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SYSTEMATICS AND EVOLUTION OF LATE PALEOCENE AND EARLY EOCENE OXYAENIDAE (MAMMALIA, CREODONTA) IN THE CLARKS FORK BASIN, WYOMING

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Abstract.— Oxyaenidae is a family of archaic carnivorous mammals included in the mammalian order Creodonta. The major oxyaenid radiation occurred in North America during the late Paleocene and early Eocene, while smaller radiations occurred in Europe and Asia in the Eocene. Three subfamilies are represented in early Cenozoic sediments in the Clarks Fork Basin of northwestern Wyoming: Tytthaeninae (new), Palaeonictinae, and Oxyaeninae. Tytthaenines are represented by one genus: Tiffanian–Clarkforkian *Tytthaena*; palaeonictines are represented by two genera: Tiffanian–Clarkforkian *Dipsalodon* and Clarkforkian–Wasatchian *Palaeonictis*; oxyaenines are represented by two genera: Clarkforkian–early Wasatchian *Dipsalidictis*, and Wasatchian *Oxyaena*. The North American oxyaenine radiation is characterized by progressive development of shearing dentitions and larger body size. Most European creodonts previously described as oxyaenines are either palaeonictines or non-oxyaenid hyaenodontids, however two species of *Dipsalidictis* are present in Europe.

INTRODUCTION

The mammalian families Oxyaenidae and Hyaenodontidae represent two distinct radiations of archaic predatory carnivores. These families are conventionally classified together in a single order Creodonta, but Oxyaenidae appeared in the middle Tiffanian (late Paleocene) of North America (Gingerich, 1980a) while Hyaenodontidae appeared in the earliest Wasatchian (Gingerich, 1986, 1989), suggesting that they may have had different geographical centers of origin. The major diversification of Oxyaenidae took place in North America, while smaller radiations occurred in Europe (Lange-Badré, 1979, 1987) and Asia (Granger, 1938). Oxyaenids made their last appearance in the middle Eocene in North America and in Asia.

Five oxyaenid genera are known from the Clarks Fork Basin of Wyoming: one tytthaenine, *Tytthaena*, two oxyaenines, *Dipsalidictis*, and *Oxyaena*, and two palaeonictines, *Palaeonictis* and *Dipsalodon*. Our objective here is to review the systematics of oxyaenids, examine species-level evolutionary change in *Dipsalidictis* and *Oxyaena*, and compare European representatives to the better known North American radiation of Oxyaenidae.

We use stratigraphic superposition to order successive localities in the Clarks Fork Basin. This provides an independent temporal framework for examination of species level evolutionary change. The stratigraphy of the Clarks Fork Basin and its faunal succession have been discussed in a series of papers by Gingerich et al. (1980), Rose (1981), and Gingerich (1982, 1983, 1986, 1989). Biostratigraphic zonations of the Tiffanian, Clarkforkian, and Wasatchian land-mammal ages used in this paper are those developed by Granger (1914), Gingerich (1976, 1983, 1986, 1989), Schankler (1980), Rose (1981), Archibald et al. (1987), and Gunnell (1989).

Fossil localities prefaced by SC are University of Michigan localities in the Sand Coulee area of the Clarks Fork Basin. Those prefaced by FG, MP, and GR are University of Michigan localities in the Foster Gulch, McCullough Peaks, and Greybull River regions of the northern and central Bighorn Basin, while those prefaced with YM are Yale-Michigan localities in the central Bighorn Basin.

INSTITUTIONAL ABBREVIATIONS

Institutional abbreviations used in this paper are as follows:

AMNH	– American Museum of Natural History, New York
BMNH	– British Museum of Natural History, London
Basel-TS	– Naturhistorisches Museum, Basel
FMNH	– Field Museum of Natural History, Chicago
MNHN	– Muséum National d'Histoire Naturelle, Paris
RAM	– Ray Alf Museum, Claremont
UCMP	– University of California, Museum of Paleontology, Berkeley
UM	– University of Michigan, Museum of Paleontology, Ann Arbor
USNM	– United States National Museum, Washington
YPM-PU	– Princeton collection at Yale Peabody Museum, New Haven

HISTORY OF STUDY

In 1875 Cope proposed the name Creodonta as a suborder of Insectivora. He distinguished Creodonta from other insectivores based on the following characters: femur with a third trochanter; small brain with large olfactory bulbs; transverse glenoid fossa of the squamosal with both pre- and postglenoid processes; unfused scaphoid and lunate; trochlea of the astragalus ungrooved and smooth; astragalar articular surface of the distal tibia smooth and ungrooved; stout distal fibula with large astragalar articular surface; and a cuboid that articulates with the head of the astragalus, but with the astragalar head lacking a distinct cuboid articular facet.

Cope erected a new order Bunotheria in 1877 and included Creodonta, Mesodonta, Insectivora, Tillodontia, and Taeniodonta in it as suborders. Cope (1877) placed the families Ambloctonidae (including *Ambloctonus* and *Palaeonictis*), Oxyaenidae (including *Stypolophus*, *Oxyaena*, *Pterodon*, and *Patriofelis*), and Arctocyonidae (including *Arctocyon*, *Miacis*, *Uintacyon*, and *Didymictis*) in Creodonta.

Osborn and Wortman (1892) raised Creodonta to ordinal status and included six families: Palaeonictidae (= Ambloctonidae), Oxyaenidae, Miacidae, Proviverridae, Mesonychidae, and Arctocyonidae. Wortman (1901) returned Creodonta to Carnivora as a suborder that included the families Oxyclaenidae, Arctocyonidae, Mesonychidae, Oxyaenidae, and Hyaenodontidae.

Matthew (1909), in the first major revision of North American early Cenozoic carnivorous mammals, retained Creodonta as a suborder of Carnivora. Matthew also included Fissipedia, Pinnipedia, and Archaeoceti as suborders within Carnivora. Within Creodonta he recognized three superfamilies: Eucreodi, Pseudocreodi, and Acreodi.

Matthew's Eucreodi (also termed "adaptive Creodonta" by Matthew) consisted of the families Arctocyonidae and Miacidae, and were distinguished by the following characteristics: either no carnassial dental development or carnassial pair formed by P^4 and M_1; claws compressed and pointed, not fissured at the tip; paraxonic manus and pes; no fibular calcaneal facet; no supratrochlear foramen of the humerus.

Matthew's Pseudocreodi (also termed "inadaptive Creodonta" by Matthew) included the families Oxyaenidae and Hyaenodontidae and were characterized as follows: carnassial teeth either M^1/M_2 or M^2/M_3; claws fissured at tip; manus and pes mesaxonic; fibular calcaneal facet present; supratrochlear foramen of the humerus present; some forms cursorial.

Matthew's Acreodi consisted of Mesonychidae (included in "inadaptive Creodonta" by Matthew) and Oxyclaenidae (also termed "primitive Creodonta" by Matthew). Acreodi were characterized as lacking carnassial shearing teeth, having "primitive" teeth with blunt cusps, and having tritubercular upper molars and tuberculosectorial or triconodont lower molars.

In 1910, Osborn followed Matthew and included Creodonta as a suborder of Carnivora along with Fissipedia and Pinnipedia. He removed Archaeoceti from Carnivora and put it in Cetacea.

Matthew (1915) retained his 1909 classification with some minor reshuffling. Creodonta was kept a suborder of Carnivora and included four superfamilies, Procreodi (Arctocyonidae and Oxyclaenidae), Eucreodi (Miacidae), Pseudocreodi (Oxyaenidae and Hyaenodontidae), and Acreodi (Mesonychidae and Triisodontidae).

In 1938 Denison published a revision of the Pseudocreodi and altered Matthew's 1915 classification slightly. He removed Procreodi and changed some familial assignments. In his suborder Creodonta he recognized three superfamilies: Pseudocreodi (Oxyaenidae and Hyaenodontidae); Acreodi (Mesonychidae and Arctocyonidae); and Eucreodi (Miacidae). Denison removed Oxyclaenidae and Triisodontidae from Creodonta.

Gregory and Hellman (1939) kept most of Denison's classification with some alterations. They recognized four superfamilies within Creodonta including Procreodi (Arctocyonidae), Acreodi (Mesonychidae), Pseudocreodi (Oxyaenidae and Hyaenodontidae), and Amphicreodi (Palaeonictidae). Palaeonictidae had been earlier viewed as a subfamily of Oxyaenidae. Gregory and Hellman removed Eucreodi (Miacidae) from Creodonta and put it in Fissipedia.

Simpson's (1945) classification of mammals followed Matthew (1915), but he erected new superfamily names. In Simpson's suborder Creodonta he included the following superfamilies: Arctocyonoidea (Matthew's Procreodi) with the family Arctocyonidae; Mesonychoidea (Matthew's Acreodi) with the family Mesonychidae; and Oxyaenoidea (Matthew's Pseudocreodi) with the families Oxyaenidae and Hyaenodontidae. Simpson also included Creotarsiidae in Creodonta, *incertae sedis*. Both Simpson (1945) and Butler (1946) returned Palaeonictidae to subfamilial status within Oxyaenidae.

Later, following suggestions by Ameghino (1901), Simpson (1936), Gazin (1941), and Kretzoi (1943), both Romer (1966) and Van Valen (1966) removed Mesonychidae and Arctocyonidae from Creodonta (to Condylarthra) and reconstituted Creodonta. Romer (1966) raised Creodonta to ordinal status and included two suborders within it, Deltatheridia (Deltatheridiidae or Palaeoryctidae and Micropternodontidae), and Hyaenodontia (Oxyaenidae and Hyaenodontidae). Van Valen (1966) did away with the term Creodonta altogether by erecting a new order Deltatheridia, including Oxyaenoidea and Palaeoryctoidea in it as superfamilies. Van Valen (1967) included these two superfamilies along with a third, Hyaenodontoidea in the suborder Hyaenodonta.

McKenna (1975) and Savage (1977) returned Creodonta to ordinal status within the Grandorder (McKenna) or Superorder (Savage) Ferae. Within Creodonta McKenna recognized the families Hyaenodontidae and Oxyaenidae, while Savage included these two families in his superfamily Oxyaenoidea. Oxyaenidae and Hyaenodontidae are the only two families now included in Creodonta by most authorities. We recognize three subfamilies within Oxyaenidae, Tytthaeninae (new), Palaeonictinae, and Oxyaeninae. It is possible that machaeroidines (*Machaeroides* and *Apataelurus*) also belong with oxyaenids (Dawson et al., 1986).

SYSTEMATIC PALEONTOLOGY

Order CREODONTA Cope, 1875
Family OXYAENIDAE Cope, 1877

Subfamily **TYTTHAENINAE**, new subfamily

Included genera.—Tytthaena.
Diagnosis.—Oxyaenids of small size with no well developed postmetacristae on P^4 or M^1; M_2 smaller than M_1; lower molars with narrow talonids.

Tytthaena Gingerich, 1980a

Tytthaena Gingerich, 1980a, p. 571.

Type species.—Tytthaena parrisi.
Included species.—T. parrisi, T. lichna (new combination).
Diagnosis.—Differs from *Oxyaena* and *Dipsalidictis* in lacking well developed postmetacristae on M^1. Differs from palaeonictines in having a narrow P_4 lacking an entoconid, and in having a sectorial P^4 as in oxyaenines.

Tytthaena parrisi Gingerich, 1980a

Tytthaena parrisi Gingerich, 1980a, p. 571, figs. 1-3.

Holotype.—YPM-PU 22352, left dentary with erupting P_4 and fully erupted M_1.
Type locality.—Cedar Point Quarry, middle Tiffanian beds (Ti-3), Fort Union Formation, Bighorn Basin, Wyoming.
Age and distribution.—All specimens except one are known from the type locality. The single exception is an isolated lower molar from the Chappo Type locality (middle Tiffanian) of southwestern Wyoming (Gunnell, in preparation).
Discussion.—Only the single molar from the Chappo Type Locality has been discovered since the original description of *T. parrisi* by Gingerich (1980a). *T. parrisi* remains the oldest known oxyaenid. As Gingerich (1980a) pointed out, it shares its closest similarities with palaeoryctid insectivores and suggests that oxyaenids probably arose from that group. Measurements of *T. parrisi* are as follows: YPM-PU 22352 (holotype), M_1 length [L] = 7.1 mm, width [W] = 4.2 mm; YPM-PU 22353, M_2 L = 6.6 mm, W = 3.9 mm; YPM-PU 21454, P^4 L = 7.6 mm, W = 6.5 mm; M^1 L = 6.5 mm, W = 8.6 mm; UM 81154 (Chappo), M_2 L = 6.4 mm, W = 3.7 mm.
Referred specimens.—YPM-PU 21454, 22352, 22353, UM 81154.

Tytthaena lichna (Rose, 1981)

Oxyaena? lichna Rose, 1981, p. 109, fig. 57-58.

Holotype.—UM 71170, left dentary with P_4 and fragments of M_{1-2}.
Type locality.—UM locality SC-74, middle Clarkforkian beds (Cf-2), Fort Union Formation, Clarks Fork Basin, Wyoming.
Age and distribution.—T. lichna is known from early and middle Clarkforkian beds (zones Cf-1 and Cf-2) in the Clarks Fork Basin.

Diagnosis.—*T. lichna* differs from *T. parrisi* in being smaller (approximately 10%), and in having a lower M_2 with an anteroposteriorly compressed trigonid, a smaller entoconid, and lacking an entoconulid (Gingerich, 1980a).

Discussion.—Rose (1981) tentatively assigned this species to *Oxyaena* but was aware that it probably belonged elsewhere. He felt that it most closely resembled *Oxyaena*, but upon further study of these specimens we feel that it belongs with *Tytthaena*. It closely resembles *T. parrisi* in size and overall morphology, and lacks any trace of the exaggerated shearing crests typical of *Oxyaena* (see below). *Tytthaena* resembles *Dipsalidictis* in having trigonids on lower molars wider than long. *T. lichna* is still very poorly known but we think that it is probably more closely related to *T. parrisi* than to any other species. *Tytthaena* remains a plausible common ancestor for oxyaenines and palaeonictines (Gingerich, 1980a). Measurements of *T. lichna* are as follows: UM 71170, P_4 L = 5.6 mm, W = 3.1 mm; UM 71803, M_2 L = 6.2 mm, W = 3.9 mm.

Referred specimens.—UM 71170, 71681, and 71803.

Subfamily PALAEONICTINAE Denison, 1938

Included genera.—*Palaeonictis*, *Ambloctonus*, *Dipsalodon*, *Dormaalodon*.

Dipsalodon Jepsen, 1930b

Dipsalodon Jepsen, 1930b, p. 524. Simpson, 1937, p. 13. Denison, 1938, p. 174. Rose, 1981, p. 111.

Type species.—*Dipsalodon matthewi*.

Included species.—*D. matthewi*, *D. churchillorum*.

Diagnosis.—*Dipsalodon* differs from *Palaeonictis* in having M_2 only slightly smaller than M_1, in having less reduced metaconids on lower molars (especially M_2), in having more closed molar trigonids, and in having broader molar talonids.

Dipsalodon churchillorum Rose, 1981

Dipsalodon, new species, McKenna, 1980, p. 330
Dipsalodon churchillorum Rose, 1981, p. 111, fig. 59.

Holotype.—YPM-PU 17846, left P_3-M_2, right P_3, left P^4, associated fragments.

Type locality.—Princeton Storm Quarry, section 21, T57N, R100W, Fort Union Formation, Park County, Wyoming.

Age and distribution.—The holotype is from the late Tiffanian (zone Ti-5), late Paleocene, in the Clarks Fork Basin. Rose (1981) referred two additional specimens to this species from middle Clarkforkian beds in the Purdy Basin, Teton County, Wyoming. Another specimen here referred to *D. churchillorum* (FMNH 2609) is from Plateau Valley, Piceance Basin, Colorado of late Paleocene (either late Tiffanian or early Clarkforkian) age.

Diagnosis.—*D. churchillorum* differs from *D. matthewi* in being smaller, in having relatively shorter premolars, and in having a relatively smaller M_2.

Discussion.—*Dipsalodon churchillorum* resembles later species of both *Dipsalodon* and *Palaeonictis*. *D. churchillorum* resembles *Palaeonictis* in its smaller M_2 relative to M_1, and its open molar trigonid on M_2. It resembles *D. matthewi* in having broader molar trigonids than *Palaeonictis*, and in having a better developed P_4 talonid basin with an entoconid present. *Dipsalodon churchillorum* is intermediate in morphological detail between later *D. matthewi* and *Palaeonictis* and is a plausible common ancestor for both lineages. Measurements of *D. churchillorum* are provided in Table 1.

Referred specimens.—YPM-PU 17846, AMNH 56137, AMNH 86865, FMNH 2609, UM 67177, 71189.

Dipsalodon matthewi Jepsen, 1930b
Fig. 1

Dipsalodon matthewi Jepsen, 1930b, p. 524, Pl. 10, figs. 8-9. Simpson, 1937, p. 13. Denison, 1938, p. 174, figs. 6, 11. Rose, 1981, p. 111.
?Dipsalodon matthewi, McKenna, 1980, p. 330

Holotype.—YPM-PU 13152, left dentary P_2-M_2, right dentary C_1-M_2.

Type locality.—SE1/4, section 14, T56N, R101W, Park County, Wyoming. This is Jepsen's "Locality 2" (1930b).

Age and distribution.—All known specimens are from the middle Clarkforkian (zone Cf-2). *D. matthewi* is known only from northwestern Wyoming.

Diagnosis.—*Dipsalodon matthewi* differs from *D. churchillorum* in being larger, in having a less reduced M_2, and in having relatively longer premolars.

Description.—The upper dentition of *Dipsalodon matthewi* has not been described previously. UM 82392 is a right maxilla of *D. matthewi* with P^3-M^1 (Fig. 1). The specimen is from UM locality SC-62, located near the top of Clarkforkian zone Cf-2 (middle Clarkforkian).

P^3 is a three rooted tooth with a prominent paracone. The metacone is strong and nearly as high as the paracone. It is separated from the paracone by a narrow, deep notch. There is no protocone, but there is a distinct shelf that extends lingually and dorsally from the base of the paracone. There is an anterior basal cusp (parastyle) developed on an anterior extension at the base of the paracone. This anterior extension is separated from the protocone shelf by a deep notch. P^3 has a well developed posterior cingulum that wraps around the metacone and extends anteriorly to the base of the paracone on its buccal aspect. P^3 measures 15.5 mm in length and 11.5 mm in width.

P^4 is the largest tooth in the upper dental series (L = 15.8 mm, W = 17.6 mm). It is dominated by a very tall paracone (measuring 17.9 mm from enamel base to tip) that is slanted posteriorly. The metacone is well developed, but is barely half the height of the paracone. There is a distinct anterior basal cusp, but it is not extended into a shelf as it is in P^3. The protocone is well developed, positioned on the lingual margin of a strong lingual shelf. As in P^3, a posterior cingulum extends from the base of the lingual shelf around the metacone to the buccal aspect of the anterior basal cusp. There is heavy wear along the posterolingual portion of the paracone and the lingual aspect of the metacone. The posterior portion of the lingual shelf and the buccal aspect of the protocone are also heavily worn.

M^1 has a paracone and metacone of equal height. There is a small parastyle and a distinct metastyle, the latter of which is centrally located on a relatively short postmetacrista. The protocone is prominent and there is a well developed paraconule and metaconule. The trigon basin is deep and there is no trace of a hypocone. A small buccal cingulum extends from the parastyle to the base of the postmetacrista. There is a tiny cuspule on the buccal aspect of the postmetacrista. The posterolingual surface of the metacone and the lingual aspect of the postmetacrista are heavily worn as is the posterolingual surface of the paracone. The anterior surface of the paracone and the lingual aspect of the parastyle also exhibit extensive wear. M^1 measures 13.8 mm in length and 17.2 mm in width.

The maxilla is broken posterior to M^1. There is a single, large root present for M^2. It is not possible to determine if M^2 possessed only this single root or was double rooted.

Discussion.—Upper dentitions of *Palaeonictis occidentalis* are represented by a number of specimens including: AMNH 110 (holotype), AMNH 16116, USNM 19325, USNM 19366, USNM 19328, YPM-PU 16140, and UM 65707. The maxilla of *Dipsalodon matthewi* (UM 82392) described above differs from *P. occidentalis* by having a relatively broader M^1 with a more bulbous paraconule and metaconule. The P^4 paracone is more strongly slanted posteriorly and is relatively taller than in *P. occidentalis*. P^3 of *D. matthewi* has a better developed and

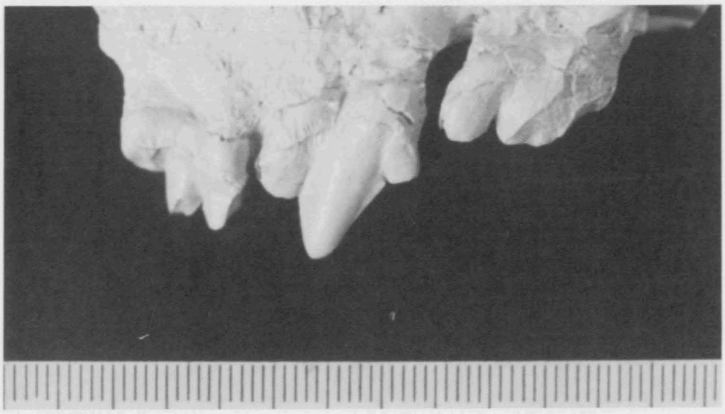

FIG. 1—Upper dentition of *Dipsalodon matthewi* (UM 82392). Right maxilla with P^3-M^1 in buccal view. Note posterior slope of paracone on P^4. Scale is in mm.

more distinct lingual expansion than does *P. occidentalis*. The lingual expansions (protocone shelves) of both P^3 and M^1 are more constricted anteroposteriorly in *Dipsalodon matthewi*.

Palaeonictis peloria (see below) and *Dipsalodon matthewi* are similar in size and gross morphology. Assignment of UM 82392 to *D. matthewi* instead of *P. peloria* is based on two considerations. First, the differences noted above between *P. occidentalis* (the Wasatchian palaeonictine representative) and UM 82392 suggest that this specimen does not belong to *Palaeonictis*. Second, Rose (1981) assigned UM 66167 to *D. matthewi* based on a fragmentary lower dentition. Associated with this specimen is the buccal half of a right M^1, showing the paracone, metacone, and postmetacrista. This specimen agrees in size and morphological detail with UM 82392, indicating that this specimen belongs with *Dipsalodon matthewi*. Measurements of *D. matthewi* are provided in Table 1.

Referred specimens.—UM 66167, 69671, 71465, 82392, and 91099.

Cf. *Dipsalodon* sp. Rose, 1981

cf. *Dipsalodon*, ?undescribed species, Rose, 1981, p. 133, fig. 60.

Discussion.—This enigmatic specimen (UM 71172) consisting of a broken lower premolar (P_3 or P_4) and a molar trigonid (M_1) was described by Rose (1981). No new information has become available since the original description. Its relationships to other oxyaenids remain unknown at this time.

Palaeonictis De Blainville, 1842

Palaeonictis De Blainville, 1842, p. 79. Osborn, 1892, p. 104. Matthew, 1915, p. 57. Denison, 1938, p. 175. Bown, 1979, p. 87. Rose, 1981, p. 113. Kihm, 1984, p. 128.

Type species.—*Palaeonictis gigantea.*

Included species.—*P. gigantea, P. occidentalis, P. peloria.*

Diagnosis.—*Palaeonictis* differs from *Dipsalodon* in having M_2 much smaller than M_1, in having a relatively smaller metaconid on M_2 with a more open trigonid, and in having a less well developed talonid on P_4 that lacks an entoconid cusp.

TABLE 1—Upper and lower tooth measurements of Palaeonictinae from the Clarks Fork Basin. All measurements in millimeters. Level represents meters above the base of the Fort Union Formation in the Clarks Fork Basin. Those levels enclosed in parentheses are estimated using biostratigraphic indicators and locality information. Prefixes for localities are FG-Foster Gulch, GR-Greybull River, MP-McCullough Peaks, SC-Sand Coulee, and YM-Yale-Michigan. All numbers are UM specimens except for 13152 (YPM-PU specimen, holotype of *Dipsalodon matthewi*), 17846 (YPM-PU specimen, holotype of *Dipsalodon churchillorum*), 2609 (FMNH specimen, referred specimen of *D. churchillorum*), and 18077 (YPM-PU specimen, holotype of *Palaeonictis peloria*). L = length, W = width

Upper dentition			P^3		P^4		M^1	
Specimen	Locality	Level	L	W	L	W	L	W
Dipsalodon churchillorum								
17846	Storm	0730	--	--	13.4	14.4	--	--
2609	Piceance	--	--	--	13.8	14.2	--	--
71189	SC-233	0755	14.1	9.8	--	--	--	--
Dipsalodon matthewi								
82392	SC-62	1380	15.5	11.5	15.8	17.6	13.8	17.2

Lower dentition			C_1		P_2		P_3		P_4		M_1		M_2	
Specimen	Locality	Level	L	W	L	W	L	W	L	W	L	W	L	W
Dipsalodon churchillorum														
17846	Storm	0730	--	--	--	--	--	--	11.8	7.3	12.5	8.1	12.1	7.7
67177	SC-86	0840	--	--	--	--	10.8	7.2	--	--	--	--	--	--
Dipsalodon matthewi														
13152	Jepsen 2	(1370)	--	--	10.5	6.4	14.5	8.0	14.9	9.2	14.2	9.3	13.2	9.3
66167	SC-74	1150	--	--	--	--	--	--	--	--	--	--	14.5	8.2
91099	MP-56	(1300)	--	--	--	--	--	--	--	--	13.6	8.5	--	--
Palaeonictis peloria														
18077	SC-55	1425	18.6	15.6	--	--	14.9	9.9	15.6	11.6	17.1	10.5	13.9	10.1
66505	SC-48	1425	--	--	10.5	6.9								
67445	SC-153	1505	--	--	--	--	--	--	--	--	16.5	8.7	--	--
Palaeonictis occidentalis														
65180	SC-7	1645	--	--	--	--	--	--	--	--	12.5	7.9	--	--
65398	SC-41	1560	--	--	--	--	11.5	8.0	13.7	8.9	--	--	--	--
66460	SC-96	1750	--	--	--	--	--	--	13.1	9.2	--	--	--	--
73596	SC-113	2050	--	--	--	--	11.7	8.0	--	--	--	--	--	--
77221	FG-42	----	13.3	6.0	9.9	6.2	11.7	8.1	13.4	8.6	13.8	9.2	11.7	7.7
83379	SC-54	1700	13.2	9.1	9.1	6.9	10.3	7.3	12.4	7.9	13.5	8.0	--	--

Palaeonictis peloria Rose, 1981

Palaeonictis peloria Rose, 1981, p. 113, fig. 61.

Holotype.—YPM-PU 18077, left dentary with P_3-M_2, associated left C_1.
Type locality.—UM locality SC-55, early Eocene, Willwood Formation, Park County, Wyoming.
Age and distribution.—Palaeonictis peloria is only known from the late Clarkforkian (Clarkforkian zone Cf-3) in the Clarks Fork Basin.
Diagnosis.—P. peloria differs from the other species of *Palaeonictis* in being significantly larger with a very heavy, robust mandible.
Discussion.—No new material of significance has been collected since Rose (1981) described this species. Measurements of *P. peloria* are provided in Table 1.
Referred specimens.—YPM-PU 18077, UM 65640, 66505, and 67445.

Palaeonictis occidentalis Osborn, 1892

Palaeonictis occidentalis Osborn, 1892, p. 104, figs. 5F, 7A, Pl. 4, figs. 1-5. Matthew, 1915, p. 58. Denison, 1938, p. 175, figs. 5-6, 9, 11, 14, 16.
Palaeonictis cf. *occidentalis*, Bown, 1979, p. 87.
Palaeonictis sp., Kihm, 1984, p. 128, Pl. 8, figs. 6-9.

Holotype.—AMNH 110, anterior part of skull, right dentary, collected in 1891 by J. L. Wortman.
Type locality.—South side of the Greybull River along Dorsey Creek, Bighorn Basin, Wyoming.
Age and distribution.—The holotype is probably early Graybullian in age (Wasatchian zone Wa-3), while other specimens are known from the Clarks Fork Basin and northern Bighorn Basin ranging through the early and middle Wasatchian (zones Wa-1 through Wa-4). Gingerich (1989) reported one specimen from the earliest Wasatchian (Wa-0). Kihm (1984) reported five specimens of *Palaeonictis* from the Piceance Basin in Colorado (possibly latest Clarkforkian, see Gunnell, 1989) that we tentatively assign to this species.
Diagnosis.—P. occidentalis differs from *P. peloria* in being smaller, differs from *P. gigantea* in being significantly larger. It also differs from *P. peloria* in having M_2 smaller relative to M_1, and in having a less robust dentary and symphysis.
Discussion.—Palaeonictis occidentalis is the only palaeonictine known from Wasatchian sediments in the Clarks Fork Basin. It is very similar to the European species *P. gigantea*, differing from that species only by its larger size. No new morphological details can be gathered from the specimens in the University of Michigan collections. Measurements of *P. occidentalis* are provided in Table 1.
Referred specimens.—UM 63905, 65180, 65398, 65707, 66460, 71138, 73459, 73596, 77221, 83379, 87005, 87080, 87758, 93556, and 93561.

Ambloctonus cf. *A. priscus*

Discussion.—One UM specimen (UM 91477 from locality MP-75) can be referred to *Ambloctonus*. The specimen consists of an M_2 trigonid that compares favorably in size and morphology with *Ambloctonus priscus* Matthew (1915).

Subfamily OXYAENINAE Wortman, 1902

Included genera.—*Dipsalidictis*, *Oxyaena*, *Patriofelis*, and *Protopsalis*.

Dipsalidictis Matthew, 1915

Dipsalidictis Matthew, 1915, p. 63. Jepsen, 1930a, p. 128. Gingerich, 1989, p. 31.
Dipsalidictides Denison, 1938, p. 167.
Oxyaena (in part), Matthew, 1915, p. 47. Jepsen, 1930a, p. 128. Simpson, 1937, p. 13. Denison, 1938, p. 167. Van Valen, 1966, p. 79. Bown, 1979, p. 85-86. McKenna, 1980, p. 330-331. Rose, 1981, p. 107.
Oxyaena sp., McKenna, 1960, p. 94. Van Valen, 1965, p. 658. Rich, 1971, p. 29. Hooker, 1980, p. 102. Hooker et al., 1980, p. 41. Russell et al., 1982a, p. 59. Russell et al., 1982b, p. 20.

Type species.—*Dipsalidictis platypus.*
Included species.—*D. platypus*, *D. aequidens* (new combination), *D. transiens* (new combination), *D. krausei* (new species).
Diagnosis.—*Dipsalidictis* differs from *Oxyaena* in having lower molar trigonids wider than long, in having better developed metaconids on lower molars, in having relatively shorter paralophids on lower molars, and in having relatively shorter postmetacristae on upper M^1 (see Gingerich, 1989).
Discussion.—Denison (1938) moved the type species of *Dipsalidictis* (*D. platypus*) to *Oxyaena* and placed *D. amplus* Jepsen (1930a) in a new genus *Dipsalidictides*. He felt that *D. platypus* differed from *Oxyaena* only in its smaller size while *D. amplus* was sufficiently different to warrant generic distinction. Both Van Valen (1966) and Rose (1981) maintained the distinction between *Dipsalidictides* and *Oxyaena* (although Rose questioned this and felt that it was possible that the two forms were congeneric). Van Valen (1966) maintained the distinction based upon the presence of a double-rooted P_1 in *Dipsalidictides* and differences in what he termed angle Q (the angle the metacrista makes with a line joining the paracone and metacone on M^1, as seen in occlusal view). This angle is approximately 120 degrees in *Dipsalidictides* and between 135 to 150 degrees in *Oxyaena* (Van Valen, 1966).
For reasons given in our generic diagnoses, we think that Matthew's (1915) separation of *D. platypus* from other oxyaenids is correct (see also Gunnell, 1988; Gingerich, 1989), and we use *Dipsalidictis* to accommodate all Clarkforkian and most early Wasatchian oxyaenines. In this way, all oxyaenines with molar trigonids wider than long with moderate shearing specializations (see below) are included in a single genus.

Dipsalidictis krausei, new species
Fig. 2, 3, 6F, 7B,E,H

Oxyaena transiens (in part), Rose, 1981, p. 105, figs. 54-55.

Holotype.—UM 69331, skull, left and right dentaries, and associated postcranial elements.
Type locality.—UM locality SC-195 ("Krause Quarry"), middle Clarkforkian beds (Clarkforkian zone Cf-2), Willwood Formation, Clarks Fork Basin, Wyoming.
Age and distribution.—The holotype is from middle Clarkforkian beds (Cf-2), while additional specimens are known from early and late Clarkforkian beds (Cf-1, Cf-3). *D. krausei* is unknown outside of the Clarks Fork Basin.
Diagnosis.—*Dipsalidictis krausei* differs from *D. platypus* in being significantly larger, differs from *D. aequidens* in being smaller and in having less robust premolars, differs from *D. transiens* in having narrower lower molar talonids, a more anteroposteriorly compressed M_1 trigonid, and less robust premolars with P_4 lacking or having a very small anterior basal cusp.
Etymology.—Named for Dr. David W. Krause who discovered the quarry from which the type specimen came and in recognition of his many contributions to the understanding of Paleocene and Eocene mammalian evolution.

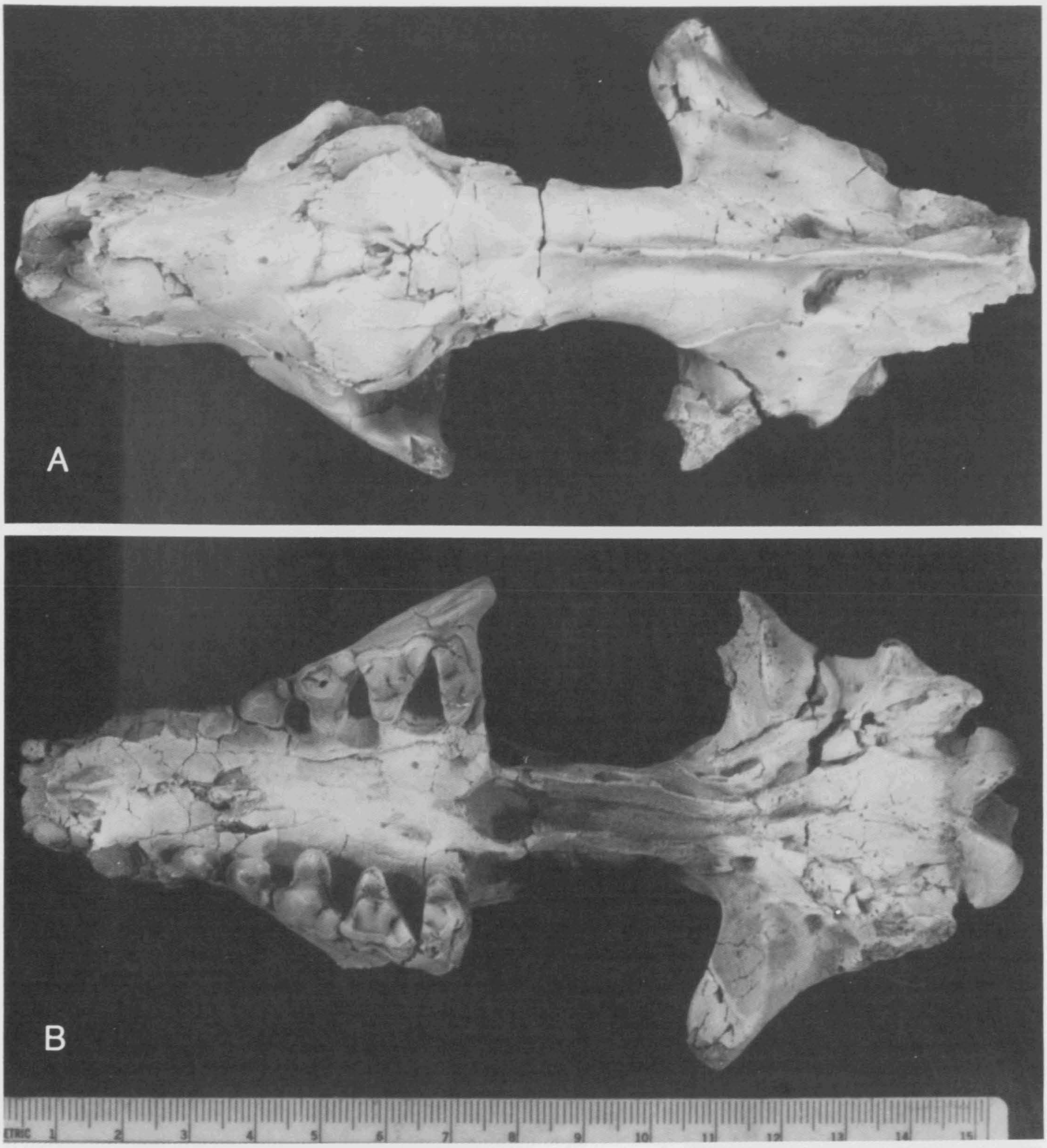

FIG. 2—Skull of *Dipsalidictis krausei*, UM 69331 (holotype). A, dorsal view; B, ventral view. Note strong postorbital constriction, guttered zygomatic processes, and heavy sagittal and occipital crests. Scale is in mm.

Description.—UM 69331 preserves most of the skull and lower dentition of *D. krausei*. The dental formula is 3.1.4.2 for the upper series and 2.1.4.2 for the lower series. The upper lateral incisors are preserved and are caniniform and larger than either of the two more central incisors (judging by alveoli of the latter two teeth). There is a short diastema between I^3 and the canine, which, judging from the alveolus, was large and projecting. P^1 is not preserved but was a single rooted tooth. P^2 is double rooted and dominated by a single cusp (paracone). It has a small cuspule along its posterior margin. P^3 is triple rooted, although there is no distinct

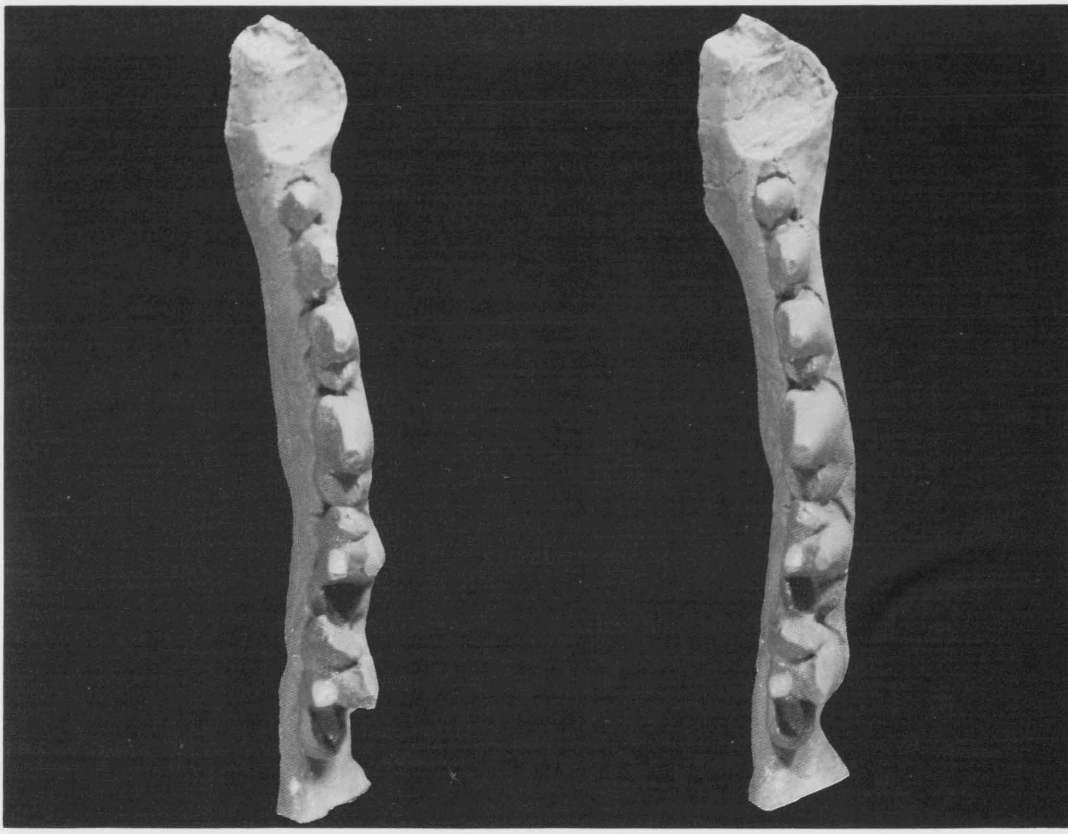

FIG. 3—Stereophotograph of lower dentition of *Dipsalidictis krausei*, UM 69331 (holotype). Occlusal view. Left dentary preserves alveolus for C_1 and intact crowns of P_{1-4}, M_{1-2}. Scale is in mm.

protocone. There is a small lingually projecting shelf giving the tooth a triangular outline in occlusal view. P^4 has a large paracone and a smaller metacone on the buccal half of the tooth. The protocone is well developed. A weak parastyle is also present. M^1 is of a typical oxyaenine form, with paracone and metacone placed close together and of equal height. There is a small parastyle. The metastyle is expanded into a moderate postmetacrista. The protocone is quite small and there is only a slight development of a trigon basin. There is a small paraconule and metaconule. A weak lingual cingulum is present but there is no hypocone. M^2 is anteroposteriorly compressed with a large paracone and a small metacone. There is a distinct parastyle that extends into a small preparacrista. The protocone is present but very low, and there is a paraconule but no metaconule. As in M^1, M^2 also has a weak lingual cingulum.

The lower incisors and canines are not preserved. Judging from alveoli, the lateral incisor was larger than the central incisor. The canine was large, oval in cross-section and projecting. P_1 is a small, single rooted, single-cusped tooth. P_2 is only slightly larger than P_1, is double rooted, and has a small posterior cuspule. P_3 is similar to P_2 except that it is larger with a better developed posterior cusp. P_4 is larger than P_3 but is similar in morphology, differing only in having a much better developed talonid cusp and by having a tiny anterior basal cuspule or fold. This anterior fold is not present on all specimens of the species. M_1 has a large protoconid and smaller, lower paraconid and metaconid, with the metaconid being slightly higher than the paraconid while the paraconid is more robust than the metaconid. The trigonid is wider than long as is typical of *Dipsalidictis*. The talonid is low and narrow but well developed. The talonid basin is shallow. M_2 is similar to M_1 in morphology but is slightly larger. The talonid of M_2 is narrower than that on M_1.

The skull of UM 69331 (see Fig. 2) has suffered very little distortion and is missing only the left and right zygomatic processes, the right mastoid and paroccipital processes of the exoccipital, both canines and first premolars, and I^{1-2} on both sides. There is some breakage of the mid-palate, the orbits, and the subnasal regions. The skull is 141 mm long. There is strong postorbital constriction with a small cranial cavity and relatively large olfactory bulbs (typical of most oxyaenids, see Matthew, 1909, and Denison, 1938). There is a prominent sagittal crest that arises at the confluence of the temporal lines and extends posteriorly to join the occipital. The occipital is expanded dorsally and laterally together with the parietals to form large muscular attachment surfaces. The dorsal surface at the base of the zygomatic process of the temporal is guttered, indicating large, heavy temporalis musculature. The postorbital process is small. There is no ossified auditory bulla.

The basicranial region of this specimen is particularly well preserved. The basioccipital dominates the posterior half of the basicranium. It is quite robust with a strong midline crest. As the basioccipital joins the basisphenoid it bulges ventrally to form two rounded projections. A deep groove is formed between these projections that continues anteriorly onto the basisphenoid. The basisphenoid continues anteriorly to join pterygoid plates that are wide and long. The glenoid fossae are relatively deep with strong postglenoid processes. There is a relatively well developed preglenoid crest present, a feature that appears to unite Oxyaenidae (see Matthew, 1909; Denison, 1938). The mastoid and paroccipital processes are robust and extend laterally, posteriorly, and slightly ventrally. The otic fossa is bounded posterolaterally by the mastoid and paroccipital processes, medially by the basioccipital, and anterolaterally by the postglenoid process of the temporal.

The path of the carotid artery can be traced along the lateral aspect of the basioccipital as a shallow groove. It passes over the edge of the basioccipital just posterior and medial to the posterior apex of the promontorium, and then passes around the medial aspect of the base of the promontorium anteriorly to enter the foramen lacerum medium. A small, shallow groove across the posterior aspect of the promontorium indicates the presence of a small stapedial artery. There is no indication of an additional carotid branch that travelled to the foramen lacerum medium across the external surface of the promontorium as Matthew (1909) described for *Limnocyon* (see MacPhee, 1981, for additional discussion of mammalian carotid circulatory patterns).

The promontorium has an elongated pear-shape, tapering anteriorly. Its apices are oriented anteromedially and posterolaterally. Its ventrolateral surface is smoothly rounded. There is a large cochlear fenestra dorsal to the posterior apex. Dorsal, lateral, and anterior to the cochlear fenestra is the vestibular fenestra, deep in the mesotympanic fossa.

UM 69331 preserves both dentaries. The body of the mandible is quite slender and gracile. It deepens slightly below M_2 and anteriorly at the symphysis. There are three mental foramina, one below I_3, one below the anterior root of P_2, and a third below the posterior root of P_3. The masseteric fossa is relatively deep. The coronoid and condylar crests are prominent. The mandibular foramen below the anterior aspect of the coronoid process is well developed. The articular condyle is at the level of the tooth row, a condition typical of most carnivorous mammals. The symphysis begins below the anterior root of P_3.

Discussion.—Dipsalidictis krausei is the most primitive species of *Dipsalidictis.* Carnassial shearing specializations are only moderately developed in *D. krausei.* It has simple premolars and a less specialized dentition that resembles *D. transiens* from the Wasatchian and may have given rise to that species. Early *D. krausei,* because of its primitive nature and age, may well have been ancestral to all later species of oxyaenines. Measurements of *D. krausei* are provided in Tables 2-3, summary statistics in Table 4.

Referred specimens.—UM 66180, 66199, 66309, 66700, 66924, 69331 (holotype), 69908, 71679, 71680, 71775, 79849, 80434, and 83429.

TABLE 2—Measurements of upper teeth of Oxyaeninae from the Clarks Fork and northern Bighorn Basins. All measurements in millimeters. Level represents meters above the base of the Fort Union Formation in the Clarks Fork Basin. Those levels enclosed in parentheses are estimated using biostratigraphic indicators and locality information. Prefixes for localities are the same as in Table 1. All numbers are UM specimens except 13153 (YPM-PU specimen, holotype of *Dipsalidictis amplus*), 15857 (AMNH specimen, holotype of *Dipsalidictis platypus*), and 16118 (AMNH specimen, holotype of *Oxyaena transiens*). L = length, W = width.

			C^1		P^2		P^3		P^4		M^1		M^2	
Specimen	Locality	Level	L	W	L	W	L	W	L	W	L	W	L	W
Oxyaena forcipata														
86948	MP-16	2250	--	--	--	--	--	--	--	--	21.4	12.2	11.3	21.0
75718	SC-303	2110	--	--	--	--	--	--	--	--	19.4	15.1	--	--
Oxyaena gulo														
65297	SC-34	1850	--	--	8.4	5.5	--	--	15.3	15.0	16.3	15.5	7.4	16.1
68114	SC-133	1750	--	--	--	--	--	--	--	--	13.1	13.0	--	--
79545	SC-213	1760	--	--	--	--	--	--	--	--	14.4	13.6	--	--
Dipsalidictis transiens														
13153	--	1590	--	--	--	--	8.4	4.9	12.0	11.2	9.9	13.2	4.6	13.6
16118	--	1540	--	--	--	--	6.2	4.1	12.6	11.5	--	10.5	--	--
73777	SC-288	1560	--	--	--	--	--	--	12.8	12.4	--	--	--	--
76230	SC-41	1560	9.4	6.7	--	--	--	--	--	--	--	11.5	--	--
80063	SC-54	1700	--	--	--	--	--	--	12.2	12.0	12.6	12.7	--	--
86433	SC-46	1700	--	--	--	--	--	--	--	--	10.5	10.1	--	--
Dipsalidictis platypus														
15857	SC-67	1520	6.1	4.8	--	--	--	--	--	--	10.1	8.0	--	--
66137	SC-67	1520	--	--	--	--	--	--	--	--	9.5	9.5	4.7	10.6
79382	SC-6	1530	--	--	--	--	--	--	--	--	--	10.6	--	--
Dipsalidictis aequidens														
68871	SC-189	1275	14.1	9.9	--	--	10.3	8.0	14.0	12.6	13.8	14.1	8.0	13.4
Dipsalidictis krausei														
69331	SC-195	1255	--	--	5.8	4.2	8.5	6.0	11.5	12.1	11.4	12.4	7.2	13.3
71679	SC-72	1435	--	--	--	--	--	--	--	--	10.0	11.6	--	--

Dipsalidictis aequidens (Matthew, 1915)
Fig. 4

Oxyaena aequidens Matthew, 1915, p. 47, fig. 41. Simpson, 1937, p. 13. Van Valen, 1966, p. 79.
Oxyaena aequidens (in part), Rose, 1981, p. 104.

Holotype.—AMNH 16070, left and right lower teeth, collected in 1912 by Walter Granger and William Stein.

Type locality.—The holotype is from seven miles east of the mouth of Pat O'Hara Creek, Clarks Fork Basin, Wyoming. This area is near UM localities SC-61, SC-119, and SC-120. These localities span the boundary between Clarkforkian zones Cf-1 and Cf-2. The holotype is probably from earliest Cf-2 because Granger and Stein concentrated on "Ralston beds" (Willwood Formation) while working in this area (for a discussion of the relationship between time stratigraphic and rock stratigraphic units in this area see Rose, 1981; for a discussion of the history of collecting in this area see Gingerich, 1980b).

TABLE 3—Measurements of lower teeth of Oxyaeninae from the Clarks Fork and northern Bighorn Basins. All measurements in millimeters. Level represents meters above the base of the Fort Union Formation in the Clarks Fork Basin. Those levels enclosed in parentheses are estimated using biostratigraphic indicators and locality information. Prefixes for localities are the same as in Table 1. All numbers are UM specimens except 3425 (RAM specimen from near Emblem, Wyoming), 13153 (YPM-PU specimen, holotype of *Dipsalidictis amplus*), 15857 (AMNH specimen, holotype of *Dipsalidictis platypus*), 16118 (AMNH specimen, holotype of *Oxyaena transiens*), 19544 (YPM-PU specimen from SC-136), and 21215 (YPM-PU specimen from Sand Coulee area). L = length, W = width.

			C_1		P_2		P_3		P_4		M_1		M_2	
Specimen	Locality	Level	L	W	L	W	L	W	L	W	L	W	L	W
Oxyaena forcipata														
75208	GR-007	(2300)	16.3	11.7	--	--	--	--	17.5	10.2	--	--	--	--
86948	MP-016	(2250)	14.7	11.7	--	--	13.9	8.2	17.4	9.9	19.1	11.4	21.9	12.6
91559	MP-076	(2200)	--	--	--	--	--	--	--	--	19.2	10.7	--	--
94269	MP-173	(2150)	15.0	10.5	10.9	5.7	12.5	7.7	16.7	10.4	17.8	10.3	19.6	12.6
95021	MP-173	(2150)	16.1	11.5	--	--	--	--	--	--	--	--	20.5	12.4
94410	MP-170	(2150)	--	--	--	--	--	--	--	--	--	--	18.6	10.2
64123	YM-421	(2150)	--	--	--	--	--	--	--	--	18.4	10.0	--	--
64137	YM-421	(2150)	--	--	--	--	--	--	16.6	11.1	--	--	--	--
3425	--	(2140)	13.3	9.3	--	--	12.1	7.3	16.2	9.1	15.8	9.2	19.2	10.6
92585	MP-122	(2100)	--	--	--	--	12.7	7.1	16.7	9.1	15.9	9.4	19.9	11.6
Oxyaena intermedia														
69712	SC-146	2065	--	--	--	--	--	--	--	--	14.9	8.3	--	--
86995	MP-017	(2110)	--	--	--	--	--	--	--	--	14.5	9.0	18.0	10.5
91927	MP-086	(2150)	--	--	--	--	--	--	13.8	8.0	13.6	7.5	--	--
64037	YM-420	--	--	--	10.0	5.6	--	--	14.5	8.3	14.0	7.7	--	--
Oxyaena gulo														
67416	SC-046	1700	--	--	--	--	--	--	--	--	--	--	14.2	9.1
63670	YM-90c	(1800)	10.8	6.8	--	--	8.1	5.0	12.6	7.1	13.2	7.4	13.6	8.4
65287	SC-032	1815	10.3	7.5	7.6	4.9	11.2	6.9	--	--	--	--	15.5	9.4
76734	SC-003	1935	12.4	8.6	--	--	--	--	14.4	8.1	--	--	--	--
Dipsalidictis transiens														
13153	--	1590	8.3	6.6	--	--	6.8	4.0	10.4	5.5	--	--	11.8	7.4
16118	--	1540	--	--	--	--	8.5	4.8	10.8	6.1	--	--	11.7	7.7
68201	SC-161	1665	--	--	--	--	--	--	--	--	11.0	6.5	--	--
73777	SC-288	1560	--	--	6.9	4.1	--	--	11.7	6.5	--	--	--	--
76230	SC-041	1560	10.1	7.3	--	--	--	--	--	--	--	--	--	--
80063	SC-054	1700	--	--	--	--	--	--	--	--	12.0	7.2	13.1	8.8
80704	SC-161	1665	9.1	6.2	--	--	9.0	5.1	11.8	6.4	11.5	6.7	12.3	8.0
82460	SC-161	1665	--	--	--	--	--	--	--	--	11.4	6.4	--	--
86025	SC-161	1665	--	--	--	--	--	--	--	--	11.4	7.1	14.5	9.1
Dipsalidictis platypus														
15857	SC-067	1520	7.7	5.3	--	--	--	--	--	--	8.3	5.3	9.3	6.1
21215	--	1370	--	--	--	--	--	--	8.0	4.5	--	--	--	--
66137	SC-067	1520	--	--	--	--	--	--	--	--	8.6	5.3	9.9	6.2
72955	SC-020	1380	--	--	--	--	--	--	--	--	8.5	5.4	--	--
Dipsalidictis aequidens														
19544	SC-136	1200	--	--	--	--	--	--	12.4	7.3	10.9	7.6	--	--
65039	SC-019	1370	--	--	--	--	--	--	12.9	7.9	--	--	13.6	8.4
67024	SC-120	1300	13.6	10.2	6.3	5.0	9.5	6.5	13.2	7.6	--	--	14.2	9.0
68869	SC-188	1280	--	--	--	--	8.4	5.6	12.7	7.0	--	--	13.3	8.5
68879	SC-190	1270	--	--	--	--	8.4	5.9	--	--	--	--	13.6	8.6
87806	SC-117	1370	13.4	11.2	--	--	--	--	13.0	7.8	--	--	14.7	9.0
Dipsalidictis krausei														
66180	SC-074	1150	9.6	6.9	6.0	3.9	7.5	4.7	10.2	6.0	10.8	6.3	12.2	7.7
69331	SC-195	1255	--	--	5.6	4.2	7.1	5.2	9.0	6.2	10.8	6.6	12.3	7.5
80434	SC-074	1150	--	--	--	--	--	--	--	--	10.9	6.5	--	--
66309	SC-090	1455	--	--	--	--	--	--	--	--	10.4	6.0	--	--

TABLE 4—Summary tooth statistics for Clarks Fork and Bighorn Basin *Dipsalidictis krausei*. Abbreviations: N, number of individuals; OR, observed range of measurements; S, standard deviation; V, coefficient of variation; L, length; W, greatest width. All measurements in millimeters.

Measurement		N	OR	Mean	S	V
Upper dentition						
P^2	L	1	5.8	--	--	--
	W	1	4.2	--	--	--
P^3	L	1	8.5	--	--	--
	W	1	6.0	--	--	--
P^4	L	1	11.5	--	--	--
	W	1	12.1	--	--	--
M^1	L	2	10.6 - 11.4	10.70	--	--
	W	2	11.6 - 12.4	12.00	--	--
M^2	L	1	7.2	--	--	--
	W	1	13.3	--	--	--
Lower dentition						
C_1	L	1	9.6	--	--	--
	W	1	6.9	--	--	--
P_1	L	1	4.0	--	--	--
	W	1	3.2	--	--	--
P_2	L	2	5.6 - 6.0	5.80	--	--
	W	2	3.9 - 4.2	4.05	--	--
P_3	L	2	7.1 - 7.5	7.30	--	--
	W	2	4.7 - 5.2	4.95	--	--
P_4	L	2	9.0 - 10.2	9.60	--	--
	W	2	6.0 - 6.2	6.10	--	--
M_1	L	4	10.4 - 10.9	10.72	0.22	2.1
	W	4	6.0 - 6.6	6.35	0.26	4.2
M_2	L	2	12.2 - 12.3	12.25	--	--
	W	2	7.5 - 7.7	7.60	--	--

Age and distribution.—*Dipsalidictis aequidens* is known from Clarkforkian beds (zones Cf-2 and Cf-3) in the Clarks Fork Basin. Van Valen (1966) reported a single specimen (AMNH 55499) from beds north of Mason Pocket, near the settlement of Ignacio, Colorado, that probably represents this species. It is likely that these beds are Clarkforkian in age, not Tiffanian as Van Valen believed.

Diagnosis.—*D. aequidens* differs from *D. platypus* in being much larger. It differs from *D. transiens* and *D. krausei* in being larger and in having more robust and relatively larger premolars (especially P_4).

Discussion.—*D. aequidens* approaches *Oxyaena* in its moderately well developed M^1 postmetacristae and M_2 paralophids. It also has a well developed maxillary excavation between M^1 and M^2, typical of *Oxyaena*. However, *D. aequidens* remains primitive in having lower molar trigonids wider than long and by having its shearing crests less well developed than is typical of *Oxyaena*. It also retains a metacone on M^2 that seems to be lost in all *Oxyaena* species. Measurements of *D. aequidens* are provided in Tables 2-3, summary statistics in Table 5.

Referred specimens.—UM 65038, 65039, 66768, 67024, 68869, 68871, 68873, 68879, 69326, 69549, 80243, 85994, and 87806.

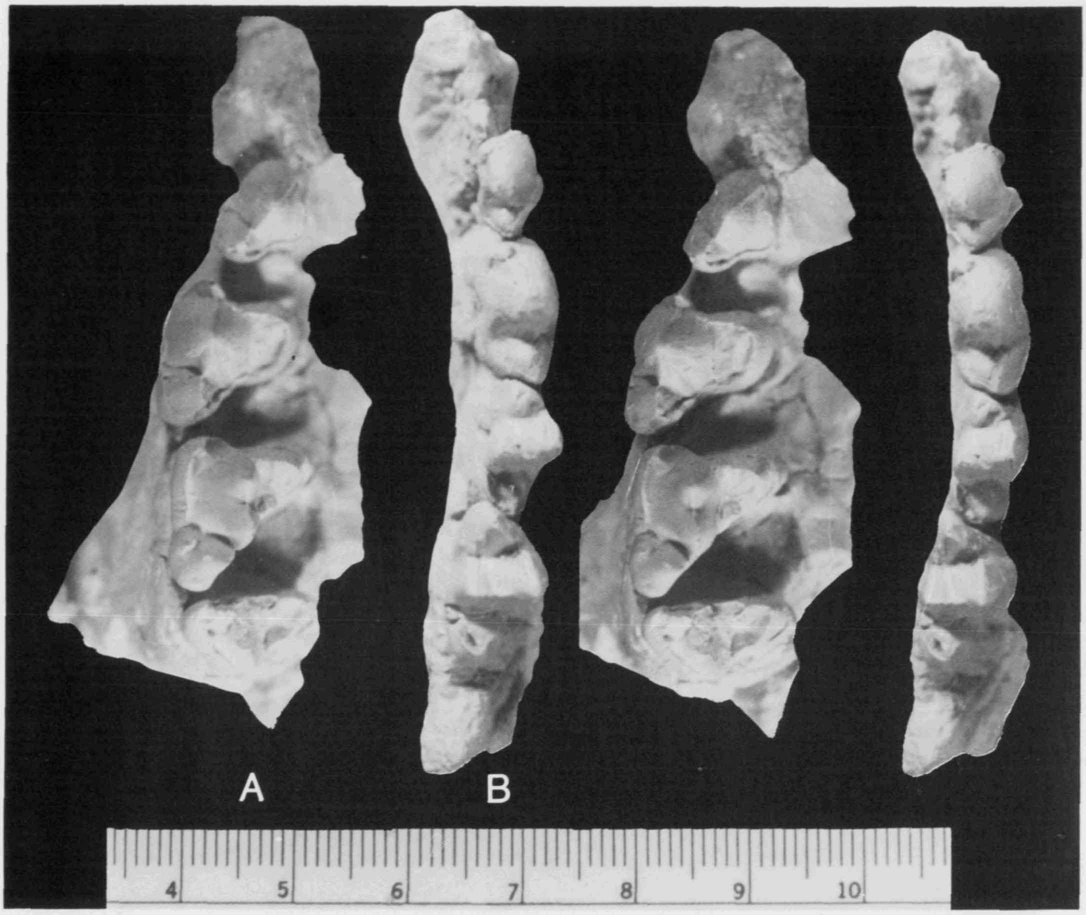

FIG. 4—Stereophotographs of upper and lower dentition of *Dipsalidictis aequidens*. A, UM 68871, right maxilla with P^3-M^2 in occlusal view. B, UM 87806, right dentary with P_3-M_2 in occlusal view. Note robustness of lower premolars. Scale is in mm.

Dipsalidictis platypus Matthew, 1915
Fig. 6C,D,G, 7C,F,I

Dipsalidictis platypus Matthew, 1915, p. 65, figs. 54-56. Gingerich, 1989, p. 31, fig. 19.

Oxyaena platypus, Denison, 1938, p. 167, figs. 8, 11, 25b, 26a-b,e. Van Valen, 1966, p. 79. Gingerich, 1980a, p. 573, fig. 3a. McKenna, 1980, p. 330. Rose, 1981, p. 107, fig. 56.

Holotype.—AMNH 15857, broken palate with right C^1, P^4, left P^4-M^1, left dentary with C_1, P_1, M_{1-2}, right dentary with broken P_4-M_1, and associated postcranial elements.

Type locality.—The holotype is recorded as coming from three miles north of the settlement of Ralston, Park County, Wyoming, on the southeast side of Polecat Bench. This is UM locality SC-67, as confirmed by discovery of an additional part of the holotype at this locality in the early 1980s (Gingerich, 1989).

Age and distribution.—The holotype is from the earliest Wasatchian, zone Wa-0. Other specimens are known from Clarkforkian beds in zones Cf-2 and Cf-3, and from Wasatchian zone Wa-1. The species is known only from northwestern Wyoming.

TABLE 5—Summary tooth statistics for Clarks Fork and Bighorn Basin *Dipsalidictis aequidens*. Abbreviations as in Table 4. All measurements in millimeters.

Measurement		N	OR	Mean	S	V
Upper dentition						
C^1	L	1	14.1	--	--	--
	W	1	9.9	--	--	--
P^3	L	1	10.3	--	--	--
	W	1	8.0	--	--	--
P^4	L	1	14.0	--	--	--
	W	1	12.6	--	--	--
M^1	L	1	13.8	--	--	--
	W	1	14.1	--	--	--
M^2	L	1	8.0	--	--	--
	W	1	13.4	--	--	--
Lower dentition						
C_1	L	2	13.4 - 13.6	13.50	--	--
	W	2	10.2 - 11.2	10.70	--	--
P_2	L	1	6.3	--	--	--
	W	1	5.0	--	--	--
P_3	L	3	8.4 - 9.5	8.77	0.64	7.2
	W	3	5.6 - 6.5	6.00	0.46	7.6
P_4	L	5	12.4 - 13.2	12.84	0.30	2.4
	W	5	7.0 - 7.9	7.52	0.37	4.9
M_1	L	1	10.9	--	--	--
	W	1	7.6	--	--	--
M_2	L	5	13.3 - 14.7	13.90	0.56	4.1
	W	5	8.4 - 9.0	8.70	0.28	3.3

Diagnosis.—*Dipsalidictis platypus* is significantly smaller than all other known Clarkforkian and Wasatchian oxyaenines.

Discussion.—New material from UM locality SC-67 is virtually indistinguishable from the holotype in both morphology and preservation. Postcranial elements of this species were illustrated by Matthew (1915) and Gingerich (1989), and these are also discussed below. Study of the postcranial elements continues (Gunnell, 1988; Rose and Gunnell, in prep.). Measurements of *D. platypus* are provided in Tables 2-3, summary statistics in Table 6.

Referred specimens.—UM 66137, 67255, 71678, 72955, 73406, 74080, 79382, 83616, 86231, 93379, and 95108.

Dipsalidictis transiens (Matthew, 1915)

Fig. 6B

Oxyaena transiens Matthew, 1915, p. 47, figs. 42-43. Denison, 1938, p. 168. Van Valen, 1966, p. 79. McKenna, 1908, p. 330.
Oxyaena transiens (in part), Rose, 1981, p. 105.
Oxyaena sp., near *O. transiens*, Bown, 1979, p. 85, figs. 51d-e.
Oxyaena sp., McKenna, 1960, p. 94. Davidson, 1987, p. 119.
Dipsalidictis amplus Jepsen, 1930a, p. 128, Pl. 4, figs. 1-2.
Dipsalidictides amplus (Denison, 1938), p. 167, figs. 6,8. Van Valen, 1966, p. 79. Bown, 1979, p. 86, fig. 52a. Rose, 1981, p.105.

TABLE 6—Summary tooth statistics for Clarks Fork and Bighorn Basin *Dipsalidictis platypus*. Abbreviations as in Table 4. All measurements in millimeters.

Measurement		N	OR	Mean	S	V
Upper dentition						
C^1	L	1	6.1	--	--	--
	W	1	4.8	--	--	--
M^1	L	2	9.5 - 10.1	9.80	--	--
	W	3	8.0 - 10.6	9.37	1.30	13.9
M^2	L	1	4.7	--	--	--
	W	1	10.6	--	--	--
Lower dentition						
P_4	L	1	8.0	--	--	--
	W	1	4.5	--	--	--
M_1	L	3	8.5 - 8.6	8.53	0.06	0.7
	W	3	5.3 - 5.4	5.33	0.06	1.0
M_2	L	2	9.3 - 9.9	9.60	--	--
	W	2	6.1 - 6.2	6.15	--	--

Holotype.—AMNH 16118, left and right dentaries, right P_3-M_2, left P_3, M_{1-2}, right maxilla P^2-M^1 and left M^1 fragment.

Type locality.—Three miles southeast of the mouth of Pat O'Hara Creek, Clarks Fork Basin, Wyoming, from Sandcouleean beds.

Age and distribution.—The holotype is from early Wasatchian beds (Wa-1) in the Clarks Fork Basin. Additional specimens from the Clarks Fork Basin are known from Wasatchian zones Wa-0 and Wa-2. Several specimens are known from the Sand Creek facies of the Willwood Formation in the central Bighorn Basin (Bown, 1979). These specimens are from early Graybullian beds (Wa-3). There are four fragmentary specimens reported by McKenna (1960) from the Four Mile fauna in Colorado that we assign to this species. They are also early to middle Wasatchian in age (zones Wa-2 and Wa-3). Davidson (1987) reported the presence of some fragmentary oxyaenine teeth from the Laramie Basin in southeastern Wyoming that we assign to this species. These also are early to middle Wasatchian in age.

Diagnosis.—*D. transiens* differs from *D. platypus* in being larger and in having better developed postmetacristae and paralophid shearing crests. It differs from *D. aequidens* in being smaller and in having less robust premolars. *D. transiens* differs from *D. krausei* in having a better developed paralophid shearing crest on M_2, in having a larger M_2 relative to M_1, and in having slightly more robust lower premolars, often with a well developed anterior accessory cusp.

Discussion.—*D. transiens* is quite similar to *Oxyaena gulo*. It has a relatively elongate postmetacrista on M^1 and the paralophid of M_2 is extended into a relatively well developed cutting blade. *D. transiens* does not have as high a protoconid on M_2. *D. transiens* also has the *Dipsalidictis* lower molar trigonid configuration (trigonids wider than long) and retains a M^2 metacone.

Van Valen (1966) states that since the types of these species come from different levels in the Graybullian, *D. transiens* should be retained as a primitive subspecies of *O. gulo*. The type of *O. gulo* was collected in 1910 by William J. Sinclair and Walter Granger along Elk Creek, near their Dry Camp 5, south and west of the settlement of Basin, Wyoming. This

TABLE 7—Summary tooth statistics for Clarks Fork and Bighorn Basin *Dipsalidictis transiens*. Abbreviations as in Table 4. All measurements in millimeters.

Measurement		N	OR	Mean	S	V
Upper dentition						
C^1	L	1	9.4	--	--	--
	W	1	6.7	--	--	--
P^3	L	2	6.2 - 8.4	7.30	--	--
	W	2	4.1 - 4.9	4.50	--	--
P^4	L	4	12.0 - 12.8	12.40	0.37	2.9
	W	4	11.2 - 12.4	11.78	0.53	4.5
M^1	L	3	9.9 - 12.6	11.00	1.42	12.9
	W	5	10.1 - 13.2	11.60	1.34	11.6
M^2	L	1	4.6	--	--	--
	W	1	13.6	--	--	--
Lower dentition						
C_1	L	3	8.3 - 10.1	9.17	0.90	9.8
	W	3	6.2 - 7.3	6.70	0.56	8.3
P_2	L	1	6.9	--	--	--
	W	2	4.1	--	--	--
P_3	L	3	6.8 - 9.0	8.10	1.15	14.2
	W	3	4.0 - 5.1	4.63	0.57	12.3
P_4	L	4	10.4 - 11.8	11.18	0.68	6.1
	W	4	5.5 - 6.5	6.13	0.45	7.3
M_1	L	5	11.0 - 12.0	11.46	0.36	3.1
	W	5	6.4 - 7.2	6.78	0.36	5.3
M_2	L	5	11.7 - 14.5	12.68	1.16	9.1
	W	5	7.4 - 9.1	8.20	0.72	8.8

area corresponds to the early Wasatchian (probably early Graybullian, Wasatchian zone Wa-3). Most Clarks Fork Basin specimens of *O. gulo* are from early Graybullian (Wasatchian zone Wa-3), although some are from near the top of Wasatchian zone Wa-2.

The type of *D. transiens* was collected in the Clarks Fork Basin, three miles southeast of the mouth of Pat O'Hara Creek. This locality description corresponds to UM locality SC-40. This locality is in the early Sandcouleean (zone Wa-1). The type of *D. transiens* is poorly preserved, but preservation is sufficient to confirm the differences discussed above. From the evidence available, it appears that *Dipsalidictis* persisted until the late early Wasatchian when it was gradually replaced by *Oxyaena*, at or near Biohorizon A (Schankler, 1980).

Van Valen (1966) maintained a specific distinction between *Dipsalidictides amplus* and *D. transiens* (his *Oxyaena transiens*) based on his assertion that *D. amplus* had a double rooted P_1. No documentation was provided for this assertion. Jepsen (1930a), in his original description stated that P_1 was single rooted. Denison (1938) included *D. amplus* in oxyaenids, which he characterized as having single rooted lower first premolars. The type of *D. amplus* is broken and distorted anterior to P_2, making P_1 root morphology difficult to determine. It seems unlikely that *D. amplus* had a double rooted P_1 as no other known oxyaenid exhibits this characteristic. We feel that, while *D. amplus* is somewhat different morphologically, it is not distinct enough to warrant specific separation from *D. transiens*.

Jepsen (1930a) felt that the buccolingually compressed P^3 of the type specimen of *D. amplus* was justification for placing *D. amplus* with *D. platypus* in a genus distinct from *Oxyaena*. Matthew had originally described *D. platypus* as lacking a P^3 protocone or lingual extension. Other specimens of *D. platypus* do have protocones or lingual extensions on P^3, indicating that this character is quite variable, at least in *Dipsalidictis* species. We are hesitant to use a buccolingually compressed P^3 as a specific character, preferring to place *D. amplus* in *D. transiens* as a junior synonym. Measurements of *D. transiens* are provided in Tables 2-3, summary statistics in Table 7.

Referred specimens.—UM 63680, 63970, 64659, 65322, 66361, 67258, 68201, 68446, 72204, 72851, 73777, 75174, 75305, 75341, 75783, 76216, 76230, 76423, 79094, 79989, 80004, 80063, 80181, 80397, 80536, 80704, 82460, 85277, 85279, 85324, 85325, 85341, 86025, 86433, 86497, 87046, 87050, 87074, 87077, 87588, 87939, and 92137.

Oxyaena Cope, 1874

Oxyaena Cope, 1874, p. 11; 1875, p. 9; 1877, p. 95; 1884a, p. 260; 1884b, p. 313. Guthrie, 1967, p. 16. Kihm, 1984, p. 125. McKenna, 1980, p. 331. Osborn, 1892, p. 109. Osborn, 1900, p. 276. Schankler, 1980, p. 105. Wortman, 1899, p. 140.
Oxyaena (in part), Matthew, 1915, p. 46. Denison, 1938, p. 167. Van Valen, 1966, p. 79. Rose, 1981, p. 104.

Type species.—*Oxyaena lupina.*

Included species.—*O. lupina*, *O. gulo*, *O. intermedia*, *O. forcipata*, *O. simpsoni*, *O. pardalis.*

Diagnosis.—*Oxyaena* differs from *Dipsalidictis* in having a well developed carnassial shearing dentition including a long postmetacrista on M^1, and a long, often flaring, paralophid on M_2. It also differs from *Dipsalidictis* in having lower molar trigonids longer than wide, in having reduced metaconids on lower molars, in having heavier premolars, and in having a more anteroposteriorly compressed M^2 that lacks a metacone.

Oxyaena gulo Matthew, 1915
Fig. 5C

Oxyaena gulo Matthew, 1915, p. 53, figs. 47-48. Denison, 1938, p. 168, figs. 5-6, 8, 11. McKenna, 1980, p. 331. Van Valen, 1966, p. 79. Schankler, 1980, p. 105.
Oxyaena sp. nr. *O. gulo*, Kihm, 1984, p. 128.

Holotype.—AMNH 15199, right maxilla with C^1, P^3-M^2, right dentary with C_1, P_1-M_1, collected in 1910.

Type locality.—Graybullian beds of the Bighorn Wasatch near Elk Creek, Bighorn Basin, Wyoming (dry camp 5 of Sinclair and Granger, see Sinclair and Granger, 1911; Gingerich, 1980b).

Age and distribution.—*O. gulo* is known from the late Sandcouleean and early Graybullian (Wasatchian zones Wa-2, Wa-3) in the Clarks Fork Basin. The holotype is from the early Graybullian (zone Wa-3) of the central Bighorn Basin, while many other specimens also come from this horizon in the Bighorn Basin. Kihm (1984) reported a single specimen from Wasatchian beds in the Piceance Basin that we assign to this species.

Diagnosis.—*Oxyaena gulo* differs from *O. intermedia* and *O. forcipata* in being smaller, in having a smaller anterior basal cusp on P_4, in having a narrower M_2 talonid, in having less well developed postmetacristae on P^4 and M^1, and in having less robust upper and lower premolars. It differs from *O. forcipata* in retaining a stronger metaconid on M_2.

Discussion.—*Oxyaena gulo* differs from its later descendants by the degree to which the carnassial shearing system is developed. In *Dipsalidictis*, the development of elongated postmetacristae and paralophids remains relatively constant, while through the *Oxyaena* lineage these features become progressively emphasized (see below). *Oxyaena gulo* has developed this shearing system to a degree beyond that seen in any *Dipsalidictis* species, but not to the de-

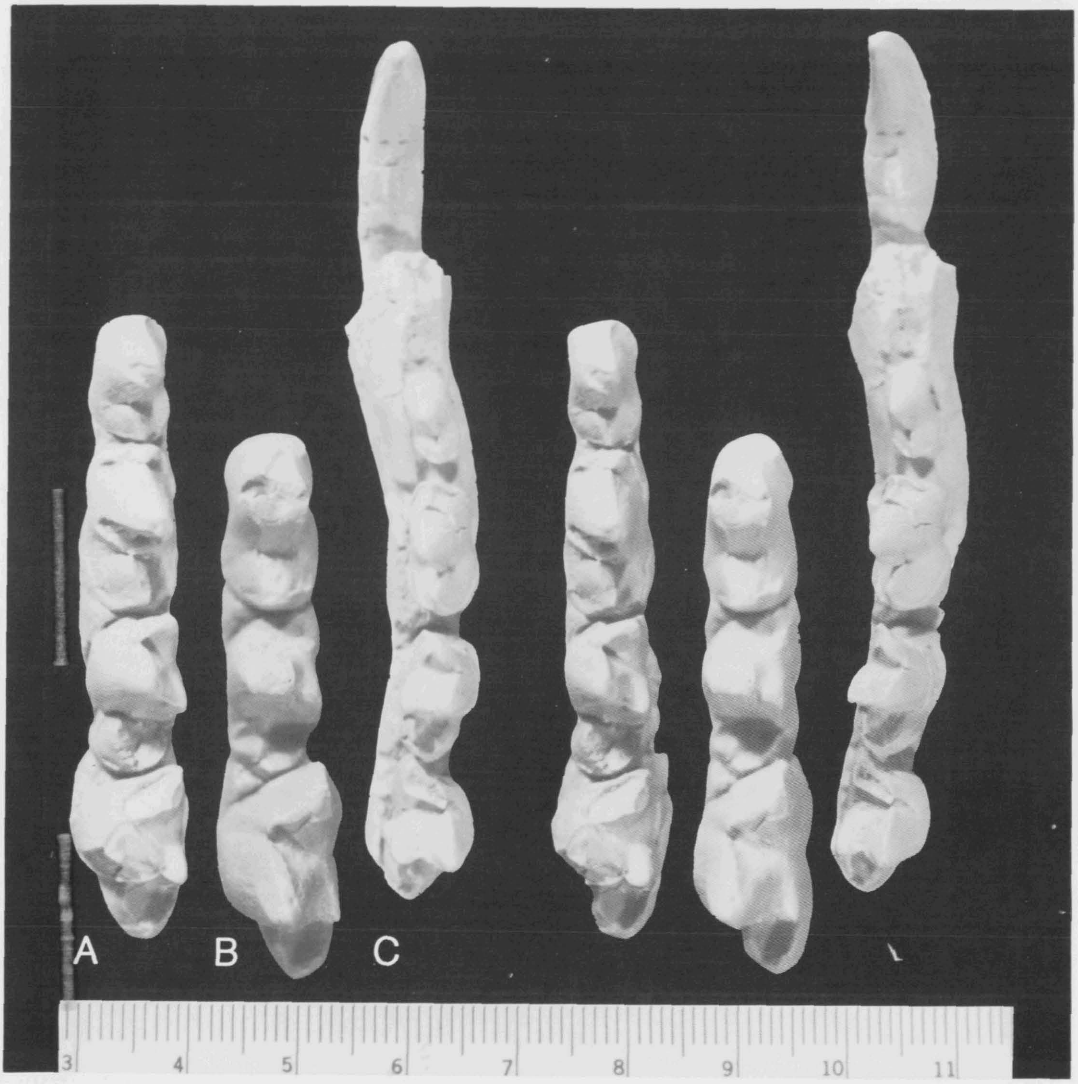

FIG. 5—Stereophotographs of lower dentitions of *Oxyaena* species. A, *Oxyaena intermedia* (composite of UM 61767, 69712, and 93585), left P_3-M_2 in occlusal view. B, *Oxyaena forcipata* (UM 92585), left P_4-M_2 in occlusal view. C, *Oxyaena gulo* (UM 63670), right dentary with C_1, P_3-M_2 in occlusal view. Scale is in mm.

gree found in its descendant species *O. intermedia*. Measurements of *O. gulo* are provided in Tables 2-3, summary statistics in Table 8.

Referred specimens.—UM 61766, 63577, 63670, 63685, 63826, 63827, 63918, 65168, 65266, 65287, 65297, 67032, 67143, 67161, 67416, 68114, 69511, 71539, 71669, 75822, 76551, 76553, 76734, 76797, 76807, 77138, 79185, 79301, 79545, 81874, 82724, 82778, 85635, 85846, 86815, 86856, 86869, 86889, 86895, 87178, 87278, 87286, 87651, 90994, 93831, 93862, 93968, 95061, 95087, and 95227.

TABLE 8—Summary tooth statistics for Clarks Fork and Bighorn Basin *Oxyaena gulo*. Abbreviations as in Table 4. All measurements in millimeters.

Measurement		N	OR	Mean	S	V
Upper dentition						
P^1	L	1	5.2	--	--	--
	W	1	4.2	--	--	--
P^2	L	1	8.4	--	--	--
	W	1	5.5	--	--	--
P^4	L	1	15.3	--	--	--
	W	1	15.0	--	--	--
M^1	L	3	13.1 - 16.3	14.60	1.61	11.0
	W	3	13.0 - 15.5	14.00	1.35	9.3
M^2	L	1	7.4	--	--	--
	W	1	16.1	--	--	--
Lower dentition						
C_1	L	3	10.3 - 12.4	11.17	1.10	9.8
	W	3	6.8 - 8.6	7.63	0.91	11.9
P_2	L	1	7.6	--	--	--
	W	1	4.9	--	--	--
P_3	L	2	8.1 - 11.2	9.65	--	--
	W	2	5.0 - 6.9	5.95	--	--
P_4	L	2	12.6 - 14.4	13.50	--	--
	W	2	7.1 - 8.1	7.60	--	--
M_1	L	1	13.2	--	--	--
	W	1	7.4	--	--	--
M_2	L	3	13.6 - 15.5	14.43	0.97	6.7
	W	3	8.4 - 9.4	8.97	0.51	5.7

Oxyaena intermedia Denison, 1938
Fig. 5A

Oxyaena intermedia Denison, 1938, p. 168, fig. 5. Van Valen, 1966, p. 79. Schankler, 1980, p. 105.
Oxyaena forcipata, Kihm, 1984, p. 125.
Oxyaena forcipata (in part), Matthew, 1915, p. 49, figs. 45-46.

Holotype.—AMNH 15183, left and right maxillae and dentaries, collected in 1910.

Type locality.—Middle Graybullian beds, near Elk Creek, Bighorn Wasatchian, Bighorn Basin, Wyoming.

Age and distribution.—The holotype is from middle Graybull beds (Wasatchian zone Wa-4). *O. intermedia* is also known from the late Graybullian in the Clarks Fork Basin and northern Bighorn Basin (zone Wa-5) and from the middle Wasatchian in the Piceance Basin in Colorado.

Diagnosis.—*Oxyaena intermedia* differs from *Oxyaena gulo* in being significantly larger and in having wider molar talonids. It differs from *O. forcipata* in being slightly smaller, in having a distinct metaconid on M_2, and in having less well developed postmetacristae on M^1 and less well developed paralophids on M_2.

TABLE 9—Summary tooth statistics for Clarks Fork and Bighorn Basin *Oxyaena intermedia*. Abbreviations as in Table 4. All measurements in millimeters.

Measurement		N	OR	Mean	S	V
Lower dentition						
P_2	L	1	10.0	--	--	--
	W	1	5.6	--	--	--
P_4	L	2	13.8 - 14.5	14.15	--	--
	W	2	8.0 - 8.3	8.15	--	--
M_1	L	4	13.6 - 14.9	14.25	0.57	4.0
	W	4	7.5 - 9.0	8.13	0.68	8.3
M_2	L	1	18.0	--	--	--
	W	1	10.5	--	--	--

Discussion.—Denison (1938) recognized this species as distinct from *O. forcipata* based on a less well developed shearing mechanism. In most other respects *O. intermedia* resembles *O. forcipata* quite closely and there is little doubt that *O. intermedia* is directly ancestral to *O. forcipata*. *O. intermedia* is also very similar to *O. gulo*, differing only in its greater size and overall robustness of its teeth. Taken together, these *Oxyaena* species make a very plausible ancestor-descendant lineage. Specimens from the Piceance Basin, described by Kihm (1984) as *Oxyaena forcipata*, are assigned to *O. intermedia* based on size and described morphology. Measurements of *O. intermedia* are provided in Tables 2-3, summary statistics in Table 9.

Referred specimens.—UM 61767, 63704, 63846, 63892, 63900, 63902, 64037, 69712, 86828, 86995, 87981, 88338, 91927, 92486, 93585, 93741, and 93758.

Oxyaena forcipata Cope, 1874
Fig. 5B, 6A,E, 7A,D,G

Oxyaena forcipata Cope, 1874, p. 12; 1875, p. 9; 1877, p. 105, Pl. 35, figs. 7-12, Pl. 36, figs. 1-6, Pl. 37, figs. 1-5; 1884a, p. 260, fig. 3; 1884b, p. 318, Pl. 24c, figs. 11-16, Pl. 24d, figs. 1-18. Denison, 1938, p. 169, figs. 27, 31. Guthrie, 1967, p. 16. Osborn, 1892, p. 109. Schankler, 1980, p. 105.
Oxyaena lupina, Osborn, 1892, p. 108, fig. 9. Wortman, 1899, p. 140, figs. 1-2, Pl. 7.
Oxyaena ultima Denison, 1938, p. 169, figs. 1,5.
Oxyaena forcipata (in part), Matthew, 1915, p. 49.
Oxyaena sp. cf. *O. lupina*, Kihm, 1984, p. 127.

Holotype.—USNM 1029, left and right dentaries.

Type locality.—San Jose Formation, San Juan Basin, New Mexico.

Age and distribution.—*O. forcipata* is known from many localities in New Mexico, Wyoming, and Colorado of late Graybullian and Lysitean age (Wasatchian zones Wa-5 and Wa-6).

Diagnosis.—*Oxyaena forcipata* differs from all other Bighorn Basin species of *Oxyaena*, except *O. intermedia* in being significantly larger. It differs from *O. intermedia* in being slightly larger, in having a longer and larger postmetacrista on M^1, in having a tiny or absent metaconid on M_2, and in having molar trigonids much longer than wide.

Discussion.—*Oxyaena forcipata* is not known from the Clarks Fork Basin proper, but it is known from surrounding areas (Foster Gulch and McCullough Peaks) in the northern Bighorn Basin.

O. forcipata has the most advanced carnassial shearing dentition of any Bighorn Basin oxyaenine. The features that distinguish *Oxyaena* from *Dipsalidictis* are highly developed in

TABLE 10—Summary tooth statistics for Clarks Fork and Bighorn Basin *Oxyaena forcipata*. Abbreviations as in Table 4. All measurements in millimeters.

Measurement		N	OR	Mean	S	V
Upper dentition						
P^3	L	1	14.5	--	--	--
	W	1	10.8	--	--	--
M^1	L	2	19.4 - 21.4	20.40	--	--
	W	2	12.2 - 15.1	13.65	--	--
M^2	L	1	11.3	--	--	--
	W	1	21.0	--	--	--
Lower dentition						
C_1	L	5	14.7 - 16.3	15.08	1.12	8.0
	W	5	9.3 - 11.7	10.94	1.04	9.5
P_3	L	4	12.1 - 13.9	12.80	0.77	6.1
	W	4	7.1 - 8.2	7.58	0.49	6.4
P_4	L	6	16.2 - 17.5	16.85	0.50	3.0
	W	6	9.1 - 11.1	9.97	0.78	7.8
M_1	L	6	15.8 - 19.2	17.70	1.52	8.6
	W	6	9.2 - 11.4	10.20	0.82	8.1
M_2	L	6	18.6 - 21.9	19.95	1.15	5.8
	W	6	10.2 - 12.6	11.67	1.06	9.0

this species. The postmetacrista of M^1 is greatly expanded, as is the paralophid of M_2. The trigonid of M_2 is opened and rotated to facilitate an even greater shearing surface along the front of the paralophid (prevallid), and the M_2 metaconid is greatly reduced or lost. Measurements of *O. forcipata* are provided in Tables 2-3, summary statistics in Table 10.

Referred specimens.—UM 64080, 64123, 64137, 64327, 73263, 75208, 75478, 75718, 75730, 82424, 82449, 86948, 91178, 91255, 91287, 91409, 91559, 92585, 93486, 94269, 94410, 94474, 95021, 95240, and 95251.

POSTCRANIAL SKELETON

Postcranial elements of oxyaenids are relatively rare. There are few significant postcranial remains of palaeonictines, while oxyaenine postcranials are poorly known from Clarkforkian and early Wasatchian sediments. New specimens in the UM and USGS collections are being studied by Rose and Gunnell, and will be reported elsewhere. However, there are some preliminary differences that can be noted between *Dipsalidictis* and *Oxyaena* (Figs. 6 and 7). Some of these differences are probably related to differences in body size (Gunnell, 1988).

Dipsalidictis has a more circular radial head, while in *Oxyaena* the radial head is more ovoid. Along with this, the ulnar articular surface on the radial head extends around nearly one-half the circumference of the head in *Dipsalidictis*, while it is restricted to the medial aspect of the head in *Oxyaena*. The shaft of the radius is bowed laterally in *Dipsalidictis* while it is straight in *Oxyaena*. All of these features suggest that *Dipsalidictis* was capable of supination and pronation (at least, to some degree), while *Oxyaena* had a radius designed more for weight bearing with less mobility at the wrist.

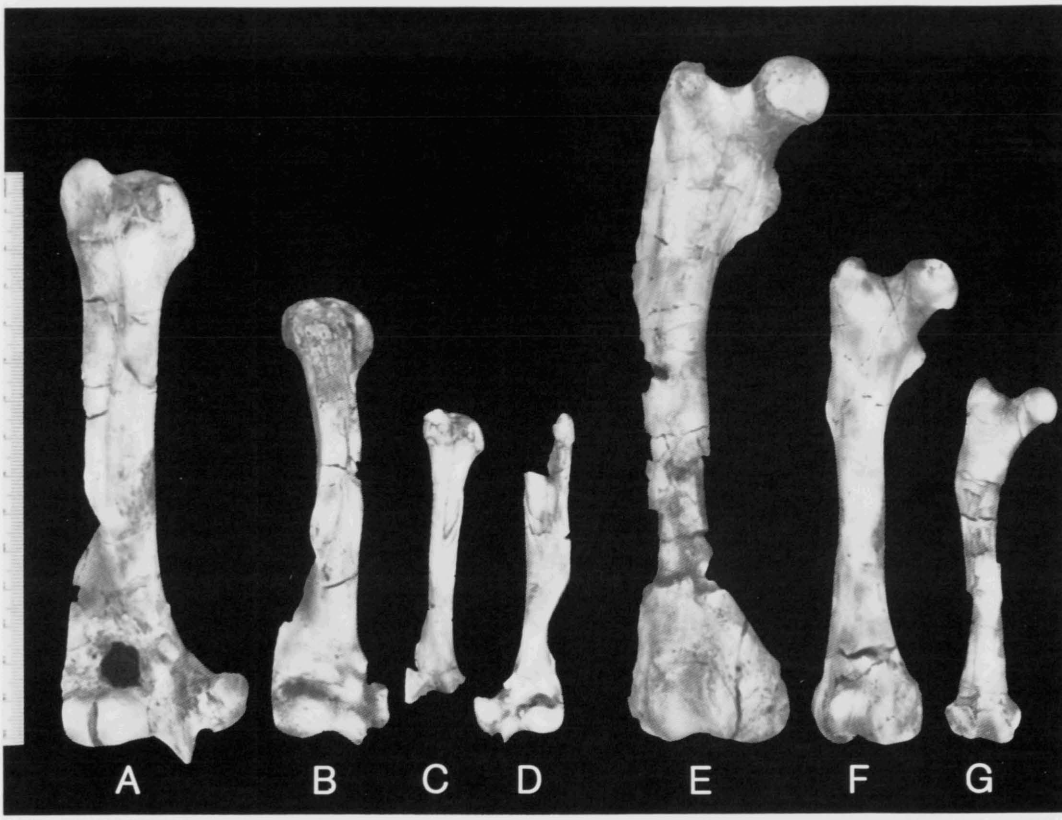

FIG. 6—Postcranial elements of *Oxyaena* and *Dipsalidictis*. A-D, anterior views of humeri. E-G, anterior views of femora. A, *Oxyaena forcipata* (UM 94269), right humerus. B, *Dipsalidictis transiens* (UM 85324), right humerus. C and D, *Dipsalidictis platypus* (AMNH 15857, holotype), right and left humeri. E, *Oxyaena forcipata* (UM 64037), right femur. F, *Dipsalidictis krausei* (UM 69331, holotype), right femur. G, *Dipsalidictis platypus* (AMNH 15857, holotype), right femur. Scale is in mm.

On the humerus, *Dipsalidictis* has a circular head (flattened proximally), while *Oxyaena* has a more ovoid or cylindrical head, suggesting a more limited range of motion in the latter genus. *Dipsalidictis* femoral characteristics include a relatively small, triangular lesser trochanter, and a relatively narrow patellar groove. In *Oxyaena* the lesser trochanter is relatively larger and semicircular, while the patellar groove is relatively broader. Both of these probably reflect the greater size of *Oxyaena*. *Dipsalidictis* has a sharply-angled distal tibial astragalar facet and a distal fibula with a very small or no calcaneal facet, a small flat astragalar facet, and a very small or no tibial facet. In *Oxyaena* the distal tibial astragalar facet is flatter and broader. The distal fibula has a small but distinct calcaneal facet, a large flat astragalar facet, and a small tibial facet.

Dipsalidictis has a very dorsoplantarly compressed astragalar head, a medially placed astragalar foramen, and a circular sustentacular facet that does not extend to the plantar base of the head. *Dipsalidictis* has a flattened fibular facet that extends laterally into a small fibular process. *Oxyaena* also has a dorsoplantarly compressed astragalar head, but it is not as flattened as in *Dipsalidictis*. *Oxyaena* has a more laterally placed astragalar foramen and has a sustentacular facet that extends to the medioplantar base of the head. The fibular facet is large and extends into a large, flaring, lateral fibular process.

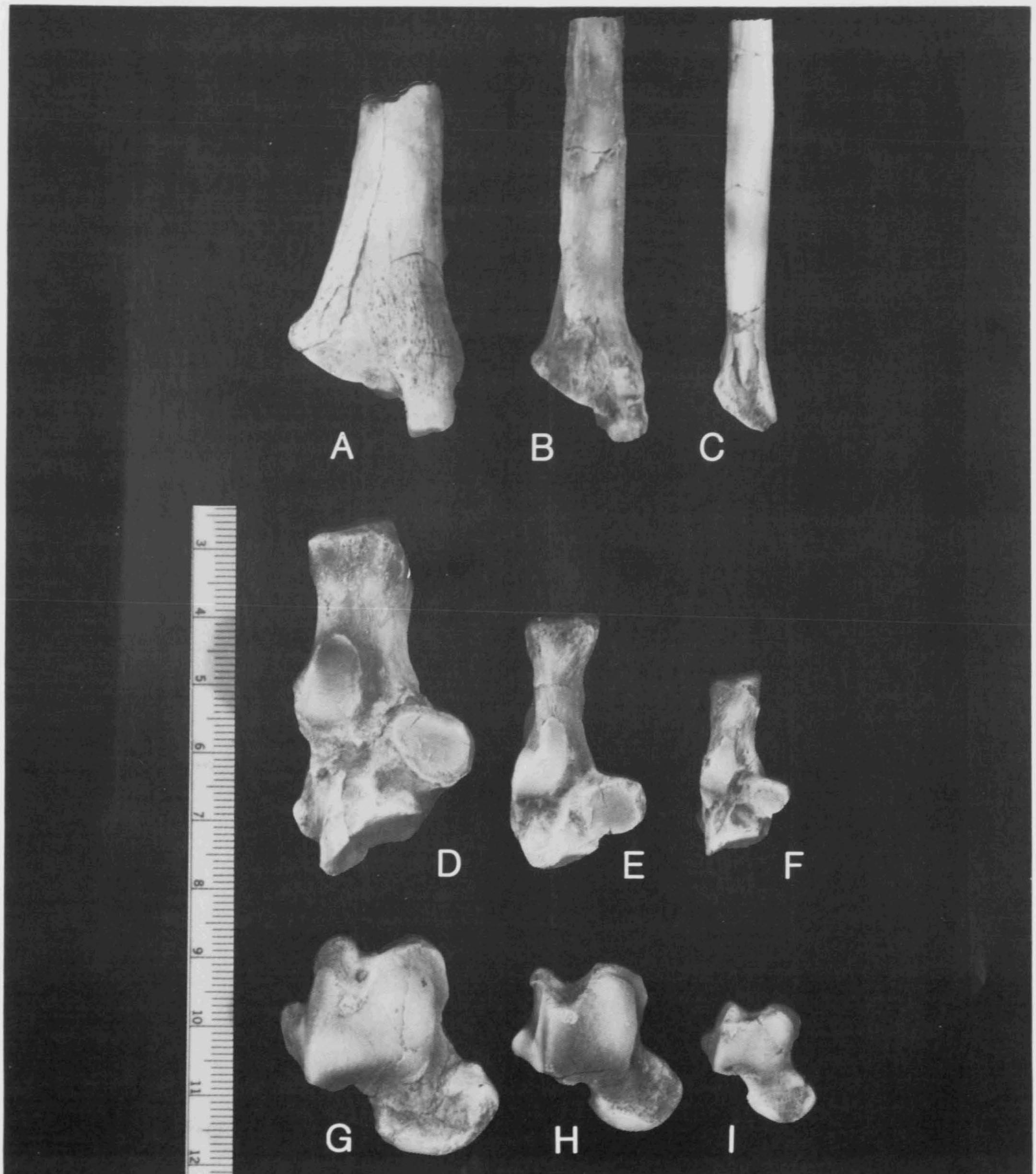

FIG. 7—Postcranial elements of *Oxyaena* and *Dipsalidictis*. A-C, anterior views of right distal tibiae. D-F, dorsal views of right calcanea. G-I, dorsal views of right astragali. A, *Oxyaena forcipata* (UM 64037, right distal tibia. B, *Dipsalidictis krausei* (UM 69331, holotype), right distal tibia. C, *Dipsalidictis platypus* (AMNH 15857), right distal tibia. D, *Oxyaena forcipata* (UM 64037), right calcaneum. E, *Dipsalidictis krausei* (UM 69331, holotype), right calcaneum. F, *Dipsalidictis platypus* (AMNH 15857, holotype), right calcaneum. G, *Oxyaena forcipata* (UM 64037), right astragalus. H, *Dipsalidictis krausei* (UM 69331, holotype), right astragalus. I, *Dipsalidictis platypus* (AMNH 15857, holotype), right astragalus.

Dipsalidictis has a more vertical (dorsoplantarly) oriented astragalar facet on the calcaneum and lacks or has a tiny calcaneal fibular facet. *Oxyaena* has a flatter astragalar calcaneal facet

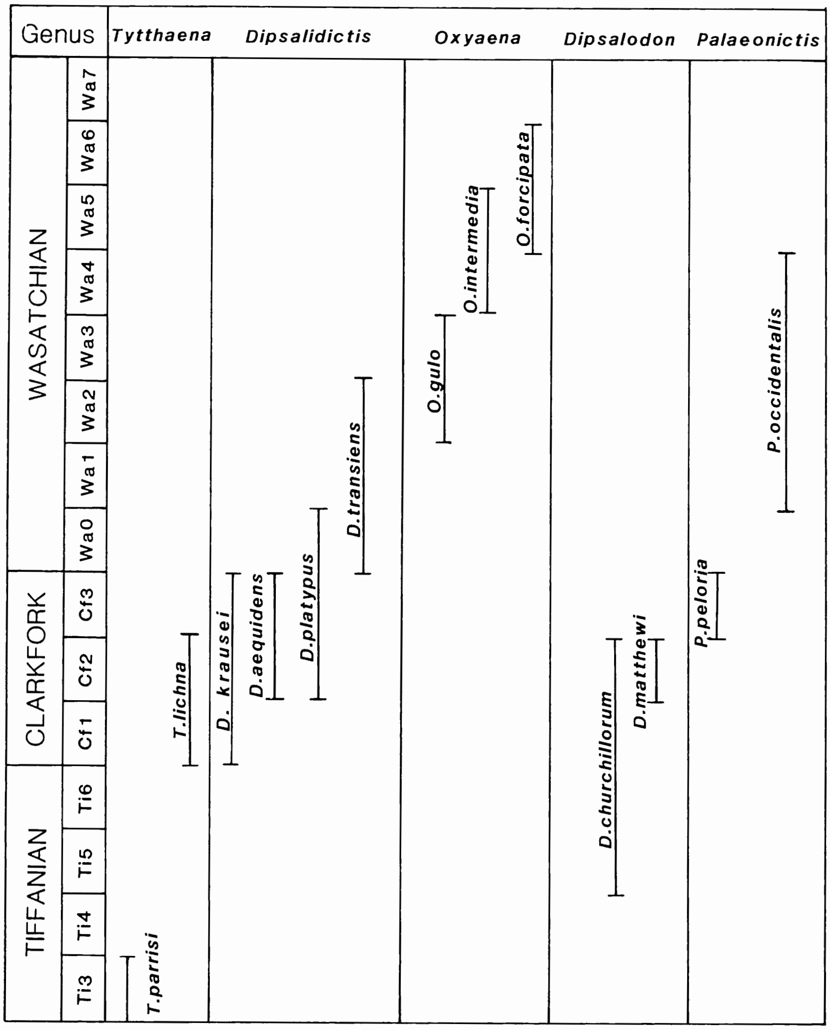

FIG. 8—Stratigraphic distribution of late Paleocene and early Eocene species of Oxyaeninae and Palaeonictinae in the Bighorn and Clarks Fork basins, Wyoming, with land-mammal ages subdivided into biostratigraphic zones. Note that maximum taxonomic diversity of Oxyaenidae was in middle Clarkforkian, when six distinct lineages are represented.

(oriented more mediolaterally) and has a distinct fibular facet. The cuboid is relatively longer and narrower in *Dipsalidictis*, while it is relatively short and broad in *Oxyaena*. *Dipsalidictis* has relatively long, gracile metatarsals that are only moderately spreading, while *Oxyaena* has relatively shorter and broader metatarsals that are more strongly spread.

All of the structures of the pes noted above indicate that *Oxyaena* had a foot developed for weight bearing, while *Dipsalidictis* had a more mobile, less robust foot structure (Gunnell, 1988). Gingerich (1990) developed a computer program predicting body mass from long bone lengths and diameters for generalized mammals. Using this program we have predicted body weights for species of *Dipsalidictis* ranging from 3 to 8 kilograms. *Oxyaena forcipata* (the only species with complete enough postcranial elements) has a predicted body weight of nearly 20 kilograms. This is consistent with foot structure as discussed above. It is likely that *Dip-*

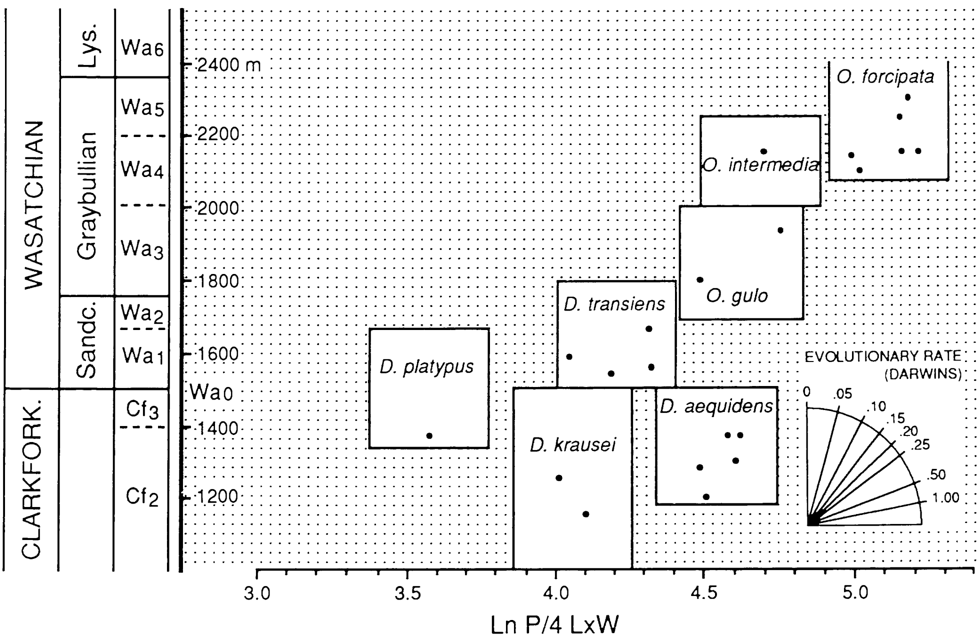

FIG. 9—Evolutionary change in size of lower fourth premolar (P_4) in Oxyaeninae of the northern Bighorn Basin and Clarks Fork Basin, Wyoming. Abscissa is natural logarithm of tooth area (length × width), and ordinate is meter level above the base of the Fort Union Formation. Closed circles represent individual specimens.

salidictis was partially arboreal (scansorial), while *Oxyaena* was probably an ambulatory terrestrial predator.

STRATIGRAPHIC DISTRIBUTION OF OXYAENIDAE IN THE CLARKS FORK BASIN

Figure 8 summarizes the stratigraphic distribution for oxyaenines and palaeonictines in the Clarks Fork Basin. *Tytthaena* ranges from middle Tiffanian (Ti-3 for *T. parrisi*) through middle Clarkforkian (Cf-1 through Cf-2 for *T. lichna*).

Dipsalidictis ranges from early Clarkforkian through early Wasatchian. *Dipsalidictis krausei* ranges from early Clarkforkian (Cf-1) through late Clarkforkian (Cf-3), *D. aequidens* from middle through late Clarkforkian (Cf-2 through Cf-3), *D. platypus* from middle Clarkforkian through middle Sandcouleean (Cf-2 through Wa-1), and *D. transiens* from early Sandcouleean (Wa-0) to early Graybullian (Wa-3).

In the *Oxyaena* lineage, *O. gulo* ranges from late Sandcouleean through early Graybullian (Wa-2 through Wa-3), *O. intermedia* from middle through late Graybullian (Wa-4 through Wa-5), and *O. forcipata* from late Graybullian through Lysitean (Wa-5 through Wa-6).

Among palaeonictines, *Palaeonictis peloria* is known only from the late Clarkforkian (Cf-3), while *P. occidentalis* is known from the middle Sandcouleean through middle Graybullian in the Clarks Fork Basin (Wa-1 through Wa-4). *Dipsalodon churchillorum* is present from late Tiffanian (Ti-5) through middle Clarkforkian (Cf-2). *D. matthewi* is only recorded from the middle Clarkforkian (Cf-2).

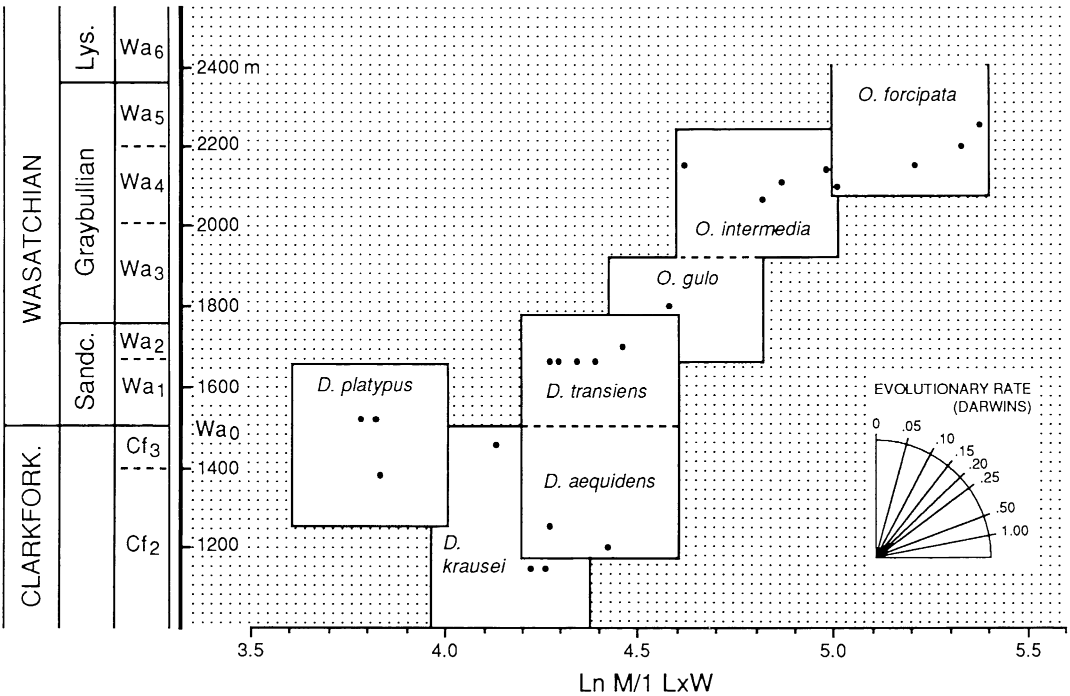

FIG. 10—Evolutionary change in size of lower first molar (M_1) in Oxyaeninae of the northern Bighorn Basin and Clarks Fork Basin, Wyoming. Abscissa is natural logarithm of tooth area (length × width), and ordinate is meter level above the base of the Fort Union Formation. Closed circles represent individual specimens.

CLARKS FORK BASIN OXYAENINAE RADIATION

Figures 9-11 summarize the radiation of oxyaenines in the Clarks Fork Basin. These figures plot lower fourth premolar area and lower first and second molar areas against stratigraphic level for *Dipsalidictis* and *Oxyaena* species in the Clarks Fork Basin. The earliest lineage represents a *Dipsalidictis krausei–Dipsalidictis aequidens* group. Based only on lower first and second molar size, these two species could probably be included in a single species. However, a plot of lower fourth premolars shows that these specimens can be separated into two distinct species. Among the other species, *Dipsalidictis platypus* is clearly discernible from the rest. The remaining species, *D. transiens*, is known from the early Wasatchian and occurs with *O. gulo* during the early Graybullian.

Oxyaena gulo may have arisen directly from *D. transiens*, although it is probable that *Oxyaena gulo* represents an immigrant species, suddenly appearing in the early Graybullian and rapidly replacing *Dipsalidictis*. *O. gulo* gave rise to *O. intermedia* through probable anagenesis, which in turn gave rise to *O. forcipata* by the same means. The change from *O. gulo* to *O. forcipata* involved an increase in overall body size and change in the carnassial shearing system.

Morphological features that separate *Oxyaena* from *Dipsalidictis* are already evident in *O. gulo* (see Tables 5 and 6). The lower molars have trigonids longer than wide reflecting the opening and twisting of molar trigonids to bring molar paralophids (prevallids) into a configuration to form long, broad shearing surfaces. The characteristic M_2 expansion of the paralophid (to extend the shearing surface) is moderately developed in *Oxyaena gulo*. Postmetacristae on upper first molars have been expanded to form shearing blades to oppose those

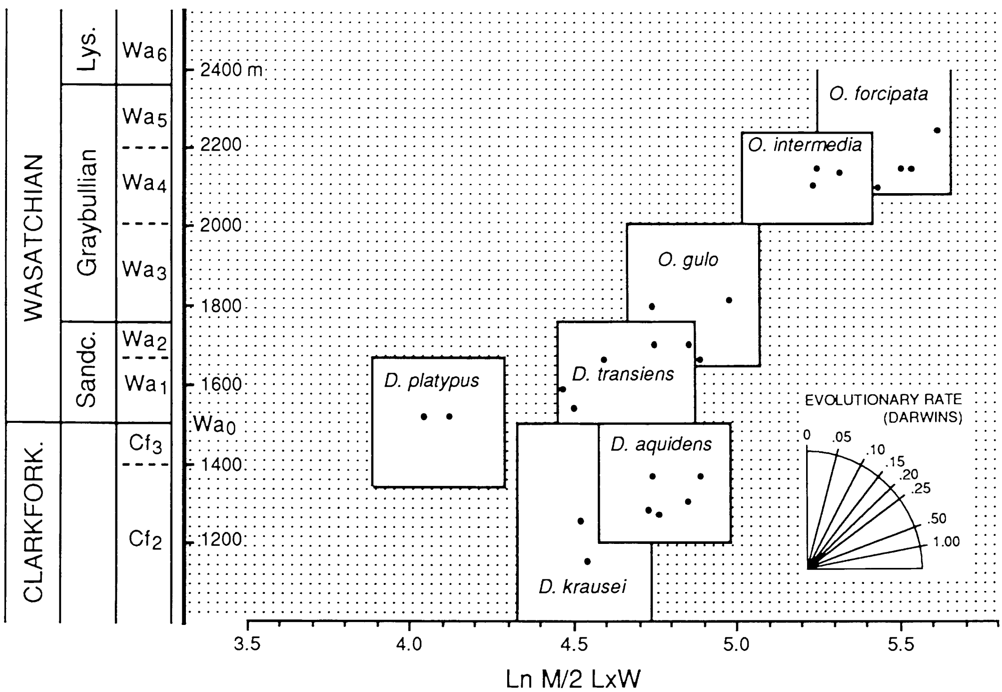

FIG. 11—Evolutionary change in size of lower second molar (M_2) in Oxyaeninae of the northern Bighorn Basin and Clarks Fork Basin, Wyoming. Abscissa is natural logarithm of tooth area (length × width), and ordinate is meter level above the base of the Fort Union Formation. Closed circles represent individual specimens.

of the M_2 (also postmetacristae on P^4 are expanded to serve the same function with M_1). The maxillary excavation between M^1 and M^2 has deepened to allow a long excursion of the paralophid across the postmetacrista.

Tables 11 and 12 give quantitative measurements that reflect the trends discussed above. Table 11 provides measurements used to quantify these morphological attributes for each of the species discussed. Table 12 gives a statistical summary of these data by species. Most *Dipsalidictis* specimens have lower molars with trigonids wider than long (Figs. 12-13). Trigonid length/width ratios range from 0.90 to 0.96 for M_1, and 0.83 to 1.02 for M_2. Most *Oxyaena* specimens have lower molar trigonids longer than wide, with length/width ratios ranging between 0.97 and 1.17 for M_1, and 1.00 and 1.36 for M_2.

We calculated a ratio of M_2 paralophid length divided by M_2 trigonid width (PALD, Fig. 14) to indicate the size of the paralophid relative to tooth size (Tables 11-12). *Dipsalidictis* has paralophids moderately wider than trigonids (ranging between 1.11 and 1.23), while *Oxyaena* has progressively enlarged paralophids relative to M_2 trigonid width (1.17 to 1.28 in *O. gulo*, increasing to 1.25 to 1.42 in *O. forcipata*).

To reflect changes in M^1 postmetacristae, we calculated a ratio between postmetacrista length and tooth width for upper first molars (PMTC, see Table 12 for summaries and Fig. 15). *Dipsalidictis* has PMTC ratios under 0.56, indicating that postmetacristae were about half as long as the width of M^1. *Oxyaena* has similar PMTC ratios for *O. gulo* and *O. intermedia*, while in *O. forcipata* this ratio reaches 0.64, giving a postmetacrista two-thirds as long as M^1 is wide.

Dipsalidictis shows no progressive trend towards specialization of a carnassial shearing system but remains relatively constant throughout its range. *Oxyaena*, on the other hand,

TABLE 11—Summary measurements for upper and lower teeth of Oxyaeninae. All measurements in millimeters. Levels represent meters above the base of the Fort Union Formation in the Clarks Fork Basin. Locality prefixes are the same as in Table 1. All numbers are UM specimens except those as noted in Tables 1 and 2. L = length, W = width, Paralophid = length of the paralophid of M_2 measured anterolingually to posterobuccally, PALD = length of paralophid of M_2 divided by width of trigonid of M_2, Postmetacrista = length of the postmetacrista of M^1, PMTC = postmetacrista length divided by M^1 width.

Specimen	Locality	Level	M_1 trigonid L/W	M_2 trigonid L/W	Para-lophid	PALD	Postmeta-crista	PMTC
Oxyaena forcipata								
75208	GR-7	(2300)	1.15	--	--	--	--	--
82449	MP-6	(2250)	--	1.36	14.2	1.42	--	--
86948	MP-16	(2250)	1.08	1.30	15.5	1.35	7.7	0.64
91559	MP-76	(2250)	1.22	--	--	--	--	--
3425	--	(2140)	1.08	1.22	13.6	1.28	--	--
64123	YM-421	(2130)	--	1.12	11.9	1.25	--	--
75718	SC-303	2110	--	--	--	--	7.9	0.52
92585	MP-122	(2100)	1.17	1.19	14.7	1.34	--	--
Oxyaena intermedia								
86828	FG-87	(1960)	--	1.04	12.6	1.25	--	--
69712	SC-146	2065	1.06	--	--	--	--	--
86995	MP-17	(2120)	1.12	1.11	11.2	--	--	--
Oxyaena gulo								
61766	YM-389	(1980)	--	--	--	--	6.6	0.56
63670	YM-90c	(1800)	0.97	1.14	10.5	1.25	--	--
65287	SC-32	1815	--	1.12	11.9	1.28	--	--
65297	SC-34	1850	--	--	--	--	7.2	0.46
68114	SC-133	1750	--	1.08	9.8	1.27	6.4	0.51
76734	SC-3	1935	1.09	--	--	--	--	--
79545	SC-213	1760	--	--	--	--	7.0	0.52
67416	SC-46	1700	--	1.00	10.3	1.18	--	--
87278	FG-103	(1770)	1.09	--	--	--	--	--
87286	FG-103	(1770)	1.08	--	--	--	--	--
87651	MP-23	(1790)	--	1.00	11.0	1.17	--	--
Dipsalidictis transiens								
13153	--	1590	--	0.85	8.7	1.18	4.6	0.35
16118	SC-40	1540	--	0.92	8.6	1.12	5.6	0.53
75341	SC-15	1630	--	1.02	10.8	1.27	6.4	0.47
68201	SC-161	1665	0.95	--	--	--	--	--
73777	SC-288	1560	--	0.88	10.0	1.23	--	--
76230	SC-41	1560	--	--	--	--	6.3	0.55
80063	SC-54	1700	0.93	0.86	10.0	1.14	6.3	0.46
80704	SC-16	1665	0.96	0.83	9.0	1.13	--	--
82460	SC-161	1665	0.95	--	--	--	--	--
86025	SC-161	1665	0.90	0.98	10.0	1.20	--	--
86433	SC-46	1700	--	--	--	--	5.0	0.50
86497	SC-47	1690	--	0.90	9.6	1.19	--	--
Dipsalidictis platypus								
15857	SC-67	1520	0.89	0.84	6.8	1.11	--	--
21215	--	1370	0.91	0.83	7.2	1.20	--	--
66137	SC-67	1520	0.92	0.90	7.2	1.16	4.2	0.44
72955	SC-20	1380	0.85	--	--	--	--	--
79382	SC-6	1530	--	--	--	--	4.5	0.42
Dipsalidictis aequidens								
19544	SC-136	1200	0.92	0.90	10.5	1.22	--	--
65039	SC-19	1370	0.88	0.88	9.9	1.18	--	--
67024	SC-120	1300	--	0.88	10.4	1.16	--	--

TABLE 11 (continued)

Specimen	Locality	Level	M_1 trigonid L/W	M_2 trigonid L/W	Para-lophid	PALD	Postmeta-crista	PMTC
Dipsalidictis aequidens (continued)								
68869	SC-188	1280	0.93	0.85	9.9	1.16	--	--
68871	SC-189	1275	--	--	--	--	5.7	0.40
68879	SC-190	1270	--	0.78	9.8	1.14	--	--
80243	SC-53	1405	0.92	0.83	10.2	1.13	--	--
85994	SC-19	1370	0.88	--	--	--	--	--
87806	SC-117	1370	0.93	0.90	10.6	1.15	5.7	0.42
Dipsalidictis krausei								
66180	SC-74	1150	0.94	0.81	8.9	1.16	--	--
69331	SC-195	1255	0.92	0.88	8.7	1.14	5.7	0.46
69908	SC-136	1200	--	0.88	9.5	1.14	--	--
71775	SC-171	1090	0.88	--	--	--	--	--
80434	SC-74	1150	0.92	--	--	--	--	--
71680	SC-50	1425	--	0.90	8.3	1.17	--	--
71679	SC-72	1435	--	--	--	--	5.4	0.45
66309	SC-90	1455	0.85	--	--	--	--	--

TABLE 12—Mean measurements of upper and lower teeth reflecting the development of efficient shearing dentitions in *Dipsalidictis* and *Oxyaena*. L/W = length/width, PALD = M_2 paralophid length divided by M_2 trigonid width, PMTC = M^1 postmetacrista length divided by M^1 width. Sample size N is given in parentheses.

Genus and species	M_1 trigonid L/W	M_2 trigonid L/W	PALD	PMTC
Dipsalidictis krausei	0.90 (5)	0.87 (4)	1.15	0.46 (2)
Dipsalidictis aequidens	0.91 (6)	0.86 (7)	1.16	0.41 (2)
Dipsalidictis platypus	0.89 (4)	0.86 (3)	1.16	0.43 (2)
Dipsalidictis transiens	0.93 (5)	0.91 (8)	1.18	0.48 (6)
Oxyaena gulo	1.06 (4)	1.07 (5)	1.23	0.51 (4)
Oxyaena intermedia	1.09 (2)	1.08 (2)	1.25	--
Oxyaena forcipata	1.14 (5)	1.24 (5)	1.33	0.58 (2)

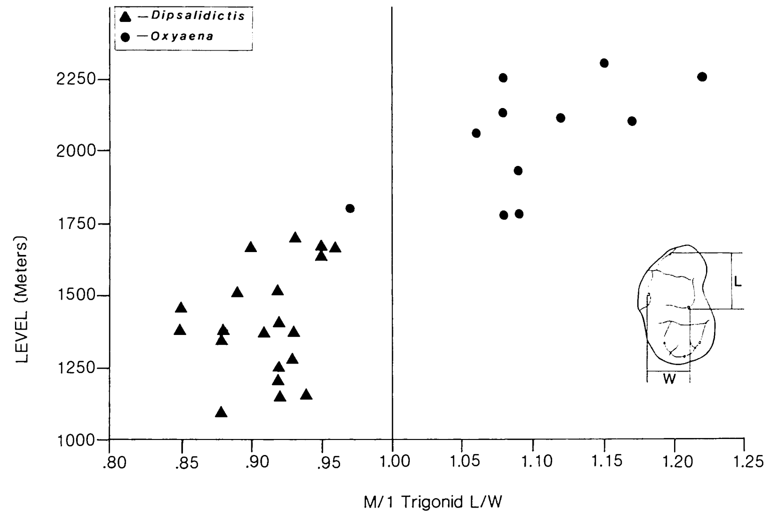

FIG. 12—Evolution of trigonid shape of lower first molar (M_1) in Oxyaeninae of the northern Bighorn Basin and Clarks Fork Basin, Wyoming. Abscissa is trigonid length (L) divided by trigonid width (W). Ordinate is meter level above the base of the Fort Union Formation. Levels of some specimens estimated from associated fauna (see Table 11). Heavy vertical line is L/W ratio of 1.00 (length and width equal). Note two distinct groups, with *Dipsalidictis* (triangles) falling below 1.00 and *Oxyaena* (circles) falling above in most cases.

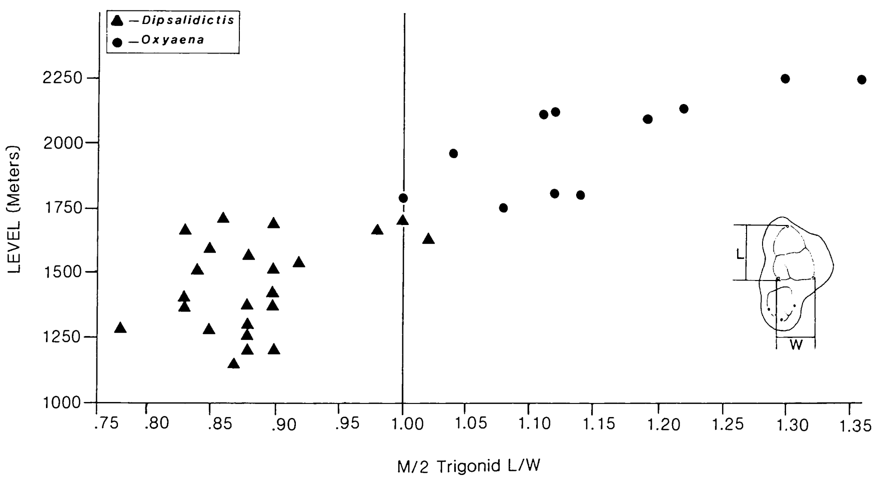

FIG. 13—Evolution of trigonid shape of lower second molar (M_2) in Oxyaeninae of the northern Bighorn Basin and Clarks Fork Basin, Wyoming. Abscissa is trigonid length (L) divided by trigonid width (W). Ordinate is meter level above the base of the Fort Union Formation. Levels of some specimens estimated from associated fauna (see Table 11). Heavy vertical line is L/W ratio of 1.00 (length and width equal). Note two distinct groups, *Dipsalidictis* (triangles) falling below 1.00 and *Oxyaena* (circles) falling above in most cases.

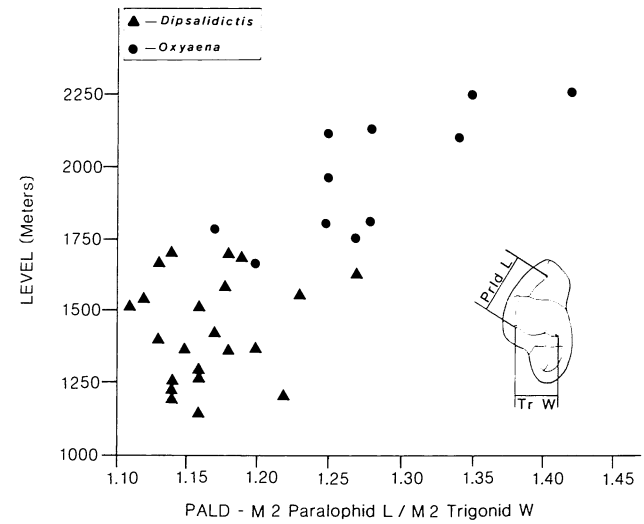

FIG. 14—Evolution of trigonid shape of lower second molar (M_2) in Oxyaeninae of the northern Bighorn Basin and Clarks Fork Basin, Wyoming. Abscissa is paralophid length divided by trigonid width (PALD). Ordinate is meter level above the base of the Fort Union Formation. Note low PALD ratios for early species (*Dipsalidictis*, triangles), with little change through stratigraphic range of genus. *Oxyaena* (circles) has larger PALD ratios and shows a strong trend of increasing PALD through stratigraphic range of genus.

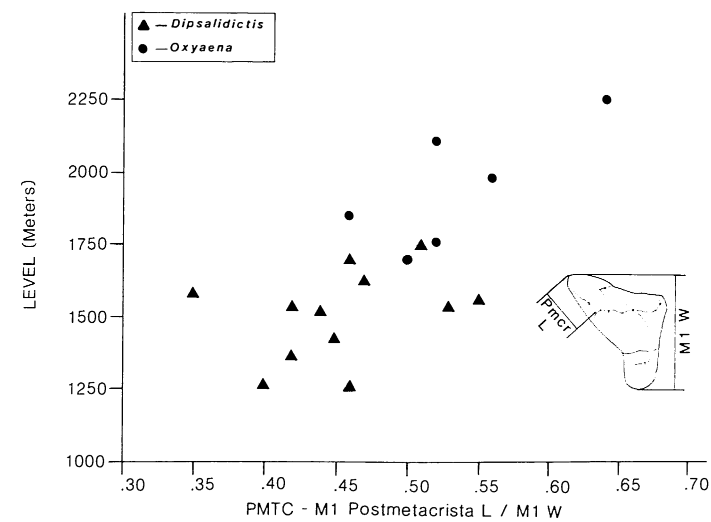

FIG. 15—Evolution of carnassial shearing on upper first molar (M^1) in Oxyaeninae of the northern Bighorn Basin and Clarks Fork Basin, Wyoming. Abscissa is length of postmetacrista divided by crown width (PMTC). Ordinate is meter level above the base of the Fort Union Formation. Note lower PMTC ratios in lower part of section (*Dipsalidictis*, triangles), and increase for those specimens in higher part of section (*Oxyaena*, circles), particularly in latest specimens (*Oxyaena forcipata*).

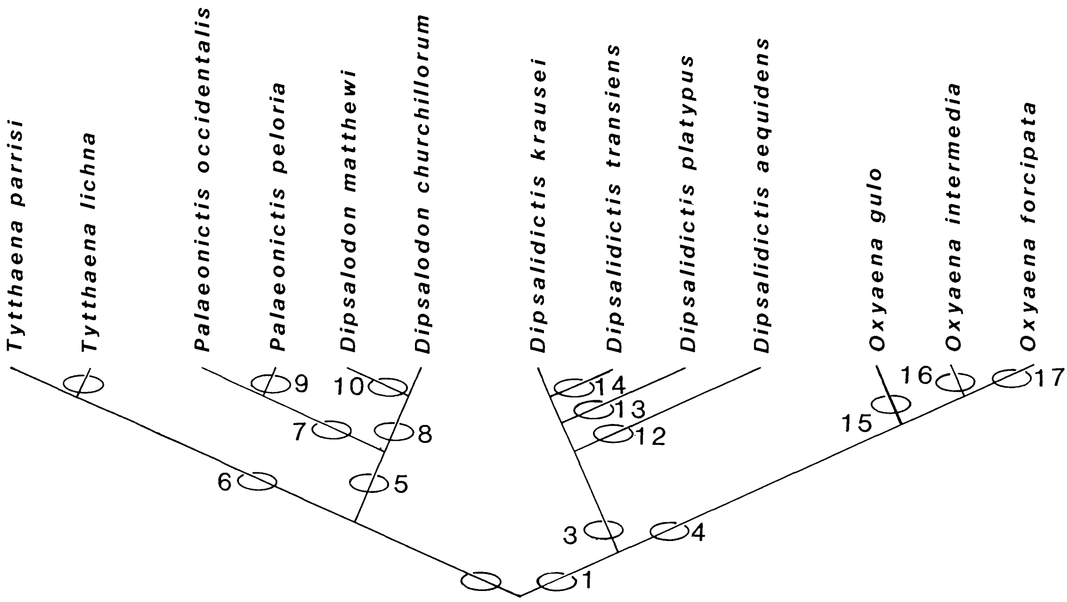

FIG. 16—Cladogram showing relationships among species of Bighorn Basin and Clarks Fork Basin Oxyaenidae, as currently understood. Nodes are represented by the following characteristics: (1) M_1 and M_2 approximately same size; M^1 postmetacrista developed. (2) M_2 smaller than M_1; M^1 postmetacrista weak to absent. (3) M^2 with metacone present; no maxillary excavation between M^1 and M^2; lower molar trigonids wider than long; gracile premolars; astragalar head very flattened. (4) M_2 larger than M_1; M^2 metacone absent; maxillary excavation present; lower molar trigonids longer than wide; lower molar paralophids and M^1 postmetacrista well developed; short broad cuboid. (5) Larger size; accessory cuspules developed on P_4; P_4 robust; (6) Small size; narrow molar talonids; P_4 narrow, lacking entoconid. (7) M_2 much smaller than M_1; M_2 with reduced metaconids. (8) P_4 with well developed talonid; P_4 entoconid present; molar trigonids relatively closed; molar talonids broad. (9) Large size; very heavy mandible and symphysis; robust premolars. (10) Larger size; M_2 less reduced relative to M_1; relatively long premolars. (11) Smaller size; M_2 with anteroposteriorly compressed trigonid; M_2 entoconid reduced; molar entoconulid absent. (12) Maxillary excavation between M^1 and M^2 present; larger size; robust, enlarged premolars. (13) Small size. (14) M_2 larger relative to M_1; more robust premolars; P_4 with anterior basal cusp. (15) Smaller size; M_2 with relatively narrow talonid; weaker postmetacrista on P^4 and M^1; M_2 metaconid strong. (16) Larger size; molar talonids wide; M_2 metaconid present but reduced. (17) M_2 metaconid tiny or absent; M_2 trigonid very open with expanded paralophid; well developed, elongate M^1 postmetacrista.

shows a progressive development of all aspects of this shearing mechanism. Figure 16 summarizes relationships within Bighorn Basin Oxyaenidae as currently understood.

EUROPEAN OXYAENIDAE

The European record of Oxyaenidae is poorly known, although both Palaeonictinae and Oxyaeninae appear to be represented in the early Eocene. *Palaeonictis gigantea*, the type species of the genus, was described by de Blainville (1842) from the *Lignites de Soissonais* (early Ypresian) at Muirancourt in France, and it has long been known from the *Argile Plastique* (early Ypresian) of Meudon (Teilhard de Chardin, 1922). *P. gigantea* is also known from the early Ypresian at Mutigny in France, and Dormaal in Belgium (Godinot et al., 1978; Russell et al., 1982a, 1982b). Lange-Badré (1987) recently described a new palaeonictine, *Dormaalodon woutersi*, based on an isolated M_2 from Dormaal.

Oxyaenines have been described from a number of European Eocene localities, although most of these have turned out to represent either *Palaeonictis* or hyaenodontids. We have examined original specimens or casts of most of the relevant material and make the following observations:

(1) The earliest European records of oxyaenines are at Dormaal, Meudon, and Pourcy. A left M_1 trigonid (MNHN AC-656) from Meudon has been referred to *Palaeonictis* (Teilhard de Chardin, 1922) and to *Oxyaena* (Gingerich, 1976), but comparison with specimens described here indicates that this probably represents a small species of *Dipsalidictis*. It differs from *Oxyaena* in having a trigonid wider than long (see above), in having a well developed metaconid that is as tall as the paraconid, and in having a less open (lingually) trigonid. In all of these features it resembles *Dipsalidictis* more closely than *Oxyaena*, and it is most reminiscent of middle Clarkforkian *Dipsalidictis krausei* from North America. Van Valen (1965) described several specimens from the Blackheath Beds at Abbey Wood (early Ypresian) in England as cf. *Oxyaena* sp. These are the lingual portion of a right M^1 (BMNH 15128), a buccal portion of left M^1, and a buccal portion of a right P^4. We refer all to *Dipsalidictis* sp. (small).

(2) Another specimen from Abbey Wood mentioned by Van Valen (1965) as *Oxyaena* is BMNH 31788, a right M_2 complete except for a missing paraconid. This represents a different species of *Dipsalidictis* most similar to North American *Dipsalidictis aequidens*, differing only in having a slightly higher protoconid with a slightly less robust metaconid. We assign this to *Dipsalidictis* sp. (large). MNHN Louis-60-Py is a right P_4 from Pourcy. It differs from *Oxyaena* by being much broader, with heavier blunter cusps. It too is most similar to *Dipsalidictis aequidens* from the middle Clarkforkian of North America, and we assign this too to *Dipsalidictis* sp. (large). Thus there appear to be two species of *Dipsalidictis*, small and large, in the early Ypresian of Europe.

(3) Late Ypresian oxyaenines from Sinceny and the London Clay could be referred to either *Dipsalidictis* or *Oxyaena*. Rich (1971) assigned UCMP 83754, a left M_1 from Sinceny, to *Oxyaena* sp. because it appeared to have a trigonid longer than it is wide. Our measurements indicate that the trigonid is approximately the same width as length (6.5 mm). The metaconid is slightly reduced and somewhat higher on the lingual flank of the protoconid, as in *Oxyaena gulo*, but it lacks the more open trigonid with the flaring prevallid typical of *Oxyaena*. We retain the oxyaenine specimens from Sinceny and the London Clay in *Dipsalidictis* sp., although a case can be made for affinity with *Oxyaena*. In many ways these specimens are similar to *Dipsalidictis transiens* from North America (late *D. transiens* resembles early *O. gulo* very closely, see above).

(4) Quinet (1966) described *Oxyaena*(?) *casieri* from Dormaal, based on a left P_4. Lange-Badré (1987) correctly referred this species to *Palaeonictis gigantea*.

(5) Rich (1971) named *Oxyaena menui* from Cuis in the *Sables à Unios et Teredines* (late Ypresian) of the Paris Basin. *Oxyaena menui* is very similar to *Propterodon* (Stehlin, 1940), as represented by Basel-Cuis TS-339. This is also the case for MNHN Louis-68-Gr, a left mandible with P_4 from Grauves that Rich (1971) referred to cf. Oxyaenoidea or cf. Hyaenodontoidea. Both specimens are hyaenodontids and probably represent *Propterodon*.

(6) Matthes (1967) described a new genus and species, *Oxyaenoides bicuspidens*, as an oxyaenine from locality XIV in the Geiseltal lignites (middle Eocene). Van Valen and Mellett (1968) correctly pointed out that this species is a hyaenodontid. Filhol (1881) named *Oxyaena galliae* from the middle or late Eocene of Quercy. This was later moved to a new genus *Paroxyaena* by Martin (1906). Denison (1938) regarded *Paroxyaena* as a palaeonictine rather than oxyaenine, an interpretation supported by Van

Valen (1966). More recently, Lange-Badré (1979) has shown that *Paroxyaena* is a hyaenodontid.

In conclusion, European oxyaenids are represented by a small radiation during the early Eocene. Two palaeonictine genera, *Palaeonictis* and *Dormaalodon*, and two oxyaenine species of *Dipsalidictis* are present in the early Ypresian. Later, in the late Ypresian late early Eocene, a single European lineage of *Dipsalidictis* is known.

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