

Form, function and fibres: a preliminary study of the Swartkrans fossil birds

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Fossil bird bones from the Swartkrans cave estimated at about one million years old have been identified to family level. Differences in humerus and sternum structure were noted. This led to an investigation into flight styles and behaviour as well as the muscle structure and function of the modern representatives of three families (Phasianidae - francolins; Columbidae - pigeons; Tytonidae - barn and grass owls) in an attempt to understand why the bones in these families were so distinctive.

Key words: fossil bird bones, flight muscles, muscle histology, histochemistry.

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Introduction

The Swartkrans cave is situated in the Krugersdorp district of the Transvaal near the famous Sterkfontein and Kromdraai caves. During the 1979 - 1986 excavation of this cave a fairly large collection of bird bones from four stratigraphic levels was recovered (Watson *in press*). The four stratigraphic levels excavated range in age from 11 000 years BP to 1,8 million years BP. The three older deposits thought to be between 1 and 1,8 million years old are renowned for their hominid component and rich mammalian fauna (Brain *et al.* 1988).

An extensive grid system was erected over the site and standard archaeological procedures and techniques were utilised to recover the bones. The substrate was decalcified breccia and by passing it through a two tiered sieve, fine enough to recover microfauna, whatever bones were present in it were recovered.

In this preliminary study only the bird bones from Member 3 (about 1 million years old) have been looked at in any detail. Member 3, also known as the 'fire member', has yielded a convincing number of burnt bones indicating the controlled use of fire (Brain & Sillen 1988). The bird bones from Swartkrans have

never been described before and it is hoped to describe the entire bird collection in detail in the future.

Findings and methods

A total of 237 bones have been assigned to 11 bird families (Fig. 1). This was done first by identifying the bones to skeletal part, and then by using the extensive comparative skeletal collection built up by the Department of Birds at the Transvaal Museum. The skeletal elements were assigned to families. The identification of bird bones beyond family level is a time consuming task and much of the work in this field in southern Africa is of a pioneering nature. It is generally recognised that any skeletal element has characteristics shared by members of a particular family and thus assigning a bone to a family is largely possible and realistic (Gilbert *et al.* 1985). When trying to narrow an identification to genus or species level, measurement is employed and subtle features need to be examined in detail using a suitably large comparative collection.

During the initial identification process of the Member 3 bird bones it became clear that certain skeletal elements were better represented than others (Fig. 2). More than a quarter (25,7 %) of all the bones assigned to families were humerus pieces. The coracoid had also survived well; the ulna, tibiotarsus and tarsometatarsus were also well represented. The fact that these bones are better represented than other skeletal parts is probably due to the fact that they are the more robust skeletal elements. In the case of the sternum, the keel of which is generally very delicate, the more robust proximal end is the portion that tends to survive and be represented in the palaeontological record.

Although individual skeletal elements were easily recognisable there was great variation in form and size. With reference to a comparative collection the bones were assigned to different families all of which are still represented in this area today (Tarboton *et al.* 1987). Having done this it was possible to calculate the minimum number of individuals represented in the collection and in each family (Fig. 1). Of the total of 50 individuals in the collection 12 belonged to the family Phasianidae (guinea fowl and francolins). All the bones assigned to this family were too small to be guinea fowl and were thus assumed to be francolins with which they compared favourably. It was possible to sex these individuals because male francolins have characteristic spurs on their tarsometatarsi. At least four of the individuals were males.

The cave is believed to have been a lair for carnivores and a shelter for early man during the depositional phases in question (Brain 1981). It is interesting to speculate how the remains of the particular families identified found their way into the cave. Members of most of the families may well have been either preyed upon or scavenged and brought back to the cave for consumption. The remains of cave dwelling species are also not hard to account for but the presence of the raptor remains needs further elucidation.

Form and function

It was at this stage that I began to wonder why, for example, a humerus from the Phasianidae

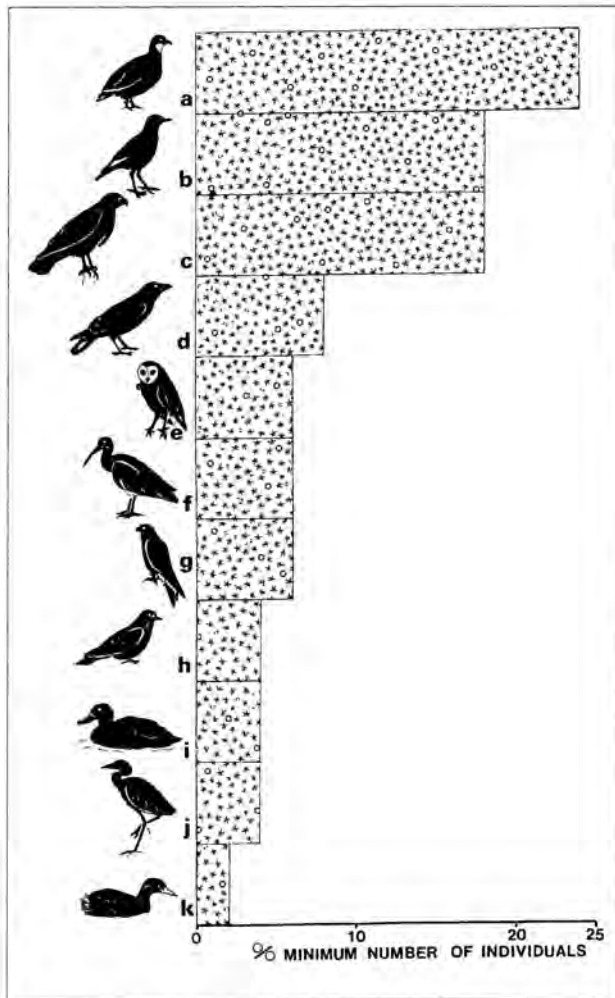


Fig. 1. The bird families identified in the Swartkrans Member 3 deposit represented as % minimum number of individuals. $n = 50$.
 a. Phasianidae
 b. Sturnidae
 c. Accipitridae
 d. Corvidae
 e. Tytonidae
 f. Threskiornithidae
 g. Falconidae
 h. Columbidae
 i. Anatidae
 j. Ardeidae
 k. Podicepsidae.

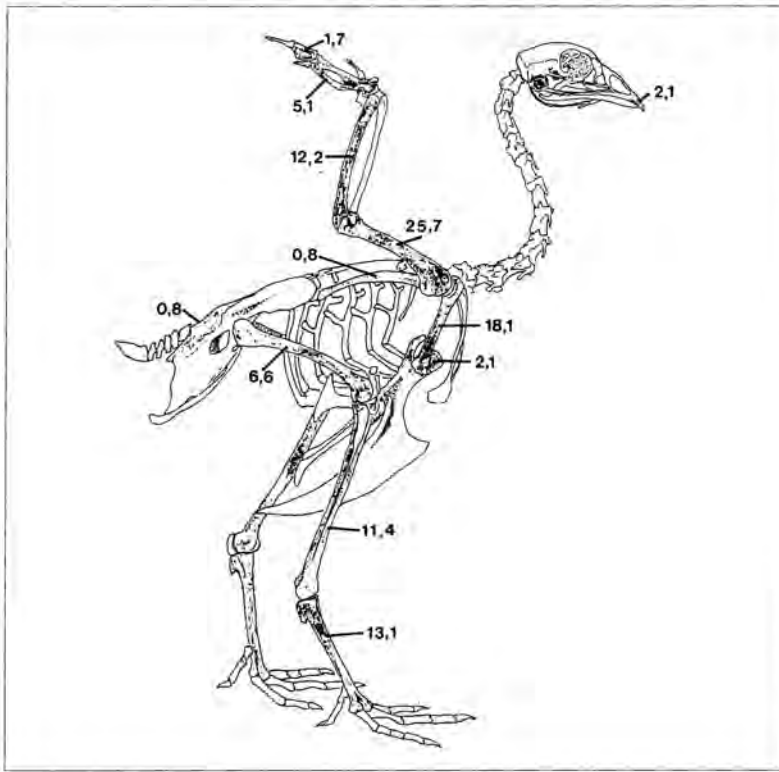


Fig. 2. Percentage skeletal part representation of the fossil bird collection identified to family level.

was physically so different from that belonging to a member of the Columbidae (pigeons and doves). How does function influence form? For this pilot study it was decided to concentrate on three families and on two skeletal elements. The families decided on were the Phasianidae, the Tytonidae (grass and barn owls) and the Columbidae. The skeletal elements were the humerus and the sternum. These bones were selected because both are involved in flight and because their morphology differs markedly in the three families in question. Although over fifty muscles are required for bird flight (George & Berger 1966), the two major flight muscles are the pectoralis, responsible for the powered downstroke, and the supracoracoideus which is responsible for the powered upstroke

(George & Berger 1966). Both these muscles originate on the keel of the sternum and insert on the proximal humerus (Fig. 3).

It appears that the relative development of the keel in different birds is directly related to the development of the pectoralis and supracoracoideus muscles (George & Berger 1966). The larger the keel the stronger the flying ability on the whole — in fact the flightless ratite birds including the ostrich and the kiwi have no keel to the sternum at all (George & Berger 1966). Membranes extend between the various processes of the sternum and these too serve as areas of origin for these large flight muscles. In general the pectoral muscle is much larger than the supracoracoideus and averages 15,5 % of the body weight, with

very little scatter from the mean in different birds (George & Berger 1966). It has been noted that the supracoracoideus is largest in birds that make a quick takeoff from a standing start and is especially small in cuckoos and owls (George & Berger 1966). The galliforms to which the fowls and francolins belong are well known for rocketing out of bushes when alarmed; they have relatively large supracoracoideus muscles. A rapid wingbeat frequency and periods of strong but brief flight suggest the need for a stronger powered upstroke (Vanden Berge 1975).

The humerus is the largest wingbone and contains, in nearly all birds, an air chamber in its shaft which is an outgrowth of the interclavicular air-sac. The marrow cavity is limited to the ends of the bone (George & Berger 1966) whereas in mammals the shaft of the long bone is where the marrow cavity is situated. The pectoral muscle inserts on the ventral aspect of the deltoid crest by means of fleshy fibres. The supracoracoideus inserts on the dorsal surface of the humerus just distal to the articulation head by means of a tendon (George & Berger 1966; Vanden Berge

1975). This tendon passes through the triosseal canal, which functions as a pulley allowing the ventrally situated muscle belly to raise the humerus and the wing (George & Berger 1966). The deltoideus muscle, another elevator of the humerus, inserts on the dorsal aspect of the deltoid crest (Fig. 3). The main extensor of the forearm, the humerotriceps muscle arises from the shaft of the humerus throughout nearly its entire length, and the main flexor of the forearm, the biceps brachii, arises by means of a tendon from the internal tuberosity on the proximal end of the humerus.

The Phasianidae (using francolins as an example) have large sternums with very deep keels (Fig. 4a). The sternum also has two long processes on each side. The large fleshy pectoral and supracoracoideus muscles originate here. The humerus is a largely unelaborate bone of medium length with a ventrally angled deltoid crest of smallish proportions and a strong scar on the dorsal surface where the tendon of the supracoracoideus attaches. The wings of galliform birds to which the Phasianidae belong, are short and rounded for rapid takeoffs. Their flight is generally rapid and not sustained (Maclean 1984). The sternum and humeral structure in respect of size and muscle attachments bears this out well. Francolins are well known to be the favoured prey of many carnivores including man. Besides being palatable, the meat return especially in the breast area is very high. In addition these birds are largely terrestrial, taking to the trees only when alarmed and to roost, making hunting them relatively easy. Understandably their feather colouring is usually cryptic.

The sternum of the Columbidae is fairly deep and when viewed from the side is rounded and not as extensive as that in the Phasianidae (Fig. 4b). There is one process which when compared to that of the francolins is relatively short. Nevertheless the pectoralis - supracoracoideus complex which arises from it is well

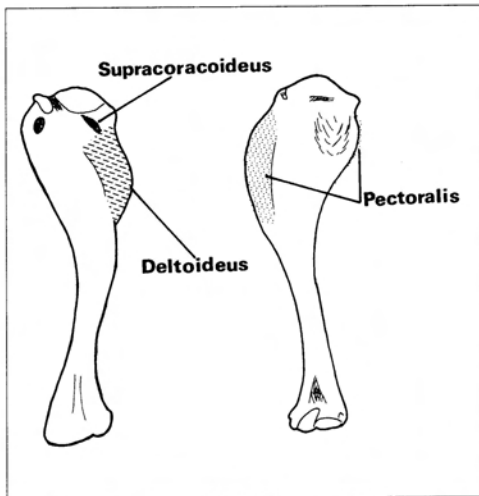


Fig. 3. Sites of muscle insertions of three of the flight muscles on the proximal humerus, dorsal and ventral views shown.

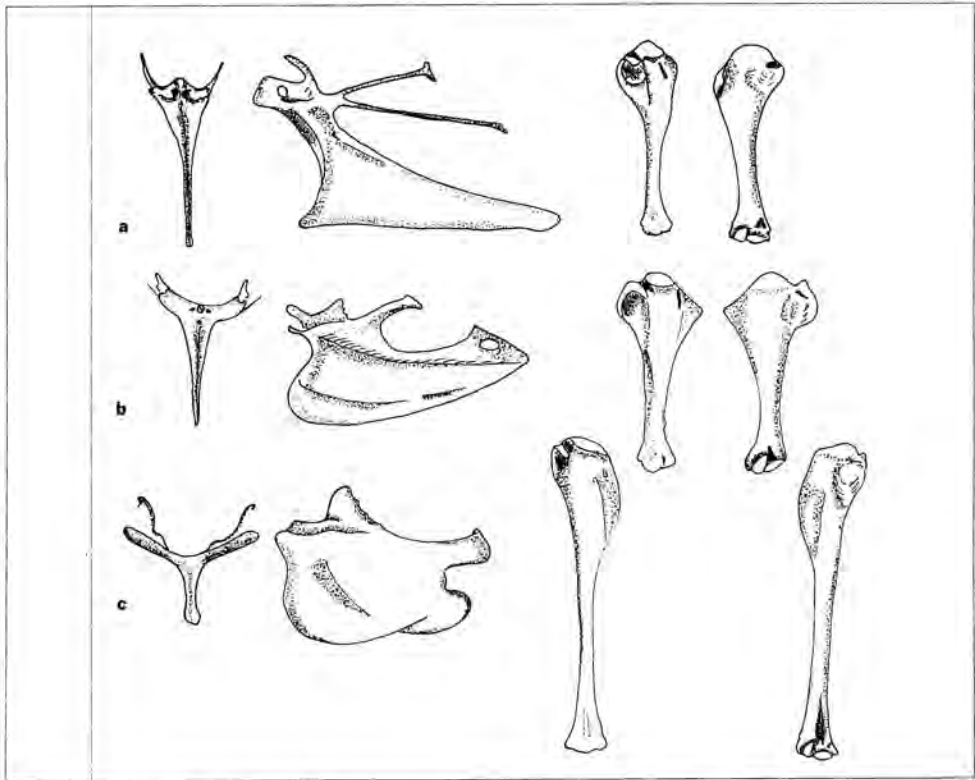


Fig. 4. Anterior and lateral views of the sternums and the dorsal and ventral views of the humerus' respectively of
 a: Family Phasianidae (*Francolinus levaillantoides*)
 b: Family Columbidae (*Columba guinea*)
 c: Family Tytonidae (*Tyto capensis*).

developed and helps in giving pigeons and doves the robust bodies we are familiar with. The humerus is a fairly short, robust bone with a large triangular deltoid crest. The area of insertion for the supracoracoideus muscle is well developed and is evident as a linear scar. The Columbidae are strong fliers and the use of pigeons as messengers in the world wars and for racing bears this out. Their flight is usually powerful and direct (Maclean 1984) and the keel and humerus structure in these birds suggests these attributes. In most species the wings are rounded but there is specific variation in wing length.

The Tytonidae include the barn and the grass owls. In this family the keel of the sternum is

relatively shallow and is rounded when viewed from the side (Fig. 4c). There are no processes on the sternum. The humerus is a long slender bone with a well-developed deltoid crest which is angled slightly ventrally. The insertion site of the supracoracoideus muscle is unremarkable which is probably to be expected as this muscle is not well developed. Barn owls use a flap and glide mode of flight while quartering the ground for prey. They may hover when scanning the ground; sometimes they beat the bushes to flush out prey and they may hunt from a perch (Maclean 1984). The bone structure observed here lends itself to this type of flight.

These birds have long, broad and rounded

wings (Maclean 1984) allowing for a large wing surface area. This is a recommendation in birds of prey as they have to be able to rise from the ground and fly with their prey which may be quite weighty (Ruppel 1977). The fossil owl bones found at Swartkrans may well be barn owl bones — their size appears to be comparable. Barn owls are known to have inhabited the cave for roughly the last two million years (Brain 1981), the plentiful microfaunal remains, almost certainly arising from owl pellets, indicate this.

Fibres

Finally the histochemistry and histology of the pectoralis and supracoracoideus muscles are interesting to look at. Three types of avian muscle fibres exist: white fibres, red fibres and intermediate fibres.

White fibres are broad, pale fibres which contain much glycogen and practically no fat (George & Berger 1966), (Table 1). Glycogen is rapidly converted into energy and where white fibres predominate, rapid flight is common.

Red fibres are narrow fibres with a rich blood

supply, much myoglobin (the muscle form of haemoglobin in the blood), many mitochondria (the powerhouses of the cell), and a rich fat supply. Minimal glycogen is found in these fibres. (George & Berger 1966) (Table 1). These fibres are conducive to sustained flapping flight.



The intermediate fibres are intermediate in structure and make-up to the red and white fibres. They are believed to have developed in birds where quick action became more frequent and sustained. They are found in birds that use a soaring and gliding type of flight (George & Berger 1966).

As seen in Table 1 the fibre types and their relative abundance in the major flight muscles of the three families in question are ideally suited to the types of flight practiced by the birds in question.

Conclusions

Although only two bones from three families were examined with respect to two of the major flight muscles it became clear that function influences form significantly. It is possible to interpret the form of the same

Table 1
Explanation of the muscle fibre types, some of their attributes and their status in two of the major flight muscles

<p>FIBRE TYPES</p> <p>W I R</p> <p>WHITE INTERMEDIATE RED</p>	<p>FAST RAPID FLIGHT SOARING + FLIGHT LONG SUSTAINED FLIGHT</p>	<p>GLYCOGEN</p> 	 <p>MITOCHONDRIA AND FAT</p>
<p>PHASIANIDAE COLUMBIDAE TYTONIDAE</p>	<p><u>PECTORALIS</u> (DOWN STROKE)</p> <p>W, I, R R, W I</p>	<p><u>SUPRACORACOIDEUS</u> (UP STROKE)</p> <p>W, I, R R, I, W R, W, I</p>	

skeletal element in different families with regard to muscle development and function. This in turn relates positively to the behaviour and habits of the birds in question. Even the fibre types within the muscle groups examined seem specifically suited for the flight patterns practiced.

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