larger phasic bursting activity which correlated with contralateral limb support (Figure 23a, c). No phasic bursting is seen during uncoupled locomotion when analysed relative to breath (Figure 23b).

4.3.2 APPENDICOCOSTALIS

The bursting activity of the appendicocostalis is consistent with an inspiratory function (Figure 17, 18, 19). Significantly greater phasic bursting activity is seen when the geese are resting on the sternum (Figure 24a) as opposed to standing (Figure 24b). Before a hissing event (when standing) there is a corresponding increase in the bursting of the appendicocostalis muscle consistent with a larger inspiration (Figure 20). The appendicocostalis muscle also has some locomotor function (Figure 18, 19). During respiration when locomotion is coupled there is phasic bursting activity which correlates with the onset of inspiration (Figure 25a). The biphasic bursting activity during uncoupled locomotion (relative to breath) is consistently larger when associated with contralateral limb support (Figure 25b). The EMG activity is cleaner during uncoupled locomotion analysed relative to breath than relative to stride (Figure 25c).

Figure 17: Representative electromyographic (EMG) traces of the external intercostal (green), appendicocostalis (red) and external oblique (blue) muscles during A) sitting and B) standing. The external intercostal demonstrates no bursting activity when either sitting or standing. The appendicocostalis has significantly increased inspiratory bursting when sitting than standing. The external oblique demonstrates expiratory bursting when standing. The rectified EMG trace, from Goose A, is sampled relative to breath extending from onset of expiratory airflow to end of inspiratory airflow.

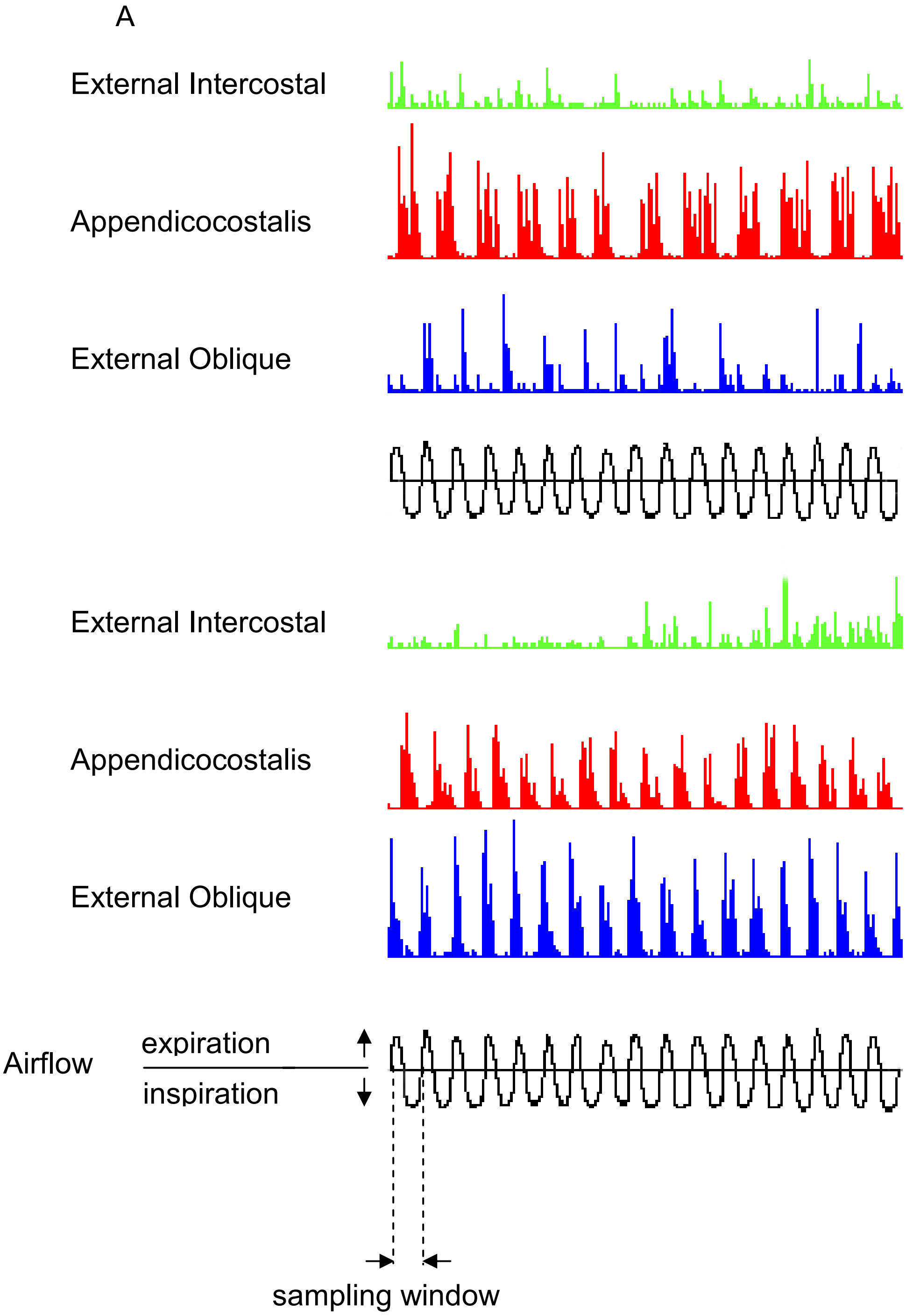

A
External Intercostal
Appendicocostalis
External Oblique
External Intercostal
Appendicocostalis
External Oblique
Airflow
expiration
inspiration
sampling window

Figure 18: Representative electromyographic (EMG) traces of the external intercostal (green), appendicocostalis (red) and external oblique (blue) muscles of Goose D during coupled walking. The rectified EMG trace, from Goose A, is sampled both relative to breath (black trace) - extending from onset of expiratory airflow to end of inspiratory airflow and relative to stride (yellow trace) – footfall is indicated by pink boxes which represent contralateral limb support and black boxes which represent ipsilateral limb support. During coupled breathing the geese breathe at one breath per step and coordinate inspiration with footfall. The external intercostal is a primarily a locomotor muscle and its activity is contralateral to footfall. The appendicocostalis has a dual locomotor and inspiratory function and the external oblique are expiratory.

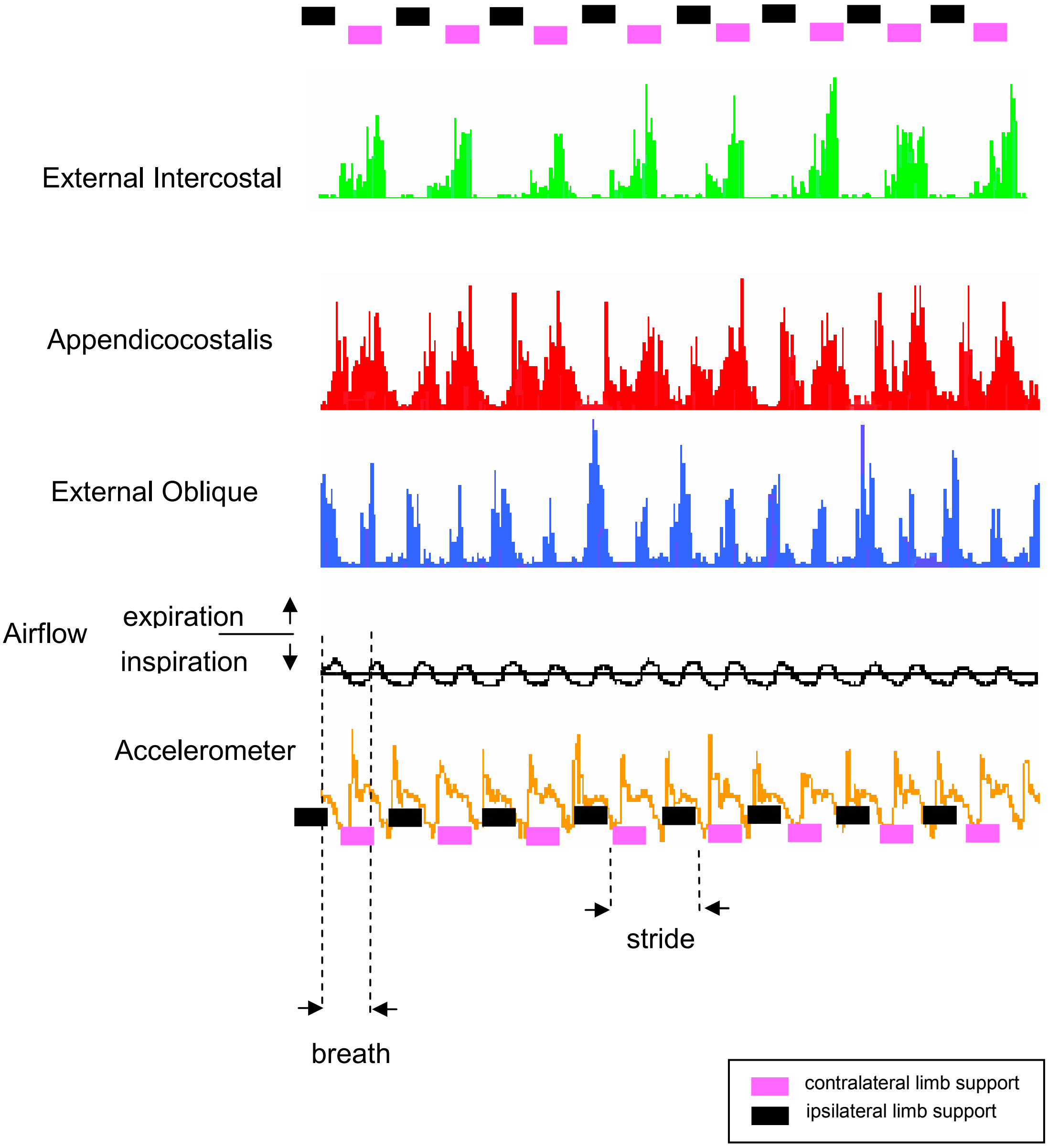

External Intercostal
Appendicocostalis
External Oblique
Airflow
expiration
inspiration
Accelerometer
stride
breath
contralateral limb support
ipsilateral limb support

Figure 19: Representative electromyographic (EMG) traces of the external intercostal (green), appendicocostalis (red) and external oblique (blue) muscles of Goose D during non coupled walking. The rectified EMG trace, from Goose A, is sampled both relative to breath (black trace) - extending from onset of expiratory airflow to end of inspiratory airflow and relative to stride (yellow trace) – footfall is indicated by pink boxes which represent contralateral limb support and black boxes which represent ipsilateral limb support. External intercostal activity is contralateral to footfall indicating the external intercostal is a locomotor muscle. The appendicocostalis has a dual locomotor and ventilatory function and the external oblique is expiratory.

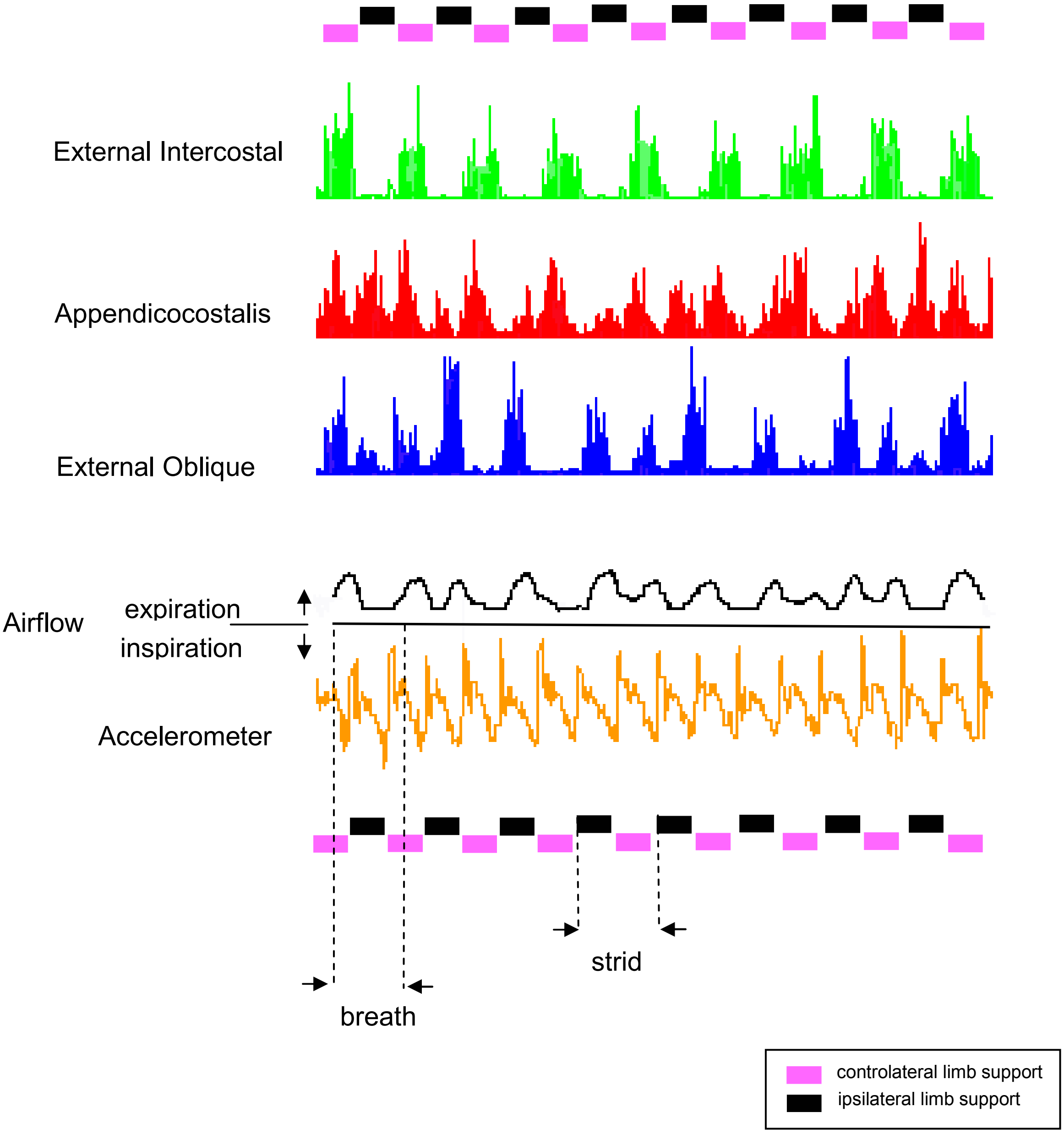

External Intercostal
Appendicocostalis
External Oblique
Airflow
expiration
inspiration
Accelerometer
strid
breath
controlateral limb support
ipsilateral limb support

Figure 20: Representative electromyographic (EMG) traces of the external intercostal (green), appendicocostalis (red) and external oblique (blue) muscles during a threat (hissing) event when standing. The rectified EMG trace, from Goose A, is sampled relative to breath extending from onset of expiratory airflow to end of inspiratory airflow. The external intercostal demonstrates no respiratory bursting during hissing. The appendicocostalis demonstrates a large increase in bursting activity before the hissing event consistent with a larger inspiration. The external oblique demonstrates larger bursting during the hissing event consistent with a large expiration.

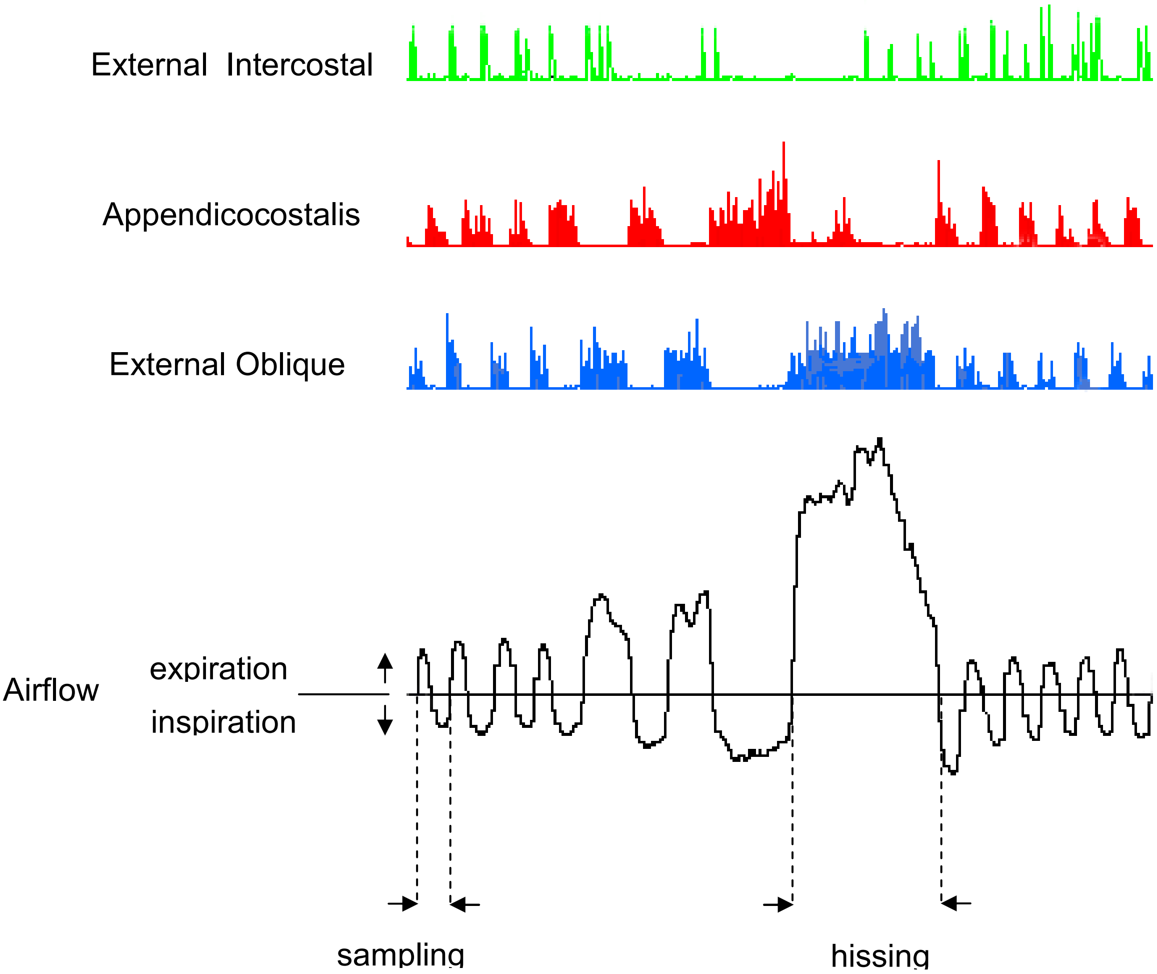

External Intercostal
Appendicocostalis
External Oblique
Airflow
expiration
inspiration
sampling
hissing

Figure 21: Representative electromyographic (EMG) traces of the external intercostal (green), appendicocostalis (red) and external oblique (blue) muscles of Goose A during a threat (hissing) event whilst the animal was walking. The rectified EMG trace, from Goose A, is sampled both relative to breath (black trace) - extending from onset of expiratory airflow to end of inspiratory airflow and relative to stride (yellow trace). External intercostal activity is unaffected by the large increase in both inspiration and expiration associated with hissing. The external oblique demonstrates a large increase in bursting activity consistent with a large expiration.

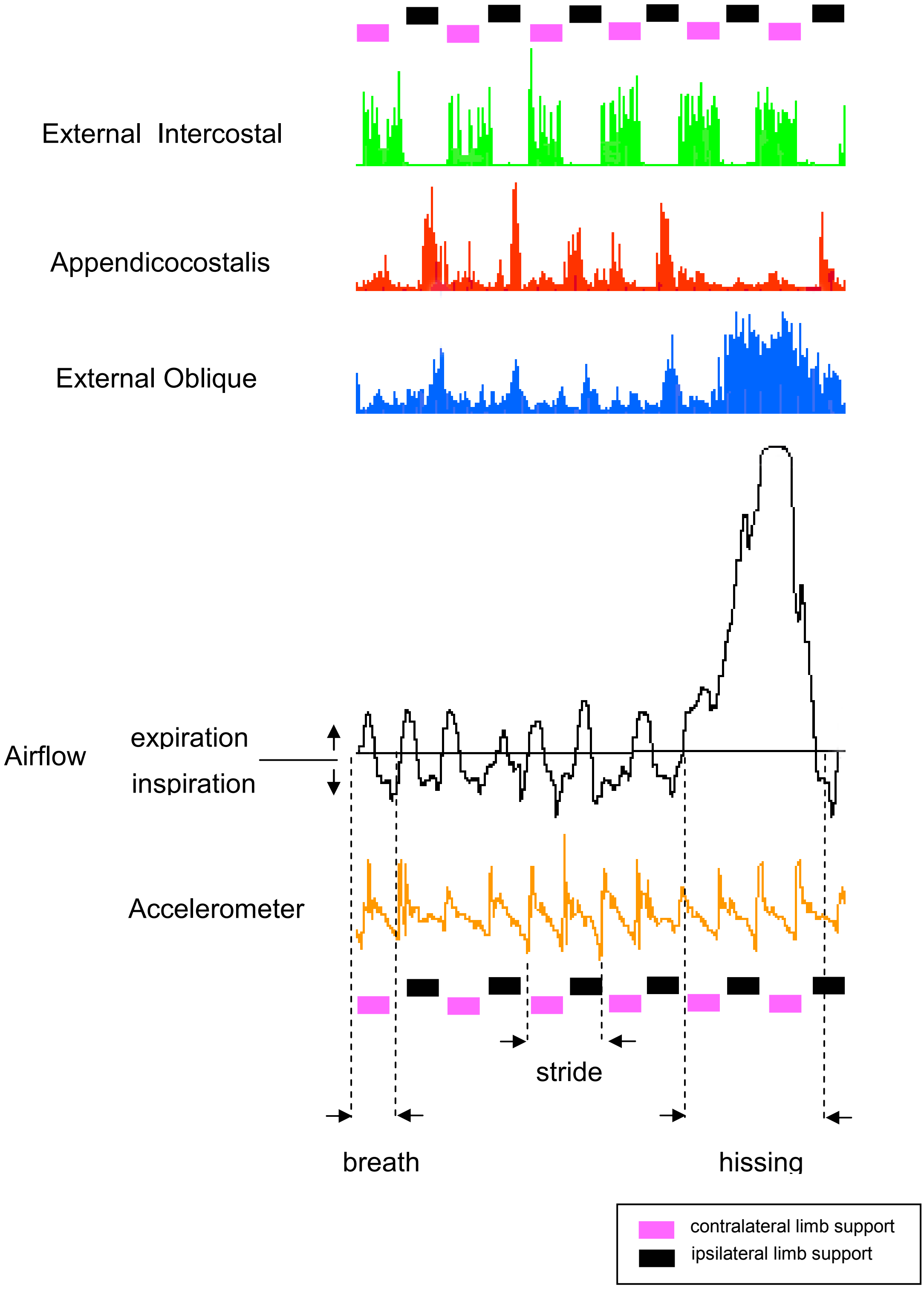

External Intercostal
Appendicocostalis
External Oblique
Airflow
expiration
inspiration
Accelerometer
stride
breath
hissing
contralateral limb support
ipsilateral limb support

Figure 22: Representative ensemble average electromyographic activity of the middle (space between the 5th and 6th ribs) external intercostal muscle during sitting (A) and standing (B). Data presented are from Goose A and are averaged over 20 breaths and shown here for one breath cycle. The external intercostal demonstrates no phasic bursting when the goose is either sitting or standing.

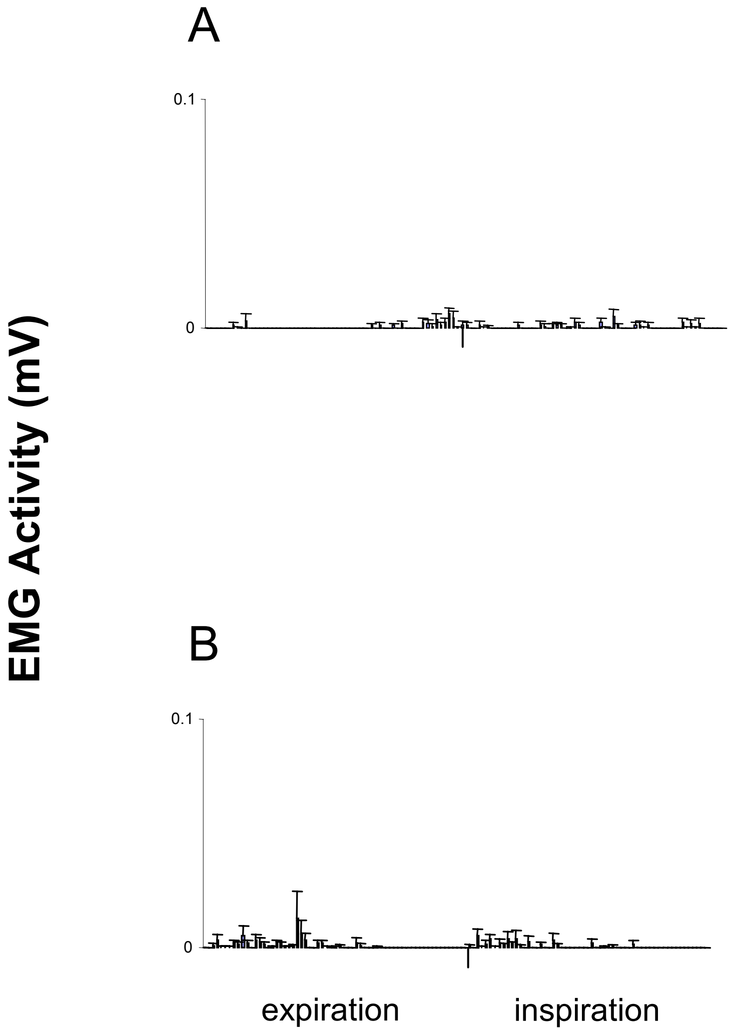

A
0.1
0
EMG Activity (mV)
B
0.1
0
expiration
inspiration

Figure 23: Representative ensemble average electromyographic activity of the middle (space between the 5th and 6th ribs) external intercostal muscle during A) coupled walking, B) not coupled walking by breath and C) not coupled walking by stride. Data presented are from Goose A and are averaged over 20 breaths, shown here for one breath cycle or one stride length as indicated on graph. The external intercostal is a locomotor muscle and its activity is contralateral to limb support.

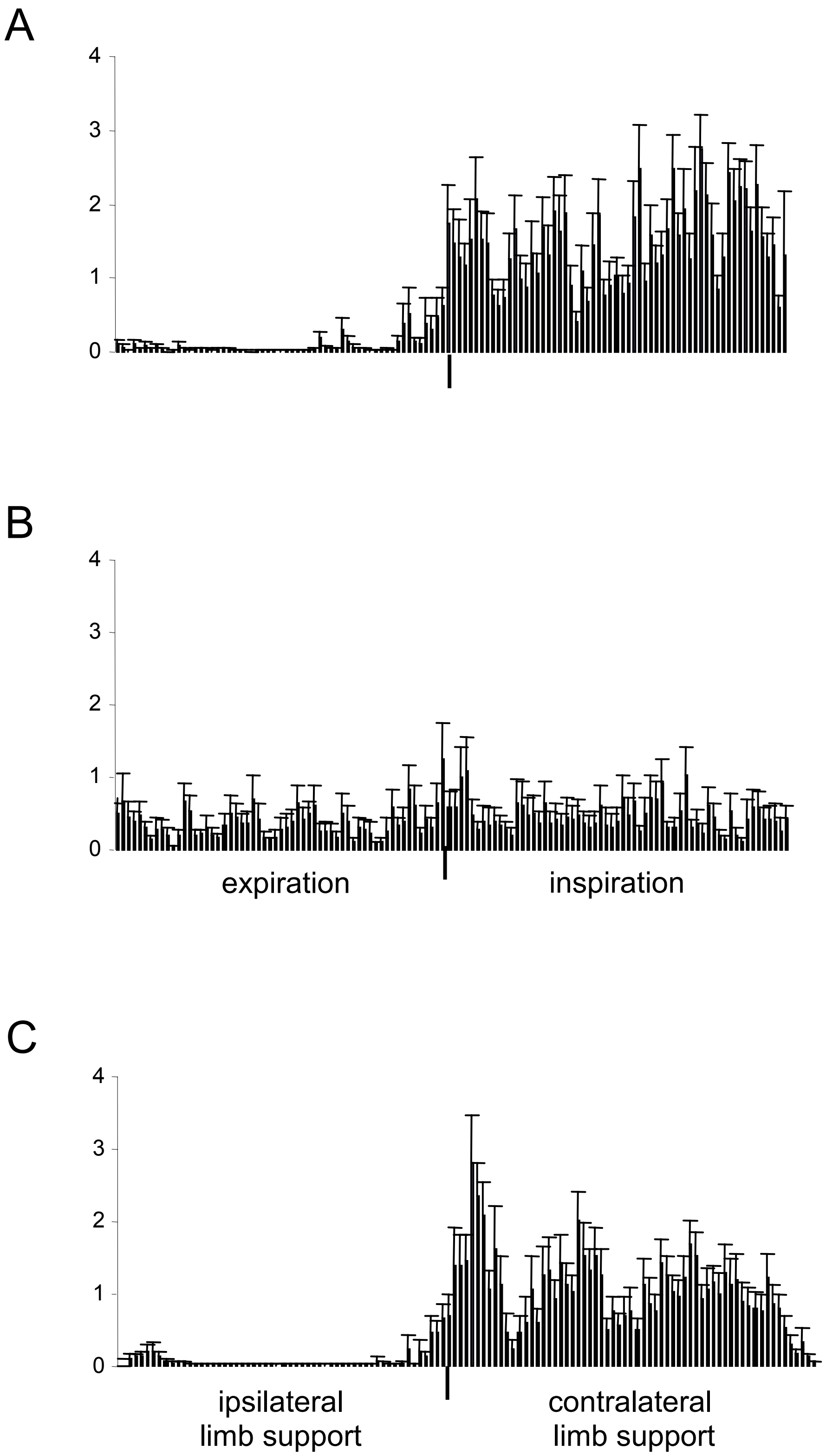

A
4
3
2
1
0
B
4
3
2
1
0
expiration
inspiration
C
4
3
2
1
0
ipsilateral limb support
contralateral limb support

Figure 24: Representative ensemble average electromyographic activity of the appendicocostalis muscle in the middle (space between the 5th and 6th ribs) during sitting (A) and standing (B). Data presented are from Goose A and are averaged over 20 breaths and shown here for one breath cycle. The appendicocostalis is an inspiratory muscle, with increased bursting in the sitting posture.

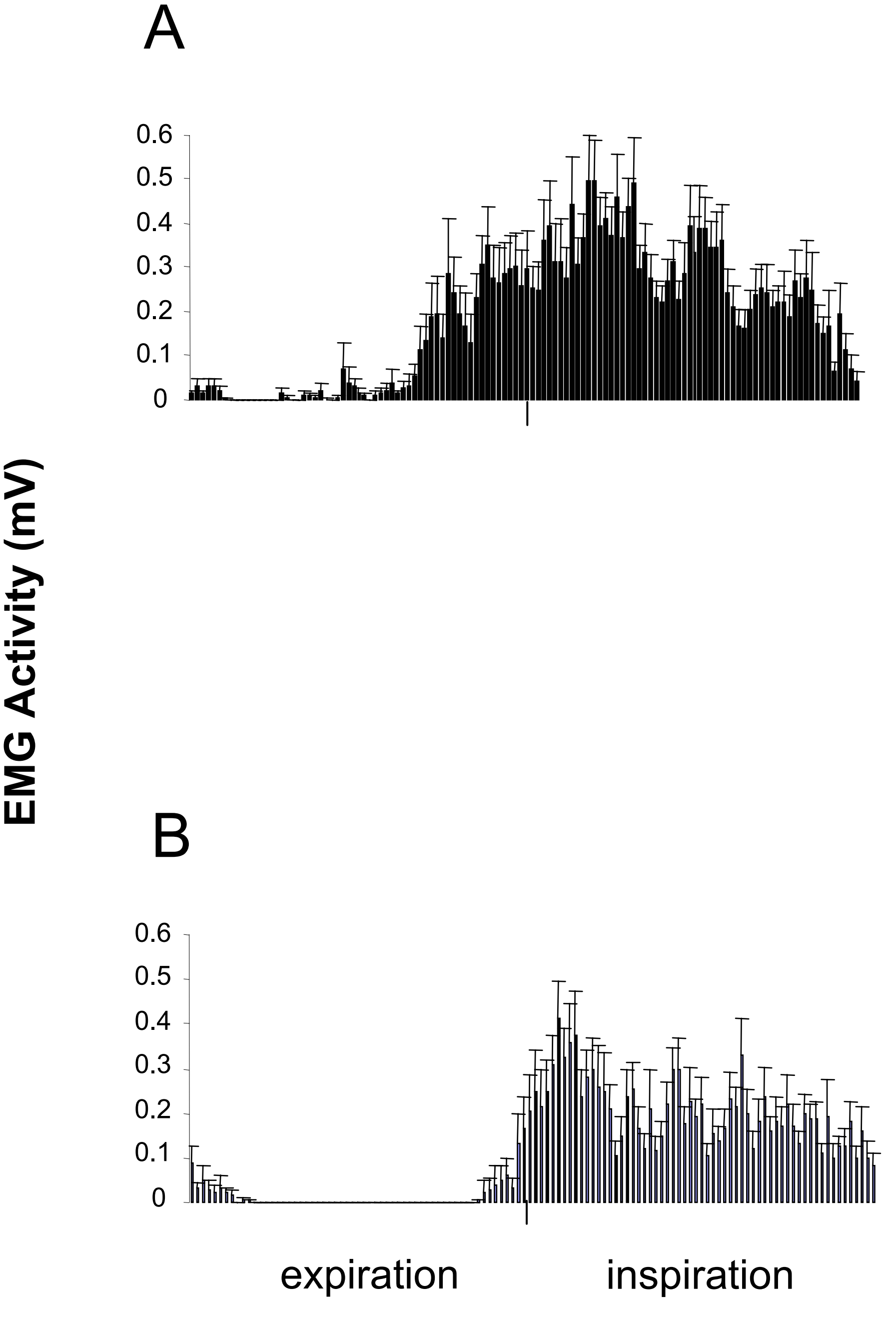
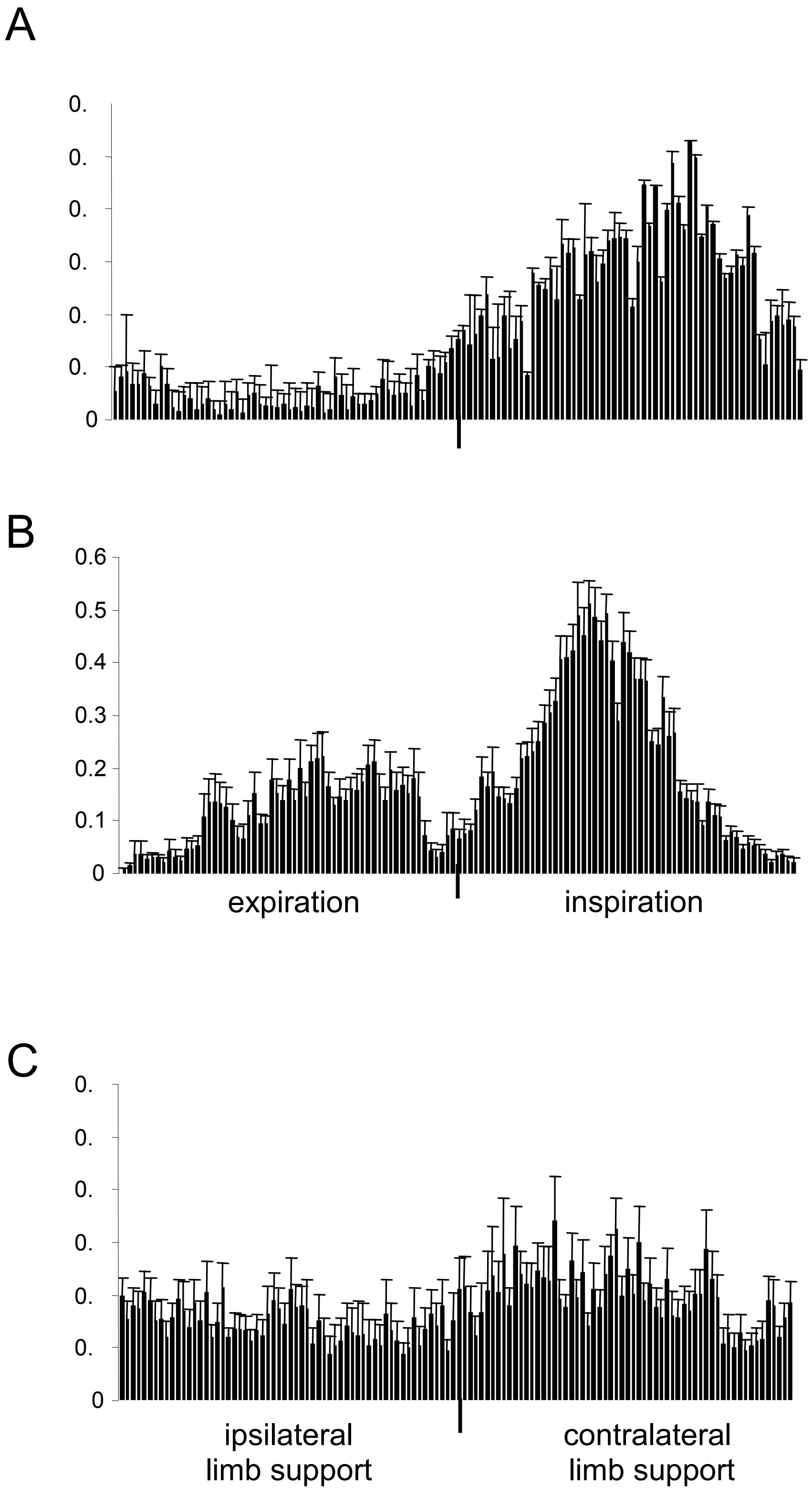

A
0.6
0.5
0.4
0.3
0.2
0.1
0
EMG Activity (mV)
B
0.6
0.5
0.4
0.3
0.2
0.1
0
expiration
inspiration

Figure 25: Representative ensemble average electromyographic activity of the middle (space between the 5th and 6th ribs) appendicocostalis muscle during A) Coupled Walking, B) Not Coupled Walking by Breath and C) Not Coupled Walking by Stride. Data presented are from Goose A and are averaged over 20 breaths, shown here for one breath cycle or one stride length as indicated on graph. The appendicocostalis muscle has a dual locomotor and ventilatory function being active during inspiration and contralateral limb support.


A
0.
0.
0.
0.
0.
0.
0
B
0.6
0.5
0.4
0.3
0.2
0.1
0
expiration
inspiration
C
0.
0.
0.
0.
0.
0.
0
ipsilateral limb support
contralateral limb support

4.3.3 External oblique

The external oblique muscle demonstrates bursting activity consistent with an expiratory function (Figure 17, 18, 19). There is no bursting activity during sitting (Figure 26a) however there is phasic bursting during expiration while standing (Figure 26b). In large expirations associated with hissing (when standing) or running there is a corresponding increase in EMG activity consistent with a larger expiration (Figure 20, 21). When analysed for coupled and uncoupled breathing (relative to breath), there is phasic bursting activity which is consistent with an expiratory function for this muscle (Figure 27a, b). When uncoupled locomotion is analysed relative to stride no clear bursting activity is associated with either ipsilateral or contralateral limb support (Figure 27c).

4.4 DISCUSSION

The muscles investigated in this study can be grouped into the following functional categories (as outline in the materials and methods). The external intercostal is a locomotor muscle (Group 1); the appendicocostalis muscle is primarily involved in inspiration but also supports locomotion (Group 3); the external oblique muscle is an expiratory muscle (Group 4).

4.4.1 The Locomotor Function of the External Intercostal

The external intercostal muscle demonstrates no ventilatory bursting during quiet breathing when either sitting or standing, during the large expirations and inspirations associated with hissing or in the uncoupled ensemble averages analysed relative to breath. However, the external intercostals are active during controlateral limb support when running. The low correlation between the breath averages when analysed relative to breath or stride for all geese (Table 5) indicates that the external intercostal muscle has no significant ventilatory function during normal breathing or running in the Giant Canada Goose.

The idea that the external intercostal muscles are involved in locomotion is not new (Carrier, 1991; Carrier, 1993; Carrier, 1996). However, the locomotor role of the external intercostal muscles demonstrated in this study contradicts previous results, which report both inspiratory and expiratory activity (Kadono et al., 1963; Fedde et al., 1964). Methodological differences may account for these conflicting results. EMG in

Figure 26: Representative ensemble average electromyographic activity of the middle (space between the 5th and 6th ribs) external oblique muscle during sitting (A) and standing (B). Data presented are from Goose A and are averaged over 20 breaths and shown here for one breath cycle. The external oblique muscle is expiratory muscle demonstrating bursting activity during standing but not sitting.

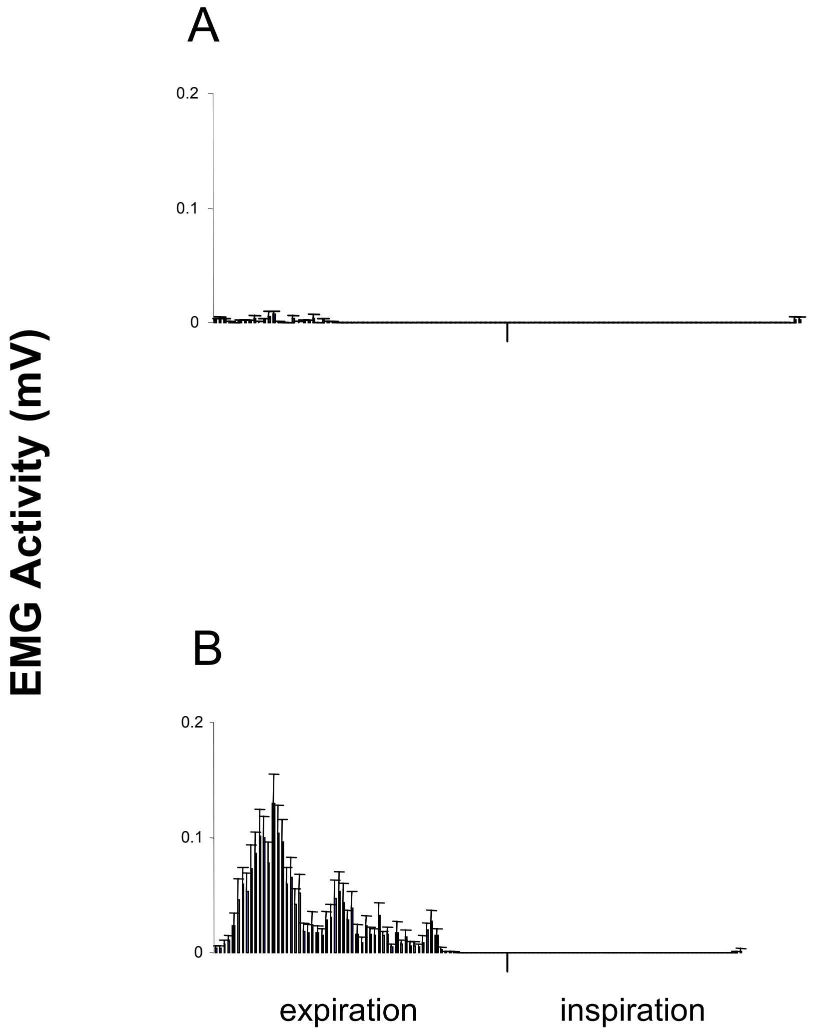

EMG Activity (mV)
A
0.2
0.1
0
B
0.2
0.1
0
expiration
inspiration

Figure 27: Representative ensemble average electromyographic activity of the middle (space between the 5th and 6th ribs) external oblique muscle during A) Coupled Walking, B) Not Coupled Walking by Breath and C) Not Coupled Walking by Stride. Data presented are from Goose A and are averaged over 20 breaths or 20 strides, shown here for one breath cycle or one stride length as indicated on graph. The external oblique is a respiratory muscle and is active during expiration.

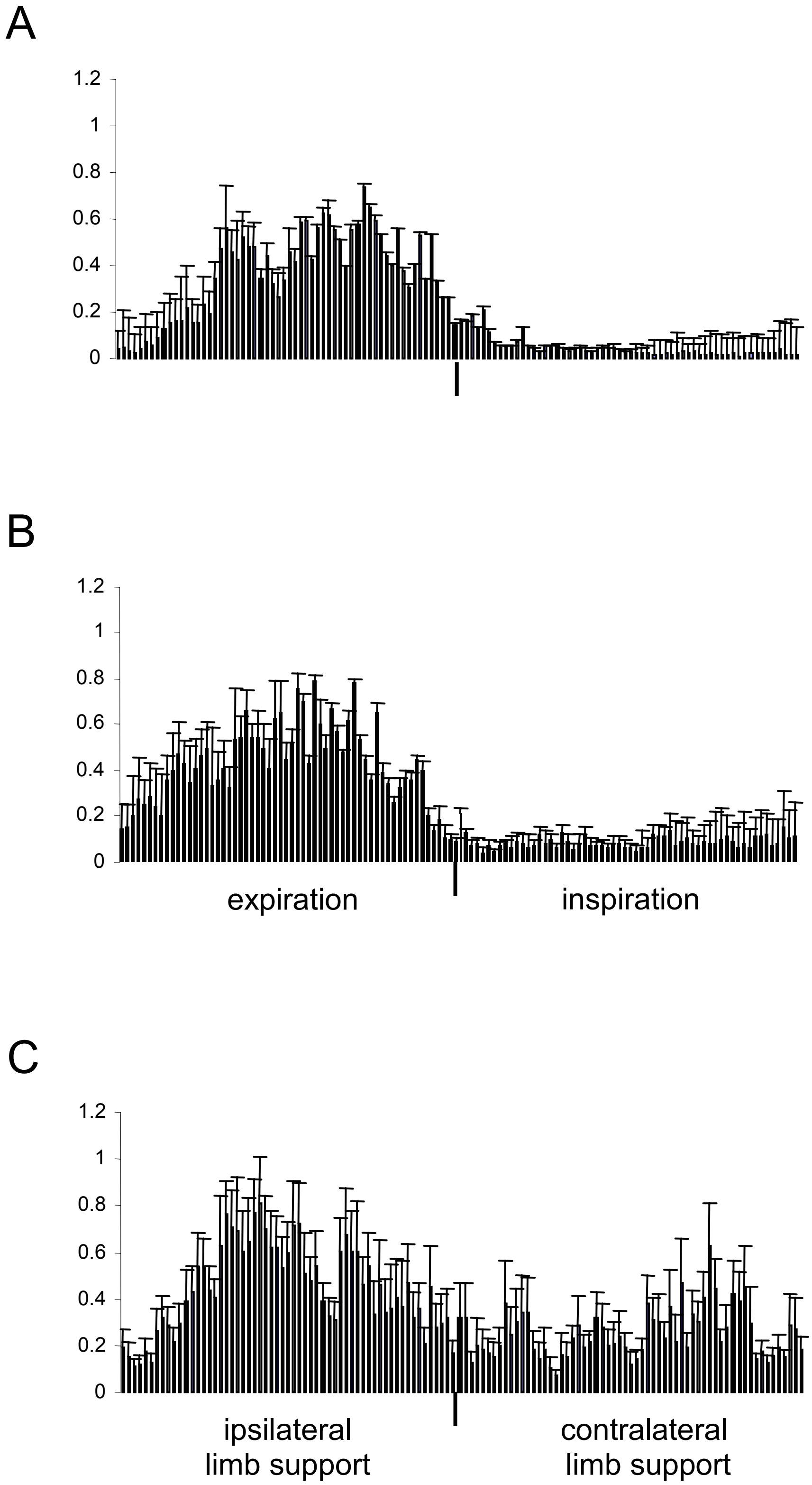

A
1.2
1
0.8
0.6
0.4
0.2
0
B
1.2
1
0.8
0.6
0.4
0.2
0
expiration
inspiration
C
1.2
1
0.8
0.6
0.4
0.2
0
ipsilateral limb support
contralateral limb support

Table 5: Coefficients of determination (r^2) for coupled and uncoupled stride averages and between coupled and uncoupled stride averages for the external intercostal, appendicocostalis and external oblique muscles for geese A-D. The external intercostal is a locomotor muscle indicated by the high correlation r^2 when analysed relative to stride. The appendicocostalis has a dual locomotor and ventilatory function and is affected by coupling indicated be the equally relatively low r^2. The external oblique is a respiratory muscle indicated by the high correlation r^2 when analysed relative to stride.

Muscle	Coefficient of Determination (r^2)							
	Goose A		Goose B		Goose C		Goose D	
	Breath	Stride	Breath	Stride	Breath	Stride	Breath	Stride
External Intercostal	0.05	0.73	0.04	0.59	0.006	0.47	0.06	0.60
Appendicocostalis	0.23	0.20	0.36	0.25	0.25	0.25	0.41	0.36
External Oblique	0.85	0.004	0.71	0.01	0.81	0.03	0.70	0.003

the current study was performed on un-anaesthetised and unrestrained birds using patch electrodes. Kadono et al., (1963) performed EMG experiments on chickens that were fixed on their side to wooden boards, while Fedde (1964) conducted EMG experiments on anaesthetised birds in a supine position, restrained by the wings. Both experiments were performed with needle electrodes. Fedde et al (1964) reported no change in EMG activity when birds were moved from the supine to upright body position. However, the exact placement of needle electrodes cannot be confirmed in living animals and failure rates of up to 50% can be expected due to needle movement (Loeb & Gans, 1986). Inherent difficulties in maintaining the exact placement of needle electrodes whilst moving the bird from the natural to supine position, coupled with the anaesthetising and restraining of the birds may have masked any electrical changes in the muscles and could account for the lack of an observed difference in muscle activity (Fedde, 1987).

The locomotor role demonstrated in this study does not preclude the external intercostals from contributing to ventilation. In dogs the intercostal muscles have been found to be primarily locomotor muscles, however they can contribute to ventilation when the work of breathing is increased (Deban and Carrier, 2002). It is possible that during laboured breathing, in restrained (Kadono et al., 1963) or supine birds (Fedde et al., 1964), the external intercostals are recruited into assisting breathing. The external intercostals may be described as accessory breathing muscles; because they do not contribute to quiet breathing but can be recruited to assist in ventilation when the work of breathing is increased. Controlled experiments, in unrestrained and un-anaesthetised geese, altering the work of breathing would be beneficial.

The external intercostal activity during locomotion is contralateral to limb support. When animals run on a level surface braking in the forward direction occurs during the first half of the step. This requires activity in extrinsic limb muscles associated with limb protraction. However, at the same time the swing limb is also undergoing protraction on the opposite side of the body. During level running in the dog the external intercostal muscles provide postural support which stabilises the rib cage and trunk and provides a strong base for the appendicular muscles to apply forces to the limbs and ground (Carrier, 1996; Deban and Carrier, 2002). However, in dogs the activity of the external intercostal is ipsilateral to limb support. In dogs the activity of intercostal muscles suggests they stabilise the trunk against the shearing forces produced by the limb protractor muscles (Carrier, 1996; Deban and Carrier, 2002). Geese have relatively large and heavy feet; therefore the shear forces may be larger on the swing limb (contralateral) side of the body as the limb undergoes protraction.

Additional experiments are required to further elucidate the locomotor activity of the external intercostal muscles during running. Experiments on the direction of the ground reactive force would establish the angle of the reaction vectors associated with footfall and confirm the direction and magnitude of the shearing force. If the external intercostal muscles are involved in counteracting shearing forces on the swing limb then manipulating the centre of mass of the geese by increasing the mass of the distal limb should increase the activity of the external intercostal muscle. Furthermore, in specialised running birds, such as the guinea fowl, that have lighter feet, the activity of the external intercostal muscle may be ipsilateral to hind limb support (Carrier pers. com)

4.4.2 DUAL FUNCTION OF THE APPENDICOCOSTALIS

The action of the appendicocostal muscles is independent of that of the external intercostal musculature, suggesting distinct motor control in these two muscle groups. The appendicocostalis muscles have a dual locomotor and ventilatory function; they are active during the inspiratory phase of ventilation in standing and sitting *B. canadensis maximus*, and demonstrate biphasic activity during locomotion. The inspiratory activity of the appendicocostalis muscles demonstrated in this study thus confirms the hypothesis of Zimmer (1935).

During breathing while standing, contraction of the appendicocostalis muscles would move the vertebral ribs cranially in a fixed plane and, in conjunction with the other inspiratory muscles (Table 5), move the sternum ventrally. Bursting activity increases when movements of the sternum are restricted by sitting. When sternal movements are restricted the appendicocostalis muscles must work to move the vertebral ribs cranially against the fixed sternum, which causes flexing around the kinetic joint between the vertebral and sternal ribs and expansion of the thoracic cavity via lateral flaring of the rib cage (as demonstrated in Chapter 3). The activity of the appendicocostalis muscles during locomotion is consistent with a dual respiratory and locomotor function. The activity of the appendicocostalis muscle is consistently larger during contralateral limb support; suggesting the muscle may play some role in stabilising the forces exerted on the trunk during running.

4.4.3 Function of the External oblique

The external oblique muscle is a ventilatory muscle, being active during expiration in quiet standing breathing. The abdominal muscles of birds are known to contribute to expiration by moving the sternum dorsally (Brainerd, 1999). The importance of the external oblique in sternal movement is confirmed by the lack of bursting when sternal movements are restricted during sitting. The aponeuroses of the finger-like projections of the external oblique muscle insert onto the base of the uncinate processes in *B. canadensis maximus*. It appears that the uncinate processes are acting as a brace for the external oblique muscle to move the sternum dorsally during expiration. Bursting activity for the external oblique muscle was cleaner during coupled and uncoupled breathing (analysed relative to breath) than uncoupled breathing analysed relative to stride. The low correlation between coupled stride averages (Table 5) indicates that the external oblique muscle is ventilatory and plays no role in stabilising the trunk during locomotion.

4.4.4 Implications of Coupling Breathing and Locomotion

In mammals (Young et al., 1992) and birds (Nassar et al., 2001) the resonant frequency of the respiratory system is entrained to the locomotor system. Coupling of wingbeat frequency and respiration in a 1:1 ratio in the Canada goose has been demonstrated to significantly reduce the mechanical cost of breathing (Funk et al., 1993; Funk et al., 1997). Furthermore, the coupling of breathing and footfall in running Guinea fowl is also thought to provide some reduction in the cost of breathing (Nassar et al., 2001). However, mechanical links between breathing and locomotion may also compromise the ability to cope with the increased metabolic and thermoregulatory demands of exercise (Lee and Banzett, 1997).

The dual role of the appendicocostalis muscle and the ability to recruit the external intercostal muscles into assisting ventilation during laboured breathing may have implications for the neuronal control of breathing. There is little research into the role of the nervous control and coordination of ventilation relative to locomotion, which perhaps reflects the difficulty of such experiments (Deban and Carrier, 2002). However, utilising different combinations of muscles during respiration is suggestive of a functional overlap in the ventilatory muscles which may circumvent any locomotor-ventilatory conflict (Deban and Carrier, 2002).

4.4.5 CONCLUSIONS

The uncinate processes in birds are involved in both inspiration and expiration. The muscles of the uncinate processes, the Mm appendicocostales, are active during inspiration, while the uncinate processes may act as a brace for the insertion of the external oblique muscle to move the sternum dorsally during expiration. The external intercostal muscles are locomotor muscles; however they can be recruited into assisting ventilation when the work of breathing is increased. Just as the Mm appendicocostales have a supplementary locomotor function. During flight the forces exerted onto the trunk may differ from those exerted during running, so the present experiments cannot be applied to locomotion in general. In light of the methodological differences between the present and previous studies, further EMG experiments of other putative respiratory muscles (listed in Table 4, Chapter 3) in un-anaesthetised and unrestrained birds and using patch or sew-through electrodes would be beneficial.

CHAPTER 5

UNCINATE PROCESSES AND THEIR IMPLICATIONS FOR THE BREATHING MECHANICS OF MANIRAPTORAN DINOSAURS

5.1 INTRODUCTION

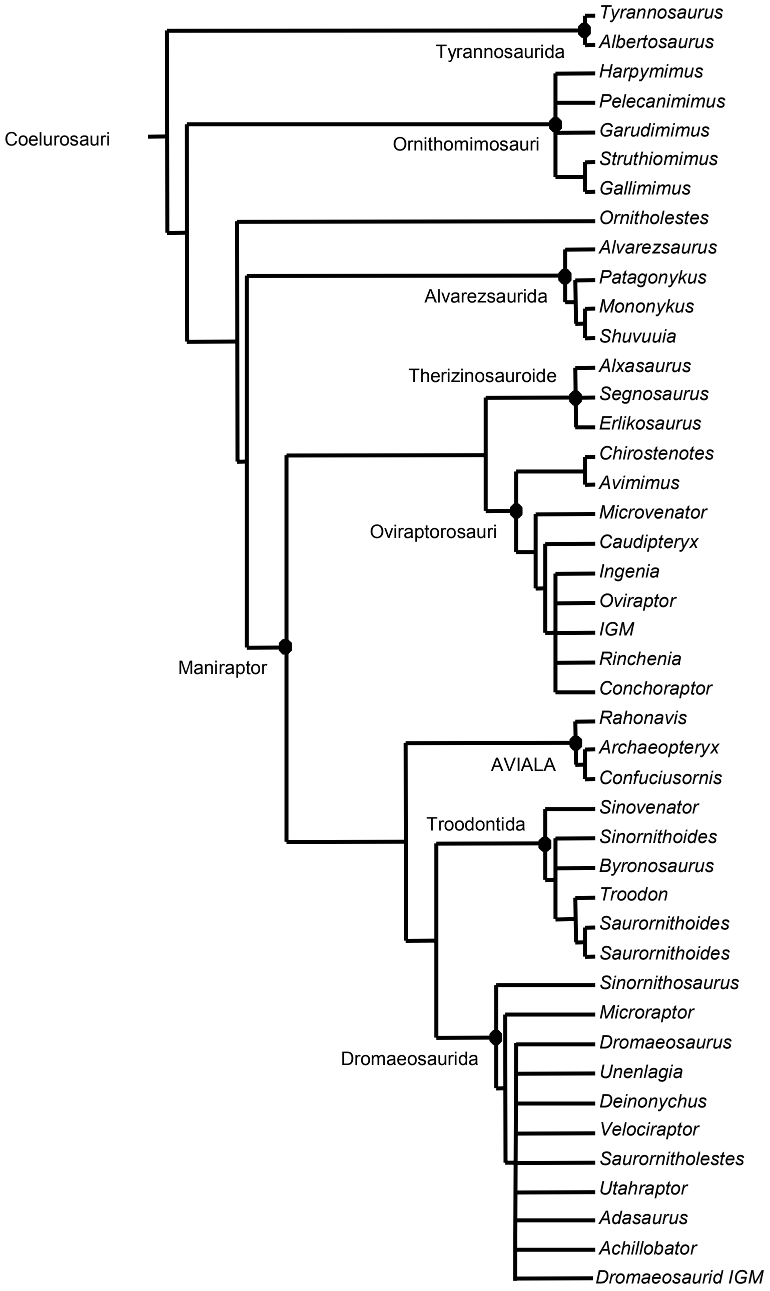
Over 130 years ago, Thomas Huxley first proposed that dinosaurs may have been the direct ancestors of birds (Huxley, 1868, 1870). However, the discovery of Euparkeria (~1910) lead to the prevalence of the thecodont hypothesis; that dinosaurs, pterodactyles, birds and crocodiles evolved from basal archosaurs, a view reinforced by Gerhard Heilmann (Heilmann, 1926). The rediscovery and description of deinonychus re-ignited the bird-theropod hypothesis (Ostrom, 1973, 1975, 1976) and subsequent phylogenetic analyses not only confirmed the bird-theropod link but demonstrated that the dromaeosaurids, such as *Velociraptor*, are the sister group to birds (Gauthier, 1986).

Cladistic analyses of the origin of birds have identified a suite of 'avian' characteristics (Gauthier, 1986; Holtz, 1994, 1996; Clark et al., 2002). For example, basal theropod dinosaurs have light bones and a three-toed foot. Moving along the theropod lineage towards the birds; there is a reduction and loss of manual digits five and four, an increasingly lightened skeleton and a reduction in the number of tail vertebrae. In coelurosaurs the arms are long and the first toe is behind the metatarsals, and the scapula is longer and more strap-like. Fused clavicles, which were thought to confound the bird dinosaur relationship (Feduccia and Martin, 1998), are in fact basal to the tetanurae (Padian and Chiappe, 1998). The pelvis and ischium become disparate in length and finally, in the dromaeosaurs and *Archaeopteryx*, the pubis begins to point downwards instead of forwards, the anterior projection on the foot of the pubis is lost, the tail becomes shorter and the semilunate carpal allows hyper-flexing of the wrist.

5.1.1 Phylogeny of the Maniraptoran Dinosaurs

Recent discoveries and cladistic techniques have improved our understanding of the phylogenetic relationships between the theropod dinosaurs (Clark et al., 2002). The most parsimonious analyses place birds as the descendents of maniraptoran dinosaurs (Figure 28). The sister group relationship between the dromaeosaurs and birds has been confirmed by a decade of detailed cladistic analyses (Chiappe and Witmer, 2002). Uncinate processes are an osteological character on the vertebral (thoracic) ribs of most extant birds and are found in some maniraptoran dinosaurs (Figure 28). Despite the homology and function of these processes in maniraptoran dinosaurs being unknown, they are thought to represent

Figure 28: Summary cladogram of Coelurosaurian dinosaurs showing the occurrence of ossified uncinate processes (modified from Clark et al., 2002). Ossified uncinate processes are reported in *Caudipteryx zoui* (Qiang, 1998), *Ingenia yanshini* (Barsbold, 1981), *Oviraptor philoceratops* (Osborn, 1924), IGM 100/42 'Big Mamma' (Clark et al., 1999, pers obs), Microraptor (Xu et al., 2003), *Deinonychus antirropus* (Ostrom, 1969), *Saurnitholestes langstoni* (pers. obs), *Velociraptor mongoliensis* (Tomida and Sato, 1995, pers. obs). Uncinate processes: + ossified uncinate processes present; --- ossified uncinate processes absent; ? presence of ossified uncinates unknown. Material: C – complete postcranial skeleton; I – incomplete postcranial skeleton; F – fragmentary postcranial skeleton.



	Uncinate Processes Present	Material	Reference
Tyrannosaurus	—	C	Osborn
Albertosaurus	—	C	Russell
Harpymimus	—	I	Barsbold & Perle
Pelecanimimus	—	C	Barsbold
Garudimimus	—	I	
Struthiomimus	—	C	Lambe,
Gallimimus	—	C	Osmolska et al.,
Ornitholestes	?	I	Osborn
Alvarezsaurus	?	I	Bonaparte
Patagonykus	?	I	Novas
Mononykus	?	I	Perle et al.,
Shuvuuia	?	I	Chiappe et al.,
Alxasaurus	?	I	Russell and Dong
Segnosaurus	?	I	Perle
Erlikosaurus	?	F	Barsbold & Perle
Chirostenotes	?	I	Gilmore
Avimimus	?	I	Kurzanov
Microvenator	?	F	Ostrom
Caudipteryx	+	C	Qiang
Ingenia	+	C	Barsbold
Oviraptor	+	C	Osborn
IGM	+	C	Clark et al., (1999), Pers
Rinchenia	?	F	Barsbold
Conchoraptor	?	F	Barsbold
Rahonavis	?	I	Forster et al.,
Archaeopteryx	—	C	Elzanowski
Confuciusornis	—	C	Hou et al.,
Sinovenator	?	I	Xu et al.,
Sinornithoides	?	I	Russell and Dong
Byronosaurus	?	I	Norell et al.,
Troodon	?	F	Leidy
Saurornithoides	?	F	Barsbold
Saurornithoides	?	F	Osborn
Sinornithosaurus	?	I	Xu et al.,
Microraptor	+	C	Xu et al.,
Dromaeosaurus	?	F	Matthew and Brown
Unenlagia	?	F	Novas
Deinonychus	+	C	Ostrom
Velociraptor	+	C	Osborn (1924), Pers.
Saurornitholestes	+	F	Pers.
Utahraptor	?	F	Kirkland
Adasaurus	?	F	Barsbold
Achillobator	?	I	Perle et al.,
Dromaeosaurid IGM	?	F	Clark et al.,

another morphological characteristic linking them to birds (Fucheng et al., 2001; Hou et al., 1996; Hwang et al., 2004; Prum, 2003; Wellnhofer, 1990).

Here I will take a phylogenetic approach to reviewing the occurrence of ossified uncinate processes in the coelurosaurian dinosaurs and investigate the morphology and possible function of the uncinate processes in the maniraptoran *Oviraptor* and *Velociraptor* dinosaurs. A functional analysis of the uncinate processes in maniraptoran dinosaurs can be viewed against their evolutionary transition to modern birds.

5.2 UNCINATE PROCESSES AND THE MANIRAPTORAN DINOSAURS

5.2.1 OVIRAPTORIDAE – IGM 100/42, CITIPATI OSMOLSKAE (NORELL ET AL., 2001)

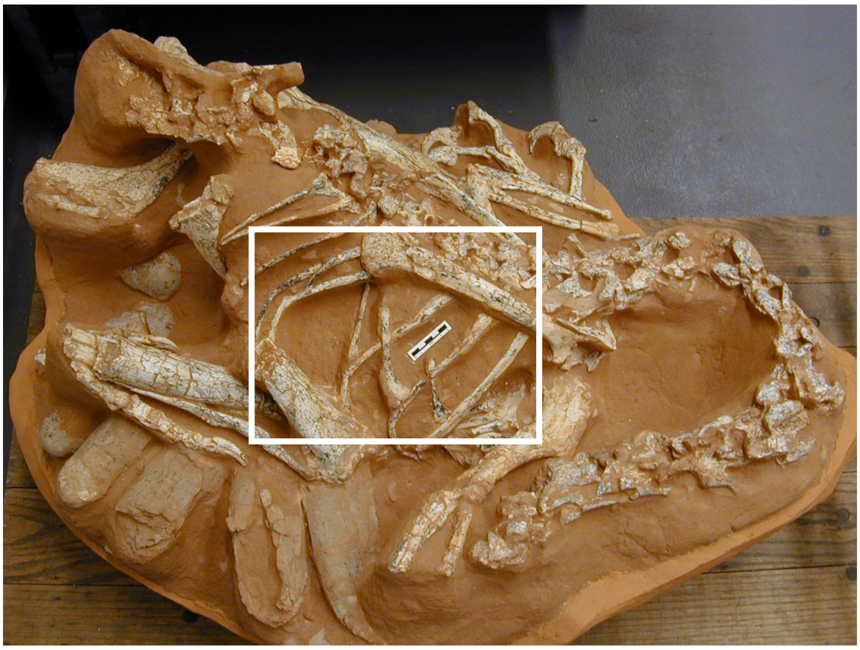
The oviraptors were small (2.5m long, 0.75m hip height), with slender limbs and grasping hands. The skull is short and deep with endentulous jaws (Barsbold et al., 2000). Specimen IGM 100/42, the 'Big Mama' specimen was found in the Late Cretaceous of Mongolia in a brooding position over a clutch of eggs (Norell et al., 1995; Clark et al., 1999). AMNH 6517 has four ossified uncinate processes present on the first four thoracic ribs on the right hand side of the skeleton. The uncinate processes extend caudally from the proximal surface at the midpoint of the thoracic ribs and overlap the following rib. The uncinate processes are flattened, broad, bell shaped at the base, taper towards the tip and has a characteristic 'L-shaped' morphology (Figure 29a). The processes on the first and fourth ribs are reduced in length and thickness. However, the uncinate processes on the second and third ribs are uniform in length, thickness and morphology. The processes are not ossified to the ribs, and may have been attached by cartilage (Figure 29b). The processes themselves would not have been mobile against the thoracic rib and may have been attached to the rib they extend from by a ligament, as found in modern birds.

5.2.2 OVIRAPTORIDAE - 'ROMEO AND JULIET', CITIPATI OSMOLSKAE (NORELL ET AL., 2001)

Two juvenile *Oviraptor* specimens, IGM 100/1002, have recently been discovered from the Late Cretaceous in Mongolia (Norell, et al., 2001). The two specimens are referred to as the 'Romeo and Juliet' specimens as they died together and appear to be 'holding hands'.

Figure 29: A) Oviraptorid, *Citipati osmolskae* 'Big Mama brooding oviraptor', Specimen No: 100/42, Mongolian Academy of Natural Sciences, Mongolia, B) rib-cage showing the 4 prominent uncinate processes extending caudally from the proximal surface at the midpoint of the 1st - 4th thoracic ribs. The uncinate processes are not fixed to the thoracic ribs and may have been attached by cartilage, scale bars 5cm.

A



B

The specimens are more disarticulated than the brooding *Oviraptor*, which may reflect the large amount of cartilage in juvenile specimens (Lyman, 1994) or that disruption of the skeleton occurred during scavenging. The thoracic region is more disarticulated than the remainder of the skeleton (Figure 30a). However, despite almost complete skeletons and the excellent preservation under nearly identical conditions to the 'brooding' *Oviraptor* (M Norell pers. comm.), the uncinate processes have been lost from all of the thoracic ribs. One individual isolated uncinate process is visible associated with the 'Romeo' specimen (Figure 30a, b), indicating how readily the uncinate processes could be lost in otherwise complete but somewhat disarticulated skeletons.

5.2.3 DROMAEOSAURIDAE - VELOCIRAPTOR MONGOLIENSIS (OSBORN, 1924)

Velociraptor mongoliensis was a small (1.8m long, 0.5m hip height), carnivorous dinosaurs from the Late Cretaceous of Mongolia. The *Velociraptor* had a narrow skull, ossified tendons stiffening the tail, and a functionally didactylus foot in which the second pedal digit was raised above the ground; the first and third digits bore the weight (Paul, 1988). The 'fighting dinosaur' specimen (MPD 100/25) is preserved in 'mortal combat' with a protoceratops (*Protoceratops andrewsi*). Ossified uncinate processes were first described in MPD 100/25 by Paul (Paul, 1984; 1988). Five uncinate processes are present on the left hand side of the specimen, extending caudally from the proximal edge at the midpoint of the third to the seventh thoracic ribs, and extend to the edge of the second following rib (Figure 31a, b). The uncinate processes are flattened and uniform in morphology; they are thin and taper towards the tip. The uncinate process on the seventh rib is reduced in size and length and has broken off from the thoracic rib. The uncinate processes on the first and second thoracic ribs are missing. The processes are not ossified to the rib and may have been attached by cartilage and an aponeurosis to the thoracic rib (Figure 31c).

Ossified uncinate processes are also present in a second currently undescribed *V. mongoliensis* specimen (MPD 100/54) from the Late Cretaceous of Mongolia. Five broken partial uncinate processes are visible on the right hand side of the specimen (Figure 32) and two ossified articulated uncinate processes are visible on the left hand side of the specimen; extending from the midpoint of the thoracic ribs (Figure 32). The broken uncinate processes on the right hand side of the specimen reinforce how easily these small bones can destroyed during fossilisation or excavation. The uncinate processes extend from

Figure 30: A) Oviraptorid, *Citipati osmolskae*, from the Late Cretaceous of Mongolia, part of the so called ‘Romeo and Juliet’ specimen. This is the ‘Romeo’ specimen No: IGM 100/1002. The specimen is more disarticulated than IGM 100/42, particularly the rib cage. A single isolated uncinate process is visible in top right hand corner of the specimen indicating how easily these small bones could be lost in otherwise complete specimens and B) close up of isolated uncinate process demonstrating the L-shaped morphology and tapering towards the tip of the process, scale bars 5cm.

A

B

Figure 31: A) *Velociraptor mongoliensis* and *Protoceratop andrewsi* the ‘fighting dinosaurs’ locked in mortal combat, specimen No: MPD 100/25, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia, scale bar 50cm, B) rib-cage showing prominent uncinate processes extending caudally from the proximal surface at the midpoint of the 3rd-7th thoracic ribs, scale bar 5cm, C) close up of the articulation of the uncinate processes to the thoracic ribs the processes are not fixed to the rib and may have been attached by cartilage, scale bar 3cm.


A
B
0 1 cm 4 5

C

Figure 32: *Velociraptor mongoliensis* specimen No: MPD 100-54, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia. Rib-cage showing partial uncinate processes (indicated by arrows) extending caudally from the proximal surface at the midpoint of the thoracic ribs on the right hand side of the specimen and two complete articulated uncinate processes (indicated by arrows) on the left hand side of the specimen, scale bar 5cm.


0 1 cm 4 5

the 3rd to 7th thoracic ribs as in MPD 100/25. The uncinate processes are identical in morphology to the uncinate processes of MPD 100/25. They are flattened, thin and taper towards the tip and span to the edge of the second following rib. The uncinate processes are not ossified to the thoracic rib and may have been attached by cartilage as previously described for MPD 100/25. A pathology is present on the second thoracic rib, on the right hand side of the skeleton. It appears as if the rib was broken however the injury wasn't fatal as there is evidence of calcification (Figure 32).

5.2.4 DROMAEOSAURIDAE - SAURORNITHOLESTES LANGSTONI (SUES, 1977, 1978)

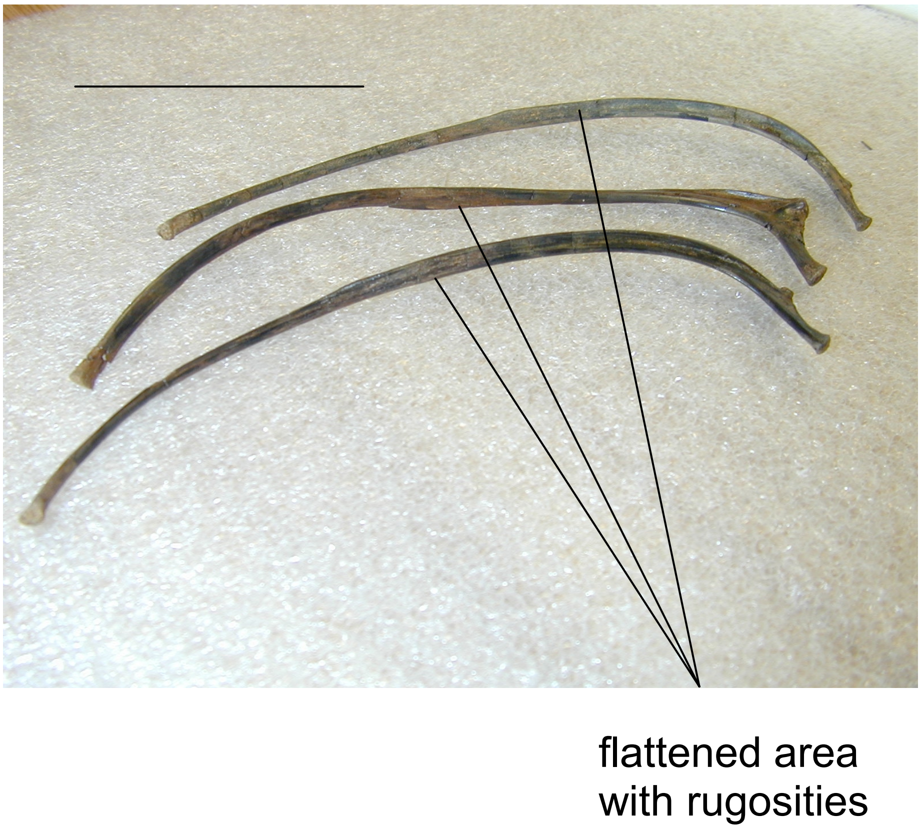
Little is known of these dinosaurs except fragmentary skull pieces and some post-cranial skeletal remains (Sues, 1977, 1978). However, as uncinate processes are present in many other members of the dromaeosauridae (Figure 28) their presence can be hypothesised in *Saurornitholestes*. Three isolated thoracic ribs from one individual (TMP 88.121.39), without uncinate processes, are known from the Late Cretaceous of the Judith River Formation of Alberta. The absence of uncinate processes is not surprising given the fragmentary remains. In the *Velociraptor* specimens the uncinate processes extend from the proximal surface at the midpoint of the thoracic ribs. On each of the *Saurornitholestes* ribs there are characteristic flattened areas, with rugosities on the leading edge which correspond to the exact region where, if present, the uncinate processes would be attached by an appendicocostalis like muscle (Figure 33a, b). These rugosities and flattened regions may provide evidence of uncinate processes on the ribs of other poorly preserved or disarticulated skeletons of maniraptoran dinosaurs in which ossified uncinate processes can be hypothesised but are not present. The ribs are morphologically similar to those of the *V. mongoliensis* specimens, in particular the MPD 100/54 specimen described earlier.

5.3 TAPHONOMY AND UNCINATE PROCESSES IN THE FOSSIL RECORD

The occurrence of ossified uncinates is patchy among the maniraptoran dinosaurs (Figure 28), indicating either they were not present or they may have been lost during fossilisation. As described earlier, the best examples of ossified uncinates within the maniraptoran dinosaurs are found in the *Oviraptor* and *Velociraptor* specimens (Paul, 1988). In these specimens the uncinate processes are not ossified to the ribs and may have been attached by cartilage. Cartilage does not readily fossilise as it has a lower structural density than

Figure 33: A) Three thoracic ribs of *Saurornitholestes langstoni*, Specimen No: RTMP 88.121.39 from the Late Cretaceous of the Judith River Formation, Alberta, Canada, demonstrating characteristic flattened regions at the midpoint of the thoracic ribs, which correspond to the location of the uncinate processes in other maniraptoran dinosaurs, scale bar 5cm, B) Rib cast from RTMP 88.121.29, demonstrating close up of rugosities on thoracic ribs where, if present, the uncinate process of the preceding rib would have been attached. These rugosities may provide evidence for the occurrence of ossified uncinate processes in the absence of the processes themselves, scale bar 1cm.

A



B

bone (Lyman, 1994). If, in other maniraptoran dinosaurs, the uncinate processes were also cartilaginously attached to the thoracic ribs they may have been lost during disarticulation, weathering or scavenging of the skeleton. Furthermore, the uncinate processes themselves are small fragile bones which, if they did remain associated with the skeleton, may be easily overlooked when fossils are being collected from the field. A re-examination of existing maniraptoran ribs, which are reported to lack uncinate processes, looking for flattened characteristic regions with rugosities on the thoracic ribs may provide evidence for uncinate processes in the absence of the processes themselves.

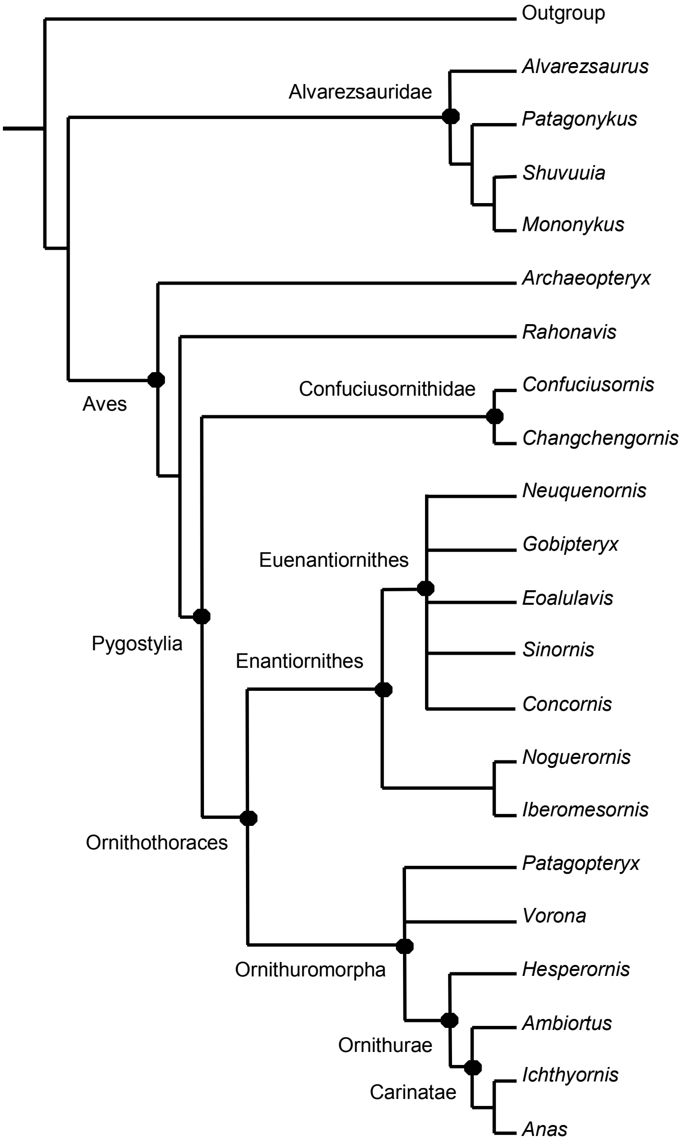
The brooding *Oviraptor* and fighting *Velociraptor* specimens in 'life' positions are unusually well preserved remains of nearly complete skeletons. The dinosaurs were probably buried alive and death was instantaneous. Osmolska (1993) suggested the animals may have been buried by the collapse of sand banks whilst fighting or protecting eggs. Sedimentological studies have confirmed the eolian nature of the sands (Jerzykiewicz, 1993), which lead to the suggestion that the animals may have been buried either during a sandstorm (Unwin et al., 1995) or by drifting sand (Carpenter, 1998). However, Martin (2001) proposed that the sudden deposition of wet sand onto the dinosaurs within alluvial fans, caused by rainstorms may account for the taphonomy of these fossils. Wet sand is much heavier than dry sand and may have limited the movement of the animals trapped within it, before suffocation.

Taphonomic conditions which appear to favour the preservation of ossified uncinate processes include rapid burial with little or no modification of remains by scavenging or weathering i.e. allowing the bones to remain *in situ*. Within the maniraptoran dinosaurs ossified uncinate processes appear to be synapomorphic for the dromaeosaurs and oviraptorids (Figure 28).

5.4 UNCINATE PROCESSES AND THE BASAL BIRDS

Until recently *Archaeopteryx*, *Hesperornis* and *Icthyornis* represented our entire knowledge of the evolution of Mesozoic birds. The discovery of *Gobipteryx* (Elzanowski, 1974) signalled the beginning of a renaissance in our understanding of the evolution of the early birds. The number of described early bird species tripled in the 1990's (Chiappe and Witmer, 2002) which has improved understanding of the evolutionary transformations of avian characteristics and the phylogenetic relationships between the basal birds. Ossified uncinate processes are rare amongst the basal birds (Figure 34), which may in part be due

Figure 34: Summary cladogram of basal birds showing the occurrence of ossified uncinate processes (modified from Chiappe, 2002). Ossified uncinate processes appear to be synapomorphic for the Ornithurae and are reported in *Hesperornis* (Marsh, 1880) and the modern birds. Uncinate processes: + ossified uncinate processes present; - ossified uncinate processes absent; ? presence of ossified uncinates unknown. Material: C – complete postcranial skeleton; I – incomplete postcranial skeleton; F – fragmentary postcranial skeleton.



	Uncinate Processes Present	Material	Reference
Outgroup			
Alvarezsaurus	?	I	Bonaparte (1991)
Patagonykus	?	I	Novas (1996)
Shuvuuia	?	I	Perle et al., (1993)
Mononykus	?	I	Chiappe et al., (1998)
Archaeopteryx	—	C	Elzanowski (2002)
Rahonavis	?	I	Forster et al., (1998)
Confuciusornis	—	C	Hou et al., (1995)
Changchengornis	?	I	Ji et al., (1999)
Neuquenornis	?	I	Chiappe and Calvo (1994)
Gobipteryx	?	I	Sanz et al., (1996)
Eoalulavis	—	I	
Sinornis	—	C	Sereno & Rao (1992)
Concornis	—	I	Sanz et al., (1995)
Noguerornis	?	I	Lacasa-Ruiz (1989)
Iberomesornis	—	I	Sanz & Bonaparte (1992)
Patagopteryx	—	I	Alvarenga & Bonaparte (1992)
Vorona	?	I	Forster et al., (1996)
Hesperornis	+	C	Marsh (1880)
Ambiortus	?	I	Kurochkin (1982)
Ichthyornis	?	I	Marsh (1880)
Anas	+	C	Welty (1962)

to the absence of complete articulated skeletons and the incompleteness of the fossil record. The *Archaeopteryx* specimens are complete, articulated and preserved with soft tissue remains such as feathers. There are 11-12 pairs of thoracic ribs, with no trace of separate sternal ribs and no uncinate processes are present (Elzanowski, 2002).

It is possible that uncinate processes may be present in the *Archaeopteryx* specimens but have been overlooked during description of the specimens. However, given the articulated preservation and detailed descriptions (Wellnhofer, 1974, 1988, 1992, 1993; Elzanowski, 2002) this would appear to be unlikely. However, a re-examination of the *Archaeopteryx* specimens specifically looking for ossified uncinate processes or evidence of their attachment (as previously described in *Saurornitholestes*) may be worthwhile. Uncinate processes have been lost in at least two species of modern birds, the Emus (*Dromaius hollandiae*) and the Screamers (Anhimidae); indicating uncinate processes are not a pre-requisite for an air-sac system or flight. Therefore despite the inference of a functional link between the evolution of an air-sac system and the occurrence of ossified uncinates (Hou et al., 1996); the absence of uncinate processes in *Archaeopteryx* does not provide evidence for or against air sacs or insight into the flight capability in *Archaeopteryx.* The occurrence of uncinate processes in the dromaeosaurs and *Oviraptor* and their absence from *Archaeopteryx*, which is more closely related to modern birds (Clark et al., 2002) (Figure 34), raises an interesting paradox of why they were 'lost' and then regained in the ornithurines.

5.5 DISCUSSION

5.5.1 UNCINATE PROCESSES: HOMOLOGY OR HOMOPLASY?

The occurrence of ossified uncinate processes in the maniraptoran dinosaurs and basal birds may be too disparate to be phylogenetically informative. A re-examination of existing specimens specifically looking for evidence of ossified uncinate, as previously described in *Saurornitholestes* would be beneficial. The sister group relationship between the Dromaeosaurs and the modern birds and the location and general morphology of the uncinate processes in the maniraptoran dinosaur suggest they may be homologous to the uncinate processes in modern birds. However the occurrence of ossified uncinate processes in the maniraptoran dinosaurs and basal birds is patchy (Figure 28, 34). Within the maniraptoran dinosaurs ossified uncinates occur in the Oviraptorids and the

Dromaeosauridae but they are absent in the Troodontidae and Avialae; the group most closely related to modern birds. The fossil record of the Troodontidae is poor, with incomplete or fragmentary post cranial remains known for all current species (Figure 28), which may explain the absence of ossified uncinate processes in this clade. Within the basal birds ossified uncinate processes are present, and appear to be synapomorphic, only for the Ornithurae (Figure 34).

Given the current phylogenetic distribution of the uncinate processes in the maniraptoran dinosaurs and the basal birds it appears unlikely that they are homologous to the uncinate processes in modern birds. Homology would require the evolution of uncinate processes once in the maniraptora (Figure 28, 34) and their repeated independent loss in the Archaeopteriformes, Confuciusornithidae, Enantiornithes and *Patagopteryx* and then reappearance in the Ornithurae. The most parsimonious explanation for the appearance and subsequent disappearance of ossified uncinate processes in the fossil record is that they are an example of homoplasy between maniraptorans and modern birds.

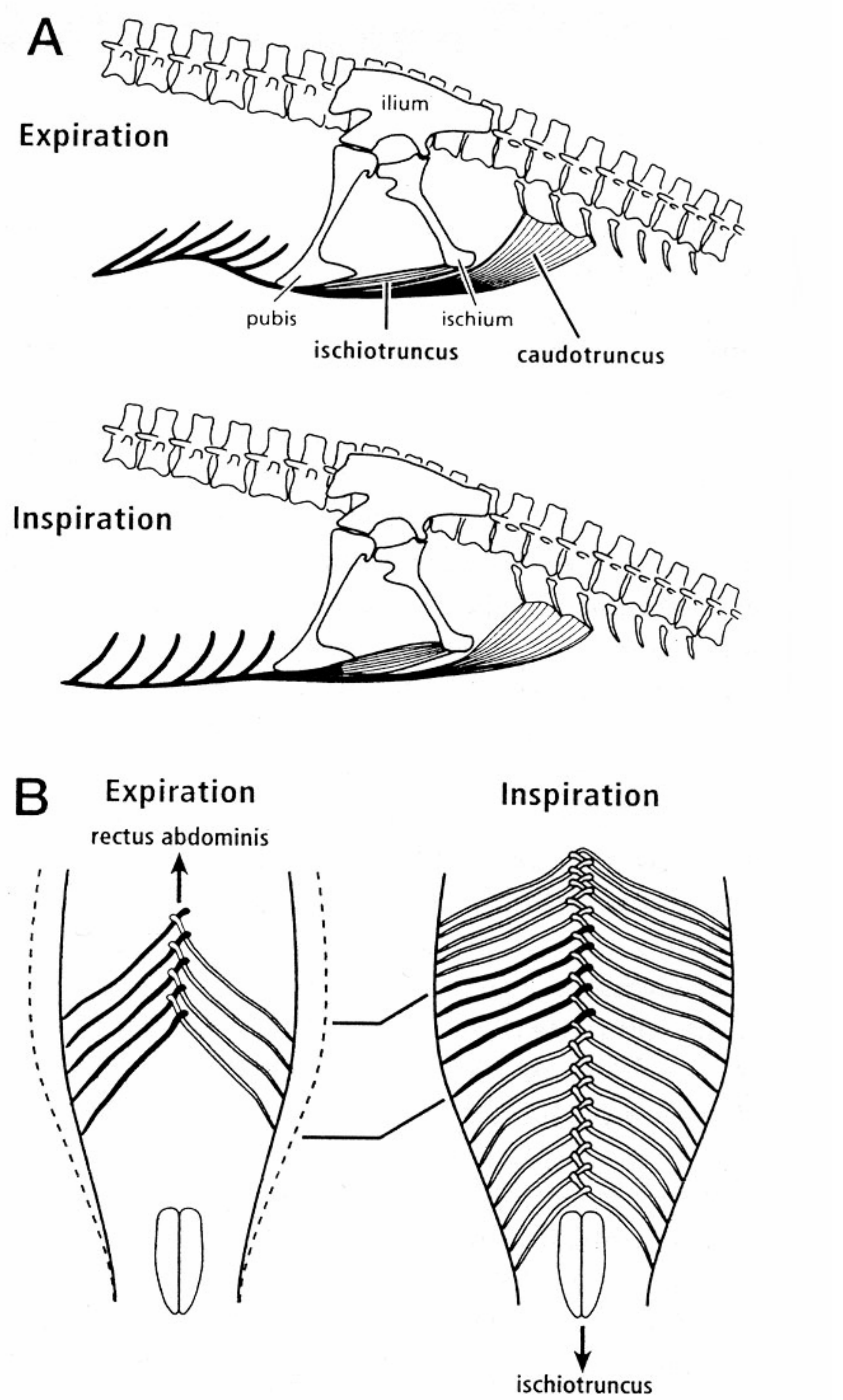
5.5.2 FUNCTION OF THE UNCINATE PROCESSES IN MANIRAPTORAN DINOSAURS

Based in part on the occurrence of ossified uncinate processes, secondarily flightless dromaeosaurs have been hypothesised to be more closely related to the modern birds, caudipterygians and the oviraptorosaurs than to *Archaeopteryx* (Paul, 1988). However, the unifying characteristics of flightless birds are consistently paedomorphic trends (such as visible sutures, atrophy of the forelimb and large vertebrae and hindlimbs) which are absent in the 'secondarily flightless' maniraptoran dinosaurs (Dawson et al., 1994; Feduccia, 1996). Furthermore, the morphology of the uncinate processes in the extant flightless birds is very different to the 'flightless' maniraptoran dinosaurs. In walking or running birds the uncinate processes are reduced in length.

The uncinate processes of the *Velociraptor* and *Oviraptor* specimens (as described earlier) extend from the same region of the thoracic ribs as the uncinate processes in birds. However, unlike the bipedal running birds, they are not reduced but are intermediate to long in length and morphologically resemble those of the swimming, flying and diving birds. Given the relatively short, stiff back and bipedalism of the maniraptoran dinosaurs uncinate processes are unlikely to have been involved in aiding dorsiflexion of the trunk during locomotion (Perry, 2001). Extant birds are highly derived which makes direct comparisons with the maniraptoran dinosaurs problematic. Furthermore, in the absence of fossilised soft tissues and lungs the breathing mechanics of maniraptoran dinosaurs are open to speculation. Ossified uncinate processes are not a prerequisite for the development of an air-sac system, as there are extant birds which lack uncinates but have fully functioning air sacs (Del Hoyo et al., 1992). However, based on indirect osteological evidence, modern analogies and extant phylogenetic bracketing, the presence of a putative air-sac system in theropod dinosaurs has been hypothesised (Paul, 1988; Perry, 1983, 1989, 1992, 2001; Burnham, 2000).

The *Velociraptor* and *Oviraptor* specimens have well developed gastralia in the ventral belly wall (Claessens, 2004). Gastralia are plesiomorphic for amniotes and are derived from the dermal body armour of Paleozoic amphibians (Romer, 1956). Gastralia have been postulated to participate in lung ventilation by preventing the inward movement of the belly wall (Lambe, 1917; Perry, 1983; Claessens, 1997, 2004). However, gastralia have recently been hypothesised to play a more dynamic role in archosaur ventilation (Carrier and Farmer, 2000a; Claessens, 2004). There are no known species which have gastralia but which also lack pubic and ischial symphyses (Carrier and Farmer, 2000a). In non-avian theropods the pubis was elongated with cranial and caudal expansions at the distal end. The ventral margin of the expanded distal end, known as the boot, aligns with the distal end of the ischium such that a parasagitally located ischiotruncus muscle could affect gastral movements (Carrier and Farmer, 2000a). The gastralia of non-avian theropods are highly derived, cross the midline and are articulated with two gastralia from the opposite side of the body. This arrangement constitutes a lever arm which through association of hypaxial musculature could have narrowed or widened the cuirassal basket (Figure 35) (Carrier and Farmer, 2000a). If the medial ends of the gastralia were drawn caudally by the ischiotruncus muscle; lateral and ventral movement of the belly wall would occur (Carrier and Farmer, 2000a; Claessens, 2004). The ischium would have functioned as the origin for the ischiotruncus muscle and the expanded foot of the pubis would have acted to direct the force of the muscle. For this proposed breathing mechanism to work effectively a caudotruncus muscle which inserts onto the gastralia is required. Specialised gastralia and pelvic girdles, coupled with the presence of pneumatic openings in the presacral vertebrae in *Oviraptor* and dromaeosaurs (Britt et al., 1998), further support the presence of air sacs and therefore avian-like breathing mechanics in theropod dinosaurs.

Figure 35: Illustration of the proposed mechanism of breathing in maniraptoran dinosaurs. A) Lateral view of the action of the ischiotruncus muscle on the gastral basket during inspiration and expiration and B) ventral view of the gastralia showing the lever mechanism which allows lateral expansion of the abdominal cavity (from Carrier and Farmer, 2000 with permission).


A
Expiration
ilium
pubis
ischium
ischiotruncus
caudotruncus
Inspiration
B
Expiration
rectus abdominis
Inspiration
ischiotruncus

5.5.3 MECHANICS OF BREATHING IN MANIRAPTORAN DINOSAURS

Given the presence of the rugosities on the thoracic ribs of *Saurornitholestes,* the uncinate processes in maniraptoran dinosaurs may have been attached by an appendicocostalis like muscle extending from the proximal edge of the uncinate process and attaching onto the following rib. A ligament similar to that found in modern birds may have supported the uncinate process on the thoracic rib it originated from. The uncinate process pulls on this ligament which translates to cranially movement of the rib. The probably cartilaginous attachment of the uncinate process to the thoracic rib may facilitate twisting of the rib which would translate to lateral movements of the gastral basket. The external oblique is the most superficial of the sheet like abdominal muscles in birds and originates at the inferior surface of the uncinate processes and from the lateral margin of the pubis. Irrespective of the homology or homoplasy of the uncinate processes in the maniraptoran dinosaurs and the modern birds, where present they may have played a role in expansion of the rib cage, movements of the gastral basket and therefore ventilation of the postulated air sac ventilatory system.

CHAPTER 6

GENERAL DISCUSSION

6.1 SUMMARY AND CONCLUSIONS

6.1.1 THE UNCINATE PROCESSES IN BIRDS

The uncinate processes in most extant birds are bony structures that extend from the posterior margin of the vertebral ribs proximal to the midpoint. Uncinate processes occur on those ribs which align with the large muscle mass of the sternum and are reduced or lacking on the first and last ribs. The function of the uncinate processes has been the subject of much speculation. The putative role as an accessory respiratory structure is a central theme of the present dissertation. Should it be possible to support this hypothesis or refute alternative ones for extant birds (as described in Chapter 1) by analogy the ossified uncinate processes in some extinct maniraptoran dinosaurs may allow us to functionally interpret the breathing mechanics of these extinct animals. To this end, establishing structure-function correlations of the uncinate processes is important as a detailed understanding of their function in extant birds is required before significance can be attributed to dinosaurs.

The function of the uncinate processes in extant birds was examined using a combination of morphological, phylogenetic and physiological techniques. The length of the uncinate processes was measured in 88 skeletons of extant birds. Sister group comparisons were used to examine the phylogenetic determination of uncinate morphology. The mechanics of breathing in standing and sitting birds was examined using x-ray cinematography. The activity of three respiratory muscle groups (the external intercostal, appendicocostalis and external oblique) was examined in un-anaesthetised and un-restrained geese using patch and sew through electrodes.

The results obtained in this study are summarised as follows:

1) The uncinate processes extend caudally from the proximal surface at the midpoint of the vertebral ribs.
2) The uncinate processes are reduced in length on the first and last ribs in extant birds.
3) The length of the uncinate processes is important as they act as a lever arm for movement of the ribs in a fixed plane about their articulation on the vertebral column.

4) The length of the uncinate processes varies with the locomotor mode of extant birds and not with phylogenetic position.
5) Uncinate processes are short in walking birds, of intermediate length in swimming and flying birds and the longest in the diving birds.
6) The uncinate processes are functionally linked to movements of the vertebral ribs and sternum during breathing.
7) Standing birds breathe by dorsoventral rocking of the sternum. When movements of the sternum are restricted the birds switch to breathing by lateral flaring of the rib-cage.
8) The external intercostals are primarily locomotor muscles but can assist breathing when the work of breathing is increased.
9) The M. appendicocostalis has a dual locomotor respiratory role but it primarily an inspiratory muscle drawing the vertebral ribs forward which translates into ventral movements of the sternum.
10) The activity of the appendicocostal muscle increases when dorsoventral rocking of the sternum is restricted, and may facilitate lateral movement of the ribs.
11) The external oblique is an expiratory muscle and is active during standing breathing.

In conclusion the uncinate processes in birds are an integral component of the breathing apparatus. Uncinate processes are involved in inspiration through the appendicocostal muscle and may also act as the insertion of the external oblique muscle which is active during expiration in standing birds. The present results clearly demonstrate that EMG experiments on avian musculature should be conducted on un-anaesthetised and unrestrained birds using patch or sew-through electrodes.

6.1.1.1 Further Observations and Future Directions

Given the increased length of the uncinate processes in diving birds, the distal insertion of the appendicocostal muscle may further improve the mechanical advantage of the uncinate processes. An increase in the mechanical advantage may be beneficial when moving the proportionately longer ribs and elongated sternum of the diving birds. The parrots (e.g. lorikeets, *T. haematodus*), and the kiwi (*A. haasti*) have triangular projections which extend from the base of the uncinate processes (as described in Chapter 2). A broad base or triangular projection extending from the uncinate process may provide a better attachment for the external oblique muscle and could be functionally linked to an increase in expiratory effort which may occur during calling in the parrots or egg laying in the kiwi. Future work examining the insertion of the appendicocostal and external oblique muscles in birds with different uncinate processes may further elucidate their function. Furthermore, future work examining the additional muscles of the thoracic region that insert on or near the uncinate processes in extant birds, in particular the posterior and anterior serratus muscles may identify the function of the uncinate processes during flight.

Ossified uncinate processes are absent in two species of extant birds the Emu (*D. novaehollandiae*) and the Screamers (Anhimidae). Given the functional link between uncinate length and sternal morphology, the role of the uncinate processes in moving the sternal mass (including the heavy flight muscles) during breathing and the reduction in length (and therefore function) of the uncinates in the walking/running birds, their loss in the Emu is not surprising. The absence of uncinate processes in the Screamers is puzzling since these birds fly, swim and dive. The loss of the uncinate processes therefore has no implications for the evolution or presence of an air-sac ventilatory system; however it may have implications for the breathing mechanics. Future EMG and x-ray cinematography experiments examining the mechanics of breathing when resting on the sternum may elucidate the respiratory function of the intercostal musculature in the Screamers.

6.1.2 UNCINATE PROCESSES AND THEIR IMPLICATIONS FOR THE BREATHING MECHANICS OF THE OVIRAPTORID AND DROMAEOSAURID DINOSAURS

In the absence of preservation of the internal organs and musculature in fossil species, the breathing mechanics of dinosaurs can only be approached indirectly. A better understanding of the breathing mechanics and respiratory biology of the maniraptoran dinosaurs may have implications for understanding if they were homeothermic endotherms (Perry, 2001).

The occurrence and general morphology of the uncinate processes were examined in the Dromaeosaurid; two specimens of *Velociraptor mongoliensis* (MPD 100/25 and MPD 100-54), in *Saurornitholestes langstoni* (RTMP 88.121.39) and in the Oviraptorid dinosaurs; *Citipati osmolskae* (IGM 100/42) and the 'Romeo and Juliet' specimens (IGM 100/1002). The phylogenetic distribution of uncinate processes was also examined in the coelurosaurian dinosaurs in an attempt to better understand the phylogenetic origin of these processes to those of modern birds.

The results obtained in this study are summarised as follows:

1) Ossified uncinate processes are present in the Oviraptoridae and Velociraptoridae.
2) The uncinate processes of the *Oviraptor* and *Velociraptor* dinosaurs extend from the proximal surface at the midpoint of the thoracic ribs and are intermediate to long in length.
3) The uncinate processes in the *Oviraptor* and *Velociraptor* specimens are not rigidly fixed to the thoracic ribs and may have been cartilaginously attached.
4) The uncinate processes in the *Oviraptor* and *Velociraptor* are morphologically similar to those of extant birds suggesting a similar functional role.
5) Uncinate processes are absent in *Saurornitholestes langstoni* however flattened areas and rugosities on the thoracic ribs provide evidence for their presence and subsequent loss.
6) Uncinate processes are inconsistent in the fossil record of the maniraptoran dinosaurs and basal birds.
7) The paucity of uncinate processes may be due to the incompleteness of the fossil record and the ease with which these small, fragile and cartilaginously attached bones might be lost during fossilisation of excavation.
8) The occurrence of ossified uncinates in the oviraptorids and dromaeosaurid dinosaurs is an example of homoplasy between the maniraptoran dinosaurs and modern birds.

Bipedal running or walking birds have short uncinate processes whereas bipedal running *Oviraptor* and *Velociraptor* dinosaurs have intermediate to long processes. The uncinate processes in these dinosaurs most closely resemble those of diving birds. The long uncinate processes in the diving birds may be functionally linked to rapid and forced inspiration upon resurfacing (as described in Chapter 2). Therefore I hypothesise that the uncinate processes in maniraptoran dinosaurs may have been an integral component of costal and gastralial movements to facilitate rapid and forceful breathing. The uncinate processes in the maniraptoran dinosaurs may have been attached to the following rib by an appendicocostalis-like muscle, which may have moved the ribs cranially during inspiration as in birds. A ligament extending from the dorsal edge of the uncinate processes may also have been attached to the thoracic ribs. The uncinate processes in the dinosaurs are long; therefore, distal insertion of an appendicocostalis-like muscle would improve the mechanical advantage. The proposed cartilaginous attachment of the uncinate processes to the ribs may have allowed some lateral movement. Furthermore, an external oblique-like muscle may have functioned during expiratory movements of the gastral basket and rib cage.

Although the gastral basket is not homologous to the keeled sternum of extant birds, its movements in the maniraptoran dinosaurs may be analogous to the movement of the avian sternum. Dorsoventral and lateral movements of gastralial basket in conjunction with costal movements may have ventilated the hypothesised thoracic and abdominal air sacs. The presence of uncinate processes and kinetic gastralia demonstrate a mechanism for facilitating the ventilation of air sacs exists in these maniraptoran dinosaurs, suggesting these were active animals with a high metabolic rate.

The following scenario is hypothesised for the breathing mechanics of the maniraptoran dinosaurs *Oviraptor* and *Velociraptor*:

During inspiration; contraction of an appendicocostalis-like muscle, attaching the uncinate processes to the following ribs, would move the ribs forward and twist them laterally; simultaneous contraction of an ischiotruncus muscle would move the gastral basket laterally and ventrally causing expansion of the thoracic cavity. During expiration; contraction of the rectus abdominus and an external oblique like muscle would pull the gastral basket anteriorly causing elevation and cause lateral compression of the ventral body wall. The ribs may return to their original position either by elastic recoil or by contraction of the hypaxial musculature. Ventral movements of the gastral basket may be analogous to the ventral movements of the sternum in modern birds which facilitates the bellows like ventilation of the air-sacs.

6.1.2.1 Further Observations and Future Directions

Ever since Richard Owen's first attempts at restoring Megalosaurus in 1854 to the Jurassic Park films of the 1990's, attempts have been made to reconstruct dinosaurs. However, reconstructions are often hampered by inaccuracies; from Owen's first attempt to reconstruct an entire animal based on fragmentary remains, models are often based on incomplete or misleading information. The inaccuracy of many reconstructions may be explained by the rapidly changing nature of palaeontology with new fossil discoveries. However, reconstructions remain a powerful tool for conveying current ideas and theories in modern palaeontology. Modern reconstructions, using three-dimensional computer models, have gone beyond the physical appearance of the animals and are starting to ask questions about the functional morphology, biomechanics and biology of dinosaurs.

Three-dimensional computer models have been used to examine a wide range of aspect of dinosaur biology including the biomechanics of neck movement and feeding (Stevens and Parrish, 1999), locomotion (Carrier et al., 2001; Christian et al., 1999), the centre of mass of dinosaurs (Henderson, 1999) and the evolution of flight (Dial, 2003). Computer models are advantageous as many of the fossils involved are too awkward, fragile and heavy to be moved manually. Computer models also allow multiple hypotheses to be simultaneously tested. In addition post-depositional distortion often alters the bones and may disrupt articulation sites (Stevens and Parrish, 1999). Models themselves are inherently simple but they can help us in understanding ideas or concepts. However, it is important to be aware of the limitations of computer reconstructions. Accurate modelling of any soft tissue components such as muscles and tendons may be problematic.

We intend to incorporate the information gathered from this dissertation on the function of the uncinate processes in extant birds into a 3-dimensional computer model of the breathing mechanics in dinosaurs. When reconstructing the breathing mechanics of maniraptoran dinosaurs, the fixed articulation of the rib heads and their fixed plane of motion enable the maximum excursions of the ribs and subsequent volume change of the thoracic cavity to be calculated. An examination of the ribs themselves looking for evidence of Sharpey's fibres may provide evidence for the angle of insertion of the intercostal and appendicocostalis like muscles and therefore the direction of the force vectors. Future development of an accurate 3-dimensional computer model will allow hypotheses into the function of the uncinate processes and gastralia during respiration in the maniraptoran dinosaurs to be tested.

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