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MAMMALIAN PALEONTOLOGY ON A GLOBAL STAGE: PAPERS IN HONOR OF MARY R. DAWSON

Edited by

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Cover illustration: Artist's depiction of the living Laotian rodent *Laonastes aenigmamus* standing upon lacustrine strata containing a well-preserved skeleton of the early Miocene rodent *Diatomys shantungensis*. Mary Dawson and her colleagues were the first to recognize that *Laonastes* is a surviving member of the otherwise extinct rodent clade Diatomyidae (see contribution by Flynn in this volume). Original art of Mark A. Klingler.

Frontispiece: Portrait of Mary R. Dawson painted by Gina Scanlon.

A NEW LARGE, HYPERCARNIVOROUS OXYAENID (MAMMALIA, CREODONTA) FROM THE MIDDLE EOCENE OF THE WIND RIVER FORMATION, NATRONA COUNTY, WYOMING

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ABSTRACT

Malfelis badwaterensis, **gen.et sp. nov.**, represented by a nearly complete juvenile skull, isolated I^{1-2}, P^1, DP^2, and a fragment of the dentary from the same individual (CM 62590), is described from the early middle Eocene (Gardnerbuttean, early Bridgerian) of the Wind River Formation, Wyoming in North America. *M. badwaterensis* preserves a unique combination of characters that set it apart from all other creodonts including the presence of a P^1 and reduced M^2, a carnassial complex from DP^{3-4}–M^1 with reduced protocones, simplified trenchant P^{2-3}, and M^1 with conjoined metacone and paracone, and metastylar blade. *M. badwaterensis* is referred to the Oxyaenidae based on the well-developed metastylar blade of M^1, a reduced M^2, and loss of M^3. This new creodont was perhaps the largest of all animals from the type locality, which has yielded nearly 80 species of mammals.

INTRODUCTION

A new genus and species of oxyaenid creodont, *Malfelis badwaterensis*, is described based on a nearly complete skull (CM 62590) from the Wind River Formation of Wyoming. This new genus is very large (total skull length is approximately 30 cm). The type skull is from a juvenile that has a highly derived carnassial complex involving the DP^{3-4}–M^1 while retaining a permanent M^2 that is erupting and apparently vestigial. The genus is perhaps the largest mammal from the type locality in the Gardernerbuttean interval or early Bridgerian of the uppermost part of the Wind River Formation. Other genera of oxyaenid creodonts in the Wind River Formation faunas of this age include *Patriofelis* and *Protopsalis.*

The creodonts are among the most important and diverse of the carnivorous mammals from the middle Paleocene through late Oligocene of North America. According to Gunnell (1998), the order Creodonta is represented in North America by three families—Oxyaenidae, Hyaenodontidae, and Limnocyonidae—with as many as 27 genera. The Oxyaenidae are represented by the genera *Tytthaena, Dipsalidictis, Oxyaena, Patriofelis, Protopsalis, Palaeonictis, Ambloctonus, Dipsalodon, Machaeroides,* and *Apataelurus.* The Hyaenodontidae are represented by *Prototomus, Gazinocyon, Arfia, Sinopa, Tritemnodon, Proviverroides, Pyrocyon, Acarictis, Hyaenodon, Hemipsalodon,* and *Ischnognathus*. The Limnocyonidae are represented by *Limnocyon, Thinocyon, Prolimnocyon,* and *Oxyaenodon*. Morlo and Gunnell (2003) have reconsidered the family ranking of the Limnocyonidae and now include the group as a subfamily within the Hyaenodontidae. In sum, more than 68 species of creodonts are known from North America, where they range in age from the Tiffanian (middle Paleocene) through the early Arikareean (late Oligocene). New species and generic-level taxa are known but not formally proposed by Rose (1981) and Ivy (1993). The order is also known from Asia (early Eocene to late Miocene) and Europe (early Eocene to early Miocene), and in Africa (early Eocene to late Miocene) where most authors suggest it originated [see, for example, Gingerich and Deutsch (1989), Gunnell and Gingerich (1991), and Gheerbrant et al. (2006)].

Institutional abbreviations are as follows: **AMNH**, American Museum of Natural History; **CM**, Carnegie Museum of Natural History; **UCM**, University of Colorado Museum; **UU**, University of Utah. Other abbreviations include: **MS**, measured section number; and **U**, unit number within measured section. Measurements were taken with digital calipers. CT-scans were analyzed through eFilm™Lite™ software (2003). A total of 246 lateral slices were analyzed through the maxillary and premaxillary regions of the skull (14 cm).

HISTORY OF INVESTIGATIONS

The taxonomic history and systematic organization of the Creodonta has been long and problematic. It has been complicated by phylogenetic interpretations, misinterpretations, and changing perceptions of taxonomic relationships within the order since its first definition by Cope in 1875.

In 1853, Leidy described the first specimens of North American creodonts and placed them in three species of *Hyaenodon* from the Oligocene beds of "Nebraska Territory." Leidy (1869) later proposed the family Hyaenodontidae to differentiate *Hyaenodon* from other carnivorous mammals based on their primitive morphology and carnassial specializations. To further define the hyaenodontids, Leidy (1871) described a new genus and species, *Sinopa rapax,* from the Bridger Formation of Wyoming. Later, Cope (1872) followed Leidy and described *Stypolophus* and *Prototomus.* Cope (1875) generated the first definition of the order Creodonta, although earlier descriptions of both hyaenodontids and oxyaenids existed outside of a well-defined taxonomic order. Scott (1892) later synonymized *Stypolophus* and *Prototomus* with *Sinopa,* which when added with the *Hyaenodon* specimens, firmly established the family Hyaenodontidae.

The first oxyaenid, *Patriofelis ulta*, was proposed by

Leidy in 1870. Cope (1877) provided the first description of the family Oxyaenidae based upon "*Stypolophus, Oxyaena, Pterodon,* and perhaps *Patriofelis.*" Later, Cope (1884) revised this definition by removing *Stypolophus* and adding *Prototomus.* A further revision came from Osborn and Wortman (1892), when they redefined the family by removing all genera except *Oxyaena* and placing *Patriofelis, Palaeonictis,* and *Ambloctonus* into the Palaeonictidae. In a series of papers, Wortman (1894, 1899, 1901) later redefined and enhanced our understanding of creodonts and our knowledge of oxyaenids by returning *Patriofelis* to the latter family. In 1901, Wortman defined the Limnocyoninae as a subfamily within the Oxyaenidae.

Matthew produced his exceptional and still unsurpassed monographic treatment of the Bridger carnivores in 1909, including a complete revision of the creodont taxa known at the time. He recognized two families, the Oxyaenidae and the Hyaenodontidae, including the limnocyonines in the former. He added a new genus of saber-toothed creodont, *Machaeroides,* which together with *Apataelurus* (Scott, 1938), represented an additional branch of the early Eocene radiation of the creodonts.

Denison (1938) completely revised the Oxyaenidae and referred both the Limnocyoninae and Machaeroidinae to the Hyaenodontidae. Within the oxyaenids, Denison included two subfamilies, Oxyaeninae (including the genera *Dipsalidictides, Oxyaena, Protopsalis, Patriofelis,* and *Sarkastodon*) and Palaeonictinae (including *Dipsalodon, Palaeonictis, Ambloctonus,* and *Paroxyaena*).

Since these earlier studies, both the Oxyaenidae and the Hyaenodontidae have undergone numerous additions and changes at the family level. More recent studies by Mellet (1976), Gingerich (1980), Gingerich and Deutsch (1989), Gunnell and Gingerich (1991), McKenna and Bell (1997), Gunnell (1998), Rose (2006), and Gheerbrant et al. (2006) have continued to define the order further and realign perceived affinities. The order is still generally divided into two distinct families, the Hyaenodontidae and the Oxyaenidae. Although the limnocyonines have been recognized formerly as a distinct family of creodonts (Gazin 1946; Gunnell 1998), Denison (1938) and Van Valen (1966) have indicated their transitional status between the Oxyaenidae and the Hyaenodontidae. Morlo and Gunnell (2003) have recently allied them with the Hyaenodontidae. Matthew (1909) and Polly (1996) have discussed the postcranial morphology of the creodonts in depth to help define and establish the systematic distinctions within the order.

SYSTEMATIC PALEONTOLOGY
Class Mammalia Linnaeus, 1758
Order Creodonta Cope, 1875
Family Oxyaenidae Cope, 1877
Subfamily Oxyaeninae Cope, 1877

Diagnosis.—Creodont taxa that have lost the M^3 and have a sectorial metastylar blade on P^4 and M^1.

Included North American genera.—*Malfelis, Oxyaena, Patriofelis,* and *Protopsalis.*

Malfelis, new genus

Type species.—*Malfelis badwaterensis,* new species.

Included species.—Type species only.

Age and distribution.—Early Bridgerian Land Mammal Age (Gardnerbuttean), middle Eocene, of western North America (Stucky 1984b; Krishtalka et al. 1987; Robinson et al. 2004).

Diagnosis.—A large oxyaenid creodont similar in size to *Patriofelis* and *Protopsalis*, and the larger species of *Oxyaena.* Differs from *Oxyaena* in having a reduced, vestigial M^2. Differs from *Oxyaena* and *Protopsalis* in having an M^1 with conjoined paracone and metacone in line with a strong metastylar blade and a reduced protocone. Differs from *Protopsalis* and *Patriofelis* in having less robust premolars. Differs from *Patriofelis* in retaining a P^1 and M^2, in having a larger protocone on M^1, and having the M^1 located on the posterior margin of the maxillary plate and not extending onto the zygomatic arch. The upper dental formula is 3–1—4–2. The snout is long and constricted posterior to the canines, resembling *Limnocyon* in skull proportions. There are two large paired parietal foramina as in *Patriofelis*, but these differ in being subequal in size and located medially on the parietal, rather than posteriorly as in *Patriofelis.*

Etymology.—*Malo,* bad, *felis*, cat (Latin).

Malfelis badwaterensis, new species
(Figs. 1–7)

Holotype.—CM 62590, complete skull with right DP^{3-4}, right M^1, and left M^{1-2}; right P^2 and left M^2 erupting; alveoli for right DP^{1-2}, right and left DC^1 roots in alveoli; and isolated left I^1, right I^2, left DP^2 and right DP^2; basioccipital and occipital condyles missing.

Type locality and horizon.—CM locality 34, UCM locality 81023, Davis Ranch (also known as Sullivan Ranch), Natrona County, Wyoming. Found in situ by RKS in MS9-U3, at top of gray mudstone, 2.1 m thick. This horizon is below the main fossil-bearing red mudstone layer at Davis Ranch [MS9-U6; UCM Locality 79042; see Stucky (1984a, p. 306)]. Fossils from U3 may be distinguished from those of U6 by a lack of concretionary matter on the bones, gray brown color of the fossils, which weather to gray, and dark blackish brown (not reddish brown) enamel.

Age and distribution.—Early Bridgerian Land Mammal Age (Gardnerbuttean Land Mammal Subage), earliest middle Eocene, of western North America, from the Lost Cabin Member of the Wind River Formation (Stucky 1984a).

Diagnosis.—As for genus.

Etymology.—Named for the now extinct settlement of Badwater, Wyoming.

Included specimens.—Holotype only. A single upper molar figured by Denison (1938, fig. 8, upper right) as *Patriofelis ferox* may also represent this taxon, but no reference is given to the locality or disposition of this specimen, which has not been examined.

Description

The type, the only known specimen of *M. badwaterensis* of certain location and age, consists of a crushed skull, isolated incisors and deciduous premolars, and a small fragment of the ramus of the left dentary. The premaxillaries are very fragmentary and preserve neither incisors in place nor their alveoli. Roots of the deciduous canines are within the skull but the teeth are badly damaged and their crowns occur as isolated fragments. Alveoli are present for the right P^1 and DP^2; the left side of the skull is badly damaged. The right DP^{3-4}–M^1 are fractured, but not to the extent that it would prevent their basic morphology from being described. The

left DP^4 has a damaged paracone and metacone region but preserves the metastylar blade. The left M^1 shows excellent preservation, and lingual to its posterior root is a simple M^2 contained within the maxillary bone that is vestigial and in the process of erupting. Two permanent incisors, P^1, two DP^{2}s, tips of both canines, and additional tooth fragments were found in the matrix surrounding the palatal region of the skull during preparation.

A computed tomography scan (CT-scan) of the skull reveals the presence of P$^{2-4}$ in the maxillary bones above the alveoli and deciduous premolars and permanent canines above the deciduous canines (Figs. 1–2). Comparative measurements for all teeth of *M. badwaterensis* and *Patriofelis ulta* are provided in Table 1. Measurements for unerupted teeth are based on interpolation from the CT-scans.

Deciduous dentition.—The deciduous canines are laterally compressed. The fragmentary remains of the crowns of the canines are sharp with a lingual wear facet and slight serrated edges on the posterolingual margins. There are very modest crenulations of the enamel. The length of the canines cannot be determined due to the fragmentary nature of the specimens. The permanent canines are contained in the maxillary bones above the deciduous canines as shown in the ct-scans (Figs. 1, 2H–J).

The right and left DP^{2}s differ slightly in overall size and height (Table 1; Fig. 3). Anteriorly, DP^2 is round and smooth. A ridge descends from the apex of the major cusp posterolabially and wraps around downward to the lingual base. A lingual cingulum at the base joins a small posterolingual cuspule or shelf. The crown of P^2, which is described below, occurs above the alveoli for the DP^2 and is visible deep within the bone of the maxilla. Diastemata
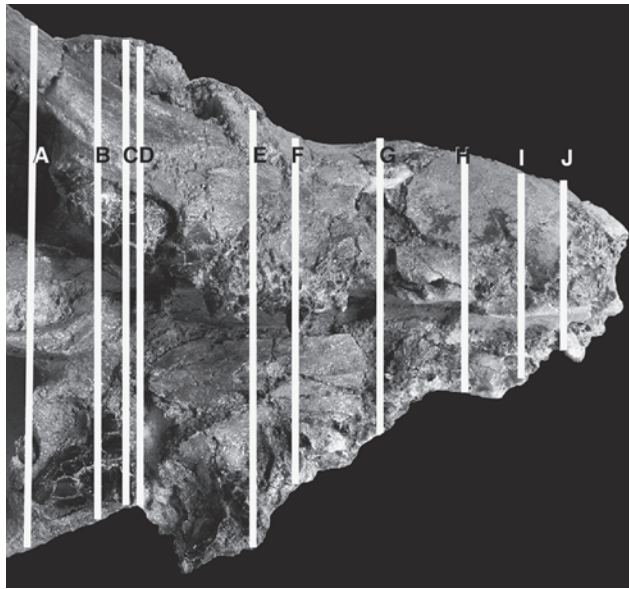

Fig. 1.—Palatal view of *Malfelis badwaterensis* showing positions of CT-scan images provided in Figure 2. A total of 246 slices across the snout from the middle of M^2 to the premaxilla were imaged over a length of 14.2 cm.

separate the DC, P, and DP^2 (Fig. 4). Whether these diastemata are maintained in the adult cannot be determined.

The DP^3 is three-rooted and has a single dominant paracone. There is no indication of a metacone, and the metastylar blade is long and sectorial (Fig. 5). There is a small parastyle and the protocone is distinct but small compared to that of P^3 in larger oxyaenids such as *Patriofelis* or *Protopsalis* (Gazin 1957; Guthrie 1971, fig. 7c; following Gunnell 1998). The DP^3 protocone is equivalent in size to that of M^1 and slightly larger than that of DP^4. There are no cingula on the tooth. Wear facets are present on the apical surface of the paracone and on the lingual surface of the metastylar blade. The DP^3 is not as robust as P^3 in *Oxyaena* and much less robust than the permanent premolars in *Patriofelis* or *Limnocyon*. In these taxa the P^4 is very likely to have been involved in bone-crushing, whereas in *Malfelis* the deciduous premolars are sectorial, suggesting that they would have functioned chiefly in shearing and only minimally in bone-crushing.

The paracone and metacone are distinct on DP^4, with the metacone being approximately twice as large as the paracone (Fig. 5). A wear facet runs anteroposteriorly in a straight line across the lingual sides of the paracone and metacone, and a second, larger facet, 15.3 mm in length, descends the apex of the metacone posteriorly along the metastylar blade. The blade is slightly bowed lingually. The vestige of a stylar shelf lies in immediate proximity to the metacone. The protocone is very reduced and smaller in size than that of DP^3. The protocone is reduced comparatively in width and lies immediately lingual to the midpoint of the centrocrista. The paraconule and metaconule are absent, and there is no cingulum on any part of the protocone. A small wear facet is present on the lingual surface of the protocone. The parastylar area is damaged, but based on the close approximation of the tooth to the posterior margin of DP^3, the parastyle would have been very small.

Permanent dentition.—Both the left I^1 and right I^2 are small and laterally compressed compared with those of *Patriofelis* (Fig. 3A–B). Cingula occur on the medial and lateral surfaces of the left I^1, running from the sharp, conical tip to the base of the enamel. The medial cingula are flared about halfway from the tip of the tooth. A wear facet is located on the mediolingual apex of the main cusp. The right I^2 is larger than I^1 and has a complete lingual cingulum. The apex is conical, and the medial cingulum is flared and slightly larger than that on I^1. There are no wear facets on the tooth.

The right P^1 has a single root that has a lingual bifurcated indentation along its length (Fig. 3E). The alveoli for this tooth in the skull have a distinct separation that might suggest the tooth were two-rooted were it not for the actual tooth being preserved (Fig. 4). The tooth is simple and recurved posteriorly, and it has slightly crenulated enamel. There is a small wear facet on the lingual side descending posteriorly along the posterior margin of the apical portion of the tooth.

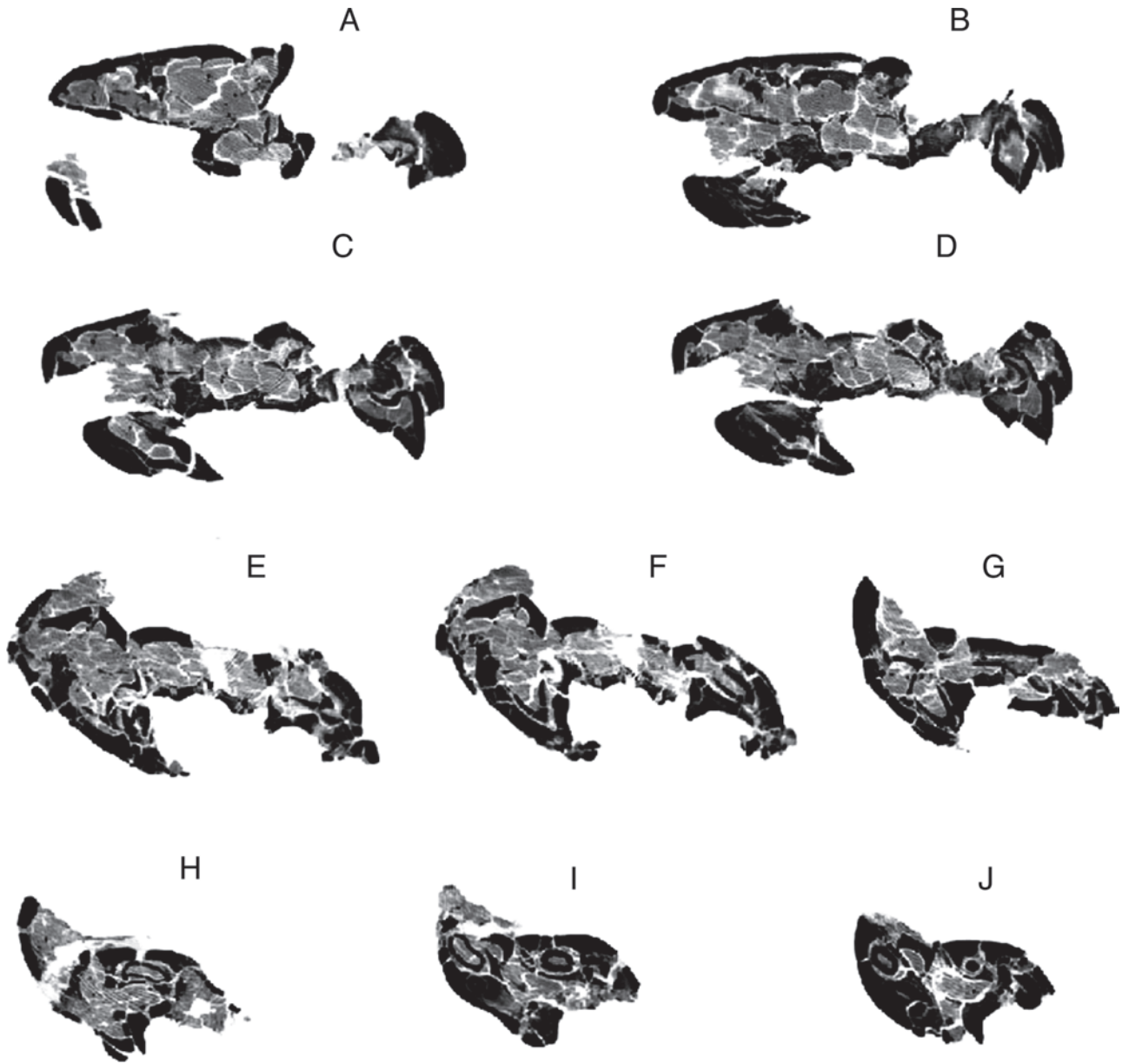Description of P$^{3-4}$ is based on the CT-scans (Figs. 1,

Fig. 2.—CT-scan images spanning the maxilla of *Malfelis badwaterensis* (see Fig. 1 for placement of individual slices). (**A**) Scan 2.246, cross-section at posterior margin of the maxilla. On the far right, the posterior metastylar region of left M^1 and cross-section through erupting left M^2 are visible. (**B**) Scan 22.246, cross-section midway along the metastylar blade of left M^1. (**C**) Scan 36.246, cross-section showing posterior root of right M^1 and lingual root of left M^1. (**D**) Scan 40.246, cross-section across lingual portion of the left M^1 at the protocone showing the posterior portion of the anterior root of the right M^1. There are no remnants of enamel or tooth fragments above the first upper molars, demonstrating that these teeth are permanent. (**E**) Scan 95.246, cross-section across right DP^4 anterior to the protocone and directly through the medial portion of the right P^4. The paracone/metacone crest of right P^4 is visible labially and the protocone is visible lingually, directly above the lingual margin of the right DP^4. (**F**) Scan 101.246, cross-section showing anterior portion of the right P^4 and left P^4; only enamel from these teeth is visible. (**G**) Scan 143.246, cross-section through erupting left P^3 and right P^3 at their approximate midpoint. Erupting teeth are simple with no indication of a protocone or lingual shelf. (**H**) Scan 177.246, cross-section through the right P^2, which is erupting into the DP^2 alveoli and is visible externally. The tooth is anteroposteriorly elongated and simple in morphology, with no cingula or lingual expansion. Above the right P^2 is the posterior open portion of the left C^1 root. Because of distortion of the skull due to crushing, the right C^1 root is not visible in this scan. (**I**) Scan 199.246, cross-section through the most posterior portion of the root of the right DC^1 and the mid-portion of the root of the left C^1. Note roots of the left DC^1 and left C^1 on the right side of the image. (**J**) Scan 217.246, cross-section at middle of left DC^1 and right DC^1. Both permanent canines appear above roots for the deciduous canines. An apparent root fragment for the right P^1 is just below the root of right DC^1.

TABLE 1. Comparative measurements (in mm) of the teeth of *Malfelis badwaterensis* and *Patriofelis ulta.* When tooth loci are preserved bilaterally, measurements are provided for both left (L) and right (R) tooth crowns. Measurements for length and width of the permanent premolars in *M. badwaterensis* are estimates based on interpolation of Ct-scan results. Measurements for M^1 of *M. badwaterensis* are incomplete due to crushing and eruption in the maxilla.

|	Measurement	*Malfelis badwaterensis,* CM 62590	*Patriofelis ulta,* UU B50
I^1	Length	4.1	8.4
	Width	2.2	5.0
	Height	5.9	12.1
I^2	Length	4.2	12.1
	Width	2.6	8.8
	Height	6.9	13.7
DC^1	Length	17.3	
	Width	12.0	
	Height	Broken	
C^1	Length		20.6
	Width		16.4
	Height		26.7
P^1	Length	8.1	Absent
	Width	5.1	
	Height	8.5	
DP^2	Length	L, 10.7; R, 10.6	Absent
	Width	L, 6.0; R, 6.2	
	Height	L, 8.6; R, 8.7	
P^2	Length	12 (estimate)	10.9
	Width	8 (estimate)	9.3
	Height	Not Measured	8.3
DP^3	Length	22.7	Absent
	Width	16.3	
	Height	18.6	
P^3	Length	18 (estimate)	17.5
	Width	13 (estimate)	17.0
	Height	Not measured	14.5
DP^4	Length	30.5	Absent
	Width	16.8	
	Height	17.7	
P^4	Length	24 (estimate)	17.3
	Width	20 (estimate)	23.5
	Height	Not measured	20.9
M^1	Length	L, 28.9; R, 29.0	18.3
	Width	L, 22.1; NA	14.1
	Height	L, NA; R, 17.6	19.2
M^2	Height	7.6	Absent
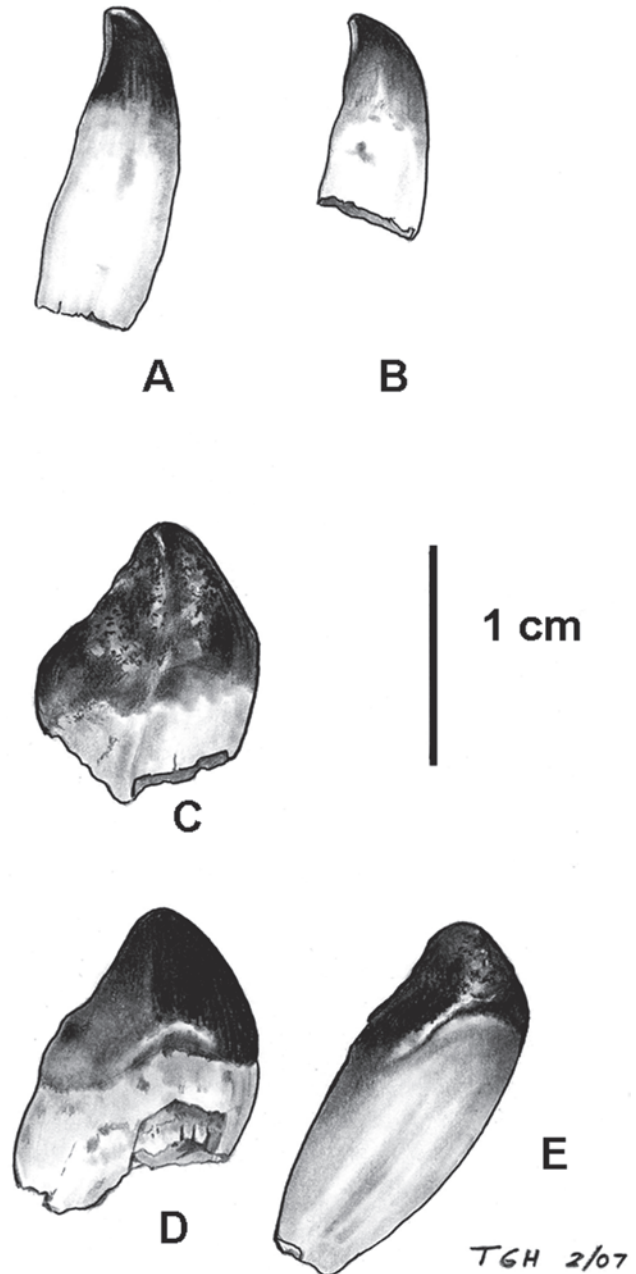
Fig. 3.—Artistic reconstructions of upper incisors and premolars of *Malfelis badwaterensis*. (**A**) left I^2 in distal view; (**B**) right I^1 in mesial view; (**C**) right DP^2 in lingual view; (**D**) left DP^2 in labial view; (**E**) right P^1 in lingual view.

2E–G). The P^2 crown is visible within the alveoli for DP^2, but both P^3 and P^4 are contained within the maxilla. The P^2 is a simple, anteroposteriorly elongated tooth without a protocone but with some lingual crown expansion. This description similarly applies to the P^3, which has no cusp or ridge in the position of a protocone. The P^4 has a well-developed parastyle, a single labial ridge (lacking a distinctive paracone and metacone), and a long metastylar blade measuring approximately 12 mm in length. The protocone is very well-developed with a sharp and robust lingual cusp.

The protocone of M^1 is reduced and equal in size to that of DP^4 (Figs. 5–6). A strong lingual cingulum wraps around the base of the protocone. The paraconule is absent and the metaconule is reduced compared to that in oxyaenids. A small notch occurs between the metaconule and the post-protocrista. The metacone is the dominant cusp and is much
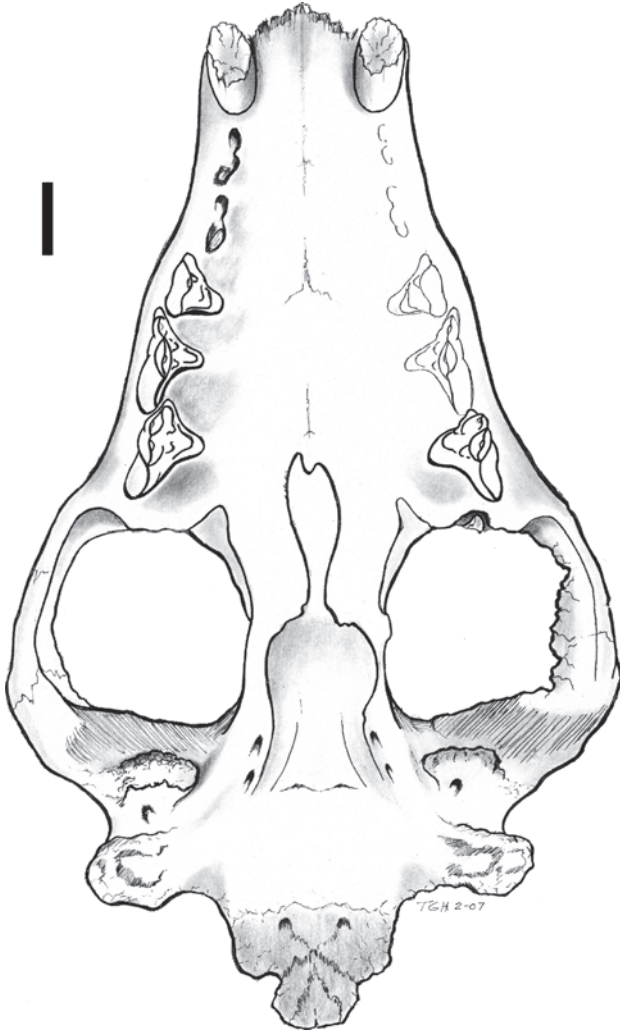
Fig. 4.—Artist's restoration of the skull of *Malfelis badwaterensis* in palatal view. Actual teeth preserved in the holotype are in heavy outline including the right DC^1, right $DP^{3–4}$–M^1, left DC^1, and left $M^{1–2}$. Several features are noteworthy on the specimen: the snout is long relative to the neurocranium; the M^1 does not extend onto the zygomatic arch; there is no anterior glenoid process; and the mastoids are large. Scale bar equals 2 cm.

Fig. 5.—Artist's restoration of the morphology of right $DP^{3–4}$–M^1 of *Malfelis badwaterensis* (above); and photograph of the same tooth loci as they are currently preserved in the holotype, CM 62590 (below). Note that the posterior margin and root of M^1 does not extend onto the zygomatic arch.

The erupting tooth is small (approximately 4.5 mm across the lingual face), if not vestigial, and has a simple conical cusp with a slight lingual cuspule. In the CT-scans there appears to be a small labial shelf that is about 3 mm wide. The specimen is damaged in the area where the right M^2 would be located.

Skull.—Overall, the skull has a short neurocranium with a relatively long snout (Fig. 4). Deep embrasures are located behind DP^3–M^1, where the trigonids of the lower molars

more pronounced than the paracone. The paracone and metacone are united to form a single crescentic shearing crest that continues onto the postmetacrista, which is slightly deflected lingually toward the metastylar ridge. There is no stylar shelf and lingually there is a slight cingulum in the metastylar region. A notch separates the postmetacrista from the metastylar blade. The M^1 posterior root does not extend onto the zygomatic arch as it does in *Patriofelis*. The enamel is moderately crenulated and the parastyle is small and reduced compared to *Oxyaena*. The M^1 is a newly erupted tooth without any wear facets, although some apical abrasion may be present along the metastylar blade and at the apex of the paracone and metacone.

The left M^2 is erupting within an alveolus located lingual to the posterior margin of M^1 on the palate (Figs. 1, 2A, 6).
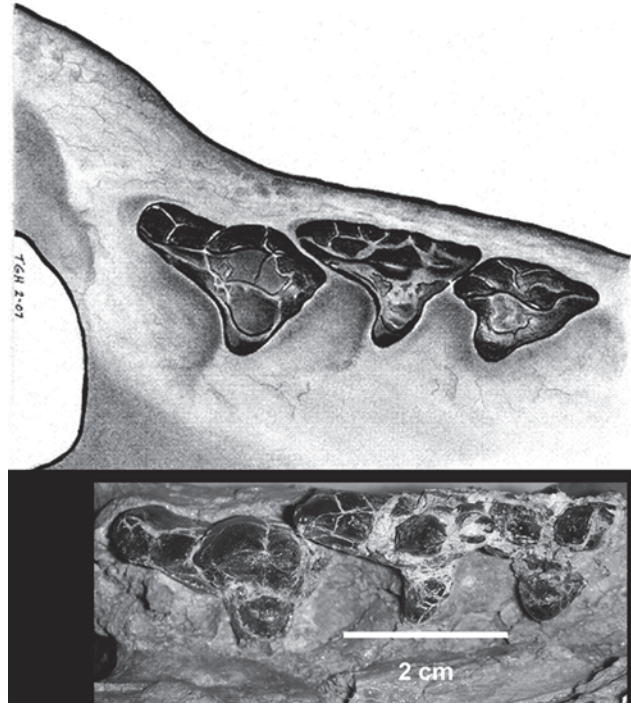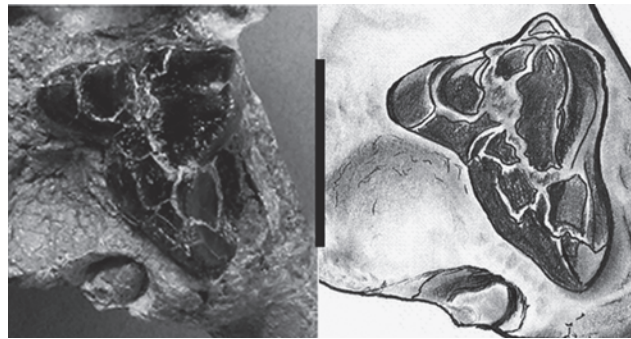

Fig. 6.—Photograph of left $M^{1–2}$ of the holotype of *Malfelis badwaterensis*, CM 62590 (left); and artist's restoration of these teeth (right). Note that M^2 is contained in the maxilla and is in the process of erupting. Scale bar equals 2 cm.

occlude. Based on the embrasures, there were three carnassials in the lower jaw (presumably dP_4, $M_{1–2}$) with the M_2 erupting and not in occlusal contact with the M^1. The palate is strongly arched and not flat as in *Patriofelis*.

The mastoid processes are massive. The pterygoid plate for attachment of the pterygoid muscles is large and extends posterolingually along the palatal process of the maxilla. The narial opening is relatively narrow and constricted midway along the palate, opening into a much larger opening posterior to the humulus of the pterygoid as in *Limnocyon*.

The glenoid fossa is broad but does not have an anterior process or ridge as it does in *Oxyaena* and *Patriofelis*. This suggests much more mobility in the dental apparatus for this juvenile. The postglenoid foramen is small and located medially about halfway between the base of the postglenoid process to its crest.

The foramen ovale is smaller than the alisphenoid canal and is comparatively larger in *Patriofelis*. There is a narrow constriction across the alisphenoids that is approximately 26 mm at its narrowest point. In *Patriofelis ulta* (UU B50; Gazin 1957) this constriction is 40 mm in width at its narrowest point.

In overall proportions the snout is long (186 mm, estimated from the front of the skull to the fronto-parietal suture) compared to the neurocranium (110 mm), yielding a total skull length of approximately 296 mm (Figs. 4, 7). The snout is constricted anterior to the zygomatic arch behind the infraorbital foramen that is located above the posterior root of the DP^3. The snout is wider anterior to this margin.

The paroccipital processes enclosing the posterior margin of the orbits are prominent, unlike those in *Patriofelis*, providing a constriction posterior to the orbit much as in *Hyaenodon*. This suggests that the orbits were relatively small, being approximately 20 mm in diameter.

The sagittal crest is convex and very well developed, much more so than in *Patriofelis,* rising from just above the top of the two parietal foramina to a height of approximately 22 mm. Although the skull is crushed or flattened in this region, the strength of this crest was very prominent with its highest point midway along the neurocranium. The sagittal crest is arched upward and the nuchal crest lies below its highest point. The neurocranium is comparable in size to that in *Patriofelis.*

There are two large, subequal parietal foramina located midway between the nuchal crest and the frontoparietal sutures on each parietal. Their positions vary on each side of the skull; on the right side the foramina are separated by 5.7 mm whereas on the left side they are 11 mm apart. In *Patriofelis*, the only other creodont in which these are known, the foramina are located farther posteriorly and the anterior foramen is much larger than the posterior one (Gazin 1957). In addition, the posterior foramen in *Patriofelis* is located posteromedially to the anterior foramen and not directly in alignment.

Dentary.—A fragment of the ascending ramus of the left lower jaw that preserves the posterior alveolus for the ultimate lower molar is massive compared to that of *Patriofelis.* It is nearly twice as wide, despite the fact that the cranium and facial region of *P. ulta* is very similar in size to that of *M. badwaterensis.* Nothing is known of the postcranial skeleton of *Malfelis*.

Fig. 7.—Holotype skull of *Malfelis badwaterensis* (CM 62590). Left lateral view showing the position of the two equal-sized parietal foramina below the well-developed sagittal crest, as well as the general proportions of the snout and neurocranium.

Discussion.—*Malfelis badwaterensis* preserves a unique combination of characters that set it apart from other Eocene Creodonta. These include the following: the snout is long and moderately narrow compared to *Oxyaena* and *Patriofelis*; P^1 is present, and a diastema separates P^1 and P^2; DP^{3-4}–M^1 preserve a reduced protocone; the paracone and metacone on DP^4 and M^1 are conjoined near their apices, forming a short but distinct centrocrista blade that is separated by a small notch from the long metastylar blade; M^2 is present, albeit as a small vestigial tooth bud; the molar row does not extend onto the zygomatic arch; the metacone on M^1 exhibits a longer and slightly parabolic, blade-like structure that is unlike the more cuspate paracone; there are paired foramina on the parietal; and there is no preglenoid crest or ridge. This combination of characters sets *Malfelis* apart from all other described creodonts.

Unlike *Patriofelis* and *Limnocyon*, the snout is elongate and the P^2 and P^3 are relatively small and uncrowded. This contrasts dramatically with the premolar complex of both *Limnocyon* and *Patriofelis*, which have robust premolars with inflated bases and protocones that are developed for bone-crushing. P^4 has a dominant protocone, but also retains a long metastylar blade as well as a sharp paracone. On the other hand, the M^1 of *Malfelis* compares favorably to the shearing apparatus of *Patriofelis*. The M^1 has a small parastyle and a conjoined paracone and metacone, which are connected along the centrocrista by the blade-like post-paracrista and premetacrista with a notch between them. The metastylar blade is very long and distinct, but forms a continuous shearing carnassial ridge from the apex of the metacone to the end of the metastylar area at the extreme posterior end of the tooth. In *Malfelis* the protocone is distinctive and greatly reduced compared to *Oxyaena,* but much more prominent when compared to *Patriofelis*. Unlike *Patriofelis*, *M. badwaterensis* retains an M^2 that is relatively smaller in size than that of *Oxyaena* and may be vestigial. We ally *Malfelis* to the oxyaenids largely because of the loss of the M^3 and the vestigial and medial position of the M^2. In addition, the conjoined paracone and metacone and the position of the metastylar blade are similar to the carnassial morphology found in *Patriofelis* and differ from that of *Protopsalis*, in which the paracone and metacone are more separate (Guthrie 1971).

PALEOBIOLOGY

Undoubtedly, *M. badwaterensis* was an obligate predator. The long snout and relatively gracile premolars suggest that it was not a bone-crusher at this stage in its life history. Among all known North American creodonts, this juvenile *Malfelis* has the longest carnassial battery. It is somewhat comparable to that found in larger species of adult *Hyaenodon.*

The fossil horizon immediately above that from which the type specimen was recovered preserves the most diverse mammalian fauna of any early to middle Eocene locality, with nearly 80 species of mammals known (Stucky 1990). Specimens of *Patriofelis* and *Protopsalis* are known from this horizon (CM 37327, 43451). *Patriofelis, Protopsalis,* and *Malfelis* were the top predators and would have hunted such animals as titanotheres (*Palaeosyops borealis*), early rhinoceroses and tapirs (*Hyrachyus* sp., *Heptodon* sp.), uintatheres, and other medium to large-sized mammals. The distinctive hypertrophy of the premolars indicate that *Patriofelis* was a bone-crusher, whereas the relatively gracile premolars and long snout of *Malfelis* suggest that it was more of a pursuit predator. Importantly, *Malfelis badwaterensis* and *Protopsalis* were the largest mammals from this part of the early Bridgerian of the Wind River Basin, being larger than animals on which they preyed.

ACKNOWLEDGMENTS

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