

Article V.—OSTEOLOGY OF PATRIOFELIS, A MIDDLE
EOCENE CREODONT.

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PLATE I.

HISTORY AND SYNONYMY.

The genus *Patriofelis* was originally established by Dr. Leidy, in the 'Proceedings' of the Philadelphia Academy, March, 1870, p. 10, upon the fragmentary portions of the rami of both lower jaws, which were obtained by Dr. Hayden in the Bridger Baisin, Wyoming, the year previous. In August, 1872, Prof. Marsh described (Amer. Jour. Science, Vol. IV, p. 10) from the same locality, some remains of a "gigantic Carnivore" which he referred to a new genus and species under the name of *Limnofelis ferox*. According to Prof. Marsh's statement, his specimen consists of portions of the skull, fragments of the lower jaw, some vertebræ, and other less important parts of the skeleton. In the same paper he describes a second species under the name of *Limnofelis latidens*, from a last upper premolar, which was obtained in the same horizon. Prof. Cope, in the 'American Naturalist' of 1880 (Vol. XIV, p. 745), proposed a third genus from teeth and limb bones, which were collected by the writer in the Wind River Baisin in the summer of 1879. To these remains Prof. Cope gave the name *Protopsalis tigrinus*. Prof. Scott has described in the 'Journal of the Philadelphia Academy,' 1886 (Vol. IX, p. 174), some remains of a large Creodont from the Bridger formation, which he referred to Prof. Cope's genus *Protopsalis*. A new species of this genus was proposed by the writer (Bull. Amer. Mus. Nat. Hist., Vol. IV, p. 98, 1892), under the name of *P. leidyianus*, from a specimen in the Princeton Collection.

The material collected by the American Museum Expedition into the Bridger Baisin now enables me not only to give an unusually full description of the osteology of the species of
[May, 1894.] [129] 9



Patriofelis, but to establish the synonymy of the three generic names that have been proposed.

A careful comparison of Marsh's description of *Limnofelis ferox* with Prof. Cope's figures and description of *Protopsalis tigrinus* leaves little doubt of the generic identity of the two specimens. Both of them, moreover, agree so perfectly with our specimens, that I do not hesitate to refer them to the same genus. Marsh's description is characteristically brief and imperfect, but enough is stated to indicate that the last lower molar of *Limnofelis* is the same as that of *Protopsalis*, which is in turn like that of *Patriofelis*. Marsh's specific name *ferox* is therefore adopted, since it has priority. A comparison of our specimens with Leidy's type of *Patriofelis ulta* reveals a difference only in size, our largest specimen being at least one-third larger in every way. I am therefore convinced that *Limnofelis* and *Protopsalis* do not present any characters, so far as known, which will enable one to separate them generically from the genus originally proposed by Leidy, namely, *Patriofelis*.

The specimens upon which this paper is based were found in the Bridger Basin at widely separated localities. The most complete is from the Henry's Fork region; several other specimens of both the species were found at Twin Buttes, and their remains are likely to occur wherever the exposures contain fossils. The larger species, *P. ferox*, is one of the largest Creodonts known, and equaled in size a full-grown black bear. The head was disproportionately large and massive, almost equaling in this respect an adult lion. The smaller species, *P. ulta*, was about one-third smaller. In both, there was a long and powerful tail, broad plantigrade feet, which, together with other characters presently to be considered, lead to the conclusion that they were aquatic in habit.

The subject is considered under the following heads: *History and Synonymy*; *Osteology*; *Comparison with other Creodonts*; *Comparison with the Seals*; *Probable Habits*; *Classification and Species*.

I.—OSTEOLOGY.

MATERIALS FOR DESCRIPTION.—The most important specimen in our collection, pertaining to the larger species, consists of an almost complete skeleton remarkably well preserved. The skull and lower jaws are present, but unfortunately somewhat damaged. The teeth are mostly wanting, but in the lower jaw the fangs of the entire series are preserved, so that their number can be determined. The facial part of the cranium is, moreover, considerably damaged, but at least two of the upper molars are sufficiently preserved to admit of a determination of their structure. With the exception of some of the cervicals and the first two or three dorsals, the vertebral column is complete and well preserved. Nearly all the ribs of one side are present, as are also a number of the sternebræ. The fore limb is represented by a scapula, part of a humerus, ulna, and radius, and nearly all the manus. The pelvis is wanting, but both hind limbs are well nigh complete. In a second specimen, somewhat smaller, one ramus of the lower jaw, bearing the premolars and a damaged first molar, is present, together with many important parts of the limbs. A third specimen includes a part of the hind foot with the greater part of the pelvis. A fourth specimen contains the pelvis, hind feet, vertebræ, humerus, scapula, ulna, radius, and part of the fore foot.

SKULL.—The single skull of *Patriofelis* contained in the collection is considerably damaged. When found it had already been weathered out of its matrix, and consisted of a heap of fragments. These, after much labor, have been put together and the result is a fairly satisfactory skull. Of this the posterior part, including the condyles, occiput, mastoid processes, brain-case, glenoid cavities and the zygomatic arches, is tolerably perfect. The greater portion of the top of the skull is also preserved, including both postorbital processes with the divergent roots of the sagittal crest posteriorly almost to the point of their junction, together with the greater part of the right nasal bone to its anterior free extremity. There is also a part of the left maxillary, reaching from its point of junction with the frontal forwards

and downwards in front of the infraorbital foramen, so as to include the roots of the first two premolars and the posterior wall of the left canine alveolus. The anterior portions of the zygomatic arches, moreover, have attached to them the posterior parts of the maxillaries, which, upon the left side, contain the last molar in position with the roots of the one immediately in advance of it. The posterior termination of the infraorbital is also indicated. There is in addition to the parts already mentioned the right anterior wall of the anterior nares, showing the alveoli of the canine, together with the lateral incisor, that is not connected by actual contact with the rest of the facial bones.

I have thus described at length the pieces as they actually exist for the reason that there is a possible source of error in the

construction of the face. The top of the skull is not connected by contact with the rest of the bones, and it may be placed too far forwards; but taking into consideration the sweep of the divergent branches of the sagittal crest, the position of the post-orbital processes, as well as other points, I am led to believe that it is approximately correct. The whole skull as thus restored is remarkable for its large size and general robustness as compared with the rest of the skeleton. Its size is quite equal to that of a lion, while the size of the body is but little if any larger than that

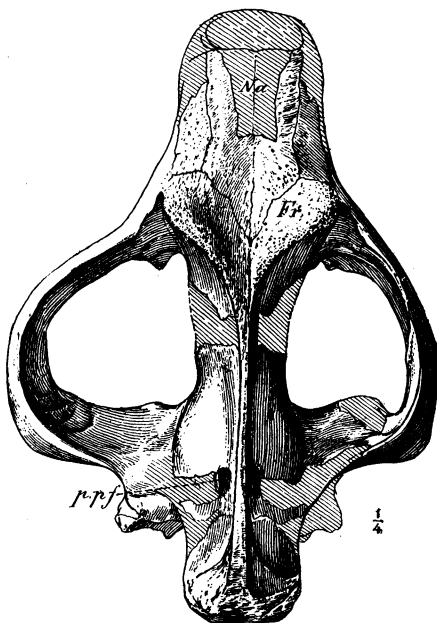


Fig. 1. *Patriofelis ferox*. Skull from above,
 ✕ natural size.

of a black bear. The face is extremely short and broad, with high, wide anterior nares. Behind the postorbital processes the

skull is much constricted, as in the seals, and there is a correspondingly long interval between the postorbitals and the anterior termination of the brain cavity. The sagittal crest is unusually high and prominent, and is continued far in advance of the brain cavity, as in the sea-lion ; it terminates posteriorly in a comparatively narrow, massive, overhanging occiput. Just above the posterior roots of the zygomatic arches at the base of the sagittal crest are seen two large postparietal foramina, which lead downwards into the lateral sinuses.

The zygomatic arches are remarkably heavy and widely expanded. The glenoid cavities have great lateral extent, and are provided with anterior and posterior glenoid processes, as in many of the fissiped Carnivora and the sea-lion. The mastoids are large and prominent ; the paroccipitals are conspicuous and closely applied to them. The tympanic bullæ are not preserved. The basioccipital is relatively broad and deeply marked for muscular insertion. The condyles are small in proportion to the size of the skull, and the foramen magnum is higher than it is wide, as in the seals. The occiput is relatively narrow, of great vertical extent and overhangs the condyles, as in the feline skull.

The *foramina* cannot be determined with a great deal of satisfaction, but some of them are sufficiently preserved to admit of

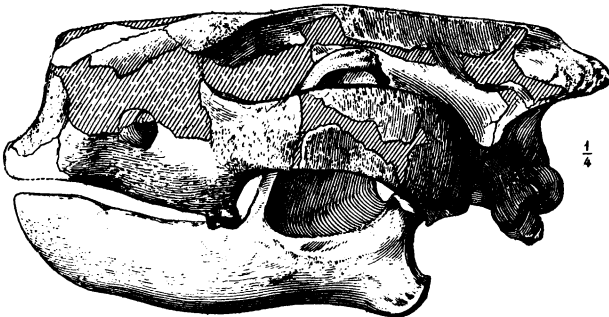


Fig. 2. *Patriofelis ferox*. Skull from side, $\frac{1}{4}$ natural size.

description. The optic foramina cannot be made out, but there is a distinct sphenoidal fissure, which is apparently not confluent with the foramen rotundum, as it is in the sea-lion. A very distinct and well-marked groove extends from the opening of the

foramen ovale, forwards to the opening of the foramen rotundum, and undoubtedly indicates the presence of an alisphenoid canal. The presence of a foramen lacerum medium cannot be determined, but a deep groove in the side of the basioccipital represents a large carotid canal, which would be completed were the tympanic bullæ in position. The region of the posterior lacerated and condyloid foramina is too much broken to show them distinctly. There are no post glenoid foramina. The stylomastoid has its usual position, and forms a deep groove between the mastoid and paroccipital process. There is another foramen of considerable size which opens backwards and downwards upon the posterior wall of this process. This foramen appears to be peculiar, and is not represented in any of the modern Carnivores.

The *brain-case* is very small in proportion to the size of the skull. While the skull is considerably larger than that of the sea-lion, the actual capacity of the cranial cavity is less than one-third as great. Its walls are remarkably thick. The cerebellum was entirely uncovered by the cerebral lobes, and the tentorium

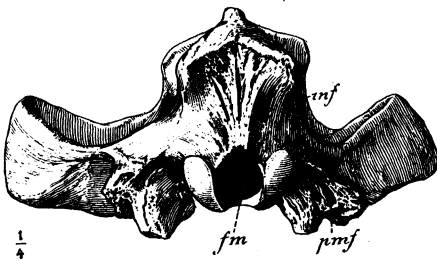


Fig. 3. *Patriofelis ferox*. Skull, occipital view,
 1/4 natural size.

was very little, if any, ossified. The cerebral cavity shows that there were at least two longitudinal or suprasylvian convolutions, much as in the more primitive carnivorous brain. There is no satisfactory evidence of a crucial sulcus. The cerebellum was relatively large, and the walls of its

cavity are unusually thick. The roof is marked by a deep longitudinal furrow for the lodgment of the vermis of the cerebellum.

The *lower jaw* partakes of the nature of the skull, and is remarkably heavy and robust. The horizontal rami are short and deep. The symphysis is rather short, and the chin abruptly rounded. The last molar is placed close against the base of the coronoid process, which rises rapidly and does not overhang the condyle. The masseteric fossa is wide and deep; the condyles,

which are placed low, have great transverse extent and a scroll-like pattern, as in the cats. The angle is well rounded and little produced, as in *Oxyæna*. The inferior dental canal is large and situated below the level of the tooth line. The inferior border of the jaw is nearly straight.

The *dentition* is but very little known, and our material does not, unfortunately, throw very much light on the subject. From Leidy's type specimen of *P. ulta* the number of molars and premolars in the lower jaw was determined to be five, of which three have been considered Pms. and two Ms. There were either four or five teeth in the upper jaw belonging to this series. I am inclined to the opinion that there were only four, of which three were Pms. and one M. Although the roots of the first two premolars above are preserved in the fragment of maxillary attached to the skull, it is difficult to determine whether the first one was single or double rooted. Now in *Oxyæna* there are four Pms. and two Ms. in the upper jaw, of which the first Pm. is single rooted and the last M. is transverse to the long axis of the jaw. In *Patriofelis* the last tooth is not transverse, and if *Patriofelis* is descended from *Oxyæna* directly, which I think the evidence demonstrates beyond question, the last upper tooth of *Patriofelis* must represent a single molar, since it would have been manifestly impossible for the transverse tooth to become again longitudinal. The transverse position is the first step in its disappearance. In the same way it may be determined that if the first Pm. is single rooted it represents the first Pm. of *Oxyæna*, and if two rooted it represents the second Pm., in which case there would therefore be only four teeth behind the canine. In our specimen it has the appearance of being two rooted, and I therefore consider the formula to be I. $\frac{3}{2}$,^(*) C. $\frac{1}{1}$, Pm. $\frac{3}{3}$, M. $\frac{1}{2}$.

The structure of the last upper tooth of *Patriofelis* is not distinctly shown in our specimen on account of the extreme wear of the crown; enough is preserved, however, to show that it had a well-developed sectorial structure. The para- and metacones are apparently completely fused so as to form an anterior blade, the posterior blade being furnished by the prolongation of the heel, as in *Oxyæna* and *Hyænodon*. If there were an internal cusp in the unworn tooth it must have been small. There is

another upper tooth in the collection from another individual, which I take to be either a first molar or the last premolar. It repeats the structure of the tooth just described, with the exception that the anterior blade is relatively larger. It has three roots, of which two are anterior and one posterior, and the internal cusp was rudimentary or wanting. The structure of the anterior teeth is entirely unknown. The canines were large and powerful, and there were probably three incisors above. The outer one, judging from its alveolus, was considerably enlarged.

A fragmentary specimen of a lower jaw in our collection shows that there were but two pairs of incisors below. These are crowded in such a way that the median one has a position almost immediately in advance of the outer one; the canine was large and slightly compressed laterally. The anterior (second?) premolar is placed very obliquely to the tooth line; it has a simple crown and two roots. The third is likewise two rooted, but the crown is not preserved. The fourth premolar is the largest of the series; its crown consists of a single principal cone, to which are added an anterior and posterior basal cusp. Of these the posterior or talon is the larger, and there is some indication of a second small internal cusp to this part of the tooth; this is suggested by the breadth and thickness of the talon at its base; it is shown in Leidy's type of *P. ulta*. The crown of the first lower molar is broken beyond recognition, but if we are to judge from Cope's specimen from the Wind River, as well as from Leidy's type, it has a structure very similar to the corresponding tooth of *Oxyæna*, with a more reduced talon. The last molar of the lower series is not preserved in any of our specimens. It has, however, been described by Marsh, and agrees so perfectly with the tooth figured by Cope, as well as that of Leidy's type, that its structure may be regarded as fully determined. The whole tooth bears a striking resemblance to the sectorial of the cat.

VERTEBRÆ, RIBS, AND STERNUM.—Almost the entire vertebral column is preserved in our best specimen of *Patriofelis*. Counting from the sacrum forwards there were sixteen vertebræ in position, so that there is no chance for error as regards this much of the

dorso-lumbar series. Of this number six are lumbar and the remaining ten are dorsal. As there are thirteen ribs of one side present in this same specimen, it is evident that there are at least three dorsals missing. I have therefore added these three vertebræ from another individual. There may have been one or two more, but I am led to believe that the number thirteen is approximately correct. This is the number usually found in the cats, but in the seals there are fifteen, and in the sea-otter there are fourteen dorsals.

The Atlas.—The general form of the atlas more nearly resembles that of the felines than any other of the existing Carnivora. This is especially seen in its vertical flattening, in marked contrast with the high arch and great vertical diameter of the neural canal of the sea-lion and sea-otter. Although the transverse processes are somewhat damaged in the single specimen which we possess, yet it is evident that they had a considerable lateral expansion, and are placed relatively high up on the sides of the bone, as in the cat, and not at its base, as in the sea-lion and sea-otter. In many of the Carnivora the transverse processes have a very marked backward direction, but this does not seem to have been the case in *Patriofelis*. There is a strong ridge occupying the upper anterior surface of the transverse process, which, so far as I am at present aware, is peculiar to *Patriofelis*.

The way in which the vertebral artery pierces the transverse process of the atlas in the different groups of the Carnivora is subject to considerable variation, as well as the form and direction of the transverse processes themselves, and in some of them, at least, these features are highly characteristic. In all of the Felidæ which I have had the opportunity of studying, the canal pierces the transverse process at its extreme posterior edge, where it is thickened and joins the body of the bone. The superior edge of this posterior border slightly overhangs the inferior edge. The process itself, moreover, in its fore and aft extension, is more or less parallel with the long axis of the neural canal. This character appears to be very constant in the Felidæ, and so far as we know the structure of the atlas in the more generalized Nimravidæ, it is true of them also. In the Canidæ, upon the other hand, the foramen for the vertebral artery is situated well in

advance of the posterior border of the process, and instead of having a fore and aft direction, as in the cat, pierces the process almost vertically from above. In the Viverridæ and Hyænidæ the position of the foramen is very much as in the cats. There is, however, an important difference between these two families and the felines in the character of the canal where the artery enters the suboccipital foramen in the anterior part of the atlas. The difference consists in the formation of a bony bridge in this situation which gives to the suboccipital foramen a double opening in the hyænas and civets, whereas it is single in the cats. It is interesting to note, however, that in *Haplophoneus* the suboccipital foramen has a double opening, as in the Viverridæ and Hyænidæ. Among the bears and mustelines, the lower edge of the posterior border of the process is extended backwards considerably, and the upper surface of the process is marked by a strong ridge. This ridge corresponds to the superior lip of the posterior border of the transverse process in the cat. In the more typical seals the vertebral foramen is greatly enlarged, while in the sea-lion it is of more normal proportions, and its arrangement, as well as that of the transverse process, is very much as in the bears.

The *axis* does not offer any characters of unusual importance. The neural spine is large and overhangs the posterior zygapophyses, very much as in the cats. The centrum is circular in section at its posterior extremity, and not depressed and oval as in the cat. Upon its inferior surface the centrum exhibits a strong keel, much more pronounced than in any of the modern Carnivores. The odontoid process is missing.

In the succeeding cervical vertebræ the centra are convex in front and concave behind. They present a circular section at their extremities, and are strongly keeled beneath. The neural spine of the sixth cervical is preserved, and indicates a proportionately greater height than is seen in any of the cats. The transverse processes are not sufficiently preserved to admit of description.

The *dorsals*, as already stated, are very probably thirteen in number, and in the anterior part of the region have relatively small bodies, with well-marked convex surfaces in front and

concave faces behind. This convexity and concavity gradually decreases towards the posterior part of the region until in the lumbar the central faces are nearly plane. In a like manner the centra increase rapidly in size posteriorly. The neural spines are not preserved, and their relative lengths cannot be determined, but judging from their roots they are relatively high and strong, as in the cats. The anterior and posterior zygapophyses are flattened oval facets which are directed upwards and downwards in the anterior ten of the series. The postzygapophyses of the tenth, however, become abruptly rounded or cylindrical, and are received into corresponding grooves in the succeeding vertebra. In the remaining dorsals, as well as the lumbar series, these articular processes become further complicated by the formation of a double tongue and groove, a character which, so far as I am now aware, is not found in any other carnivorous or creodont mammal. In the postzygapophyses the groove is superior and the cylindrical part inferior, while in the anterior zygapophyses this order is reversed. At the point where the zygapophyses change their character so abruptly, metapophyses and anapophyses appear and are well developed from this backwards. It is moreover at this point that the transverse process for the articulation of the tuberculum of the rib disappears, and the neural spine changes from a backward to a forward direction.

The *lumbar*s, six in number, have large plane-faced centra, with a strongly developed inferior keel, which gives to them a somewhat trihedral form. The neural spines are strong and unusually broad, especially those of the last three vertebræ. The distal ends of the spines of the anterior three vertebræ are more or less thickened and tuberos. All the lumbar have well-developed transverse processes, as well as anapophyses and metapophyses.

The *sacrum* is made up of three vertebræ, of which two unite with the ilia at the sacro-iliac synchondrosis. The bone is relatively broad and heavy, in keeping with the large size of the lumbar in advance of it, and the powerful tail behind. The neural spines are present, although smaller in every way than those of the lumbar series.

The *tail* is well nigh complete, and consists of twenty-eight caudals. The proximal ones are large and strong, with well-

developed transverse processes and complete articular processes. The neural canal and articular processes cease at the tenth from the sacrum, after which they present the pattern usually seen in the caudal region of the long-tailed Carnivora. There were numerous chevron bones, but none of them have been preserved.

The Ribs.—As already remarked there are thirteen ribs of one side preserved, together with numerous fragments of those of the other side. As this number agrees so well with the number of dorsals I am persuaded to believe that there cannot have been more than one or two pairs more than this number at the very utmost. The first rib is somewhat remarkable for its shortness and stoutness, together with the unusual size of its articular processes. It is considerably flattened, as are the succeeding three, after which they become more and more rounded. The last three have no tubercula, and articulate directly with the bodies of the dorsals.

The Sternebræ.—There are six sternal bones preserved in the more complete skeleton. These resemble the corresponding bones of the sea-lion more than those of the felines in their relative robustness and greater breadth. They are moreover much shorter than in any of the fissiped Carnivora.

FORE LIMB.—The fore limb of *Patriofelis* differs materially from that of the fissiped Carnivora in the proportions of the various segments. The scapula, humerus, and ulna are of about equal length, while the radius and manus also compare very closely in this respect. In the fissiped Carnivora, on the other hand, the scapula is very generally shorter than either the humerus or ulna, the length of the ulna equals, or may exceed that of the humerus, and the length of the radius is always greater than that of the manus. In the Pinnipedia the proportionate lengths of the component segments are again different. The scapula is always longer than the humerus, the ulna is longer than the scapula, and the manus is again longer than the ulna. One of the chief peculiarities of the fore limb of the seal consists in the enlargement of the scapula and the elongation of the manus. In this respect, there-

fore, the fore limb of *Patriofelis* is more like that of the seals than the land Carnivores.

The *scapula* is relatively longer and broader than that of the cats, dogs, or bears. The prominent spine divides the external surface in such a manner that the greatest breadth of the two fossæ are about equal, whereas the greatest breadth of the infra-spinous fossa in the cat, dog and bear, always exceeds that of the supra-spinous fossa. In the Otariidæ, at least among the seals, it is the supra-spinous which is the larger.

The head of the scapula presents a rather shallow pyriform glenoid cavity, and is joined to the body of the bone by an exceedingly short neck. As a result of this arrangement the acromion, which is unusually large, overhangs the shoulder joint to a greater extent than is seen in any of the recent genera. The tubercle for the attachment of the long head of the biceps is well developed, and occupies its usual position on the dorsal or external portion of the neck on the coracoid side. The coracoid process is of moderate proportions, and is rather obtuse, as in the bears and dogs, differing in this respect from the cats, in which it is produced and pointed. On the axillary border, at the point of junction of the head with the body, is seen a well-marked roughened depression for the tendinous origin of a part of the *teres minor*. The spine is large and prominent, and is terminated proximally by a remarkably well-developed acromion. To this is added a large overhanging metacromion, whose dimensions greatly exceed that of the feline scapula, in which it is best developed of all the Carnivora. The glenoid or axillary border is thickened and raised above the general level of the infra-spinous fossa, and towards its posterior termination shows a relatively small though distinct area for the origin of the *teres major*. This area is unusually large in the bears and seals.

The *humerus* is remarkable for the enormous development of the deltoid crest, the great prominence of the supinator ridge, as well as the lateral flattening of the shaft. The bone is relatively short and robust, not exceeding the scapula or ulna in length, and the shaft is moderately bent. The head is small, laterally compressed, and its articular surface is prolonged backwards so as to overhang the posterior border of the shaft to an unusual degree.

The bicipital groove is single, deep and narrow, the tuberosities are quite prominent and robust, and are deeply marked for ligamentous attachment. The greater tuberosity rises above the level of the articular surface, and is somewhat compressed from side to side, having a very slightly oblique direction to the long axis of the head. This is more pronounced in the cat, and becomes almost transverse in the sea-lion. The deltoid crest is almost as prominent as it is in the sea-lion, and occupies at least five-eighths of the entire length of the bone. In this particular the humerus differs markedly from that of all the land Carnivora and approaches that of the seal. The distal portion of the bone shows a powerful supinator ridge, and deep and well-marked antecubital and anconeal fossæ. There is apparently no supertrochlear foramen, but a large entepicondylar foramen is present. The trochlea is relatively broad, and the outer margin is thin and produced downward almost as far as the inner border. The anterior face of the articular surface is convex on the outer side, and is received into the cup-shaped head of the radius. It is not so convex as in the cat but is more like that of the sea-lion. A large part of the trochlea is occupied by the head of the radius, so that pronation and supination must have been somewhat limited.

The *ulna* is a strong bone, and is remarkable chiefly for the length of its olecranon process. In this respect it exceeds any of the modern Carnivora. In the dog and black bear the olecranon is only about $10\frac{1}{2}$ per cent. of the entire length of the ulna; in the puma it is about $12\frac{1}{2}$ per cent.; in the sea-lion it is about $17\frac{1}{2}$ per cent.; while in *Patriofelis* it is nearly $24\frac{1}{2}$ per cent. The posterior wall of the sigmoid cavity is elevated more than is usual in the Carnivora, as is also the case with the coronoid process. The shaft is laterally flattened and deeply grooved upon the outside. There is also a shallower groove found upon the inside. The shaft is deepest at the coronoid process by reason of a considerable backward curve, which it makes in this situation. The distal end is fashioned into a short, though stout, styloid process which articulates with the cuneiforme.

The *radius* is short and robust. Its head is oval in section, and covers a large part of the humeral trochlea. It is probable that

the movements of pronation and supination were more or less limited. The distal end of the bone is considerably expanded, but it does not exhibit the deep tendinal sulci which are seen in the modern Fissipedia. In this respect it is more like that of the sea-lion. It also shows a tendency towards the distal flattening of the shaft, a feature so conspicuous in the radius of the sea-lion. The distal articular surface is relatively small, and does not show separate facets for scaphoid or lunar, as one would be led to infer.

The Manus.—The carpus of *Patriofelis* is like that of the other Creodonta, in that the scaphoid, lunar and centrale are free. The *scaphoid* has about the same proportions and the general form of that of the cat, if the lunar and centrale were removed. Proximally it shows a single convex facet for articulation with the radius. Laterally it is applied very closely to the lunare by a nearly vertical facet, the proximal surface of the two bones forming a continuous convex surface. It is owing to this fact that the distal articular surface of the radius exhibits but a single facet. Distally but two facets can be distinguished, one for the trapezium, and another for the trapezoid and centrale. That for the trapezium is the larger of the two, in consequence of the abnormally large size of this latter bone.

The *lunare*, as stated above, is strongly convex from before backwards on its proximal aspect, and is closely applied to the scaphoid. Below it is strongly saddle-shaped, and articulates with the magnum, centrale and unciforme. It joins the cuneiforme by a moderately well-defined facet.

The *cuneiforme* is relatively large, and resembles the corresponding bone in the carpus of the bear. It presents a strong lateral process, which, when the bone is placed in its natural position on the unciforme, reaches over and almost touches the fifth

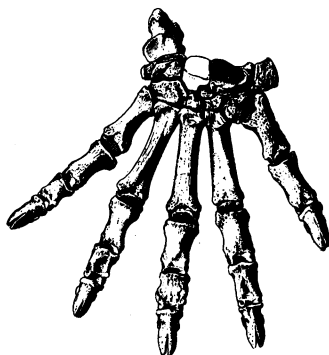


Fig. 4. *Patriofelis ferox*. Right manus, $\frac{1}{2}$ natural size.

metacarpal. The facet for articulation with the styloid process of the ulna is a wide, transversely extended groove, which is separated from the pisiforme facet by a high, transverse ridge. The distal surface has a cup-shaped facet where it articulates with the unciforme.

The *pisiforme* is robust and has a rather short, expanded tuber, which is very rugose for tendinous attachment. Otherwise this bone closely resembles that of the bear.

The *unciforme* differs from both that of the bears and felines in that it has considerably less vertical depth in proportion to its width. The cuneiforme facet is less vertical than in these forms, and the facet for the lunar is more on the summit of the bone. Distally there are two facets distinguishable, which serve as points of articulation for metacarp. IV and V.

The *magnum* is very much like that of the cat, and has practically the same relations to the surrounding bones. It is excluded from contact in front with the scaphoid by the intervention of the centrale. The broad shelf-like projection upon its radial side is occupied exclusively by the centrale, and the trapezoid does not overlap it, as is the case with the cats; in this respect it resembles the bears more than the cats. Distally it presents a single surface for articulation with metacarp. III.

The *centrale*, the smallest element of the carpus, is somewhat irregularly shaped, and articulates with the following bones: above, its principal contact is with the scaphoid, but it also touches the lunar; upon the ulnar side it articulates with the magnum, while below it is supported by the magnum and trapezoid. Upon the radial side it is more or less wedge-shaped, and lies between the scaphoid and trapezoid. In the coössified scapho-lunar of the cat and the bear, that prominent wedge of bone which extends down upon the radial side of the head of the magnum, and rests upon the ledge of this latter bone, undoubtedly represents the centrale.

The *trapezoid* is proportionately small, and does not lap over upon the magnum as it does in the cat. It is apparently not placed so high in the carpus as usual in the Carnivora, and therefore does not permit of the second metacarpal projecting above the level of the others, as so very frequently happens when the

bones are closely articulated. It articulates above by two distinct facets with the centrale and scaphoid, and upon the ulnar side with the magnum ; upon the radial side with the trapezoid, while below it supports the second metacarpal. It has essentially the same shape as in most of the fissiped Carnivora.

The *trapezium* is chiefly remarkable for its unusual size. It is almost equal to the unciforme and greatly exceeds the corresponding bone in the carpus of the modern Fissipedia. Above it has a large facet for articulation with the scaphoid, and a smaller one by which it articulates with the centrale. Upon the ulnar side there is a facet for articulation with the trapezoid and the inner side of metacarpal II, while distally there is a rather large flattened articular surface by which it supports the first metacarpal. It is of much interest to note that in its size and general form this bone of *Patriofelis* resembles the aquatic Carnivores much more than it does any of the Fissipedia. In the sea-lion the trapezium is larger than the unciforme ; its transverse diameter is almost if not quite equal to its vertical diameter ; there is a large facet for the scapho-lunar and the facet for articulation with the first metacarpal is not convex from side to side. In the Fissipedia, on the other hand, the vertical diameter is always the greatest, the facet for contact with the scapho-lunar is relatively small, and the facet for the first metacarpal is convex from side to side. Now in *Patriofelis* the greatest diameter of the trapezium is transverse, there is a large contact with the scaphoid, and the facet for the first metacarpal is like that of the sea-lion. The corresponding bone of *Oxyæna* resembles that of *Patriofelis* very closely.

Of the *metacarpals* the third and fourth are about equal in length and the longest, after which comes the second, fifth and first in the order mentioned. In the matter of size and robustness of the shaft, metacarpal I holds the first place, although there is some reason to believe that in the specimen here figured this bone is slightly pathological, which makes it appear larger than it would otherwise be if such were not the case. In the bone of the opposite side we have unfortunately only the proximal end preserved, so that this point cannot be fully determined. At all events it can be stated that metacarpals I and V were well

developed and relatively much larger and stronger than in the Fissipedia. One noticeable feature about the metacarpals is that the interlocking is but very slightly developed, and that the foot was broad and the toes well spread apart, which would lead to the conclusion that it was webbed. The distal ends of the metapodials all possess distinct keels, which are confined to the palmar half of the articular surfaces. The dorsal portion of these surfaces present that peculiarly distinctive hemispherical pattern so characteristic of the Fissipedia, and which appears to be altogether different in the seals. No especial mention need be made of the phalanges, further than to state that they are rather broad, depressed, and slightly curved, as in the Fissipedia.

The bony *claws* differ markedly from those of the Fissipedia, in that they are not laterally compressed and pointed, as is universally the case in this group, but follow the pattern of the Creodonta in having a deep cleft at their distal extremities. So far as is known, this character appears to be a very constant one in all the Creodonts, and is one of the features by which they can be easily recognized. The claws in *Patriofelis* are not so much depressed as they are in other Creodont genera, notably *Mesonyx*, and they are, moreover, considerably curved. There does not appear to be any trace of the bony hood or sheath enclosing the base which is developed to a greater or less extent in all the modern Fissipedia. There is another feature of the claws which is worthy of note, and that is the development of the subungual process. In the sea-lion this process is so large, especially in the fore limb, that it constitutes the greater part of the bone, and there is but the faintest trace of that part which bears the corneous sheath; yet a distinct depression upon the dorsal surface marks its position. The subungual process is not so large in the three middle digits of the hind foot, and the bony claws are well developed. In all the ungual phalanges there is a large, distinct foramen (the subungual foramen) which pierces the process transversely. This is more marked in the hind than the fore foot. In the Fissipedia, on the other hand, the subungual process is comparatively small, confined to the posterior part of the bone, and never overshadows the true bony claws, as it does in the seals. Traces of the subungual foramen exist, but they are

minute and inconsiderable. In *Patriofelis* the subungual process is well developed, and extends forward, beyond the middle of the under surface of the claw, and the foramen is large and distinct, as it is in the sea-lion. In this respect the claws of *Patriofelis* are intermediate between those of the Fissipedia and the Pinnipedia.

HIND LIMB.—The *pelvis* presents a number of marked anatomical characters which are apparently not found in any of the modern Carnivora at least. The ilium is well developed, and in proportion to the entire length of the pelvis exhibits about the same relative length as in the dog, cat and bear, and is therefore much greater than in the sea-lion. The chief peculiarity of the ilium of *Patriofelis* is its very unusual shape. It may be described as consisting of a strong trihedral bar of bone, the superior border of which is expanded into a broad lamina with a concave external surface. It therefore presents three distinct surfaces, of which one is directed internal, one upwards and outwards, and the other downwards and outwards. Of the two external surfaces the upper one, which served for the fleshy origin of the median gluteal muscle, is the larger and, as already stated, very concave. The inferior external surface is of less extent, and does not present any especial feature of interest further than to indicate a rather unusual size for the large gluteal muscle. The anterior end of the ilium is thickened and everted. A short distance in front of the acetabulum is seen a prominent roughened area for the tendinous origin of the *rectus femoris*. The acetabulum is rather shallow, and, as in the sea-lion, the roof of the cavity is not so thick and strong as it is in the fissiped Carnivores. It has a broad cotyloid notch, as in the dog.

The *ischium* is relatively broad and flat, with a prominent and somewhat elongated spine. There is little or no thickening of the bone at its posterior end to form the ischial tuberosities as in the Fissipedia, in this respect resembling the sea-lion. The obturator or thyroid foramen is large, slightly oval in form, and the two pubes are not united by bone at the pubic symphysis, which is long. The anterior edge of the symphysis lies consider-

ably behind the acetabulum and not opposite its middle as in the Fissipedia. The ilio-pectineal eminence is prominent and intermediate in size between that of the dog and sea-lion.

The *femur* is large and powerful. It exceeds the tibia both in length and size. The globular head is set upon the shaft by a moderately short well-constricted neck, and exhibits a slight pit for the attachment of a *ligamentum teres*. The greater trochanter is strong and rises to a level with the head of the bone. It is roughened for muscular attachment, and has a deep digital fossa. The lesser trochanter is well developed, and is connected with the greater trochanter by a faint though well-curved intertrochanteric line. As in all the Creodonts, there is a small though distinct third trochanter. In its upper portion the shaft is flattened from before backwards, but in its lower part becomes more cylindrical, and at its distal extremity is especially thickened. The rotular groove is well developed but does not extend so high up on the shaft as in the terrestrial Carnivores. In the strictly cursorial forms, such for example as the Canidæ, the upper extremity of the rotular groove extends to a point in front of the shaft, much higher than do the condyles upon the opposite side of the bone. In the sea-lions and the seals in general the reverse of this is true. In *Patriofelis* they are about equal in this respect. The condyles are not flattened from before backwards as in the sea-lion, and there is a peculiar thickness of the bone where they join the shaft, very much as in *Hyænodon* and *Oxyæna*. Of the two condyles the inner one is slightly the longer, the disparity being about equal to that seen in the puma.

The *patella* does not present any characters of unusual importance. It may be said of it, however, that it is relatively large and rather closely resembles that of the fissiped Carnivores.

The *tibia* is shorter than the femur, and is in every way more slender and delicate. If the length of the femur be expressed by 10, that of the tibia would be 8 or thereabout. The head of the bone is relatively broad with a moderately well-developed spine. The cnemial process is not so prominent as it is in either the dog or the puma, but it is thicker and extends down the shaft for a greater distance. It is, however, much better developed than it is in the sea-lion, in which it may be said to be almost entirely

absent. The distal end of the bone exhibits a strong internal malleolus, and an articular surface which shows but the faintest trace of that division into tongue and groove so highly characteristic of the higher Carnivora. The surface is directed strongly outwards.

The *fibula* is unusually stout, quite as much so as in the sea-lion, but there is no tendency to bony union with the tibia, as in the seals. The proximal end is considerably expanded and roughened for muscular attachment. The shaft is straight, nearly cylindrical and expanded into a distal extremity. When the tibia and fibula are articulated and the femur placed in position the fore and aft plane of the proximal extremity of the tibia is directed slightly inwards towards the body, while the same plane of the distal extremity is directed somewhat outwards. It results from this that the tibia has a decided twist, which causes a distinct outward rotation of the foot. In the sea-lion this torsion of the tibia is very prominent, which together with certain modifications of the tarsus does not permit the foot to be moved in a line with the long axis of the body, and gives to the animal that very peculiar and awkward gait upon the land. In the terrestrial Carnivora, on the other hand, there is no torsion of the tibia visible, and the foot moves freely in the direction of the long axis of the body. This matter will again be discussed when we come to speak of the probable habits of *Patriofelis*.

The *pes* presents a number of interesting characters. It is short and spreading in contradistinction to the narrow, elongated, compressed type of the more typical cursorial Carnivora. The *astragalus* is very primitive in that the trochlea is but faintly indicated, and the head is placed upon the body in a very oblique position. If the fibular facet be taken to indicate a fore and aft direction, then the head projects inwards at an angle of 45° or thereabout. It is nearly as great as it is in the sea-lion, and very much greater than in any of the terrestrial Carnivora. The neck is notably short and stout, and its constriction much less pronounced than is usually the case. The tibia and fibular facets form nearly a right angle at their point of junction, whereas in the sea-lion it is an obtuse angle, and in the Fissipedia it is an acute angle. The trochlea or tibial facet is rather short from

before backwards, slightly prolonged upon the neck, as in the seals and *Hoplophoneus*, and with a rather prominent antero-external angle, but not so great as in the sea-lion. There is a large and distinct astragalar foramen which is placed at the posterior termination and a little to the outer side of the trochlea. This foramen,

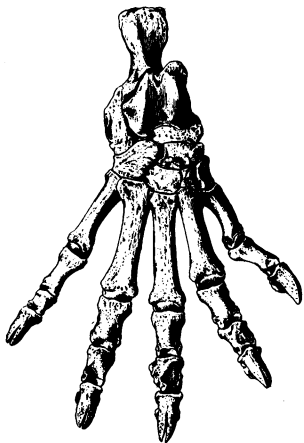


Fig. 5. *Patriofelis ferox*.
Right pes, $\frac{1}{4}$ natural size.

as is well known, is highly characteristic of the primitive forms of many orders of mammals, and it is of especial interest to note that the seals are among the very few living forms in which it has been retained. It is also present, though small, in the Miocene genus *Hoplophoneus*. The calcaneal facet is rather flat from before backwards, as in the sea-lion and *Hoplophoneus*, and does not have the deep saddle shape as in the Fissipedia. It is separated from the sustentacular facet by a moderately deep, wide groove. The sustentacular facet has its usual position but displays some characters peculiarly its own. It is continuous with the navicular facet

by a narrow band around upon the inner side of the head, whereas in all the other forms in which these two facets are united it is always upon the outer or fibular side of the head. The facet for the navicular is oval and flattened from above downwards. While it articulates with the cuboid as well as the navicular, this articular surface is not divided.

The *calcaneum* has a short, stout tuber, somewhat laterally compressed beneath the astragalar facet, but produced into a thick more or less rounded tuberosity at its posterior extremity. The tuber is relatively much shorter than in any of the terrestrial Carnivores and approaches that of the sea-lion. The characteristic shortness of the heel in the seals is not due so much to the absolute brevity of the bony process as it is to the unusual backward prolongation of the astragalar facet, and there is in consequence a high degree of mobility of this latter bone upon the calcaneum. The astragalar facet is rather flat, and is not so

steeply arched as in the dog, cat, or bear. It displays a more gentle curve, and spreads back further upon the tuber, as in *Hoplophoneus* and the sea-lion. The sustentacular facet is small, circular, and does not become continuous with the cuboidal facet, as is the case in the sea-lion. The facet for the cuboid is oval, cup-shaped, and the antero-external angle is produced in such a manner as to give it a marked obliquity in conformity with the peculiar shape of this latter bone. There is a broad, thick, ledge-like process upon the outside and near the distal end, which has generally been accepted as a mark of a plantigrade gait. In the human foot this process serves for the attachment of the annular ligament, and is deeply grooved for the passage of the long and short peroneal tendons. It is of much greater size in the calcaneum of *Patriofelis* than in that of the bear. It is also large in the sea-lion.

The *cuboid* is a highly characteristic bone in the tarsus of *Patriofelis*. Proximally it has two facets separated by a distinct antero-posterior ridge, one of which is for the astragalus and the other for the calcaneum. If the bone be held in a vertical position, the facet for the calcaneum is wholly upon the outer side, and forms the external boundary of the bone, but as the cuboid is not placed vertically in the tarsus the facet is directed upwards and outwards when the bone is in its natural position. This great obliquity of the calcaneal facet is very unusual, and is not found in any of the living forms except the seals and the South American musteline genus *Galictis*. In neither of them, however, is it so highly developed as in *Patriofelis*. Distally there is a large concave facet which supports the fourth and fifth digits. Internally it articulates by a single facet with the astragalus and ectocuneiforme. The *navicular* presents the usual form found in the Carnivora, and does not call for especial mention. The *cuneiforme* bones, moreover, display the usual pattern of the Fissipedia, the internal one not being especially enlarged, as in the seals.

The *metapodials* are five in number, and like those of the fore foot, show comparatively little interlocking. They are shorter proportionately than in the dog or cat, but are equally, if not more, robust. They are about equal to those of the black bear in length, but are stouter in every way. The fourth is the longest

and strongest of the series, after which comes the third, second, fifth and first, in the order named. They all possess distinct keels and globular-shaped heads upon their distal extremities. The *phalanges* resemble those of the fore foot in their form and general proportions, with the exception of their slightly greater length. The bony claws are all fissured at their extremities, and the subungual processes and foramina are well developed.

There yet remain to be mentioned in connection with the limbs two bones which, although they were not found in position, give every evidence of being a *radial sesamoid* and a *tibiale* (?). The radial sesamoid is relatively large, and is located at the inner extremity of the scaphoid, where it is found in the dog and bear. It appears to be altogether absent in the sea-lion. It is compressed from before backwards, and is slightly hollowed out at its distal end. The *tibiale* (?) has a similar shape to that of the radial sesamoid, but is not so large and not so much flattened. It articulates by a very distinct facet with the ento-cuneiforme, very much as in the dog, and not apparently with the ento-cuneiforme and navicular, as it does in the sea-lion, in which it is unusually large.

II.—COMPARISON WITH OTHER CREODONTS.

A.—COMPARISON WITH *OXYÆNA*.

In the foregoing description very little mention has been made of the nearly-related genus *Oxyæna*. The species of this genus, as is well known, have been found so far only in the older Wahsatch deposits. With the aid of the materials now in the Museum Collections I am able to give a comparative statement of the more important characters in the skeletal structure of these two genera. The species upon which this comparison is primarily based is *Oxyæna lupina* Cope, of which a somewhat fragmentary skeleton was collected by the Museum Expedition into the Big Horn Basin in 1891.

In the skull of *Oxyæna* we note the same peculiarity as regards the great disparity in size between it and the rest of the skeleton seen in *Patriofelis*. The face is short, the muzzle broad

and truncated, the skull much constricted behind the post-orbitals, and there is a long interval between the postorbitals and the anterior termination of the brain cavity. The sagittal crest is, moreover, high and prominent and extended well forward in advance of the brain-case. There are two large post-parietal foramina as in *Patriofelis*, and the glenoid cavities have anterior and posterior glenoid processes. The mastoid and paroccipital processes are prominent, and there is evidence of the existence of the same peculiar foramen piercing their posterior wall as seen in *Patriofelis*. In the lower jaw the rami are relatively deep, with a straight inferior border; the chin is abruptly rounded, the symphysis is short, the condyles well extended transversely and scroll-like in pattern; the angle is rounded and not produced into a hook, and the coronoids are broad and high.

In the teeth some important differences are to be observed, which separate the two genera very sharply. In our paper¹ we made the statement that our specimens demonstrate the existence of three incisors in the lower jaw. This, I think, is an error, for I cannot discover any evidence in support of this proposition. Cope expressed the opinion that there were only two incisors in the lower jaw, and I see no evidence for a contrary view. The dental formula, I. $\frac{2}{2}$, C. $\frac{1}{1}$, Pm. $\frac{4}{4}$, M. $\frac{2}{2}$, shows some important modifications as to the number of teeth in the molar and premolar series. In this, *Oxyæna* is the more primitive, as we would be led to infer by reason of its being the older genus of the two. *Patriofelis* has discarded one molar from the upper series, and a premolar from both the upper and lower series, if my conclusions are correct in regard to the dentition. The last lower molar has, moreover, been modified into a true sectorial tooth, consisting of only the two blades, whereas in *Oxyæna* this tooth possesses the internal cusp and the talon as well.

In the vertebral column the atlas of *Oxyæna* resembles that of *Patriofelis* very closely. The other cervicals, so far as they are known, have the same general characters as those of *Patriofelis*. The lumbar do not apparently have as highly complex zygapophyses as those of the Bridger genus, but the approach in this

¹ Fossil Mammals of the Wahsatch and Wind River Beds, Bull. Amer. Mus., Vol. IV, 1892, p. 108.



direction is very marked. *Oxyæna*, like *Patriofelis*, had a long and powerful tail, the sacrum being unknown.

Of the fore limb the scapula is somewhat fragmentary, but the greater part of both heads is preserved. The glenoid cavity has the same general form as in *Patriofelis*; as in this genus, moreover, the neck is very short, the spine rising almost immediately behind the border of the cavity. The spine itself is considerably damaged, so that the question of the acromion and the metacromion cannot be determined, but if we are to judge by the great similarity between the heads of the two bones, it is highly probable that a metacromion was present. In the humerus we note a most striking similarity. The deltoid crest is prominent and extends almost the entire length of the shaft; there is an entepicondylar foramen, but no intercondylar foramen. The humeral trochlea is very similar in the two genera, and the internal condyle is extended downwards into a broad flange-like process. The ulna has the same powerful olecranon process, and is deeply grooved, as in *Patriofelis*. Of the radius very little is known. The manus is strikingly like that of *Patriofelis*, with the exception that it is more slender and weaker in every way. In the carpus there is a free scaphoid and lunar, a centrale is present, and the trapezium is singularly enlarged, as it is in *Patriofelis*. The metacarpals have about the same relationship to each other as in the Bridger genus, and the interlocking is comparatively slight. The phalanges appear to be somewhat longer, and the claws not so deeply cleft as in *Patriofelis*. The subungual processes are well developed, and the foramen is present and large.

In our *Oxyæna* material the pelvis is not well represented, but Scott says of it:¹ "The pelvis differs from that of the typical Creodonts in having an expanded ilium, and wide, flattened ischium," a character which agrees well with *Patriofelis*. The femur appears to be a trifle shorter in proportion to its size, the distal end is more flattened from before backwards, and the rotular groove is not so well marked. There is a small, though distinct, third trochanter, and the head of the bone has a pit for the *ligamentum teres*. Of the tibia we note the same general

¹ A Revision of the North American Creodonta. Proceed. Philad. Acad., 1892, p. 315.

form in the proximal extremity, with the exception of the unusually weak development of the cnemial crest, which is quite as flat as it is in the seals. In its distal extremity the astragalar facet is relatively small, but very little grooved, and not so oblique as in *Patriofelis*. The fibula is large and has the same character as in the Bridger species. The pes is remarkably similar in the details of its construction to that of *Patriofelis*. The astragalus has the same flat tibial facet; there is a large astragalar foramen, and the head is set upon the body of the bone so as to be very oblique. In the calcaneum the tuber is short, the astragalar facet is long and little arched, and the cuboidal facet is very oblique. The cuboid, moreover, shows the same remarkable oblique facet for the articulation with the calcaneum, and it also has a large facet where it joins the astragalus. The metapodials are not completely known, but what knowledge we do have of them, renders it all but certain that there are no important differences between the Wahsatch and Bridger genera. Indeed, the similarity between the limb structure of the two forms is so great that did we not know that there are considerable differences in the teeth we would not hesitate to refer them to one and the same genus.

B.—COMPARISON WITH HYÆNODON.

This genus, as is well known, comes from the Lower Miocene or White River deposits. Although much of the skeleton has been described, very little apparently is known of the hind limb. A comparison of the skull of *Patriofelis* with that of *Hyænodon* shows some important differences, which to my mind render it extremely doubtful whether they should be placed in the same family. The general form of the skull is strikingly like that of the dog, the muzzle is long, narrow and pointed, in marked contrast with that of *Patriofelis*, which is short, broad and truncated. The skull is moderately constricted behind the orbits it is true, but the long interval between the postorbitals and the anterior termination of the cranial cavity is not found; it is about equal in this respect to the dog and the cat. The sagittal crest is not extended in advance of the brain cavity as it is in *Patriofelis*. The lachrymal is extended out upon the face, as was noted by

Scott,¹ a character which is not found in *Oxyæna* at least. The anterior glenoid process is wanting, the mastoid is much reduced, and there is a post glenoid foramen present. The mandibular condyles have comparatively little lateral extension, and the angle of the jaw is produced into a blunt hook-like process, which has a strong inclination inwards. The rami are long, shallow and much curved upon the inferior border; the chin is long and pointed, and the symphysis singularly elongated. These characters stand out in bold relief from those already noted in *Oxyæna* and *Patriofelis*.

In the dentition again there are three incisors in the lower jaw as well as three true molars, whereas both *Patriofelis* and *Oxyæna* have only two. In the fore limb the scapula is unknown, the humerus has the usual Creodont characters, which may also be said to be true of the ulna and radius. The carpus differs from that of *Patriofelis* and *Oxyæna* in the proportions of some of the bones, but in the enlargement of the trapezium it resembles them. In the hind limb the ilium is said by Scott (l. c.) to be feline in appearance and to have the gluteal surface little expanded. He also describes a large contact between fibula and calcaneum. The transverse processes of the atlas are also stated by this author to be imperforate.

These characters, it seems to me, weigh strongly against the conclusion that there is any near relationship between *Hyænodon* and either *Patriofelis* or *Oxyæna*, as is believed by Scott. *Hyænodon*, moreover, is the most modern of all the Creodonts, and if it has been derived from *Oxyæna* it must have been from a species much more primitive than any yet known belonging to that genus. I think it much more probable that *Stypolophus* was the ancestor of *Hyænodon*, since in this form we have all the conditions satisfied, so far at least as we know its osteology. This cannot be satisfactorily determined, however, until we know the Uinta representative of the White River Creodont.

C.—COMPARISON WITH PALÆONICTIS.

There is but one other family with which it is necessary to compare *Patriofelis*, and that is the Palæonictidæ. Unfortunately

¹ Some Little-known Creodonta, Journal Philad. Academy, Vol. I, 1886, p. 177.

we know very little of the osteology of either of the two genera composing this family. They are both short muzzled types, and in one at least (*Palæonictis*) there was a full complement of incisors in the lower jaw. The upper molars do not exhibit the sectorial pattern of either *Oxyæna* or *Patriofelis*, and it is highly probable that they form a distinct family. I have elsewhere¹ called attention to their relationship with the Felidæ.

III.—COMPARISON WITH THE SEALS.

It yet remains to compare the skeleton of *Patriofelis* with that of the modern Pinnipedia. This group, as is well known, is the most distinct and aberrant of all the Carnivora. The large number of trenchant anatomical characters by which they are distinguished from their nearest allies is strong presumptive evidence of the fact that their ancestry is to be traced far back into Tertiary times. It is moreover highly probable that much of the extreme modification by which they are now characterized will not be found to pertain to their ancestors, inasmuch as no Creodont or primitive Carnivore is known whose limb structure would lead one to suppose that it was exclusively aquatic, as the seals now are.

There is, however, much evidence to convince us, as I will presently attempt to show, that this group at least of Oxyænidæ included animals accustomed to seek their food in the water, and were partially adapted to an aquatic life.

The *principal osteological characters* of the Pinnipedia may be briefly summarized as follows:² In the *skull* the face is remarkably short, the interorbital constriction pronounced, and there is a long interval between the anterior termination of the brain and the postorbital processes when they exist. There is no lachrymal bone or canal, and there is a large vacuity in the inner wall of the orbit. The brain-case is broad, and in the least specialized forms is surmounted by a high and prominent sagittal crest, which

¹ Fossil Mammals of the Wahsatch, Bull. Amer. Mus., Vol. IV, 1892, p. 96.

² See Prof. J. A. Allen's 'Monograph of the North American Pinnipeds,' U. S. Geol. Survey, F. V. Hayden, 1880, a most important work; also 'The West Indian Seal,' *Monachus tropicalis*, by the same author. Bull. Amer. Mus., Vol. II, 1887, pp. 1-34.

extends forwards to the postorbitals. There may or may not be an alisphenoid canal or an anterior glenoid process present. The mastoids are conspicuous, and the tympanic bullæ are either conspicuous and inflated or small and rugged. There is no postglenoid foramen. The teeth have an unusually simple pattern. The true molars are never more than two, and the entire molar and premolar series never consist of more than six teeth. The incisors in the lower jaw of both the temporary and milk series never exceed two pairs. The *vertebræ*, in some of them at least, show marked traces of the complex articulations of the pre- and postzygapophyses of the lumbar region, so common in the Creodonts. The *feet* are pinniform, with the digits of the manus decreasing in length and size from the first to the fifth; the true ungual processes of the ungual phalanges are either distinct and terminal or altogether abortive, in which case, they are replaced by subungual processes, which are always large, the first three being pierced by a foramen. The trapezium is as large or larger than the unciforme; the ulna has a powerful and elongated olecranon process; the humerus is shorter than the scapula, and has an enormous deltoid crest which extends nearly the whole length of the shaft; the entepicondylar foramen is either present or absent. The scapula is broad with a well-developed supraspinous fossa, and a short neck and rudimental metacromion process.

In the *pelvis* the ilia are short with the anterior border much everted; the pubes barely meet in a short symphysis which lies behind the acetabulum and is never ankylosed. The cotyloid notch is much reduced or altogether absent, and there is no pit for the *ligamentum teres*.

The *femur* is remarkably short, much compressed from before backwards, the digital fossa is small or absent, and there is no third trochanter. The fibula, which is large, is coössified with the tibia; the cnemial crest is weak or absent, and the tibia has a very decided twist. The tibia-astragalar facet is plane, without the tongue and groove of the Fissipedia; in some of them at least (*Zalophus*) there is a vestigial astragalar foramen present. The tuber of the calcaneum is short; there is large contact between the astragalus and cuboid, and the calcaneo-cuboidal facet is

very oblique, as in *Patriofelis* and *Oxyæna*. To this should be added the large size of the external calcaneal tubercle. In the pes the first and fifth digits are the largest, with the three middle ones shorter and subequal. Of the ungual phalanges the subungual processes are well developed and perforated by the subungual foramen.

The Pinnipedia are divided into three families, of which the Otariidæ are in many respects the most primitive. This is seen more especially in the characters of the hind limbs, which can support the body in the ordinary way, and can be used to a considerable extent for progression upon the land, whereas in the more typical seals (Phocidæ) this is not the case. Other characters which cause them to be regarded as the most primitive members of the group are seen in the presence of postorbital processes, the high sagittal crest, an alisphenoid canal, an anterior glenoid process, small and rugged tympanic bullæ, a prominent mastoid process, a rudimental cotyloid notch of the acetabulum, presence of trochanter minor of the femur, and a more normal astragalus, which frequently shows distinct traces of the astragalar foramen. They are more specialized than the Phocidæ in the following characters: absence of entepicondylar foramen of humerus, rudimental condition of the true ungual processes in all the digits of the manus, absence of digital fossa of femur, which however is not found in all the Phocidæ, and lack of complication of the lumbar zygapophyses.

From a careful survey of the foregoing osteological characters of the Pinnipedia, in connection with what we already know of the development of the Carnivora from the Creodonta, I think that the following propositions may be fairly deduced: (1) *They are descended from ancestors in which the tibia-astragalar facet was not grooved*, for the reason that there is no Carnivore known in which the groove has ever been obliterated when once formed.¹ The ungrooved astragalus is characteristic of all the Creodonta, with the exception of one family, Mesonychidæ. (2) *They are descended from a short muzzled type in which there was great reduction of the true molars, and comparatively little reduction of the*

¹ Even in such an exclusively aquatic form as the sea otter the astragalar groove is very distinct, notwithstanding the fact that the digits of the pes are highly modified.

premolars, for the reason that there are never more than two true molars and very frequently one.¹ (3) *They are descended from a type in which the incisors of the lower jaw were reduced to two pairs.* This proposition I regard as established from the fact that none of them possess more than the two pairs in the lower jaw in the adult dentition, and according to Allen,² there are only two pairs of incisors in the lower jaw in the milk dentition of the Otariidæ, which seems to point to the fact that they were lost at an extremely early period. (4) Their ancestors possessed in addition the following important characters: Skull with interorbital region constricted and long between postorbitals and the anterior termination of the brain-case; an alisphenoid canal; an anterior or preglenoid process; a prominent mastoid; a metacromion process of the scapula; an entepicondylar foramen of the humerus and a prominent deltoid crest; a long and powerful olecranon; an enlarged trapezium; a free scaphoid, lunar and centrale; a short unanchylosed pubic symphysis; a femur with a digital fossa; an unreduced fibula; an astragalar foramen; a cuboid with a very oblique facet for the calcaneum and a large contact with the astragalus; a calcaneum with a relatively short tuber and ungual phalanges, with well-developed and large, perforated subungual processes. (5) Their ancestors were, judging from these characters, not exclusively, but semi-aquatic in habits, with limbs fitted for progression upon the land.

If now we examine the skeleton of *Patriofelis* in connection with these probable ancestral characters of the seals, we find that there are some striking features of likeness between the two groups. These characters, moreover, are found in such widely different parts of the skeleton, that I think they can hardly be due to convergence or parallelism.

Features common to Patriofelis and the Seals.—In the skull we note the *short muzzle* and long much-constricted region between the postorbitals and the anterior termination of the brain-case; there is an alisphenoid canal present, as well as a well-developed preglenoid process; the mastoids are prominent in both, and there is no postglenoid foramen. There are but two pairs of

¹ See Huxley's 'Anatomy of Vertebrate Animals,' p. 363.

² Loc. cit., p. 3.

incisors in the lower jaw, and the molar dentition is much reduced. In the fore limb the humerus is shorter than the scapula, and provided with a great deltoid crest and an entepicondylar foramen. The scapula is large, with short neck and metacromion process. The ulna has the same powerful olecranon, which, together with the prominent deltoid crest, however, appears to be very common among the Creodonts. The trapezium is enlarged; the feet are broad and spreading, and in the ungual phalanges, the subungual processes are largely developed.

In the vertebral column, as already noted, some of the seals (notably *Phoca vitulina*) show marked traces of the complex articulation of the lumbar zygapophyses. The pubic symphysis of *Patriofelis* is short, lies behind the acetabulum, and is not ankylosed. The fibula is large and un-reduced in both groups; the trochlea of the astragalus is not grooved; the tuber of the calcaneum is short, and the cuboid has a very oblique calcaneal facet and a large contact with the astragalus. The foot is broad and spreading, and the ungual phalanges have perforated subungual processes.

PROBABLE HABITS OF PATRIOFELIS.

From the structure of the limbs more than any other feature in the osteology of *Patriofelis*, I am led to conclude that it was aquatic or semi-aquatic in habits. The broad, flat, plantigrade feet, with their spreading toes, suggest at the first glance their use for swimming. The eversion of the feet, together with the general clumsiness of the limbs, point, moreover, to the fact that the animal was not an active runner. Now, if the animal was aquatic, what was the nature of its food? It certainly could not have been fish, for the reason that the remains of fishes are very scarce in the Bridger sediments. If, however, we can form any judgment from their remains, I think that it can be safely stated that the Bridger Lake *literally swarmed with turtles*, and if *Patriofelis* frequented the water, it is highly probable that they formed a staple article of its diet. This supposition accords well with the great strength and power of the jaws, together with the robust and much-worn condition of the teeth. There is another fact which may be mentioned in this connection, which has a direct

bearing upon this conclusion, and that is the existence of coprolites in the Bridger sediments containing fragments of turtle shells. This, while it is not at all conclusive, yet demonstrates that there was an animal living on the borders of the ancient lake, that was accustomed to capture turtles for food, and from what has already been stated, I think that animal was *Patriofelis*. He was, perhaps, not as expert a swimmer as the seals now are, but was sufficiently active in the water to capture turtles. When the lake disappeared, it can be conjectured that *Patriofelis* took to the open sea, and finally came to feed upon fish exclusively. It is further conceivable that in their new habitat their swimming power was gradually increased, and, owing to the soft nature of their food, the great strength and power of the jaws were gradually lost, and the teeth became gradually modified into the simple degenerate organs which constitute the dental equipment of the modern Pinnipedia.

IV.—CLASSIFICATION AND SPECIES OF PATRIOFELIS.

It will be seen from what has already been stated that *Patriofelis* is a member of the Creodonta. Various efforts have been made from time to time to give an exact definition of this group, but these definitions have as yet proven very unsatisfactory. That the Creodonta stand in general antecedent relationship to the Carnivora is now abundantly demonstrated, but whether the Carnivora arose from one or several stems of the Creodonta, is still an open question. It is held by Cope and Scott that all the Fissipedia are descended from the Miacidæ of the Creodonta. I have expressed a contrary opinion, with Schlosser, in regard to the cats.

One of the chief osteological distinctions between the Creodonta and the Carnivora consists in the union of the scaphoid, lunar and centrale in the carpus of the Carnivora, whereas they are free in the Creodonta. There are, moreover, such characters as the fissured ungual phalanges, the complex articulations of the lumbar vertebræ, the relative size and degree of convolution of

the cerebral hemispheres, and a number of other characters of less importance which serve to distinguish these groups from each other. It must be borne in mind, however, in considering these differences, that if the Carnivora have been derived from the Creodonta, the distinctions between them must have been exceedingly slight at the point where they actually meet, and that any definition which can be given will, according to the very nature of the case, fail. There is considerable evidence to show that wherever the Creodonta continued beyond the Lower Miocene they took on certain characters which now so sharply distinguish the Carnivora. In the Miocene genus *Hyænodon*, the cerebral hemispheres were almost, if not quite, as well convoluted as their carnivorous cotemporaries, and in the European species of the same genus, according to Scott, the scaphoid, lunar and centrale were united as well. In a like manner many of the Miocene Carnivora show marked traces of their Creodont ancestry. This is especially seen in the flat astragalus and the remains of the suture uniting the scaphoid and the lunar, as well as the simpler type and less convoluted cerebral hemispheres. It would appear, therefore, that these groups, being incapable of exact definition, have lost much of their original significance, and are now to be regarded as mere matters of convenience in classification. The same may be said of the Insectivora with relation to the Creodonta.

The systematic position of *Patriofelis* within the Creodonta is not difficult to discover. Its general skeletal structure is so much like that of *Oxyæna* that, notwithstanding the differences in the teeth, they must be placed in the same family. *Oxyæna* is the older form, and has the more primitive dentition, but the differences are not greater than we would be led to anticipate in the ancestral genus. I think that it can be accepted as demonstrated that *Patriofelis* is the direct descendant of *Oxyæna*, which may have likewise given off a branch which terminated in the modern seals. It is somewhat doubtful whether this branch leads through *Patriofelis*.

Regarding the relationship of *Patriofelis* to *Hyænodon* I have spoken on a former page. I do not think that they can be consistently associated in the same family.

The family definition may now be stated as follows :

Oxyenidæ.—Muzzle short and truncate ; interorbital region constricted and elongated ; sagittal crest extended well in advance of the brain-case. A pre-glenoid process and no postglenoid foramen ; an alisphenoid canal and prominent mastoid. Lachrymal bone not extended out upon the face. Two pairs of lower incisors. Trapezium enlarged ; pubic symphysis not ankylosed ; fibula unreduced ; calcaneo-cuboidal facet very oblique ; cuboid having large contact with astragalus. Fibula not articulating with calcaneum.

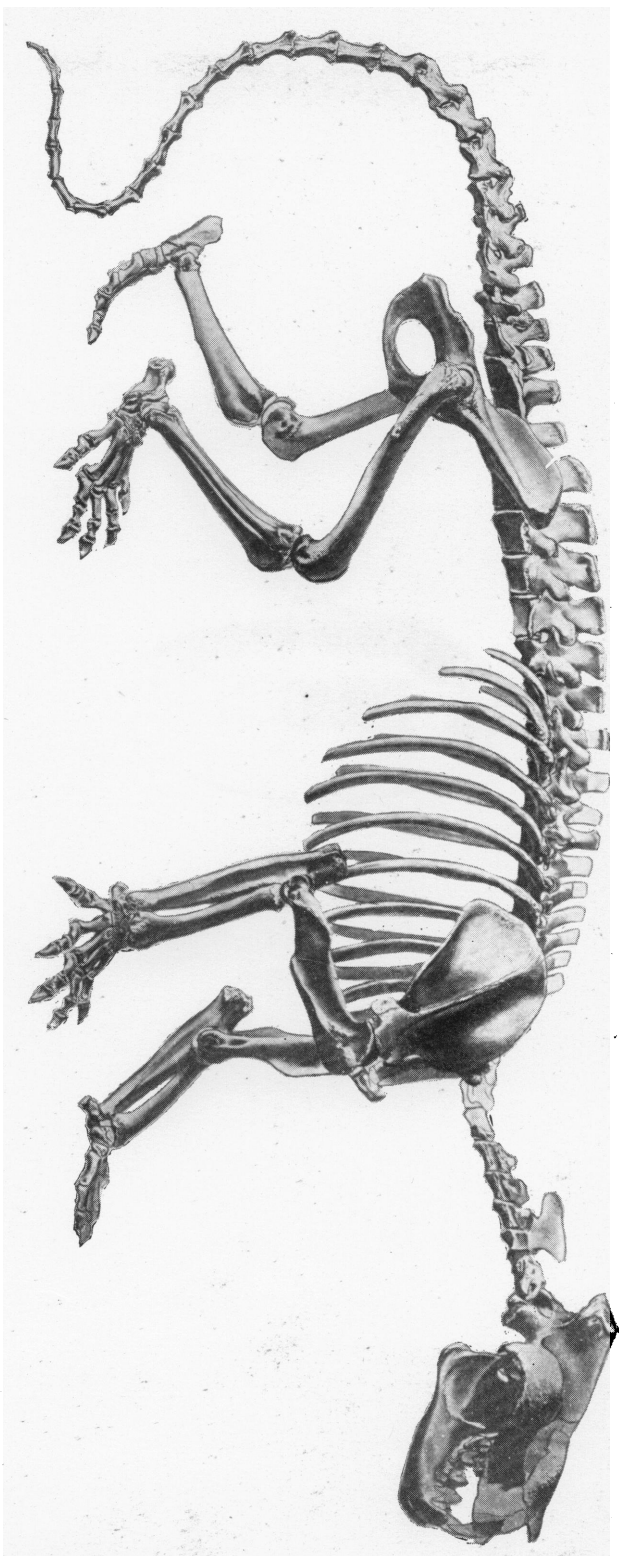
Oxyæna Cope.—Premolars in the lower jaw 4, molars 2. Last superior molar transverse.

Patriofelis Leidy.—Premolars in lower jaw 3 ; molars 2, Last superior molar longitudinal.

The species are not numerous, and it is indeed questionable whether more than three should be referred to *Patriofelis*. Leidy's type species *P. ulta* is easily distinguished by its small size ; it is scarcely more than half as large as *P. ferox*. I have chosen to regard Cope's species *P. tigrinus* as distinct chiefly on account of its having come from an older formation, although there is no character observable in the fragmentary specimen of *P. tigrinus* to warrant such a belief. When we have better specimens of it, however, it will doubtless show a nearer relationship to *Oxyæna* than to the Bridger species. There is yet another species which was described by the writer¹ under the name of *Patriofelis leidyæ*.² It was stated at the time that its reference to the genus *Patriofelis* is doubtful. I am now convinced that it does not belong here, but is probably a forerunner of the Miocene *Nimravidæ*. Until more of it is known it is impossible to give to it a generic definition, and I therefore refrain from proposing a new name.

¹ Fossil Mammals of the Wahsatch, Bull. Amer. Mus., Vol. IV, 1891, p. 98.

² This species, together with the figure of it, is erroneously attributed by Zittell, in his 'Handbook of Palæontology,' to Osborn.



RESTORATION OF PATRIOFELIS FEROX.
 $\frac{1}{2}$ Natural Size.

