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A SKULL OF THE BRIDGER MIDDLE EOCENE CREODONT, PATRIOFELIS ULTA LEIDY

(With 4 Plates)

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INTRODUCTION

Discovery of a remarkably well preserved skull and lower jaws of the Bridgerian creodont carnivore *Patriofelis* was made by Golden York for the University of Utah. Not only is this by far the most nearly complete known for *Patriofelis,* but almost certainly belongs to the heretofore very poorly represented genotypic species, *P. ulta.* The specimen was found in 1953 while prospecting [1] Bridger exposures about 20-25 miles east of Kemmerer, Wyo., north of Granger and not far from the Green River. Mr. York's description of the location would place it in or near T. 22 N., R. 111 W. The exact horizon is not certain but the specimen is reported to have come from near the top of the section as exposed locally in the hill or bench. The exposures in this general area are of the Bridger formation as shown on the 1955 edition of the Geologic Map of Wyoming. Moreover, there seems no doubt but that only the lower part of the Bridger is represented in this portion of the basin.

I am greatly indebted to Dr. William Lee Stokes, head of the department of geology at the University of Utah, for giving me the opportunity of examining and describing this unusual specimen. Dr. Joseph T. Gregory at Yale University, Dr. Glenn L. Jepsen at Princeton University, and Dr. George G. Simpson at the American Museum of Natural History aided significantly in permitting examination and study of type and related materials in collections under their care. The specimen was skillfully prepared, removing it from the much-

[1] Mr. York's fieldwork was supported by a grant from the Research Fund of the University of Utah.

indurated nodule in which it was found, by Franklin L. Pearce. The wash drawings accompanying this paper were made by William D. Crockett.

PREVIOUS STUDIES

Matthew has briefly outlined the history of investigation relative to *Patriofelis* up to 1909. A recapitulation, however, with additional details, and comments on more recent studies, may not be unwarranted.

Patriofelis was first described by Leidy in 1870 from a pair of lower jaws (U.S.N.M. No. 105) collected by Hayden in 1869 near Fort Bridger. A major portion of both rami are represented, including alveoli for all the cheek teeth, but portions of the crowns of P_4-M_2 are preserved only on the left side. Leidy did not so indicate, but it is evident from his illustrations of the right ramus published in 1873 (pl. 2, fig. 10) that the tooth portions shown were drawn in reverse from the opposite side. Leidy first regarded his new form, *Patriofelis ulta,* as probably belonging to the cat family, but in 1873 regarded it as "perhaps intermediate to the feline and canine animals."

In the meantime (1872) Marsh described the new genus, *Limnofelis,* with two new species, *L. ferox* and *L. latidens,* based essentially on a lower jaw portion with M_2 (Y.P.M. No. 11865) from Henry's Fork and a last upper premolar (Y.P.M. No. 10904) from the Grizzly Buttes respectively. Later in the same year, with additional material at hand, he proposed the new generic name *Oreocyon* for *Limnofelis latidens.* Marsh did not discuss the possible relationships of these animals, other than to compare their size with that of a lion and to state that the lower canine and premolars of *O. latidens* "somewhat resemble those in the Hyaena." He later concluded, however, that *Limnofelis* was apparently related to the cats, but nowhere did he discuss the possible relationship to Leidy's *Patriofelis* from the same beds.

Although rather generally ignoring Marsh's names, Cope worked out a rather orderly arrangement of the creodonts and in 1880 (figured in 1884a) described as new the form *Protopsalis tigrinus* on the basis of two lower molars (A.M.N.H. No. 4805), a canine and certain bone elements from the lower Eocene Wind River beds. He included this genus tentatively, as he had earlier allocated *Patriofelis,* in his family Oxyaenidae, which he regarded (1884a) as ancestral to the Felidae. The same year (1884b), however, he abandoned this idea in favor of the Miacidae as the ancestral group.

In 1892, Wortman, in a part of a joint paper with Osborn on the

Wasatch and Wind River fauna, discussed and refigured the type of *Patriofelis ulta* and named as new the species ?*Patriofelis leidyanus,* based on a jaw portion in the Princeton collections (No. 11375) including, as was later shown, only deciduous teeth. Although uncertain as to the generic reference for his new species, he believed that it indicated for *Patriofelis,* along with *Palaeonictis,* an ancestral position with respect to the true felids. Scott in his revision of the creodonts in 1892 also included *Patriofelis* in the Palaeonictidae, but placed *Protopsalis* along with *Oxyaena* in the Hyaenodontidae! He recognized, however, that *Oreocyon* Marsh, and hence that part of *Limnofelis* which had been named *L. latidens,* was a synonym of *Patriofelis,* but tentatively placed *Limnofelis* in synonymy with *Protopsalis.* Nevertheless, he followed Cope's later thinking in deriving the Felidae as well as other modern Carnivora from the Miacidae.

Wortman's most significant contribution to the study of *Patriofelis* appeared in 1894 and included a detailed description of the mounted skeleton and other newly acquired materials in the American Museum. He placed both *Limnofelis* and *Protopsalis* in synonymy with *Patriofelis,* concluded that only two species were represented, the large *P. ferox* and smaller *P. ulta,* and transferred the group to the Oxyaenidae. No reference was made to Marsh's *Oreocyon latidens;* presumably he regarded this as something different. Furthermore, the species that he had earlier named ?*Patriofelis leidyanus* was believed not to represent *Patriofelis,* but a form which might be the forerunner of the Nimravidae. Adams, in 1896, following Wortman's suggestion, gave ?*P. leidyanus* the new generic name *Aelurotherium,* and because of it regarded the Felidae as polyphyletic. Wortman, in 1899, placed this genus in the *Palaeonictidae,* separate from the Oxyaenidae, and in 1901 placed his species *A. leidyanum* in synonymy with Marsh's *Limnofelis latidens* as *Aelurotherium latidens.* This procedure, however, was in error as the immature lower jaw of *Limnofelis latidens,* with which comparison was made and which he figured as a type, was not the type but a referred specimen, and hence could not carry the name. The actual type of *Limnofelis latidens,* and hence of *Oreocyon latidens,* was a P^4 which Wortman in a later part of the same paper referred to *Patriofelis ferox,* clearly listing *Limnofelis latidens* as a synonym of *Patriofelis ferox.* Also in 1901 he described the new species *Aelurotherium bicuspis* on the basis of a lower cheek tooth, which he regarded as M_1 (Y.P.M. No. 11755). Although now recognizing that the known lower premolars of *Aelurotherium* were deciduous, he defended his 1892 conclusions as to the ancestral position of *Aelurotherium* with respect to the Oligocene

felids, resting them rather largely on his interpretation of M_1 as essentially the carnassial tooth of the lower series.

Osborn (1907, fig. 95, E) reillustrated the teeth in the type of *A. leidyanum* indicating that all were deciduous and belonged to *Patriofelis,* but Matthew, in 1909, demonstrated the synonymous position of *Aelurotherium,* as well as *Limnofelis, Oreocyon,* and *Protopsalis,* with *Patriofelis,* correctly identifying the various teeth in the types. As to whether all the species that he placed in synonymy with *P. ferox,* however, represent that species and none *P. ulta,* may be doubted.

In addition to describing the skeleton of *Patriofelis ferox,* Wortman, in his 1894 paper, pointed out a number of characters that he believed indicated that *Patriofelis* or a closely related form gave rise to the pinnipeds. This suggestion was criticized by Osborn in 1900, and in 1902 Wortman defended his conclusion, taking a strong stand against Osborn's views, but was again refuted, this time by Matthew in 1909. Kellogg, in 1922, discussed at length such evidence as had been presented on the origin of the pinnipeds, but deduced that a case for the Oxyaenidae had not been demonstrated, nor had Matthew's suggestion of an arctoid fissiped ancestry solved the problem.

Matthew's (1909) monographic study of the Bridger carnivores and insectivores included a review and restudy of the known material of *Patriofelis,* as well as a taxonomic revision. The four species that he recognized are indicated as representing four distinct stratigraphic units and include as the oldest *Patriofelis tigrinus* (Cope) from the Wind River beds; a species from the Huerfano B beds originally referred by Osborn (1897) to *P. ulta,* but named *Patriofelis coloradensis* by Matthew; the genotypic species *Patriofelis ulta* Leidy from Bridger B; and Marsh's *Patriofelis ferox* from the upper Bridger levels. In 1915 he decided that *P. coloradensis* represented *Ambloctonus* rather than *Patriofelis.*

Later discussions of *Patriofelis* included a review by Thorpe (1923) in which an attempt was made to revive *Patriofelis latidens.* Thorpe recognized the error in Wortman's taxonomic procedure in arriving at the name *Aelurotherium latidens,* but seems to have committed a similar error in regarding the lower jaws, Y.P.M. No. 10940, as the type of *Oreocyon latidens,* whereas the holotype of *Limnofelis latidens* is No. 10904, a last upper premolar. Although Marsh's characterization of the genus *Oreocyon* was based on referred materials, the type species was clearly that which he originally described as *Limnofelis latidens* and hence cannot have a different type specimen.

In his revision of the "Pseudocreodi," Denison (1938) revived

Protopsalis for the Wind River form *P. tigrinus* Cope because he felt that the carnassial construction exhibited had not attained the *Patriofelis* stage, and restored Huerfano B *Ambloctonus coloradensis* to *Patriofelis,* largely on the basis of characters of the lower jaw proper. A new species, *Patriofelis compressa,* was described, characterized by slender premolars, on a lower jaw (A.M.N.H. No. 17017) also from the Huerfano B stage in Colorado.

P. M. Butler (1946) in a discussion of the evolution of carnassial dentitions in certain creodont subfamilies indicated the changes that took place in the development of the Oxyaeninae, culminating in *Patriofelis.* In his treatment of the various subfamilies he gave no preferred arrangement of these into families, but did discuss the general characteristics of the superfamilies or tribes as named by Matthew.

TAXONOMIC SUMMARY

The taxonomic arrangement adopted here is essentially that of Matthew, modified by Denison, but with minor differences and a corrected synonymy as far as known material can be interpreted. Although species are not redescribed, annotations are included where pertinent and a key is added.

OXYAENIDAE Cope, 1877

OXYAENINAE Trouessart, 1885

PATRIOFELIS Leidy, 1870

Synonyms.—Limnofelis Marsh, 1872.
Oreocyon Marsh, 1872.
Protopsalis Cope, 1880.
Aelurotherium Adams, 1896.

Type.—Patriofelis ulta Leidy, 1870.

Discussion.—The number of incisors above and below for the middle Eocene or Bridger members of this genus is two in the material at hand, although Matthew has indicated (1909) that the number is three in the lower jaw, based partly on the appearance of alveoli in A.M. No. 12078. If Matthew has correctly interpreted No. 12078, the number of lower incisors in *Patriofelis* is variable as in *Oxyaena.* Moreover, *Patriofelis* has been characterized as lacking the second upper molar. Its presence, however, is variable, as a vestigial M^2 may occur, possibly characterizing lower Bridger *P. ulta* (and Huerfano species ?).

PATRIOFELIS ULTA Leidy, 1870

Synonyms.—Limnofelis latidens Marsh, 1872; *Oreocyon latidens* (Marsh), 1872.

Type.—Lower jaws with P_4-M_2 (incomplete) in left ramus (U.S.N.M. No. 105).

Referred material.—The upper premolar (P^4 according to Marsh, Wortman, and Thorpe, but P^3 according to Matthew) upon which Marsh based the species *Limnofelis latidens* is decidedly smaller than either P^3 or P^4 in A.M. No. 13145—the skull material described by Matthew as *Patriofelis ferox.* Its length is about intermediate between that of P^3 and P^4 in the skull of *P. ulta* described in this paper. Moreover, this premolar is reported to be from the Grizzly Buttes and hence lower Bridger, the horizon which seems characterized by *P. ulta.* Hence, *Limnofelis latidens* and *Oreocyon latidens* are more likely synonyms of *Patriofelis ulta* rather than, as Wortman (1902) and Matthew (1909) indicate, of *P. ferox.*

Besides the University of Utah skull and jaws (No. B50) belonging to *Patriofelis ulta,* there is in the U. S. National Museum (No. 21365) a right mandibular ramus of this species, with P_2-P_4 partially erupted, Dp_4 loose, and M_1 and M_2 but little worn. The lower molars are only slightly smaller than in the type, but the horizon represented is believed to be very low in Bridger C, immediately above the Green River shale just to the northeast of Twin Buttes.

PATRIOFELIS FEROX (Marsh), 1872

Synonyms.—Patriofelis leidyanus Wortman, 1892; *Aelurotherium leidyanum* (Wortman), see Adams 1896.
Aelurotherium latidens Wortman (not Marsh), 1901.
Aelurotherium bicuspis Wortman, 1901.
Patriofelis latidens Thorpe (not Marsh), 1923.

Type.—Fragment of left ramus of mandible with M_2 (Y.P.M. No. 11865).

Referred material.—Included among the materials referred to *Patriofelis ferox* are the type specimens of the above species placed in synonymy. These are the immature lower jaw with Dp_2-Dp_4 (P.U. No. 11375) of *P. leidyanus;* the lower jaw with a canine, Dp_3, Dp_4, and M (Y.P.M. No. 11756), which was "another specimen" in Marsh's description of *Limnofelis latidens,* but which Wortman indicated as a type for *Aelurotherium latidens;* the lower cheek tooth regarded by Matthew Dp_4 (Y.P.M. No. 11755) of *Aelurotherium bicuspis;* and the symphysial portion of a pair of lower jaws with

C–P_4 (Y.P.M. No. 10940) which was among the "additional remains" Marsh had when he proposed *Oreocyon* for *L. latidens,* and which Thorpe regarded as the type of *O. latidens* when he attempted to preserve the species name *Patriofelis latidens.*

Additional materials of *Patriofelis ferox,* including the mounted skeleton composed of A.M. Nos. 1507 and 1508 in the American Museum, are listed by Matthew (1909, p. 420). In the National Museum, besides the unused portions of A.M. No. 1508 (U.S.N.M. No. 5916) received in an early exchange, there are several parts of a comparatively large skull (U.S.N.M. No. 21364) obtained in the upper Bridger, probably C, to the north of the saddle between Sage Creek Mountain and Cedar Mountain, and the right ramus of a lower jaw, mentioned by Denison (p. 173) as exhibiting Dp_2–Dp_4 with M_1 erupting (U.S.N.M. No. 13318), from the upper part of Bridger C between Sage Creek and Hickey Mountain. M_1 in the latter specimens is not completely exposed, but its size is clearly much greater than in *P. ulta.*

PATRIOFELIS (PROTOPSALIS) TIGRINUS (Cope), 1880

Type.—Two lower molars, a lower canine, and certain bone elements (A.M.N.H. No. 4805).

Discussion.—The type of this species is reported by Matthew (1915) to be from the Lost Cabin beds of the Wind River series. No additional specimens are known. I have retained *Protopsalis* as a subgenus rather than completely suppressing it in *Patriofelis* as Matthew did in 1909, and in preference to recognizing full generic rank as Denison did in 1938. *Protopsalis* appears to be structurally intermediate between *Oxyaena* and typical *Patriofelis,* but possibly a little closer to *Patriofelis,* although there is greater difference between it and *Patriofelis* than between the middle Eocene species of *Patriofelis.* This can perhaps be best represented by regarding it as a distinct subgenus. Nevertheless, *P.* (*Protopsalis*) *tigrinus* is a rather gigantic form and surely is not the species which gave rise to the comparatively small lower Bridgerian forms of *Patriofelis.*

?PATRIOFELIS COLORADENSIS Matthew, 1909

Type.—Left ramus of mandible with C–P_4 and M_2 (A.M. No. 2691).

Discussion.—I suspect, as did Denison (1938), that this species belongs to *Patriofelis* rather than *Ambloctonus* where Matthew placed it in 1915. In addition to characters cited by Denison, I note that

Osborn's (1900, fig. 8) illustration of the jaw shows the interval for missing M_1 smaller than would seem possible for this tooth in *Ambloctonus*. Moreover, *Ambloctonus* is not otherwise known from beds as late as Huerfano B or lower Bridger.

PATRIOFELIS COMPRESSA Denison, 1938

Type.—Left ramus of mandible with C–M_2 (A.M. No. 17017).

Discussion.—Slightly larger, though close to ?*P. coloradensis* in size, this form is apparently distinguished by relatively slender premolars. No information is available on the extent to which this character is variable in *Patriofelis*. It comes, moreover, from the same beds as ?*P. coloradensis*.

KEY TO SPECIES OF PATRIOFELIS

M_2 with small talonid
  Very large ..... *P. (Protopsalis) tigrinus*
M_2 without talonid
  Large (P_2-M_2, 78-84 mm.)*..... *P. ferox*
  Intermediate size (P_2-M_2, 75.5-76.0 mm.)*
    Vestigial M_2 ..... *P. ulta*
  Small
    Lower premolars robust (P_2-M_2, 60 mm.)*....?*P. coloradensis*
    Lower premolars slender (P_2-M_2, 65 mm.)*.....*P. compressa*

* Measurements according to Denison, except second specimen of *P. ulta*.

DESCRIPTION OF THE SKULL AND JAWS OF PATRIOFELIS ULTA

Attention was called by Scott (1913) to the resemblance in relative body proportions of *Patriofelis* to an otter. The short, broad, and low snout of the skull is perhaps even more otterlike than he had realized. The general appearance of the skull was not hitherto known, as that of *Patriofelis ferox* which Wortman (1892) described (A.M. No. 1507) was considerably restored and the portions of the top of the skull were evidently placed too high, so that the rostrum has the appearance of much greater depth than in the University of Utah specimen. The latter shows a small amount of crushing dorsoventrally below the frontal region, but it is so nearly complete that the extent of deformation is evident and would in no way account for the depth indicated in the larger animal.

Dorsal aspect.—In dorsal view (pl. 1) the remarkable shortness and breadth of the rostral portion of the skull is clearly evident. The nasals are broad forward but taper posteriorly to near the frontomaxillary sutures on either side where they abruptly widen and then

taper to a point between the frontals, producing a pattern resembling an arrowhead pointing posteriorward. The frontals are decidedly broad forward but taper posteriorly toward the parietals. Between the postorbital processes the frontal area or plateau is slightly concave, a condition that I do not attribute to the compression which has taken place between this surface and the posterior part of the palate. At the position of the postorbital processes the frontals are bluntly inflated, and moderately prominent temporal ridges extend posteriorly to their union forming the sagittal crest at about the juncture of the frontal and coronal sutures. The parietals are elongate and slender, and support a moderately well developed sagittal crest that slopes downward and backward, although increasing in depth toward the supraoccipital. The supraoccipital is missing from the *P. ulta* skull, but from other material of the genus it is known to extend far backward and a little upward, forming a remarkably developed inion. The greatest constriction of the slender braincase is across the parietals between the temporal part of the frontals and the anterior margin of the squamosals where these pairs approach each other closest. Posterior to the constriction the superior and lateral surface of the cranium formed by the squamosal sweeps widely out onto the broad and massive zygomatic processes. At the deepest part of the temporal fossa, a very large vascular foramen penetrates the parietals on each side of the sagittal crest. This is accompanied by a smaller foramen posterolateral to it on each side close to the squamosal but also within the parietal.

Lateral aspect.—In lateral view (pl. 2) the premaxilla is seen to rise as a narrow rim of bone along the anterior margin of the maxilla and form the lateral rim of the broad but possibly somewhat depressed anterior narial aperature. The premaxilla is rapidly pinched out posteriorward between the nasal and maxilla. The maxilla as exposed laterally is anteroposteriorly short, although the nasal process extends posteriorly above the lachrymal as it rises onto the dorsal surface, and the malar process extends prominently backward beneath the malar or jugal. The large infraorbital foramen penetrates the maxilla above the anterior root of P^3, well forward of the orbital rim and about midway dorsoventrally. The lachrymal bone is prominently displayed on the dorsolateral surface of the rostrum anterior to the orbital rim and forms the anterior margin of the orbit. Extending downward to the anterior extremity of the jugal and separated from it by a marked notch, it almost or quite excludes the maxilla from participation in the formation of the rim. The lachrymal foramen is concealed just within the orbital fossa posterior to a small process on

the lachrymal bone formed by the above notch. The jugal is comparatively deep and strong, articulates in a much-extended contact with the maxilla below and inward, and shows almost no evidence of a postorbital process. Posteriorly, the squamosal portion of the zygoma is particularly deep and sturdy. The transversely elongate postglenoid process extends strongly downward and forward, forming with a prominent process on the outer part of the anterior margin of the glenoid fossa a combination which almost locks the condyle of the lower jaw in place. Unfortunately the mastoid and exoccipital portions of the skull are incomplete; however, sufficient remains to note that the posterior profile of the occiput is nearly vertical beneath the inion.

The orbits of *Patriofelis ulta* are not large but are decidedly dorsal in their position on the face. This is effected by the flattened to concave frontal area between them and by the deep zygomae below. Not only are the orbits high but the plane of the orbital rim faces decidedly upward because of the outward sweep of the jugal. The anterior margin of the orbit is well forward, about over the middle or anterior portion of P^4.

It is only in the orbital fossa that there is any evidence of dorsoventral compression of the skull; nevertheless, the noticeable fracturing and distortion are not so severe that details of the foramina penetrating bone in this area cannot be determined, although certain of the sutures are obscured. The large posterior opening of the infraorbital canal is just below and slightly median to the lachrymal foramen, at the anterior apex of the orbital plate of the maxilla. Posterior to the infraorbital opening, a little over 2 centimeters, and about on the same level, there is a large, anteroposteriorly elongate sphenopalatine foramen, and immediately below the latter is a much smaller, though prominent, posterior palatine foramen.

In the posterior portion of the orbital fossa, a separate optic foramen seems indicated by an opening about $1\frac{1}{2}$ centimeters anterior and dorsal to the sphenoidal fissure. The large sphenoidal fissure, directly below the most constricted portion of the cranium, evidently transmitted not only the third, fourth, first branch of the fifth, and sixth cranial nerves as customary, but also the second branch of the fifth or trigeminal, inasmuch as the foramen rotundum does not appear to have become separated from the sphenoidal fissure (Wortman believed them separate), at least not externally, in this group of animals. Moreover, the sphenoidal fissure must also have transmitted the external carotid artery, as the anterior opening of the alisphenoid canal, which, when present as in modern bears and dogs, opens into the

foramen rotundum, was evidently confluent anteriorly with the sphenoidal fissure. The posterior opening of the alisphenoid canal is surely represented by the clearly defined foramen immediately anterior to the foramen ovale (agreeing here with Wortman's interpretation).

Ventral aspect.—In the over-all appearance of the skull in ventral view (pl. 3), one notes the short, broad palate, elongate mesopterygoid and basicranial portion, and widely swinging, massive zygomae. The palate in greater detail shows the premaxillae not much extended forward of the canines and nearly straight across the front of the incisors. The anterior palatine foramina are close to the incisors and median to the canines. They appear nearly circular when viewed from somewhat forward of the palate. The posterior palatine foramina are on the forward portion of the suture between the maxillae and palatines, medial to the fourth premolars. The posterior nares are covered beneath by the palate to a point farther back than the posterior border of the orbital plate of the maxilla on either side, about medial to the posterior margin of the carnassials. The mesopterygoid fossa is extremely elongate anteroposteriorly and the forward portion is partially constricted below by inwardly directed lower margin of the ascending plate of the palatines. Posteriorly the fossa is more open as the pterygoids along their lower margins diverge toward the hamular processes. The posterior margin of the pterygoids, above the hamular process, sweeps abruptly upward and posterolaterally just inward of the foramen ovale, apparently extending almost to the notch representing the foramen lacerum medius. Particularly noteworthy is the union of the pterygoids across the roof of the mesopterygoid fossa, concealing the presphenoid and the anterior portion of the inferior surface of the basisphenoid. Anterior to this the evidence is not so clear, but there seems no doubt but that the palatines are also united through a median suture completely removing the presphenoid from participation in the mesopterygoid fossa, not, however, the vomer, the median ridge of which can be seen emerging from the nasal cavity.

In the basicranial area only the basisphenoid, basioccipital, and periotics are preserved posteromedial to the squamosals and alisphenoids. The basioccipital is broad as well as elongate, evidently occupying a relatively large area of the basicranial region. The basilar tubercles for the *recti capitis* muscles on the forward portion of this bone are elongate and well developed, reaching their greatest prominence forward at the suture between the basioccipital and basisphenoid. Posterolaterally, the basioccipital is perforated by a broad and flattened condylar or hypoglossal foramen which joins a prominent

vascular canal before entering the foramen magnum. Medial to the hypoglossal foramen and extending ahead to the lateral margin of the basioccipital, a broad and distinct anterolaterally directed groove, evidently occupied by the internal carotid, as suggested by both Wortman and Matthew, rises into the large aperture representing the foramen lacerum medius just ahead of the medial portion of the petrosal. The exposed surface of the basisphenoid is triangular in shape with the anterolateral sides bound in part by the alisphenoids and forward by the V-shaped margin of the pterygoids. About midway forward on the anterolateral margin on each side, at the anterior extremity of a shallow groove from the foramen lacerum medius, there is a foramen which extends forward above the pterygoid, evidently the pterygoid canal for the *Vidian* nerve. Parallel and lateral to this on the surface of the alisphenoid are two or three sharp grooves or striae, extending between the posterior margin or lip of the foramen ovale to the position on the margin of the aperture corresponding to the eustachian foramen. Still more lateral and nearly parallel to the foregoing, but on the squamosal, is the straight and deeply impressed fissura Glaseri, for the chorda tympani nerve, sharply limiting the glenoid surface and postglenoid process medially and extending backward to a recess in the squamosal directly opposite the fenestra ovalis. The posterior surface of the postglenoid process shows a number of dorsoventral ridges and grooves near the lower margin, and a very broad and shallow depression near its medial margin extends upward and is confluent with a comparatively large postglenoid foramen (Wortman thought this to be absent) close to the fissura Glaseri.

Petrosal.—The petrous portion of the periotic is exhibited in the anterolateral portion of the large otic fossa lateral to basioccipital. It does not appear to separate completely the foramen lacerum medius from the foramen lacerum posterius as the medial margin of the petrosal shown on the left side approaches close but does not touch the basioccipital. The outline of the petrosal as exposed ventrally cannot be fully determined because the margin is somewhat damaged and incomplete; nevertheless the most conspicuous feature of this element is the downward- and forward-directed buttonlike promontorium. A fairly large fenestra rotunda faces backward and slightly outward. An elongate groove on the petrosal extending backward from a position immediately outward from the lateral margin of the fenestra rotunda is not explained but suggestion is made that this may have covered the stapedial muscle dorsally, or possibly the stapedial artery. The slightly smaller fenestra ovalis is forward and a little above the fenestra rotunda and faces laterally and somewhat forward.

The ventral aperture of the stylomastoid foramen is destroyed on both sides but sufficient remains of the walls of the foramen to indicate that it may not have been completely closed medially. A small portion of the mastoid projects medially, in front of the stylomastoid foramen and beneath its continuation as the facial canal, almost to the petrosal posterolateral to the fenestra rotunda. Immeditely lateral to the stylomastoid foramen and confluent with it, as exposed in the broken section, is a larger cavity (or canal?) that may have contained the stylohyal. The facial canal is open anteriorly at least as far as a point just ahead of the fenestra ovalis. Here the facial nerve may have entered the petrosal, although slight damage obscures the relationship. On the other hand, a large aperture on the dorsal surface of the petrosal, posteromedial to the promontorium, may have conducted the facial nerve, in which case it was uncovered ventrally through most of its course. The large aperture referred to is not otherwise accounted for. A prominent epitympanic recess is noted, apparently in the squamosal, opposite the fenestra ovalis and at the posterior extremity of the fissura Glaseri.

Upper dentition.—In a superficial way the teeth (pl. 3) of *Patriofelis,* as noted by Marsh, show an interesting resemblance to those of the hyena. Although the form of the palate is rather like that in *Crocuta,* the pattern of the upper teeth is perhaps less hyena-like than it is in the lower series. The carnassials in each, of course, are not homologous. The upper cheek tooth series in *Patriofelis ferox* was described by Matthew (1909), but the anterior part of the dentition was not known. The University of Utah specimen demonstrates that there are only two upper incisors and that M^2 may be present so that the formula for the genus may be written

$$I\frac{2}{2\text{-}3?},\ C\frac{1}{1},\ P\frac{3}{3},\ M\frac{1\text{-}2}{2},$$

with M^1 and M_2 as carnassials.

The upper incisors are simple teeth with conical crowns exhibiting enamel distributed a little higher on the outer side, and a prominent lingual cingulum that is carried nearer the apex of the crown medially. The median incisor is comparatively small with a transversely flattened root, whereas the lateral of the two is decidedly large and more caninelike in appearance. Its root is more nearly circular in cross section, but with the posterolateral surface somewhat flattened. The canine is very robust and heavy rooted, approximately oval in cross section—not flattened or saberlike. These teeth have been much blunted by wear.

There is no P^1. P^2 is simple and two rooted with a very broad

posterior portion. There is a small posterior cusp placed buccally and a brief shelf posterolingually, but without a deuterocone. P^3 is three rooted with a small anterior cuspule and a large tritocone not as high as the primary cusp. The deuterocone, though damaged, is seen to be well developed and about median in position. In P^4 the small anterior cusp is higher or nearer the apex of the primary cusp and the tritocone is about as large as the primary cusp but more bladelike in appearance. The talon carries a well-developed crestlike deuterocone and is anteroposteriorly broader and more anterior in position than that of P^3. M^1, the carnassial, has been converted entirely to a shearing blade. This tooth is rather worn lingually, but it is apparent that the anterointernal root did not support a talon or deuterocone. M^2 is a small peglike tooth anterolingual to the posterior margin of M^1.

An interesting feature of the *Patriofelis* upper dentition is the extent to which it is carried outward and posteriorly on the strong zygoma as in cats and hyenas, and the fossil form, *Hyaenodon*—quite unlike the bears, and possibly dogs. Also, as noted by Matthew (1909), the upper cheek teeth are inclined inward, very much so in the posterior part of the series, so that the shearing surface, particularly of M^1, is vertical. The outer wall of M^1 is nearly horizontal and the angle that it makes with the shearing surface is, in consequence, not particularly acute. Also, as a result of this, the vestigial M^2 is implanted at an angle, dorsal to the crown of M^1, so that it is almost concealed in the ventral view. Its small crown scarcely reaches the plane of shear on M_1 immediately ventral to it.

Mandible.—The *Patriofelis* jaws (pl. 4), as Matthew (1909) has noted, are deep and massive. The symphysis is deep and elongate, and although Matthew considered it as not co-ossified, I find the two rami are firmly united. When it was necessary to separate the jaws so as to remove them from the skull during preparation, breakage for the most part occurred to one side through the canine alveolus. The anterior margin of the symphysis is a little less abrupt than Matthew has shown for *P. ferox,* curving gently into the comparatively straight lower margin of the horizontal ramus. The depth of the jaw beneath the tooth row is nearly uniform, though a little shallower beneath the posterior root of P_4 as shown for *P. ferox*. The mental foramina are variable and on the right side two are located one above the other beneath the anterior part of P_2, and two side by side beneath the posterior root of P_3 and the anterior root of P_4. On the left side two slightly larger foramina are located, one beneath P_2 and the other beneath P_3. There is also an irregular display of foramina beneath the incisors close to the anterior margin of the symphysis.

Neither the angle nor the top of the coronoid process are complete on either side of the *P. ulta* mandible, but it is seen that the slope of the anterior margin of the ascending ramus is not so steep as shown for *P. ferox*. The condyle is transversely very elongate and carries the articular surface well forward along the inferior as well as the superior surface. The outer portion of the superior surface extends down on the anterior part of the condyle where articulation occurs with the well-developed process anterior to the glenoid surface of the squamosal, almost locking the lower jaw in place, as in some mustelids. The masseteric fossa would appear to be weakly defined near the lower margin of the jaw but is deeply impressed in the upper portion. The deeper part of the fossa is limited downward by a ridge which extends forward from just below the condyle. The crest bounding the fossa anterodorsally extends downward and forward from the anterior margin of the coronoid process, but disappears upon reaching a position almost below the posterior margin of M_2.

On the medial surface of the jaw it is seen that the symphysis extends posteriorly to a position below about the anterior margin of P_4 and exhibits a deep pit forward near its posterior limit for certain muscles, including the geniohyoid and probably a part of the digastric. The inferior dental foramen is located above the shallow vascular notch in the lower border of the jaw and about opposite the ridge on the outer surface that limits the deeper part of the masseteric fossa ventrally. Posterior and ventral to the inferior dental foramen the medial surface of the jaw is distinctly concave. There is no particular indication of a sulcus mylohyoideus.

Lower dentition.—As noted above, the hyena-like appearance of the teeth (pl. 4) in *Patriofelis* is most noticeable in the lower series, particularly the premolars. The resemblance in the molar series is between nonhomologous carnassials and is upset by the presence of the small M_1 in *Patriofelis*.

The number of lower incisors is clearly two in the University of Utah specimen. The smaller, medial incisor is distinctly posterior to the lateral tooth and rather flattened transversely. The lateral incisor is less procumbent and shows a relatively broad anterior surface. The crowns of both are blunt with wear. The canines have massive roots and are comparatively close together, much crowding the incisors. Their crowns are likewise considerably worn.

P_2 is neither crowded nor oblique as in *P. ferox*. It shows a short diastema between it and the canine, and though small, is relatively broad and two rooted. It carries a minute cuspule anterior to the principal cusp and a low, blunt cusp on the talonid. P_3 is similar but

much larger and broader, with a relatively larger and transversely flattened talonid cusp. Like P_4, this tooth shows a distinct backward tilt. P_4 is larger than P_3 and has higher cusps, also the talonid shows a more pronounced crest on its lingual margin. The backward tilt of this tooth is rather pronounced, so that the outer margin of the talonid is much lower than that of the trigonid, or than any of the other teeth. M_1 is small and crowded with a comparatively large paraconid portion, although this part of the tooth is rather obscured by wear. The metaconid is developed as an upward and posterolingually directed spur from the protoconid. The talonid is low, much worn, and almost completely hidden lingually by the anterior root of M_2. M_2, of course, is the shearing tooth and possibly a trifle longer than P_4. It lacks any trace of a talonid. The posterior blade along its cutting edge is longer than the anterior, and projects backward and upward rather strikingly.

In addition to the backward tilt noted for P_3 and P_4, all the cheek teeth, as noted by Matthew (1909), tilt distinctly outward. As with the inward tilt of the upper teeth, this orients the shearing surface of P_3 and P_4, as well as that of the carnassial, nearly vertical. It is noted also that the outer shearing surfaces are dorsoventrally more elongate than the lingual walls. The crown of each tooth has a noticeably greater buccal than lingual height.

MEASUREMENTS IN MILLIMETERS OF SKULL AND MANDIBLE OF *Patriolefis ulta* LEIDY, UNIV. UTAH NO. B50

Skull:	
Greatest length from anterior margin of premaxillae to two small processes on superior margin of foramen magnum	248.
Length from anterior margin of nasals to vertical portion of occiput above foramen magnum	227.
Length from anterior margin of premaxilla to posterior wall of glenoid surface medially	178.
Length of palate from anterior margin of premaxilla to anterior margin of posterior narial aperture	100.5
Greatest length of nasals	78.0
Distance between lateral margin of anterior narial aperture and anterior margin of orbit	52.5
Greatest width across zygomae	183.
Width across nasals anteriorly	40.
Width between orbits dorsally	76.
Width across postorbital processes of the frontals	70.
Width of cranium at constriction	38.
Width of palate between canines	31.
Width of palate posteriorly, between M^2's at alveoli	81
Upper dentition:	
Over-all length of dentition from anterior surface of lateral incisor to posterior margin of M^1	105.

Length of cheek tooth series, P^2-M^1, inclusive	68.5
I^2 (at alveolus), anteroposterior diameter: transverse diameter	9.0 : 4.0
I^3 (at alveolus), anteroposterior diameter: transverse diameter	13.0 : 10.0
C (at alveolus), anteroposterior diameter: transverse diameter	23.0 : 16.0
P^2, anteroposterior diameter: transverse diameter posteriorly	11.2 : 8.0
P^3, anteroposterior diameter externally: transverse diameter perpendicular to outer wall	17.8 : 19.0[a]
P^4, anteroposterior diameter externally: transverse diameter perpendicular to outer wall	18.5 : 22.0[a]
M^1, anteroposterior diameter	21.5
M^2, greatest diameter	4.0
Mandible:	
Length from anterior margin of symphysis to posterior surface of condyle medially	177.
Length of symphysis	60.
Posterior margin of M_2 (at alveolus) to posterior surface of condyle medially	76.
Lower dentition:	
Anterior margin of lateral incisor to posterior margin of M_2 (at alveoli)	103.
Length of cheek tooth series, P_2-M_2 (at alveoli) inclusive	76.
I_2 (at alveolus), anteroposterior diameter: transverse diameter	6.5 : 3.0
I_3 (at alveolus), anteroposterior diameter: transverse diameter	7.8 : 5.0
C (at alveolus), anteroposterior diameter	21.0
P_2, anteroposterior diameter: transverse diameter at talonid	10.5 : 7.2
P_3, anteroposterior diameter: transverse diameter at talonid	13.3 : 9.5[a]
P_4, anteroposterior diameter: transverse diameter at talonid	17.8 : 11.6
M_1, anteroposterior diameter: transverse diameter at trigonid	16.0 : 8.5
M_2, anteroposterior diameter: transverse diameter	18.6 : 10.0

[a] Approximate.

SUMMARY OF RELATIONSHIPS

The position of *Patriofelis* in the Oxyaenidae, as the culminating stage of the Oxyaeninae in North America, seems firmly established, although it should be noted that a later survival of the subfamily is believed represented by the genus *Sarkastodon* (Granger, 1938) in the upper Eocene of Asia. The genus *Oxyaena* is first recognized in the Clark Fork Paleocene and carries through the lower Eocene represented by several species. An intermediate form, *Protopsalis,* here regarded as a subgenus of *Patriofelis,* is known from the Lost Cabin level of Wasatchian time and *Patriofelis* proper characterizes the upper Huerfano as well as both upper and lower levels of Bridger Middle Eocene. The lower Bridger species *Patriofelis ulta* may well be the forerunner of larger *Patriofelis ferox,* and although in turn evidently derived from *Oxyaena* through the *Protopsalis* stage, the

known species *P.* (*Protopsalis*) *tigrinus* was clearly not in the direct line of development.

Wortman (1894, 1902, and 1906) was strongly convinced that *Patriofelis* was aquatic or semiaquatic in habit and in or near the line of descent of the pinnipeds. He also advanced the idea that *Patriofelis* may have "preyed on numerous species of turtles that inhabited the Bridger lake." While his reasoning and analysis of the possibilities are thought provoking, as far as the position of the Oxyaenidae with respect to the pinnipeds is concerned, I am unable to agree. Nevertheless, there would seem from Wortman's argument some justification for believing that *Patriofelis* may have been partially aquatic in habit. I am particularly impressed by the over-all otterlike body proportions and the rather otterlike structure of the rostrum of the skull. On the other hand, the teeth are basically so very much like those of a hyena that I greatly suspect a carrion-feeding habit, if this can be reconciled with the foregoing, or, as Wortman has postulated, a diet of fresh-water turtles.

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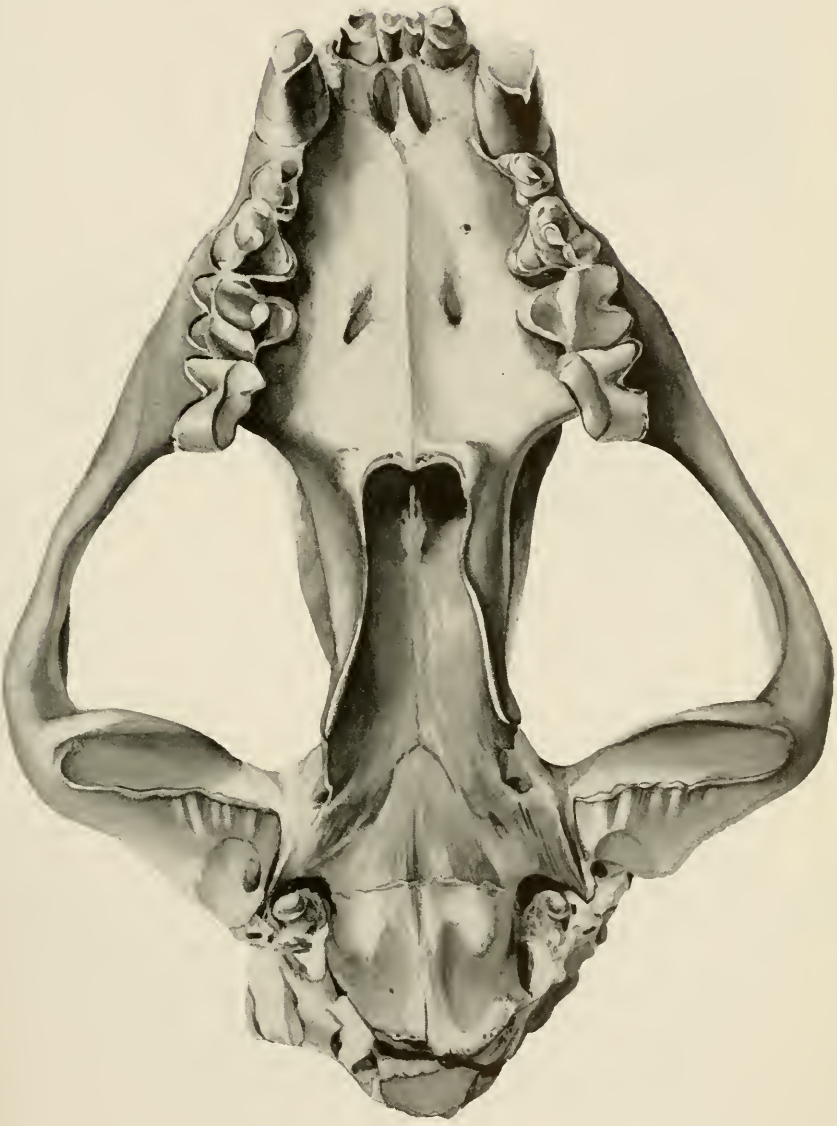
PATRIOFELIS SKULL FROM THE BRIDGER MIDDLE EOCENE

Patriofelis ulta Leidy: Skull (Univ. Utah No. B50), dorsal view. Approximately three-fifths natural size.

PATRIOFELIS SKULL FROM THE BRIDGER MIDDLE EOCENE

Patriofelis ulta Leidy: Skull (Univ. Utah No. B50), lateral view. Approximately three-fifths natural size.



PATRIOFELIS SKULL FROM THE BRIDGER MIDDLE EOCENE

Patriofelis ulta Leidy: Skull (Univ. Utah No. B50), ventral view. Approximately three-fifths natural size.

PATRIOFELIS MANDIBLE FROM THE BRIDGER MIDDLE EOCENE

Patriofelis ulta Leidy: Mandible (Univ. Utah No. B50), dorsal view (above), lateral view of right ramus (below). Approximately three-fifths natural size.