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The morphology of the bill apparatus in the Steller's Sea Eagle

Alexander Ladyguin

Moscow State University, Science Park, Educational-Research Center "Ecosoil", 119899, Moscow, Russia.
e-mail: ladygin@rc.ru

INTRODUCTION

The osteology of birds has been more thoroughly investigated than any other anatomical system in that group of animals. Being made up of many individual parts, each with numerous details, the skeleton offers more evident possibilities for study than other systems. Bones also make up most of the fossil evidence.

The avian skull and mandible have featured largely in systematic accounts (e.g. Huxley 1867, Pycraft 1898, Barnikol 1952, Fisher 1944), and have attracted much attention as to function (e.g. Lakjer 1926, Hofer 1950, Bock 1970, Dzerdjinskiy 1972, 1986, Hertel 1994). Study of the avian skull rests in part on research during developmental stages, as in the adult few suture lines are retained. Some phases of development have been investigated by Parker 1890, Marinelly 1936, Jollie 1957, Sushkin 1899, 1902. Some species of Falconiformes were investigated by Parker 1873, Sushkin 1899, Fisher 1944, Jollie 1977, Hertel 1994, Ladygin 1994. No detailed investigation of the skull of sea eagles has been undertaken.

MATERIAL AND METHODS

Twenty-one skulls of Steller's Sea Eagle *Haliaeetus pelagicus*, 12 skulls of White-tailed Sea Eagle *H. albicilla* and 18 skulls of Bald Eagle *H. leucocephalus* were examined. Five adult, 4 subadult and 3 eaglet (4 weeks old) skulls were included in the myology study.

Jaw muscles of three adult Steller's Sea Eagle and one adult White-tailed Sea Eagle were dissected. I drew original illustrations in pencil, using a dissecting microscope and drawing scale tools for all anatomical figures, final figures were inked.

The figures have been sketched directly from the specimens; they are not designed to present exact dimensions or proportions. The figures give an impressions of the particular structure described and any significant relationships which it might have with other structures.

Measurements (Table 1, Fig. 1) were taken with digital calipers in millimeters, and all analysis was made using the SYSTAT statistical package.

Specimens studied were housed at: Zoological Museum of the Moscow State University, Vertebrate Department of the Biology Faculty of the Moscow State University, Zoological Museum of the Zoological Institution of St. Petersburg, American Museum of Natural History,

Table 1. Sea eagle skull measurements.

Cranium	Beak	Mandible
Total length = length from occiput to tip of beak in straight line (Fig. 1, A)	Total length = length from naso-frontal hinge to tip of beak	Total length = maximum length along ramus
Total width = maximum skull width across postorbital processes	Tomial length = length from anterior part of nares to tip of beak	Maximum width = width in the region of articulation
Occipital width = maximum width of occipital region	Tomial width = width at anterior part of nares	Articular length = length from articular to tip of mandible
Maximum height = maximum height of the base of the cranium (Fig. 1, B)	Tomial depth = depth at anterior part of nares	
	Tomial cord = length from anterior part of nares to tip of the beak (Fig. 1, D)	
	Tomial arch = curved length from anterior part of nares to tip of the beak	
	Tomial arch radius = length from cord to point of maximum curvature (Fig. 1, E)	
	Maximum height = height at the anterior part of nares	

All anatomical materials used in this study were obtained from birds killed by accident .

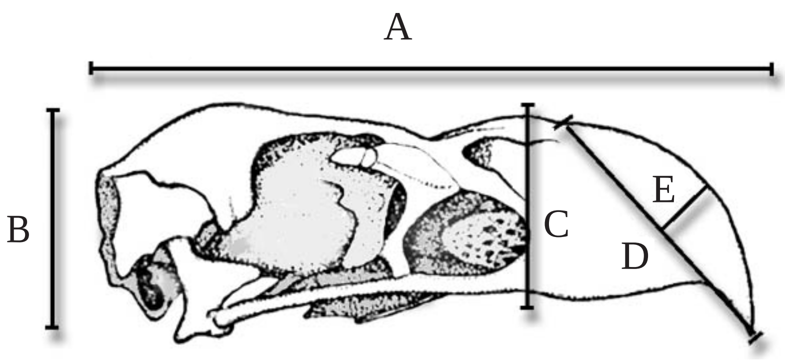

Fig. 1. Measurements used to calculate cranial indexes.

Zoological Museum of the Zoological Institution of Halle (Germany), Paleontological Institution, private collections.

Table 2. Morphological characteristics of Steller's Sea Eagle skulls (N = 15).

Characteristics	Average length ± SD (mm)
Length of skull	146.0 ± 27.8
Width of skull	71.0 ± 9.5
Height of skull	40.0 ± 8.0
Length of cranium	69.5 ± 12.0
Length of the upper jaw	82.0 ± 9.5
Length of the low jaw	117.0 ± 11.5
Height of the upper jaw	35.0 ± 2.0
Width of the upper jaw	29.5 ± 6.5
Width of the lower jaw	70.2 ± 5.4
Diameter of the orbital	35.5 ± 9.9

Phylogenetic remarks

Steller's Sea Eagle is a member of the Genera *Haliaeetus*, Family *Accipitridae*, Order *Falconiformes*, Class *Aves*.

This is a small group of large Accipitrids, that feed mostly fish and includes such well studied birds as the Bald Eagle and White-tailed Sea Eagle.

Definition and orientation

Basically, the head skeleton can be divided into three parts: cranium (or, more correctly, neirocranium), primary upper jaw and lower jaw. These three elements are connected to one another by a complex of bones, ligaments and muscles. We will considered these elements of the skull separately, and then discuss the interactions between them that allows them to work as a single biomechanism.

RESULTS AND DISCUSSION

General description

The skull of the Steller's Sea Eagle is one of the most massive among all Accipitrids, including griffons (*Gyps* sp.) and other vultures (Table 2).

Cranium

The cranium is the large, durable capsule that protects the brain, eyes, and hearing capsules. The cranium provides a stable base for the connection of most ligaments and jaw's muscles. The Steller's Sea Eagle's cranium is very hard, all bones are well developed, and most cranium foramens, as is typical in other birds of prey, are absent.

Viewed from above the skull of the Steller's Sea Eagle is elongated-triangular with a rounded base. The cranium is usually flattened above and rounded behind. It has distinct cerebral bulges and a shallow median gutter. The median depression may extend forward and become accentuated in the brow region. The cranium is laterally widened. The ear area is easily characterized. The depressor mandibulae has an extensive origin beginning lateral and posterior to the squamosal articulation of the quadrate (Fig. 2).

The cranium of Steller's Sea Eagle has some characteristic processes. The zygomatic process, to which the *Musculus adductor mandibulae externus* is connected, is short and blunt. The articular process is exposed at the edge of the tympanic cavity. It is large and has a distinct, lateral ridge, which makes it triangular in cross-section. The base of the skull is inflated. The parasphenoid bulges ventrally either side of the midline. The occipital condyle is exceptionally wide, and has median, posterior and ventral grooves. The basiparasphenoid area

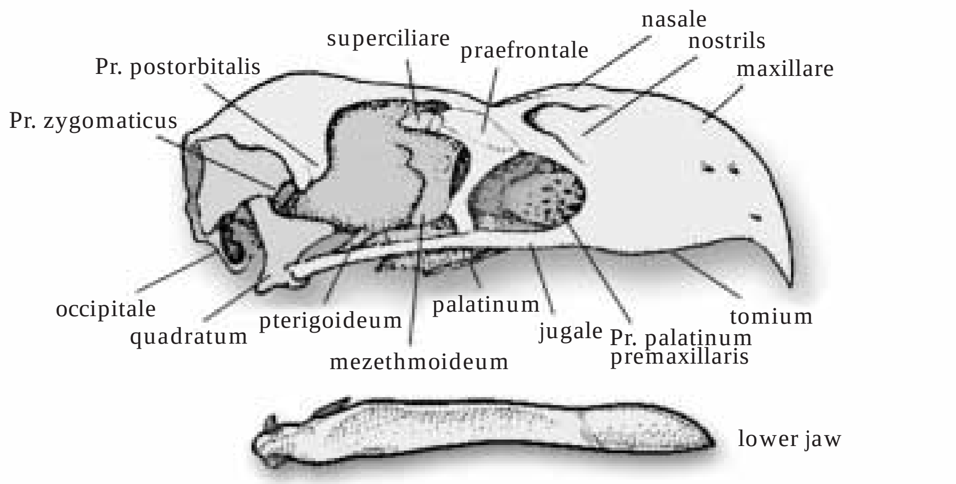

Fig. 2. Lateral view of Steller's Sea Eagle skull.

is triangular. The basiparasphenoid processes are low, rounded ridges extending out to either side. They are separated medially by a small median basyparasphenoid process. Posterior to the latter and anterior to the condyle, the basioccipital bone has the form of a low ridge instead of a pit.

The tympanic articulations are well developed, the Eustachian tubes are partly open and the anterior wall of the anterior tympanic recess has a blunt, hornlike alaparasphenoid process. The basipterigoid processes are developed only in the chicks and disappear in the adult birds.

The basitympanic process width, the distance between the lateral points of the basiparasphenoid plate, ranges from the 55 to 65% of the postemporal width, measured across the skull at the zygomatic processes.,This is the widest among all Accipitrids.

Viewed posteriorly, the tympanic margin has a characteristic sigmoid shape. Viewed laterally, this margin is accutely angled at the junction of the squamosal and exoccipital. A posterior tympanic process occurs in Steller’s Sea Eagle, but involves an outgrowth of the dorsal rim.

The lateral basiparasphenoidal processes are low rounded lumps showing variously scrawled, minor ridges or tubercles. The exoccipital process is a somewhat triangular, bluntly-tipped, ventro-anterior projection at the ventral margin of the tympanic cavity.

The interorbital septum is not perforated in adult birds, which is unusual for birds of prey and may suggest a relatively small orbit. Normally, within the limit of space in the bird’s skull, the large orbits crowd out less important structures, and the interorbital septum in many raptorial species is quite narrow and even perforated. Perforation is attenuated the bones and skull as a whole, but in Steller’s case probably, the skull as a whole must be more secure and this reason dictates any bones to be faster.

The olfactory capsule, which encloses the olfactory nerve, is narrow. The palatine processes of the maxillae are well separated, and approach those of the desmognathous palate.

The prefrontal is well developed and is free. It is connected via sindesmos with the frontal and the lateral side of ethmoid. The supraorbital process is broad with a truncated tip. The posterior margin is squared for the reception of the small nasal gland, which lies between the prefrontal and the orbit margin. The superciliare form is a small cycle-like bone attached to the posterior edge of the supraorbital process.

The orbital process of the prefrontal is free, but in part supported by the lateral mezethmoid plate. This robust processes widens out into a somewhat spatulate ending; the distal portion is elongated (correlated with the deepening of the upper mandible). The ventral caudal ends of these processes are in contact with the medial part of the mezethmoid, been hang upon, but not fused with it.

The vomer is formed of lateral components. This bone is a thin, laterally compressed, splint lying in the septum between the internal nares. The anterior end exhibits small reduction in size. The tip of the vomer is free. The vomer appears to be rooted to the rostrum parasphenoid by fibers. The vomer is associated with the anteropterigoids h, in the adult, are indistinguishably fused to the palatines. The vomer appears to be rooted to the anteropterygoids by fibers.

The final element of the palate,the pterigoid, articulates antero-medially with the palatine and posterolaterally with the quadrate. The anterior articulation of the pterigoid, as viewed ventrally, is a straight line. The pterygoid process is formed from the anteropterygoid, which is fused with the palatine. The palatine fossa is well excavated and is bounded medially by a strongly developed choanal ridge.

When viewed from below, the quadrate, one of the most complicated of skull bones, has a distinctly triangular shape, the base is forward, and the outer side shortest. Seen from above, the eagle quadrate has a shallow, rounded notch on its outer posterior margin, and the inner process juts straight medially (protrude straight inward) as part of the relatively straight posterior margin

The Steller’s quadrate has a large, long and wide Pr. orbitalis, which starts from the medial part of the bone’s corpus and is directed inside and forward. The lateral surface of this well developed process provides space for the large Musculus adductor mandibulae posterior.

A pneumatic foramen is found on the dorsal medial surface of this inner process. The cavity of the articular portion is continuous with the tympanic cavity through the foramen.

Upper jaw

The bill in adult sea eagles is bright yellow, unlike those of most other adult raptors; in the subadult the bill is brownish with some yellow lines. The upper jaw has a very sharp, long hooked beak.

The Steller’s Sea Eagle bill is unusually long for Accipitrids (but typical for sea eagles)

Table 3. Average (± SD) of cranial indices in Steller's (*N* = 15) and White-tailed Sea Eagles (*N* = 12).

Index letter	Indexes	Steller's	White-tailed
A	Length of lower jaw symphysis / maximum length of the lower jaw	0.23 ± 0.06	0.20 ± 0.05
B	Diameter of the orbit/length of the cranium	0.47 ± 0.07	0.41 ± 0.05
C	Maximum height of the upper jaw / maximum height of the cranium	0.87 ± 0.10	0.55 ± 0.12
D	Width/height of the upper jaw	0.36 ± 0.09	0.40 ± 0.08
E	Length of the upper jaw/length of the skull	0.55 ± 0.09	0.46 ± 0.08
F	Length of the upper jaw / length of the cranium	1.20 ± 0.01	0.70 ± 0.02

(cranial index F = 1.2, Table 3), and very deep, even for sea eagles (cranial index C = 0.87, Table 3). The upper jaw is even longer then the cranium, and has about the same depth. Such unusual proportions are not found in other Falconiformes.

The shape of the upper part of the bill above the nares is large, inflated and atypical arched. This area of the skull is quite important because the cranium and beak are connected here and this articulation is subjected to large amounts of force during feeding. The arched, bulbous form this area exhibits in cross section provides structural strength necessary when during feeding.

The narial aperture is usually triangular-ovoid. The external naris is located in the ventroanterior portion of the lateral wall of the vestibular chamber. Anteriorly the vestibule is well ossified, although a gap or small fissure usually occurs between it and the premaxilla. Posteriorly the wall is incomplete below the median naris. The lateral margin of the median naris is essentially part of the ventral process of the nasal and dorsal part of nasal process of the maxilla.

The bony nasal septum extends back to the craniofacial gap. It is normally not perforated or it has has irregular perforations; the membranous nasal septum is never perforated.

The frontonasal hinge is simple. The prefrontal bones (articulate) directly, without any overlap against the lateral edge of the frontal and nasals. This contact, when viewed dorsally, creates a straight anterio-posterior line.

The rostrum-labial bar hinge is characterized by the long pointed spine of the premaxilla which projects posteriorly along the labial bar and the slim anterior tip of the jugal.

The palatal is desmognathous - well developed palatine processes contacts each other and are completely fused. This characteristic also might serve to reinforce the Steller’s skull against lateral forces that must occur during the ripping of food items.

The palatal aspect of the rostrum (as in all Accipitrids) has the tip of the praemaxilla braced by ossification of the ventral margin of the nasal septum. This is called the septal bar. The palatal vacuity is vestigial and divided by this bar. In Steller's Sea Eagle the contact and fusion of these maxillary processes has crowded out the septal bar, and it is reduced it to a

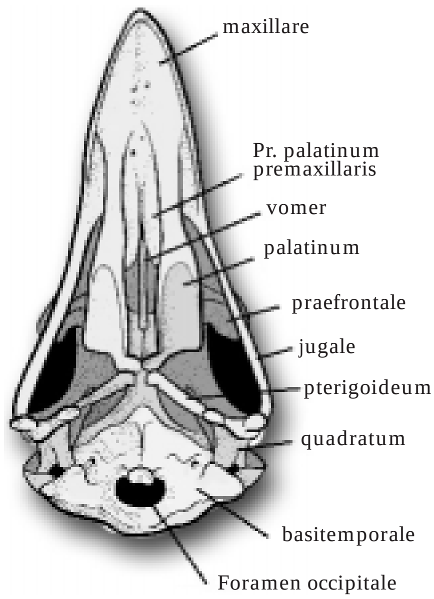

Fig. 3. Ventral view of Steller's Sea Eagle skull, ventral view.

fibrous vestige.

The palatal surface of the tip of the rostrum has a characteristic median grove formed by the difference in the levels of the palatine processes of the premaxilla and the septal bar. In this grove lies a median ridge formed by the septal bar.

The tomium is straight, not toothed. The tomial margin of the premaxilla is deeply grooved in the region of the hook. These grooves appear to be sites of growth for the tip of the horny sheath. The tomial margin of the premaxilla is posterior to this groove. Viewed laterally, it presents an even, somewhat sigmoid, curved outline.

The posterior palatal process of the premaxilla is weakly developed. It lies lateral to the anterior end of the palatine. The jugale is a long narrow bone, and connects the latero-ventral end of the beak to the lateral part of the quadrate. There are no specific characteristics of the jugale in the Steller's Sea Eagle.

Lower jaw

When viewed from above, the lower jaw is strongly triangular. It is relatively long and strong. In comparison with other Accipitrids; the Steller's lower jaw is relatively deep and has a well developed lateral surface, where powerful skull muscles find ample space for attachment.

Skull ligaments

The ligamental apparatus (Fig. 3) of the Steller's skull is very typical for birds.

The quadrato-maxillae articulation is regulated by three ligaments: *Ligamentum jugo-mandibulare internum*, *Lig. jugo-mandibulare externum* and *Lig. postorbitale*. The *Ligamentum jugo-mandibulare internum* which connects the caudal edge of the jugal to the caudal edge of the lower jaw after turning behind the jaw articulation, attached to the caudal edge of the lower jaw

The *Lig. jugo-mandibulare externum* connects the caudal edge of the jugale and the lateral surface of the lower jaw just anterior to the jaw articulation.

The *Lig. postorbitale* connects the postorbitalis processes of the cranium and the lateral surface of the lower jaw.

All three ligaments are very strong and short in comparison to other birds of prey.

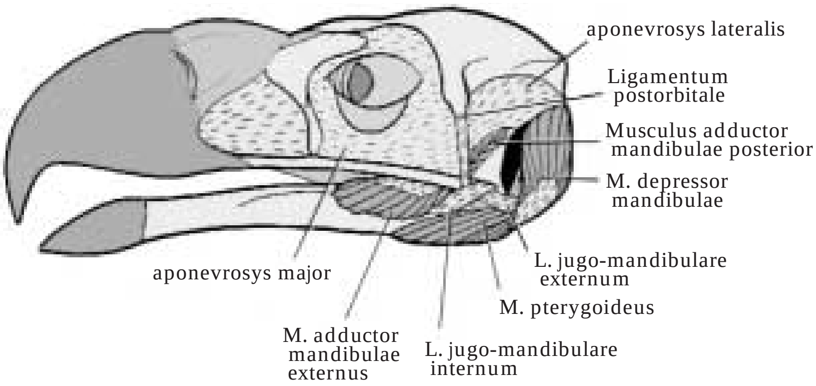

Fig. 4. Ligaments and the muscles on the lateral surface of the Steller's Sea Eagle skull.

The *Lig. occipito-mandibulare* is covered by the *M. depressor mandibulae*. It connects the caudal edge of the lower jaw to the ventral surface of the cranium. This ligament is also quite strong, but is relatively long.

The head muscles

Steller’s Sea Eagle head muscles are very powerful (Fig. 4).

The *Musculus adductor mandibulae externus* is well developed and covers a wide area on the lateral surface of the mandible. This is the most important and well-developed skull muscle. It lifts the lower jaw and clamps upper and lower jaws together. For this task this muscle in Steller’s eagle fills a large areafrom the jaw’s articulation to the mouth This is not the right word, but I don’t know what you want to saycorner.

The *M. pterygoideus* is also well developed and also covers a large area on the lateral surface of the lower jaw just under the end of the *M. depressor mandibulae*.

In most Accipitrids this muscle is less developed and does not occupy the whole of the lateral surface. *M. pterygoideus* in cooperation with the Musculus adductor mandibulae externus depresses the upper jaw, and works with that muscle to clamp the jaws together. Given the way in which sea eagles feed, (fixing a food item with the foot and tearing relativelysmall pieces from it) this muscle is quite important because it fit reinforces the upper jaw against untucking.

Depressor mandible is a muscle of great interest. The origin of this muscle is restricted to the tympanic rim and caudal surface of the cranium. The insertion of this muscle is on the caudal surface of the mandible. Depressor mandible opens the jaws. It is well developed in comparison with other Accipitrids and probably adds to the general reinforcement of Steller’s skull.

Other muscles are morphologically similar to those found in other Accipitrids.

The hyoid apparatus

The basyhyal is round (or slightly flattened above and rounded below.) in cross-section and lacks any indication of a keel. The enthoglossal ossification is composed of elongated rods with articulation areas at their mid-points. Generally, the hyoid apparatus in Steller's is similar to that of most Accipitrids. It is relatively undeveloped and delicate (Ladygin 1994).

CONCLUSION

From this survey of features, the Steller's Sea Eagle type can be characterized as follows:

The desmognathous palate is formed by the palatal processes of the maxillae meeting at the middle, behind and below an ossification of the ventral margin of the nasal septum which extends forward to the tip of the bill. The vomer is a vertical midline plate, which is bilateral posteriorly. The nasal vestibule is partly ossified forming a median perforated septum and partial walls in anterioriorly and ventrally. The narial opening, framed by the nasal bone, is roughly triangular in shape and obstructed by ossification in the lateral vestibular wall. The rostrum is large and strongly hooked; the premaxillary and narial portions are of about equal length. The fronto-nasal hinge is simple; the prefrontal is well developed, free and has a superciliary bone associated with its supraorbital processes. The cranium is strongly contoured with cerebral bulges, a median groove and grooves above the orbital margins; the orbital margins are only slightly extended. The zygomatic and articular processes of the squamosal are well developed. The basipterigoid processes are vestigial in the adult, and the mandibulae lack a posterior fenestra. The basyhial is not keeled. The upper jaw in Steller's eagle is extraordinarily massive when compared to those of other sea eagles, its depth accounting greatly for the massive appearance.

Birds jaws are powerful 'tools' used for feeding, especially in the birds of prey. The Steller's eagle's strong, very curved bill is the perfect implement for food riping and tearing large carcasses into small pieces that are easy to swallow. The main food of Steller's eagle are large fish, sometimes weighing about 6-7 kilograms, similar to the eagle's own mass. In the Bering and Ochotskoe seas the main fish species upon which they feed are the anadromous salmon. Fish skin is tough and difficult to tear. But field observations suggest that Steller's Sea Eagles can consume about 900 g of fish in 3-4 minutes. In comparison, White-tailed Sea Eagle feeding at the same locations spend about 18 minutes to consume the same amount, and Golden Eaglerequires 28 minutes (Ladygin 1994, 1996).

Field research in Kamchatka (Ladygin 1992, 1994, 1997) has shown that Steller7s SEa Eagle occur in large aggregations on the wintering grounds, and at these aggregations many aggressive interactions between tens of eagles occur during feeding, behavior that is similar to groups of vultures feeding on a single carcasse. In the case of the Steller's Sea Eagle strong competition between individuals exists at feeding places during wintertime. The time necessary for food preparation can be a key factor in survival. Because of this, morphological structures that can reduced time of feeding should be considered adaptive and are promoted.

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