

**Beak morphology in extant birds with
implications on beak morphology in
ornithomimids**

Master-thesis by
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2007

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Abstract

Ornithomimosaurs are only one out of several dinosaurian groups that at some point evolved beaks. The morphology of this beak and its relation to dietary habits have long been debated. Birds and turtles are the primary extant beaked organisms. Many studies have previously been conducted with the emphasis on beak shape and sensory organ topography in relation to feeding habit and behaviour. Few have, however, focused on both external and internal morphology and their correlations. This study focuses on comparative anatomy between extant birds and ornithomimid dinosaurs in an effort to reconstruct the beaks of these gracile dinosaurians. The results show a close relation in shape between the examined birds and the ornithomimids, and point towards a beak suited for omnivory (feeding on animals small enough to swallow whole) or high-fibre herbivory.

Introduction

The many different shapes and sizes of the beak or bill of birds (*rostrum* in Latin) are thought to mainly be the result of adaptations to different ecologies. Accordingly, beak morphology can tell us important aspects of the birds' ecology. For instance the beaks of Anseriform birds (ducks and geese) are flattened dorso-ventrally, laterally expanded, and have vertical lamellae on the overlapping margins of the upper and lower jaw, which makes them adapted to filter small invertebrates and plants from the water; whereas Falconiform birds (birds of prey) have a sharp beak with a curved anterior part suited for tearing off flesh. Other birds have long probing bills or short powerful beaks to crack open nuts.

The beak itself consists of the upper and lower jawbones with a horny cover called *ramphotheca*. The terminology used on different parts of the beak is given in Figure 1. In many birds like albatrosses and gulls this covering surrounds the nostrils, but in parrots and birds of prey the ramphotheca extends only as far back as to the anterior border of the external nares. Posterior to this the rostrum is covered with skin and feathers. The horny sheath is made up of β -keratin (Bragulla *et al.* 2003 and Wu *et al.* 2004a). The same substance is found in bird feathers and in reptile scales (e.g. crocodilians, squamates, chelonids and rhynchocephalids) – here along with α -keratin (Wu *et al.* 2004a). In mammalian hooves, claws, and hair only α -keratin is found (Bragulla *et al.* 2003 and Wu *et al.* 2004a). Presumably mammals either diverged from the bird and reptilian lineage before β -keratin production evolved, or they lost it secondarily from their ancestor (Wu *et al.* 2004a). Keratin growth-rate may vary between species, and the location of the keratin producing layer also depends on the positions of maximum wear on the beak. The production zone is located near the point of wear so that the beak will always have a sufficiently thick layer of keratin covering it. If the production zone is located too close to the zone of wear zone, keratin will accumulate and de-sensitize the area (Gerritsen 1988).

In addition to the beak of birds, beak-like structures are found in a large variety of animal groups. The Platypus is popularly considered a beaked mammal. However, I will not discuss the platypus bill further here since it differs in important aspects from bird bills - it is a leathery coating rather than a horn-covered bill and it does not contain β -keratin as it belongs to a mammal. More closely related presently found bill structures are those in chelonids (turtles and tortoises) in which the ramphotheca covers the premaxilla, maxilla and the dentary (Wyneken 2001).

To find further similar structures we have to look into the fossil record. Here we come across several groups which during their evolutionary history developed a horny cover in the oral region. The earliest recorded reptiles with beak-like structures are the Permian *Diictodonts*, which are mammal-like reptiles (Sullivan *et al.* 2002), and the Triassic archosaurs *Silesaurus opolensis* (Dzik 2003) and *Effigia okeeffeae* (Nesbitt 2007) (only anterior most on the dentary in *S. opolensis*). Whether these organisms produced β -keratin or not remains unknown. Any evidence for either would be an important contribution to the understanding of mammal and reptile evolution.

Several dinosaur groups evolved beaks, especially among the ornithischian dinosaurs. Stegosaurids, Ankylosaurids, Ceratopsids and Hadrosaurs all evolved beaks in one form or another – the latter a duck-like bill and the other three a beak more like that of a parrot or turtle. This feature was presumably not something inherited by the most recent common ancestor of these four groups, and therefore probably evolved independently in at least some of the groups. In saurischian dinosaurs beaks were only present in later forms. Among theropods we find these structures in the more derived forms such as oviraptorids and ornithomimosaurs, whereas the more primitive forms still retained teeth. Since these two groups belong to different clades, in which the primitive forms have teeth, beaks have had to evolve separately in these two groups (Figure 2). Moreover, since we find beaks in both ornithischians and saurischians but not in their common ancestors the structure must have evolved at least twice (which would be the most parsimonious explanation), in dinosaurs alone. Regarding birds the fossil record shows that beaks evolved at least three times (Figure 2).

So why have so many groups of animals evolved a beak-like structure? It is hypothesized that it might have been advantageous in handling food items and nesting material (Chiappe 2007). Other advantages may be in probing feeding habits where a smooth keratin-covered surface would reduce friction. One might also hypothesize that a beak is less costly to produce than a robust jaw with teeth. It probably also contributes in lightening of the skull, which in early non-flying birds would be a pre-adaptation to flight. Several publications produced during the last few years on growth factors in the avian beak show that the genetical developmental program for teeth still lies dormant in the avian genome (Harris *et al.* 2006, Wu *et al.* 2004(a and b) and 2006, and Chiappe 2007). This was particularly well proven in a paper by Harris *et al.* (2006), where they managed to grow teeth in a chicken mutant by altering the oral/aboral junction early in development. They also concluded that their model permits regional growth of teeth, as seen in many non-avian dinosaurs and birds (e.g. Hesperornis). The origin of beaks is difficult to explain. However, in all egg-laying species the young develop an egg tooth used to cut/crack open the egg shell, which is made up of the same substance as the beak itself. It would appear that it is an easy structure to evolve as it has evolved independently in so many groups.

As mentioned above, ornithomimids were one of the dinosaurian families in which beak-like structures evolved. The evolution of beaks in Ornithomimosaurs is thought to have happened via stages of reduction of teeth in the upper jaw and dentary, as seen in the reduced maxillary tooth-row in *Pelecanimimus* and the edentulous upper jaw and posterior dentary of *Harpymimus* and *Shenzhousaurus* (Ji *et al.* 2003 and Pérez-Moreno *et al.* 2004). Ornithomimosaurs are represented by eleven different species worldwide. Seven of which are Asian (*Shenzhousaurus orientalis*, *Harpymimus oklandikovi*, *Garudimimus brevipes*, *Archaeornithomimus asiaticus*, *Gallimimus bullatus*, *Sinornithomimus dongi*, and *Anserimimus planinychus*), one European (*Pelecanimimus polydon*), and three North

American (*Ornithomimus velox*, *Ornithomimus edmontonicus*, and *Struthiomimus altus*). They were a group of rather gracile theropod dinosaurs found in Cretaceous rocks in North America, Asia, and Europe. They had robust legs for running and three long fingers on each hand. Later forms of these dinosaurs evolved beaks while more primitive forms like *Pelecanimimus* retained teeth (Perez-Moreno *et al.* 1994). Classification within ornithomimidae (Figure 3) has been based primarily on postcranial material because few well-preserved skulls have been excavated until relatively recently. The new skulls along with more postcranial skeletons have led to revisions regarding the interrelationship of these groups as well as to the relationship between ornithomimids and other theropods (Russell *et al.* 1972, Ji *et al.* 2003).

In addition to interrelationships between ornithomimosaur their diet has also been the subject of debate. Everything from carnivore and omnivore to herbivorous and filter-feeding habits has been suggested (Osmólková *et al.* 1972, Nicholls *et al.* 1985, Norell *et al.* 2001, and Barsbold *et al.* 1990). A herbivorous or omnivorous diet might appear better supported by evidence as specimens with gastroliths have been found (Kobayashi *et al.* 2001 and 2003). Two specimens with preserved remains of the ramphotheca have also been recovered (*G. bullatus* and *O. edmontonicus*), showing that the keratin covered at least the ventral surface of the premaxilla and the rostral part of the dentary. The columnar property of the ramphotheca of *G. Bullatus* led Norell *et al.* (2001) to hypothesize a filter-feeding behaviour for ornithomimosaur. This was rejected by Barrett (2005) who argued that the columnar structures were an integral feature of the ramphotheca and not lamellae as in Anseriform birds. He also postulated that filter-feeding would not have been sufficiently effective to cope with the energy-need of these animals, and that the ramphotheca combined with gastroliths were more consistent with high-fibre herbivory.

In this study the properties of bird rostrums – bone and ramphotheca - and the rostral part of the skulls of two North American representatives from the family *Ornithomimidae* – *Ornithomimus edmontonicus* (Sternberg 1933) and *Struthiomimus altus* (Osborn 1917) – will be examined. The results will be used to try to reconstruct the keratin sheath in these two. It will also be discussed whether this gives new information regarding the dietary habit of ornithomimosaur. Little has previously been done on avian jaw morphology. To quote Zusi (1993): “Avian systematic in the twentieth century has focused on the species and subspecies levels, emphasizing on external morphology, rather than on comparative anatomy and phylogeny at higher levels”.

The key questions to answer in this study will be:

1. Which bones are covered by ramphotheca?
2. Which properties of these bones tell us that they are covered by ramphotheca (surface, size, and relation to other bones in the skull)?
3. Do the ramphothecal properties vary along the rostrum?
4. Are any of this transferable to ornithomimids?

Materials and Methods

To get a rough idea of general skull-shape in the different bird orders compared to that of the dinosaurs in question, morphometric measures were taken of both groups and an ordination analysis was performed on the dataset. Skulls from the bird orders that were found to be morphologically closest to the ornithomimid skulls according to the ordination analysis were chosen for further use in the comparative analysis.

Dataset

The data were gathered in co-operation with Stig Olav K. Jansen who was conducting a similar analysis, on the oviraptorids.

Measurements were selected that would best represent the general shape of the skulls, and different ratios of these were used in the ordination analysis. We only used measurements performed on specimens in lateral view, as one of the ornithomimid skulls was preserved in this orientation. Furthermore we did not use any measurements of the mandible, as this was not entirely revealed in all the ornithomimid skull casts. The measure definitions chosen are listed below, and the dataset is presented in appendix 2.

Measurements chosen:

1. Skull length (**S_L**) – total length at maximum.
2. Cranium height (**C_H**) – measured from the basioccipital to the top of the skull.
3. Cranium length (**C_L**) – measured from above the posterior margin of the antorbital fenestra to the posteriormost point.
4. Rostrum length (**R_L_1**) – measured in a straight line from above the antorbital fenestra to the tip of the rostrum.
5. Rostrum length (**R_L_2**) – same as above, but measured along the surface.
6. Rostrum height at mid-length (**R_H**)
7. Rostrum curvature (**Cur**) – R_L_2 divided by R_L_1 .

Ordination

To perform the analysis PAST version 1.61 was used. We ran a PCA-analysis with the var-covar setting.

The result is presented in Figure 4. The ordination plot shows that Psittaciformes and Oviraptorids are only connected to each other (distinguished by having the most curved rostrums) and not to any other groups. To the left in the plot Ornithomimids fall into line with Struthioformes, Procellariiformes, and Anseriformes along axis 1. Some separation is apparent in axis 2, which is due to differences in rostrum-height to skull-height ratio. Within Galliformes one taxon diverges from the other two. This is *Numida meleagris* which has a distinct bony crest on the top of its head. More skulls could have been used in this analysis, but it was only conducted to show general differences in skull morphology.

Skulls

Procellariiformes was one of the groups close to the ornithomimid skulls in the ordination analysis, three skulls of representatives from *Diomedidae* (albatrosses) were examined, and one skull of *Pachyptila sp.* from the family *Procellariidae*.

The second group close to the ornithomimids was Anseriformes. Examination of one skull of the species *Clangula hyemalis* (Long-tailed Duck) was conducted. A skull of a Peking duck

(breed of domestic duck) was dissected to determine the extent and properties of the anseriform ramphotheca.

The third group chosen was Galliformes. One skull of the species *Meleagris gallopavo* (wild turkey) was examined.

The fourth and last group included in this analysis was Struthioformes (ostriches). Here one skull of the species *Struthio camelus* (African ostrich) was analysed. In addition another specimen of the same species was dissected to determine the extent and properties of the struthioform ramphotheca.

Skulls used for thorough examination:

Ornithomimus edmontonicus (TMP 2002.00.5) - a cast of the right lateral side and a photography of the left lateral side of the skull of specimen (TMP 95.110.1), located at the Royal Tyrell Museum of Palaeontology, Alberta, Canada. The skull is somewhat compressed laterally which has caused some crushing in the mandible and snout. This specimen is briefly discussed by Norell *et al.* (2001) in an article on the beaks of ostrich dinosaurs.

Struthiomimus altus (TMP 90.85.1) - a cast of the skull TMP 90.26.1 from the Royall Tyrell Museum of Palaeontology, Alberta, Canada. The skull is referred by Kobayashi *et al.* (2005b) *Struthiomimus altus*. The skull show some crushing of the cranium due to dorsal compression which has also resulted in some displacement of certain bones and some lateral expansion of the upper jaw (especially the left side). Some surface damage on the premaxillaries and maxillaries are also apparent. No lateral compression is visible.

PROCELLARIFORMES

Diomedidae (A-1, A-2 and A-3) - three non-recorded skulls borrowed from the Biological Institute at the University of Oslo. Being without name or number the skulls were temporally numbered for the purpose of this analysis.

The first skull (A-1) has a relatively complete exterior, but the cranium interior is missing. On this specimen the ramphotheca has been removed to reveal the underlying bone-surface. The second skull (A-2) is complete, and has maintained its ramphotheca. The third skull (A-3) lack the mandible, but is otherwise complete and with ramphotheca.

Specimen A-2 and A-3 were used to theoretically reconstruct the removed ramphotheca on specimen A-1. A more thorough examination was carried out on A-1, which lack a horny sheath, as the sub-ramphothecal structures are of importance when comparing with the fossil material.

Pachyptila sp. (ZMO 1337) - the skull is complete with both upper and lower jaw, but without any ramphotheca.

GALLIFORMES

Meleagris gallopavo (ZMO 2820) - a complete skull without ramphotheca.

ANSERIFORMES

Clangula hyemalis (ZMO 5907) - a relatively complete skull - only the right quadratojugal-jugal-maxilla complex is damaged and the posterior of the cranium is crushed – without ramphotheca. As well as one dissected Peking duck specimen.

STRUTHIOFORMES

Struthio camelus (ZMO 2644) - complete skull of one adult of the species without ramphotheca, as well as one dissected specimen of the species (unnumbered).

Other skulls used in this study:

Order	Species	No.		Order	Species	No.
Anseriformes	<i>Cygnus cygnus</i>	ZMO 2931		Galliformes	<i>Numida meleagris</i>	ZMO 1362
Anseriformes	<i>Somateria spectabilis</i>	ZMO 5056		Passeriformes	<i>Corvus seapulatus</i>	ZMO 1157
Anseriformes	Unknown	ZMO 5582		Passeriformes	<i>Corvus albicollis</i>	ZMO 1156
Anseriformes	Unknown	ZMO 6025		Procellariiformes	<i>Pachyptila sp.</i>	ZMO 1034
Anseriformes	Unknown	ZMO 5365		Psittaciformes	Unknown	ZMO3540/1340(?)
Anseriformes	<i>Anas clypeata</i>	ZMO 5531		Psittaciformes	<i>Psittacus sp.</i>	ZMO 4916
Anseriformes	<i>Anser albifrons</i>	ZMO1021		Psittaciformes	<i>Psittacus sp.</i>	ZMO 4915
Anseriformes	<i>Cygnus bewickii</i>	ZMO 6258		Psittaciformes	<i>Cacatua galerita</i>	ZMO 360/65
Caprimulgiformes	<i>Podargus cuvieri</i>	ZMO 5650		Struthioniformes	<i>Struthio camelus</i>	ZMO 3636
Charadriiformes	<i>Cephus grylle</i>	ZMO 698		Struthioniformes	<i>Struthio camelus</i>	ZMO 346/65
Falconiformes	<i>Aquila albicilla</i>	ZMO 690				
Falconiformes	<i>Pernis apivorus</i>	ZMO 4036				
Galliformes	Unknown	ZMO 3141				

The Ornithomimid skull

In this section the skulls of *Ornithomimus edmontonicus* (TMP 2002.00.5, Figures 5-6) and *Struthiomimus altus* (TMP 90.85.1, Figures 7-9) are described and then compared with other previously described ornithomimosaurs. The description is of the rostral part of the skull and of the entire mandible.

Ornithomimus and Struthiomimus

SYSTEMATIC NOMENCLATURE

DINOSAURIA Owen, 1842

THEROPODA Marsh, 1881

ORNITHOMIMO AURIA Barsbold, 1976

ORNITHOMIMIDAE Marsh, 1890 *sensu* Smith and Galton 1990

ORNITHOMIMUS Marsh, 1890

Ornithomimus edmontonicus Sternberg, 1933.

And

STRUTHIOMIMUS Osborn, 1917

Struthiomimus altus Osborn, 1917

General skull morphology

The overall shape of the two skulls examined here is very similar, both being gracile and equipped with large orbits and long edentulous rostrums. *O. edmontonicus* (TMP 2002.00.5) and *S. altus* (TMP 90.85.1) differ from one another in the ordination-analysis but this is because the skull of *S. altus* (TMP 90.85.1) is crushed and made measuring difficult. No doubt, if complete, the difference between the two would be less marked.

Skull openings

The external narial openings are located anterior-most on the snout on both specimens, and are bordered dorsally, anteriorly, and ventrally by the premaxillaries, and posteriorly by the nasals. The openings are in lateral view oval in shape, and tilt slightly forward. In dorsal view the nares of *S. altus* (TMP 90.85.1) are positioned close together and comprise the major part of the snout. This is possibly also the case in *O. edmontonicus* (TMP 2002.00.5) but it is obscured because of lateral compression.

The antorbital fossa contains the antorbital fenestra, the maxillary fenestra and the premaxillary fenestra. The antorbital fossa is approximately one-third of the skulls total length (70 mm in TMP 2002.00.5), and the antorbital fenestra is approximately half the length of the antorbital fossa. The size of the antorbital fenestra relative to the antorbital fossa cannot be determined in *S. altus* (TMP 90.85.1) as the former is not visible on the cast, but the latter is approximately one third of the total length of the skull (65 mm).

The orbit is round in shape and is completely separated from the antorbital fenestra by the prefrontal-lacrimal-complex which connects to the jugal. In *S. altus* (TMP 90.85.1) the orbits show a more oval shape, though this could be due to compression of the skull.

Premaxilla

The premaxilla makes up the majority of the narial borders except for the posterior. The bone consists of a main body with three posterior-pointing processes. The dorsal process - which is slightly crushed in *O. edmontonicus* (TMP 2002.00.5) - makes up the dorsal ridge of the narial opening and connects to the nasals just posterior to the middle of the external nare. In *S. altus* (TMP 90.85.1) the premaxillaries wedge between the two nasal bones and end approximately at level with the anterior end of the antorbital fossa. It is likely that this is also the case in *O. edmontonicus* (TMP 2002.00.5) but this is not deducible in this specimen. The middle process is the longest, and it is wedged between the nasal and the maxilla towards the back. This and the ventral process make up the connection to the maxilla. In *O. Edmontonicus* (TMP 90.85.1) the suture makes a sharp turn backwards at level with the posterior end of the external narial opening, making the ventral process slightly longer than in the *S. altus* (TMP 90.85.1) where it is almost perpendicular to the upper jaws ventral margin.

The ventral margin of the premaxilla is pitted with foramina. The pits are mostly oval and vary in depth and inclination and become shallower towards the ventral margin of the premaxilla. The pits in *S. altus* (TMP 90.85.1) is not as conspicuous due to light crushing of the snout, so the size and depth is not clearly visible. There are also some pits located posterior to the premaxilla-maxilla connection (subnarial foraminae). On the ventral margin of *O. edmontonicus* (TMP 2002.00.5) just below the pits, there are remains of what would have been the keratinous covering, the ramphotheca which is discussed below. In *O. edmontonicus* (TMP 2002.00.5) the entire ventral margin of the premaxilla forms a cutting edge. In *S. altus* (TMP 90.85.1) the edge is only visible in the posterior third of the bone, but presumably it persists in its entire length. In *S. altus* (TMP 90.85.1) there are several small parallel grooves on the bone surface of the middle process close to the narial opening. This is not seen in *O. edmontonicus* (TMP 2002.00.5).

Maxilla

The maxilla is boomerang-shaped, in lateral view, in both specimens with two posterior-facing processes. The dorsal process is broader than the ventral and separates the nasal from the antorbital fossa and the premaxilla from the antorbital fenestra. The ventral process makes up the majority of the ventral margin of the antorbital fossa, and contact with the ventral side of the jugal at level with the posterior fourth of the margin.

In *O. edmontonicus* (TMP 2002.00.5) there are at least seven pits along the ventral margin of the maxilla from the anterior fourth of the antorbital fossa to the maxilla-premaxilla suture. There are also several pits on the main body of the maxilla that form a diagonal line between its ventral and dorsal border. These pits are not as conspicuous in *S. altus* (TMP 90.85.1) due to crushing of the surface. The anterior three fourths of the ventral margin of the maxilla form a cutting edge and get rounded towards the jugal.

Nasal

The nasal is long and slender and makes up the posterior border of the external narial opening. The nasal bones in *S. altus* (TMP 90.85.1) extend from the posterior end of the narial opening to approximately the posterior end of the prefrontal (as mentioned by Kobayashi *et al.* 2005b). The two bones in this specimen have been compressed dorsally and fractured, at approximately mid-length. In *O. edmontonicus* (TMP 2002.00.5) the two nasals have been slightly compressed laterally, causing a small ridge between them (only the right side is present in the cast and its dorsal side is facing laterally due to compression). There are about 5 foramina on each nasal bone, the first approximately above the middle of the antorbital fossa to approximately 10 mm anterior to the posterior end of the premaxilla.

Mandible

The general shape of the mandible is slender, slightly bent making a dorsal arch composed of the dorsally expanding process of the surangular. Posterior to the symphysis the dentary narrows and is spoon-shape. The mandibular is visible in both specimens and have a narrow oval shape. In *O. edmontonicus* (TMP 2002.00.5) the prearticular and splenial are visible due to missing pieces of the dentary's posterior part.

Dentary

The dentary is the longest bone in the mandible and is about half its length. The anterior fourth of the dentary forms a cutting edge on the dorsal margin which becomes more round posteriorly, and the mid-section of the dorsal margin is overlapped by the maxilla when the jaws are closed. The symphysis lies in an oblique angle and gives the dentary a shovel-like shape – as in *Gallimimus bullatus* (Osmólska 1972 and Hurum 2001) The symphysis is 36 mm long in *O. edmontonicus* (TMP 2002.00.5) and 28 mm long in *S. altus* (TMP 90.85.1). The middle transverse surface area is depressed in the posterior three fourths, making a > shaped depression (Figures 5 and 7). The main surface of the bone is smooth, except for the presence of foramina along the dorsal margin in the anterior two-thirds. The pits form a line following the dorsal margin the symphysis suture before turning backwards forming an almost circular pattern. The individual pits penetrate the bone in an angle – as in the premaxilla - and their shallow end points backwards posteriorly but becomes vertical at the symphysis. In *S. altus* (TMP 90.85.1) there is one large foramina anterior-most on the dentary and one slightly smaller at level with the posterior end of the symphysis. This is not visible on the cast of *O. edmontonicus* (TMP 2002.00.5), but it could be present on the original specimen. The anterodorsal margin of the dentary in *O. edmontonicus* (TMP 2002.00.5) bears, as on the premaxilla, remains of the ramphotheca (described below). In *S. altus* (TMP 90.85.1) the dentary-surangular-angular suture is relatively intact, and is W-shaped with a long ventral posterior-pointing projection covering the angular exteriorly. In *O. edmontonicus* (TMP 2002.00.5) the shape of the dentary-surangular and dentary-angular sutures are difficult to deduce due to missing pieces of the dentary, surangular and angular, exposing the prearticular and the splenial. However, the dentary seems to have met the angular right below the middle of the visible mandibular fenestra. The “hinge” where the surangular wedges between the medial and lateral processes of the dentary (Hurum 2001) is visible on the cast, and has been completely revealed on the left side.

Surangular

The surangular bone is about the same length as the angular. The ventral side of the bone connects to the angular in the posterior half, and the middle part makes up the dorsal border of the mandibular fenestra. The posterior half the surangular has a laterally expanding process which makes contact with the quadratojugal in the upper jaw when jaws are in closed position. The surangular is dorsally slightly overlapped by the jugal when jaws are closed. In *S. altus* (TMP 90.85.1) there is a foramen just above the middle of the surangular-angular suture. This is not visible in *O. edmontonicus* (TMP 2002.00.5) perhaps due to the nature of the preparation.

Angular

The angular is long – about as long as the surangular - with the anterior part, which wedges between the dentary and the splenial, being narrower than the posterior part. The anterior seems to expand slightly towards the end before being overlapped by the dentary. The angular makes up the ventral margin of the mandibular fenestra.

Articular

In *O. edmontonicus* (TMP 2002.00.5) the articular is horn-shaped in lateral view with the pointed end facing downwards. The connection with the angular makes up approximately two thirds of its anterior margin, the last third being the surangular-articular suture. In the studied specimen of *S. altus* (TMP 90.85.1) the articular's have been pushed forward and inwards by the compression of the skull. In the specimen described by Osborn (1917), however, the articular (at least on the left side) is complete and it shows an elongate lateral surface and semicircular cross-section. Regrettably, Osborn did not describe the bone in detail.

Ramphotheca

On the ventral and dorsal margin of, respectively, the premaxilla and dentary in TMP 2002.00.5 traces of the ramphotheca are present. The lower ramphotheca is approximately 25mm long and the upper ramphotheca about 27 mm, and when the jaws would be in closed position the keratin elements would fill the gap between the premaxilla and dentary (Norell *et al.* 2001). Both the premaxilla and the dentary have a straight anterior part of about 45mm and the preserved remains of the ramphotheca are located at the anterior part of this area, tapering posteriorly.

Other Ornithomimids

Other ornithomimid cranial material previously described includes *Gallimimus bullatus* (Osmólska *et al.* 1972 and Hurum 2001), and *Sinornithomimus dongi* (Kobayashi *et al.* 2003). All these share the same general skull morphology as *Ornithomimus edmontonicus* (TMP 2002.00.5) and *Struthiomimus altus* (TMP 90.85.1) in being slender and having large orbits and edentulous jaws. Exceptions are the shape and composition of the snout in *G. bullatus* – being longer and blunter, and in having a rising ventral margin in the premaxillary – and the relatively shorter antorbital fenestra in *S. dongi*, along with its lack of lateral foramina in the maxillary and dentary. Of other ornithomimids – *Ornithomimus velox* (Marsh 1890), *Archaeornithomimus asiaticus* (Gilmore 1933), and *Anserimimus planinychus* (Barsbold 1988) - only post cranial material is available.

Regarding more primitive ornithomimosaur, however, skulls of *Pelecanimimus polydon* (Perez-Moreno 1994), *Shenzhousaurus orientalis* (Ji *et al.* 2003), *Harpymimus oklandikovi* (Barsbold *et al.* 1984 and Kobayashi *et al.* 2005a), and *Garudimimus brevipes* (Barsbold 1981 and Kobayashi *et al.* 2005b) are available. Of these only the latter has an edentulous rostrum. *P. polydon* is considered the most primitive of the group, as it has minute teeth without interdental space in both the upper and lower jaw (Perez-Moreno 1994 and Kobayashi *et al.* 2005b). Teeth are also found in *H. oklandikovi* and *S. orientalis* but here they are restricted to the anterior portion of the dentary (Ji *et al.* 2003, Barsbold *et al.* 1984 and Kobayashi *et al.* 2005a). Except for in *H. oklandikovi*, lateral foramina in the dentary and maxillary are found in all of these taxa. Premaxillary foramina, though, are present in all taxa. Kobayashi and Barsbold (1984) hypothesized that the premaxillary of *H. oklandikovi* might have been covered by a ramphotheca as suggested for *Gallimimus* and *Ornithomimus* (Norell *et al.* 2001).

The Avian Skull

In this section I will describe the skulls of general paleognathous and neognathous birds based on these skulls: *Diomedidae* - albatrosses (A-1, A-2 and A-3, Figures 18-27), *Pachyptila sp.* - prions (ZMO 1337, Figures 28-31), *Meleagris gallopavo* – Wild turkey (ZMO 2820, Figures 14-17), *Clangula hyemalis* – Long-tailed duck (ZMO 5907, Figures 32-35), *Struthio camelus* - African ostrich (ZMO 2644, Figures 10-12). In addition the dissected specimen of the Peking duck and the *Struthio camelus* are described.

The terminology used is that given by Zusi (1993).

General skull morphology

A typical bird skull is elongate, with large orbits tapering towards the tip of a long rostrum made up of edentulous jaws which is covered by a horny sheath, known as the ramphotheca. A large number of variations exist though. Ranging from long and tubular to short and flat beaks, and high and low profile skulls. Flat rostra are likely to be wider than tubular rostra.

Skull openings

In both paleognaths and neognaths the temporal fenestrae and the antorbital fenestra have merged with the orbit. The external bony nares can be elongate and extend almost the entire length of the rostrum, or they can be restricted to, usually, the posterior part. Where they are elongate the posterior portion gets covered by membranous tissue making only the anterior part penetrating the ramphotheca (see Witmer 2001 for more on nostril position).

Premaxilla

The premaxillaries compose the majority of the rostrum having two posterior-facing processes. The dorsal one connects to the nasals posterolaterally and to the mesethmoid. The lateral process makes up the anterior and lateral border of the external nare, and connects posterodorsally to the nasal and posteroventrally to the maxilla (which anterior part it overlaps in various degrees). In some birds - especially Galliforms – the maxilla-premaxilla connection is only made via a ligament and the junction is not ossified (Figure 14). Anteriorly the two premaxillary bones fuse to form the tip of the beak. Their extent in the palate varies between different orders of birds as well as between neognaths and paleognaths (this topic is also discussed by Zusi (1993). In the paleognaths (in this study represented by *Struthio camelus* (ZMO 2644)) the palatal element of the premaxillaries are split and short compared to that of neognaths. They end laterally at their connection to the maxillaries at mid-length of the rostrum, and anteriorly at the margin of the choana. In neognaths (here represented by members of *Diomedidae*, *Pachyptila sp.*, *Clangula hyemalis*, and *Meleagris gallopavo*) the premaxillaries comprise most of the ventral part of the rostrum. They are fused all the way to the choana (if present), and then split to wedge between the maxillaries and the maxillopalatines (can also overlap the maxillaries completely). Within neognaths the posteroventral elements of the premaxillaries connect to the maxillaries and/or to the palatines (Zusi 1993). The exterior anterior surfaces of the premaxillaries are pitted with foramina in various degrees. Typical is a relatively smooth –not entirely even in most cases - surfaced posterior to a densely pitted distal tip. This is particularly apparent in Anseriforms and Struthioforms which have a maxillary nail on this area. Dense pitting is less in other birds but in most cases it is still restricted to the anterior part of the rostrum. Specimen A-1 from the *Diomedidae* family – which have a ramphotheca consisting of separate plates – has a more densely pitted apex than the Galliforms, Charadriiforms and Ciconiiforms of this study. In all birds studied here, the foramina penetrate the bone at various angles with their openings thus

pointing in different directions. Generally they point towards the margins of the bone. In the apex of Struthioforms and Anseriforms they form a flowering like pattern, starting in a perpendicular angle at the apex's mid-point and turning outwards (Figure 13).

Maxilla

The maxilla connects anteriorly to the premaxilla and nasal and is usually overlapped by the either of these in neognaths. In paleognaths the nasal does not make contact with the maxilla (Zusi 1993), and the overlapping by the premaxilla tapers posteriorly revealing more of the maxilla moving backwards. The premaxillary overlapping of the maxilla varies between bird orders and within orders and more study is needed to identify at what taxonomic level this no longer holds. In the specimens examined here the maxilla is revealed in various degrees in lateral view. But the anterior of the maxilla can be totally overlapped as well, e.g. in the Galliforms of this study (see also Chiappe 2007 on domestic chicken skulls). Posteriorly a slender process of the maxilla connects to the jugal and the quadratojugal. The palatal process of the maxilla, the maxillopalatine, overlaps the palatine dorsally and is revealed between the palatine and the vomer in ventral view. In Anseriforms the maxilla makes up the posterolateral surface of the palate, connecting with the premaxilla anteriorly and the palatines medially. In Galliform and Charadriiforms however, the maxilla wedges between the ventral process of the premaxilla and the palatine. In the overlap area between the maxilla and premaxilla there are foramina in the Procellariiforms and Anseriforms studied here. This is not seen in any of the other study specimens. The maxilla is usually separated from the margin of the external nare by the nasal, or the premaxilla, or both.

Nasal

The nasal connects laterally to the lacrimal, medially to the premaxillary and the mesethmoid, posteriorly to the frontal, and in neognaths to the maxilla ventrally - and premaxilla in the cases where this overlaps the maxilla. The bone makes up the posterior margin and part of the dorsal margin of the external nare and in neognaths, also part of the ventral margin.

Palate

The palate consists of the pterygoids, the palatines, and the vomer. The anterior of the pterygoids connect via a flexible joint to the posterior palatines in neognaths, but are fused in the paleognaths (Chiappe 2002). The palatines run on either side of the vomer and connect with the posterior of the maxillaries (*S. camelus* (ZMO 2644)) or premaxillaries (neognaths). The vomer of many paleognaths connect with either the maxillaries or the premaxillaries - neither in *S. camelus* (ZMO 2644) - and is much reduced in neognaths (Zusi 1993), which is part of their definition (Chiappe 2002).

Mandible

The general bird mandible is long and slender with a dorsally expanding process posteriorly, ending in either a pointed tip or a flat spoon like tip. Its depth varies as well as its width. Flat, shallow mandibles are also likely to be wide and vice versa.

Dentary

The dentary is the longest bone in the mandible and makes up the entire lower jaw tomia. The symphysis is either oblique (Charadriiformes, Passeriformes) or horizontal (Procellariiformes, Galliformes, Anseriformes, Falconiformes, Psittaciformes). There is a > shaped depression on the lateral surface with varying extent starting at the posterior most part of the bone (Figures 10, 15, 19, and 29). The lower jaw tomia is overlapped by the upper jaw, and it forms a

cutting edge in its entire length – except in Struthioforms and Anseriforms where the tomia is flat and rounded respectively. Along the dorsal margin of the dentary there are several foramina, except for in *S. camelus* (ZMO 2644). These appear in different patterns. In the Procellariiform birds they come in triplets diverging from each other moving anteriorly. In Anseriforms they follow the margins of the “lip” made up by the dorsal margin of the dentary. In Struthioforms and in the Galliforms studied here the foramina are restricted to the area around the symphysis. Struthioforms and Anseriforms have in the dentary as in the premaxillary a densely pitted anterior region (here the symphysis area). The foramina penetrate the bone in an angle, with their opening towards the tomia along the entire dentary.

Surangular

The surangular is long and slender with a dorsal expansion which varies in height and shape between different birds – being relatively high in the Anseriforms of this study. The surangular also have a lateral process at mid-length. Anteriorly the bone is wedged between the inner and outer processes of the dentary. The posterior connects to the articular, and the ventral to the angular. The surangular makes up the dorsal margin of the mandibular fenestra, where present.

Angular

The angular is about the same length as the surangular, and connects posteriorly to the articular, dorsally to the surangular, and its anterior wedge between the dentary and splenial. The angular makes up the ventral border of the mandibular fenestra, where present.

Articular

The articular connects anteriorly with the surangular and angular. The bone shows generally two varieties of shapes in the birds examined, either almost triangular (Struthioformes and Procellariiformes) or elongate with a crescent shaped posterior process (Anseriformes).

Ramphotheca

Diomedidae

The ramphotheca of the upper jaw on both skull A-2 and A-3 (Figures 22-27) extend as far back as to where the maxilla is reduced to a shaft-like structure laterally, and to the rugose band (Figure 20) between the narial openings dorsally. The posteriolateral edge of the ramphotheca forms a V with the pointy end towards the external nares. The upper jaw ramphotheca itself consists of mainly three separate plates – *maxillary unguis*, *culminicorn* and *latericorn* (Figures 22-27). On skull A-2 the ramphotheca has formed an anterior facing tube on the posterior edge of the narial which, in this case, makes up a fifth plate. This is not present in skull A-3, perhaps lost during the conservation process, or later, as some cracks is apparent in this area.

The mandibular ramphotheca is only present in skull A-2 as skull A-3 lacks a lower jaw. In skull A-2, it extends dorsally to the posterior end of the dentary but is a little shorter ventrally. The edges form a > shape like in specimen A-1. The lower jaw ramphotheca also consists of three different plates – *mandibular unguis*, *ramicorn* and *inter-ramicorn*.

Peking duck – dissected specimen

In this specimen the keratin cover of the rostrum was removed from the right side to determine its make up and distribution. It was found that the keratin-layer between the nostrils and the maxillary nail was thinner than that of the nail. It did not cover the posterior part of the external nares (in the underlying bone), and extended almost as far back as to the posteroventral end of the rostrum. The dorsal border of the ramphotheca was about at level

with the middle of the nostrils. The lamellae and tomia of both the upper and lower jaw were softer than the other keratinized regions, but this might be the result of the conserving ethanol the specimen was in and the fact that it is not supported with bone in this region. The maxillary nail consisted of thick layer of hard keratin which covered the foramina-rich anterior region of the rostrum.

The lower jaw ramphotheca extended back to the posteriodorsal end of the dentary, and the keratin-layer between this point and the mandibular nail was as thin as in the upper jaw. The nail too was like the maxillary nail hard and thick keratin covering the foramina region anteriormost.

Struthio camelus – dissected specimen

Though very decomposed, this specimen showed that the keratin covering the maxillaries were softer than that covering the rostral ridge and maxillary nail. This was also the case in the mandible. The mandibular nail was thicker and harder than the lateral keratin cover. The posteriodorsal border of the upper jaw ramphotheca was approximately at level with the middle of the nostrils, and the posteroventral border was in about half-length of the bony external nare. The posterior border of the lower jaw ramphotheca was approximately at the posterior end of the dentary depression (Figure 10).

Comparison of ornithomimids and birds

The description of the avian and ornithomimid skulls in the former chapters reveals that features of most interest are the ramphotheca supporting bones (see avian ramphotheca description) viz., premaxilla, maxilla, dentary, and to some extent, the nasals. A comparison of these bones in birds and ornithomimids was therefore made.

General skull morphology

The overall shapes of the ornithomimid and avian skulls are relatively similar (see ordination analysis), but differ in important areas. One, is the relative length of individual bones (see below), another is the location of skull openings. In birds the temporal fenestrae have fused with the orbit and form a large opening – argued to facilitate enlargement of the brain (Chiappe 2007), whilst they are separated in the ornithomimids. The antorbital fenestra has shifted backwards in birds compared to in theropods and is separated from the orbit by the lacrimals connection to the jugal bar-complex. In some birds this separation is lost and the antorbital fenestra joins the orbit and the temporal fenestrae (Zusi 1993). The external narial openings are also “pushed” backwards in birds (one exception being the kiwi in which they are located far anteriorly. But this is a secondary trait) being in the posterior part of the rostrum compared to being anteriorly in ornithomimids. However, some other birds have elongate narial openings extending almost the entire length of the rostrum (as mentioned in the introduction).

Premaxilla

This bone is radically different in birds and ornithomimids. In the latter it constitutes only the anterior part of the rostrum compared to nearly the entire rostrum in birds (except in *S. camelus* (ZMO 2644) where its extent is similar to that of ornithomimids). Even so, it is still confined to the same space in the jaw – relative to the skull openings. It still forms the anterior, ventral and part of the posterior and dorsal margins of the external nares as it does in the ornithomimids. The general surface of the bone is rather smooth except for in the foramina regions in both avians and ornithomimids (at least in the areas not affected by compression). What seems to be typical of the keratin covered regions is that they generally contain foramina and the surface is overall more uneven - presumably to contain vascular tissue and sensory organs, and to more firmly connect the ramphotheca to the bone. The foramina topography itself is different in each avian order. In Procellariiformes the ventral and anterior part of the premaxilla have foramina, but in the Anseriforms and Struthioniforms the foramina are restricted to the anterior area – where also the maxillary nail is also located. Passeriformes have foramina along the ventral margin of the premaxillaries, but not as much in the anterior area than in Procellariiform birds. However, *Pachyptila sp.* (ZMO 1337) which has the same ramphothecal configuration as the Diomedeids, does not show the same amount of rostral aggregation of foramina (could be size related).

Maxilla

The maxillary bone in all ornithomimosaur (in which skull material is available) contributes to a major part and the upper jaw's ventral margin as in other theropods. A difference worth noting, however, is that the posterior part of the maxillary – making up the ventral border of the antorbital fenestra – is a very thin process of the bone in ornithomimosaur (Parks 1928, Barsbold 1981, Perez-Moreno *et al.* 1994, Ji *et al.* 2003, Kobayashi *et al.* 2005 a and b, and 2003) while being much more robust in most other theropods, e.g. *Dromaeosaurus* (Currie 1995).

The anterior surface of the maxilla is in *O. edmontonicus* (TMP 2002.00.5) is pitted but less so along the ventral margin than in *S. altus* (TMP 90.85.1). This could, however, have something to do with preservation and/or the cast making. Though, with only these casts at hand *S. altus* (TMP 90.85.1) show more resemblance to extant birds in this feature. Both procellariiform birds show the same foramina pattern, but neither the ostrich nor the anseriforms have this. The latter two groups only exhibit an anterior accumulation of foramina but at the same time these groups are the only ones in this study to clearly show differentiation in the ramphotheca where the keratin cover is softer and thinner posterior to the maxillary nail.

Nasal

The nasals of ornithomimids differ from that of birds in that the nasals are restricted to a dorsal frontal-premaxillary extension, whilst in birds the nasals also make up the posterolateral part of the rostrum and are much shorter, due to the extension of the premaxillaries.

Mandible

The overall shape and configuration of the mandible is very similar in birds – not just the birds of this study (see Zusi 1993, and Chiappe *et al.* 2002 for examples of more bird configurations) - and ornithomimosaurs (see Hurum 2001 for additional ornithomimid mandibles). The dentary is generally the longest bone in the mandible, followed by the surangular, angular, splenial and prearticular. In both groups the angular is overlapped by the dentary (exteriorly) and the splenial (interiorly), and the surangular is overlapped by the interior and exterior process of the dentary (dorsally).

The feature most striking with the dentary bone of both birds and ornithomimosaurs, and also in sea turtles (personal observation), is the > shaped depression (Figures 5, 7, 10, 15, 19, and 29) on the posterior area. The size and strength varies, but this area marks the point, if present, where dorsal margin foramina start to appear (e.g. the albatrosses described here) or, in some cases, the junction between the rough and smooth surface on the dentary. When describing the specimens with ramphotheca it was noticed that the keratin cover extends as far back as to where the margins of the dentary depression appears. In the birds studied the ramphotheca extends equally far back on both upper and lower jaws.

The mandible too has foramina like those on the premaxilla and/or the maxilla. In the ornithomimids and procellariiforms they appear along the dentary's dorsal margin and follow the curve at the symphysis. In Anseriforms and Struthioforms, however, foramina only appear anteriormost where they are covered by the mandibular nail and similarly the maxillary nail, in the upper jaw. But as mentioned earlier these birds also have a different keratin configuration than that of the procellariiform birds.

Discussion

The above descriptions point to a large divergence in cranial skeletal composition between birds and ornithomimids. One apparent difference is the merging of both temporal fenestra with the orbit, and loss of the postorbital bone in birds. These features lighten the skull and facilitate the development of an enlarged brain. There are also the differences in extent of the bones in the upper jaw (see section on comparison above), which result in repositioning of the external nares – although relative position is retained. One question asked in this study was whether or not there are only a certain set of bones bearing the ramphotheca? This would have

implications, for instance, as to how an enlarged beak would evolve, either by enlarging these bones or evolve ramphotheca growth on other bones as well. The examination showed that most birds have ramphotheca on both the maxilla and premaxilla (and partially on the nasal and palatine in some birds – e.g. Diomedeidea). This is also observed in extant turtles (Wyneken 2001). The maxilla in birds are greatly reduced (Zusi 1993), a property which can be explained in at least two different ways. The first is that this may facilitate cranial kinesis which is observed in most birds (Zusi 1984 and Bout 2001) whereby a more proximal placement of the antorbital fenestra would be preferable to obtain as much vertical thrust on the rostrum as possible since the reverse would give a more horizontal thrust and hinder a sufficient lift of the beak (Zusi 1984). A second explanation for reduced maxilla in birds is that a proximal placement of the external nares was preferable to facilitate, for instance, probing for food in mud or water to prevent either of these to enter the nostrils and thus enabling breathing while feeding. Reduction of the maxilla in both cases would consequently lead to a compensatory lengthening of the premaxilla to maintain the length of the rostrum. Russel (1972) argued that the skull of *Dromiceiomimus breviteritus* (NMC 12228) was kinetic, as the anterior end of the frontals and the frontal-nasal junction are thin in this specimen. Later examination done by Nicholls and Russel (1981) showed that the specimen described by Russel (1972) is referable to *Ornithomimus edmontonicus*. The long antorbital fenestra, however, does not support cranial kinesis, although lowering of the quadrate relative to the jugal-maxilla connection could compensate for the lack of vertical thrust – which is what is illustrated in Russell's (1972) drawings of NMC 12228.

In a beaked organism one would expect to find that the ramphotheca have similar tomia extent in both the upper and lower jaw, this to be able to effectively use the force produced by the muscles. A hard surface against a soft surface would absorb much of the pressure produced. This is also what is observed in birds and turtles (Wyneken 2001), and is therefore what should be expected for ornithomimids. The tomial extent of the mandibular ramphotheca therefore gives the tomial extent of the upper jaw ramphotheca. Also, in birds the antorbital fenestra is not covered by the ramphotheca. The thin ventral border of the antorbital fenestra, made up by the maxilla, in ornithomimids is an indication that this area would not have been exposed to any severe mechanical forces perpendicular to the bone such as when biting. This is a clue to whether one would expect this area to be covered with keratin or not. If the maxillary projection was not directly used to implement biting-force on food items it is not very likely to have been so. This area is also present in birds but is shifted backwards, as mentioned in the comparison above. As predicted for the ornithomimids above, this area is not part of the pressure-surface in extant birds and is not covered with keratin.

The mandibles of the birds and ornithomimids studied here are very similar in shape as well as in surface features. This suggests a similar ramphotheca configuration, which in birds is only supported by the dentary. The posterior border of the ramphotheca is shown to be the > shaped depression in the bone (Figures 10, 15, 19, and 29). This feature is also present in the ornithomimids discussed here (Figures 5 and 7) and probably marks the posterior end of the ramphotheca here as well. The ornithomimid dentary are most similar to that of Charadriiforms – the latter group was also mentioned (there represented by sea gulls - *Larus*) by Hurum (2001) - in the way the anterior of the dentary has a shovel-like shape. It is also similar to the Anseriform dentary in the rounded posterior tomia that is overlapped by the upper jaw.

Beak presence has in many studies been associated with the presence of foramina or pits where teeth are lacking (Dzik 2003, Apesteguía 2004). This is, however, by no means any

obligate association as there are several other groups of animals with teeth that also have these foramina including Crocodilians, monitor lizards, Dromaeosaurs, and Tyrannosaurids. Another argument against such an association is the fact that the ramphotheca also covers areas not having any foramina at all, such as culmen in birds. These areas do, however, have grooves for containing blood-vessels or have a rough surface. The occurrence of pitted surfaces combined with lack of teeth and the formation of a cutting edge will generally suggest the presence of a beak. Studies on upper and lower jaw foramina have been conducted in some birds, especially anseriforms and charadriiforms (Elner 2005, Nebel 2005 and Berkhoudt 1980). These studies show that the small foramina actually house for sensory cells (generally tactile) as well as for blood supply. In birds these sensory cells come in two types: Herbst corpuscles, which detect stimuli perpendicular to the surface and Grandry corpuscles which detect tangential movement (Berkhoudt 1980). A study done by Berkhoudt (1980) on the mechanoreceptors in the mallards bill showed that the corpuscle in some areas are contained within a tube-like papilla which has a keratinized lid, and that these papillae are positioned in the pits in the bone underneath the maxillary and mandibular nail. Detailed investigations of the papillae themselves showed that the corpuscles within them were divided into two layers, the Grandry corpuscles above (more distal) than the Herbst corpuscles. The papillae pits found in the mallard are consistent with the foramina found in the anteriormost part of the upper and lower jaws of the Anseriform birds of this study. As described, the anteriormost part of the upper- and lower jaws are densely pitted. Another feature mentioned in this study is that these foramina protrude through the bone in an angle, making the keratinized papilla lid always pointing towards the margins of the bill, thus causing the receptors to be more sensitive to stimuli coming from the edges of the bill. Similar foramina were also found in the other birds of this study. The Procellariiform birds in general have a line of foramina along the ventral margin of the upper jaw (in the premaxilla) and three rows of foramina in the dentary's dorsal margin. The foramina in these birds penetrate the bone in an angle as well. The jaws of the ornithomimids too have pits along the tomia and in the area of the symphysis. In his study, Berkhoudt (1980) also discussed the localization of the different kind of corpuscles with respect to feeding habits in an attempt to see if one could explain why the sensory organs are positioned the way they are. Such comparisons would be useful in order to reconstruct foraging behavior in the ornithomimids as well. However, a more detailed study would have to be done on the distribution on sensory receptors. It is, however, likely that the edges/tomia immediately in contact with food items will be equipped with tactile sensors. Both ornithomimids here are well equipped with foramina in the anterior surface of the rostrum. In the dentary these point dorsally, towards the ramphotheca remains in *O. edmontoensis*. This suggests that this portion of the rostrum had a central role in foraging. Also the presence of a rounded tomia in the posterior part of the rostrum indicates that the beak was not used to grasp or tear food-items. A round posterior followed by a sharp anterior is what we find in Anseriforms and Struthioforms.

Except for in the presence of a maxillary- and mandibular nail (which is indicated by a densely pitted surface) no correlations between heterogeneity in the ramphotheca and skeletal structure were found. It is, however, probable that it is related to feeding habit. Softer and/or thinner keratin layer gives a more sensitive surface, and a thick hard surface is useful to open and tear food items.

Conclusion

The beaked ornithomimosaur is likely to have had a mandibular ramphotheca which posterior border would be the > shaped depression in the dentary (Figures 5 and 7). The mandibular tomia would be covered to approximately where the maxillary connects to the

jugal. The keratin would have formed a cutting edge anteriorly (following the skeletal framework) and be flattened posteriorly. It is likely that the keratin was harder in front, since this is the part preserved in *O. edmontonicus* (TMP 2002.00.5). The upper jaw ramphotheca would have covered the entire tomia (ventral margin) back to approximately the maxilla-jugal suture, the same length as the dentary ramphotheca. The lateral and dorsal border remains uncertain after this study. Two morphologies, however, seem more likely than others. One (Figure 36 case A) being that the ramphotheca covered only the ventral margin and its perimeter, and terminated dorsally at the anterior part of the external nares (as seen in turtles, ostriches, and most neognath birds with elongate bony nares. One exception being members of the genus *Larus* - gulls). In this case the nares would be covered by muscular tissue and skin posteriorly. The other possibility (Figure 36 case B) being that the ramphotheca covered the rostrum from approximately the antorbital fenestra and forward (as seen in most other birds). In the latter case the keratin sheath would probably also have covered the external nares, in a similar fashion to Procellariiform birds. The beak of *S. altus* (TMP 90.85.1) and *O. edmontonicus* (TMP 2002.00.5) were probably much alike due to similarity in skull-structure. Barrett (2005) argues that the beak of *Gallinimus* and *Sinornithomimus* may have been less extensive than that of *Ornithomimus* and *Struthiomimus* because of less pitted maxillary and premaxillary surfaces. Alternatively this is an indication of differences in feeding habits, though this is likely to be reflected in beak morphology as well.

Regarding dietary habits the tomial morphology suggests an omnivore (animals small enough to swallow whole) or herbivore diet. This is consistent with findings of gastroliths in the ornithomimid digestive system (Kobayashi *et al.* 1999), and it also fits the habit described by Russel and Nicholls (1985) where the ornithomimid arms were argued to be adapted to grasping branches to reach food items.

I suggest that future studies in this area should put a greater emphasis on histology to see whether the bone-structure in the area covered by ramphotheca shows any anomaly compared to the rest of the skull (especially in the junction from cover to non-cover). Histological examination of the foramina in birds with comparisons to ornithomimids (and other theropods) might also reveal if they are connected to keratin growth-zones, or if they can throw light on the type of sensory papillae present.

Acknowledgments

Thanks to my supervisors Jørn H. Hurum (Museum of Natural History University of Oslo) and Glenn-Peter Sætre (Biological Institute at the University of Oslo) for guiding me through the last two years, to Prof. David L. Bruton (Museum of Natural History University of Oslo) for guidance whenever needed and for proof-reading this paper, to Rinchen Barsbold (Director of the Paleontological Centre, Mongolian Academy of Sciences) for giving me the opportunity to study the specimens on display in his exhibition of Mongolian dinosaurs in Reggio de Calabria Italy, to Phil J. Currie (University of Alberta - Edmonton, Alberta, Canada) and Darren Tanke (Royall Tyrell Museum, Alberta, Canada) for acquiring the casts and photographs of the Ornithomimids examined in this study, and finally thanks to Øyvind Enger for acquiring the Peking duck and ostrich skulls used in the analysis.

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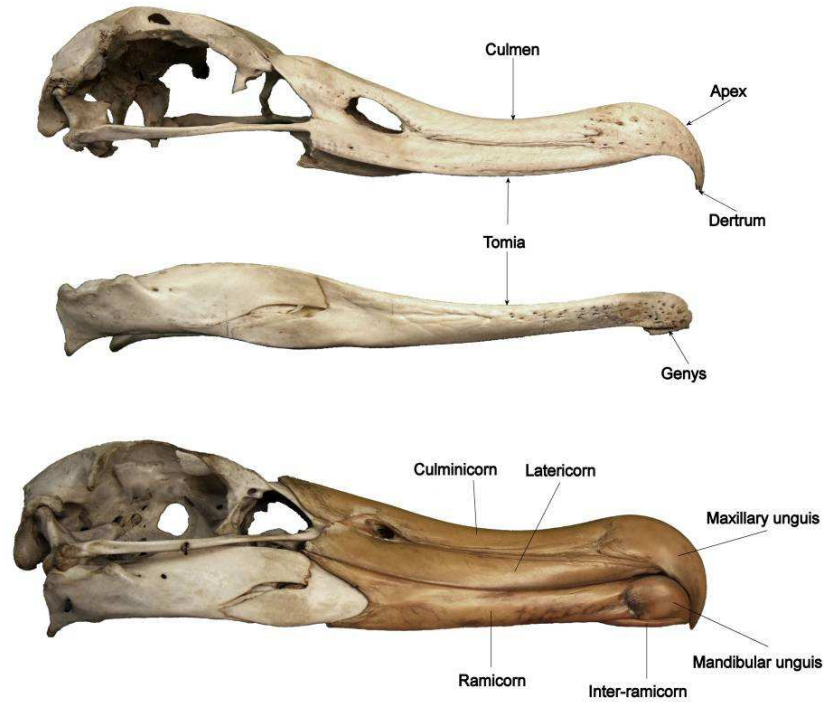


Figure 1
Beak terminology after Kiyota *et al.* (2000), and Newton (1896). Note that in many birds the ramphotheca is fused into one continuous cover.

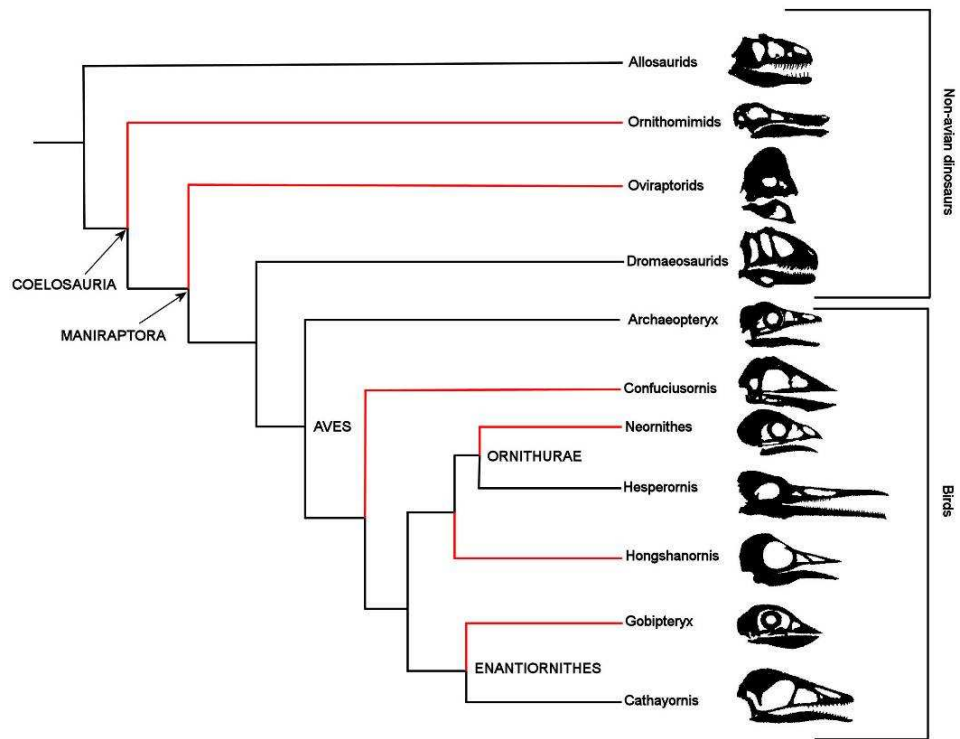


Figure 2
Evolution of toothlessness (indicated by red lines). Figure adapted from Chiappe (2007). The toothlessness status of *Hongshanornis* is still controversial. Note that the ornithomimids and the oviraptorids evolved beaks independently of each other.

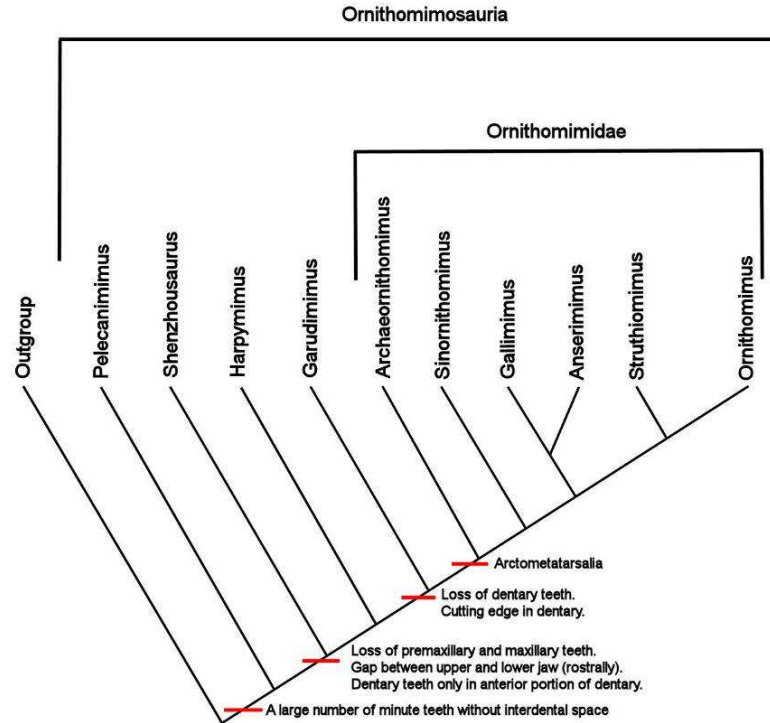


Figure 3

Cladogram of Ornithomimosauria adapted from Kobayashi and Barsbold (2005). *Dromiceiomimus* has been removed as it has been shown to be referable to *Ornithomimus edmontonicus* by Russel (1972). Note that teeth are lost gradually.

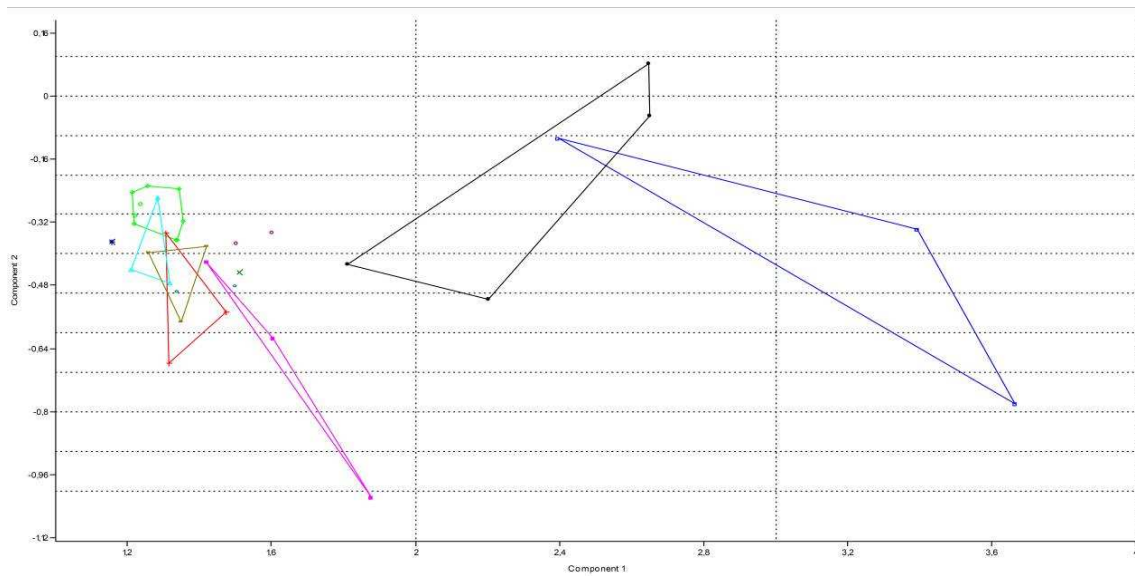


Figure 4

PCA-results. Eigenvalue for axis 1 = 85,7%, and for axis 2 = 9,0%. Green: Anseriformes, Light blue: Procellariiformes, Brown: Struthioniformes, Pink: Galliformes, Black: Psittaciformes, Red: Ornithomimidae, Blue: Oviraptoridae.

A-1



A-2

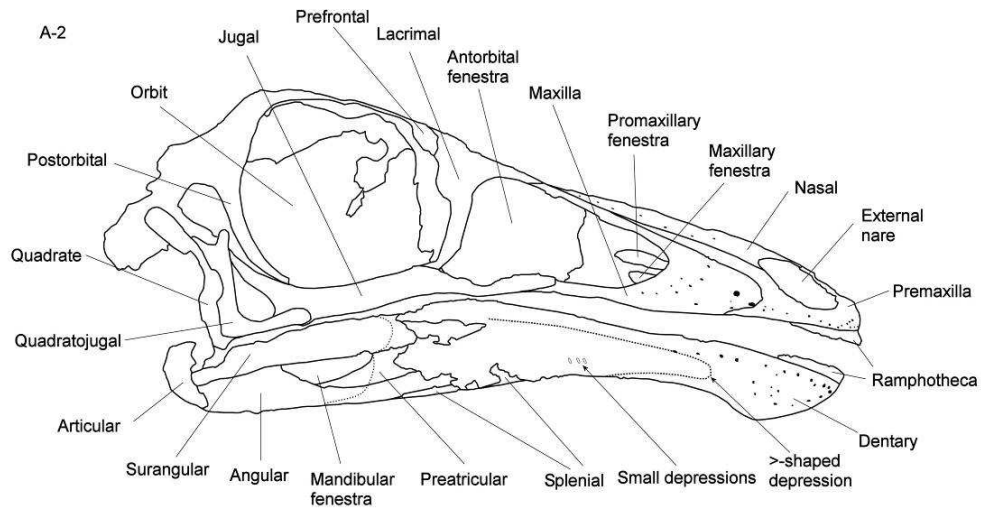


Figure 5

The skull of *Ornithomimus edmontonicus* (TMP 2002.00.5) in lateral view. Note the preserved remains of the ramphotheca anteriormost in the rostrum.

A-1



A-2

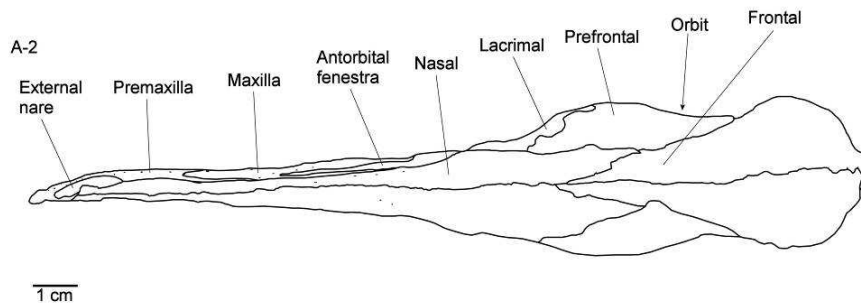


Figure 6

The skull of *Ornithomimus edmontonicus* (TMP 2002.00.5) in dorsal view.

A-1

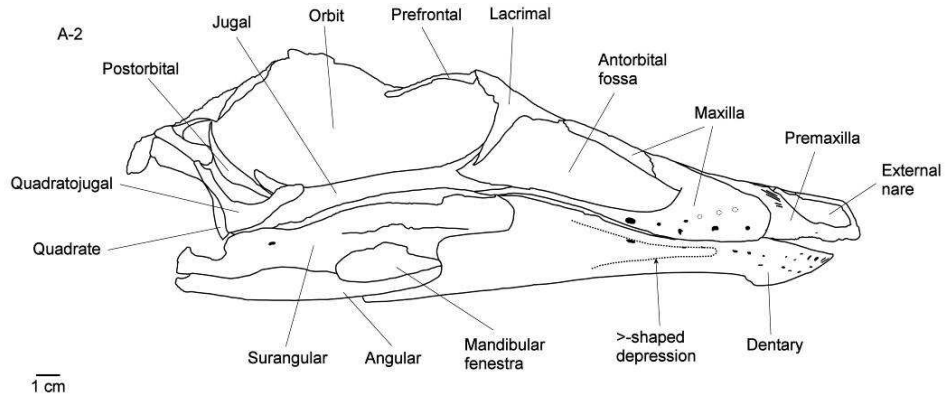


Figure 7
The skull of *Struthiomimus altus* (TMP 90.85.1) in lateral view.

A-1

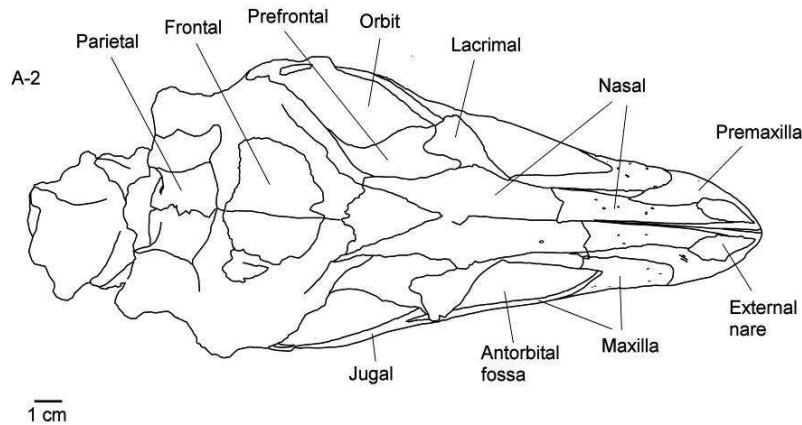
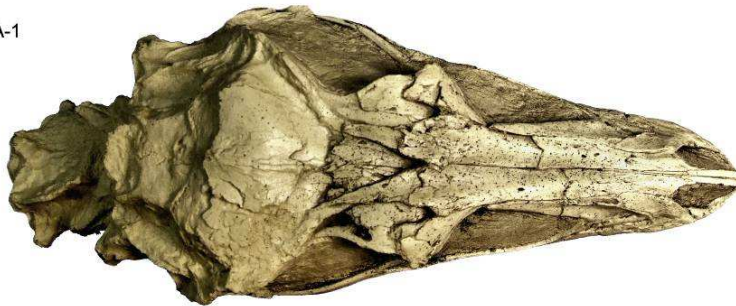


Figure 8
The skull of *Struthiomimus altus* (TMP 90.85.1) in dorsal view.

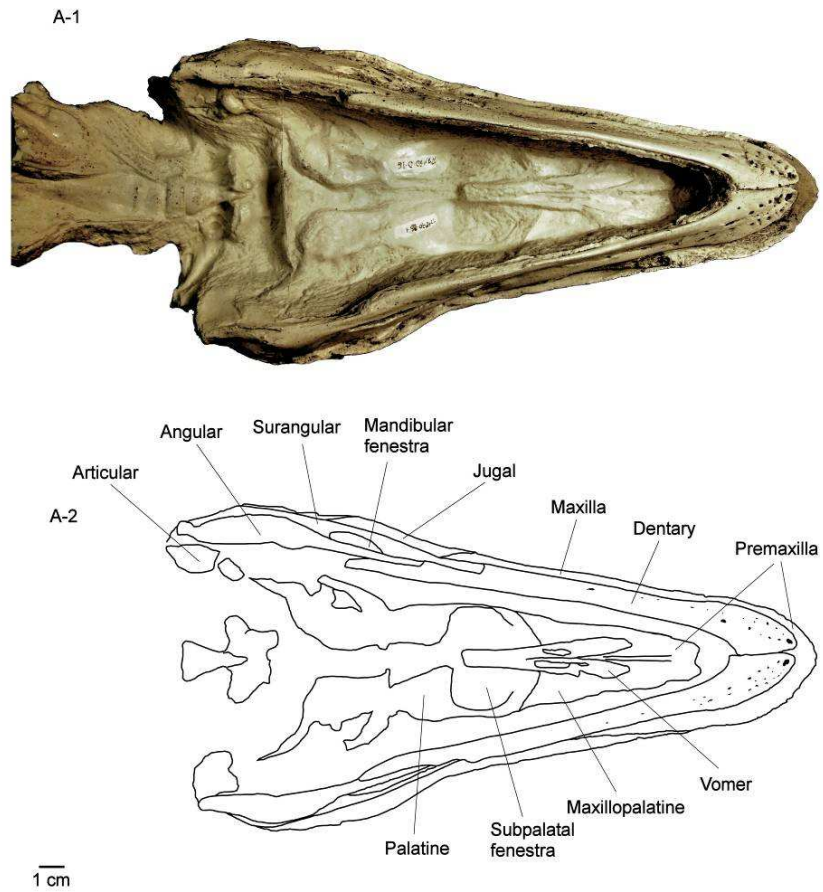


Figure 9
The skull of *Struthiomimus altus* (TMP 90.85.1) in ventral view.

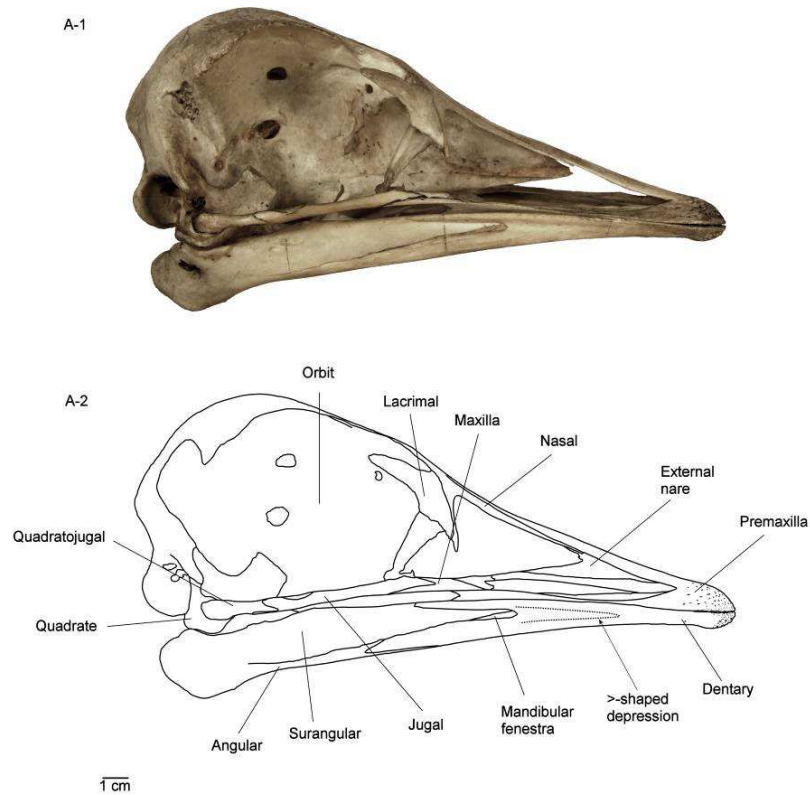


Figure 10
The skull of *Struthio camelus* (ZMO2644) in lateral view.

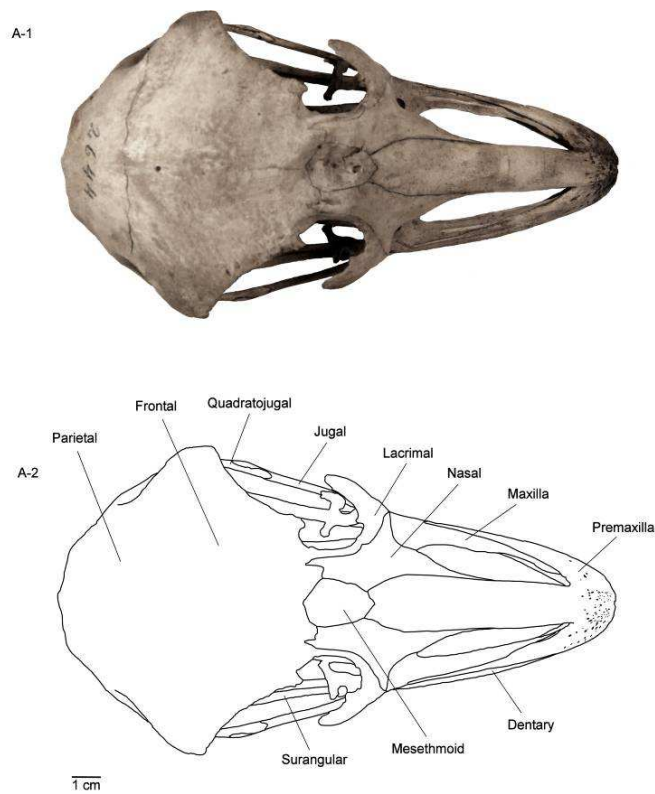


Figure 11
The skull of *Struthio camelus* (ZMO2644) in dorsal view.

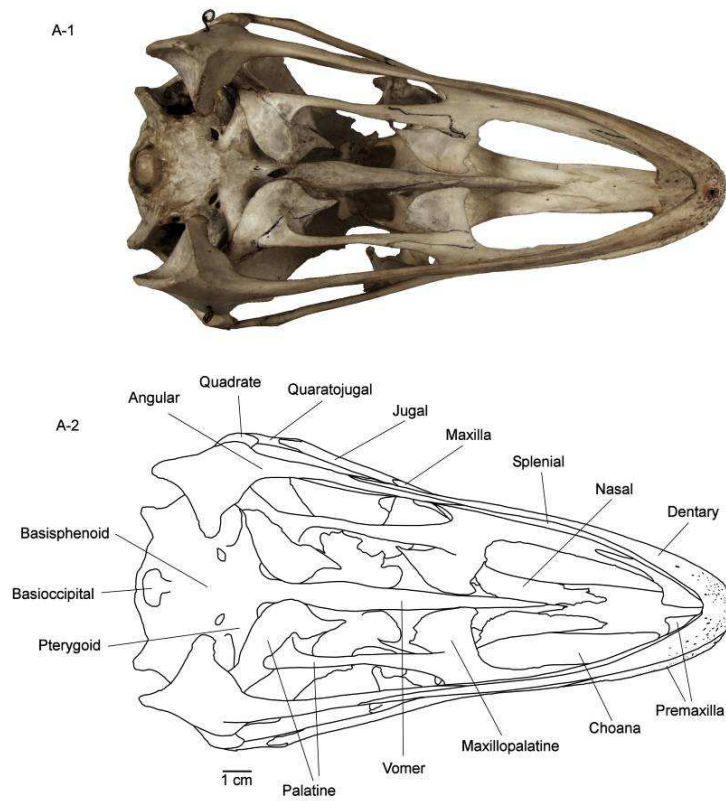


Figure 12
The skull of *Struthio camelus* (ZMO2644) in ventral view.

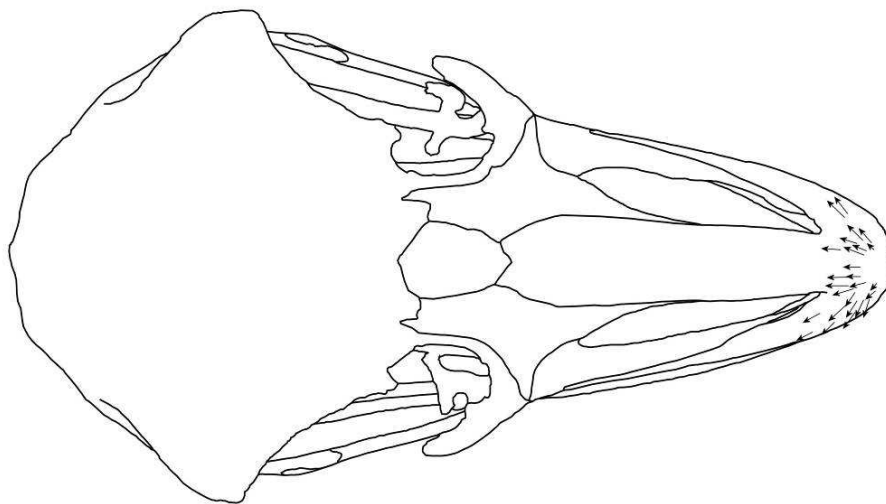
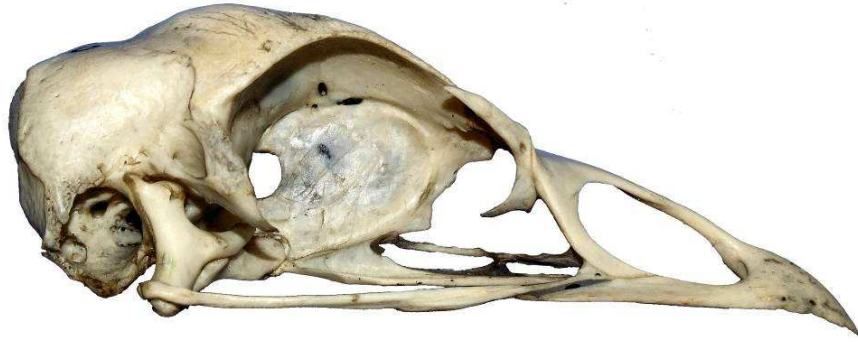


Figure 13
Schematic drawing of *Struthio camelus* (ZMO 2644) showing orientation of foramina.

A-1



A-2

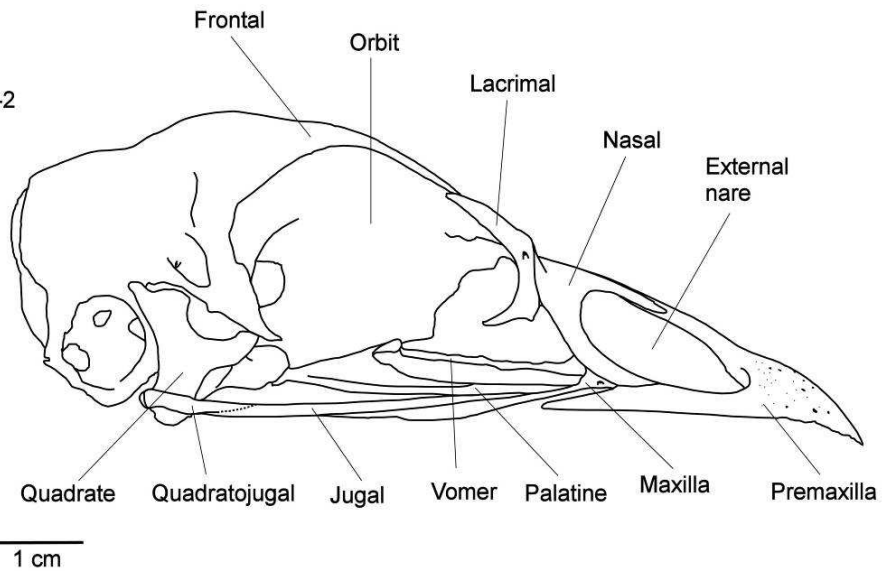


Figure 14
The skull of *Meleagris gallopavo* (ZMO 2820) in lateral view.

A-1



A-2

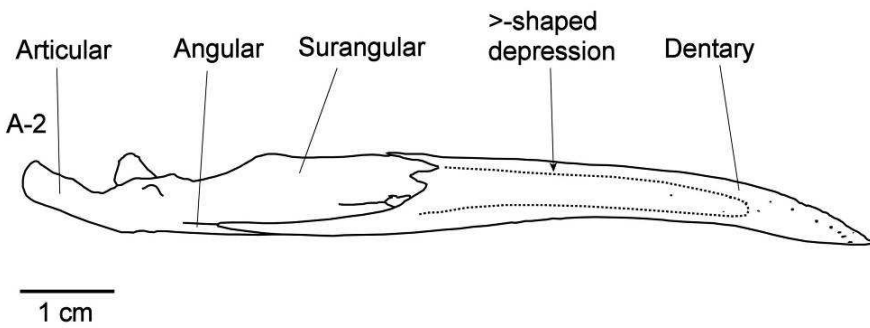


Figure 15
The mandible of *Meleagris gallopavo* (ZMO 2820) in lateral view.

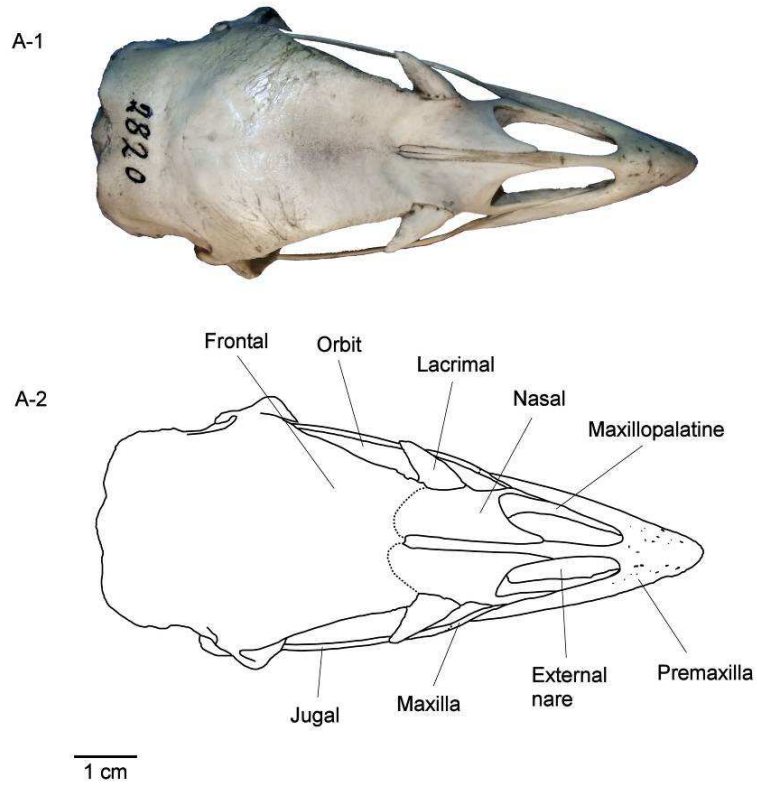


Figure 16
The skull of *Meleagris gallopavo* (ZMO 2820) in dorsal view.

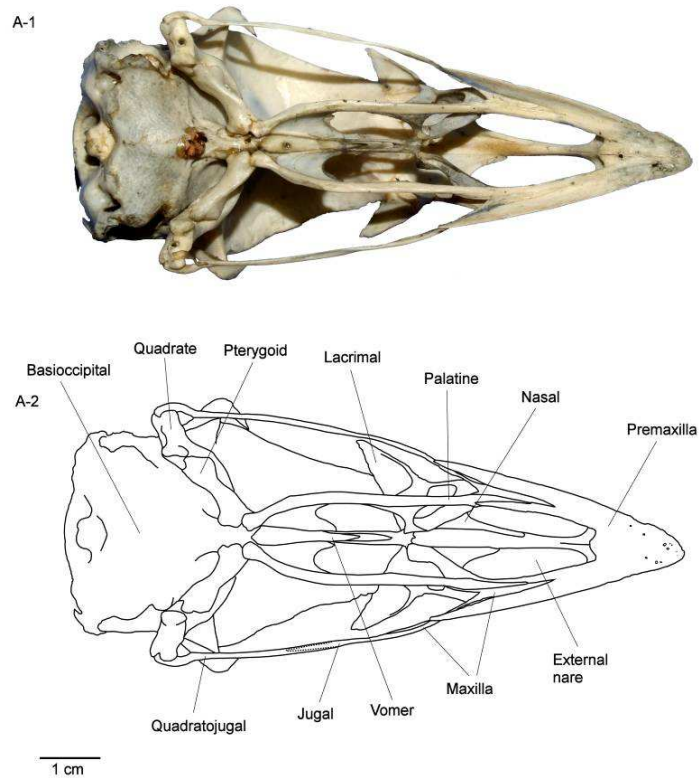


Figure 17
The skull of *Meleagris gallopavo* (ZMO 2820) in ventral view.

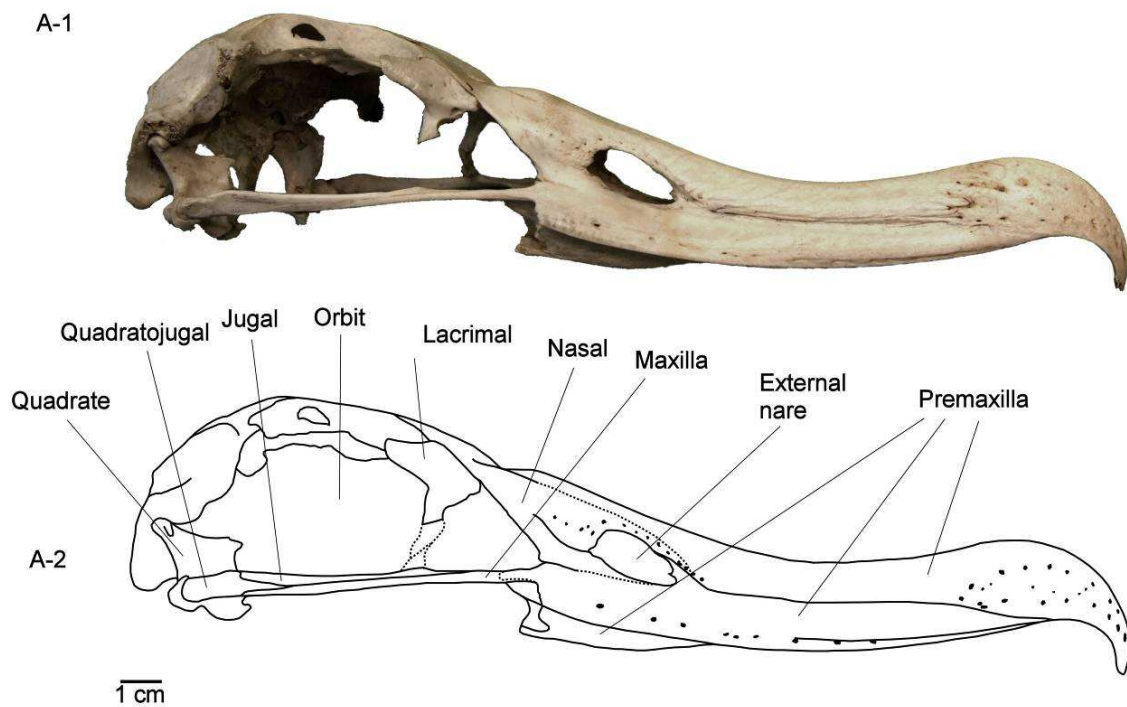


Figure 18
Diomedidae skull (A-1) in lateral view.

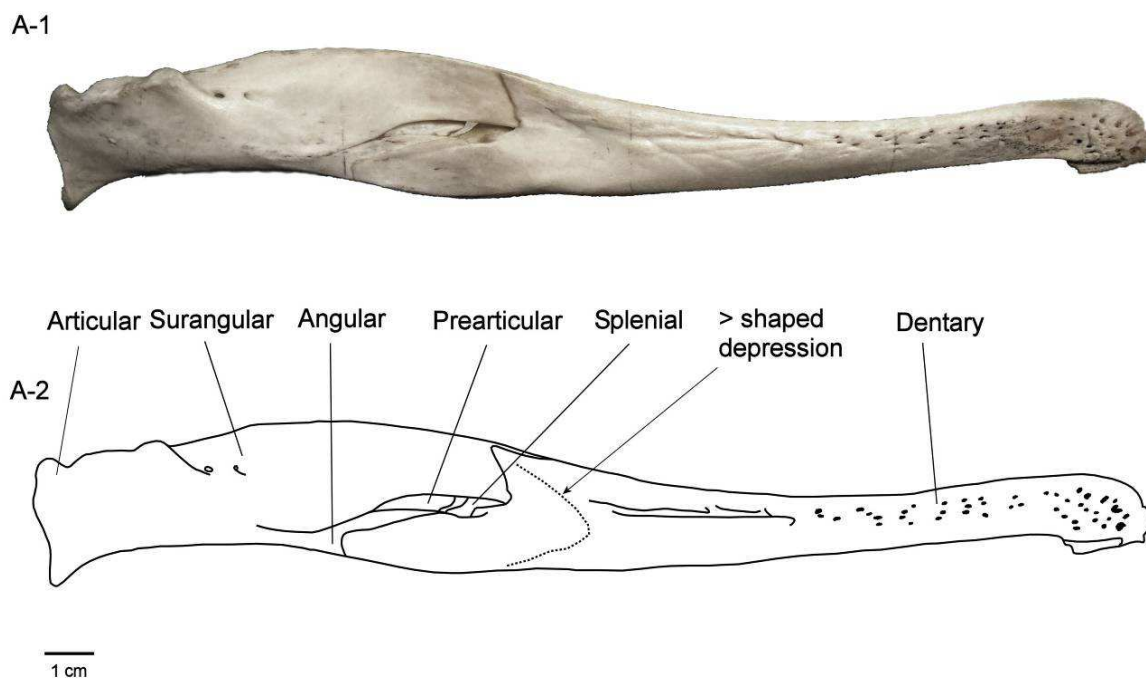


Figure 19
Diomedidae mandible (A-1) in lateral view.

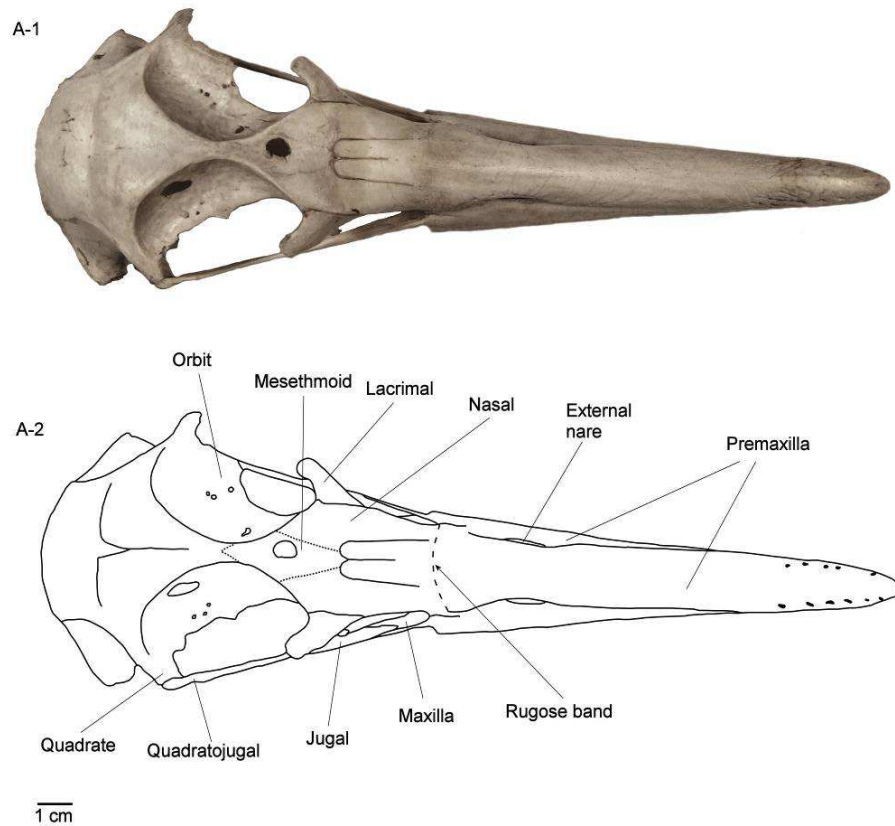


Figure 20
Diomedidae skull (A-1) in dorsal view.

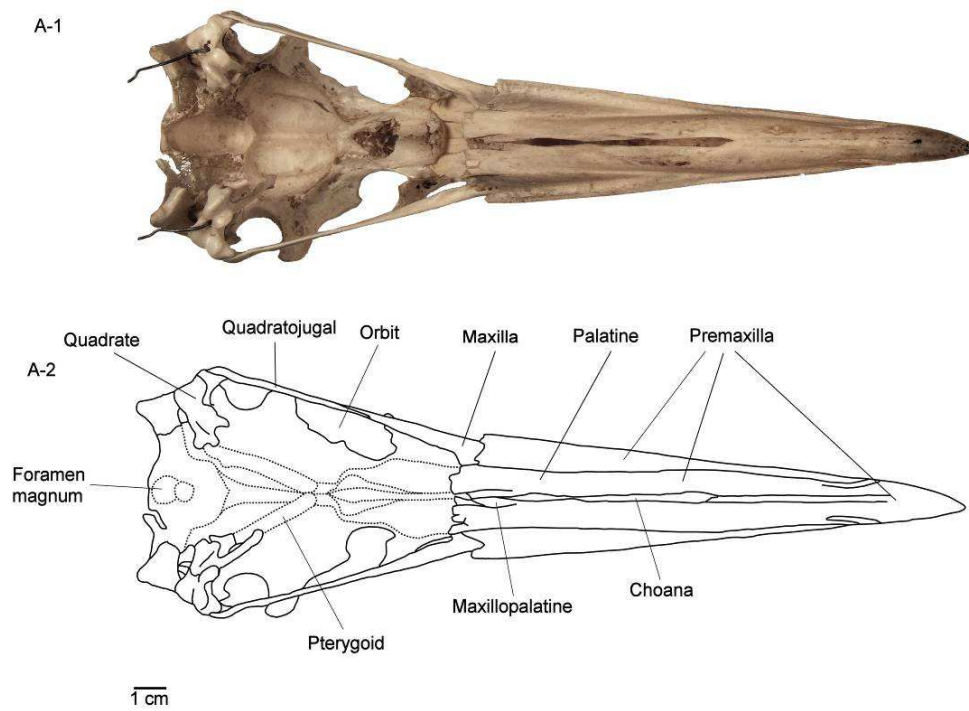


Figure 21
Diomedidae skull (A-1) in ventral view.



1 cm
Figure 22
Diomedidae skull (A-2) in lateral view.



1 cm
Figure 23
Diomedidae skull (A-2) in dorsal view.



1 cm
Figure 24
Diomedidae skull (A-2) in ventral view.



1 cm

Figure 25
Diomedidae skull (A-3) in lateral view.



1 cm

Figure 26
Diomedidae skull (A-3) in dorsal view.



1 cm

Figure 27
Diomedidae skull (A-3) in ventral view.

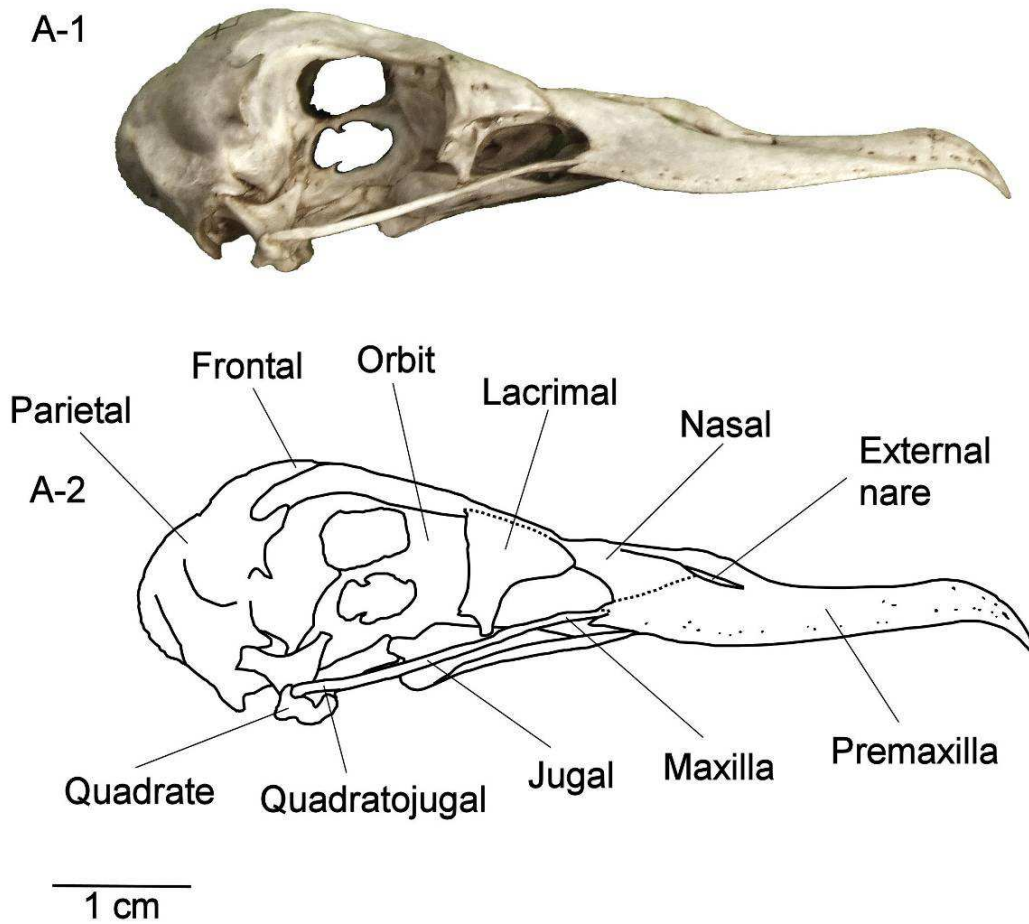


Figure 28
The skull of *Pachyptila* sp. (ZMO 1337) in lateral view.

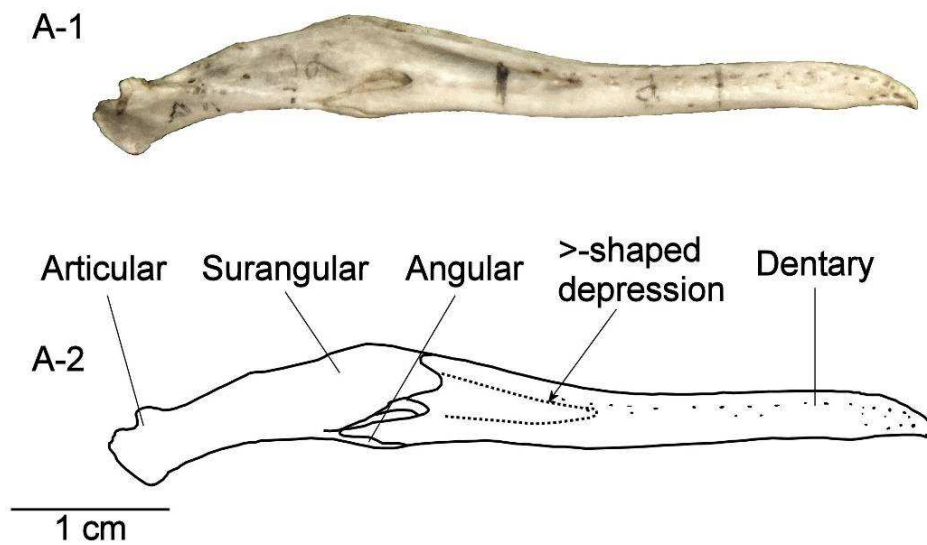


Figure 29
The mandible of *Pachyptila* sp. (ZMO 1337) in lateral view.

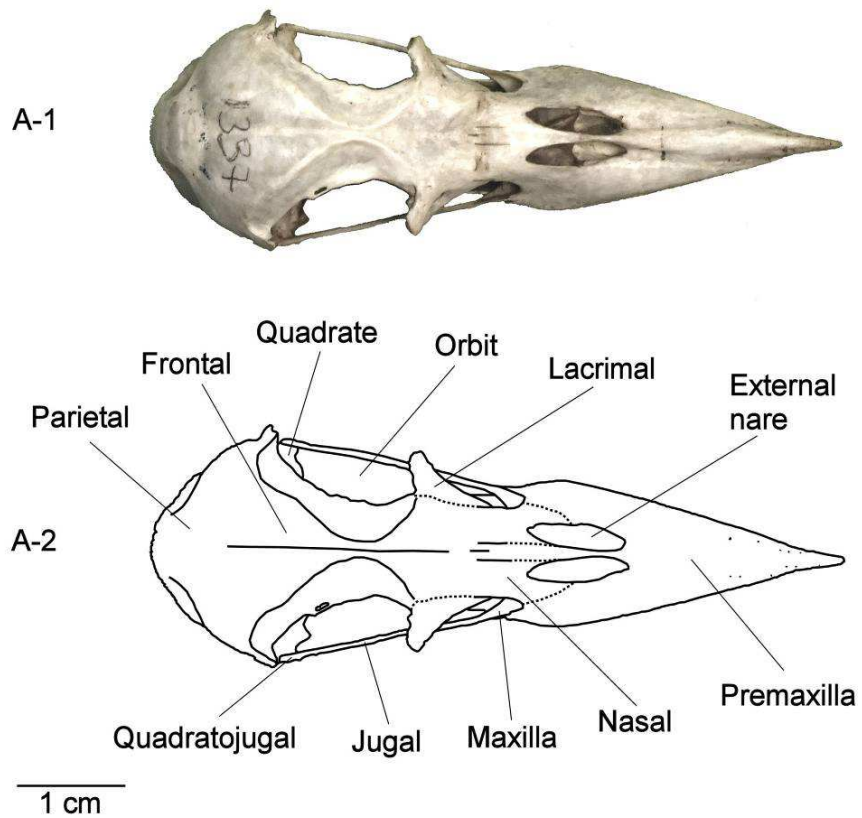


Figure 30
The skull of *Pachyptila* sp. (ZMO 1337) in dorsal view.

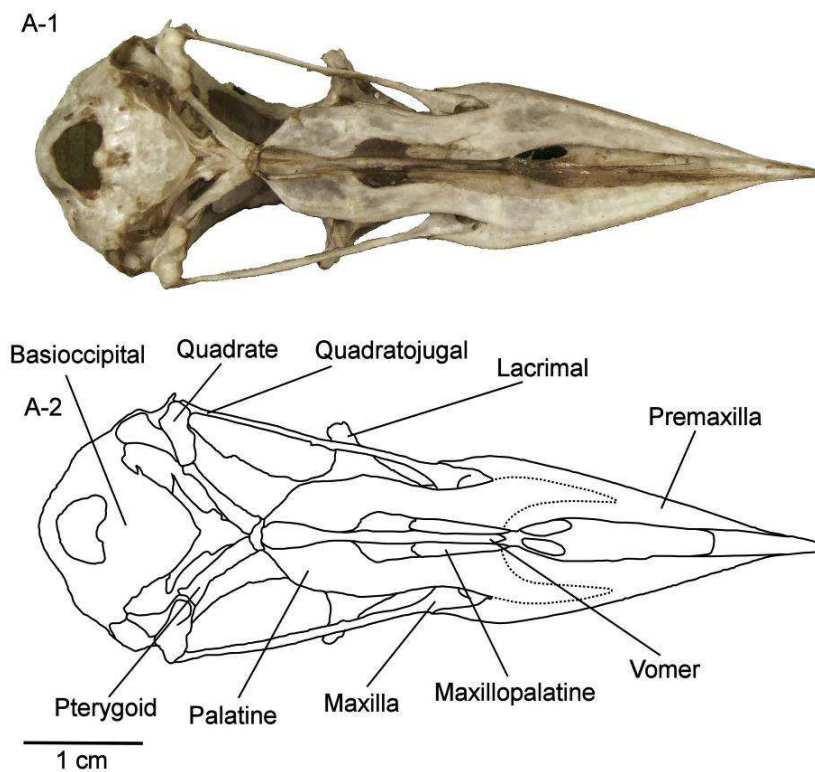
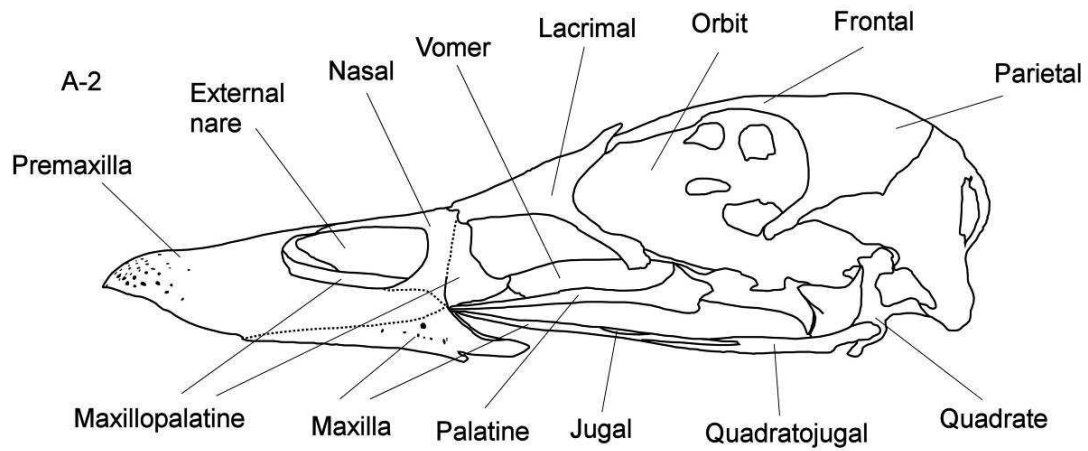


Figure 31
The skull of *Pachyptila* sp. (ZMO 1337) in ventral view.

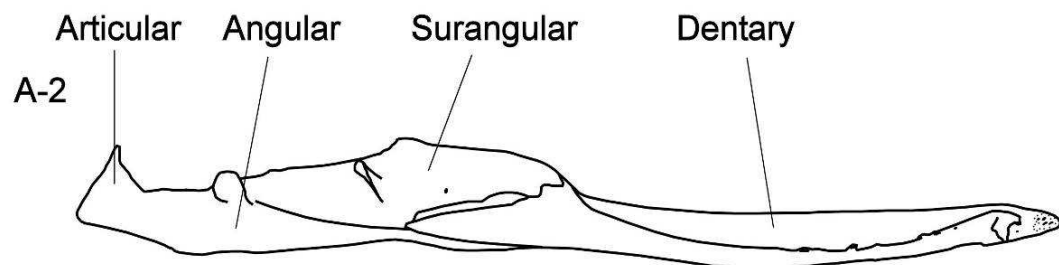
A-1



1 cm

Figure 32
The skull of *Clangula hyemalis* (ZMO 5907) in lateral view.

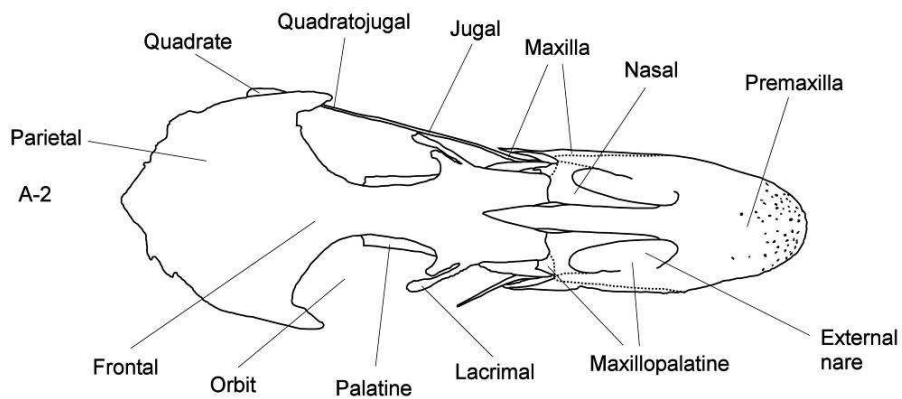
A-1



1 cm

Figure 33
The mandible of *Clangula hyemalis* (ZMO 5907) in lateral view.

A-1

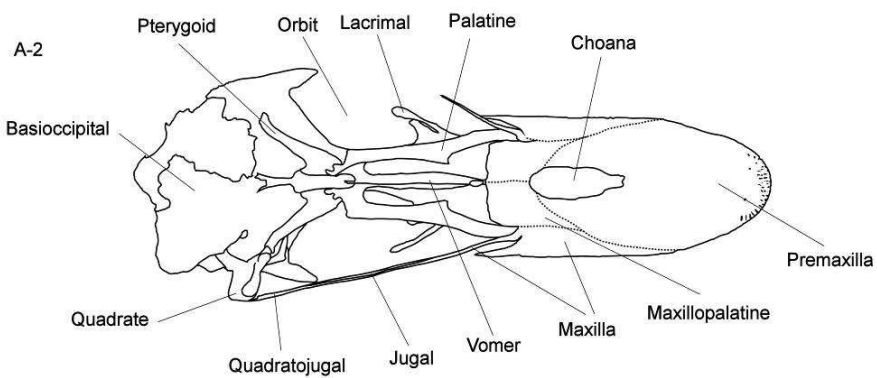
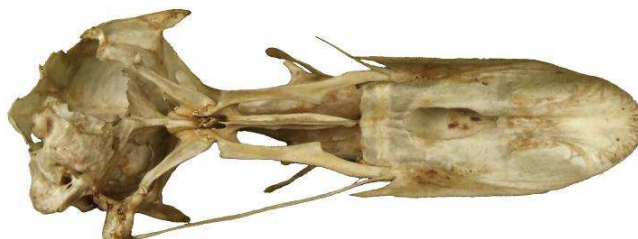


1 cm

Figure 34

The skull of *Clangula hyemalis* (ZMO 5907) in dorsal view.

A-1



1 cm

Figure 35

The skull of *Clangula hyemalis* (ZMO 5907) in ventral view.

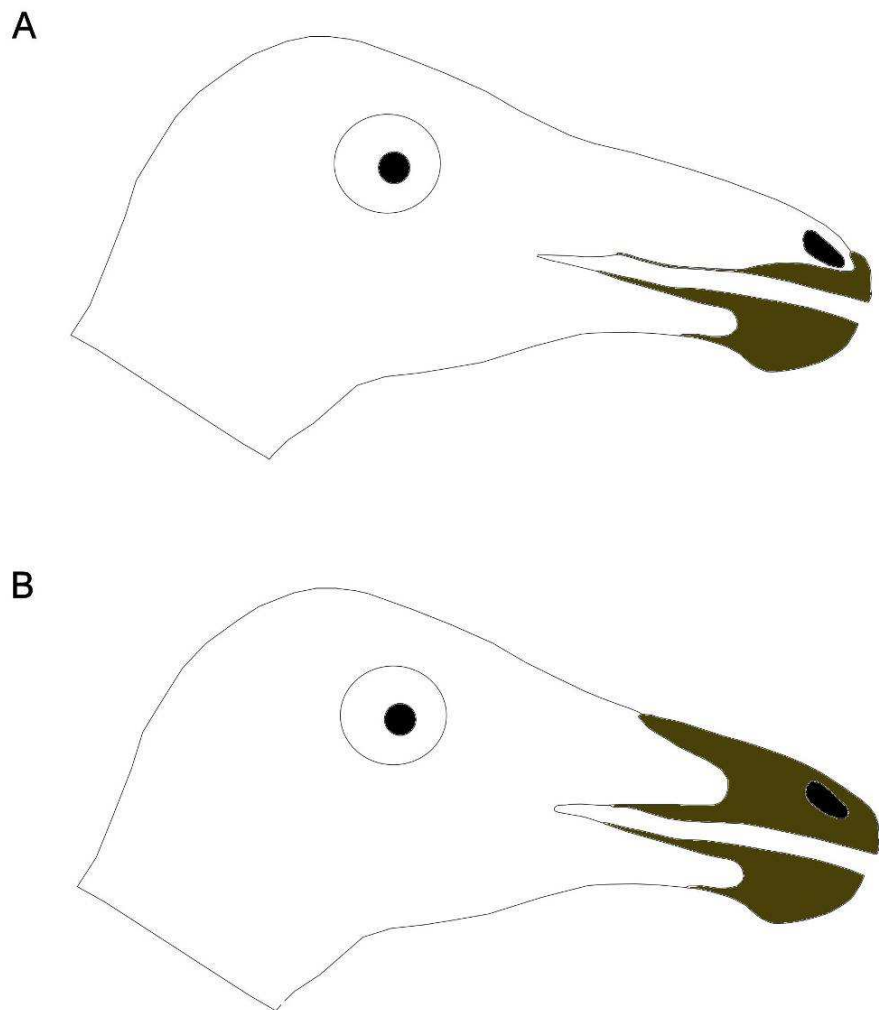


Figure 36
Schematic reconstruction of the ornithomimid beak (case A and B from conclusion).

Appendix 2 - Dataset

Group	Species	No.	L_R/L_S	Cur	H_C/L_S	H_R/H_C	H_C/L_C
Anseriformes (1)	<i>Cygnus cygnus</i>	ZMO 2931	0,49	1,10	0,23	0,37	0,45
Anseriformes (2)	<i>Cygnus bewickii</i>	ZMO 6258	0,50	1,08	0,24	0,34	0,49
Anseriformes (3)	<i>Somateria spectabilis</i>	ZMO 5056	0,47	1,10	0,25	0,64	0,46
Anseriformes (4)	<i>Clangula hyemalis</i>	ZMO 5907	0,41	1,06	0,25	0,52	0,43
Anseriformes (5)	?	ZMO 5582	0,43	1,09	0,27	0,32	0,47
Anseriformes (6)	?	ZMO 6025	0,36	1,18	0,35	0,33	0,55
Anseriformes (7)	?	ZMO 5365	0,41	1,17	0,33	0,36	0,55
Anseriformes (8)	<i>Anas clypeata</i>	ZMO 5531	0,53	1,07	0,20	0,41	0,42
Anseriformes (9)	<i>Anser albifrons</i>	ZMO 1021	0,48	1,18	0,27	0,44	0,52
Caprimulgiformes	<i>Podargus cuvieri</i>	ZMO 5650	0,49	1,25	0,34	0,56	0,68
Charadriiformes	<i>Cephus grylle</i>	ZMO 698	0,53	1,03	0,24	0,28	0,51
Falconiformes (1)	<i>Aquila albicilla</i>	ZMO 690	0,45	1,35	0,34	0,61	0,61
Falconiformes (2)	<i>Pernis apivorus</i>	ZMO 4036	0,34	1,35	0,39	0,33	0,59
Galliformes (1)	?	ZMO 3141	0,48	1,34	0,43	0,46	0,84
Galliformes (2)	<i>Numida meleagris</i>	ZMO 1362	0,43	1,57	0,70	0,29	1,23
Galliformes (3)	<i>Meleagris gallopavo</i>	ZMO 2820	0,47	1,20	0,33	0,47	0,63
Ornithomimidae (1)	<i>Ducky</i>	TMP90016	0,54	1,10	0,25	0,50	0,54
Ornithomimidae (2)	<i>O. edmontonicus</i>	TMP2002.00.5	0,58	1,05	0,35	0,41	0,84
Ornithomimidae (3)	<i>G. bullatus</i>	X625	0,47	1,22	0,40	0,46	0,75
Oviraptoridae (1)	<i>Conchoraptor gracilis</i>		0,29	2,15	0,42	0,82	0,58
Oviraptoridae (2)	<i>Oviraptor sp. 1</i>		0,56	3,00	0,46	1,18	1,04
Oviraptoridae (3)	<i>Oviraptor sp. 2</i>		0,58	3,05	0,64	1,41	1,53
Passeriformes (1)	<i>Corvus seapulatus</i>	ZMO 1157	0,56	1,14	0,30	0,38	0,67
Passeriformes (2)	<i>Corvus albicollis</i>	ZMO 1156	0,55	1,23	0,32	0,57	0,71
Procellariiformes (1)	<i>Pachyptila typicus</i>	ZMO 1337	0,48	1,18	0,23	0,31	0,44
Procellariiformes (2)	<i>Albatross sp. 1</i>	AL-1	0,67	1,14	0,22	0,38	0,65
Procellariiformes (3)	<i>Pachyptila typicus</i>	ZMO 1034	0,52	1,09	0,28	0,22	0,58
Psittaciformes (1)	1340?	ZMO 3540	0,29	2,44	0,34	0,90	0,48
Psittaciformes (2)	<i>Psittacus sp. 1</i>	ZMO 4916	0,33	1,63	0,47	0,39	0,70
Psittaciformes (3)	<i>Psittacus sp. 2</i>	ZMO 4915	0,33	2,00	0,57	0,42	0,86
Psittaciformes (4)	<i>Cacatua galerita</i>	ZMO 360/65	0,26	2,45	0,43	0,78	0,58
Struthioniformes (1)	<i>Struts</i>	ZMO 2644	0,49	1,18	0,37	0,25	0,73
Struthioniformes (2)	<i>Struts</i>	ZMO 3636	0,44	1,10	0,31	0,32	0,56
Struthioniformes (3)	<i>Struts</i>	ZMO 346/65	0,48	1,24	0,30	0,41	0,59

Table 1

Ratio of measurements used in the ordination analysis.