

**Beak morphology in oviraptorids,
based on extant birds and turtles**

M.Sc. Thesis by
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Abstract

Oviraptorids are one of several groups of dinosaurs, which have evolved beaks. Of extant beaked animals, birds and turtles are the best known. In this study, an anatomical comparison between oviraptorids, extant birds and turtles was made to try to reconstruct the beak in oviraptorids. The results show a close similarity in mandibular beak shape of parrots and oviraptorids, whereas turtles deviate. In the upper jaw, the oviraptorids show more resemblance to the latter group. The same bones, namely the premaxilla but also the maxilla and the nasal, were covered by ramphotheca in almost all the groups of birds, as well as in oviraptorids and turtles. Comparative evidence suggests that oviraptorids may have had a beak suited for an omnivorous diet, and the diet primarily consists of small prey, but also eggs, nuts and hard seeds.

Keywords: oviraptorids, parrots, turtles, ramphotheca, skull anatomy, crest.

Introduction

The beak or bill has many different forms and sizes, and is found in several different animal groups, where birds and turtles are the best known. The beak has evolved to suit the way of feeding; some beaks are long and thin, others short and powerful, or long and flat like the duck bill. The beak itself consists of a keratin layer called ramphotheca, which covers the upper and lower jaw bones. The turtle beak consists of the same keratin composition as the bird beak, but is distinctly different in shape. Several dinosaurs appear to have a beak or a beak-like structure, and there are many speculations about different beak shapes. Oviraptorids are known to have a beak-like structure.

Oviraptorids are bird-like dinosaurs, mainly living in Mongolia in the Late Cretaceous, but also found in China, North America and England. The very first oviraptorid was discovered in Mongolia on top of a nest, surrounded by eggs. It was crushed laterally, poorly preserved, and was described as *Oviraptor philoceratops* by Osborn (1924), which means “predator that loves to eat the eggs of horned dinosaurs”. *Oviraptor philoceratops* was for a long time the only species found in the order Oviraptorosauria, and the order was the less known of the theropods groups. However, several spectacular discoveries during the last two decades made it to one of the best known theropod groups. The discovery of two nesting places with several embryos and adults at Ukhaa Tolgod, Mongolia (Norell *et al.* 1994, Norell *et al.* 1995, Clark *et al.* 1999) and Bayan Mandahu, China (Dong & Currie 1996), together with several other specimens, made a good base for interpreting the skeletal anatomy (Clark *et al.* 2002b).

A complete crested oviraptorid skull and postcranial skeleton of an adult specimen (IGM 100/42) and four apparently juvenile specimens from Zamyn Khondt in Mongolia were described by Barsbold (1981, 1983a, 1986, 1988). They gave important information about the oviraptorids, but were misinterpreted to belong to *Oviraptor philoceratops*. Due to this erroneous assignment, *Oviraptor philoceratops* has often been displayed as a crested dinosaur, even though the holotype shows no evidence of having a crest (Smith 1993, Clark *et al.* 2001, Clark *et al.* 2002a, Maryańska *et al.* 2002, Xu *et al.* 2002, Senter 2007). IGM 100/42 is now grouped under the subfamily Oviraptorinae (Osmólska *et al.* 2004). Barsbold (1986) described *Conchoraptor gracilis*, a skull with a partial skeleton and several other partial skulls without the characteristic crest, but with large elongated narial openings. In the same paper he also described a crested oviraptorid as *Oviraptor mongoliensis*, but after a re-examination (Barsbold 1997) he found significant differences and placed it under the genus *Rinchenia*. The name remained as a *nomen nudum* until it was used as *Rinchenia mongoliensis* by Osmólska *et al.* (2004).

The discovery of *Caudipteryx* led to many intensive studies and debates of the relationship between birds and dinosaurs. *Caudipteryx* was feathered but flightless and had four teeth in the premaxilla (Osmólska *et al.* 2004). Gastroliths, like those in some herbivorous dinosaurs and modern birds, have been found preserved in at least two specimens of *Caudipteryx* (Ji *et al.* 1998). Several paleontologists were suspicious that feathers, one of the characteristics which define modern birds, arose much earlier than the modern birds (Peters 1985, Padian *et al.* 2001). Witmer (2002:p.14) declared in his article: “The presence of unambiguous feathers in an unambiguously non-avian theropod has the rhetorical impact of an atomic bomb, rendering any doubt about the theropod relationships of birds ludicrous.” This led to an interesting hypothesis: if more primitive flightless dinosaurs had feathers, the hypothesis that the origin of flight came with the origin of the feathers is fundamentally decoupled (Ji & Ji 2001). Oviraptorids had feathers with the diagnostic features of shafts and barb, similar to those found in modern birds (Zhang & Zhou 2000, Zhou 2004, Norell & Xu 2005).

Some paleontologists concluded that the oviraptorosaurid dinosaurs *Caudipteryx* and *Protarchaeopteryx* are not theropod dinosaurs at all, but flightless birds which evolved from a yet unknown taxon unrelated to dinosaurs (Feduccia 1999), whilst others hold that all birds evolved from Archosauria (Martin & Czerkas 2000, Martin 2004). Based on a mathematical comparison of the body proportions of flightless birds and non-avian theropods, Jones *et al.* (2000) found that *Caudipteryx* was a bird and not a theropod dinosaur. However, after re-examining the limb proportions, an analysis of the latter method was made, and Dyke & Norell (2005) came to the opposite conclusion. In a controversial article, Maryańska *et al.* (2002) placed the oviraptorids under Aves, and claimed that oviraptorids are actually secondarily flightless, and belong within Avialae as flightless birds. The result was also supported by Paul (2002). Later Lü *et al.* (2004) modified the dataset from Maryańska *et al.* (2002), and came to the same conclusion. These analyses were so convincing that they were included in several paleontological textbooks, like “Vertebrate Paleontology Third Edition” by Benton (2005). In “The Dinosauria Second Edition” Osmólska *et al.* (2004) placed the group back under

Maniraptoriformes and Oviraptorosauria. In his extensive phylogenetic article, Senter (2007) used most of the data from the work of Maryańska *et al.* (2002) and Lü *et al.* (2004), and his conclusion was quite different from theirs. He placed the oviraptorids back under Oviraptorosauria, and re-arranged several of the oviraptorosaurid groups (Fig. 1). He also said that the oviraptorosaurian taxonomy is likely to be changed in the future, due to low decay indices and bootstrap values (Senter 2007).

An oviraptorosaurian dinosaur from China with several characters closer to more typical theropods, *Incisivosaurus gauthieri*, was described by Xu *et al.* (2002b). It had a low skull and toothed jaws, a pair of premaxillary teeth, like the rodent incisors, and small maxillary teeth with large wear facets. This kind of dental features were until then unknown among the theropods, and indicate a herbivorous diet.

The diet of oviraptorids has not been discussed in detail. Some paleontologists suggest that oviraptorids have been omnivorous, while Barsbold (1986) believed that they were amphibious dinosaurs, their long muscular tail used for propulsion through the water, and adapted to eat much harder food than eggs, such as mollusks. Later Barsbold *et al.* (1990) meant that they had typical terrestrial hind limbs. Also Smith (1990, 1993) pointed out that oviraptorids could not be amphibious dinosaurs. He also argued that oviraptorids were not omnivorous, egg-eaters, nor mollusk eaters, but rather herbivores, with the sharp edges of the jaws cutting off leaves and other fibrous matter. Glut (1997) maintained that the oviraptorids were herbivorous, because the skull was too fragile for a diet on hard food.

Little has been done on avian jaw morphology. Zusi (1984) & Bühler (1981) describe the different ways of mobility in the upper jaws. Most birds have prokinesis, where the upper jaw moves at the point where it is attached to the skull. In rynchokinesis, the upper jaw is flexed upwards or downwards at some point along the jaw. Even though the beak in oviraptorids was bird-like in many ways, prokinesis and rynchokinesis were most likely absent in the oviraptorids (Barsbold 1983a). In this study I will try to find out which properties can predict a ramphothecal cover on the rostral bones in birds and turtles, and I will examine three Mongolian oviraptorid skulls; The Zamyn Khondt specimen (Barsbold 1981, 1983a, 1986, 1988), *Oviraptor* sp. and *Conchoraptor gracilis*. Based on the results of the anatomic features of birds and turtles, I will try to reconstruct the keratin sheath in the Zamyn Khondt specimen.

The key questions to answer in this study are:

- What properties in the bone structure indicate they were covered with ramphotheca? (Surface, size, relationship to other bones)
- Which bones are covered by ramphotheca in birds and turtles?
- Does the ramphotheca always follow the rostral bones?
- Can this knowledge be transferred to oviraptorids?
- What did the beak of oviraptorids look like?
- What was the dietary habit of oviraptorids?

Materials and Methods

Dataset

The dataset was collected together with Espen Madsen Knutsen, who wrote a similar thesis on ornithomimids (Knutsen 2007). Measurements were selected to best represent the general shape of the skulls, and different ratios of these were used in an ordination analysis. I only used measurements performed on specimens in lateral view, as one of the oviraptorid skulls was preserved in this orientation. I did not use any measurements of the mandible, as this was not always complete in all the oviraptorid skull casts studied. Since there is no antorbital fenestra in turtles, the posterior end of the nasal sutures was used as the posterior point in measuring R_L_1 and R_L_2. The definitions of measurement are listed below, and the dataset is presented in appendix 2.

Measurements chosen:

1. Skull length (**S_L**) – total length.
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 dorsal surface.
6. Rostrum height at mid-length (**R_H**)
7. Rostrum curvature (**Cur**) – R_L_2 divided by R_L_1 .

Ordination

I used PAST version 1.74 (Hammer *et al.* 2001) to perform an ordination analysis on different skulls (Tab. 1), and ran a PCA-analysis with the var-covar setting. From the results of the PCA-analysis (Fig. 2), I selected which skulls I wanted to compare with the oviraptorids.

Terminology and Abbreviations

The terminology is from Weishampel, Dodson & Osmólska (2004). Institutional names are abbreviated as follows: BM, Bergen Museum - Natural History, Bergen, Norway; IGM, Mongolian Academy of Sciences, Ulan Baatar, Mongolia; PMO X, Fossil cast collection, Geological Museum, University of Oslo, Norway; ZMO, Zoological Museum, University of Oslo, Norway.

Selection of Comparative Groups

The ordination plot shows that Psittaciformes and oviraptorids are morphologically rather similar; they both have very curved rostrums. The Testudines are also rather similar to Psittaciformes and oviraptorids. 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

The ordination analysis shows that there are two groups that resemble oviraptorids with respect to beak and skull morphology, namely Psittaciformes and Testudines. The Psittaciformes samples include two skulls of *Psittacus* sp., one skull of *Ara* sp., and one skull of *Cacatua galerita* (sulphur-crested cockatoo). The Testudines samples include *Caretta caretta* (Loggerhead turtle) and *Eretmochelys imbricate* (Hawksbill turtle) from the family *Cheloniidae*, together with two skulls of *Amyda cartilaginea* (Asiatic soft-shell turtle) from *Trionychidae*, and *Geochelone nigra* (Galápagos giant tortoise) from *Testudinidae*.

The skulls used in the examination:

OVIRAPTOROSAURIA

Zamyn Khondt specimen (IGM 100/42), Figs. 3, 4, 34. The original skull, located at the Mongolian Academy of Sciences, Ulan Baatar, Mongolia. The skull is damaged, especially on the crest, and the left posterolateral surface is crushed. It is stabilized with epoxy, which cause a shining coat on the surface. This specimen is discussed by Barsbold (1981, 1983a, 1986, 1988), Clark *et al.* (2001), Clark *et al.* (2002a), Clark *et al.* (2002b), Maryańska *et al.* (2002), Osmólska *et al.* (2004), Xu *et al.* (2002a), Smith (1992), Holtz (2007), and Senter (2007).

Conchoraptor gracilis (PMO X677), Fig. 5. A cast of a *Conchoraptor gracilis* skull from a private collection. It appears to be a juvenile specimen, especially when compared to the *Conchoraptor gracilis* described by Barsbold (1986). The cast is slightly crushed laterally, and is only partially prepared. The surface shows signs of being sand abraded.

***Oviraptor* sp.** (PMO X678), Figs. 6, 7. A cast of an *Oviraptor* sp. skull from a private collection. The specimen is presented in left lateral view. The skull is crushed laterally, the crest is slightly distorted, and the nasal area is partly damaged. The posterior part is a little squeezed down on the side facing the matrix. The surface shows the same wear as in *Conchoraptor gracilis* (PMO X677).

PSITTACIFORMES

Cacatua galerita (ZMO 360/65), Figs. 8-11. A complete Sulphur-Crested Cockatoo skull without ramphotheca.

***Psittacus* sp.** (ZMO 4915 & ZMO 4916), Figs. 12, 13. Two complete skulls without ramphotheca of small parrots. Specimen ZMO 4915 has a damaged orbit on both sides. In specimen ZMO 4916 the left palatine is broken, and there is slight damage around the orbit.

Ara sp. (ZMO 1340), Fig. 14. A complete macaw skull without ramphotheca. The skull also shows some traces of the ramphotheca.

Ara sp. (ZMO 688), Figs. 15, 16. A complete macaw skull with ramphotheca. The skull looks very similar to *Ara sp.* (ZMO 1340), and it is damaged on the left side of the posterior part. Some parts of the quadratojugal, the quadrate and the posteriormost part of the lower jaw are either broken or missing, as is most of the left squamosal.

TESTUDINES

Caretta caretta (ZMO 19/62), Figs. 17-20. A complete Loggerhead turtle skull without ramphotheca.

Eretmochelys imbricate (ZMO 12/74), Fig. 21. A complete Hawksbill turtle skull without ramphotheca.

Amyda cartilaginea (ZMO 7104 & ZMO 7105), Figs. 22-26. Two complete Asiatic soft-shell turtle skulls, ZMO 7104 without ramphotheca, and ZMO 7105 with ramphotheca. ZMO 7105 lacks the quadratojugal on both sides.

Geochelone nigra (ZMO 296), Figs 27-30. A complete Galápagos giant tortoise skull without ramphotheca.

Other skulls used in this study:

Order	Species	No.	Order	Species	No.
Anseriformes	<i>Cygnus cygnus</i>	ZMO 2931	Procellariiformes	<i>Diomedeidae</i> sp.	ZMO A-1
Anseriformes	<i>Somateria spectabilis</i>	ZMO 5056	Procellariiformes	<i>Diomedeidae</i> sp.	ZMO A-2
Anseriformes	Unknown sp.	ZMO 5582	Procellariiformes	<i>Diomedeidae</i> sp.	ZMO A-3
Anseriformes	Unknown sp.	ZMO 6025	Procellariiformes	<i>Pachyptila</i> sp.	ZMO 1337
Anseriformes	Unknown sp.	ZMO 5365	Procellariiformes	<i>Pachyptila</i> sp.	ZMO 1034
Anseriformes	<i>Anas clypeata</i>	ZMO 5531	Psittaciformes	<i>Ara maracana</i>	ZMO 6080
Anseriformes	<i>Anser albifrons</i>	ZMO 1021	Psittaciformes	<i>Coracopsis nigra</i>	ZMO 7183
Anseriformes	<i>Cygnus bewickii</i>	ZMO 6258	Psittaciformes	<i>Cacatua leadbeaten</i>	ZMO 5585
Anseriformes	<i>Clangula hyemalis</i>	ZMO 5907	Psittaciformes	<i>Platycercus splendens</i>	ZMO 6079
Caprimulgiformes	<i>Podargus cuvieri</i>	ZMO 5650	Psittaciformes	<i>Poicephalus meyeri</i>	ZMO 1375
Charadriiformes	<i>Cephus grylle</i>	ZMO 698	Psittaciformes	<i>Psittacus</i> sp.	ZMO 5584
Coraciiformes	<i>Rhinoplax vigil</i>	ZMO 2669	Psittaciformes	<i>Psittacus</i> sp.	ZMO 6281
Falconiformes	<i>Aquila albicilla</i>	ZMO 690	Psittaciformes	<i>Psittacus erithacus</i>	ZMO 1377
Falconiformes	<i>Pernis apivorus</i>	ZMO 4036	Psittaciformes	<i>Psittacus erithacus</i>	ZMO 5459
Galliformes	Unknown sp.	ZMO 3141	Struthioniformes	<i>Struthio camelus</i>	ZMO 2644
Galliformes	<i>Meleagris gallopavo</i>	ZMO 2820	Struthioniformes	<i>Struthio camelus</i>	ZMO 3636
Galliformes	<i>Numida meleagris</i>	ZMO 1362	Struthioniformes	<i>Struthio camelus</i>	ZMO 346/65
Oviraptorosauria	<i>Rinchenia mongoliensis</i>	PMO X679	Struthioniformes	<i>Casuaris casuaris</i>	BM 3123
Passeriformes	<i>Corvus seapulatus</i>	ZMO 1157	Testudines	? <i>Caretta caretta</i>	ZMO 7260
Passeriformes	<i>Corvus albicollis</i>	ZMO 1156	Testudines	<i>Chelonia mydas</i>	ZMO 5/12-1925

The Oviraptorid Skull

In this section the skull of the Zamyn Khondt specimen (IGM 100/42) (Barsbold 1981, 1983a, 1986, 1988), Figs. 3, 4, 34, is described, and then compared with *Oviraptor* sp. (PMO X678), Fig. 5, and *Conchoraptor gracilis* (PMO X677), Figs. 6, 7. The description is of the rostral part of the skull and of the entire mandible.

Oviraptor and *Conchoraptor*

SYSTEMATIC NOMENCLATURE

DINOSAURIA Owen, 1842
THEROPODA Marsh, 1881
COELUROSAURIA Huene, 1914
OVIRAPTOROSAURIA Barsbold, 1976
OVIRAPTORINAE Barsbold, 1976
OVIRAPTORIDAE Barsbold, 1976

Genus indet.

Oviraptorid Zamyn Khondt specimen

Genus CONCHORAPTOR Barsbold, 1986
***Conchoraptor gracilis* Barsbold, 1986**

General skull morphology

Both IGM 100/42 and the *Oviraptor* sp. (PMO X678) have a big crest on the top of the head (Figs. 3, 5). The crest on IGM 100/42 is more anteriorly situated than the crest of *Oviraptor* sp. (PMO X678), which is slightly crushed laterally, and is slightly thinner and higher. The oviraptorids have a very compact look, but have several fenestrae in the crest. The *Conchoraptor gracilis* (PMO X677) is quite similar to the oviraptorids, but differs from other taxa of oviraptorids in this study, because of its lack of a head crest (Fig. 6). It is also slightly laterally deformed.

Skull openings

The external narial openings on IGM 100/42 and *Oviraptor* sp. (PMO X678) have a slightly oval form, almost round, and are located above the antorbital fenestra. Their margins consist of the premaxilla dorsally, ventrally and anteriorly, and posteriorly and interiorly by the nasal. In *Conchoraptor gracilis* (PMO X677) the external narial openings are bean shaped in lateral view, and the openings tilt slightly backwards. The antorbital fossa contains the antorbital fenestra and the maxillary fenestra in both IGM 100/42 and *Conchoraptor gracilis* (PMO X677), but in *Oviraptor* sp. (PMO X678) only the antorbital fossa is visible. The antorbital fossa is relatively small, being only 1/4 of the size of the

orbit. The orbit is round and very big relative to its cranial height, and is completely separated from the antorbital fenestra by the prefrontal-lacrimal-complex, which connects to the jugal. The orbit makes up one third of the cranial height in IGM 100/42 and *Oviraptor* sp. (PMO X678), and half the cranial height in *Conchoraptor gracilis* (PMO X677) which lack this large crest, and has therefore a lower skull height.

Premaxilla

The premaxilla makes up most of the rostrum, and also most of the external narial borders, except posteriorly. It constitutes the anteriormost part of the palate, and the ventral margin forms a cutting edge. The lateral surface is rugose, and has several foramina. It connects to the maxilla posteroventrally, the lacrimal posteriorly and the nasal dorsally, and it makes up the entire tomia in the upper jaw. The ventral cutting edge is jagged in IGM 100/42 and *Conchoraptor gracilis* (PMO X677) (Figs. 3, 6). In all of the oviraptorids, the premaxilla together with the maxilla makes up the secondarily palate. The palatal surface of the premaxilla is overlapped by the maxilla (Fig. 34), and the maxilla is formed as two shelves, with two longitudinal bulges separated by a shallow groove on each (Elzanowski 1999). The four ridges have a top on the posterior end (Fig. 34).

Maxilla

The maxilla in oviraptorids contains two tooth-like caudomedial processes (Figs. 3, 5, 6, 34), which connects to the vomer (Osmólska 1976, Elzanowski 1999). The maxilla is robust, and forms the ventral boarder of the antorbital fossa, and it connects to the premaxilla anteriorly and dorsally, and the jugal posteriorly. Internally the maxilla connects to the palatine posteriorly and premaxilla anteriorly. When viewed laterally, the maxilla in IGM 100/42 forms the entire interior part of antorbital fossa, as well as the posterior part of the upper jaw. The ventral part is shifted inwards, and forms the lateral surface curved longitudinal (Fig. 34). In *Oviraptor* sp. (PMO X678) the maxilla starts as two thin bones that fuse into one, but in *Conchoraptor gracilis* (PMO X677) the maxilla is almost hidden in matrix, only showing a thin straight bone.

Nasal

The nasal is located on the posterior and interior side of the external narial openings, and it connects to the premaxilla anteriorly, the lacrimal laterally and the frontal posterodorsally. The nasal, together with the frontal, makes up the crest in IGM 100/42 and *Oviraptor* sp. (PMO X678) (Figs. 3, 5). In *Conchoraptor gracilis* (PMO X677) the nasal is two almost square plates, with many pneumatic openings (Fig. 7). *Oviraptor* sp. (PMO X678) also has a lot of pneumatic openings, but the nasal is placed vertically because of the crest, and not horizontally as in *Conchoraptor gracilis* (PMO X677).

Mandible

The mandible is short and compact, and it is pointed anteriorly. It has a large heart-shaped external mandibular fenestra (Figs. 4, 5, 6). The height of the mandible on the highest point is almost 1/2 of the length, and the height at the mid length of the mandible is 3 to 4 times higher than in the ends. The anterodorsal margin functions as a cutting edge, and extends as far back as the upper jaw ramphotheca overlap. The anteriormost part of the mandible is pointed upwards and forwards. The surangular and

the angular are fused together, and it is difficult to see any sutures. The bones on the medial side are still covered in matrix in *Conchoraptor gracilis* (PMO X677) and *Oviraptor* sp. (PMO X678), and a description is therefore impossible.

Dentary

The dentary is about half the length of the mandible and is the longest bone in the mandible. It contains the anterior, dorsal and ventral borders of the mandibular fenestra, and it makes up the entire tomia in the lower jaw. The lower jaw tomia is overlapped by the upper jaw tomia, and they form a cutting edge in the entire length of the tomia. The dentary connects to the angular posteroventrally and the surangular posteriorly. The lateral side of the dentary is rugose, and there are several foramina all along the dorsal margin. These foramina are all around the dentary with a very high density.

Avian skulls used in this study

General skull morphology

Most of the birds used in this study have elongate skulls with large orbital openings, and is thinner towards the tip of the rostrum. The rostrum is long and covered with ramphotheca. However, a typical Psittaciformes skull is almost round (Figs. 8, 12, 13, 14, 15). The orbits are very large compared to the skull size. Many of the bones, like the quadrate and the jugal process, are not ossified. They are connected to each other with ligaments, so that they can move even more in relation to each other, than in other birds.

Skull openings

The external narial openings in Psittacidae are round, placed high up on each side of the beak, and resemble each other in the whole group. However, they are much larger in *Cacatua galerita* (ZMO 360/65) than in the *Ara* sp. (ZMO 1340), 1/5 vs. 1/10 compared to the beak height. In the two skulls of *Psittacus* sp. (ZMO 4915 & ZMO 4916), the external narial openings are 1/8 of the beak height. Their borders consist of the premaxilla dorsally, ventrally and anteriorly, and posteriorly by the nasals. In Psittaciformes, both the antorbital fenestra and the temporal fenestra are separated from the orbit, in contrast to other birds (Figs. 8, 14, 15). In juveniles the prefrontal-lacrimonal-complex, which surrounds the orbit, is not fully developed (Figs. 12, 13). The antorbital fenestra is formed as a triangle in front of the orbit, and the opening is bordered by the prefrontal-lacrimonal-complex posterolaterally, the maxilla-jugal-complex ventrally and premaxilla anteriorly. The temporal fenestra is placed behind the orbit, in front of the quadratojugal. The orbit is round and makes up half of the cranial height, and is completely separated from antorbital fenestra by the prefrontal-lacrimonal-complex.

Rostrum

The premaxillas and nasals form the rostrum in parrots, which is connected to the frontal and the maxilla-jugal-complex with ligaments, and the junction is not ossified. Internally it connects to the palatine. The nasal bone is completely fused with the premaxilla and the two premaxilla bones have also fused. It is impossible to see any sutures, but as in any other birds and reptilians the nasal is to be found at the posterior part of the external narial openings. The premaxilla makes up the anterior and lateral borders. The ventral margin of the premaxilla forms a cutting edge, and the anteriormost part is pointed ventrally. The surface is rugose, and there are several foramina beneath where the ramphotheca has been (Figs. 8, 12, 13, 14).

Maxilla-jugal-complex

The maxilla-jugal-complex consists of the maxilla, the jugal and the quadratojugal. In Psittaciformes the three bones have fused together, making a thin round bone, which connects only with ligaments to the premaxilla anteriorly, and to the quadrate posteriorly (Figs. 8, 11). It is completely separated from the lacrimal, but makes up the ventral border of the antorbital fenestra.

Palate

The pterygoids, the palatines and the vomer make up the palate, and they are all connected to each other only with ligaments (Fig. 11). The palatine connects anteriorly to the premaxilla, and is dorsally connected to both the vomer and the pterygoids. The pterygoids are connected anteriorly to the vomer and the palatines, and posteriorly to the quadrate. The vomer has been ossified to the rest of the skull, and has become an attaching point to the pterygoids and the palatines. The palatines are situated vertically, but slightly tilted outwards ventrally, whilst the pterygoids are thin and round, like the maxilla-jugal-complex.

Mandible

The mandible is pointed anteriorly, and the anterodorsal margin functions as a cutting edge, and extends as far back as the dental. In *Psittacus* sp. (ZMO 4915 & ZMO 4916) and the *Ara* sp. (ZMO 1340) the dentary height is 1/2 of the mandible length, but only 1/3 in *Cacatua galerita* (ZMO 360/65). This is due to the anteriormost part of the mandible being pointed upwards and forwards in *Cacatua galerita* (ZMO 360/65), whilst in the other three skulls the mandible ends vertically at the highest point of the mandible (Figs. 9, 13, 14). Some parrots, like the two skulls of *Psittacus* sp. (ZMO 4915 & ZMO 4916) and the *Ara* sp. (ZMO 1340), has a small mandibular fenestra. In *Cacatua galerita* (ZMO 360/65) there is no mandibular fenestra, but the mandible is longer than in the other three skulls.

Dentary

The dentary is the longest bone in the mandible, and makes up 40-50 percent of the mandible. It also makes up the entire tomia in the lower jaw, and it is overlapped by the upper jaw tomia, and forms a cutting edge in its entire length. The symphysis in parrots is either oblique as in *Cacatua galerita* (ZMO 360/65, Fig. 9) or horizontal as in the two *Psittacus* sp. (ZMO 4915 & ZMO 4916, Figs. 12, 13) and the *Ara* sp. (ZMO 1340, Fig. 14). The dentary connects to the angular posteroventrally and the surangular posteriorly. Internally it connects to the splenial posteriorly. There are several foramina on the dentary, and the dentary is rugose beneath where the ramphotheca was. There are also some foramina on the inside, but they are restricted to the anteriormost part of the dentary.

Ramphotheca

The ramphotheca is quite similar in all Psittaciformes, although there are some minor differences. The beak of the *Ara* sp. (ZMO 1340 & ZMO 688, Figs. 14, 15, 16) is more powerful than in *Cacatua galerita* (ZMO 360/65, Figs. 8, 11), having a larger palatal surface. In all skulls, the ramphotheca at the upper jaw extend as far back as the anterior part of the external narial opening dorsally, also stretching around the lateral sides of the narial opening, covering almost the entire rostrum. The ventral margin forms a cutting edge, and the anteriormost part is pointed ventrally. In the lower jaw, the ramphotheca extend as far back as the upper ramphotheca dorsally, and as far back as the symphysis ventrally, covering most of the dentary. The dorsal margin of the ramphotheca forms a cutting edge, the anteriormost part is pointed dorsally, and together with the upper ramphotheca forms a grasping beak.

Testudine skulls used in this study

General skull morphology

The Testudines are an anapsid group, which members lack temporal fenestra. Notably, the testudines do not have the nasal bone, the nasal opening being bordered dorsally by the prefrontal. Particularly in some of the marine groups, exemplified by *Caretta caretta* (ZMO 19/62) and *Eretmochelys imbricate* (ZMO 12/74), the skull roof is extraordinary heavy (Figs. 19, 21), while the crania of others, e.g. *Amyda cartilaginea* (ZMO 7104) and *Geochelone nigra* (ZMO 296), have various invaginations and secondary openings (Figs. 24, 29), paralleling the synapsid and diapsid condition. Indeed, the status of testudines as a true anapsid group is disputed.

Skull openings

The external narial opening in turtles combine before exiting the skull interior, presenting a single opening, similar to the condition found in mammals and crocodylians. However there are two distinct opening in the palate. In many of the sea-turtles, such as *Caretta caretta* (ZMO 19/62) and *Eretmochelys imbricate* (ZMO 12/74), the narial opening is half the size of the orbit, whilst in some land-turtles, e.g. *Geochelone nigra* (ZMO 296), the narial opening is the same size as the orbit. In freshwater-turtles as *Amyda cartilaginea* (ZMO 7104), the narial opening is also the same size as the orbit, but compared to other turtles, both openings are small relative to the skull size. The orbits faces laterally in the sea-turtles *Caretta caretta* (ZMO 19/62) and *Eretmochelys imbricate* (ZMO 12/74), whilst they are more forwardly facing in the land-turtle *Geochelone nigra* (ZMO 296) and in the freshwater-turtle *Amyda cartilaginea* (ZMO 7104). In some species, e.g. *Caretta caretta* (ZMO 19/62) and *Eretmochelys imbricate* (ZMO 12/74), a secondary palate is developed (Fig. 20), giving a single opening dorsally in the mouth. The orbital openings are well forward of the middle of the cranium in all species. The openings are bordered by the maxilla and the prefrontal anteriorly, and by the postorbital and the jugal anteriorly. The frontals, situated between the prefrontals and postorbitals are adjacent to the openings in some species (Figs. 19, 29) like *Caretta caretta* (ZMO 19/62) and *Geochelone nigra* (ZMO 296), and form part of the upper margin in others (Fig. 24), like in *Eretmochelys imbricate* (ZMO 12/74) and *Amyda cartilaginea* (ZMO 7104).

Premaxilla

The premaxilla consists of two small rectangular bones underneath the narial opening, and make up the anteriormost part of the skull. It constitutes the anteriormost part of the palate. In *Caretta caretta* (ZMO 19/62) and *Eretmochelys imbricate* (ZMO 12/74) the premaxilla is sponge-like, and the ventral margin forms a cutting edge. In *Geochelone nigra* (ZMO 296) the premaxilla is rugose, and the ventral margin has a blunter cutting edge than in *Caretta caretta* (ZMO 19/62) and *Eretmochelys imbricate* (ZMO 12/74). In *Amyda cartilaginea* (ZMO 7104) the two premaxillary bones are fused and are barely visible externally, and the ventral margin has a flat edge.

Maxilla and Palate

The maxilla forms the lateral margins of the narial opening, the anterior and most of the ventral margin of the orbit, and connects to premaxilla anteriorly, the jugal posteriorly, and to the prefrontal anterodorsally. In the palate the maxilla connects to the premaxilla anteriorly, the vomer ventrally, palatine posteroventrally, and the jugal posteriorly, and internally the maxilla connects to the jugal posteriorly, palatine ventrally, and prefrontal anteriorly. The ventral margin forms a cutting edge in *Caretta caretta* (ZMO 19/62) and *Eretmochelys imbricate* (ZMO 12/74), while the ventral margin has a flat edge in *Amyda cartilaginea* (ZMO 7104, Fig. 25). In *Geochelone nigra* (ZMO 296, Fig. 30) the ventral margin has a blunter cutting edge than in *Caretta caretta* (ZMO 19/62, Fig. 20) and *Eretmochelys imbricate* (ZMO 12/74).

Prefrontal

The prefrontal make up the posterodorsal edge of the narial opening and the anterodorsal edge of the orbit. The anteroventral part connects to the dorsal process of the maxilla, and to the frontal and the post orbital posteriorly. Internally, the prefrontal connects to the postorbital posteriormost dorsally, the frontal mediodorsally, the vomer medioventrally, the palatine posteroventrally, and the maxilla lateroventrally. In *Caretta caretta* (ZMO 19/62), *Eretmochelys imbricate* (ZMO 12/74) and *Geochelone nigra* (ZMO 296) the prefrontal is trapezoid in shape, with its posteriormost part laterally. In *Amyda cartilaginea* (ZMO 7104) the posteriormost part is medially.

Mandible

In *Caretta caretta* (ZMO 19/62) and *Eretmochelys imbricate* (ZMO 12/74) the mandible is pointed anteriorly, and the anterodorsal margin is formed as a cutting edge. The dentary constitute 2/3 of the mandible length, and the height is 1/5 of the mandible length, but the mandible of *Caretta caretta* (ZMO 19/62) is wider than in *Eretmochelys imbricate* (ZMO 12/74). In *Amyda cartilaginea* (ZMO 7104) the mandible is pointed anteriorly, but the anterodorsal margin is flat. The dentary constitute 90 percent of the length on the ventral side of the mandible, and 60 percent of the dorsal side. The height is 1/3 of the mandible length. The dentary in *Geochelone nigra* (ZMO 296) constitute 60 percent of the mandible length, and the height is 1/3 of the length. The anterodorsal margin is forms a blunt cutting edge.

Dentary

The dentary is the longest bone in the mandible, and constitute 60-90 % of the length in the mandible. It also forms the entire tomia in the lower jaw. The symphysis in turtles is either oblique as in the families Cheloniidae and Trionychidae (Figs. 18, 21, 23), or vertical as in Testudinidae (Fig. 28). There is a < shaped depression on the lateral surface of the dentary, and starts at the posterior part of the denary. The depression varies with different extent (Figs. 18, 21, 23). The lower jaw tomia is overlapped by the upper jaw tomia, and it forms a cutting edge in its entire length, with the exception of *Amyda cartilaginea* (ZMO 7104), where the tomia is flat and rounded respectively. There are several foramina all along the dorsal margin of the dentary, also on the inside. These foramina appear in several different patterns, those around the dentary

being closely spaced in the families Cheloniidae and Testudinidae (Figs. 18, 28). In Trionychidae they follow the dorsal margin of the dentary, with one thin row of foramina on the inside, and one on the outside (Fig. 23).

Surangular

The surangular is the next largest bone in the mandible, and makes up the posterodorsal part of the lateral surface of the mandible. It connects to the dentary anteriorly and ventrally, angular posteroventrally, the coronoid process dorsally, prearticular internal ventrally, and articular on the posterior internal surface.

Angular

The angular is a thin long bone on the inside of the mandible, slightly longer than the surangular. It connects to the dentary anteriorly and ventrally, to the prearticular dorsally, to the surangular posteriormost ventrally and internally, and to the articular posteriormost internally. The angular is visible on the lateral surface of the mandible, as a thin bone posteroventrally.

Prearticular

The prearticular is placed just above the angular, and is about the same length as the angular. It connects to the coronoid dorsally, the angular ventrally, and the articular posteriormost internally.

Articular

The articular is wedged between the surangular and the angular internally, and is round in form. The articular and the quadrate make the contact surface between the upper and the lower jaw.

Coronoid

The coronoid is placed on top of the prearticular, and is one of the smallest bones in the mandible. It connects to the prearticular ventrally, the dentary anteriorly and dorsally, and the surangular posteriorly.

Ramphotheca

Cheloniidae

The ramphotheca of both the skulls of *Caretta caretta* (ZMO 19/62) and *Eretmochelys imbricate* (ZMO 12/74) are quite similar, but the ramphotheca of *Caretta caretta* (ZMO 19/62) is more robustly constructed than in *Eretmochelys imbricate* (ZMO 12/74), and has a crushing surface inside the mouth. This is due to a wide palatal portion. In *Eretmochelys imbricate* (ZMO 12/74), especially the lower jaw is narrow and smooth (Wyneken 2001). On both skulls, the ramphotheca in the upper jaw extend as far back as the anterior part of the narial opening dorsally, also stretching around the lateral sides of the narial opening, and to the end of the maxilla laterally. The ventral margin forms a cutting edge, and the anteriormost part is pointed ventrally. In the lower jaw, the ramphotheca extends as far back as the upper ramphotheca laterally, covering most of the dentary. The dorsal margin of the ramphotheca forms a cutting edge, the anteriormost part is pointed dorsally and together with the upper ramphotheca forms a grasping beak.

Trionychidae

The ramphotheca in *Amyda cartilaginea* (ZMO 7104) occur inside the mouth, and is normally covered with outer lips. The ramphotheca on the upper jaw extends as far back dorsally as just above the ventral margin and to the end of the maxilla posteriorly. The ventral margin has a flat border in two levels, so that the edge between them forms a cutting edge with the lower ramphotheca (Fig. 26). In the lower jaw, the ramphotheca extend as far back as the upper ramphotheca laterally, covering the dorsal side of the dentary. The dorsal margin of the ramphotheca has a flat border, forming a crushing surface with the upper ramphotheca.

Testudinidae

The ramphotheca in *Geochelone nigra* (ZMO 296) is robustly constructed and has a crushing surface inside its mouth. This is due to a wide palatal portion. The ramphotheca in the upper jaw extend as far back as the anterior part of the narial opening dorsally, also stretching around the lateral sides of the narial opening, and to the end of the maxilla laterally. The ventral margin forms a cutting edge, and the anteriormost part is pointed ventrally. In the lower jaw, the ramphotheca extends as far back as the upper ramphotheca laterally, covering most of the dentary. The dorsal margin of the ramphotheca forms a cutting edge, and the anteriormost part is pointed dorsally, forming a grasping beak together with the upper ramphotheca.

Osteological comparison of oviraptorids, parrots and turtles

From the description of the oviraptorids, parrots and turtles in the previous chapters, one can see that the premaxilla, the maxilla and the dentary is of most interest. These are the bones that support the ramphotheca, sometimes together with the nasal, so these bones are therefore compared. The nasal is covered by ramphotheca only in a few samples, and then only small parts of the nasal are covered.

General skull morphology

The overall skull shape of the oviraptorids and the parrots is very similar (see the ordination analysis, Fig. 2), even though they differ in important characters. The turtles have a more elongate skull shape than the other two groups. One of the differences between oviraptorids and parrots is the relative length and size of the different bones, another difference is the location of the skull openings. The two large temporal fenestrae in oviraptorids are either completely missing in parrots, or they are very small, like in *Cacatua galerita* (ZMO 360/65, Fig. 8). The antorbital fenestra is much smaller in parrots than in oviraptorids, and is absent in turtles. The orbit in parrots, in contrast to the oviraptorids, is completely separated from the antorbital fenestra by the prefrontal-lacrimal-complex and does not connect to the jugal. The relative size of the orbit compared to the skull, is approximately the same in oviraptorids and parrots, but smaller in turtles. The external narial openings are enormous in oviraptorids compared to parrots, both placed at the posterior part of the rostrum. In turtles the internal narial openings combine into one single external narial opening, which is placed in the anteriormost part of the skull.

Premaxilla

The premaxilla in oviraptorids and parrots is radically different from the turtles. In the latter the premaxilla is often two small square bones under the external narial opening, the anteriormost part of the small rostrum. In oviraptorids and parrots the two premaxilla bones are fused to form a long and wide rostrum. The premaxilla is still confined to the same place in the jaw relative to the skull openings. It forms the anterior border of the external narial openings in all the groups, but also the ventral border in oviraptorids and parrots. The surface is rugose or sponge-like in all of the samples, showing where the premaxilla is covered by ramphotheca, and where the ramphotheca was connected with sensory organs and vascular tissue to the surface of the bones. Presumably, a rugose surface will contribute to a better attachment zone than a smooth surface.

Maxilla

The maxillary bone in all oviraptorids as in other theropods, contributes to most of the ventral side of the upper jaw. In IGM 100/42 the maxilla also forms the entire interior part of antorbital fossa (Fig. 3). This may also be the case in *Oviraptor* sp. (PMO X678) and *Conchoraptor gracilis* (PMO X677), but unfortunately the antorbital fossa is still covered with matrix, so this cannot be confirmed (Figs. 5, 6). In parrots, the maxilla has fused together with the jugal and quadratojugal forming the maxilla-jugal-complex, a thin straight bone which connects to the rostrum with ligaments. The pterygoids, the

palatines and the vomer make up the palate, and they are all connected to each other and the rostrum with ligaments, to make the beak more flexible to movement. In turtles the maxilla forms the lateral borders of the narial openings, as well as the anterolateral part of the skull.

Nasal

In oviraptorids and parrots the nasal forms the posterodorsal part of the rostrum, whilst in turtles the nasal is replaced by the prefrontal which also forms the posterodorsal part of the rostrum. The crest in oviraptorids consists of the nasal, together with the frontal.

Mandible

The dentary is normally the longest bone in the mandible of birds and turtles, followed by the surangular and the angular. One of the most striking features with the dentary bone of both birds and turtles in ventral view, is the < shaped depression (Figs. 18, 21, 23) on the posterior area. The size and strength varies, but this depression marks the point where the dorsal margin foramina appear. Sometimes it also marks the junction between the rough and smooth surface on the dentary. However, *Geochelone nigra* (ZMO 296), the parrots and the oviraptorids lack this < shaped depression on the lateral surface of the dentary, and the oviraptorids have a large mandibular fenestra in its place. Except for the large mandibular fenestra in oviraptorids, the whole mandible in parrots is very similar to the one in oviraptorids (Figs. 4, 9), and some parrot species have a small mandibular fenestra (Figs. 13, 14). Whilst the mandible in turtles is long and elongated, the mandible in oviraptorids and parrots is short and compact. The mandible, like the premaxilla and the maxilla, also has foramina. In oviraptorids and parrots they appear along the dorsal margin of the dentary, and follow the curve at the symphysis. This also applies for the testudine family Trionychidae. In the families Cheloniidae and Testudinidae, the foramina are closely spaced, and appear in different patterns all over the anterior part of the mandible. When observing the specimens with ramphotheca, one can see that the keratin cover extends as far back as to the point where the margins of the dentary depression appear. In all the birds and turtles used in this study, the ramphotheca extended equally far back on both the upper and lower jaw.

Discussion

There are many similarities in cranial skeletal composition between oviraptorids and parrots. A study of a virtual brain model of *Conchoraptor gracilis* compared with the avian brain showed that *Conchoraptor gracilis* had many similarities to extant birds, on some levels even more than *Archaeopteryx* (Kundrát 2007). One of the differences between oviraptorids and birds, except parrots, is the merging of both temporal fenestrae with the orbit and the loss of the postorbital bone in birds. These features help to lighten the skull, and to facilitate the development of the enlarged brain. The merging of the temporal fenestrae with the orbit also appears in some parrot species, whilst in others the temporal fenestrae are still separated. The turtles are an anapsid group, and do not possess any temporal fenestrae.

If one assumes that the same bones always support the ramphotheca, then this implies for how the beak has evolved. For instance, to evolve a larger beak, the ramphotheca-bearing bones would then have to enlarge, or extend the growth of ramphotheca on other bones as well. This study has shown that many extant birds and turtles have rostral ramphotheca cover on both premaxilla and maxilla, but in parrots only the premaxillary is covered, and the ramphotheca runs up to the anterior border of the external narial openings. Both oviraptorids and parrots have the external narial openings placed on the top of the powerful rostrum. In parrots, the external narial openings are covered by a muscular tissue and skin. Some birds also have ramphotheca on the nasal and the palatine, the cassowary being an extreme example. The crest in the *Casuaris casuaris* skull (BM 3123) consists of the nasal, which grows on the top of the frontal and the whole crest is covered by ramphotheca (Fig. 31) (pers. com. Anne Karin Hufthammer). In the latter case the external narial openings are covered in ramphotheca as in the Procellariiform birds (seagulls). Turtles have their external narial opening placed almost at the anteriormost part of the skull, not far from the ventral edge of the upper jaw, and covered by muscular tissue and skin.

The maxilla in birds is very reduced (Zusi 1993), and in parrots the maxilla makes a complex together with the jugal and the quadratojugal that forms the ventral border of the antorbital fenestra. In extant birds the antorbital fenestra is not covered with ramphotheca, and the extent of the upper jaw tomia controls the extent in the lower jaw. The maxilla-jugal-complex is connected between the premaxilla and the quadrate to control the beak movement. The maxilla-jugal-complex is very thin (Fig. 11) and is most likely not exposed to any strong mechanical forces when biting. It is therefore not covered by ramphotheca. This fact may be used to judge if the area is covered with keratin or not. In turtles the maxilla forms most of the anteroventral surface and is exposed to strong mechanical forces when biting. The maxilla is therefore a robust bone covered by ramphotheca. In *Chelonia mydas* (ZMO 5-12-1925), the dorsal edge of the mandible has short tooth-like structures and tall ridges of bone (Fig. 32). The short tooth-like structures becomes long tooth-like spines in the ramphotheca (Fig. 33). The maxilla in oviraptorids is robust, and forms the palate together with the premaxilla (Fig. 34). This may indicate that the maxilla was exposed to strong mechanical forces

when biting, and was covered by ramphotheca. The ventral edge of the rostrum has structures similar to the mandible in *Chelonia mydas* (ZMO 5-12-1925, Fig. 32), and this may indicate the ventral form of the ramphotheca in oviraptorids. This will be discussed later in the discussion. The ramphotheca in all of the birds and turtles measured in this study had similar tomia in both the upper and the lower jaw, so as to be able to use the force produced by the muscles more efficiently. A soft surface would absorb much of the force produced by the hard surface. Since this appears in all of the examined birds and turtles, this can also be expected in the oviraptorids.

In most birds and turtles the < shaped depression in the dentary indicates the posterior border of the ramphotheca. But since parrots lacks this depression, the rugose surface or the extent of the upper jaw tomia indicates where the posterior border of the ramphotheca is located. The mandibles of the oviraptorids and the parrots are not only very similar in shape, but also possess similar surface structures. This can indicate a similar mandibular ramphotheca configuration between the oviraptorids and the parrots. Since the overall cranial anatomy of the oviraptorids is similar to that of parrots, it is tempting to assume that the oviraptorids had quite similar cranial muscles to that of parrots (see Gadow 1891: plate 26, Burton 1974: figs. 1-3, Zusi 1993: fig. 8.13). The parrots and the oviraptorids are so similar that a mandibular symphysis was first described as a Cretaceous parrot (Stidham 1998), and later as a caenagnathid-like-non-avian theropod by Dyke and Mayr (1999). As a reply to the critic, Stidham (1999) said that assigning the mandible to anything else than an avian clade would be unparsimonious (Waterhouse 2006).

The large posterior part of the crest in IGM 100/42 is formed by the nasal and the frontal, and Barsbold (1981, 1983a, 1983b, 1988) claimed it was covered with ramphotheca as in the cassowaries. The lateral surface of the crest is full of fenestrae, but it is possible that the looser osseous tissue was not preserved in a fossilized state (Barsbold 1981, 1983a, 1983b, 1988). The latter description also relates to the other oviraptorids in my study, *Oviraptor* sp. (PMO X678), *Conchoraptor gracilis* (PMO X677) and *Rinchenia mongoliensis* (PMO X679). The main function of the crest is not clear in either oviraptorids or cassowaries. It may be used for fighting, but this does not seem likely, due to the thin and brittle crest in some of the oviraptorids (Barsbold 1988), e.g. *Oviraptor* sp. (PMO X678, Fig. 5), and to the porous nasal bone underneath the helmet in the cassowaries. Moreover, it is not strengthened with a thickening of bone structure, as in the helmeted hornbill, *Rhinoplax vigil* (ZMO 2669, Fig. 35). This can be the case in cassowaries as well, but this is not confirmed. The crest in the cassowaries is only found on mature individuals as an indicator of sexual maturity, suggesting it is may be a result of sexual selection. In addition it can also be used to move away branches and sift through leaf litter in the search for food. It is possible that sexual selection caused the crest in the crested oviraptorids. The pneumatic surface may also have been used to regulate temperature, much like the sail in *Dimetrodon* (Bramwell & Fellgett 1973). It may also be used to show vivid colors as a signal to warn off predators or to signal to conspecifics. Unlike the oviraptorids, the crest of the Helmeted Guineafowl, *Numida meleagris* (ZMO 1362), only consists of the frontal, and is covered by skin. None of the

examined species had ramphotheca on the frontal, and only a few of them had partially covered nasal bone.

In several studies, the presence of the beak has been associated with an edentulous jaw full of foramina and pits (Dzik 2003, Apesteguía 2004). But foramina and pits are also seen in toothed animals, like monitor lizards, crocodylians, dromaeosaurs and tyrannosaurids. Nevertheless, disregarding the foraminae would the occurrence of a toothless jaw in most cases suggest the presence of a beak or a beak-like structure. Studies of the foramina in birds have shown that the small foramina, in addition to blood vessels, house two types of sensory cells which are positioned to make the receptors more sensitive to stimuli from the edges of the bill (Knutsen 2007). Similar foramina were also found in my study. In the turtles, there exist a large number of foramina and pits on the surface of the jaws, except in *Amyda cartilaginea* (ZMO 7104 & ZMO 7105) which has external lips and keratin plates in the palatine (Figs. 25, 26). Instead it has a row of foramina along the flat ventral edge of the premaxilla and maxilla, underneath the chewing plates. It also has some foramina on the anterolateral surface, for blood supply and sensory receptors to the lips. The parrots have some foramina at the anteriormost part of the mandible, and a few along the anterolateral edge. In the upper jaw there is a thin row of foramina at the anteriormost part of the rostrum (Figs. 8, 14). The general rostral surface structure is very rough in all of the oviraptorids. The surface has only a few foramina, but several grooves near the cutting edge, pointing towards the edge. The grooves, however, might be foramina that have been worn down or the result of the cast making procedure.

The oviraptorids appear to be a more primitive functional form of the parrot, because of the similar cranial structure. The bones connected to the rostrum in the oviraptorids are ossified, whilst they are attached with ligaments in the parrots which make the beak flexible to movement. This means that the oviraptorids could not move their beak in the same way as parrots. The beak of the parrots is a result of specialization, and by placing the seed in the notch inside the rostrum (Fig. 16) and using the tongue and the lower jaw tomia, the parrot can peel off the hull of seeds with minimum effort (Fig. 36). Since the oviraptorids had no kinesis in the beak, they could most likely not have the same feeding technique as the parrots. However, the oviraptorids also have a specialization; the two tooth-like processes of the maxilla (Fig. 34). Osmólska (1976) claimed that since the two tooth-like processes in the holotype of *Oviraptor philoceratops* do not bear any traces of wear, they had to be covered by a horny or soft tissue. It was most likely a keratin cover, because a soft tissue cover would reduce the advantage of having teeth in the palatine. Barsbold (1981) claimed that the tooth-like processes presumably were a specialization to eat hard food, such as eggs, nuts, and hard seeds. They might have the same function as the notch inside of the parrot beak; used to keep the nut or egg in position. However, the existence of nuts in the Late Cretaceous is not completely definite, and needs to be confirmed or disapproved. Nevertheless, nuts and hard seeds were unlikely the main diet. Some paleontologists hold that oviraptorids were herbivorous, because the oviraptorid skull was too fragile for a hard food diet (Glut 1997), and that they used the sharp edges of their jaws to cut off leaves and other fibrous matter (Smith 1990, 1993). Even though gastroliths have been

found in the primitive oviraptorosaurid *Caudipteryx* (Ji *et al.* 1998), it is not likely that advanced oviraptorids had gastroliths. However, as the oviraptorid skull is heavier and stronger built than most bird skulls, and the beak is as powerful as an eagle's beak, it is more probable that the oviraptorids had an omnivorous diet, the main diet was prey. The two tooth-like processes, together with a spiny ventral edge of the ramphotheca and the palatal ridges, might have been used to hold on to the prey while it was torn apart. The palatal ridges have extensions at the posterior end, which most probably were expressed as tooth-like structures in the ramphotheca, much the same as the mandible of *Chelonia mydas* (ZMO 5-12-1925, Fig. 33). Any small structures on the ridges in the palate, and elsewhere can be destroyed during fossilization or subsequent preparation.

Conclusion

Generally would a toothless jaw with foramina along the jaw edges, together with an uneven surface, suggest the presence of a beak or a beak-like structure. Since neither the oviraptorids nor the parrots have the < shaped depression on the mandible, this cannot be used to assess the posterior extent of the ramphotheca, as discovered in other birds and ornithomimids (Knutsen 2007). The premaxilla, maxilla and partly the nasal are covered by ramphotheca in birds (Figs. 14, 15), whilst only the premaxilla and maxilla are covered by ramphotheca in turtles (Figs. 25, 26). In both groups, only the dentary is covered by ramphotheca in the mandible. The ramphotheca follows the skeletal framework, and all the surface features of the ramphotheca are also present in the underlying bone. Even though the ramphotheca consistently follows the bones it may extend beyond them in the growth direction (Figs. 32, 33), as in the beak of parrots where the beak is longer than the bone beneath (Figs. 14, 15). This study has shown that characters in beak morphology in birds also can be transferred to turtles. When the same rules apply to two groups of animals which have evolved so distinctively separate from each other, this knowledge can most likely be transferred to oviraptorids as well.

The oviraptorid mandible (Fig. 4) is very similar to the parrot mandible (Fig. 9), and the ramphotheca most likely resembled that of parrots, with the dorsal margin forming a cutting edge. The anteriormost part will grow until it meets the upper jaw ramphotheca, as in parrots. The extent of the ramphotheca in the upper jaw is much harder to predict. However, two morphologies are more likely than others. In both, the ventral margin of the ramphotheca is likely to be a spiny cutting edge which extended in the growth direction, leading to a combination of the parrot beak and the turtle beak; a sharp cutting edge as in the turtle beak, and the strength and the length of the former.

The first possible morphology (Fig. 37, case A) is that the ramphotheca cover the premaxilla up to the anterior part of the external narial opening. In this case, the external narial openings would be surrounded by a muscular tissue and skin, as in parrots and turtles. This also indicates that the pneumatic crest was covered by a muscular tissue and skin, as in *Numida meleagris*. The second morphology (Fig. 37, case B) is that the crest (the nasal bone), as well as the premaxilla and the maxilla, was covered with ramphotheca. In the latter case the external narial openings would be surrounded by ramphotheca. Since none of the examined specimens had ramphotheca on the frontal, it would be very strange if the oviraptorids did. The crest in the examined oviraptorid species is built up of both the nasal and frontal bones, which implies that the entire crest could not have been covered in ramphotheca. It is not likely that only the anterior part of the crest was covered with ramphotheca. In any case, the ridges in the palate, together with the two tooth-like processes of the maxilla, were most certainly covered by a ramphotheca with tooth-like structures, as in the mandible of the turtle *Chelonia mydas* (ZMO 5-12-1925, Fig. 33). This indicates that the whole maxilla in oviraptorids most likely was covered with ramphotheca.

Regarding the dietary habit, the tomial and palatal morphology suggests an omnivorous diet. The sharp beak, together with long arms with long sharp claws, is well adapted to catch and tear small prey. The two tooth-like caudomedial processes on maxilla may have been used to hold on to the prey. Moreover, they could also crush hard food such as eggs, nuts, and hard seeds. The suggestion that oviraptorids were herbivorous, eating only leaves and other fibrous matter, does not seem very likely, since they do not have any flat wide tomia with which to chew, and could not move their jaws sideways.

In my view further studies of the crest in cassowaries, oviraptorids and helmeted hornbills are needed; the purpose of the crest and the anatomy of the crest-bearing bones should be examined in detail. A closer look at more species of oviraptorids needs to be done, both with and without crest. Why do crestless oviraptorids also have the pneumatic surface on the top of their head? More thorough studies of the two tooth-like caudomedial processes of the maxilla should be done; they might be poison spines as in the platypus. Hopefully more new material might enlighten the habitat of oviraptorids.

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A1



A2

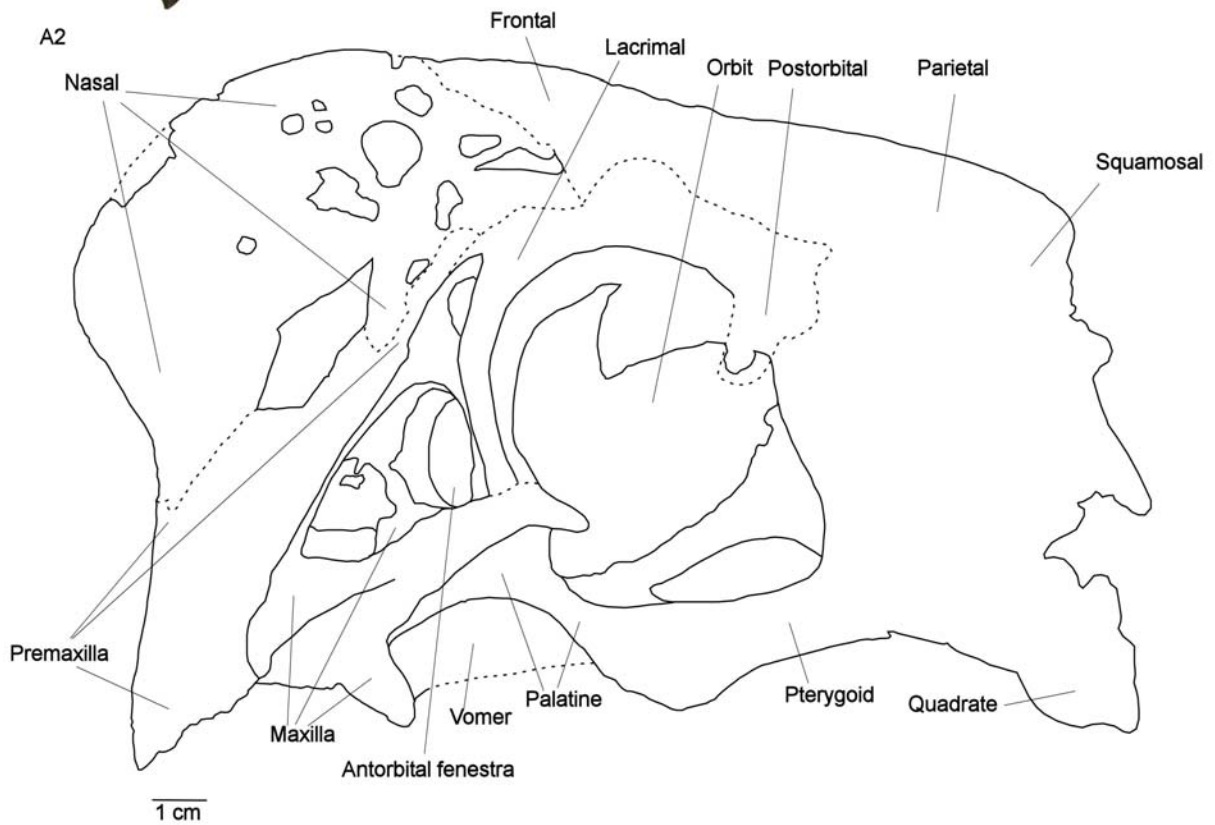


Figure 3

The skull of the oviraptorid Zamyn Khondt specimen (IGM 100/42) in lateral view. A1: The skull
A2: Explanatory drawing

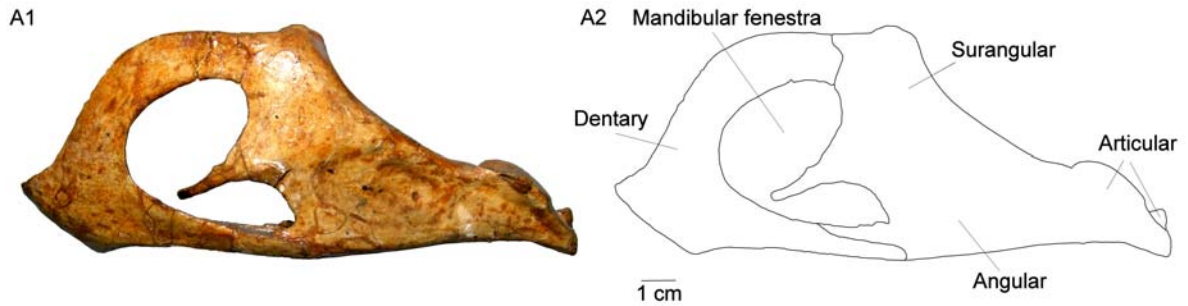


Figure 4
The mandible of the oviraptorid Zamyn Khondt specimen (IGM 100/42) in lateral view. A1: The mandible
A2: Explanatory drawing

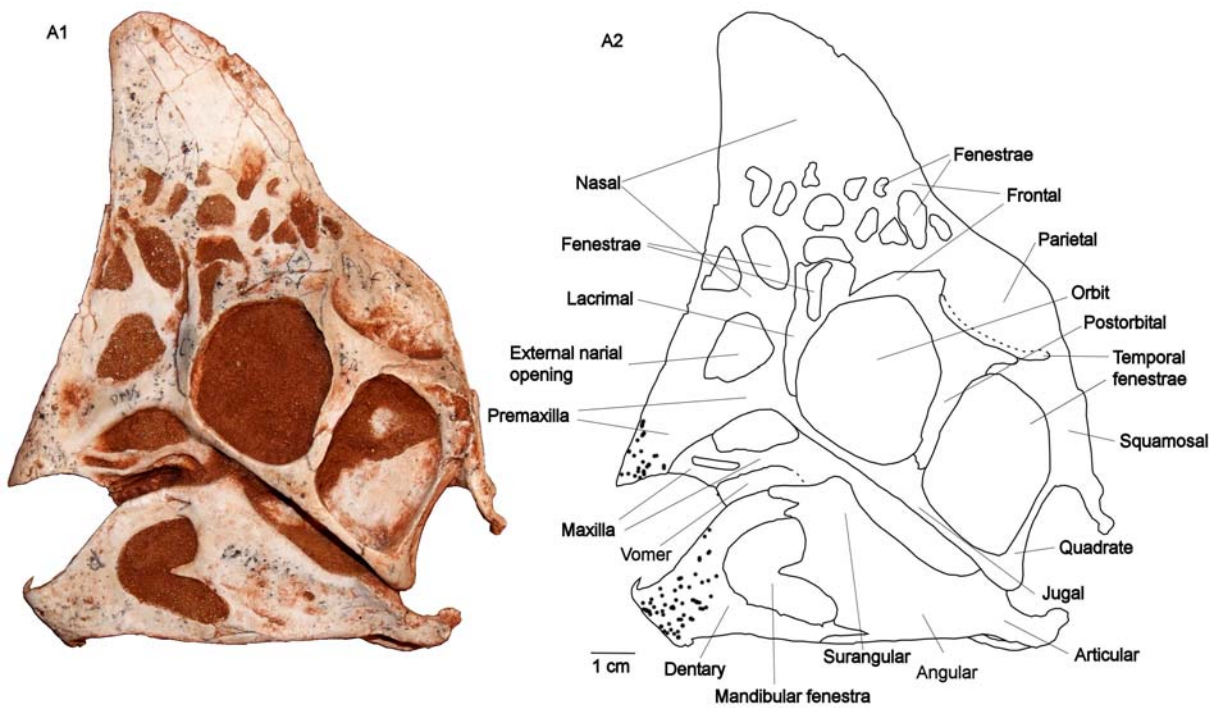


Figure 5
The skull of *Oviraptor* sp. (PMO X678) in lateral view. A1: The skull A2: Explanatory drawing

A1

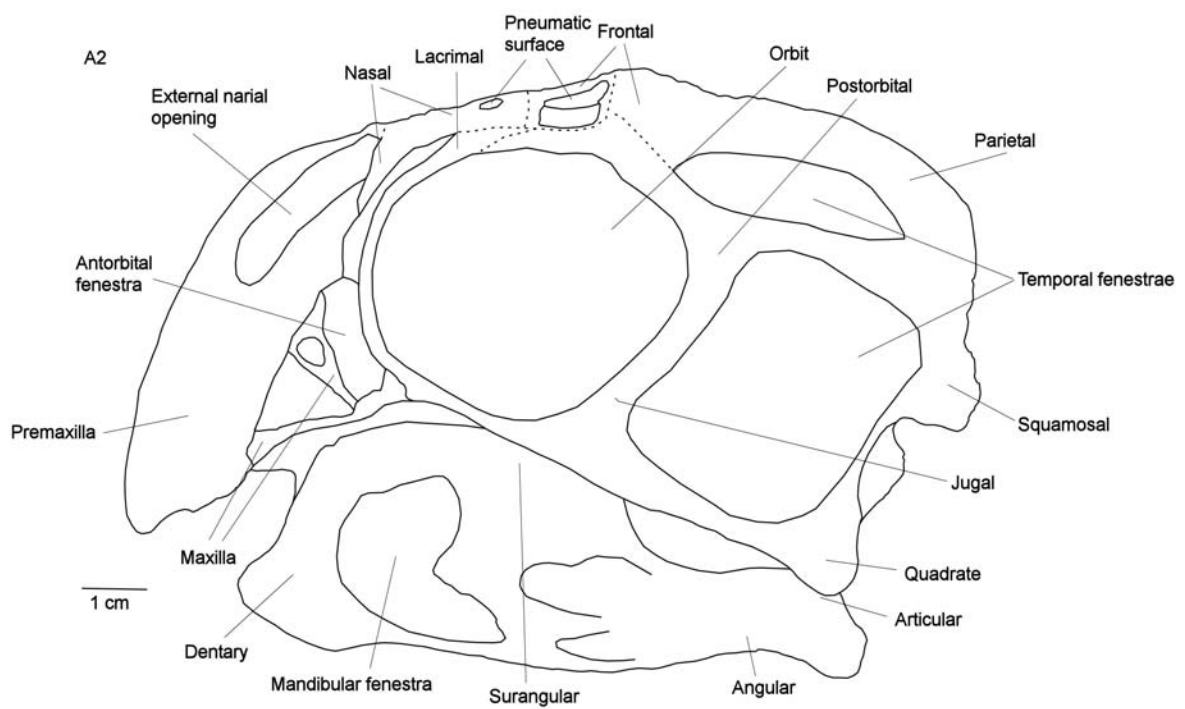


Figure 6
The skull of *Conchoraptor gracilis* (PMO X677) in lateral view. A1: The skull A2: Explanatory drawing

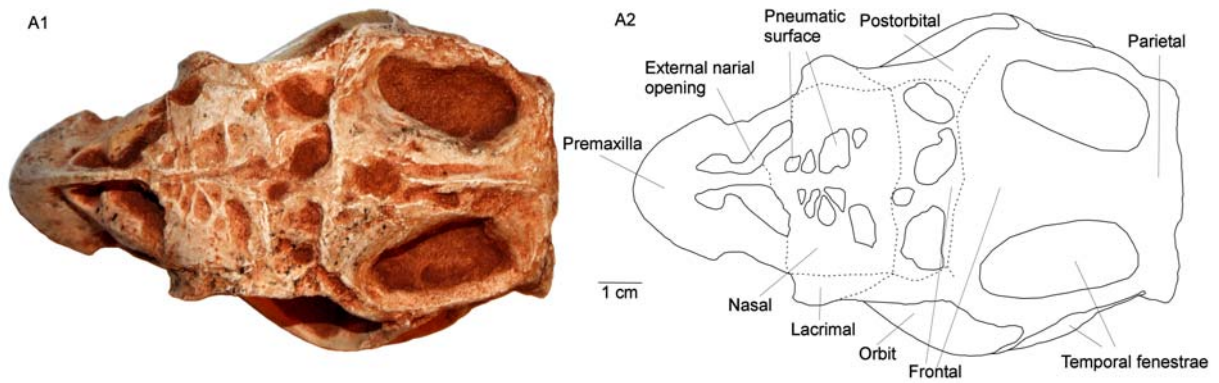


Figure 7
The skull of *Conchoraptor gracilis* (PMO X677) in dorsal view. A1: The skull A2: Explanatory drawing

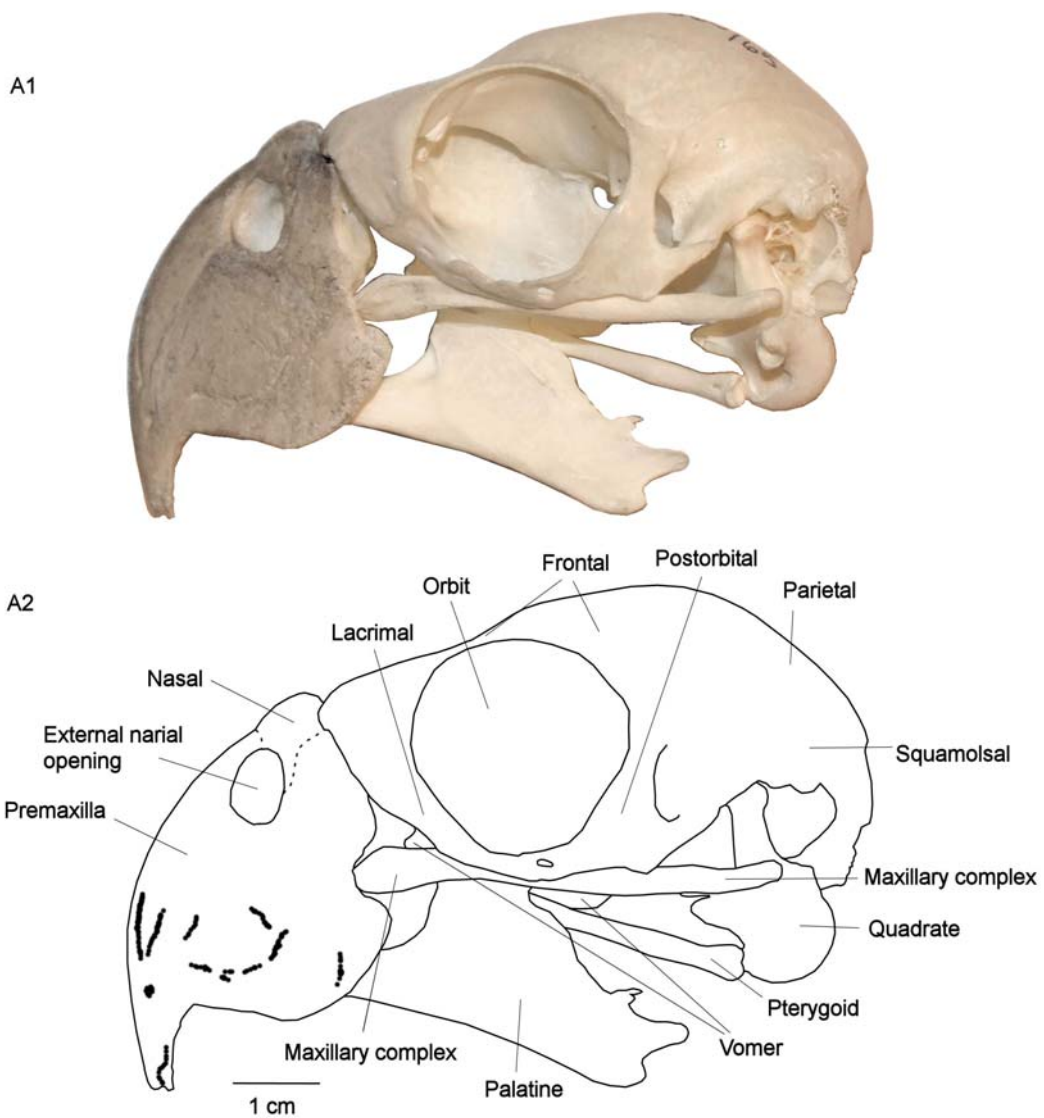


Figure 8
The skull of *Cacatua galerita* (ZMO 360/65) in lateral view. A1: The skull A2: Explanatory drawing

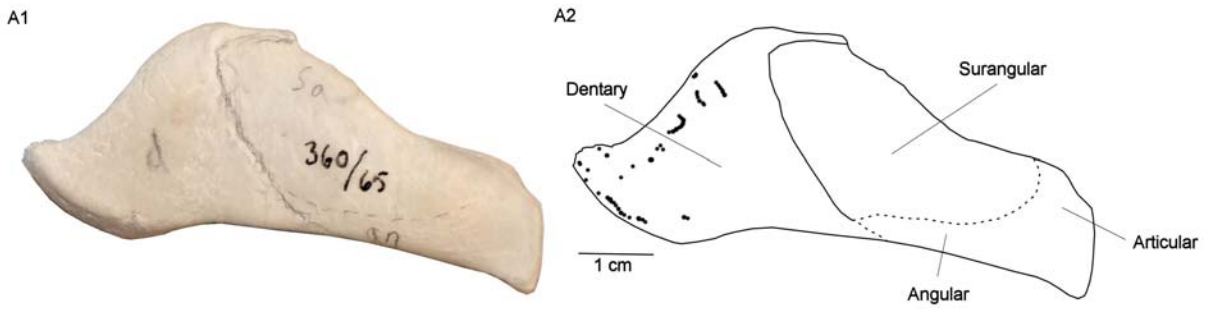


Figure 9
The mandible of *Cacatua galerita* (ZMO 360/65) in lateral view. A1: The mandible A2: Explanatory drawing

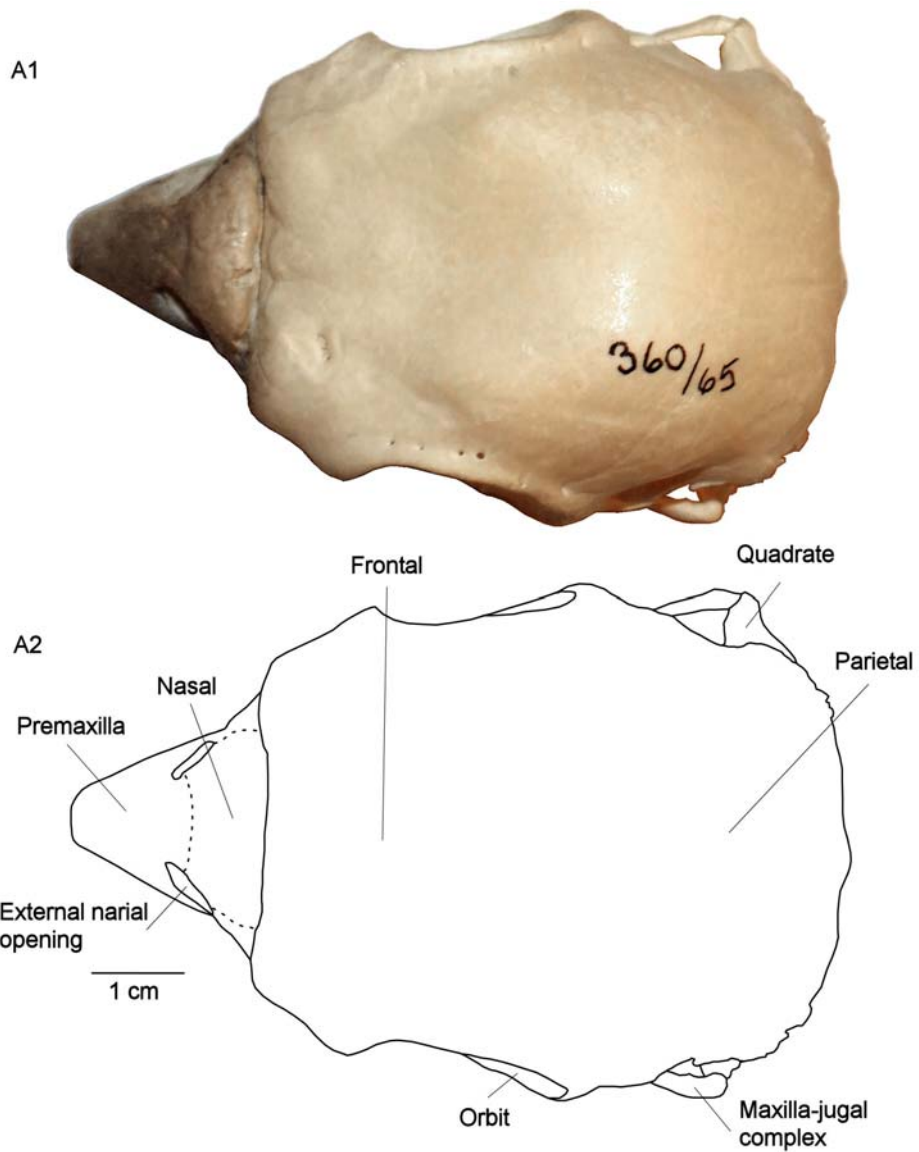


Figure 10
The skull of *Cacatua galerita* (ZMO 360/65) in dorsal view. A1: The skull A2: Explanatory drawing

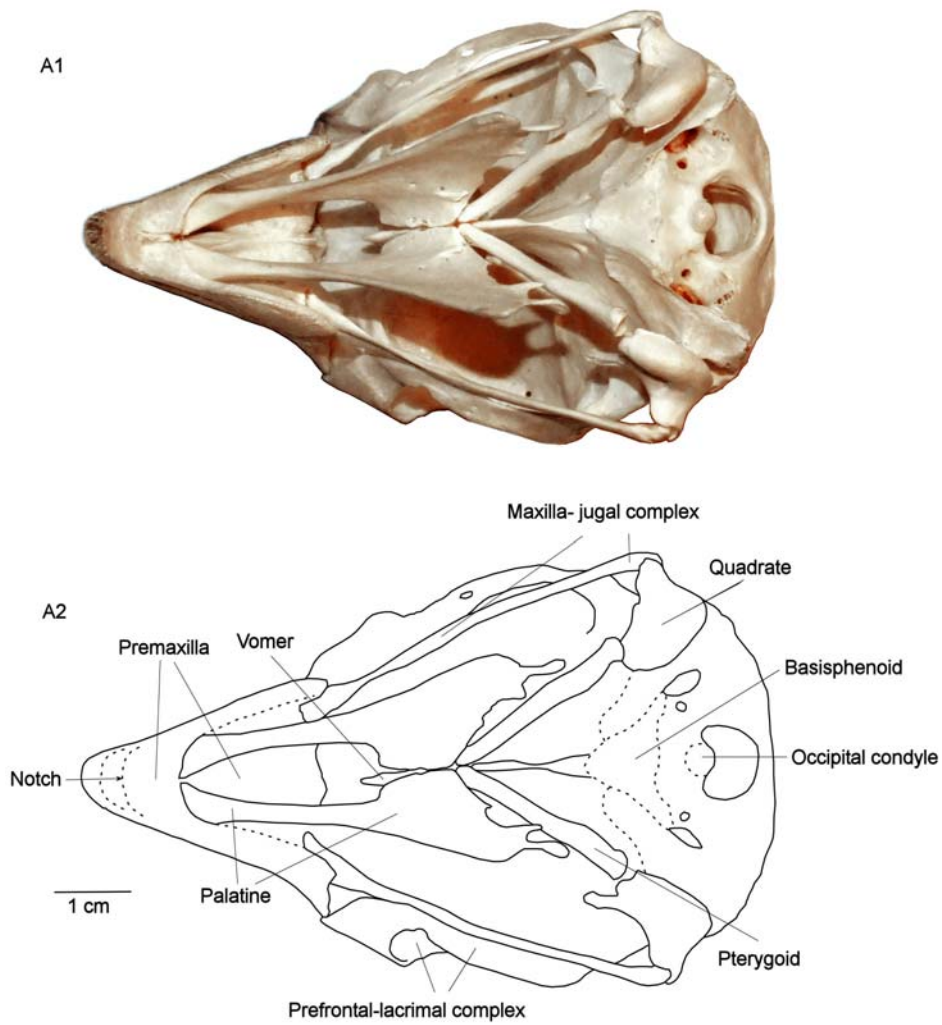


Figure 11
The skull of *Cacatua galerita* (ZMO 360/65) in ventral view. A1: The skull A2: Explanatory drawing

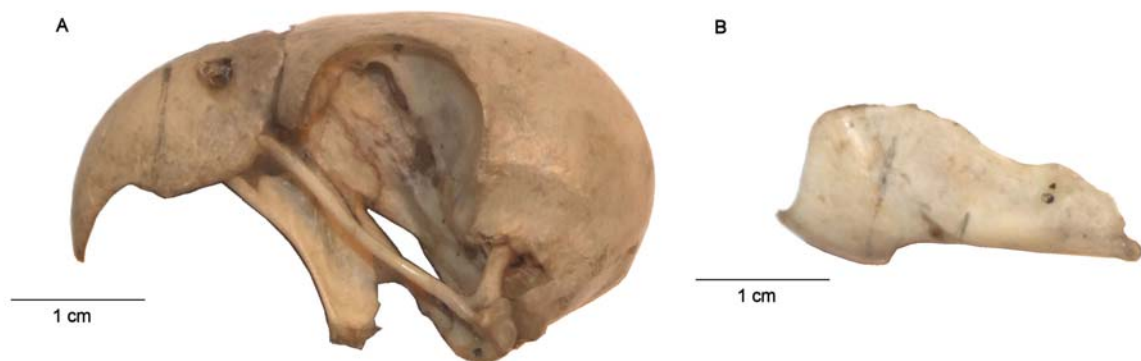


Figure 12
The skull of *Psittacus* sp. (ZMO 4915) in lateral view. A: The skull B: The Mandible



Figure 13
The skull of *Psittacus* sp. (ZMO 4916) in lateral view. A: The skull B: The Mandible

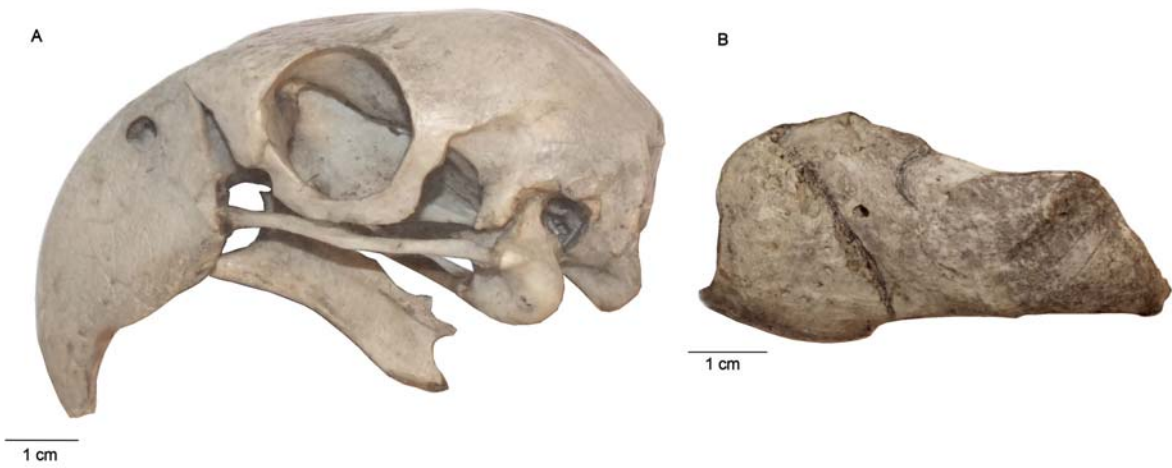


Figure 14
The skull of *Ara* sp. (ZMO 1340) in lateral view. A: The skull B: The Mandible

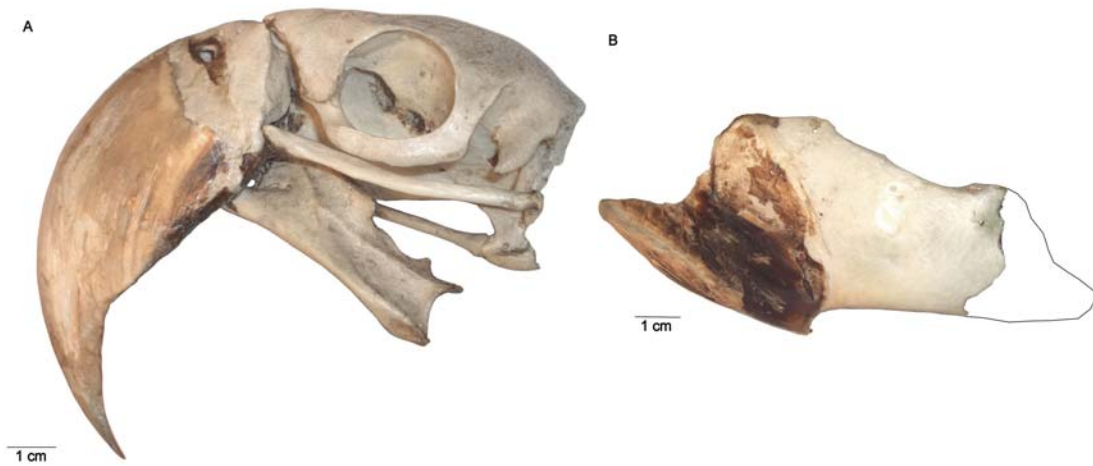


Figure 15
The skull of *Ara* sp. (ZMO 688) in lateral view. A: The skull B: The Mandible



Figure 16
The skull of *Ara* sp. (ZMO 688) in ventral view. The seed is placed in the notch.

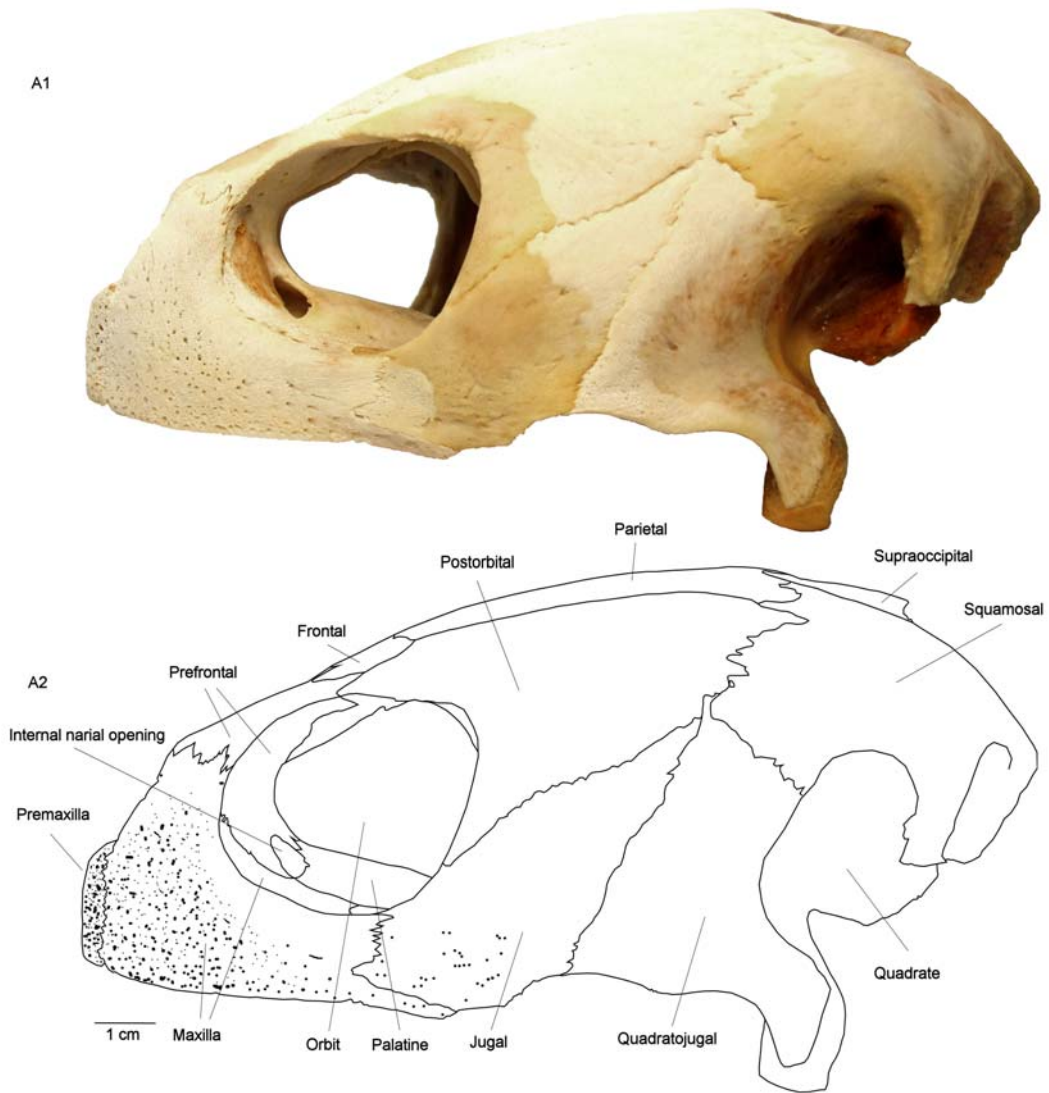


Figure 17
The skull of *Caretta caretta* (ZMO 19/62) in lateral view. A1: The skull A2: Explanatory drawing

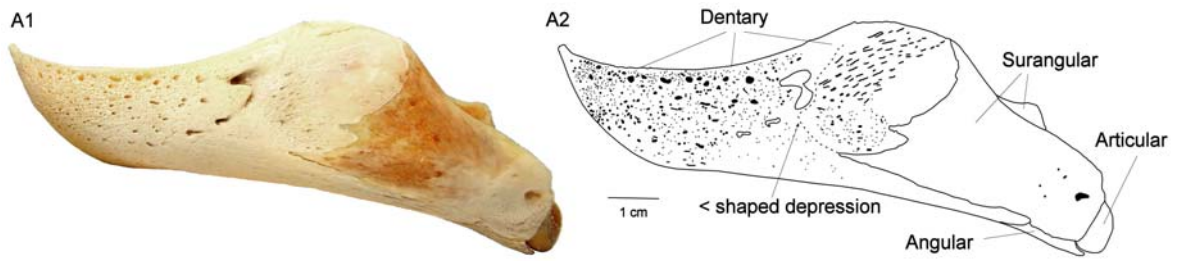


Figure 18
The mandible of *Caretta caretta* (ZMO 19/62) in lateral view. A1: The mandible A2: Explanatory drawing

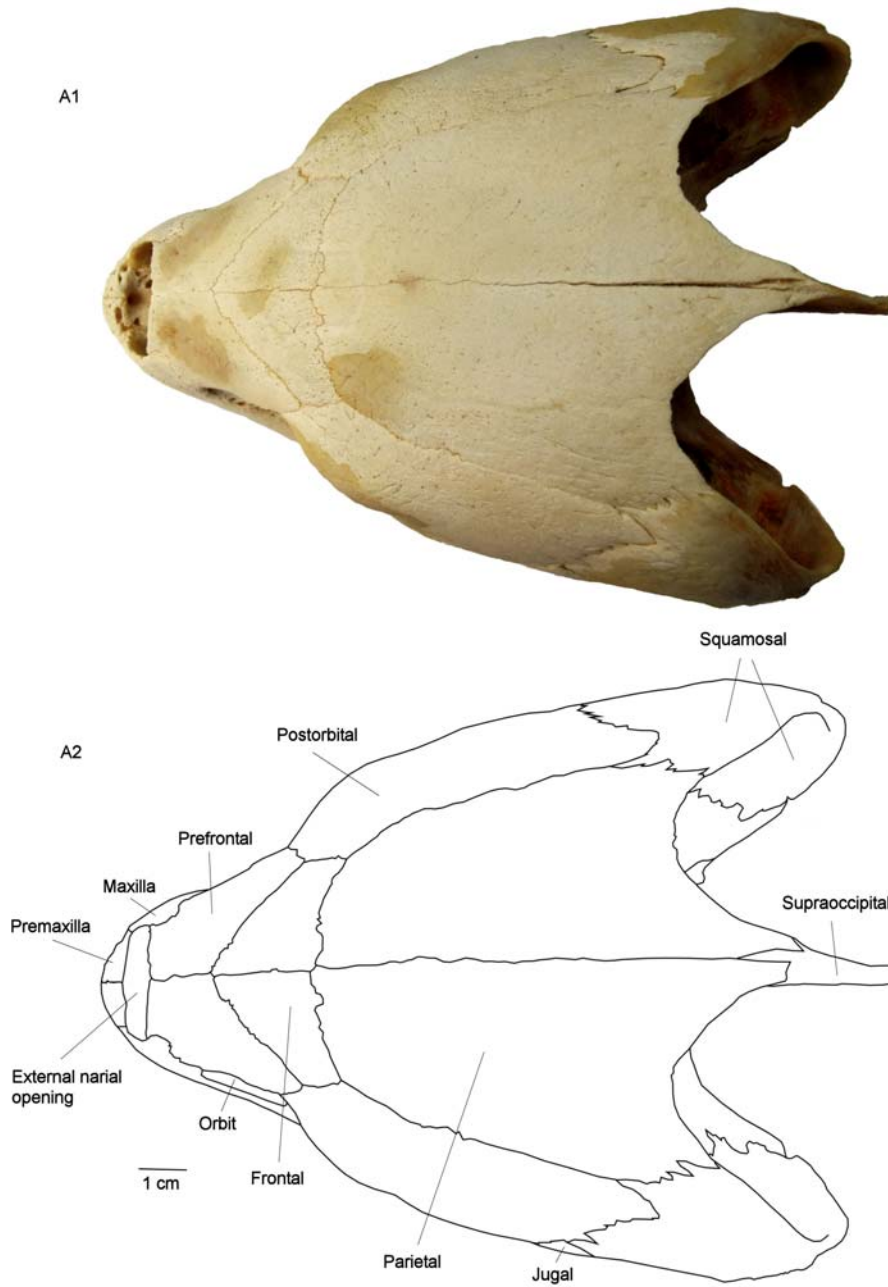


Figure 19
The skull of *Caretta caretta* (ZMO 19/62) in dorsal view. A1: The skull A2: Explanatory drawing

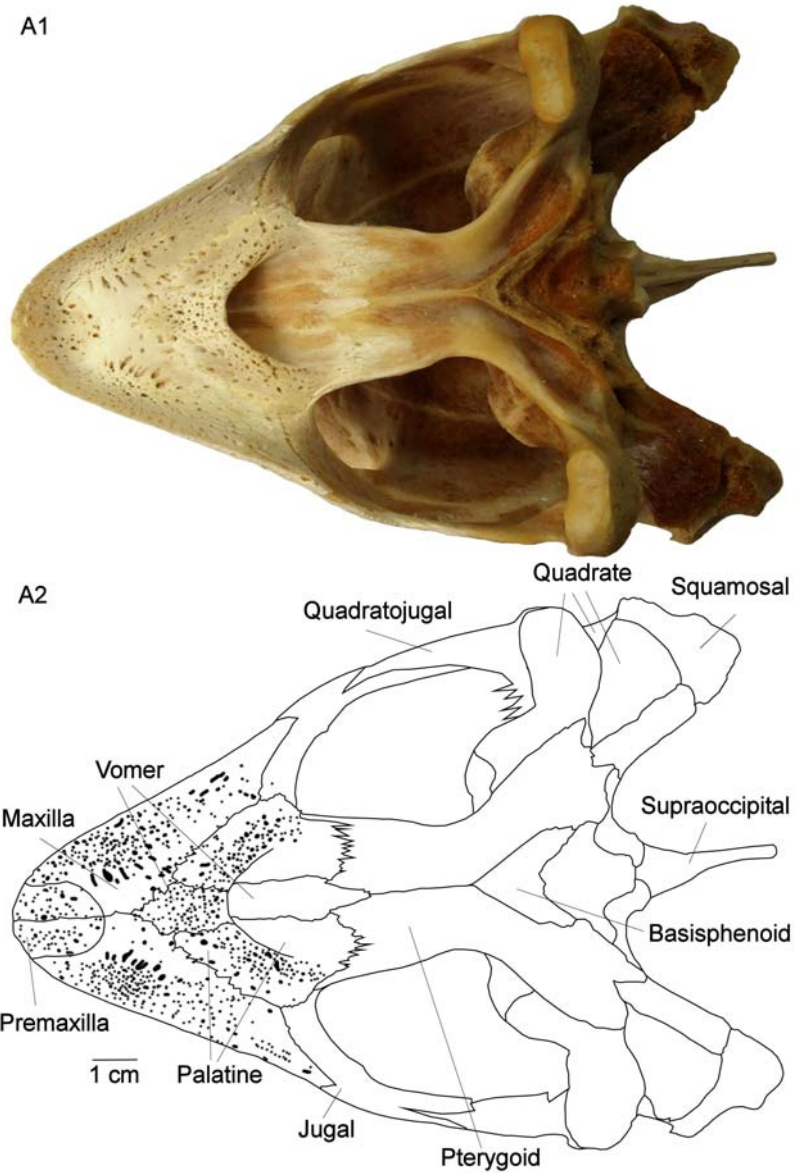


Figure 20
The skull of *Caretta caretta* (ZMO 19/62) in ventral view. A1: The skull A2: Explanatory drawing

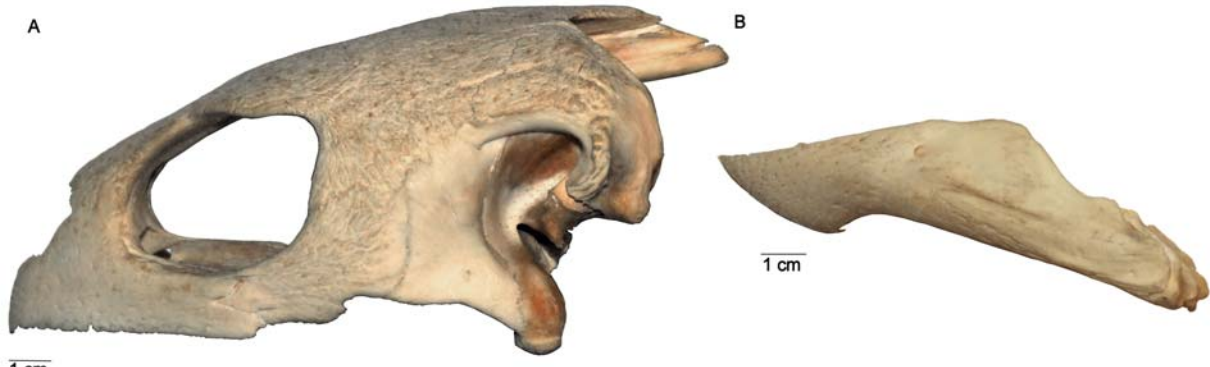


Figure 21
The skull of *Eretmochelys imbricate* (ZMO 12/74) in lateral view. A: The skull B: The mandible

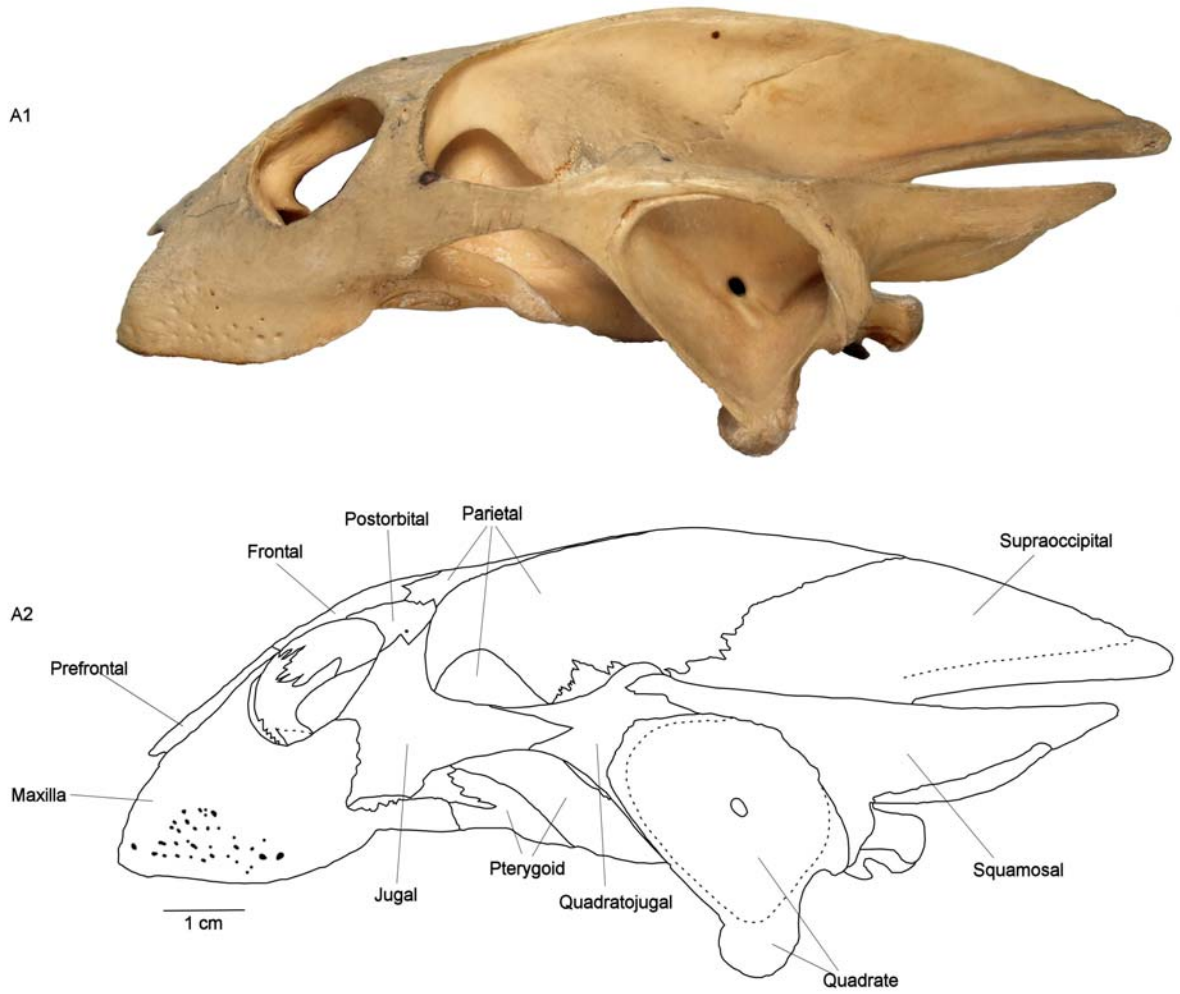


Figure 22
The skull of *Amyda cartilaginea* (ZMO 7104) in lateral view. A1: The skull A2: Explanatory drawing

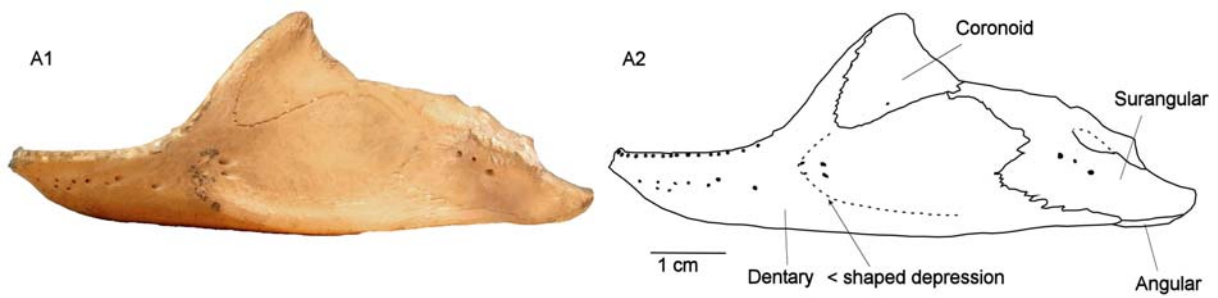


Figure 23
The mandible of *Amyda cartilaginea* (ZMO 7104) in lateral view. A1: The mandible A2: Explanatory drawing

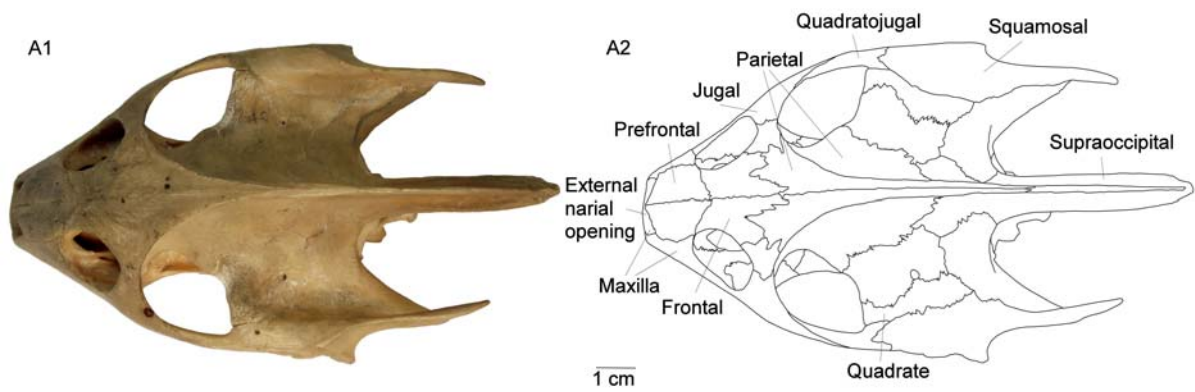


Figure 24
The skull of *Amyda cartilaginea* (ZMO 7104) in dorsal view. A1: The skull A2: Explanatory drawing

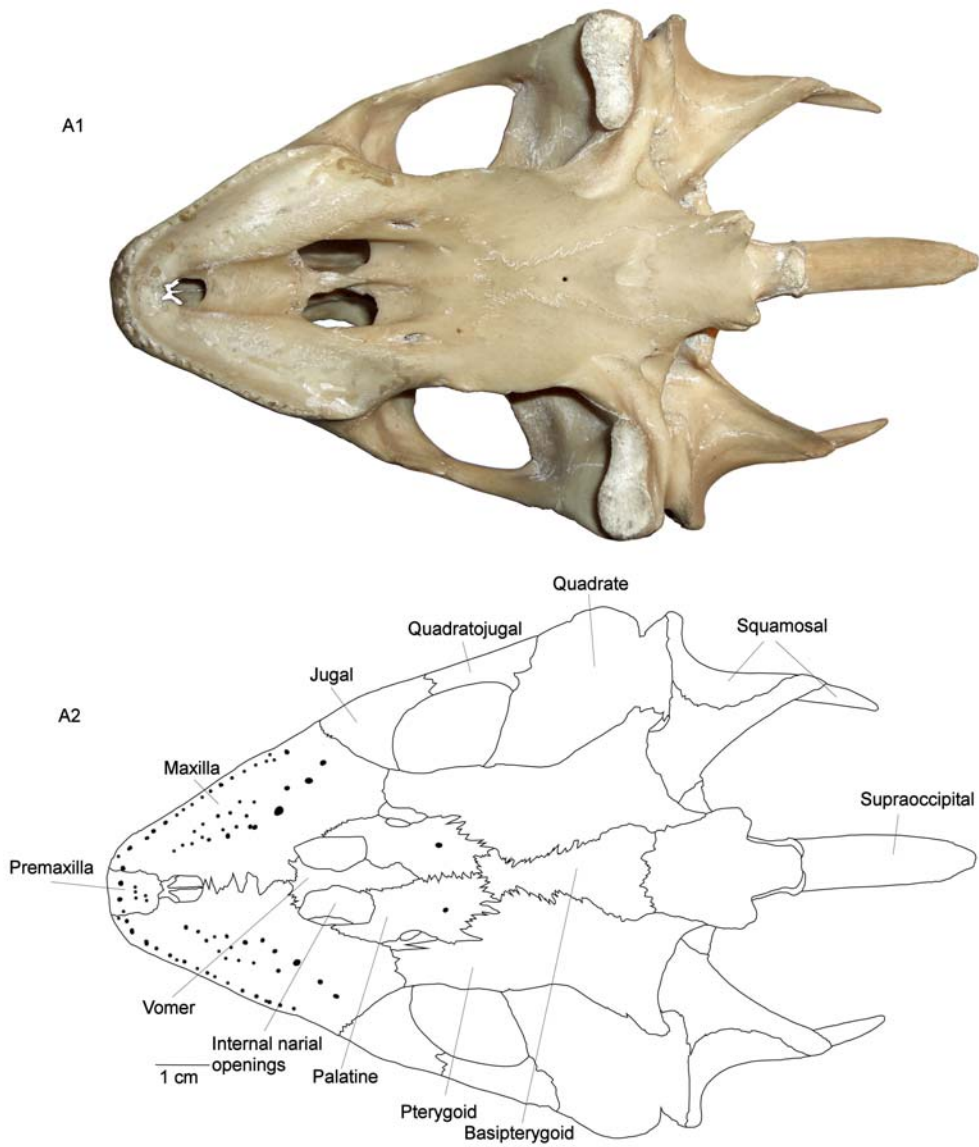


Figure 25
The skull of *Amyda cartilaginea* (ZMO 7104) in ventral view. A1: The skull A2: Explanatory drawing



Figure 26
The skull of *Amyda cartilaginea* (ZMO 7105) in ventral view. The ramphotheca is plate-formed.

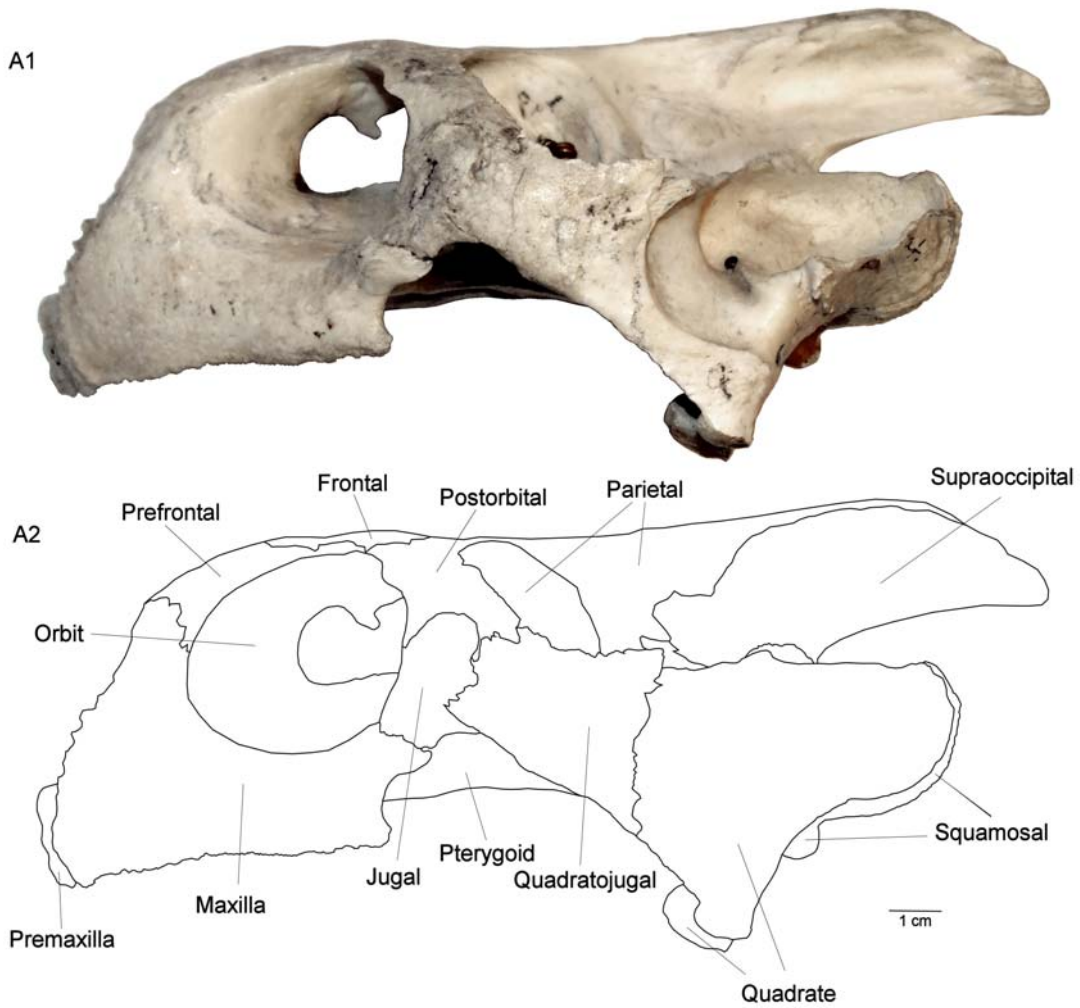


Figure 27
The skull of *Geochelone nigra* (ZMO 296) in lateral view. A1: The skull A2: Explanatory drawing

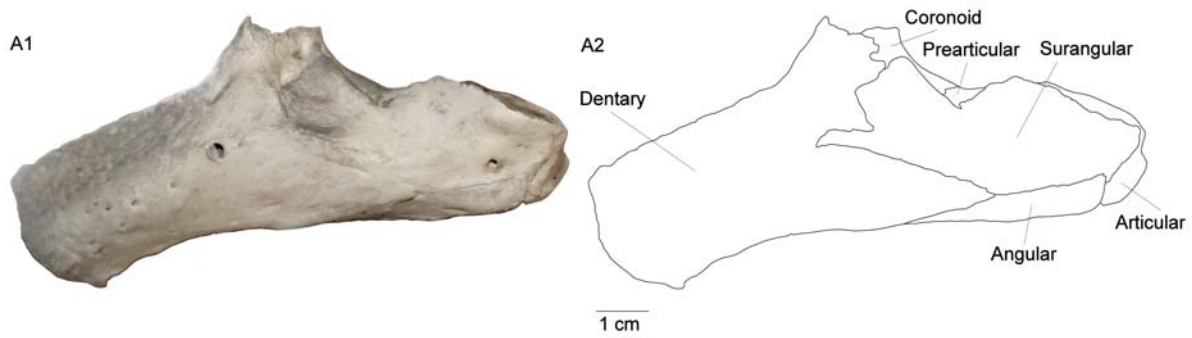


Figure 28
The mandible of *Geochelone nigra* (ZMO 296) in lateral view. A1: The mandible A2: Explanatory drawing

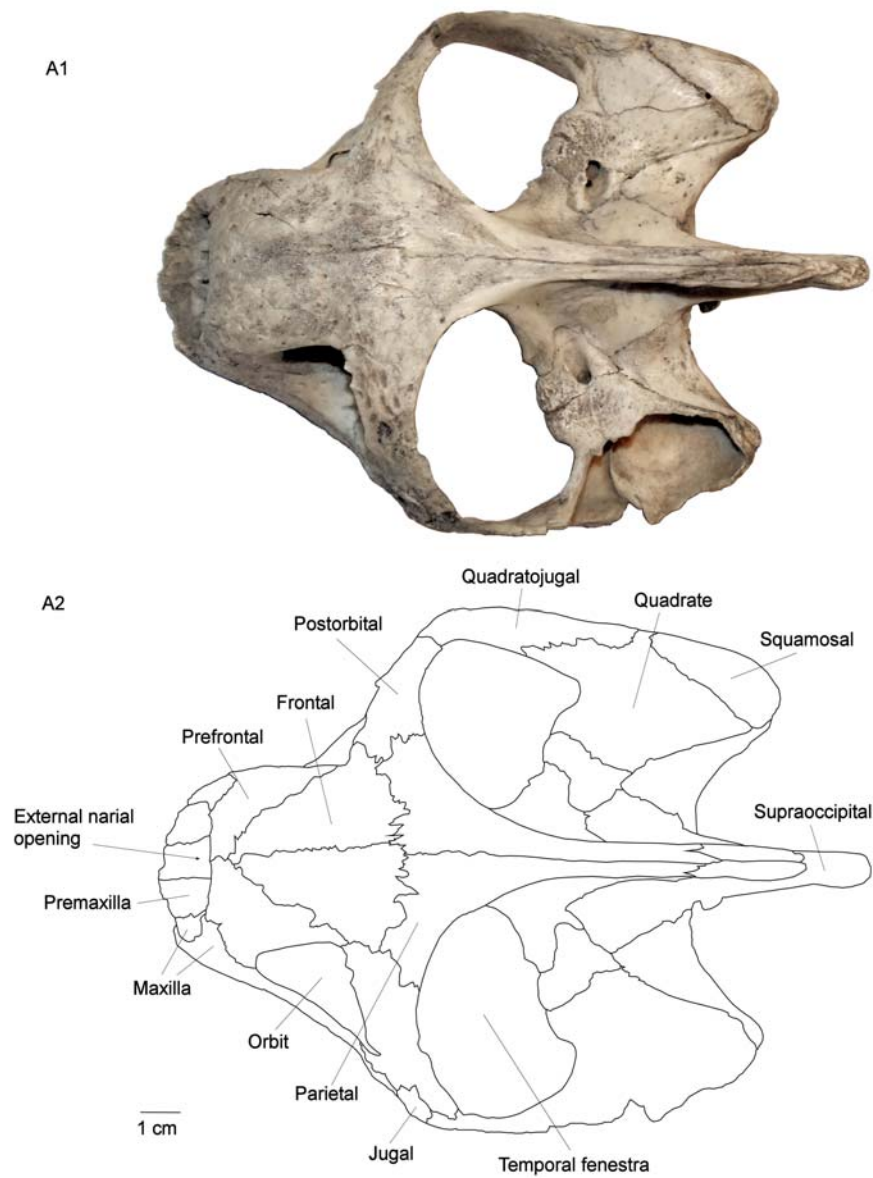


Figure 29
The skull of *Geochelone nigra* (ZMO 296) in dorsal view. A1: The skull A2: Explanatory drawing

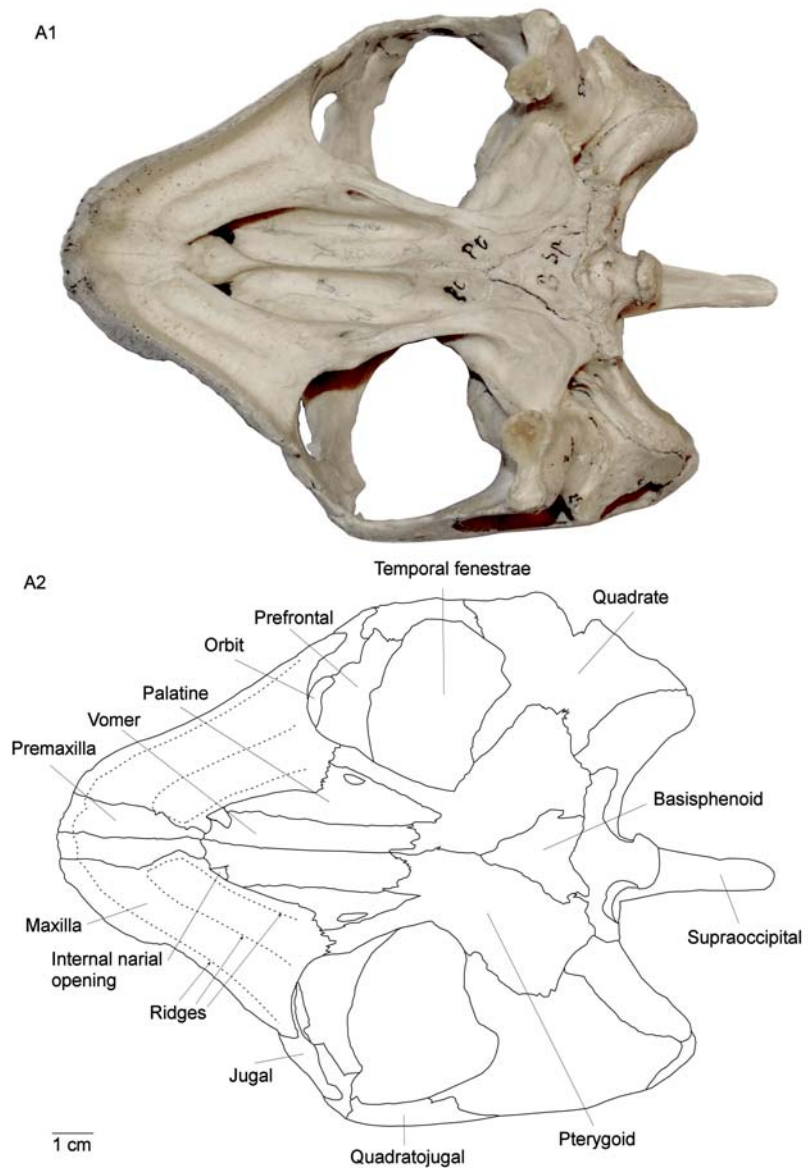


Figure 30
The skull of *Geochelone nigra* (ZMO 296) in ventral view. A1: The skull A2: Explanatory drawing

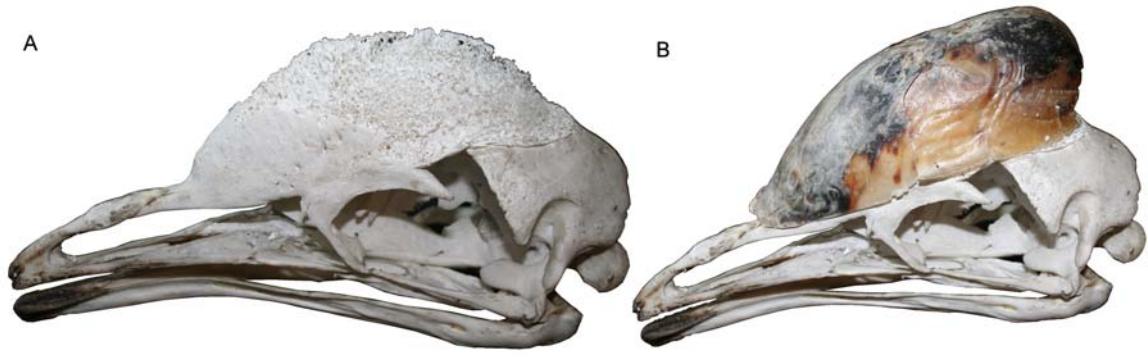


Figure 31
The skull of *Casuarius casuarius* (BM 3123) in lateral view, A: Without ramphotheca B: With ramphotheca
Photo: Anne Karin Hufthammer.

A1



A2

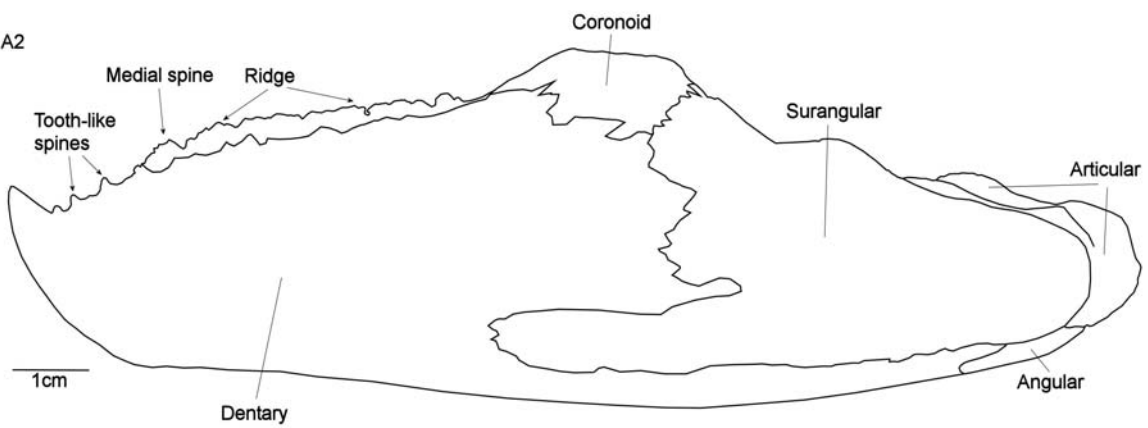


Figure 32

The mandible of *Chelonia mydas* (ZMO 5-12-1925) in lateral view, without ramphotheca. Note the tooth-like spines at the lateral surface, and the medial ridge with the medial spine. A1: The mandible A2: Explanatory drawing

Medial spine



Figure 33

The mandible of *Chelonia mydas* (ZMO 5-12-1925) in lateral view. The long tooth-like spines at the lateral surface and the medial ridge are made of ramphotheca. The large medial spine is apparently similar in shape to the two caudomedial processes of the maxilla in oviraptorids.

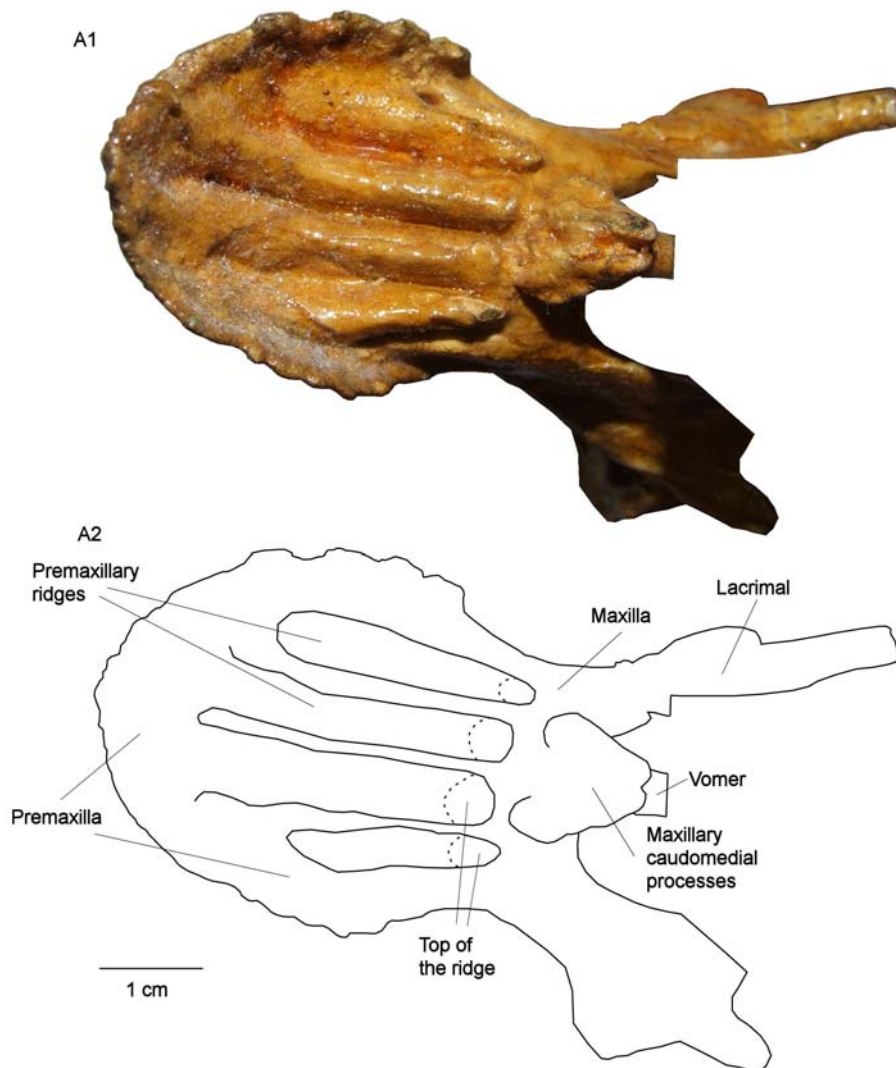


Figure 34

The anteriormost part of the rostrum of the oviraptorid Zamyn Khondt specimen (IMG 100/42) in ventral view. Note that the four ridges have a top at the posteriormost part. Also note the two tooth-like caudomedial processes of the maxilla. A1: The palate A2: Explanatory drawing

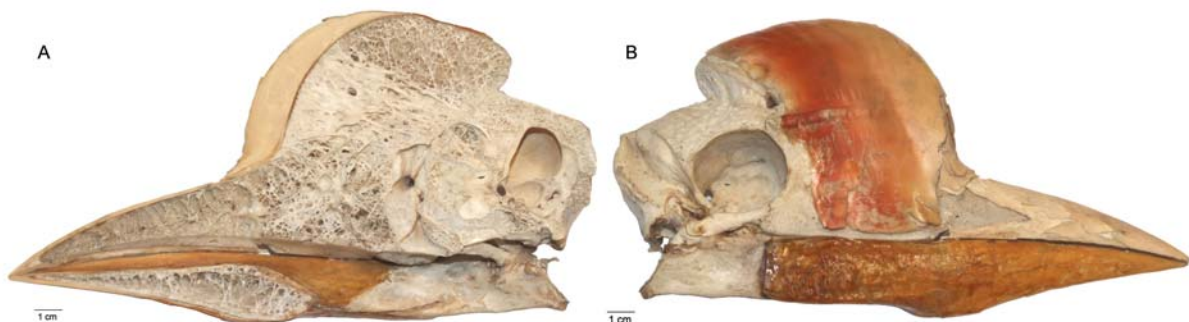


Figure 35

The skull of the helmeted hornbill, *Rhinoplax vigil* (ZMO 2669) in lateral view. Note the thickening of the bone structure and the ramphotheca on the anterior part of the crest. The crest is formed by the premaxilla. A: Internal view B: External view.

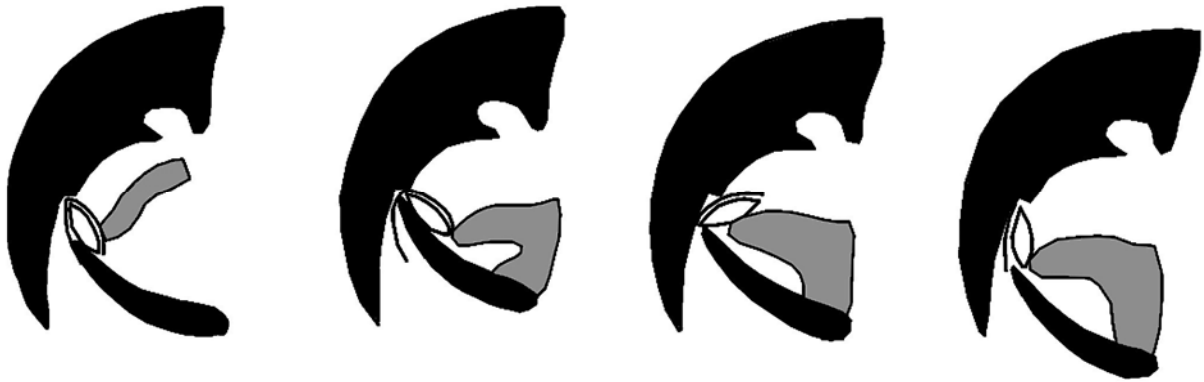


Figure 36
 Figure showing how the parrot uses the notch inside the beak to hold the seed in place, and use the tongue and the mandible to peel the hull off the seed. Adapted from Homberger (1980, abb. 1).

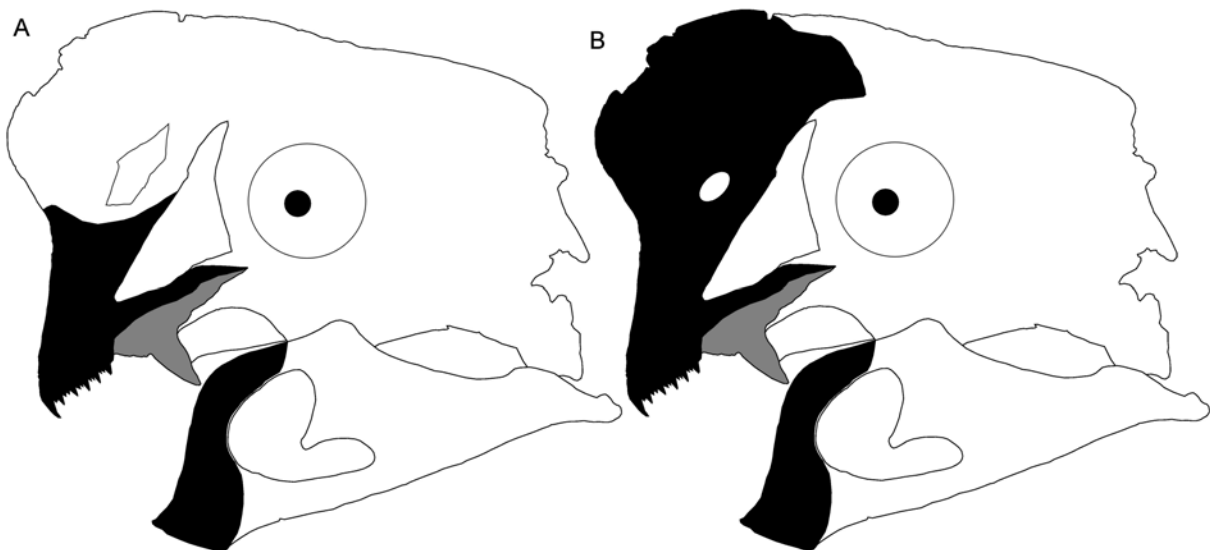


Figure 37
 The schematic reconstruction of the oviraptorid beak. Case A and B from the conclusion. The black areas are ramphotheca, and the grey area is the ramphotheca inside the mouth, covering the robust maxilla and the two caudomedial processes. The mandible has ramphotheca on the inner surface, and the skull has ramphotheca on the palate.

Appendix 2 – Dataset

Group	Species	No.	R_L_1/S_L	Cur	C_H/S_L	R_H/C_H	C_H/C_L
Anseriformes	<i>Cygnus cygnus</i>	ZMO 2931	0,49	1,10	0,23	0,37	0,45
Anseriformes 2	<i>Cygnus bewickii</i>	ZMO 26258	0,50	1,08	0,24	0,34	0,49
Anseriformes 3	<i>Somateria spectabilis</i>	ZMO 25056	0,47	1,10	0,25	0,64	0,46
Anseriformes 4	<i>Clangula hyemalis</i>	ZMO 25907	0,41	1,06	0,25	0,52	0,43
Anseriformes 5	Unknown sp.	ZMO 5582	0,43	1,09	0,27	0,32	0,47
Anseriformes 6	Unknown sp.	ZMO 6025	0,36	1,18	0,35	0,33	0,55
Anseriformes 7	Unknown sp.	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	<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	Unknown sp.	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
Ornithomimiformes	<i>Struthiomimus altus</i>	TMP 90016	0,54	1,10	0,25	0,50	0,54
Ornithomimiformes 2	<i>Ornithomimus edmontonensis</i>	TMP 2002.00.5	0,58	1,05	0,35	0,41	0,84
Ornithomimiformes 3	<i>Gallimimus bullatus</i>	PMO X625	0,47	1,22	0,40	0,46	0,75
Oviraptoriformes	<i>Conchoraptor gracilis</i>	PMO X677	0,29	2,15	0,42	0,82	0,58
Oviraptoriformes 2	<i>Oviraptor philoceratops</i>	PMO X678	0,56	3,00	0,46	1,18	1,04
Oviraptoriformes 3	<i>Rinchenia mongoliensis</i>	PMO X679	0,58	3,05	0,64	1,41	1,53
Passeriformes	<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	<i>Pachyptila typicus</i>	ZMO 1337	0,48	1,18	0,23	0,31	0,44
Procellariiformes 2	<i>Albatross sp.</i>	ZMO 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	<i>Ara sp.</i>	ZMO 1340	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	<i>Struthio camelus</i>	ZMO 2644	0,49	1,18	0,37	0,25	0,73
Struthioniformes 2	<i>Struthio camelus</i>	ZMO 3636	0,44	1,10	0,31	0,32	0,56
Struthioniformes 3	<i>Struthio camelus</i>	ZMO 346/65	0,48	1,24	0,30	0,41	0,59
Testudines	<i>Caretta caretta</i>	ZMO 19/62	0,19	2,15	0,47	0,57	0,58
Testudines 2	<i>Eretmochelys imbricata</i>	ZMO 12/74	0,19	1,90	0,35	0,60	0,44
Testudines 3	<i>Amyda cartilaginea</i>	ZMO 7104	0,16	2,00	0,30	0,63	0,36
Testudines 4	<i>Geochelone nigra</i>	ZMO 296	0,15	2,52	0,34	0,47	0,40

Table 1
Ratio of measurements used in the ordination analysis.