SOME EFFECTS OF ENVIRONMENT AND HABIT ON CAPTIVE LIONS.

By N. Hollister,

Superintendent, National Zoological Park, Washington.

INTRODUCTION.

The series of over 100 East African lions now in the collection of the United States National Museum was recently spread out for study. Marked differences between wild-killed specimens and those which had died in the National Zoological Park in Washington were at once apparent. These differences involved both the skins and skulls, and from the fact that five of the park lions were of known history and were from a locality abundantly represented by wild-killed specimens, the uniform differences between the two lots, wild and park-reared, seemed more significant than would otherwise have been the case.

The 11 Zoological Park lions preserved in the collection agree among themselves in all essential details and differ uniformly from wild-killed lions. In the following remarks, however, the notes presented, unless otherwise stated, refer to the restricted subspecies *Felis leo massaica*,[1] represented in the collection by 59 specimens, 54 wild-killed and 5 park-reared. The five park-reared animals have definite and complete records. They were captured near Nairobi, British East Africa, and comparisons of skins and skulls are made with specimens of equal age, killed in the same vicinity. All chance of error from the use of park animals of unknown origin, which might be crosses of different subspecies bred in captivity or specimens of wild forms not represented in the Museum collection, is thus eliminated.

[1] In 1910, when reporting on the mammals collected in British East Africa by John Jay White (Smithsonian Misc. Coll., vol. 56, No. 2, p. 11), I referred the Nairobi lion to *Felis leo sabakiensis* Lönnberg, described from Kilimanjaro. After working over the much more abundant material since received at the Museum I am unable to recognize this race, and now refer these lions to the earlier-named *Felis leo massaica* Neumann, described from Kibaya, German East Africa.

The wild-killed material was collected chiefly by Dr. W. L. Abbott, John Jay White, Col. Theodore Roosevelt, Kermit Roosevelt, Paul J. Rainey, and Edmund Heller.

The histories of the five Zoological Park specimens of *Felis leo massaica* have been given me by Mr. A. B. Baker, assistant superintendent of the National Zoological Park. It seems important to give his account in complete detail.

The history of the five lions from East Africa, so far as we know it, is as follows:

In May, 1909, while the Smithsonian expedition was at Nairobi, Mr. W. N. McMillan offered the lions and several other animals to the National Zoological Park, through Dr. E. A. Mearns, who reported the offer here by letter. He was authorized by cable to accept the animals on behalf of the park.

I first saw the lions September 19, 1909. They were then at Mr. McMillan's "Juja Farm," some 23 miles northeast from Nairobi. There were two males, said to be then about 20 months old, and three females, one of which was said to be about 19 months old and the other two about 27 months. All were said to be from the region about the Nairobi, but I was able to get the exact locality of only one—a male which was captured by Mr. G. L. Langridge in the Mua Hills, out some 25 miles from Machakos station. When captured it was a little larger than a house cat. I was told that all of the others were caught while small cubs. The lions were put into shipping boxes October 15 and 16, left Juja Farm on a big freighting wagon at noon October 18, and arrived at Nairobi late on the 19th. The boxes were put under a shed in the railroad freight yard there until the morning of October 26, when they were shipped by rail, and should have reached Mombasa early in the morning of the 27th, but did not arrive there until noon of the 28th, because of the derailing of the train, which made it necessary to transfer all the boxes to other cars. They were transferred to the steamship *Melbourne* shortly after noon on the 28th and arrived at Port Said at 8 p. m. November 8. They were kept on a lighter in the harbor there until November 21, when they were transferred to the "tramp" steamer *Moltkefels* sailing that day. The ship spent the night of November 25–26 at Malta, and arrived at Philadelphia December 17. The lions were forwarded from Philadelphia December 18, reached Washington early on the 19th, and were transferred to cages in the lion house at the park about noon of that day.

At Juja Farm the five lions were kept together in a stone building, perhaps 25 feet long, 15 feet from front to back, and 8 feet high. This was divided by a partition running from front to back, into two compartments, perhaps 15 and 10 feet wide. The roof was of galvanized iron. The floor was of concrete, with good drainage so that it could be washed out with a hose. All sides were tight, except the front, which was closed with an iron grating. The place was poorly lighted and the animals had little chance to get into the direct sunlight. There were low wooden shelves in the corners, which the animals seemed to occupy most of the time when not walking. The three younger lions were good tempered, but the two older females were quite savage, probably from having been teased. The shipping crates were about 3 feet wide, 5 feet long from front to back, and 3 feet 6 inches high, inside measurements. There was a steel grating in the front, with stout wire netting over it, so that a paw could not be put out. A space was left at the bottom wide enough to admit food and pan for water. This space was closed except when food or water was given. There was a ventilating opening, about 8 inches square, in the

rear end of the box fitted with a grating. This opening was covered over when the animals were shipped from Port Said to protect them from the colder weather that would come during the remainder of the journey. At the park the lions were put into cages 10 feet wide, 8 feet deep from front to back, and 7 feet high. They were kept in these for about two years and then transferred to cages 12 feet 6 inches wide, 12 feet deep from front to back, and 9 feet high. These latter cages connect with outdoor cages 20 feet wide, 33 feet deep from front to back, and 10 feet high. The lions had free access to these outside cages during the day, whenever the weather was suitable.

While they were at Juja Farm the lions were fed mainly on zebra and kongoni (*Coke's hartebeest*), which usually were to be had for the shooting within a mile of the house. The whole dressed carcass was used and the lions were given sections from any part of it. They were liberally fed and apparently had a fair proportion of bone with the meat. I gave them zebra meat till October 20, then beef, mostly neck and shoulder, till November 1. Owing to an accident on the railroad it was impossible to give them either food or water from 6 a. m. of October 26 to noon of October 28, although during the first day they were exposed to the hot sun on an open car. From November 3 to 7, three sheep, bought at Djibouti, were fed them. November 9 to 22 they had beef, and the 23d and 24th a goat each day. From November 26 to 30 beef from Malta was fed. This was hind quarter, largely "round," as I found that beef from any part of the body was priced the same, and hind quarter gave the most meat for the money. From December 1 to 16 the lions were fed on goat meat, one goat being butchered each day, or one every second day, as the supply dwindled. From December 17 they were fed on beef. At the park the lions were given cuts of beef from brisket, shoulder blade, and short ribs, with, occasionally, upper shin or shoulder cut. At first they were given 8 pounds daily, which was increased, as they grew, to 10, 12, and finally a maximum of 14 pounds during the winter months to the two males. Most of this was cold-storage beef, and occasionally it was necessary to use some that had been frozen.

All of the lions appeared to be in perfect health when shipped and when they reached the park, except that the male (No. 2297) had a small abscess in one cheek, and that all were infested with roundworm and tapeworm. The tapeworm was probably acquired from the kongoni, the meat of which I was told is generally "measly."

The male lion No. 2297 (U.S.N.M., No. 197944) died March 1, 1914, of chronic gastroenteritis. He had been ill for about 10 months, could not properly digest his food, and was emaciated. He became blind about 18 months after his arrival at the park and remained so for about three months, then began to recover his sight, the pupil, which had been fully expanded, gradually contracting as the eye responded to the light.[1]

Male No. 2367 (U.S.N.M., No. 199707) was shot July 1, 1915, as he was unfit for exhibition. Autopsy showed considerable softening at the base of the brain, but other organs appeared to be practically normal. This lion became blind about 15 months after arrival and did not regain sight. The effects of the brain lesion were first noticed about two years before death and increased until the animal was finally killed. He always ate well and was in good flesh.

Female No. 2209 (U.S.N.M., No. 176201) died March 22, 1913, from choking. She was a hasty eater, bolting her food, and this time a large piece of meat lodged in her throat and she died before help could be given. She kept in

[1] This is the only skull among the five which shows pathological conditions in the bone. The shape and general characters of the skull are exactly as in the others, but the bone is very light and flaky.—N. H.

excellent flesh, although fed only 10 pounds of beef, but sometimes, after bolting her own portion, she would rob another lioness of part of its food. She was heavily infested with ascaris worms. She was the youngest of the three lionesses. She was bred several times, but never became pregnant.

Female No. 2276 (U,S.N.M., No. 197137) was shot December 25, 1913, as she was unfit for exhibition. In November, 1912, she was removed to a hospital cage on account of her difficulty in walking. She ate well and remained in excellent flesh, but the trouble continued to increase until she was killed. The autopsy did not show any serious lesions. She was given but 10 pounds of beef per day. She came in heat several times, but would not allow the male to approach her.

Female No. 2360 (U.S.N.M., No. 199524) died of pericarditis February 14, 1915, about six weeks after the first symptoms of illness were noticed. She was the largest of the lionesses, and her daily ration was 11 pounds of beef. She was bred several times, but did not become pregnant.

Not knowing just what data you might want, I have given the history with much detail.

The conspicuous external characteristics which distinguish these McMillan lions (as the five park-reared specimens will hereafter be called) from wild-killed animals of the same age and from the same region are much darker color, more luxuriant mane, and much longer hair tufts on back of elbows. The skulls are very different in general proportions. Those of the McMillan lions are much shorter and broader than in wild animals; their zygomatic arches are more wide-spreading, and the bones of the arches are much thicker and more cylindrical. (See pls. 22–25.) These skulls have furthermore a greater rostral and mastoid breadth and numerous minor distinguishing characters. Only one of the McMillan skulls shows evidence through pathological changes of the life in captivity, and this condition has affected the quality of the bone and not the shape, as the skull agrees in all the relative dimensions with those of other park lions in perfect condition.

COMPARISON OF McMILLAN LIONS WITH WILD-KILLED SPECIMENS FROM VICINITY OF NAIROBI.

Color and External Characteristics.

At the time of their arrival in Washington the McMillan lions were the subject of remark on account of their exceedingly pale coloration. Most of us had been accustomed to the much darker park lions, usually seen in captivity, and these new arrivals seemed particularly beautiful animals because of the strange pale grayish buff coloration, which was, as a matter of fact, the normal coloration of the subspecies to which they belonged. When, after the death of the animals, the skins reached the museum, the great darkening of the general color since their arrival was at once noted. The degree of color change is in direct relation to the period of life in Washington. In the following notes on color the skins have been

observed from in front; they present a somewhat darker aspect when viewed from the rear.

Males.—Wild-killed adult males of *Felis leo massaica* are all of a very uniform color. The general appearance is that of grayish buff animal, a very light-colored lion with virtually no deep ochraceous or dark brown in the hue of the skin. The general body color is the effect of pinkish buff hairs tipped with blackish, the dark tips considerably grizzling the otherwise general pure buff coloration. The hairs of the belly, throat, and insides of limbs lack the black tips and these parts are, as a consequence, almost pure pinkish buff in color. The tufts at the back of the elbows are comparatively short, mixed buff and brown. The mane varies greatly in different animals, but averages much shorter than in captive lions, is rather coarse haired, and comparatively light in color. It is produced on the withers in a narrow line and is almost entirely wanting on the shoulders. The tail is more gray, less buff than the body, but lacks any suggestion of ochraceous.

The first male McMillan lion to die in the park was No. 197944, March 1, 1914. He had been in Washington a little over four years and was, according to Mr. Baker's records, about six years of age at the time of death. The skull shows a fully adult animal with basisphenoid suture obliterated and with a fully developed sagittal crest. The skin is considerably darker, more ochraceous buff or cinnamon buff, than in wild-killed males of the same age. The general color of the back is more cinnamon buff; the black hair tips, though present, are less conspicuous against the darker ground color and the general appearance is therefore less grizzled, more reddish. The belly, throat, and inner sides of limbs are decidedly pinkish cinnamon instead of pinkish buff, as in all wild-killed males. The tufts at the back of elbows are long, luxuriant, and silky, mixed deep black and buff—much longer and fuller than in any wild-killed animal. There is a supplemental tuft of dark brown hair on each side of the lower belly. The mane is longer, more silky, and more cinnamon buff in color than in wild-killed lions. It extends far back on the withers and laterally onto the foreparts of the shoulders in curly masses. The tail is decidedly more ochraceous and black, instead of buff and blackish as normal in the subspecies.

The second male McMillan lion (No. 199707) died in the Zoo July 1, 1915, at an age of about seven and one-half years, five and one-half years of which had been spent in Washington. The skin of this lion is decidedly darker than any other East African specimen. The appearance of the animal has been greatly changed—from a pale grayish buff to a dark brownish ochraceous. The general color of the upper parts and sides of the body is dark tawny olive; of the belly, throat, and insides of limbs cinnamon to pale ochraceous tawny. The

tufts at backs of elbows are extraordinarily long, thick, and silky of rich black and buff hairs. Whereas in wild lions of equal age the hairs of these tufts average about 60 millimeters in length and are rarely over 80, in this specimen they are 200 millimeters in length. The mane is remarkably full and is not approached in this respect nor in its deep coloration by those of wild-killed lions. It is full and wide on the withers and luxuriant on the lower neck and anterior shoulders. The whole head, face, and mane are richly tinged with deep tawny and ochraceous. The tail is rich and dark in color, the black tip offering little contrast in shade from the general color of its upper side.

Females.—The wild lioness of *Felis leo massaica* averages somewhat darker in color than the male, but the coloration in its essential elements is the same—a grayish buff general color, the effect of a pale pinkish buff ground color mixed with the blackish of the hair tips. Except in very rare cases there is little or no indication of real tawny or ochraceous in the general coloration.

The first of the three McMillan lionesses to die was No. 176201, March 22, 1913. The skin is much darker than the average wild-killed *massaica* and is very much darker than when the animal reached the Washington Zoo in 1909.

The second female (No. 197137) died December 25, 1913. The skin of this lioness is somewhat darker than the wild animal and is conspicuously cinnamon colored, not at all the grayish buff of a normal *massaica*. The belly is pure cinnamon color, not buff as in all the wild lionesses of this form. The coat is long and full.

The last female of the McMillan lions died February 14, 1915, after over five years in the Washington Zoo. The skin is very dark and has been greatly changed since its arrival. It is very much darker than any skin of a wild-killed female *massaica* in a large series, and at a short distance looks like a tawny blackish animal. It represents the extreme of change in color in the lioness as No. 199707 does in the lion. The back is dark brownish tawny olive, rich and glossy.

From the above facts it is evident that life in Washington considerably darkened the color of these McMillan lions. Young wild lions are much darker and richer colored than adults, quite the reverse of the condition in the McMillan lions. From Mr. Baker's notes it is seen that while the captive lions were kept during their stay in Africa in a virtually sunless and rather dark den, in Washington they had abundant access to out-of-doors yards. In view of the success of Mr. Beebe's experiments in increasing the pigmentation in birds by confinement in superhumid atmosphere,[1] it would

[1] Zoologica, vol. 1, No. 1. New York, 1907.

perhaps seem unnecessary to go beyond the theory that the humid climate of Washington has acted in a similar manner on these lions from the highlands of East Africa. The effect has been to change the color of living examples of *Felis leo massaica* to a darker color very much resembling that of *Felis leo nyanzæ*, the lion of the more humid Victoria Nyanza region.

While the data available do not show very great difference in mean relative humidity between the weather station at Machakos, British East Africa (near where the lions were captured), and Washington, District of Columbia, the average monthly precipitation at Washington for a term of years is considerably greater. At Entebbe, Uganda (near the type-locality of *Felis leo nyanzæ*), both mean relative humidity and monthly precipitation are higher than in Washington or in the British East African range of *Felis leo massaica*. The problem is so complex and there are so many possible factors which are little understood, that it seems unwise to hazard a positive opinion on the cause of the great color change in the McMillan lions. Alterations in the quality of light to which the animals were exposed, as well as the changes in the conditions of metabolism due to a life in captivity under abnormal treatment and diet, are factors that must be considered.

Mr. F. C. Selous,[1] after writing of the variability of the mane in lions apparently adult, says:

> Quite recently there was a fine lion in the Zoological Society's Gardens at Regent's Park which was presented by Messrs. Grogan and Sharpe. This animal was caught near the Pungwe River, in southeast Africa, and brought to England by these gentlemen when quite a small cub. When full grown it developed a very much finer mane than I believe has ever been seen in a wild lion that has come to maturity in the part of Africa from which it was brought. Similarly, some 30 years ago there was a very fine lion in the Society's Gardens which was brought by Colonel Knox from the Soudan. Colonel Knox took me to the Gardens to see this animal, and pointed out to me the fact that it had developed a far finer mane (extending much farther back over the shoulders and under the belly) than any man had ever seen in a wild lion in the country from which it came. Lion cubs brought to this country from India also grow fine manes, though I do not think that there is any record of a lion ever having been shot in India with anything more than a fairly good mane. The fact that lion cubs captured in any part of Africa or Asia, and brought up in the comparatively cool and damp climate of western Europe, always—or nearly always—grow fine manes, which usually cover the whole shoulders and often extend all over the undersurface of the body, and the further fact that in the hotter parts of Africa lions always have very scanty manes, but on the high, cold plateaus often develop good, and occasionally very luxuriant manes, appears to me to show that a heavily maned lion is a reversion to an ancient ancestral type, first evolved in Pleistocene times in a cold and inclement climate.

[1] African Nature Notes and Reminiscences, pp. 83, 84. 1908.

Mr. Selous has noted that while the eyes of wild lions are of a "flaming yellow" in color, those of animals reared in captivity are often brownish.

Skull Characteristics.

The greatest interest in the study of the McMillan lions compared with wild examples from the same region lies in the skull. The skulls of the captive animals are of a definite, uniform shape and differ from all the skulls of wild-killed lions in the Museum collection in a number of conspicuous characters. They are broader and shorter, more massive and bulky, and exhibit abundant relative differences which would be instantly accepted as of "specific" value in wild animals. The obvious reason for these great differences is that the principal muscles operating the jaws and neck (those muscles used by a wild lion in mauling and killing game, biting, gripping, and shaking) have had little influence on the shape of the bones during development. In a wild-reared lion these powerful muscles naturally and in a normal way mold the growing skull, particularly in the regions of their attachment.

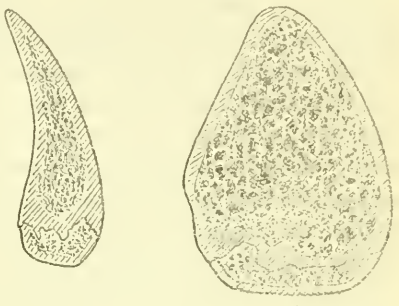
The most conspicuous peculiarities of the McMillan lion skulls are the greater (relative and actual) zygomatic breadth, the large rostra, and the great distance across the base of the skull at the mastoids. While actually measuring less in condylobasal or greatest length than many of the wild *massaica* skulls of equal age, they have a far greater zygomatic breadth than any, averaging about 30 millimeters more in males and 20 millimeters more in females. (See detailed measurements, p. 192; and pl. 24.)

All five of the McMillan lions, male and female, are, as already noted, fully adult, the skulls with basal sutures obliterated. All agree in most particulars in the differentiating characteristics, and comparisons may be made with wild-killed skulls of *Felis leo massaica* from the same vicinity and of equal age, without special designation of specimens by number. The differences are sometimes most pronounced in males.

Regions of attachment of the masseter muscle.—Contrary to the usual textbook definition of its function, the masseter muscle unquestionably furnishes the chief gripping power; it is the one most exercised during use of the canine and incisor teeth.[1] Aided by the

[1] In this connection see Keith, The Antiquity of Man, 1915, pp. 462–463. The lion, like all cats, is a biting animal of the highest type. While there is intimate relationship between the functions of the masseter and temporal muscles, and the two masses are actually connected, each nevertheless is the prime power in the definite mechanical action of separate parts of the dental row. The masseter, as stated above, has primarily to do with the front teeth (the canines and incisors), while the temporal is chiefly concerned with the molar-premolar row, and the process of cutting and chewing rather than biting and gripping.

temporal and internal pterygoid muscles, it locks the jaw and makes the grip firm. The region of its origin in the McMillan skulls is greatly changed from the wild type. The malar and the zygomatic process of the temporal bone[1] have been almost uninfluenced by the muscle and have to a certain degree retained distinctive characters of juvenility. In wild lions this muscle has exercised very great influence on the bones of the zygomatic arch. The following characters, which appear to be largely due to the nonaction of this muscle, separate easily the McMillan lion skulls of either sex from wild skulls of equal age: Zygoma more spreading anteriorly; malar very thick and wide; squamosal arm subterete and heavy, almost rounded in cross section and not at all concave on inner surface, with no superior margin for strong muscle attachment [in skulls of wild-killed specimens the squamosal arm of the zygoma is thin and light, but strong; it is greatly hollowed out on inner surface and has a sharp superior margin]. The region of insertion, the outer lateral face of the ascending mandibular ramus, is also greatly modified. In the McMillan skulls it is comparatively heavy and thick, but is smooth and poorly fitted for muscle attachment. The margin is smooth and rounded. The great zygomatic breadth of the skull of the captive lion is partly due to the rounded squamosal arm.



1 2

FIGS. 1-2.—CROSS SECTIONS OF ZYGOMATA OF WILD-KILLED AND PARK-REARED LION SKULLS, MADE AT INFERIOR POINT OF ZYGOMATICO-TEMPORAL SUTURE.—(1) WILD-KILLED (No. 155443, NAIROBI, BRITISH EAST AFRICA); (2) PARK-REARED (No. 199707, "MCMILLAN LION.") ADULT MALES OF EQUAL AGE. NAT. SIZE.

Some measurements of two old adult male skulls of equal age are as follows:

	Wild lion from Nairobi (No. 155443).	McMillan lion (No. 199707).
	Mm.	*Mm.*
Condylobasal length	335	325
Zygomatic breadth	234	264
Greatest thickness of zygoma at middle	9.3	14.8
Actual thickness of bone at middle of zygoma	4.0	11.5
Thickness at inferior zygomatico-temporal suture	14.4	29.1
Height of arch at middle, across malar and zygomatic process of temporal	31.9	36.9

[1] The masseter is attached to almost the entire length of the inner side of the zygoma, from just back of the molar tooth to the pit on the upper side of the squamosal root, and to the ventral half of the outer surface from near the maxillary tuberosity to near the glenoid surface.

Regions of attachment of the temporal muscle.—The temporal muscles, chiefly concerned with the cheek teeth rather than with the front teeth,[1] have had less influence in changing the type of skull of the captive lion, than have the masseters. The lion in captivity has, as a matter of fact, used his temporal muscles in much the normal way of a wild lion, whereas the natural function of the masseter is almost entirely discontinued in a captive animal which does not kill its own prey. As a precaution against the natural tendency of the animals to bolt their food without mastication, the lions in the Zoological Park are regularly fed pieces of meat with large bones.

The region of origin, the entire side of the skull posteriorly, is somewhat modified. The brain case has been less subjected to pressure by these powerful muscles than in the wild lion; the muscles have had less to do with moulding its shape during the process of absorption and ossification; and it, as a consequence, is less compressed laterally. Wild lion skulls of equal age have smaller braincases, more sharply marked sagittal and lambdoidal crests. The region of insertion, the inner surface of the ascending ramus, is slightly smoother in the McMillan lions, but is little modified.

Capacity of the braincase.—As stated above, external measurements of the braincase in wild lions are less than in park-reared animals of equal age. The capacity of the braincase, however, is considerably greater. Young adults of each, as usual among carnivores, have greater braincase capacity than old or aged adults. The bones forming the cranium of the Zoo lion are thicker, and the actual size of the brain is less than in wild-killed examples. In the case of the McMillan lions the capacity is about 50 cubic centimeters less in males and about 40 less in females, than in wild-killed examples of equal age from the same locality.

The "Richardson lion," from the New York Zoological Park, celebrated as the record skull for greatest breadth,[2] and the Menelik lion, the type-specimen of *Felis leo roosevelti*, are both park-reared animals of uncertain history but they show the skull characters of captive lions to a marked degree. Even the skulls of these enormous lions, although the animals represent forms unquestionably larger in a wild state than *Felis leo massaica*, have less braincase capacity than any wild-killed examples of the East African lion.

[1] A fox skull, in the Vienna Museum, with a defective left lower carnassial tooth, exhibits an asymmetrical condition because the animal used its right temporal muscle to such a degree as to develop this muscle far above the normal strength, while the left temporal muscle was very weak from little use. The right temporal ridge on the skull was pushed up almost to the sagittal line while the left temporal ridge remained below its normal elevation for that age. The occipital crest is likewise asymmetrical. (Toldt, Zool. Anz., vol. 39, pp. 176–191, figs. 1–4. July 4, 1905.)

[2] See Roosevelt and Heller, Life-Histories of African Game Animals, vol. 1, 1914, p. 225.

Following are some measurements of the capacity of the brain-case in fully adult lions:

MALES.

	No.			Cc.
Wild-killed	155443	*Felis leo massaica*	Nairobi	265
Do	182297	do	Kapiti	265
Do	182332	do	do	285
Park-reared	[1] 199707	do	Nairobi	215
Do	[1] 197944	do	do	220
Do	38246	"Richardson lion"		250
Do	144054	"Menelik lion"	[Abyssinia]	255

FEMALES.

Wild-killed	182309	*Felis leo massaica*	Ulu	245
Do	182326	do	Kapiti	255
Do	182421	do	do	245
Park-reared	[1] 197137	do	Nairobi	190
Do	[1] 199524	do	do	215

[1] McMillan lions. These are the only park-reared skulls strictly comparable with wild-killed *F. l. massaica.*

The mastoid and occipital regions.—These regions are, except for the squamosal arm of the zygoma, the most modified parts of the park-reared lion skulls. The change from the uniform type found in the wild lion is very great. The mastoid breadth in the McMillan lions is far greater than is usual in wild skulls of equal age; the mastoids are broad and spreading, with the large, smooth, postero-external surfaces next to the paroccipital process only slightly turned forward from the general occipital plane, and without sharply marked marginal ridges [in wild lions the mastoid breadth is usually much less, the sides are drawn in and forward, so that the postero-external surfaces of the mastoids lie in a position at a much greater angle from the general occipital plane; marginal ridges sharply recurved; paroccipital process longer and more angular]. (See pl. 25.)

Nondevelopment of the muscles chiefly used in lifting and shaking prey and the consequent lack of necessity for strong attachments is clearly responsible for this difference in the park-reared animals. The splenius, complexus, rhomboideus capitis, cleido-mastoid, sterno mastoid, rectus capitis posticus major, and rectus capitis posticus minor all attach to the affected parts. A powerful splenius is necessary in the wild lion, as the beast commonly carries heavy prey for long distances; the well-developed rhomboideus capitis aids in this work. The complexus and mastoid muscles are of great power in the shaking process and are, like the splenius and other closely related

muscles, naturally less developed in the animal reared in captivity. The digastric muscle, of quite another function, but powerfully developed in the cat, and having its origin on the paroccipital process and inward, bordering the posterior margin of the auditory bullæ, is no doubt somewhat responsible for the development of shape in this part of the skull as well. After a preliminary movement of the hyoid muscles, it is the chief agent for depressing the jaw. The cephalo-humeral and other muscles and the ligamentum nuchæ attach to the base of the skull but, in this problem, are of little importance.

The mastoid breadth in a wild-killed adult male lion from Nairobi (No. 155443) is 135 millimeters; in a McMillan lion of the same age (No. 199707) it is 152.

The lambdoidal ridge and occipital bones are broader in the McMillan skulls than in any skulls of wild lions. Here again the splenius and complexus muscles, through nondevelopment, have failed to influence the bone as in a normal wild lion whose life is one of tearing and shaking of strong prey.

The development of powerful neck muscles evidently begins in the wild lion at an early age. Roosevelt and Heller write of the young lion:[1]

> When the cubs are three months or so old, they habitually travel with the mother; then, instead of eating her fill at a kill and afterward returning to the cubs, the latter run up to the kill and feed at it with their mother. We found flesh and hair in the stomachs of two cubs; for they begin to eat flesh long before they stop suckling. While still very young they try, in clumsy fashion, to kill birds and small animals. By the time they are four or five months old they sometimes endeavor to assist the mother when she has pulled down some game which is not formidable, but has not killed it outright before they come up; and soon afterward they begin to try regularly to help her in killing, and they speedily begin to help her in hunting and to attempt to hunt for themselves. Evidently in their first attempts they claw and bite their prey everywhere; for we found carcasses of zebra and hartebeest thus killed by family parties which were scarred all over.

Remarks on Other Park-Reared Carnivores.

Park lions in the museum collection recorded as from Abyssinia, Sudan, and Somaliland, and others without definite history, agree in all essential details with the McMillan animals. The Menelik lion, which has been made the type-specimen of a new subspecies,[2] is virtually inseparable by any character, so far as the skull is concerned, from the McMillan lions. The differentiating characters as given in the description are exactly those separating park-reared from wild-killed specimens of the East African *massaica;* the specimen was compared with wild examples. This animal was presented

[1] Life-Histories of African Game Animals, vol. 1, 1914, pp. 165, 166.

[2] *Felis leo roosevelti* Heller, Smithsonian Misc. Coll., vol. 61, No. 19, p. 2. November 8, 1913.

to President Roosevelt by Emperor Menelik of Abyssinia and died in the Washington Zoo. All the characters of skin and skull point to a life-long captivity. The skin shows a long, full mane which connects from the neck with the elbow tuft. The colors are almost exactly as in the McMillan male longest in captivity, except that the mane is slightly darker and is curly instead of straight haired. Black manes and curly manes are individual variations found in males of equal age from one locality. One male *massaica* collected by Dr. W. L. Abbott has a much blacker mane than the Menelik lion.

An old male lion from Sir Francis Reginald Wingate, Omdurman, Sudan, which died in the Washington Zoo, is of the same type and shows all the characteristic evidence of a long life in captivity. The mane extends in a curly mass from the withers on to the shoulders, but does not connect between the neck and elbow tuft; it is largely black. This skin exhibits small tufts of hair on each side of the lower belly, like the McMillan male number 197944.

In a large series of leopard skulls in the collection a single specimen is from a park-reared animal. It can instantly be selected from the series by a blindfolded person familiar with the characteristic shape of the bone in the zygomatic arch of the McMillan lions. Wolves born and reared in the Washington Zoo from parents of known history show the same characteristic shapes of these bones when compared with wild-killed animals of the same subspecies. The differences are much less in the wolf, however, than in the great cats.

No changes in the teeth have been noted in the park-reared animals of any species, although the teeth of the McMillan lions do actually average slightly less in size than in wild-killed animals. The variation, shown in the following table, is so slight as to be of little consequence without further data:

Dental measurements of adult Felis leo massaica.

Locality.	Number.	Alveolar length of upper canine.	Upper carnassial.	Second upper premolar.	Lower molar.
Wild-killed males.					
		mm.	*mm.*	*mm.*	*mm.*
Kapiti Station	182297	27.8	40.0 × 19.9	27.5 × 13.5	28.6 × 15.3
Do	182332	26.5	37.8 × 19.2	27.2 × 13.7	28.7 × 14.5
Ulu Station	182307	24.5	37.8 × 18.8	26.7 × 13.9	28.5 × 14.2
Ulukenia Hills	182313	26.9	41.5 × 21.1	28.5 × 15.4	28.9 × 15.3
Nairobi	155443	27.8	39.3 × 18.9	27.3 × 14.0	28.8 × 14.5
Laikipia Plateau	163328	24.4	38.0 × 19.1	27.3 × 12.1	27.7 × 13.6
McMillan males.					
	197944	23.0	35.8 × 18.1	24.0 × 13.4	28.2 × 13.9
	199707	25.2	37.9 × 19.7	25.8 × 13.0	27.6 × 14.7

Dental measurements of adult Felis leo massaica—Continued.

Locality.	Number.	Alveolar length of upper canine.	Upper carnassial.	Second upper premolar.	Lower molar.
Wild-killed females.					
		mm.	*mm.*	*mm.*	*mm.*
Ulu Station	182308	23.6	35.4 × 17.7	23.8 × 11.7	25.1 × 12.7
Do	182309	24.9	38.5 × 19.4	27.7 × 14.1	28.4 × 14.6
Do	182311	20.7	33.6 × 15.9	22.3 × 11.5	24.6 × 13.2
Kapiti Station	182293	21.9	35.2 × 17.1	23.7 × 12.9	25.3 × 13.9
Do	182324	20.9	33.9 × 16.8	23.6 × 11.7	25.3 × 12.4
Do	182326	19.4	33.2 × 15.5	22.1 × 11.2	23.9 × 12.1
Do	182421	21.9	32.5 × 16.3	23.1 × 12.2	23.3 × 12.7
Do	182423	21.2	33.1 × 17.0	21.8 × 12.5	24.6 × 13.6
Wami Hill	161914	21.7	33.4 × 15.6	21.7 × 11.1	24.2 × 12.1
Kitanga	182315	23.2	35.6 × 16.5	22.2 × 12.0	25.6 × 13.2
McMillan females.					
	197137	19.1	33.6 × 15.2	22.9 × 10.5	23.8 × 11.9
	199524	19.2	32.5 × 15.4	21.7 × 11.3	22.9 × 12.4

SUMMARY.

Specimens of the exceedingly pale *Felis leo massaica* brought from the British East African highlands to Washington change from the normal pale grayish buff color of the race to a darker color, resembling that of *Felis leo nyanzæ* of the Victoria Nyanza region. The color deepens with each successive moult for five years at least. The cause of this color change is unknown, though humidity is probably a factor of some importance.

The skulls of lions and other large carnivores which habitually kill quantities of heavy game are greatly influenced in a definite way by the development of the principal muscles used in gripping, holding, tearing, biting, and shaking. If the animals are captured when young and reared in confinement these particular muscles are little developed and the bone at the region of origin or insertion is little changed by their influence. The bones then retain certain characteristics of juvenility and develop along wholly different but uniform lines from that of the wild-reared animal.

Changes in the skull which would be accepted as of "specific" or possibly of "generic" value in wild animals from different regions are thus produced in the life of a single individual within from five to seven or eight years, almost as rapidly as if by "mutation."

The primary object of this paper is to call attention to a definite case of structural modification by habit.[1] No idea of extensive specu-

[1] The value of evidence derived from this case over that furnished by experimental mutilation of young animals can easily be appreciated. Nevertheless experiments such as those recorded by Anthony and others, like the removal of the greater part of the

lation on its meaning or the possible value of the records in the study of evolution is contemplated. The opportunity for such speculation, however, is unlimited, and the temptation is great. This remarkable change has taken place in the lions under artificial treatment. Might some such a change not happen in a state of nature? At numerous times in geologic history whole groups of animals have become extinct. In fact, this is the rule, and only a few of the types known from fossil remains have left living descendants. If all the ungulate mammals of Africa or in some one extensive region were swept away in a few years by a plague like the rinderpest, would the lion die out, or would he completely change his habits in one generation and become a feeder on mice, squirrels, birds, and fruit? In the latter case, would not the enforced disuse of the powerful mechanism for the destruction of zebras, hartebeest, and larger game produce in one generation, as with the park lions, a type of skull wholly different from that now known in a state of nature?

One can easily believe that if the ordinary wild lion skulls were known only from Miocene deposits and the specimens were compared with the McMillan lion skulls, they might be regarded as representing the ancestor of the latter. The great change would naturally be regarded as the result of slow variation continued over that long period of time.

The use of zoological park material in the description of new forms of mammals should be discouraged. New names should never be based on animals in parks or on skins and skulls of specimens which have lived long in captivity.

Relative dimensions (ratio of length to breadth) of skulls is shown by the McMillan lions to be easily changed by habit or environment. Great weight has often been placed on the ratio of length to breadth, as a deep-seated character. Paleontologists, especially, value such differences much higher than do workers in recent mammals who have access to large series of closely related subspecies and are familiar with the variations they exhibit in this respect. The surprising and uniform differences in this regard between the McMillan lion skulls and the skulls of wild-reared examples of *Felis leo massaica* are, nevertheless, a revelation to all mammalogists who have seen the specimens.

left temporal muscle of a puppy at birth and the subsequent dissection of the animal at or near maturity, have shown the importance of the study of the action and growth of the muscles, exercised by peculiar habit, in the formation of species. (See especially Anthony, Bull. Sci. Anthr. Paris, ser. 5, vol. 4, 1903, pp. 119–145, figs. 1–11. Anthony and Pietkiewicz, C. R. Acad. Sci., vol. 149, 1909, p. 870, and other papers by the same authors.)

Measurements of skulls of lions.

MALES.

Locality or history.	No.	Condylobasal length.	Greatest length.	Zygomatic breadth.	Mastoid breadth.	Interorbital constriction.	Greatest thickness of zygoma at middle.	Actual thickness of bone at middle of zygoma.	Thickness at inferior malar-squamosal suture.	Height of arch at middle.	Breadth of brain case.	Length of mandible.
Wild-killed massaica.												
Kapiti Station	182297	322	373	248	135	71	8.6	8.0	15.8	35.8	112	257
Do	182332	328	372	228	138	70	7.3	5.5	11.2	30.0	111	253
Ulu Station	182307	324	....	230	142	71	8.7	6.5	14.2	31.3	....	249
Ulukenia Hills	182313	....	....	236	....	72	7.9	7.0	12.2	29.5	....	244
Nairobi	155443	335	373	234	135	70	9.3	4.0	14.4	31.9	107	256
Laikipia	163328	316	337	233	133	75	8.2	6.0	16.0	33.2	108	235
Park-reared.												
"McMillan lion"	197944	309	345	261	146	78	12.4	10.5	25.7	31.4	116	248
Do	199707	325	363	264	152	80	14.8	11.5	29.1	36.9	120	260
"Richardson lion"[1]	38246	332	366	277	139	75	13.0	12.5	20.5	30.8	124	248
"Menelik lion"[2]	144054	296	335	255	132	70	20.5	18.1	24.2	29.4	117	236
"Abyssinian lion"[3]	174639	308	333	246	128	71	12.3	11.5	27.2	31.6	112	233

FEMALES.

Wild-killed massaica.												
Kapiti Station	182293	264	294	203	120	63	7.4	4.0	10.8	25.6	....	203
Do	182324	266	299	185	111	57	7.2	4.0	9.7	26.8	94	200
Do	182326	267	299	204	117	60	7.7	3.0	9.2	29.3	99	210
Do	182421	262	292	192	119	58	6.3	4.0	9.9	25.9	98	203
Do	182423	254	282	180	112	54	6.3	3.1	9.6	23.8	93	198
Ulu Station	182308	259	290	195	115	58	6.2	5.0	11.0	25.0	98	202
Do	182309	280	306	195	122	56	6.8	4.9	11.1	25.4	97	210
Do	182311	262	285	195	114	57	6.9	5.0	9.2	24.2	96	204
Wami Hill	161914	258	291	192	114	58	7.8	4.2	9.7	24.2	98	196
Kitanga	182315	....	....	....	....	58	6.9	4.1	10.8	26.6	....	197
Park-reared.												
"McMillan lioness"	197137	265	291	209	120	59	11.0	10.0	15.4	26.9	95	200
Do	199524	265	300	224	119	64	14.6	16.0	19.0	28.1	102	206

[1] Died in Central Park Zoo, New York City. Roosevelt and Heller state (Life-Hist. African Game Animals, vol. 1, p. 225) that this is the record specimen in zygomatic width.

[2] Type specimen of *Felis leo roosevelti* Heller. From Emperor Menelik's Zoo. Presented by Menelik to President Roosevelt and died in Nat. Zoo. Park in Washington.

[3] Died in Nat. Zoo. Park, Washington. Early history unknown.

EXPLANATION OF PLATES.

PLATE 22.

(One-third natural size.)

Skull of wild-killed adult male *Felis leo massaica*. U.S.N.M., Cat. No. 155443; near Nairobi; British East Africa, 1908; collected by John Jay White.

PLATE 23.

(One-third natural size.)

Skull of park-reared adult male *Felis leo massaica*. U.S.N.M., Cat. No. 199707; captured as small cub near Nairobi, British East Africa; died in Nat. Zool. Park, Washington.

PLATE 24.

Skulls of adult female *Felis leo massaica* (one-third natural size).

Upper. Park-reared; U.S.N.M., Cat. No. 199524; captured as small cub near Nairobi, British East Africa; died in Nat. Zool. Park, Washington.

Lower. Wild-killed; U.S.N.M., Cat. No. 182326; Kapiti Station, British East Africa, 1911; collected by Paul J. Rainey.

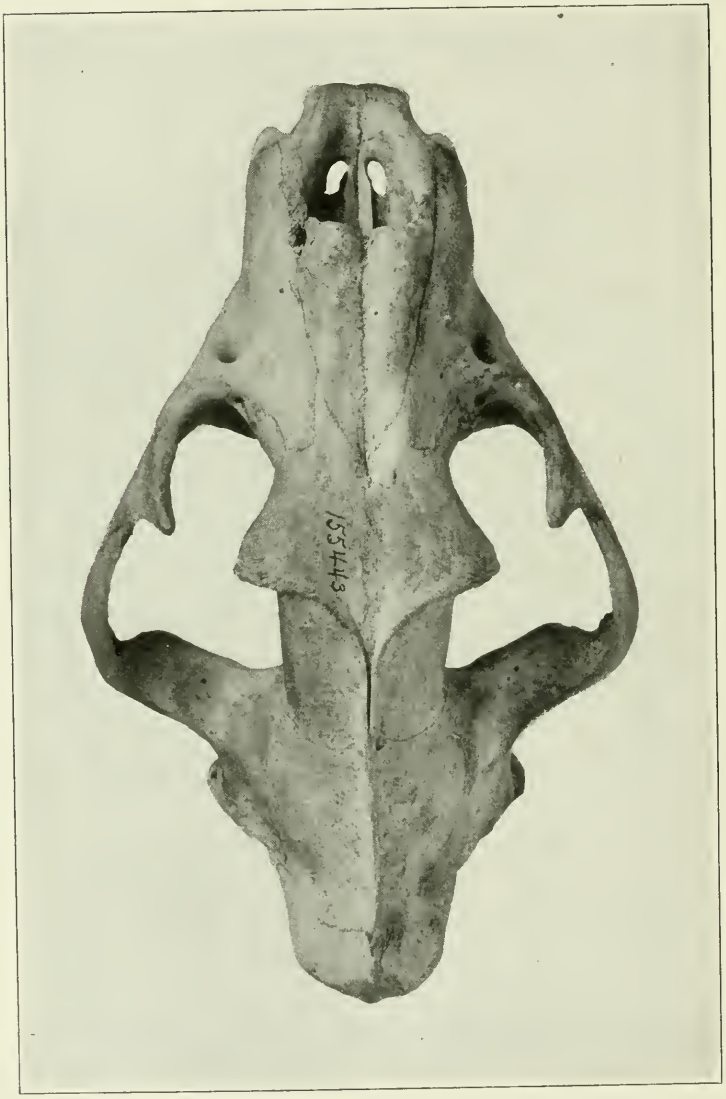
PLATE 25.

Skulls of adult male *Felis leo massaica*, occipital views (reduced; same scale).

Upper. Wild-killed; U.S.N.M., Cat. No. 155443; near Nairobi, British East Africa; collected by John Jay White.

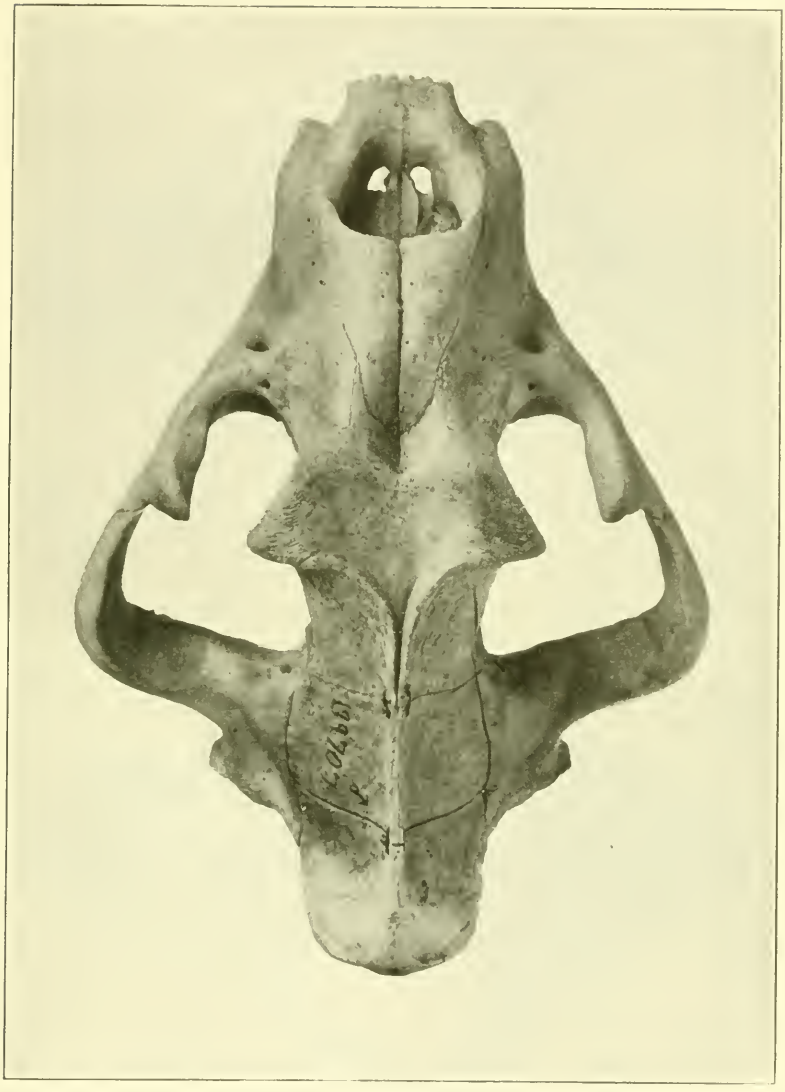
Lower. Park-reared; U.S.N.M., Cat. No. 199707; captured as small cub near Nairobi, British East Africa; died in Nat. Zool. Park, Washington.

77403—Proc. N. M. vol. 53—17——13



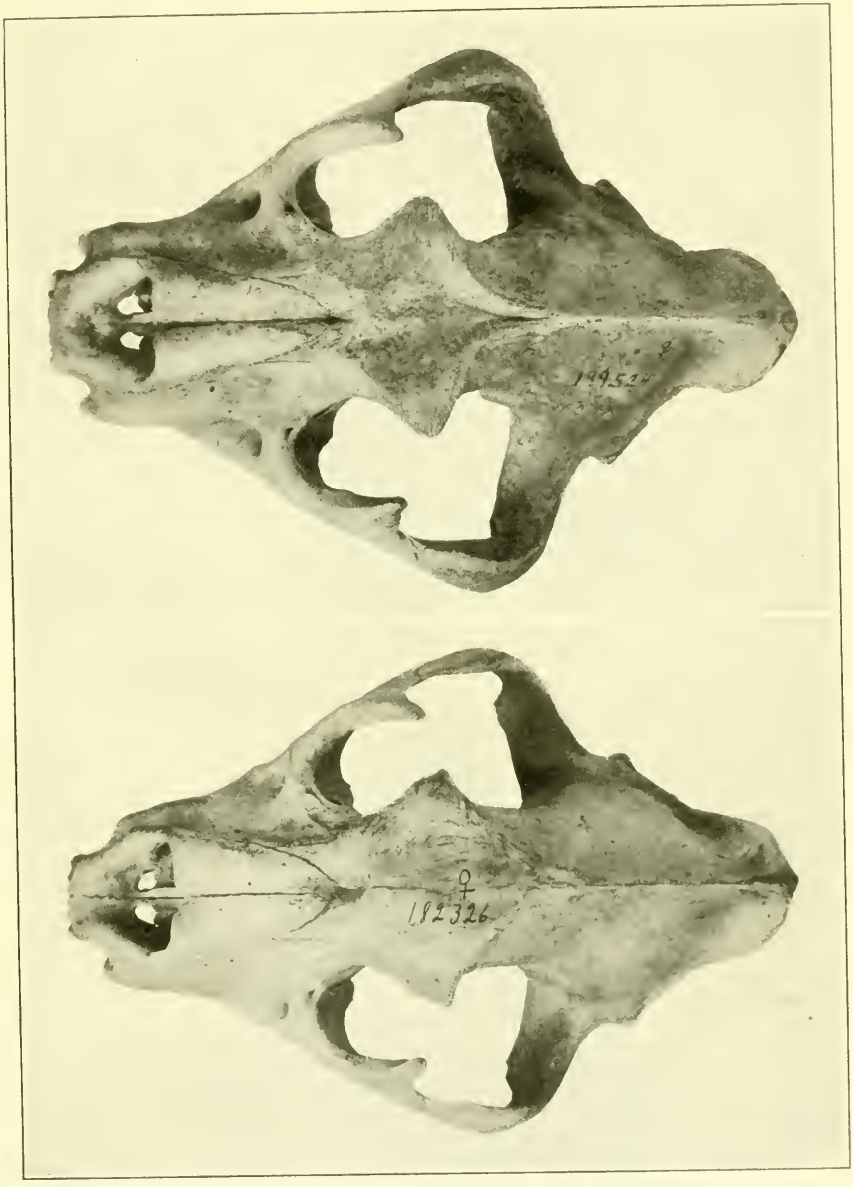
SKULL OF WILD-KILLED ADULT MALE FELIS LEO MASSAICA.

FOR EXPLANATION OF PLATE SEE PAGE 193.



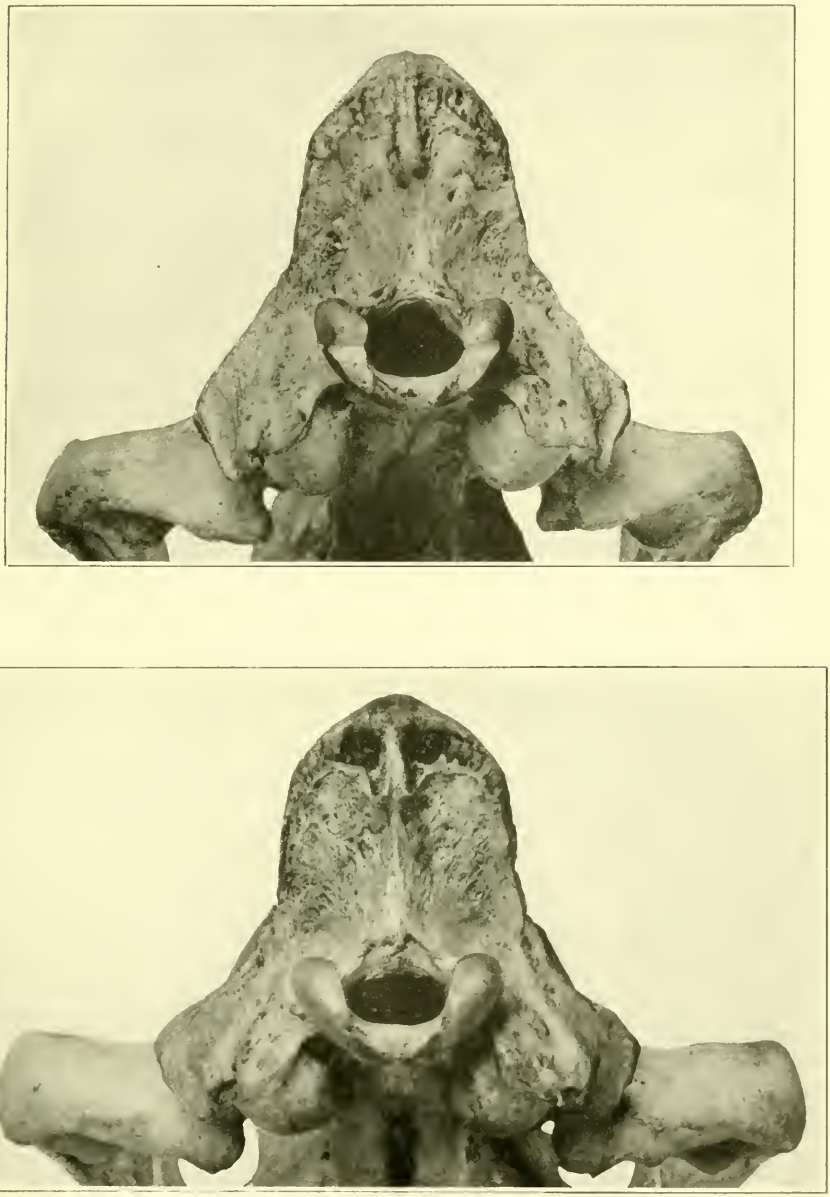
SKULL OF PARK-REARED ADULT MALE FELIS LEO MASSAICA.

FOR EXPLANATION OF PLATE SEE PAGE 193.



SKULLS OF PARK-REARED (UPPER) AND WILD-KILLED (LOWER) LIONESSES.

FOR EXPLANATION OF PLATE SEE PAGE 193.



SKULLS OF WILD-KILLED (UPPER) AND PARK-REARED (LOWER) LIONS.

FOR EXPLANATION OF PLATE SEE PAGE 193.