

CARNIVORA FROM THE LATE MIOCENE LOVE BONE BED OF FLORIDA

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Eleven genera and twelve species of Carnivora are known from the late Miocene Love Bone Bed Local Fauna, Alachua County, Florida. Taxa from there described in detail for the first time include the canid cf. *Urocyon* sp., the hemicyonine ursid cf. *Plithocyon* sp., and the mustelids *Leptarctus webbi* n. sp., *Hoplictis* sp., and ?*Sthenictis* near ?*S. lacota*. Postcrania of the nimravid *Barbourofelis* indicate that it had a subdigitigrade posture and most likely stalked and ambushed its prey in dense cover. The postcranial morphology of *Nimravid* (Felidae) is most similar to the jaguar, *Panthera onca*. The carnivorans strongly support a latest Clarendonian age assignment for the Love Bone Bed. Although the Love Bone Bed local fauna does show some evidence of endemism at the species level, it demonstrates that by the late Clarendonian, Florida had become part of the Clarendonian chronofauna of the midcontinent, in contrast to the higher endemism present in the early Miocene and in the later Miocene and Pliocene of Florida.

Key Words: Carnivora; Miocene; Clarendonian; Florida; Love Bone Bed; *Leptarctus webbi* n. sp.

INTRODUCTION

The Love Bone Bed Local Fauna, Alachua County, Florida, has produced the largest and most diverse late Miocene vertebrate fauna known from eastern North America, including 43 species of mammals (Webb et al. 1981; MacFadden & Hulbert 1990). The Love Bone Bed consists of fluvial sediments of the Alachua Formation that fill a complex stream channel deposit cut into the underlying limestone of the late Eocene Crystal River Formation (Webb et al. 1981). Field parties from the Florida Museum of Natural History excavated this locality from its discovery in 1974 until its closure in 1981. The quarry has yielded a wealth of carnivore material, in contrast to other Florida late Neogene localities such as Mixson's Bone Bed, McGehee Farm, or the Upper Bone Valley, in which carnivorans are poorly represented. Eleven genera and twelve species of carnivorans are known from the Love Bone Bed. The carnivorans are the same as or closely related to taxa from the late Miocene faunas of the Great Plains and the West Coast, and support a latest Clarendonian age (9.5-9.0 Ma) assignment for the Love Bone Bed local fauna.

The following vertebrate paleontology collections are abbreviated in the text as follows: AMNH, Ameri-

can Museum of Natural History, New York; F:AM, Frick fossil mammal collection, part of the AMNH; UF, Florida Museum of Natural History, University of Florida.

All measurements are in millimeters. The following abbreviations are used: *N*, number; *X*, mean (\pm standard error); *OR*, observed range; *CV*, coefficient of variation; *L*, length; *W*, width; *GL*, greatest length; *GTD*, greatest transverse diameter; *GTW*, greatest transverse width; *APD*, anteroposterior diameter; *TD*, transverse diameter; *GW*, greatest width.

SYSTEMATIC PALEONTOLOGY

Order CARNIVORA Bowdich 1821

Family NIMRAVIDAE Cope 1880

Genus *BARBOUROFELIS* Schultz, Schultz, and Martin 1970

BARBOUROFELIS LOVEORUM Baskin 1981

Tables 1-3

Barbourofelis lovei Baskin 1981.

Comments.—The specific epithet was emended by Hulbert (1992), because this taxon was named for Ron and Pat Love. The most notable addition to material of *Barbourofelis loveorum* from Florida since the original description (Baskin 1981) is a skull (UF 37000) illustrated in Hulbert et al. (2001:fig. 11.32b-c). Measurements are given in Table 1. This skull is from a juvenile, as indicated by the small size of the canines (*L*

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Table 1. Measurements of the skull of *Barbourofelis loveorum* and *Nimravides galiani* from the Love Bone Bed. Measurements in parentheses may be exaggerated because of the reconstruction.

	<i>Barbourofelis</i>	<i>Barbourofelis</i>	<i>Nimravides</i>
	UF 24447	UF 37000	UF 27989
Condylbasal Length	239	218	245
Maximum Length	(288)	249	290
Width palate across C	(84)	74	73
Width palate across P4	121	121	105
Length palate		99	120
Width across Interorbital constriction	89	90	66
Width of zygoma	187	165	176
Width across mastoids		103	101
Height of occipit	93	82	85

= 23.9, W = 7.3) that are similar in dimensions to deciduous canines of the holotype UF 24447 (Baskin 1981:fig. 1), and the low degree of wear on the P4, even less than that of the holotype. The high occipit of this better prepared specimen shows the expected barbourofeline morphology, as noted by Baskin (1981) in his discussion of the reconstruction of juvenile skull selected as the holotype of *B. loveorum*. Bryant (1988) analyzed the tooth eruption sequence of *B. loveorum*. He concluded that the extremely large deciduous upper canine and the delayed eruption of the permanent upper canine that was present in *B. loveorum* was a synapomorphy for all Nimravidae and further distinguished this family from the Felidae.

Postcranial Skeleton.— The skeleton of *Barbourofelis* is decidedly non-feline in structure and more closely resembles the nimravid *Hoplophoneus* (Scott & Jepsen 1936). The atlas differs from that of felids and most other carnivorans, but resembles *Hoplophoneus* and ursids in lacking alar notches. The transverse processes extend backwards and are pointed at their posterior termination as in *Smilodon*. The sacrum is wider than long, and has a large area of attachment for the pelvis. The small sizes of the posterior zygapo-

physes and the posterior articular surface indicate that *Barbourofelis* had a very short tail. The bones of the forelimb are stout, with well-developed processes for muscle attachment. The humerus has a relatively large cross-sectional area and possesses prominent pectoral, deltoid and lateral epicondylar ridges, with the pectoral and deltoid crests extending low on the humerus. The pelvis is distinct from that of felids. In lateral view, the ala (the wing of the ilium) is rotated medially into the horizontal plane. There are large areas for attachment of the iliac muscle on the ventral surface and the deep gluteal muscle on the lateral surface. The bones of the hind limb are more slender than those of the forelimb, but also possess well-developed processes for muscle attachment. The femur has a strong third trochanter and relatively small distal condyles. The shaft is bowed convex anteriorly to an even greater extent than is seen in *Smilodon*. The metapodials are robust, with large proximal processes and are easily distinguished from those of felids. Their shafts are dorsoventrally compressed and the distal articular surfaces are flattened dorsally.

Many of these features are characters that Ginsburg (1961b) considered diagnostic of a plantigrade

stance. Joints in plantigrade animals tend to be looser with a greater degree of motion. In *Barbourofelis* this is especially marked in the joint between the radius and scapholunar, which has a very rounded proximal articular surface, and those between the carpals and tarsals, between the podials and metapodials, between the metapodials themselves, and between the tibia and the astragalus. The calcaneum is short and the sustentacular facet is medially situated. The astragalus possesses a short neck and the astragalar keels are poorly developed. The metapodials are short and, when articulated, spread out in a fan. Gonyea (1976) criticized Ginsburg's (1961b) work on plantigrade posture and stated that all nimravids and felids have digitigrade posture at least for the forelimb. Although this may be true, classifying all these carnivores as simply digitigrade masks important differences in their postures. The Oligocene nimravids, *Barbourofelis*, and certain machairodontine felids such as *Smilodon* should be classified as subdigitigrade. Thus, although their metapodials were not in full contact with the substrate during locomotion, they were not nearly as perpendicular to the ground as in the fully digitigrade felines.

Gonyea (1976) used limb proportions to interpret behavior and ecology of saber-toothed carnivorans. He compared limb segment ratios of four extinct sabertooths with eight species of Recent large felids. Tables 2 and 3 present long bone measurements for *Barbourofelis loveorum*. Greatest length of metacarpal III averaged 62.0 ± 1.05 for 12 specimens; metatarsal III, 63.6 for four specimens. The intermembral index (IMI, anterior limb length/posterior limb length; anterior limb length = length of humerus + radius + third metacarpal; posterior limb length = length of femur + tibia + third metatarsal) ranged from 0.790 for *Dinictis* and 0.810 for *Felis concolor*, the puma, to 0.974 for *Smilodon* (Gonyea 1976). For *B. loveorum*, indices of 0.942, 0.949, and 0.937 were calculated for minimum, average, and maximum measurements, respectively.

The brachial (or humeroradial) index (BI) is the ratio of the length of the radius to that of the humerus. It ranges from 0.820 for *Smilodon* to 1.033 for *Acinonyx jubatus*, the cheetah (Gonyea 1976). In *Barbourofelis loveorum*, the BI is 0.700, 0.691, and 0.676, based on the minimum, average, and maximum measurements, respectively (Table 1). A value of 0.717 was computed for a radius and humerus, possibly from the same individual, of *Barbourofelis fricki* from Long Island Quarry, Kansas in the USNM collection. These values are all markedly lower than those reported by Gonyea (1976)

for extant felids, but are closest to those he reported for *Smilodon*.

The crural index (CI), the length of the tibia to that of the femur, ranged from 0.837 for *Smilodon* to 1.050 for *Uncia uncia*, the snow leopard, and *Acinonyx jubatus* (Gonyea 1976). The values for *Barbourofelis loveorum* are 0.750, 0.744, and 0.742 for the minimum, average, and maximum measurements, respectively (Table 2). The average index for two femora and two tibiae of *B. fricki* in the F:AM collection from the Jack Swayze Quarry in Kansas is 0.648. Again, these values are smaller than those reported for *Smilodon*.

The limb proportions of *Barbourofelis* are most similar to those of the machairodontine felid *Smilodon*. The hind limb is not elongated relative to the forelimb. The IMI is intermediate between that of *Panthera leo* and *Smilodon*, which has the relatively shortest hindlimbs of the "cats" investigated by Gonyea (1976). The average BI of 0.69 and CI of 0.74 for *B. loveorum* are lower than those he reported for cats. The values of these three indices are correlated with an absence of cursorial adaptations. Anyonge (1996) distinguished ambush, cursorial, and ambulatory locomotor groups in late Neogene sabertoothed carnivorans. Ambush and ambulatory species had significantly lower BI's (0.80) than cursorial species (1.01). The average CI of ambush species (0.84) was intermediate between those of ambulatory (0.69) and cursorial (0.93) species. The BI and CI values calculated for *B. loveorum* suggest an ambush species. Anyonge (1996:fig. 3) tentatively concluded that average measurements for the smaller and older *B. morrisoni* suggest it was an ambulatory species.

Gonyea (1976) associated short distal segments (low BI and CI) with extant felids from highly structured habitats, such as dense forest; and longer distal segments with those inhabiting open terrain. According to Gonyea's criteria, *Barbourofelis loveorum* was an inhabitant of dense forest. A fully digitigrade posture is best adapted for running down and capturing prey in open country. The subdigitigrade *Barbourofelis* probably stalked and ambushed its prey in a dense forest, perhaps along the stream border of the channel that formed the Love Bone Bed. Gonyea (1976) also used the relationship between the cross-sectional area of the humerus and its length as an indication of the size of prey that a cat could capture. The cross-sectional area was computed by multiplying the width and thickness of the shaft two-thirds of the way down the shaft. The cross-sectional areas of the two complete *B. loveorum*

Table 2. Measurements of the humerus, ulna, and radius of *Barbourofelis loveorum* and *Nimravides galiani* from the Love Bone Bed.

	<i>Barbourofelis</i>				<i>Nimravides</i>			
	<i>N</i>	<i>X</i>	<i>OR</i>	<i>CV</i>	<i>N</i>	<i>X</i>	<i>OR</i>	<i>CV</i>
Humerus								
GL parallel to longitudinal axis	2	270.5	260-281		3	279.7	272-292	
GTD of proximal extremity	5	53.22	51.4-55.1		3	60.70	53.5-65.0	
Greatest APD of proximal extremity	5	78.50	75.8-83.3		3	77.9	75.0-83.2	
TD at middle of shaft	3	26.83	25.8-27.5		3	27.8	26.5-30.0	
APD at middle of shaft	3	37.70	37.1-38.2		3	40.9	40.0-42.0	
GW of distal extremity	22	71.08±0.822	64.6-76.8	5.5	8	73.5	67.8-78.7	5.1
Least APD of articulating surface of ulna	22	24.53±0.316	21.7-29.1	6.0	6	25.0	22.2-28.1	7.8
Ulna								
GL parallel to longitudinal axis	6	247.7±4.03	230-258	4.0	1	297		
GW posterior surface of olecranon process	14	32.43±0.869	27.4-38.0	10.0	9	22.78±1.140	19.2-27.8	15.0
Greatest TW greater sigmoid cavity	13	32.23±0.914	28.0-39.0	10.2	8	34.50±0.886	30.2-37.7	7.3
APD across coronoid process	13	52.39±0.964	45.0-57.0	6.6	8	47.25±1.191	44.7-54.0	7.1
APD of shaft at proximal end of tendon scar	6	27.38±0.809	25.0-29.2	7.2	5	29.14	28.1-31.2	
TD of shaft at proximal end of tendon scar	6	20.37±0.970	17.8-23.9	11.7	5	14.98	13.4-17.6	
Greatest APD at distal extremity	6	27.08±0.973	23.9-29.7	8.8	2	27.65	25.5-29.8	
GW of distal extremity	6	18.85±0.533	17.2-20.6	6.9	2	15.00	13.5-16.5	
Radius								
L measured along internal border	9	186.8±1.15	182-190	1.9	2	227	211-243	
Longest diameter of proximal end	8	31.00±0.682	27.6-33.2	6.2	5	35.17±1.059	33.2-39.2	6.7
Greatest diameter taken at right angles to long diameter of proximal end	8	24.25±0.485	23.3-26.2	5.7	5	25.54±0.938	23.6-28.0	8.2
W of shaft at middle	8	23.99±0.396	23.2-25.3	4.7	3	26.03	22.7-27.9	
Thickness of shaft at middle	8	13.74±0.415	11.5-14.9	8.6	3	15.00	13.7-15.8	
GW at distal end taken normal to internal face	8	41.73±0.972	38.4-46.7	6.6	5	43.50±1.649	39.6-48.9	8.5
Greatest thickness of distal end	8	30.61±0.655	28.2-33.9	6.0	5	28.46±1.983	25.2-36.2	15.6

Table 3. Measurements of the femur and tibia of *Barbourofelis loveorum* and *Nimravides galiani* from the Love Bone Bed.

	<i>Barbourofelis</i>				<i>Nimravides</i>			
	<i>N</i>	<i>X</i>	<i>OR</i>	<i>CV</i>	<i>N</i>	<i>X</i>	<i>OR</i>	<i>CV</i>
Femur								
GL from top of greater trochanter to distal condyles	4	277.0	268-291	3.5	4	328.5	315-347	4.6
TD of proximal end, outer face of greater trochanter to inner side of head	11	71.82±0.601	69.2-75.8	2.8	11	69.34±1.421	64.0-77.1	6.8
Greatest APD of head	11	33.39±0.376	31.8-35.8	3.7	10	33.56±0.634	30.4-36.2	6.0
TD shaft at middle	6	27.87±0.842	24.2-30.2	7.4	7	26.93±0.278	26.1-27.9	2.7
APD of shaft at middle	6	21.20±0.366	20.2-22.3	4.2	7	27.04±0.599	24.5-28.9	5.9
GW of distal extremity	7	56.74±0.973	52.8-59.8	4.5	6	59.98±1.160	56.8-64.1	4.7
Greatest APD of distal extremity	7	54.87±1.050	50.2-58.0	5.1	6	55.95±1.673	52.3-61.9	7.3
GW of intercondylar notch	7	10.62±0.29	9.3-11.8	7.2	6	17.90±0.924	15.0-20.6	12.6
GW of articular surface of inner condyle	7	24.02±0.379	22.8-25.7	4.2	4	22.52	21.0-24.5	6.4
Tibia								
GL	11	206.3±1.34	201-216	2.1	4	288.8	279-302	3.3
Greatest TD of proximal end	10	54.51±0.767	50.8-58.7	4.4	7	65.73±1.580	61.8-72.8	6.4
TD of shaft at middle	11	19.08±0.335	17.1-20.6	5.8	5	27.68±0.317	26.8-28.7	2.6
Greatest TD of distal end	10	41.10±0.873	36.6-44.8	6.7	13	48.09±0.683	44.0-51.5	5.1
Greatest APD of distal end	10	27.32±0.457	25.5-29.3	5.3	13	31.35±0.598	28.7-34.7	6.9

humeri are 1028 and 1050 mm². These values fall well-above Gonyea's (1976:fig. 6) regression line for cross-sectional area of the humerus (expected values = 661 and 796 mm²) versus its length. Of the 12 taxa examined (Gonyea 1976), only *Hoplophoneus* and *Smilodon* show comparable results. These values indicate that *B. loveorum* probably took prey substantially heavier than its own body weight, such as *Teleoceras* or *Gomphotherium*. *Barbourofelis* probably stalked and ambushed its prey from dense cover, pulling down large prey with its heavily muscled, well-developed forelimbs.

Family FELIDAE Gray 1821

Genus *NIMRAVIDES* Kitts 1958

NIMRAVIDES GALIANI Baskin 1981

Tables 1-3

Comment.—Baskin (1981) described cranial and dental material of this species. A notable addition is a nearly complete skull (UF 27989) recovered in 1981 (Table 1).

Postcranial Skeleton.—The lion-sized *Nimravides galiani* is typically feline in limb structure and proportions, and in many postcranial features resembles the jaguar, *Panthera onca*. The pelvis has characters of both *Smilodon* and *Panthera*. The femur and tibia are elongate and slender. The neck of the astragalus is long. The calcaneum is lynx-like in form and has a long neck with a grooved head. Greatest length of metacarpal III averages 110.0±3.06 for six specimens; metatarsal III, 116.0±1.52 for six specimens. *Nimravides* possesses the digitigrade characters Ginsburg (1961b) detailed for modern cats. The BI values for *N. galiani* are 0.776, 0.811, and 0.832 for the minimum, average, and maximum measurements, respectively. Gonyea (1976) reported values of 0.820 for *Smilodon*, well below those of *P. onca* (0.868) or *Machairodus* (0.921). The CI values are 0.886, 0.881, and 0.870 for the minimum, average, and maximum measurements, respectively, close to those values reported for *Machairodus* (0.876) or *P. onca* (0.899). The IMI values are 0.818, 0.840, and 0.846, for the minimum, average, and maximum measurements, respectively. These are more like *Puma* (0.810) or *Uncia uncia* (0.847) than a jaguar (0.881) or *Machairodus* (0.905). Gonyea (1976) correlated elongated hind limbs, such as are present in *P. concolor*, with jumping ability. Anyonge (1996) inferred that *Nimravides*, like all large extant felids other than the cheetah, was a true ambush predator, rather than a cursor.

Discussion.—The genus *Nimravides* was established by Kitts (1958) for *Pseudaelurus thinobates* from the latest Clarendonian Black Hawk Ranch Local Fauna of California (Macdonald 1948b) and the early Hemphillian Arnett (= Port of Entry Pit) and Higgins local faunas of Oklahoma and Texas. Macdonald (1948b) derived his species from the Barstovian *P. intrepidus*. Martin and Schultz (1975) recognized that the type of *Machairodus catacopsis*, a mandibular symphysis, belonged to *Nimravides*, and was probably a senior synonym of *N. thinobates*. The symphysis is relatively large, similar in size to specimens from the early Hemphillian.

Baskin (1981) named *Nimravides galiani* from the Love Bone Bed and concluded that *Nimravides* was derived from the early Clarendonian *Pseudaelurus pedionomus* (Macdonald 1948a). He determined that although *Nimravides catacopsis* was correctly assigned to *Nimravides*, it was best to consider the species name a *nomen dubium*, given the fragmentary nature of the type specimen, the lack of precise knowledge of the age and location of the type locality, and the possibility that more than one species was present in the early Hemphillian.

Beaumont (1990) referred *Pseudaelurus pedionomus* to *Nimravides*. He recognized two subspecies from the Ash Hollow Formation: *Nimravides pedionomus pedionomus* for material from the early Clarendonian Cap Rock Member and *N. p. nebraskensis* for material from the late Clarendonian Merritt Dam Member. He distinguished *N. p. nebraskensis* from *N. p. pedionomus* by its larger size and from *Nimravides galiani* by its slightly smaller size and minor differences in the dentition. Beaumont (1990) noted the strong similarity between *N. galiani* and *N. thinobates* from Black Hawk Ranch, except for the stronger and more inclined accessory cusps on the lower premolars in the latter. He (1990:138) concluded that there was a lineage of Clarendonian *Nimravides* from *N. pedionomus* to *N. galiani* to *N. thinobates*, and declined to speculate on their possible eventual synonymies. He considered that one or more different species of *Nimravides* were present in the Hemphillian, which were more closely related to *N. thinobates* than to *N. galiani*, and that could possibly be assigned to *N. catacopsis*, but that this last would be difficult to demonstrate.

Clarendonian *Nimravides* may represent a single chronospecies as tentatively postulated by Beaumont

(1990), similar to the situation interpreted for *Epicyon saevus* or *E. haydeni* (Baskin 1998b). However, there appear to be discrete size differences as noted by Baskin (1981). The m1 and p3-m1 lengths of specimens from the Love Bone Bed (26.8 ± 1.00 , 61.9 ± 2.25) are statistically significantly larger than specimens from the Merritt Dam Member (23.9 ± 0.31 , 57.12 ± 2.72) reported by Beaumont (1990). Likewise, the m1 and p3-m1 lengths of specimens from the Love Bone Bed are statistically significantly smaller than specimens from California and Oklahoma referred to *N. thinobates* (29.2 ± 1.59 , 69.82 ± 3.66) by Kitts (1958) and Baskin (1981).

In the lower jaw of *Nimravides galiani*, p1 is absent and a very small to vestigial, single-rooted p2 is present in 10 specimens, absent in 9. The holotype of *N. pedionomus* has single-rooted p1 and p2. In specimens referred to *N. thinobates*, p2 is usually absent. In the maxilla of *N. galiani*, there is no alveolus for a tooth between the canine alveolus and P3 in UF 24482 (Baskin 1982:fig. 7A). UF 27989 has a small alveolus for P2. An additional edentulous maxilla fragment (UF 26105) is referred to *N. galiani* (P3 alveolar L = 17, P4 alveolar L = 31). Between the P3 alveoli and the alveolus for the canine are two small alveoli that are interpreted as the alveoli for unirooted P1 and P2. An M1 is present. In a maxillary fragment referred to *N. pedionomus nebraskensis* (Beaumont 1990), P2 and M1 are present.

If there is sexual dimorphism in this genus (Baskin 1981), overlap in size among the three named Clarendonian species may mainly be the result of presumably larger males from older faunas and presumably smaller females from younger faunas. The cranium from the Love Bone Bed (Table 1) may be from a large male. The P4 is longer than those reported previously from this locality. The skull has an exceptionally well-developed sagittal crest, approximately 30 mm tall midway along its length and 44 mm tall close to its posterior junction with the lambdoidal crest. The badly damaged skull of *Nimravides thinobates* from Black Hawk Ranch (Macdonald 1948b:fig. 14) is similar in size to material from the Love Bone Bed and the largest specimen from the Merritt Dam Member of the Ash Hollow Formation. In it, P2 and probably M1 are absent. The Black Hawk skull may be from a smaller female.

Family CANIDAE Gray 1821
Genus EPICYON Leidy 1859
EPICYON SAEVUS (Leidy 1859)
EPICYON HAYDENI (Leidy 1859)

Comment.—These two species are described and discussed in Baskin (1998b)

cf. *UROCYON* sp.

Figure 1 A-B

Proturocyon cf. *macdonaldi* nomen nudum, in Webb et al. 1981.

Referred Material.—UF 25696, right M1; 25697, right M2; 25698, right p4; 37947, left jaw fragment with p2; 25699, 25700, edentulous jaw fragments, all from the Love Bone Bed, Alachua County, Florida, latest Clarendonian Land Mammal Age.

Description.—The M1 is transversely elongate. The cusps are acute. The cingula on the borders of the tooth have beaded enamel. The protocone is connected by a prominent preprotocrista to a small parastyle. The external cingulum is well developed, but is constricted medially between the paracone and metacone. The metaconule is especially well developed. It is connected to the external cingulum by a weak postmetaconulecrista. The hypocone is large and is situated slightly anterior to the metaconule and internal to the protocone. A median notch separates the hypocone from the precingulum. The precingulum and postcingulum are prominent. A weak external cingulum is present on the posterointernal border of the tooth (L = 8.7, W = 10.6).

The M2 is well worn, but the cusps appear to be low crowned. The large protocone is connected to a small metaconule. The hypocone is situated on the postero-internal border of the tooth (L = 5.5; W = 6.5).

The p4 has a small posterior accessory cusp on the flank of the main cusp. The posterior border is trichant (L = 7.2; W = 3.2).

Discussion and Comparisons.—Macdonald (1948b) described the lower jaw with m2 of a fox-like canid from the late Clarendonian Black Hawk Ranch local fauna of California that he thought might be referable to *Urocyon*. Additional material of this canid in the University of California Museum of Paleontology collected since that time supports this assignment. The M1 from the Love Bone Bed is slightly larger than this material, has a more prominent metaconule and precingulum, and the hypocone is not as bent posteriorly. In development of the metaconule and other characteristics, the M1 from the Love site bears a strong resemblance to that of *Nyctereutes*, the Asian raccoon dog.

The M2 from the Love site is smaller and lower crowned than the M2 from Black Hawk Ranch. The small size of this tooth indicates the possibility that it may be referable instead to another taxon, such as

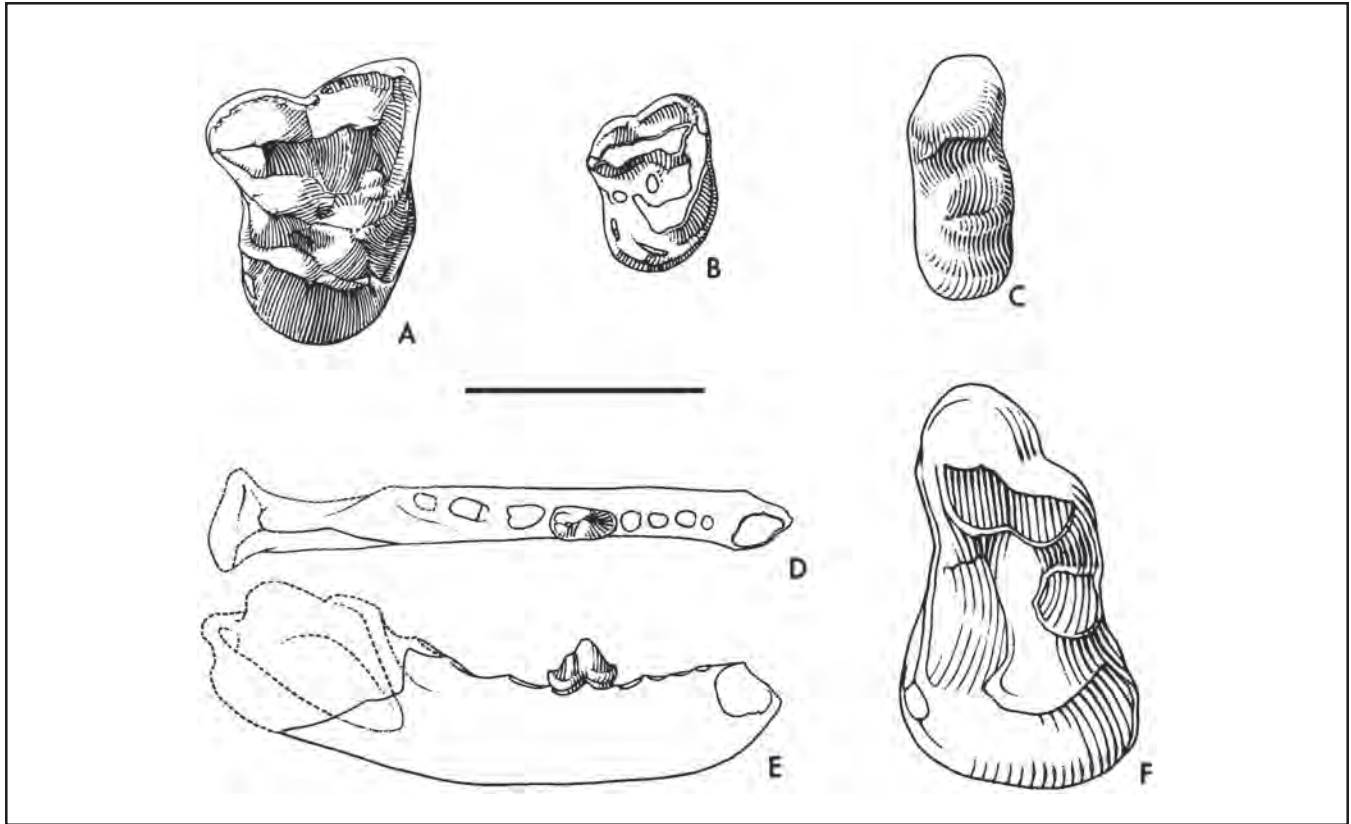


Figure 1. Cf. *Urocyon* sp., *Plionictis* sp., and ?*Sthenictis* near ?*S. lacota*. (A) cf. *Urocyon* sp., UF 25696, right M1, occlusal view; (B) cf. *Urocyon* sp., UF 25698, right M2, occlusal view; (C) *Plionictis* sp., UF 25701, right M1 occlusal view; (D) and (E) ?*Sthenictis* near ?*S. lacota*, UF 25633, right mandible with p4 occlusal and lateral views; (F) ?*Sthenictis* near ?*S. lacota*, UF 25632, right M1, occlusal view. Scale bar = 12 mm for A and B, 5 mm for C, 2.5 mm for D and E, 10 mm for F.

Leptocyon (= ?*Leptocyon* in Webb et al. 1981).

Family URSIDAE Gray, 1825

Subfamily HEMICYONINAE Frick 1926

Genus *PLITHOCYON* Ginsburg 1955

cf. *PLITHOCYON* sp.

Figure 2

Referred Material.—UF 37180, left m2; UF 37078, left tibia; UF 38010-38012, calcanea.

Description of m2.—The protoconid and smaller metaconid are situated opposite each other, close to the anterior margin of the tooth. The two cusps are joined at their bases and are separated only at their apices. A preprotocristid slopes downward from the base of the protoconid to the anterointernal corner of the tooth. It does not connect with the metaconid. The talonid is lower than the trigonid, elongate, relatively flat, and open internally. The low hypoconid is connected to the protoconid by a crest. There is a weak, low external cingulum

(L=16.6, W=12.7).

Comparisons.—The m2 is most similar to that of amphicyonids and hemicyonine ursids. Amphicyonids are known from the Hemingfordian and Barstovian of Florida. Hunt (1998a) recognized two Clarendonian amphicyonids, *Ischyrocyon* and *Pseudocyon*. In these two genera, the m2 is much higher crowned than and the hypoconid is not connected to the protoconid as in UF 37180. Late Clarendonian *Ischyrocyon* has an m2 trigonid with a large, subcentral protoconid and very reduced to absent metaconid and m2 talonid with a prominent, isolated, subcentral hypoconid. *Ischyrocyon* from the Burge has an m2 trigonid more similar to UF 37180 in having a metaconid with a preprotocristid extending anterior to it, but differs in the other features noted above. *Pseudocyon* also has a short trigonid as in UF 37180, but the metaconid is situated more medially and connected to the preprotocristid.

Hemicyonines have similar crown height and a

protoconid-hypoconid connection as in UF 37180. *Phoberocyon johnhenryi*, from the Hemingfordian Thomas Farm Local Fauna, has a longer trigonid, with the preprotocristid connecting to the metaconid and delineating a trigonid basin, as well as a metaconid that is more separate from the protoconid. Hunt (1998b) assigned the North American hemicyonines from the Barstovian to *Plithocyon* and those from the Clarendonian to an undescribed new genus for the large "*Hemicyon*" *barbouri*. The two genera are distinguished by characters of the m1, which is unknown in the Florida taxon. Hunt (1998b) states that in *Plithocyon* the protoconid and metaconid of m2 are the same height, unlike UF 37180. The Love m2 is slightly smaller than the m2 of the type of *P. barstowensis* (L=17.8, W=12.2) and much smaller than the type of "*H.*" *barbouri* (L=21.3, W=12.3). The trigonid of m2's assigned to *Plithocyon* from Barstow in the collections of the AMNH vary in morphology. Most are similar to those illustrated for European *Ursavus* (e.g., Ginsburg & Morales 1998) with an anteriorly extending preprotocristid connecting to the metaconid, defining a relatively long and shallow trigonid. F:AM 23798 from the *Hemicyon* stratum is more similar to the Florida specimen in having a short trigonid, although the preprotocristid connects to the metaconid. The m2 of the type of "*Hemicyon*" *barbouri* is heavily worn. The m2 of F:AM 54205 from the Devil's Jump Off, Cherry County, Nebraska is much larger and has a relatively longer trigonid and taller hypoconid than UF 37180.

Description and Comparisons of the Calcaneum.—The calcaneum of the Florida cf. *Plithocyon* is intermediate in appearance between those of digitigrade

carnivorans such as *Canis* and *Nimravides* and plantigrade carnivorans such as *Barbourofelis* and *Ursus*. The sustentaculum is separate from the cuboid facet. Compared with illustrations of calcanea of ursids (Stains 1973), the Love Site calcanea differ in having an ectal facet that extends further proximally and is positioned more medially, as well as possessing a trochlear process immediately distal to the ectal facet that extends nearly to the distal end. They resemble the calcaneum illustrated for the amphicyonid *Cynelos lemanensis* (Ginsburg 1977:fig. 36), but have a better-developed trochlear process. The Florida specimens also resemble the calcaneum of *Hemicyon sansanensis* (Ginsburg 1961a:fig.36-2), but the proximal end is more rounded (concave). The Love material is most similar to a hemicyonid calcaneum from the Valentine Formation of Nebraska (F:AM 68165B) and differs from a more bear-like calcaneum assigned to *Ischyrocyon* (F:AM 68157) from the Merritt Dam Member of the Ash Hollow Formation.

Family PROCYONIDAE (Gray, 1825) Bonaparte, 1850

ARCTONASUA FLORIDANA Baskin 1982

PARANASUA BIRADICA Baskin 1982

Comment.—These two species are described and discussed in Baskin (1982).

Family MUSTELIDAE (Fischer 1817) Swainson 1835

Genus *LEPTARCTUS* Leidy 1856

LEPTARCTUS WEBBI n. sp.

Figures 3-4; Table 4

Holotype.—UF 24724, right dentary fragment with c1, p2-m1.

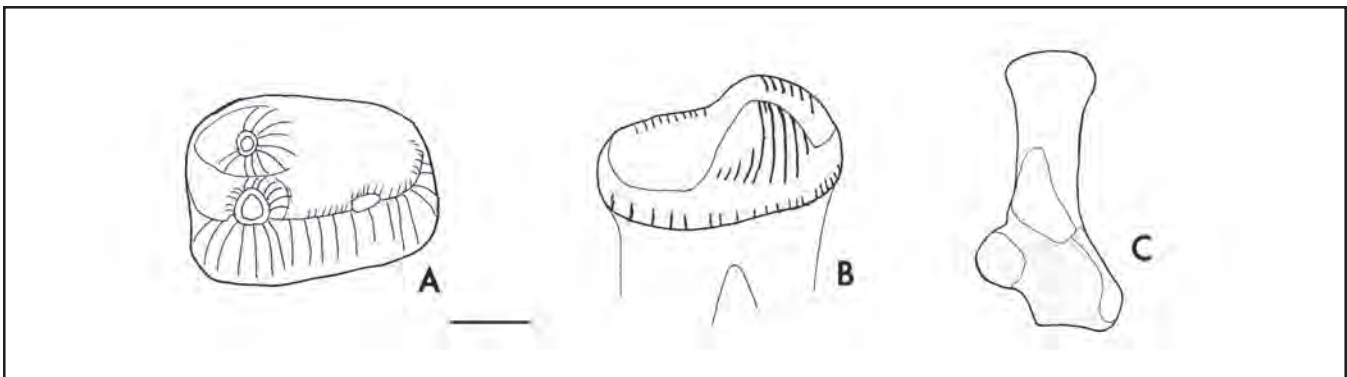


Figure 2. Cf. *Plithocyon* sp. Scale bar = 5 mm for A and B, 10 mm for C. (A) and (B) UF 37180, left m2, occlusal and internal views; (C) UF 38010, calcaneum.

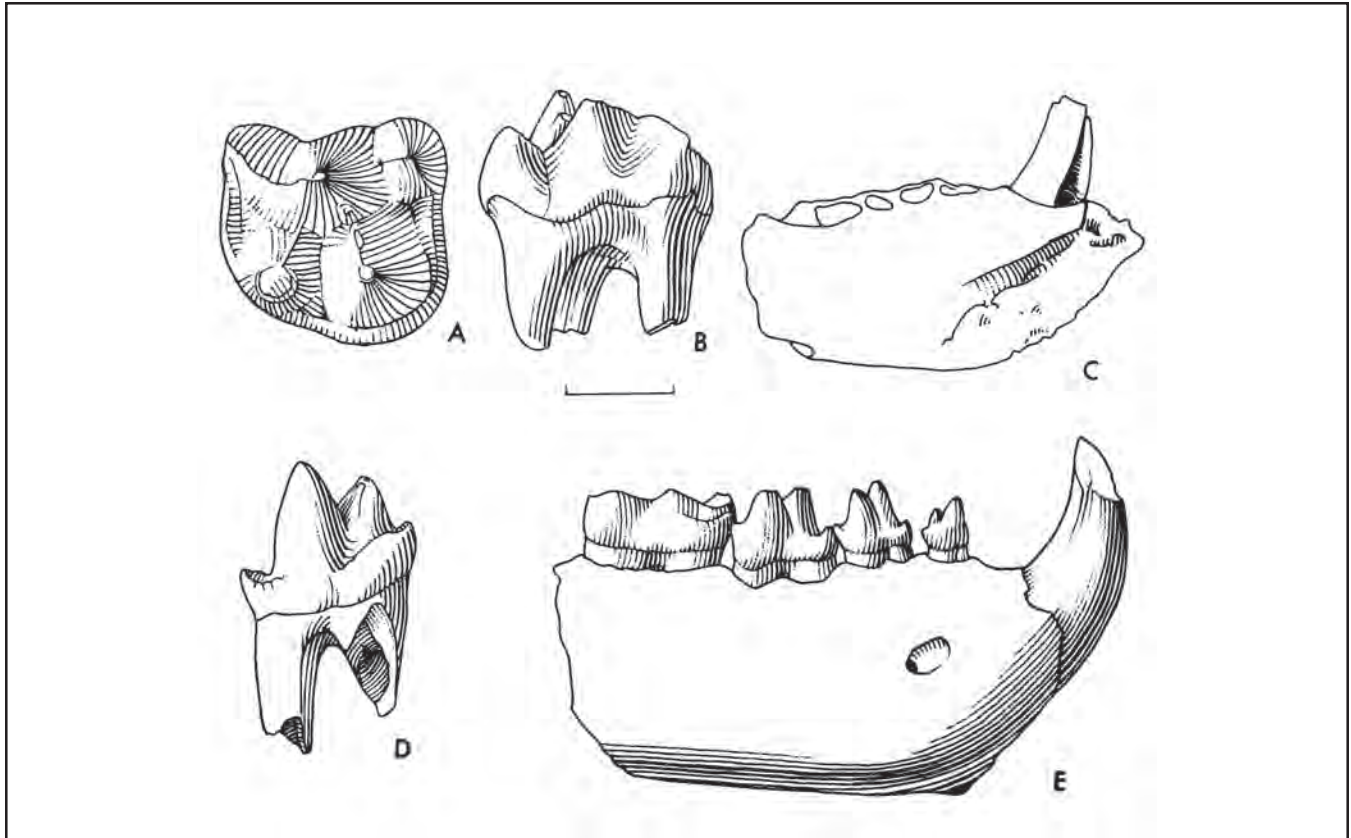


Figure 3. *Leptarctus webbi* n. sp. from the late Miocene Love Bone Bed. Scale bar = 10 mm for A-D, 15 mm for E; (A) and (B) UF 24986, right P4, occlusal and external views; (C) UF 24983, left dentary fragment with c1 external view; (D) UF 24989, right p4, internal view; (E) UF 24724, holotype right mandible fragment with C1, p2-m2, external view.

Hypodigm.—UF 24987, left P4; 24986, right P4; 24988, left M1; 24989, right p4; 24990, right m2; 24983, left dentary fragment with c1; 24982, left dentary fragment with p2-m2; 24724, holotype; 24984, 25065, left dentary fragment with m2; 37948, left dentary fragment with p3-4; 37953, left dentary fragment with p4-m1; 37952, mandible with m1; 24985, left dentary fragment; 24398, 37949, 37950, 37951, 37954, mandible fragments; 24991, left and right otic fragments; all from the Love Bone Bed, Alachua County, Florida, latest Clarendonian Land Mammal Age.

Diagnosis.—Auditory bullae apparently lacking bony projections (tympanic processes). P4 has a well-developed parastyle and hypocone. M1 is quadrate with a well-developed metaconule. The dentary is deep and massive. The lower canine has a deep anteromedial groove. The lower premolars have well developed posterior accessory cusps on the protoconid. On the m1, the subequal metaconid, protoconid, and

paraconid form an equilateral triangle, open medially.

Etymology.—Patronym for S. David Webb.

Description.—The P4 is quadrate, slightly longer than wide. The protocone is large and subequal in size to the paracone. A well-developed hypocone and the protocone are each connected to the paracone by a crest. The paracone-metacone blade is unnotched. The parastyle is subequal in size to the paracone. There is a small median cusp on the anterior cingulum. There is a moderate posterior cingulum and the internal cingulum is weak to absent.

The M1 is very worn. The protocone, paracone, metacone, and metaconule are all subequal in size, with the first three cusps forming an equilateral triangle closing off a trigon basin. The paracone and metacone are anterior to the protocone and metaconule, respectively. The metaconule is connected to the protocone by a transverse mure. There is a small metastyle on the postero-external border of the tooth and a very small

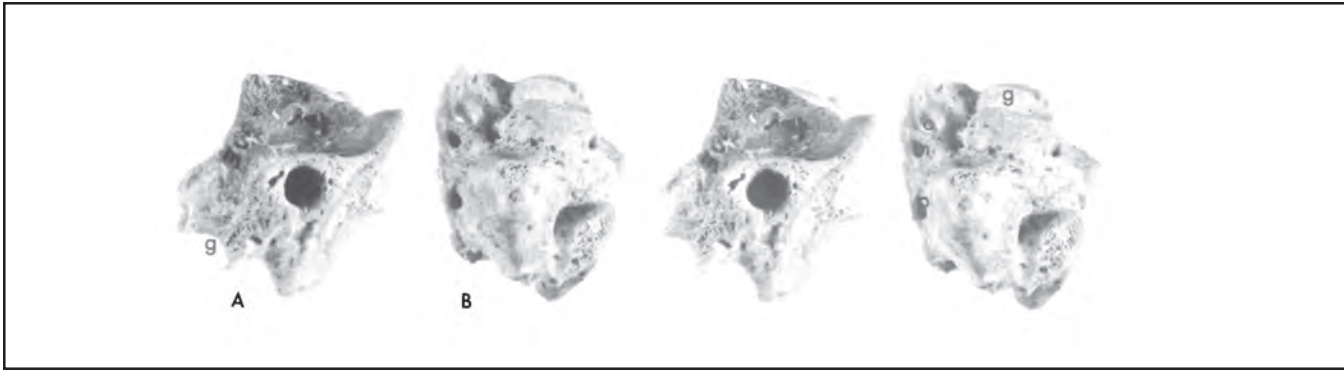


Figure 4. Stereophotographs of *Leptarctus webbi*, UF 24991, left otic fragment; g, glenoid fossa, o, foramen, ovale, m, median lacerate foramen, p, posterior carotid foramen. (A) lateral view, anterior to left. (B) ventral view, anterior to top.

mesostyle. The hypocone is on the postero-internal border of the tooth, medial to the protocone.

The mandible is heavy and increases slightly in depth anteriorly. There is a large mental foramen beneath p2; a smaller one may be located somewhat posteriorly. The ventral border of the mandible is constricted beneath the masseteric fossa. The ventral border of the masseteric fossa widens posterolabially.

The alveoli for the first and second incisors are aligned anteroposteriorly on the medial border of the ramus at the symphysis. The alveolus for the i3 is lateral to the alveoli for i1 and i2. The canine is deeply grooved medially at the base of the enamel to anteromedially at the tip. There is a small diastema between the canine and p2.

The p2 is a small tooth with two roots and a small posterior accessory cusp. It is separated from p3 by a short diastema. The p3 and p4 have a large posterior accessory cusp adjacent to, but clearly separated from the protoconid on the external border of the tooth and are widest transversely between the protoconid and posterior accessory cusp. The p3 anterior cingulum is narrow, the posterior cingulum is broad. The p4 is larger than p3 and has a relatively larger posterior accessory cusp and better developed anterior and posterior cingula.

The m1s are slightly worn. The paraconid, metaconid, and entoconid are subequal in height and slightly taller than the protoconid and hypoconid. When unworn, the five cusps were probably subequal in height. The apices of the three cusps of the trigonid form an equilateral triangle, with the metaconid slightly posterior to the protoconid and with the paraconid on the internal bor-

der, anterior to the protoconid. The protoconid is slightly anteroposteriorly elongate. The paraconid and metaconid are broadly and strongly connected to the protoconid. The trigonid opens labially through a V-shaped notch between the paraconid and metaconid. There is a wider labial opening for the deeply basined talonid between the metaconid and entoconid. On one specimen, there is a small hypoconulid on the postcristid connecting the hypoconid and entoconid. The hypoconid is connected to the protoconid by a cristid obliqua. There is a moderate to strong anterolabial cingulid and a weaker posterolabial cingulid.

The m2 is small, oval in outline, and double-rooted. The paraconid is small; the protoconid and metaconid are connected by a convex posterior cingulum. The talonid is reduced to a posterior heel.

Left and right otic fragments, presumably from the same individual, are assigned to *Leptarctus webbi* after comparison with *Leptarctus ancipidens*. The bulla is conical in shape, but is skewed anteriorly. It is fused to the surrounding bones. The distal termination of the bulla is slightly abraded, but the abraded region is small, indicating there is apparently no tympanic process. If a small tympanic process were present, it would not be double. The auditory tube is very long, passing ventral to the long and broad posterior root of the zygomatic. The external auditory meatus has a circular cross-section. The paroccipital and the much larger mastoid processes are broken off, but they both appear to have been joined to the bulla. The large stylomastoid foramen lies between the mastoid process and the bulla. An unusual feature of this auditory region is that the canalis musculotubarius opens ventrally into the foramen ovale.

The posterior carotid foramen is in the entotympanic, approximately halfway between the median and posterior lacerate foramina. The median lacerate foramen is posterior to the common opening of the foramen ovale and canalis musculotubarius. The postglenoid foramen divides in two internally. One opening communicates medially and dorsally with a foramen in a depression in the posterior root of the zygomatic adjacent to the braincase wall.

The right otic fragment is broken medially, revealing the internal structure of the bulla. Two septa radiate medially and anteriorly, respectively, from the elongate ventral lip of the crista tympanica ventrally to the floor of the bulla. A smaller third septum extends posteriorly from the medial septum. The canal connecting the fo-

ramina stylomastoideum primitivum and definitivum forms a relatively large tube on the inside of the tympanic chamber. This tube and the three septa partition the ventrolateral portion of the tympanic chamber. The epitympanic recess is a deep pit. The fossa muscularis major is extremely large.

Discussion.—The Leptarctinae are a distinct group of mustelids (Baskin 1998a). The most primitive is *Craterogale simus*, from the early Hemingfordian Runningwater Formation of Nebraska. Fourteen species of *Leptarctus*, including *L. webbi*, have been named. The earliest and most primitive species of *Leptarctus* is the early Hemingfordian *L. ancipidens*. The type species, *L. primus* (Leidy 1856), was named from an isolated P4 (L = 7.4, W = 6.3) from the late Barstovian

Table 4. Measurements taken on *Leptarctus webbi*.

	UF no.: 24986	24987	24988	24724	24982	25065	24989	37953
P4 length	10.8	9.8						
width	10.3	9.5						
M1 length			10.9					
width			10.3					
p2 length				3.5	3.4			
width				3.7	2.6			
p3 length				6.0	5.7			
width				4.6	4.6			
p4 length				7.8	8.0		8.2	8.2
width				5.2	5.4		5.7	5.9
m1 length				11.4	11.4			12.0
width				6.3	6.2			7.2
m2 length					6.2	6.4		
width					4.6	5.6		
p2-m2					35.6	(37.7)		36.5
depth below m1					15.8	15.7	15.1	15.2

Bijou Hill Fauna, South Dakota (Skinner & Taylor 1967). Matthew (1924) included the material from the early Barstovian Olcott Formation in *L. primus*. Baskin (1998a) referred the Olcott Formation *Leptarctus* to the smaller, more primitive *L. oregonensis*, first described from the early Barstovian, Mascall Formation of Oregon (Stock 1930). The P4 of *L. oregonensis* is smaller and has a smaller hypocone and parastyle and a longer metacone blade than *L. primus*.

Baskin (1998a) included late Barstovian and early Clarendonian leptarctines in *Leptarctus primus*. Dorr (1954) named *Hypsoparia bozemanensis* from the late Barstovian of Montana. Voorhies (1990a) and Webb (1969) recognized *L. primus* from the late Barstovian Valentine Formation and the early Clarendonian Cap Rock Member of the Ash Hollow Formation of Nebraska, respectively, although both made their comparisons with the Olcott specimens. Evander (1986) referred the *Leptarctus* from the late Barstovian Crookston Bridge Member of the Valentine Formation of Nebraska to *L. cf. bozemanensis*, noting that the specimens were larger than the Olcott material. Lim & Martin (2002) named *H. timmi* from the late Barstovian of South Dakota. *H. bozemanensis* and *H. timmi* differ from each other in minor details, and likely are conspecific. *Leptarctus martini* (Lim & Miao 2000) is from the late Barstovian Devil's Gulch Member of the Valentine Formation. The skull and dentition are similar to those of the holotype of *H. bozemanensis*, although the P4 and M1 are wider than long.

Lim and Martin (2002) concluded that *Hypsoparia* (Dorr 1954) is distinct from *Leptarctus*. They compared the late Barstovian *Hypsoparia* to early Barstovian Olcott Formation *Leptarctus*, rather than to the genotypic species *L. primus*. Other than the great height of the zygomatic arch, most if not all, of the characters they list as diagnostic of *Hypsoparia* can be found in other species of *Leptarctus*. Olsen (1958) did not consider the structure of the zygomatic arch sufficient to distinguish *Hypsoparia* from *Leptarctus*. In any event, Lim and Martin (2002) have not demonstrated any differences with the genotypic *L. primus*. Webb (1969) suggested that *H. bozemanensis*, with its enlarged zygomasseteric structure and large canines, is a mature male specimen of *L. primus*. Dorr (1954) thought the differences exceeded sexual variation in extant mustelids.

Hunt and Skolnick (1996) interpreted that the early Miocene paleomustelid *Megalictis* expressed a profound degree of sexual dimorphism. Extant mustelids display

a relatively high degree of sexual dimorphism (e.g., Gittleman & Van Valkenburgh 1997). The Love site sample may offer evidence of sexual dimorphism in *Leptarctus*. The left and right jaw halves (UF 24724 and 24982), although not found together, may belong to the same individual. They are similar in size and degree of wear of the teeth. These two jaw halves, UF 25065, and UF 37953 are larger in size than anterior jaw fragment UF 24983 (Fig. 3C), and edentulous jaw fragments UF 24398, UF 37949, and UF 37950, which average 14.3 mm depth of jaw below m1. The canine of UF 24983 is considerably smaller than that of the holotype (UF 24724). It is not likely, therefore, that this size difference is correlated with an age difference. The alveoli of the anterior jaw fragment indicate that the teeth in this specimen were slightly smaller than those of the holotype. This difference could be the result of individual, ontogenetic, or sexual variation.

Leptarctus neimenguensis occurs in the late middle Miocene (Barstovian equivalent) Tunggur Formation of China. *L. progressus*, probably from the late Barstovian or early Clarendonian Lower Bone Valley Fauna, of Florida is known from a damaged P4.

Leptarctus wortmani (Matthew 1924), from near Hay Springs, Nebraska, is likely from the late Clarendonian Ash Hollow Formation (Voorhies 1990a:A147). The holotype is a lower jaw with canine, erupting p3 (L = 5.1, W = 3.0), and erupted p4 (L = 6.9, W = 4.6). Matthew (1924) did not diagnose this species, distinguishing it from *L. primus*, the only other named species at that time and the one to which Wortman (1894) first assigned it, by its larger size. Specimens in the AMNH collections that best match *L. wortmani* are from the Clarendonian Hollow Horn Bear Quarry, Ash Hollow Formation, South Dakota and MacAdams Quarry, Texas.

Lim and Martin (2003) believed that *Leptarctus wortmani* was from the early Hemingfordian, Runningwater Formation. They (2003) named a new subgenus and species, *Leptarctus (Pseudoleptarctus) genowaysi*, for specimens from the Ash Hollow Formation of Nebraska. When contrasting it with *L. wortmani*, they compared it with a lower jaw (F:AM 25351) from the Runningwater Formation rather than the type. The five F:AM specimens from the Ash Hollow Formation referred to *L. genowaysi* include F:AM 49412 from Hollow Horn Bear Quarry (Lim & Martin 2003:fig. 2). F:AM specimens of *L. wortmani* from the late Clarendonian, Merritt Dam Member of the Ash Hollow Formation do show some characters in common

with *L. webbi* such as a well-developed parastyle on P4, strongly grooved c1, and strong anteroexternal cingulid on m1, but they and the type of *L. genoways* should be assigned to *L. wortmani*.

Lim and Martin (2001a) named *Leptarctus kansasensis* from three fragments of a skull with a P4 from the late Clarendonian, Selby Ranch Quarry in the Ogallala Formation of Phillips County, Kansas. It is likely conspecific with *L. wortmani*, since the P4 is similar in size to specimens from the Ash Hollow Formation.

Leptarctus desuii (Lim & Martin 2001b) is a large species, known only from a rostrum with P2-M1. It is from Carlson Quarry, Hitchcock County, Nebraska, and is assigned to the early Hemphillian, Republican River Beds. No justification is given for the stratigraphic and age assignment. Republican River is an antiquated term that is probably synonymous with Ogallala. Voorhies (1990b:117) noted that quarries along the Republican River range in age from late Barstovian to Hemphillian, although the only locality listed for Hitchcock County is late Barstovian. The large size of this specimen does suggest a Hemphillian age.

Leptarctus supremus (Lim et al. 2001), from the late early Hemphillian Box T Local fauna, Lipscomb County, Texas, is known only from a partial skull, with badly worn P4 and M1. It is another large species, similar in size to *L. desuii*, but they have not been compared. Differences in tooth proportions may be the result of the extreme wear present in *L. supremus*.

Comparisons.—The apparent absence of the tympanic process of the bulla is the most striking difference between *Leptarctus webbi* and other leptarctines in which this region is preserved (*L. ancipidens*, *L. oregonensis* from the Lower Snake Creek, Olcott Formation, *L. martini*, *L. timmi*, *L. supremus*, and *L. neimenguensis*, as well as *Craterogale*). Lim (1997) suggested the hooked processes indicate an exceptionally strong styloglossus, the muscle used for tongue retraction, which is enlarged in mammals with prehensile tongues for eating leaves or insects. Additionally, compared to the early Hemingfordian *L. ancipidens* (Olsen 1959), *L. webbi* has an additional septum in the interior of the bulla and the epitympanic recess and the fossa muscularis major are larger and deeper. In both, the foramen ovale and the canalis musculotubarius share a common opening.

The P4 of *Leptarctus webbi* is larger and more quadrate than that of *L. primus*, *L. oregonensis*, *L. ancipidens*, *L. progressus*, or *L. neimenguensis* and has a much better developed parastyle and hypocone.

The P4 of *L. martini* lacks a parastyle. *Leptarctus desuii* is smaller and has a less quadrate P4. The P4 hypocone is larger than the protocone and the parastyle appears to be less prominent than in *L. webbi*. The P4 of *L. supremus* is similar in size to *L. webbi*, although *L. supremus* has a small parastyle and is relatively narrower.

The M1 of *Leptarctus webbi* has a much larger metaconule (usually identified as a hypocone) than in *L. ancipidens*, *L. primus*, *L. oregonensis*, *L. ancipidens*, or *L. neimenguensis*. *Leptarctus desuii* is smaller and has a less quadrate M1 than *L. webbi*. The M1 of *L. supremus* is somewhat larger and is wider than long.

The lower premolars have well developed posterior accessory cusps and anterior cingula, unlike *Leptarctus ancipidens*, *L. oregonensis*, *L. primus*, or *L. neimenguensis*. As in the P4, the m1 has a much-reduced shearing function with the talonid more closed than *L. ancipidens*, *L. oregonensis*, *L. primus*, or *L. neimenguensis*. It also differs from these in having the cusps of the talonid equal in height to those of the trigonid.

Leptarctus webbi most closely resembles *L. wortmani*. Both *L. webbi* and *L. wortmani* differ from other described species in possessing well developed anterior cingula and prominent posterior accessory cusps on p3 and p4 that are offset laterally. *Leptarctus wortmani* (p2-m2 = 31.4) is smaller than *L. webbi* (p2-m2 = 35.5). Although the canine is not fully erupted, it appears to be more slender and less deeply grooved than in *L. webbi*. The p3 is not expanded transversely, there is no anterior cingular cusp, and the posterior accessory cusp is relatively small, closely appressed to the protoconid, and only slightly offset laterally. The p4 lacks an anterior cingular cusp, has a less well-developed posterior accessory cusp, and has the posterior cingulum less broad and less elevated. *Leptarctus webbi* differs from specimens of *L. wortmani* from the Ash Hollow Formation of Nebraska and South Dakota in the poor development or absence of a hypoconulid on m1 and much better development of a posterior accessory cusp on p3 and a broader p4. A skull (F:AM 25154) from *Leptarctus* Quarry in the Merritt Dam Member has a prominent tympanic process on the bulla. The P4 of the type of *L. kansasensis* has a lower and smaller parastyle than *L. webbi*.

Two other specimens appear to be referable to *Leptarctus webbi*. One is a p4, from the late Clarendonian Black Hawk Ranch local fauna of California. Macdonald (1948b) described this specimen as

a procyonine, but also discussed the possibility that it might belong to an advanced species of *Leptarctus*. Wagner and Reynolds (1983) identified this specimen as *L. wortmani*. The specimen is similar in size and morphology to the Florida material. The other is a lower jaw fragment with m1-m2, from the late Clarendonian Black Butte local fauna of Oregon (Shotwell 1963). This specimen was described as *Pliotaxidea* sp., but has been re-identified as a specimen of *Leptarctus* (Wagner 1976). Of all the described material, it most closely resembles the Florida specimens.

Genus *STHENICTIS* Peterson 1910

? *STHENICTIS* near ?*S. LACOTA* (Matthew & Gidley 1904)

Figure 1D-F; Table 5

Referred Material.—UF 25632, left M1; 25633, 25634, right mandibles with p4; 25635, 25636, edentulous mandibles; 32043 left mandible with m1 trigonid; all from the Love Bone Bed, Alachua County, Florida, latest Clarendonian Land Mammal Age.

Description.—The occlusal surface of the M1 is concave transversely and is expanded lingually. The internal border is convex. The cusps are very low. The styler shelf is well-developed external to the paracone. The paracone is connected to the slightly smaller metacone. The metacone is somewhat interior to the paracone. The external cingulum is greatly expanded external to the paracone. Wear facets are present at the locations of the remainder of the cusps. The large, transversely oval protocone is situated close to the anterior border. The hypocone occupies the internal border and a round metaconule is present midway on the posterior

border. There are three roots: a large lingual root and two labial roots. The root beneath the metacone is smaller than the root beneath the paracone.

The alveolus for the lower canine is relatively large. An alveolus for the p1 is present only in UF 32043. The p2 is offset labially. The p2 is slightly shorter than p3. The p4 is laterally compressed. The posterior accessory cusp is located slightly labial to the midline of the tooth. The anterior cingulum is narrow; the posterior cingulum broader. The m1 is elongate; m2 is single-rooted. The mandible is elongate. There are two mental foramina: a larger one beneath the p2, and a small one beneath the p3. The masseteric fossa extends to a point beneath m2.

Comparisons.—?*Sthenictis lacota* was described from the Clarendonian Little White River fauna of South Dakota as *Potamotherium lacota* (Matthew & Gidley 1904) from a jaw with canine and p1 alveoli, p2 and p3, and broken p4 and m1. It was assigned to *Paroligobunis* by Peterson (1910) and then to *Brachypsalis* by Gregory and Downs (1951:8). *Brachypsalis* is a paleomustelid with a short, deep jaw and a short, broad m1 (Baskin 1998a), unlike the South Dakota specimen. The Florida material and ?*S. lacota* were assigned to *Sthenictis* in Webb et al. (1981), because of their elongate mandibles, narrow cheek teeth, and especially, as indicated by the alveoli, the narrow elongate m1, a mellivorine character. The mandible is not as deep or massive as in the mellivorines *Hoplictis* and *Eomellivora* and the premolars are more slender. The mandible and teeth of ?*S. lacota* are approximately equal in size to material from the Love Bone Bed. The only significant difference that is observable is the usual absence of a p1 in the Florida material. A p1 is present in other species of *Sthenictis*.

The genotypic species, *Sthenictis robustus*, is a lower jaw (AMNH 8541) from the late Barstovian Valentine Formation of Fort Niobrara, Nebraska. Cope (1890) originally described this species as *Stenogale robusta*. Matthew and Gidley (1904) included the species in *Potamotherium*. Peterson (1910) referred it to a new genus, *Brachygale*, which he changed to *Sthenictis* in an errata sheet. Kretzoi and Kretzoi (2000) state that Peterson made the change because the name was supposed to be preoccupied by *Brachygalea* Hampson 1906, a lepidopteran. According to the ICZN, a one letter difference in the names of genera is not sufficient to establish homonymy. However, *Sthenictis* has been used for this genus for over 75 years (Cope & Matthew 1915, Matthew 1924) and it should be conserved.

Table 5. Measurements taken on ?*Sthenictis* cf. ?*S. lacota*.

	UF no.:	25632	25633	25634
M1 length		10.4		
width		17.2		
p4 length			11.5	11.4
width			5.6	5.2
p2-m1			(46.7)	(45.0)
p2-m2				(51.5)

The p4 and m1 of *Sthenictis robustus* are badly broken. The m1 possesses a trenchant heel. It is much smaller than the Florida material. *Sthenictis bellus* Matthew from the late Hemingfordian Sheep Creek Formation of Nebraska is much smaller than the Florida material. The p4 is a relatively more slender and sharper tooth, with the posterior heel not as broad or well developed. The m1 has a prominent metaconid. *Sthenictis dolichops* Matthew from the early Barstovian Olcott Formation of Nebraska is smaller than the Florida material. The p4 has a poorly developed posterior accessory cusp and posterior cingulum. The mandible is deeper than in the Florida specimens. The m1 has a poorly developed metaconid. *Sthenictis juturensis* Shotwell from the Clarendonian Black Butte fauna is much smaller than the Florida material. The posterior accessory cusp of the p4 is very weakly developed. The metaconid of m1 is large and the talonid slightly basined.

Gregory (1942) described a maxilla with canine and P3-M1 from the early Clarendonian Big Spring Canyon Local Fauna of South Dakota as *Martes campestris*. Baskin (1998a) referred this species to *Sthenictis*, because of relatively straight anterior margin and unexpanded interior margin of the M1. It compares well with the M1 from a nearly complete skull and associated skeleton of *Sthenictis* from the Burge Fauna in the AMNH collections (F:AM 25235). The M1s of *S. campestris* (L = 7.9, W = 14.0) and the Burge specimen are significantly smaller than that of the Love Bone Bed *?S. lacota* and have a more anteriorly situated protocone with a well-developed preprotocrista.

The wear facets on the Florida M1 (Fig. 1F) indicate that a large, well developed metaconid was probably present on m1. The M1's illustrated for *Ischyriictis zibethoides* (Ginsburg & Morales 1992:fig. 4) and *Laphyctis mustelinus* (Viret 1933:fig. 5) have a more centrally located protocone, more symmetrical external cingulum, and a broader internal cingulum. The M1 of *Hoplictis* is unknown, but is presumably similar to that of *Eomellivora*, which has a similar m1. The M1 of *Eomellivora* has a posteriorly directed external cingulum that is widest between the paracone and metacone, a metacone that is distinctly smaller than the paracone, no metaconule, and a large central protocone. The protocone articulates between the protoconid and hypoconid of m1. The Love M1 has a large oval anterior wear facet. The external part of the facet probably articulates with the protoconid of m1; the internal part, with a large metaconid. The broken surface of the m1 of *?Sthenictis lacota* is expanded lingually at the position

of the metaconid, not vertical as in *Hoplictis*. Usual absence of p1 and differences in the shape of the premolars and possible differences in the metaconid and perhaps talonid of m1 between other species of *Sthenictis* and *?S. lacota* indicate that if more material were available it might be necessary to place *?S. lacota* in a new genus.

Genus *HOPLECTIS* Ginsburg 1961a

HOPLECTIS sp.

Figure 5

Referred Material.—UF 25964, left m1; 25965, left dentary fragment with p2, p3, and broken p4 and alveoli for c1 and p1.

Description.—The incisor alveoli are very small, and the canine alveolus is relatively large. The p1 is small and single-rooted. The p2 (L = 9.1, W = 5.3) is double-rooted, with the anterior end directed labially. There is a single anteriorly directed cusp. The tooth broadens slightly posteriorly. The p3 (L = 11.8, W = 7.0) is single-cusped, slightly offset in the jaw, narrow anteriorly and broad posteriorly. The p4 (L = 14.9), although broken, appears to have been much taller than p2 or p3, with a narrow anterior cingulid. The m1 (L = 21.6, W = 9.0) is an anteroposteriorly elongate, blade-like tooth. There is a very weak anterolabial cingulid. The talonid is trenchant. There is no entoconid or metaconid. The protoconid is about one-third taller than the paraconid. There are narrow carnassial notches between the paraconid and protoconid and between the protoconid and hypoconid. There is a very weak and short cingulid low on the internal margin of the crown, midway between the paraconid and protoconid. The mandible is massive (depth below p4 = 26.8), with a broad symphysis and a chin.

Discussion and Comparisons.—Bryant (1968) described *Beckia grangerensis* as a new genus of mellivorine mustelid from the probably late Clarendonian Ellensburg Formation of Washington. She distinguished *Beckia* from *Eomellivora* on the basis of its shallower jaw, taller, more trenchant premolars, and absence of cingulids; Edwards (1976) reported a mandible of *Beckia* from the late Clarendonian part of the Contra Costa Group, California. Tedford et al. (1987) considered *Beckia* to be a junior synonym of the European subgenus *Ischyriictis* (*Hoplictis*), which immigrated to North America in the Clarendonian. Ginsburg (1961a) established the subgenus *Hoplictis* for the Burdigalian *I. florencei* and the Astaracian *I. helbingi* and subsequently raised it to generic status (Ginsburg & Morales

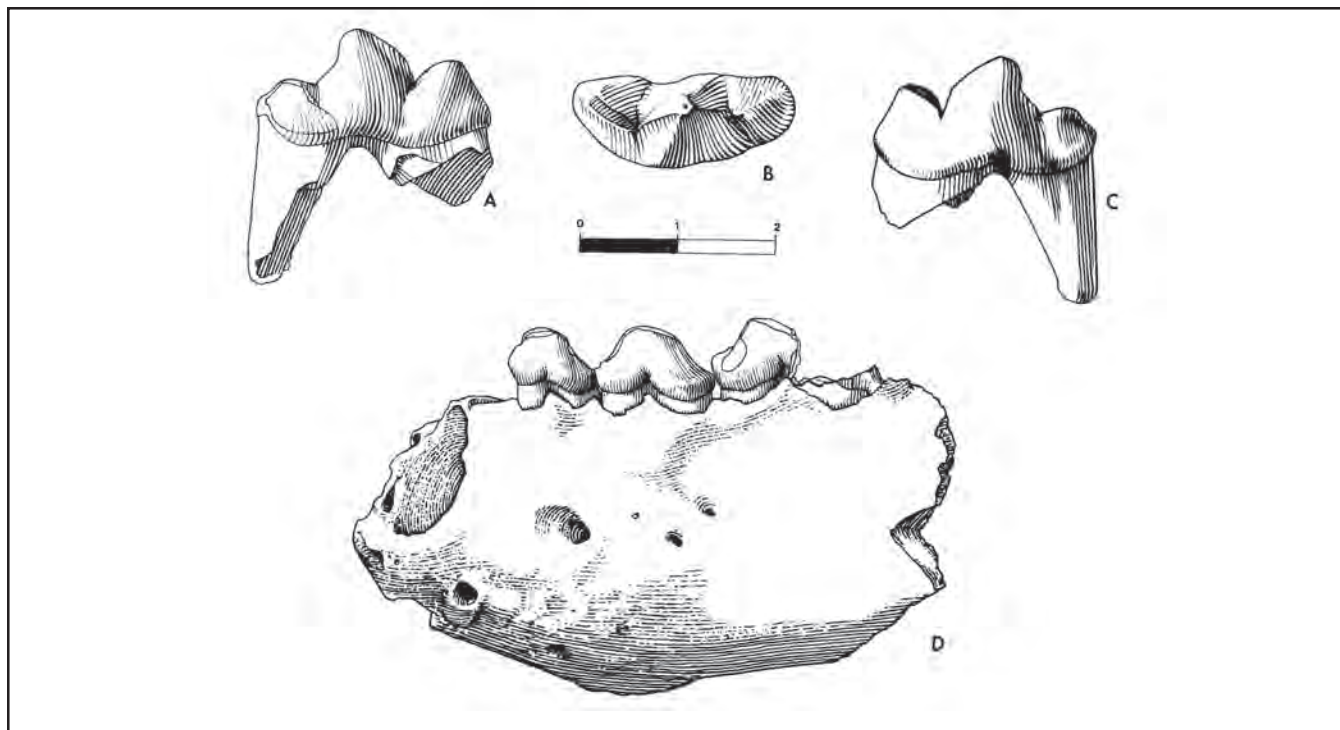


Figure 5. *Hoplictis* sp. (A-C) UF 25694, left m1, internal, occlusal and external views; (D) UF 25695, left dentary fragment, external view; scale bar = 20 mm.

1992). The m1 of *Hoplictis* differs from *Ischyriactis* in not having a metaconid. *Hoplictis helbingi* (Viret 1951) from La Grive (MN 7) is known from a p4 and an m1 that appear to be indistinguishable from those of *Beckia*.

The m1 from the Love site is larger than that of *Hoplictis grangerensis* and smaller than that of *H. helbingi*. The mandible is more massive than that of *H. grangerensis* and the p3 appears to be relatively lower than a slightly more anteriorly directed main cusp. F:AM 22264, a left ramus with p4-m1, is from the early Hemphillian Mixson's Bone Bed, Levy County, Florida. It is nearly the same size (p4: L= 14.8, W =6.1; m1: L = 21.7, W = 8.0) as the Love specimen. The p2 and p3 are crowded and offset, especially p2, which is set at approximately a 60° angle to the midline of the jaw. The posterior root of p2 is at the same level as the anterior root of p3. The p4 lacks a posterior accessory cusp, which is present in *H. grangerensis*. The m1 lacks cingulids.

Genus *PLIONICTIS* Matthew 1924

PLIONICTIS sp.

Figure 1C

Referred Material.—UF 25701, right M1, from the

Love Bone Bed, Alachua County, Florida, latest Clarendonian Land Mammal Age.

Description.—The M1 is a small, transversely elongate tooth (Fig. 1C). There are three roots: large internal and antero-external roots and a small postero-external root. The paracone is joined to and is slightly external to the subequal sized metacone. The external cingulum is widest external to the paracone. The protocone is low and is connected to the anterior border by a preprotocrista. There is no distinct hypocone on the convex internal border (L = 2.2; W = 5.3).

Discussion.—This M1 was compared with M1s of fossil mustelids in the collections of the AMNH. It most closely resembles the M1 of *Plionictis* (Matthew 1901:fig. 9) in morphology and size. Therefore it is assigned to this genus.

BIOCHRONOLOGY

The fauna of the Love Bone Bed indicates an age close to the Clarendonian/Hemphillian boundary. It shares many elements with late Clarendonian faunas, such as those from the Merritt Dam Member of the Ash Hollow Formation of Nebraska or Black Hawk Ranch of California, and with early Hemphillian faunas, such as

Mixson's and McGehee of Florida. Radiometric ages for the Merritt Dam Member of the Ash Hollow Formation range from 10.2 ± 0.7 from low in the section to 9.95 ± 0.3 Ma higher in the section (Skinner & Johnson 1984). Prothero & Tedford (2000) concluded that the paleomagnetic stratigraphy of Black Hawk Ranch is correlated with Chron4Ar (9.0-9.7 Ma). The Carnivora from the Love Bone Bed support a latest Clarendonian age assignment for this fauna (Webb et al. 1981, Prothero & Tedford 2000), slightly younger than the fauna of the Merritt Dam Member, approximately 9.0-9.5 Ma.

Cf. *Plithocyon* is significant, since the last occurrence of hemicyonine ursids in North America is from the late Clarendonian (Hunt 1998b). *Barbourofelis loveorum* (Baskin 1981) is intermediate in morphology between *B. morrissi* from the Merritt Dam Member and *B. fricki* from the early Hemphillian. *Barbourofelis loveorum* also occurs in the Black Hawk Ranch local fauna and the earliest Hemphillian Arnett local fauna of Oklahoma (Baskin 1981). *Barbourofelis fricki* is instead present at the early early Hemphillian Jack Swayze Quarry of Kansas. *Nimravides galiani* is restricted to the late Clarendonian. Beaumont (1990) considered it more derived than *Nimravides* from the late Clarendonian Merritt Dam Member of the Ash Hollow Formation and more primitive than *N. thinobates* from Black Hawk Ranch and the early Hemphillian of the Plains. *Epicyon saevus* and *E. haydeni* are at a comparable stage of evolution as these same taxa known from the Merritt Dam Member (Baskin 1998b). At McGehee, both species are present, but at Mixson's *E. saevus* is replaced by *Borophagus pugnator* (Wang et al. 1999). *E. saevus* is less derived than *E. diaboloensis* from Black Hawk Ranch. *Hoplictis* migrated to North America from Eurasia in the late Clarendonian and ranges through the early Hemphillian and is present at Mixson's. *Leptarctus webbi*, cf. *Urocyon* sp., and ?*Sthenictis* near ?*S. lacota* also support a late Clarendonian age assignment for the Love Bone Bed local fauna.

In his cladistic analysis of the Tayassuidae, Wright (1998) concluded that the Love Bone Bed peccary is more derived than the late Clarendonian Black Hawk Ranch species or Merritt Dam Member species, but more primitive than *Prosthennops* or *Mylohyus*, which first appear in the early Hemphillian. Wright (1998) identified *Mylohyus* cf. *longirostris* from Mixson's. The two species of rhinos, *Teleoceras proterum* and *Aphelops malacorhinus* may have their first occurrence at the Love Bone Bed, as does the new species of

Tapirus (Hulbert, this volume). These species are more derived than taxa from the Merritt Dam Member and also occur at Mixson's and McGehee. Nine species of horses are recognized from the Love Bone Bed (MacFadden & Hulbert 1990). Of these, *Hipparion* cf. *tehonense*, *Calippus cerasinus*, *Neohipparion trampasense*, and *Pseudhipparion skinneri* are typical of late Clarendonian faunas of the Plains, but also occur in the early Hemphillian (the latter three in Mixson's and/or McGehee; Hulbert 1988). *Cormohipparion ingenuum* is an early Clarendonian to early Hemphillian Gulf Coast endemic (Hulbert 1988). Horse species that may have their earliest occurrence at the Love Bone Bed are *Nannippus westoni*, *Cormohipparion plicatile*, *Protohippus gidleyi* (all three also at McGehee and Mixson's), and *Calippus elachistus* (also at McGehee).

Early Hemphillian immigrants, such as ground sloths (present at Mixson's and McGehee) and ursine bears are conspicuously absent in the Love Bone Bed local fauna. The beaver *Eucastor*, which occurs at the Love Bone Bed (Webb et al. 1981), is restricted to the Barstovian and Clarendonian. *Mylagaulus elassos* from the Love Bone Bed is ancestral to *M. kinseyi* at McGehee. The more derived *Calippus hondurensis* (relative to *C. cerasinus*) occurs at McGehee and Mixson's (Hulbert 1988). Similarly, the more derived and possibly immigrant gomphothere *Amebelodon* first occurs in early Hemphillian faunas such as Mixson's, and not at the Love Bone Bed, where only *Gomphotherium* is present (Lambert & Shoshoni 1998).

BIOGEOGRAPHY

The Love Bone Bed Local Fauna provides the most detailed picture of late Miocene vertebrate community organization east of the Mississippi River and allows the best comparison with the well-known contemporaneous fauna of the Plains. Tedford et al. (1987:193) stated that the Gulf Coast seemed to have been a separate biotic province during much of the Miocene and that by the Clarendonian, the Texas Gulf Coast established broad faunal continuity with the midcontinent, but Florida remained a haven for a distinctive mammalian assemblage. This is certainly true for the early Miocene. Graham (1999) characterized early Miocene vegetation of the Gulf Coast as possibly warm temperate to subtropical, in contrast to the grassy savanna and woodland vegetation of the high plains. Eight endemic mammalian genera and 15 endemic species are known from the Gulf Coast Arikarean (Albright 1998; Hayes 2000). The

Hemingfordian Thomas Farm Fauna of Florida has 27 species of mammals including three Gulf Coast endemic artiodactyl genera and 16 Gulf Coast endemic species, including four (out of nine) carnivorans.

In the middle to late Miocene, the Southeast was characterized by warm-temperate deciduous vegetation, while Nebraska was dominated by woodland and grassland (Graham 1999). The Barstovian and early Clarendonian mammal record is too poorly represented in Florida to evaluate properly. The late Clarendonian of Florida shows a decrease in Gulf Coast endemism, especially for the carnivorans. The Love Bone Bed has no endemic mammalian genera out of 40 and 13 endemic species out of 43. Among the 12 species of carnivorans, *Leptarctus webbi*, *Paranasua biradica*, and *Arctonasua floridana* are known only from Florida. *Nimravides galiani*, *Barbourofelis loveorum*, *Epicyon saevus* and *E. haydeni* are all represented in the faunas of the plains and the far west. Cf. *Urocyon* sp., *?Sthenictis* cf. *?S. lacota*, appear to be closely related to taxa from western faunas, as may be cf. *Plithocyon* sp., *Hoplictis* sp., and *Plionictis* sp.

The 20 species of ungulates at the Love site display a greater degree of Gulf Coast endemism. Of the nine species of horses, four are Gulf Coast endemics: *Nannippus westoni*, *Cormohipparion plicatile*, *Calippus elachistus* (also known from the early Hemphillian of Florida) and *Cormohipparion ingenuum* (also known from the late Miocene of Florida, the Texas Gulf Coast, and Honduras). *Teleoceras proterum*, the camelid *Hemiauchenia minima*, the dromomerycid *Pediomeryx hamiltoni*, and the new species of tapir are also only known from Love site and the early Hemphillian of Florida. There is a high relative abundance of many taxa, especially browsers, which are present, but poorly represented in contemporaneous midcontinent faunas (Webb et al. 1981). This probably reflects the more mesic conditions in the Gulf Coast Savanna region (Graham 1999) in contrast to the Plains.

By the latest Clarendonian Florida had become part of the Clarendonian chronofauna showing a major overall similarity to the faunas of the midcontinent. Certain elements of the fauna appear to have Neotropical affinities. Of the two procyonid genera (Baskin 1982), *Paranasua* appears to have evolved in the Gulf Coast province, although a specimen apparently referable to this genus is known from the early Hemphillian of Kansas. *Arctonasua*, which is related to the South American *Cyonasua* group, is more widespread both temporally and geographically, but is best known from Gulf

Coastal faunas (Baskin 1982). The llama *Hemiauchenia minima* is another Florida endemic closely related to South American taxa.

Although carnivorans are poorly known from the early Hemphillian of Florida, ungulates are well represented at Mixson's and McGehee. The early Hemphillian registered a major decrease in ungulate diversity associated with increased seasonality and aridity, with the midcontinent showing a greater decline than Florida (Webb et al. 1995). Eleven and 16 species of ungulates are known from Mixson's and McGehee, respectively. Perhaps half of these are Gulf Coast endemics. By the late Hemphillian, endemism among ungulates increased in Florida (Webb et al. 1995). This endemism declined again in the early Pleistocene. Twelve species of terrestrial carnivorans are known from the Leisey Shell Pits. Of these, only *Arctodus pristinus* and a possible new species of *Procyon* are known mainly from Florida. Of the 32 species from Leisey 1A, six are known mainly or exclusively from Florida. Morgan & Hulbert (1995:40) stated that although Blancan and Irvingtonian Florida faunas have a significant tropical component, they are more similar to western faunas. Much of the tropical influence results from immigrant xenarthrans and caviomorphs.

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