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THE PLIOCENE CANIDAE OF FLORIDA

S. David Webb

UNIVERSITY OF FLORIDA
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THE PLIOCENE CANIDAE OF FLORIDA

S. David Webb[1]

Synopsis: A new genus and species of canid, *Carpocyon limosus* is described from the Hemphillian (Middle Pliocene) Bone Valley Formation. Though showing strong omnivorous tendencies, it is not closely related to cynarctine canids; nor is it close to *Actiocyon* Stock which is here synonymized with *Alopecocyon* Camp and Vanderhoof. *Carpocyon cuspidatus* (Thorpe), new combination, from the late Barstovian (Late Miocene) of Nebraska, represents an earlier stage of evolution and suggests derivation of *Carpocyon* from *Tomarctus.*

Five species of *Osteoborus* are now known from Florida: (1) *Osteoborus dudleyi* (White), new combination, is a large, progressive species from the Bone Valley fauna. *Pliogulo* White is considered a synonym of *Osteoborus* Stirton and Vanderhoof. *Osteoborus crassapineatus* Olsen is placed in synonymy with *O. dudleyi* (White). (2) *O. orc,* new species, is a very small but advanced form from Withlacoochee River site 4A; and two less progressive species occur together in Mixson's Bone Bed, (3) *O. galushai,* a new medium-sized species, near *O. cyonoides,* and (4) a very large species near *O. validus.* The latter also occurs at McGehee Farm. (5) A species larger and even more primitive than *O. galushai* also occurs at McGehee Farm and at Hogtown Creek site II. Until it can be characterized by more adequate material, it is referred to *O. galushai.*

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[1] The author is Assistant Curator of fossil vertebrates, Florida State Museum, and Assistant Professor of zoology, University of Florida. His principal research concerns the Pliocene mammals of Florida. Manuscript received 4 November 1968.

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INTRODUCTION

Florida provides almost the only record of Pliocene terrestrial life in the eastern United States. This is so tantalizingly scant that the Florida State Museum recently has undertaken extensive paleontological exploration of the state's Pliocene terrestrial deposits. This is the ninth contribution resulting from this program.[1]

Only two species of Pliocene canidae have been described from eastern United States, as against six Miocene species. Even the Pliocene age of these taxa was doubted because of their uncertain stratigraphic provenience within the Bone Valley District (Olsen, 1956b; White, 1942). It can now be shown that the two previously named taxa are synonyms and that they are late Hemphillian (Middle Pliocene) in age. Furthermore, one new genus, three new species, and two referred species can now be added to the record of Pliocene canidae in the eastern United States.

ACKNOWLEDGMENTS

The revival of interest in Pliocene deposits in Florida began in 1962 when Clayton Ray, my predecessor at the Florida State Museum, initiated excavations at the McGehee Site. In 1963 and 1964 the Frick Corporation undertook joint sponsorship of this work with the Florida State Museum. After my arrival in 1964, the study of Pliocene deposits was broadened to include large scale exploration for new sites, as well as continued excavation at the McGehee Site. The Frick Corporation continued partial sponsorship of these operations through 1965. Subsequently this program has been supported by NSF grant GB 3862.

During these studies it became clear that the classic Bone Valley collections were confused stratigraphically and that precise field studies were required. The phosphate companies in the Bone Valley District have been most cooperative, not only offering us access to every section in every pit, but also placing valuable equipment at our service. Particular acknowledgment is due the International Minerals and Chemical Corporation for partial support of our work in the area during 1967 and 1968.

In 1939 through 1941 Ted Galusha led field parties from the Frick Laboratory of the American Museum of Natural History in intensive excavation of the Mixson's Bone Bed. I am grateful to Ted Galusha and other personnel in the Frick Lab for permission to study the canidae from Mixson's.

My understanding of carnivore phylogeny has been enhanced considerably by conversations with Donald E. Savage, Richard H. Tedford, and John E. Mawby.

ABBREVIATIONS

All measurements are given in mm, unless otherwise noted.

Institutions that have loaned materials for this study are abbreviated as follows:

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[1] Previous contributions are Brodkorb (1963); Webb (1964 and 1966); Auffenberg (1966); Rose and Weaver (1966); Weaver and Robertson (1967); Hirschfeld and Webb (1968); Webb and Tessman (1968).

CWT—Panhandle Plains Historic Museum, Canyon, Texas
FAM—Frick Laboratory, American Museum of Natural History
FGS—Florida Geological Survey, Tallahassee, Florida
MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts
UCMP—University of California, Museum of Paleontology, Berkeley, California
UF—University of Florida, Florida State Museum, Gainesville Florida
UMMP—University of Michigan, Museum of Paleontology, Ann Arbor, Michigan
YPM—Yale Peabody Museum, Yale University, New Haven, Connecticut

Certain Florida Pliocene localities are briefly described in this and other papers. More complete geographic descriptions and stratigraphic data are recorded in the locality catalog, Florida State Museum.

SYSTEMATICS

FAMILY CANIDAE Gray

SUBFAMILY CANINAE Gill

Carpocyon new genus

GENOTYPE.—*Carpocyon limosus* new species, Bone Valley Fauna of Florida, late Hemphillian age.

ETYMOLOGY.—Greek: *Karpos,* fruit; *Kyon,* dog; in reference to the presumed significance of fruit in the diet of these canids.

REFERRED SPECIES.—*Cynodesmus cuspidatus* Thorpe (1922), collected 1873 by Otto Harger (no exact date with type specimen YPM 12788), Niobrara River Fauna of Nebraska, late Barstovian age. Presumably collected from the lowermost (Crookston Bridge) member of the Valentine Formation (Skinner, *et al.,* 1968) on the basis that the bone is hard and tan and the teeth molasses-colored, as is typical of this fauna.

GENERIC DIAGNOSIS.—Medium-sized canid, larger than *Procyon lotor.* Dentition blunt, tending to wear heavily. Molars enlarged and premolars relatively reduced. P^3 with posterior accessory cusp and tending to develop strong lingual cingulum. P^4 triangular with strong parastyle, low weak paracone-metacone blade, protocone broad with no distinct crests on parastyle or paracone, weak lingual cingulum. M^1 massive, rectangular, 70 to 75% wider than long, paracone and metacone subequal, no stylar cusps, continuous labial cingulum, protoconule absent, strong metaconule subequal to and symmetrical with protocone, hypocone a blunt enlargement of lingual cingulum. M^2 relatively large, structurally similar to M^1. M_3 present in lower jaw.

Carpocyon limosus new species

Figure 1, Table 1

ETYMOLOGY.—Greek: *limosus*, hungry.

HOLOTYPE.—UF 12069, two maxillary fragments with left P^3, P^4, M^1 and zygomatic arch, and right P^4, M^1 and M^2, collected by William Thomas, September 1966.

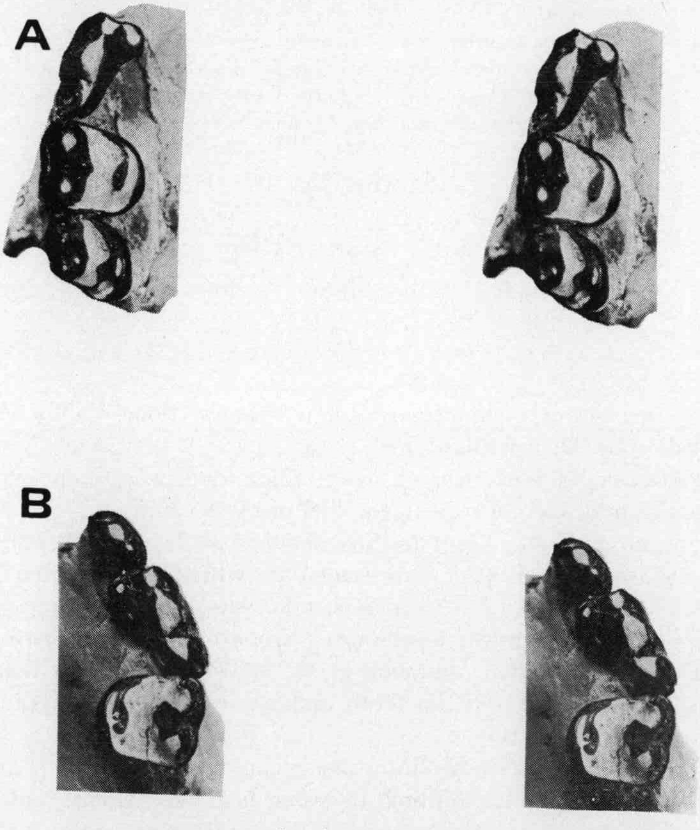

FIGURE 1. Stereoscopic views of palate of *Carpocyon limosus* new genus and species. Holotype, UF 12069. A. Left P^3-M^1. B. Right P^4-M^2. Natural Size.

TYPE HORIZON AND LOCALITY.—Palmetto Washer: *Hexameryx* Locality (UF locality catalog) about 7 miles southeast of Brewster, Polk County, Florida. In light gray medium phosphatic sands from a phosphate mine. In the same matrix and in the same individual dragline dump were found *Nannippus ingenuus* (Leidy), *Neohipparion*

Table 1. MEASUREMENTS[1] OF HOLOTYPE OF *Carpocyon limosus* (in mm)

Tooth	Length	Width
P^3	9.6	6.0
P^4	15.6	9.1
M^1	11.4	14.2
M^2	9.1	13.2

[1] Measurements of left jaw and right jaw agree on comparable teeth. Length-width measurements taken across most widely separated points of enamel. On M^2 "width" is actually an anterolabial-posterolingual measurement.

phosphorum Simpson, and *Hexameryx simpsoni* White, indicating a Hemphillian (Middle Pliocene) age.

DIAGNOSIS.—P^3 expanded lingually with distinct lingual root. P^4 with strong parastyle, short bulbous protocone, continuous lingual cingulum. M^1 with strong labial cingulum, lingual moiety nearly as wide as labial; M^2 80% as wide as M^1, posterolingually elongated.

DESCRIPTION OF TYPE.—The third premolar is anteroposteriorly elongate. There are four cusps in line: a large protocone, a smaller posterior accessory cusp, and in line with these, an anterior and a posterior cingular cusp. A weak labial cingulum extends the length of the tooth. A strong continuous lingual cingulum connects the anterior with the posterior cingular cusp and from the latter a weak cingulum extends along the posterolabial side of the tooth. The lingual cingulum broadens considerably near its middle, and this broad area is supported by a separate lingual root.

The fourth upper premolar is triangular in shape. The shearing blade is weakly developed, the paracone and metacone relatively short and blunt. The blade is oriented in a nearly anteroposterior direction as in modern canines, not obliquely as in more primitive forms. A strong parastyle lies at the anterior end of the carnassial blade. The protocone remains a distinct rounded cusp separated by a shallow valley from the parastyle and paracone. A weak but continuous lingual cingulum extends from the protocone to the posterior edge of the metacone blade. On the left carnassial shearing wear has eradicated most of this cingulum.

The molars are relatively large and heavily worn. The first upper molar is roughly rectangular in shape and nearly 25% wider than long. The paracone and metacone are broad low cusps of about the same size. No stylar cusps are present, but there is a broad continuous external cingulum. The protocone lies directly lingual to the metacone. These cusps, though broad, are low and readily wear to dentine. Replacement dentine fills the pulp cavities that become exposed under these cusps. The hypocone is also broad and low. It readily wears down and connects with the anterolingual cingulum to form a long lingual talon.

The second upper molar resembles the first, but it is a little smaller and its lingual side is skewed posteriorly giving the tooth a subtrapezoidal shape. The paracone and metacone are smaller, lower, and more closely appressed than in the first molar. The hypocone is relatively large and occupies a position wholly posterior to that of the metacone. As in the first molar, there are strong labial and anterolingual cingula. M^3 is absent.

The position of the infraorbital foramen cannot be determined from the type specimen. The anterior root of the zygomatic arch lies above the first molar. The jugal is 15 mm deep immediately posterior to its contact with the maxillary.

RELATIONSHIPS—*Carpocyon limosus* is considerably younger than *Carpocyon cuspidatus* (Thorpe) of late Barstovian age. The canoid genera to which *Carpocyon* bears a close resemblance are *Tomarctus, Cynarctus,* and *Actiocyon* (=*Alopecocyon*). *Tomarctus* (including *Tephrocyon*) ranges in age from the Arikareean through Clarendonian (Downs, 1956; Olsen, 1956a; Wilson, 1960; Macdonald, 1963); *Cynarctus* (excluding *Cynarctoides*) is recorded from the Barstovian and Clarendonian (McGrew, 1937, 1938; Hall and Dalquest, 1962), and *Actiocyon* (=*Alopecocyon*) is known from the late Clarendonian of California (Stock, 1947).

In *Carpocyon* the broad low cusps, relatively large, nearly square molars, and heavy wear on the teeth indicate adaptation to a varied diet that probably included many fruits and berries. In this aspect of its dentition the genus resembles procyonids, but in every fundamental feature, such as the shape of the carnassial and the five-cusped pattern of the molars, the dental pattern is canid.

In both its omnivorous aspect and its basically canoid pattern, the dentition of *Carpocyon* more nearly approaches that of certain species of *Cynarctus.* Recent studies of the cranial features of *Cynarctus* and its relatives by Dahr (1948), Hough (1948) and Galbreath (1956) demonstrate clearly that the cynarctines are canids, convergent in some features of their dentition with procyonids, but not, as had previously been supposed, closely related to procyonids or even ursids. *Cynarctus* (and even the older *Cynarctoides*) had in many respects become more procyonid-like than *Carpocyon.* Differences in detail are considerable, as indicated in Table 2. Evidently *Carpocyon* bears no special relationship to cynarctines. Resemblances to that group

Table 2. Comparisons of *Carpocyon*, Upper Dentition with That of Certain Other Canids

	Carpocyon	*Cynarctus*	*Alopecocyon*
P^4	parastyle strong, protocone low, anterior, close to blade, lingual cingulum low, narrow	parastyle absent, protocone large, bulbous, far lingual from blade, lingual cingulum high and broad	parastyle weak, protocone long, low anterior, far lingual from blade, grades into low, but broad, cingulum
M^1	rectangular, wider than long,	rectangular, longer than wide (even in *Cynarctoides*),	triangular, wider than long,
	metaconule and protocone subequal,	metaconule larger than protocone,	metaconule much weaker than protocone,
	labial cingulum broad and continuous	labial cingulum broken or absent	labial cingulum moderately developed
M^2	moderately enlarged	greatly enlarged	greatly reduced

are either features common to most canids or are convergently produced by similar omnivorous habits.

Actiocyon Stock (1947) from Barstovian deposits in Cuyama Valley, California is here synonymized with *Alopecocyon* Camp and Vanderhoof (1940) from Vindobonian deposits in France. The close resemblance between these genera was pointed out to me by D. E. Savage. Viret's (1933) earlier name *Alopecodon* was preoccupied by Broom's use of it in 1908 for a mammal-like reptile. De Beaumont (1964) suggests that *Alopecocyon* is a descendant of *Broiliana,* and a mustelid not a canid. Unfortunately, the absence of a braincase for *Alopecocyon* makes this a difficult point to pursue.

Alopecocyon is characterized by its short, nearly quadrangular upper carnassial and the low connate cusps of the upper molars. These procyonoid features suggest, at first glance, possible relationship to *Carpocyon limosus,* but the resemblance is remote, as Table 2 shows. Moreover the Barstovian species of *Carpocyon, C. cuspidatus,* is even more distinct from contemporaneous *Alopecocyon* than is the Hemphillian species.

The genus *Tomarctus* more nearly approaches *Carpocyon* in the fundamental features of its dentition, and certain species of that genus occur early enough to be ancestral to *Carpocyon.* The genus *Tomarctus* Cope (including Matthew's *Tephrocyon*), typified by the Barstovian species *T. brevirostris,* has been given a central place in canid phylogeny. It is generally believed to constitute the "main line" of canid evolution through most of the Miocene, giving rise to both the hyaenoid dogs, *Aelurodon* and *Osteoborus,* and to *Canis* and related modern genera. Confusion of several species of *Tomarctus* with those of *Cynodesmus* has gradually been resolved (Simpson, 1932; McGrew, 1935; White, 1942; Green, 1948; Downs, 1956; Olsen, 1956a; and Macdonald, 1963), so that a consistent definition of each is now established.

The principal features indicating the probable ancestry of *Tomarctus* to *Carpocyon* are the following:

a) stepped premolars (with strong posterior accessory and cingular cusps);

b) nearly anteroposterior orientation of carnassial blades;

c) strong parastyle on upper carnassial in many early species, for example, *T. brevirostris* Cope (genotype) and *T. rurestris* (Condon), though absent in later species such as *T. euthos* (McGrew);

d) protocone on upper carnassial low but distinctly separated anteriorly;

e) molars with metaconule large, about equal to and symmetrical with protocone (Olsen, 1956a);

f) molars lacking protoconule (this feature is probably correlated with the preceding);

g) talon of first upper molar tending to become wider anteroposteriorly and square, exemplified in *T. paulus* Henshaw, *T. temerarius* (Leidy), certain specimens referred to *T. kelloggi* (Merriam), and especially in *T.* cf. *brevirostris* described by Gazin from Skull Spring, Oregon.

The omnivorous features adumbrated in certain species of *Tomarctus* are carried to greater extremes in *Carpocyon*. In that genus the animals became larger with blunt-cusped teeth. The upper molars were enlarged with a relatively weak paracone, broad hypocone, strong lingual cingulum, and very broad external cingulum. M^2 also became large and square. The parastyle of the upper carnassial was further developed with the shearing blade tending to wear more bluntly. While the molars were enlarged, the anterior premolars were relatively reduced.

It is evident that *Carpocyon limosus* represents the culmination of adaptive trends that began in some large Hemingfordian species of *Tomarctus*. Certain Barstovian species such as *T. temerarius* (Leidy) and the Skull Spring *Tomarctus* described by Gazin (1932) may represent a continuation of this stock. The first clearcut embodiment of these trends is *Carpocyon cuspidatus* (Thorpe) of late Barstovian age.

In addition to the type palate of *C. cuspidatus,* also in the Yale collection is a lower jaw fragment collected by the same collector, assigned the same number, and preserved in the same manner as the two upper jaw fragments constituting the type. Thorpe (1922) mentions it as "a fragment of a jaw without teeth." The significance of this fragment, if properly associated, is that it indicates the presence of a long two-rooted M_2 at least 12 mm long and a rather elongate M_3 at least 6 mm long behind the lower carnassial. The jaw is 20 mm deep below M_2. These teeth further indicate the relationships of *Carpocyon* to the main line of canid evolution.

The principal advancements by *Carpocyon limosus* over *C. cuspidatus* are the following:

a) P^3 heavier cusped, and broader;
b) lingual cingulum heavier, supported by added lingual root;
c) P^4 parastyle stronger;
d) protocone less projecting, more bulbous;
e) anterior end of lingual cingulum added;
f) M^1 talon squared up (11.0 long in *C. limosus,* compared to 10.2 in *C. cuspidatus*);
g) M^2 enlarged, elongated posterolingually.

Each of these features tends to produce a heavier grinding battery. With the exceptions of (b) and (e), they augment adaptations already observed in *Carpocyon cuspidatus.* The direction of these trends, and the fact that they were intensified during the Barstovian through Hemphillian interval suggests their initiation in an early Barstovian species of *Tomarctus.*

SUBFAMILY BOROPHAGINAE Simpson

Osteoborus Stirton and Vanderhoof

Osteoborus dudleyi (White) new combination

Figure 2, Table 3

Pliogulo dudleyi White, 1941.
Osteoborus crassapineatus Olsen, 1956b.

HOLOTYPE.—MCZ 3688, a skull lacking right zygoma and all teeth except RP^3.

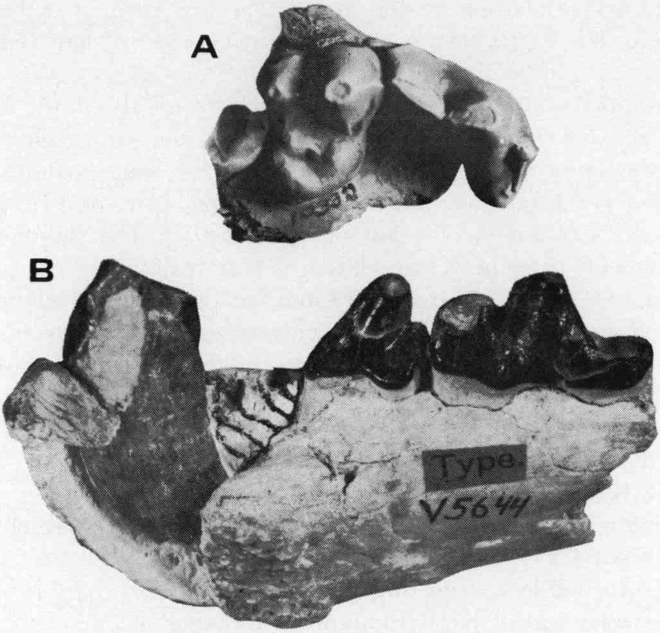

FIGURE 2. *Osteoborus dudleyi.* A. UF 10335, Left P^4-M^2. B. FGS V 5644, Left mandible, Holotype of *O. crassapineatus*. Natural Size.

TYPE LOCALITY AND HORIZON.—Phosphate pits near Mulberry, Polk County, Florida. Exact locality unknown. From Bone Valley Gravels.

REVISED DIAGNOSIS.—Moderately large species of *Osteoborus* with short face, high-vaulted cranium and deep jaws with massive canines.

Table 3. MEASUREMENTS OF THE UPPER DENTITION OF *Osteoborus Dudleyi* (in mm)

Upper Dentition	Holotype MCZ 3688	*O. dudleyi* UF 10335	UF 12401	*O. cyonoides* UCMP (largest) 30103, 30101
P^3 length x width	12.3 x 7.3			11.8 x 7.0
P^4 length x width		27.6 x 14.6		27.5 x 14.0
M^2 length x width	10[1] x 21[1]	17.5 x 23.4	16.1 x 18.5	16.7 x 23.1
M^1 length x width		9.1 x 12.0		9.3 x 14.2
P^4-M^1 min. length	38.3	38.7		
P^4-M^2 min. length		42.2		

[1] Approximate

P_1 absent, P_3 two-rooted, P_4 with posterior accessory cuspid and posterior cingulum compressed but distinct, P^4 with strong parastyle, distinct protocone and posterolingual cingulum, M_1 with strong metaconid and short bicuspid heel. Closely comparable to *O. cyonoides*, but differing in larger size, higher vaulted skull, and stronger parastyle on P^4. Comparable in size to *O. hilli*, but less progressive in premolar reduction and simplification of the upper carnassial.

REFERRED MATERIAL.—FGS V-5644, right mandible with canine and P_4-M_1, broken behind M_1 and lacking symphysis, type of *O. crassapineatus*, from the American Agriculture Chemical Company phosphate pits at Pierce, Polk County, Florida. UF 10335, right maxillary fragment with P^4-M^2 and UF 12401, RM^1, both from Palmetto Washer (UF locality catalog) near Pierce, Polk County, Florida.

SYNONYMY.—In 1941 White based a new genus and species of large carnivore on a nearly complete but essentially edentulous skull from somewhere in the vicinity of Mulberry. Although he recognized it as borophagine, he made it the type species of a new genus, *Pliogulo*. The generic name selected by White and the fact that most of his comparisons were with the wolverine has led some to suppose it a mustelid. Olsen (1956b) described a borophagine lower jaw from the same area as a new species of *Osteoborus*. Though he suggested *Pliogulo* White might be a synonym of *Osteoborus*, he failed to discuss the possibility of his specimen being referable to White's species. Study of the type specimens of both these species, as well as additional new material, makes it clear to me that only one borophagine species occurs in the Bone Valley Formation, *Osteoborus dudleyi* (White).

DESCRIPTION OF TYPE.—The type skull of *Osteoborus dudleyi* compares closely with those of other species of *Osteoborus*, particularly *O. cyonoides*, Hemphill Fauna (Matthew and Stirton, 1930) and *O. validus*, Higgins Fauna (Johnston, 1939a). The two latter species represent a more progressive stage of evolution, as indicated by the high arched cranial vault and shortened face, than *O. pugnator* and especially *O. littoralis*. The top of the skull is even higher and more rounded in *O. dudleyi* than in *O. cyonoides* and *O. validus*.

It is not surprising that differences between *Osteoborus* skulls of a progressive type and those of *Borophagus* should be so subtle in view of the direct phylogenetic relationship indicated by dental studies. Direct comparison of the skull of *Osteoborus dudleyi* with skulls of *Borophagus diversidens* from the Blanco and Cita Canyon faunas of Texas reveals certain differences in detail. The most striking difference is the broad postglenoid process in *O. dudleyi*, which extends far lateral to the external auditory meatus, whereas in *B. diversidens* the process is narrow and tightly pressed against the auditory tube. Also the postglenoid foramen faces more anteriorly in *B. diversidens* than in *O. dudleyi.* These comparisons strongly suggest that White's borophagine pertains to *Osteoborus.*

The only previously known Bone Valley material representing the upper dentition is the type skull of *Osteoborus dudleyi,* which has the alveoli for most of the teeth, but only RP^3 actually present. Additional material now includes an upper jaw with cheek teeth and an upper molar. In most respects the upper dentition of *O. dudleyi* compares closely with that of *O. cyonoides* as represented by the UCMP sample from Coffee Ranch Quarry (Hemphill Fauna) in Texas. The sample from the Coffee Ranch Quarry was used in this study as a control to indicate the range of variation in features of *Osteoborus.* The principal difference between *O. dudleyi* and *O. cyonoides* is the larger size of the Bone Valley species.

P^3 in the type of *O. dudleyi* is well worn, but retains indications of three weakly separated cusps aligned anteroposteriorly. The middle cusp is the largest and was presumably the highest. A narrow lingual cingulum occupies the lingual side of this tooth. The anterior end of P^3 lies medial to P^2 as in *O. cyonoides* rather than lateral to it as in *Borophagus pachyodon.* P^3 overlaps P^2 only slightly. P^1 lies almost directly behind the canine rather than overlapping it.

The upper carnassial is represented in the maxillary, UF 10335. The protocone protrudes rather far lingually and rises to a distinct cuspule. Although this cuspule is not common, it appears as a variant in the Hemphill sample of *O. cyonoides.* The parastyle is connected by a strong crest to the protocone. This crest is better developed than in any specimens observed from the Hemphill Fauna. The paracone and metacone contribute about equally to the carnassial blade, although the paracone is taller and more robust than the metacone. A weak cingulum occurs on the lingual side of the metacone.

In both first upper molars the protoconal shelf is rather narrow with a sharp posterolingual angle. The external cingulum is very weak. A distinct anterolingual cingulum below and immediately anterior to the protoconule occurs in both Bone Valley specimens. However the Coffee Ranch sample of *Osteoborus cyonoides* demonstrates that in M^1 all of these features may vary greatly within a population (Matthew and Stirton, 1930, Plate 28).

M^2 is rather large but offers nothing in the way of distinctive features.

The only known lower jaw of this species is a right mandible with C and P_4-M_1, from near Pierce, Bone Valley District, Florida, described by Olsen (1956b) as the type of *O. crassapineatus,* here synonymized with *O. dudleyi.*

The dimensions of the lower canine in the Bone Valley mandible are remarkably large. Olsen considered this one of the major diagnostic features of the Bone Valley *Osteoborus,* although later in the same paper he notes that this "may be just an anomalous individual that would not be representative of the borophagine population from Bone Valley Formation."

In the large sample of jaws from the Coffee Ranch Quarry, it is apparent that canine size is subject to considerable individual variation. It is also possible that a unit increase in the body size of these canids brought about an exponential increase in the size of the canine. In *O. hilli* from Axtel local fauna in Oklahoma (Johnston, 1939b) which is closely comparable in size to *O. dudleyi,* the lower canine ranges in size from an anteroposterior dimension of 12.3 mm and a transverse dimension of about 10 mm in the type specimen, to dimensions of 18.8 x 12.5 in CWT 1756. Thus the observed range of variation in a few specimens is quite wide and at the upper end approaches the dimensions of the Bone Valley jaw (19.7 x 15.3). In a specimen of *O. validus* from Higgins, Texas described by Johnston (1939a) the dimensions of the lower canine are 19 x 17.5 mm.

The very heavy wear on the canine is surprising in view of the light wear on the protoconids of P_4 and M_1. The canine is worn most heavily on the labial side, but is also heavily worn on the dorsal surface and the lingual side. Presumably the lingual surface wears against the large upper third incisor.

The symphysis in the Bone Valley mandible is extraordinarily long and deep. The symphyseal region extends as far back as the anterior root of P_4, whereas in most other *Osteoborus* specimens the posterior edge of the symphysis lies below P_3. The jaw deepens from the molar to the symphyseal region in the Bone Valley jaw, in contrast to smaller *Osteoborus* jaws that usually become more slender anteriorly. Nevertheless the jaw proportions are quite variable in modern wolves and their is little doubt that they varied considerably in populations of *Osteoborus* as well. Presumably the massive symphysis in the Bone Valley jaw is functionally related to the powerful canines.

The appearance of the alveoli in the Bone Valley jaw suggests that P_1 was absent and shows that P_3 was doubled rooted. The number of roots on P_2 cannot be judged as the critical area was broken away.

In P_4 the principal cusp is high and inclined posteriorly. An anteroposteriorly compressed posterior accessory cusp separates the principal cusp from the posterior cingulum in the fashion characteristic of *Osteoborus*. The posterior cingulum is also compressed and is best developed on the labial side. In typical *Osteoborus* fashion P_4 is set well labial to the carnassial and the jaw is bowed outward at this point.

The lower carnassial exhibits a short bicuspid heel and a distinct metaconid. The heel is well worn exposing a flat unenameled surface. By contrast the high protoconid is only lightly worn.

RELATIONSHIPS.—A critical nomenclatural point is the synonymy of "*Pliogulo*" *dudleyi* based on a skull and *Osteoborus crassapineatus* (misspelled *crassipineatus* under the type figure) based on a mandible. An extreme typologist could not be satisfied on this point because as yet no upper and lower jaws of this species have been found in association and the two type specimens certainly did not belong to a single individual. Yet that each of these specimens belongs to the genus *Osteoborus* can be demonstrated, and their similar size and provenience makes it highly probable that they came from the same population of *Osteoborus*. Agreement in size between the two specimens may be shown directly by comparing certain dimensions that are functionally correlated and indirectly by comparing each specimen to corresponding elements in closely related species that are represented by adequate samples.

In *Osteoborus* and, indeed, in late Cenozoic canids generally, the lower carnassial tooth is very close to 75% of the combined lengths of the upper carnassial and the first upper molar of the same individual. Clearly this relationship must be functionally controlled within narrow limits. In the type mandible of *O. crassapineatus* M_1 is 31.0 mm long. In the type skull of *Pliogulo dudleyi* the minimum length of P^4 and M^1, established by the alveoli, is 38.3 mm; thus the lower carnassial of *O. crassapineatus* is no more than 81%—most probably a few percent less—of the length of the corresponding teeth of *Pliogulo dudleyi*. This is a reasonably close comparison for different individuals. Similarly the length P_1-P_3 inclusive is slightly greater than P^1-P^3 in most individual canids. In *O. crassapineatus* the length of P_1-P_3 is 28.5 while in *P. dudleyi* the corresponding length of the uppers is 26.7. Furthermore, the distance from the lower canine to the posterior end of M_1 is 79.9 in *O. crassapineatus*; while in *P. dudleyi* the distance from the canine to the middle of M^1 is 79.0. Thus the two critical type specimens compare closely in functional dimensions. It should be apparent from the previous description that each specimen is referable on its own merits to *Osteoborus*. Hence the probability that the two species in question are synonymous is great. Following the rules of priority and the subjective generic and specific synonymies just indicated, the proper combination is *Osteoborus dudleyi* (White).

O. dudleyi compares most closely with *O. cyonoides* from which it differs in its consistently larger size. This is particularly evident in the huge canines and massive jaw. The skull is more highly vaulted than in *O. cyonoides*, and the parastyle of the upper carnassial is stronger than in any of the *Osteoborus* samples from the Hemphill (Coffee Ranch).

O. dudleyi agrees in size with *O. hilli* from Axtel fauna in Oklahoma (Johnston, 1939b). *O. hilli* is among the most progressive species of the genus (see following discussion of *O. orc*) and shows several advances beyond the stage of *O. dudleyi*. The last lower premolar is higher and more compressed posteriorly in *O. hilli* than in *O. dudleyi*. In the upper carnassial *O. dudleyi* retains a distinct protocone, a posterolingual cingulum, and a strong parastyle, whereas in *O. hilli* (as in *Borophagus*) all of these features are nearly suppressed.

Osteoborus orc new species

Figures 3, 4, Tables 4, 5, 6

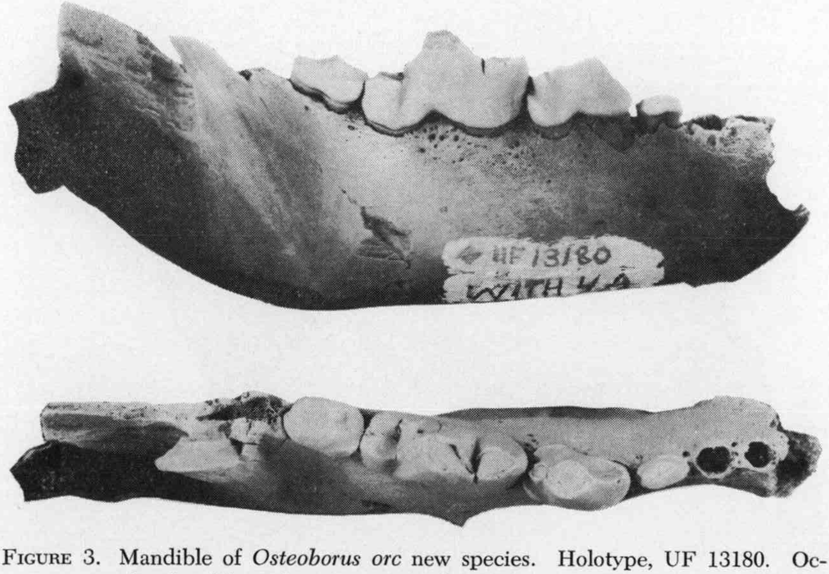

FIGURE 3. Mandible of *Osteoborus orc* new species. Holotype, UF 13180. Occlusal and lateral views. Natural Size.

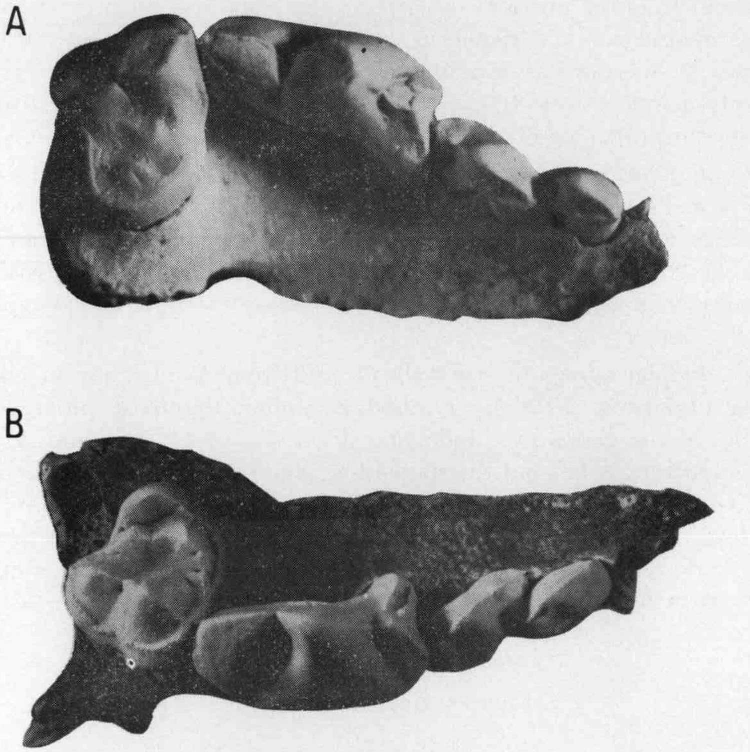

FIGURE 4. Maxillae of *Osteoborus orc* new species. A. UF 12314, occlusal view. B. UF 12313, occlusal and lateral views. ×1½

Table 4. MEASUREMENTS OF THE DENTITION OF *Osteoborus orc* (in mm)

Upper Dentition	UF 12313	UF 12314	UF 12350	UF 12316	UF 12317
C length x width			11.2 x 7.4	10.0 x 7.6	
P^2 length x width	8.4 x 4.8	7.6 x 4.2	7.2 x 4.0[1]		
P^3 length x width	11.0 x 5.9	10.8 x 5.5	11.5 x 6.0[1]		
P^4 length x width	19.5 x 11.8	18.3 x 9.9			19.4 x 9.5[1]
M^1 length x width	12.6 x 17.4	12.8 x 16.9			
C-P^3 length	29.0	27.6			
C-P^4 length	48.0	47.2			
C-M^2 length	58.5	60.0			

Lower Dentition	UF 12320	UF 12326	UF 12319	UF 12321
C length x width			11.6 x 9.7	
P_2 length x width			4.6 x 6.0	
P_3 length x width		7.9 x 5.0		
P_4 length x width		14.1 x 8.5		
M_1 length		21[1]		
M_2 length x width		10.4 x 6.9		10.0 x 6.8
C-P_4 length	44.2	41[1]		
M_1-M_3 length	38			
P_4-M_3 length	52			
C-M_3 length	76[1]			
Depth below P_4	24			
Depth below M_1				25

[1] Approximate

ETYMOLOGY.—Mytholgical. *Orc* = a ruthless carnivorous creature serving the forces of evil in the Third Age of Middle Earth (see Tolkien, 1965, especially Chapter 3, part 2).

HOLOTYPE.—UF 13180, right mandible with P_3-M_2 and alveoli for C, P_1 and P_2.

MATERIAL.—UF 12313, left maxilla with P^2-M^1; UF 12314, right maxilla with P^2-M^1; UF 12315, right maxilla and premaxilla with canine tooth and alveoli for I^{1-3} and P^{1-3}; UF 12317, two upper carnassial teeth; UF 12350, left maxilla with P^1-P^4; UF 14782, P^3; UF 12319, anterior mandibular fragment; UF 12320, right mandible with P_2, P_3 and M_2; UF 13181, left mandible with P_3-M_1; UF 12321, left mandible with M_2; UF 12326, left mandible with alveoli for P_1-P_3; UF 14783, right mandible with M_{1-2}; UF 14785, right mandible with P_1 and P_3; UF 14786, three mandibular fragments; UF 14781, P_4; UF 14784 three M_1's; UF 12323, atlas; UF 12324, two axes; UF 12332, lumbar vertebra; UF 12333, two humeri; UF 12327, four radii; UF 12328, 3 ulnae; UF 12325, two pelves; UF 12329, femur; UF 12330, two tibiae; UF 12331, 17 metapodials. Collected by Robert Allen, Norm Tessman, and Kent Ainslie, May, 1967.

TYPE HORIZON AND LOCALITY.—Withlacoochee River, locality 4A, (UF locality catalog), about 8 miles southeast of Dunnellon, Marion County, Florida. Fossil vertebrates preserved in massive green clay, filling a sinkhole developed in Inglis member of Ocala Limestone (Late Eocene). This is the second report on parts of the fauna (Hirschfield and Webb, 1968); other elements clearly indicate a Hemphillian age.

DIAGNOSIS.—The smallest known species of *Osteoborus*, with relatively shallow jaws and delicate canine teeth. Anterior premolars greatly reduced; P_1 and P^1 present or not. Length P^{1-3} 65% of length P^4-M^1. P_2 single rooted. P^2 and P_3 without distinct accessory cusp(id)s. P^4 with strong parastyle, weak protocone connected by two low ridges to parastyle. M^1 paracone much stronger than metacone; hypocone narrow and strongly skewed posterolingually; nearly continuous labial cingulum. P_4 with posterior accessory cuspid and high, wide posterior cingulum tightly appressed, advanced well beyond *cyonoides* and approaching *pugnator* in these features; anterior slope crested with cingular cusp at base. M_1 with weak metaconid, relatively shorter talonid, with basin closed in by hypoconulid much more than in *cyonoides*. M_2 elongate, with strong labial cingulum, greatly reduced trigonid, lacking entoconid.

DESCRIPTION OF MATERIAL.—P^1 is represented in both UF 12313 and 12315 by a single alveolus 3.0 mm in diameter, but in UF 12314 no alveolus for P^1 appears. P^2 and P^3 are low short teeth, closely spaced and obliquely set in the jaw, each supported by two unfused roots. The crown of P^2 consists of a principal cusp less than 4 mm high from which oblique descending crests reach the ends of the crown. On the lingual side is a weak but continuous cingulum. P^3 is similar in shape but larger. The principal cusp is about 6 mm high. Small anterior and posterior accessory cusps are indicated by swellings on the longitudinal crests.

The upper carnassial retains a strong parastyle that rises to nearly half the height of the paracone-metacone blade. It wears very heavily. A small anterior protocone is connected to the parastyle by two thin

Table 5. SKELETAL MEASUREMENTS OF *Osteoborus orc* (in mm)

ATLAS VERTEBRA	UF 12323
maximum width	ca. 78
anterior width centrum	36
maximum depth centrum	24
dorsal length centrum	16
ventral length centrum	11

AXIS VERTEBRA	UF 12324a	UF 12324b
length dorsal crest	50	ca. 55
length centrum	41	43
width across zygapophyses	32	34
anterior width centrum	28	28

FIRST LUMBAR VERTEBRA	UF 12332
length centrum	23
posterior width centrum	20
posterior depth centrum	12

HUMERUS	UF 12333a	UF 12333b
maximum distal width	48	43
maximum distal articular width	29	28
height anconeal fossa	17	12

RADIUS	UF 12327a	UF 12327b	UF 12327c	UF 12327d
maximum length	124			
proximal transverse/antero-posterior diameter	20/15		21/15	27/17
distal transverse/antero-posterior diameter	18/12	20/14		

ULNA	UF 12328a	UF 12328b	UF 12328c
proximal transverse	14		
anteroposterior diameter	25		
depth of humeral notch	19		
distal transverse/antero-posterior diameter		7/13	8/13

PELVIS	UF 12325a	UF 12325b
minimum depth ilium shaft	19	19
maximum height acetabulum	23	22

FEMUR	UF 12329
length	ca. 110
maximum width distal end	25
maximum depth distal end	30

TIBIA	UF 12330a	UF 12330b
proximal transverse/antero-posterior diameter	35/36	
distal transverse/antero-posterior diameter		23/16

Table 5. (cont.)

Metatarsal IV	UF 12331n	UF 12331o	UF 12331p
length	52	58	60
proximal transverse/antero-posterior diameter	8/12	10/12	9/13
Metatarsal V	UF 12331q	UF 12331r	
length	44	ca. 49	
proximal transverse/antero-posterior diameter	9/10	8/10	

discontinuous crests. In worn specimens the protocone appears as a mere wear surface on the basal swelling of the tooth. The carnassial blade wears along two surfaces: bluntly on the tops of the paracone and metacone, and to a lesser extent vertically on the lingual side in the usual sectorial fashion. Both wear surfaces are marked by very deep striae in the four available carnassials. A strong posterolingual cingulum lies at the top of the shearing surface.

The first molar presents a relatively high paracone and by contrast a very low metacone. In the slightly worn specimen the paracone rises 5.0 mm above the labial cingulum, whereas the metacone is only 2.7 mm higher. The labial cingulum is moderately developed, but is cut by the valley between the two principal cusps. The lingual portion of the tooth is relatively narrow with the hypocone strongly skewed posteriorly. The lingual part of this tooth most nearly resembles the slenderest, most skewed variants in the Hemphill (Coffee Ranch) Fauna from Texas (Matthew and Stirton, 1930, plate 28, figure b), but both specimens here are even more extreme.

As in *Osteoborus* generally, a cingulum extends from the hypocone around the anterolingual side of the tooth, and fades out at a point well labial to the protocone. The protocone is unusual in its relationships. The anterior crest from the protocone produces two strong cuspules and then forms a strong cingulum that borders the anterolingual slope of the paracone and joins the anterior end of the labial cingulum.

An analogous cingulum, without cuspules, runs from the metaconule posterolabially to the posterior end of the labial cingulum. These ridges are much heavier in *Osteoborus* than in *Canis lupus* or *C. latrans*.

The mandible of *O. orc* is relatively shallower than in other species. In keeping with its small size this species has rather delicate canines.

The lower premolars are closely crowded. P_1 is present in one lower jaw (UF 12319), but two other jaws lack alveoli for that tooth.

P_2 is single rooted, though a groove on the lingual side indicates that it was derived by the fusion of two roots.

P_3 presents only a low principal cusp from which longitudinal crests descend anteriorly and posteriorly. There are no accessory cusps or cingula. The tooth is supported by two roots.

The principal cusp in P_4 presents a strongly convex anterior profile, in this respect resembling *Borophagus* more than other species of *Osteoborus.* This convex anterior slope is produced by a strong anterior crest and by an anterior cingular cuspid at its base. The posterior accessory cuspid is weak, but distinct. The posterior cingulum is strongly compressed anteroposteriorly and the posterior edge of P_4 is square cut as in *Borophagus* and *Osteoborus progressus* Hibbard (1944).

The trigonid and talonid of M_2 are equal in length. The cusps of the trigonid are low, but distinct. The paraconid occupies the middle of the anterior edge of the tooth, and the metaconid lies directly opposite the protocone. A broad triangular cingulum squares up the anterolabial corner of the tooth. The talonid forms a broad shallow concavity marked only by a low hypoconid. The entoconid is absent in both specimens, one unworn, in this sample.

The skeletal remains of *O. orc* differ from those of *Canis lupus* only in proportions and in minor osteological features. The anterior part of the atlantal arch is very heavily built, the odontoid process of the axis is unusually stout, and the zygapophyses are wide and very sturdily constructed.

The limb elements are heavy jointed. The distal end of the humerus in particular is much broader than in similar sized modern *Canis.* One specimen has a well developed entepicondylar foramen that is absent in a smaller specimen. The radius and metapodials are much shorter and yet broader than the corresponding elements in *Canis lupus.* The short broad limb structure has received comment in larger species of this genus (Matthew and Stirton, 1930); it seems even more remarkable in so small a species as *Osteoborus orc.*

DISCUSSION.—*Osteoborus orc* is the smallest of the species referred to either *Osteoborus* or *Borophagus.* It falls distinctly below the range of variation in the large sample of *O. cyonoides* from the Hemphill Fauna of Texas, and it is about one-third smaller than the small California species, *O. diabloensis* Richey and *O. littoralis* Vanderhoof. An upper jaw from the Upper Snake Creek beds, referred by

Cook and Macdonald (1962) to *Borophagus* sp., approaches but does not equal this species in smallness of its dimensions.

The nearest comparison in size, as well as in other features, is with *O. progressus* Hibbard (1944) from the Saw Rock Fauna of Kansas. The comparable teeth are lower P_3, P_4, M_1 and M_2, and in these *O. orc* is 20 to 25% smaller than *O. progressus.*

A small canid maxillary from the Upper Snake Creek beds was referred by Cook and Macdonald (1962) to *Borophagus* sp. Although its premolars are comparable in size to those of *Osteoborus orc,* the critical features are inadequately known to determine its relationships. It may well belong in *Osteoborus* near *O. secundus.*

The premolars of *Osteoborus orc* are crowded and greatly reduced. In this respect *O. orc* is one of the most advanced species known (along with *O. hilli, O. pugnator,* and *O. progressus*), and is comparable with some species of *Borophagus.* For example in the two upper jaws of *O. orc* the length of P^{1-3} is 62% and 68% respectively of that of P^4-M^1, and in *Borophagus solus* the length of P^{1-3} is 64% of that of P^4-M^1. In *O. hilli* this percentage is about 60%. In most species of *Osteoborus* this percentage lies between 70% and 80% (Table 6), the premolars being less reduced.

Other progressive features of the premolars of *Osteoborus orc* are the complete suppression of the accessory cusps or cuspids on P^2, P_2, and P_3 and their near absence on P^3, weak protocone on P^4, single rooted P_2, P_4 with convex anterior slope bearing a crest and cingular cuspid, and with a compressed square-cut posterior cingulum. The very strong wear on the parastyle of the upper carnassials, noted above in three of four specimens, is accomplished by the robust principal cusp of P_4. As this cusp becomes enlarged still further (in *Borophagus*) the parastyle against which it grinds "fades" into a long vertical crest on the anterior slope of the paracone of the upper carnassial. *O. orc* approaches *Borophagus* in the heavy wear on the parastyle of P_4, but the parastyle remains strong.

The upper first molar also represents a progressive state in *Osteoborus* evolution. In the great inequality between the paracone and metacone and in the narrow skewed talon this tooth closely resembles that of *Borophagus.* The last lower molar is relatively reduced in size and lacks the entoconid, both advanced features for *Osteoborus.*

Most of these features noted in *orc* represent advanced stages in the evolution of *Osteoborus* into *Borophagus.* A number of features, such as the degree of premolar reduction, fusion of roots on P_2, narrow skewed structure of M^1, and the loss of the entoconid on M_2, suggest

Table 6. Upper Dentition Measurements of Certain Borophagine Species
(in mm)

	O. dudleyi MCZ 3688	*O. hilli* Holotype	*O. cyonoides* UC 30115	*O. littoralis* Holotype	*O. diabloensis* Holotype	*O. orc* (mean of two jaws)
Canine length	19	17.5	16	14.5		10.0
Canine width	12	11	10	ca. 7		7.6
P^{1-3} length	26.7	26.0	25.5	29.8	30.0	20.1
P^4-M^1 length	38.3	39.6	35.8	37.0	37.4	30.9
Ratio $\frac{P^{1-3}}{P^4\text{-}M^1}$	70	66	71	80	80	65

	Borophagus pachyodon Holotype	*B. pachyodon* UC 32464	*B. matthewi* Holotype	*B. solus* Holotype
Canine length	18	19	20	18.5
Canine width	11	13	13	11.4
P^{1-3} length	27.1	25.9	27.5	23.9
P^4-M^1 length	37.2	42.3	36.5	37.3
Ratio $\frac{P^{1-3}}{P^4\text{-}M^1}$	73	61	75	64

that *Osteoborus orc* might be the proximate ancestor of *Borophagus,* along with *O. secundus* and *O. progressus.* However the retention of a strong parastyle on P^4 of this species is considerably different from that of *Borophagus.* Moreover the anterior crest and cingular cuspid of P_4 are peculiar features not observed in *Borophagus* or other Hemphillian material of *Osteoborus.* These features are best developed in *Aelurodon* and therefore represent primitive characters of the borophagine tribe.

In most respects *O. orc* is a progressive species of *Osteoborus.* While not so likely ancestral to some or all species of *Borophagus* as are *O. hilli* or *O. progressus,* it is nearly as advanced. Presumably this species is from the later half of the Hemphillian age.

Osteoborus galushai new species

Figure 5, Table 7

ETYMOLOGY.—Named in honor of Ted Galusha of the Frick Laboratory for his extensive contribution to knowledge of the carnivores and to vertebrate paleontology in general.

HOLOTYPE.—Mandible with nearly complete left and right dental series, FAM 61671 and 61672.

TYPE LOCALITY AND HORIZON.—Alachua Clay, Mixson's Bone Bed sinkhole, northeast of Williston, Levy County, Florida. Associated with the Hemphillian faunule described by Leidy and Lucas (1896), and Simpson (1930).

REFERRED MATERIAL.—All from the type locality: left maxillary fragment with P^2, P^4 and alveoli for C and P^3, FAM 61675; right maxillary fragment, FAM 61557; left maxillary fragment with M^1 and M^2; FAM 61677; maxillary fragment with P^3-M^2 and alveoli for P^1 and P^2; FAM 61676; upper canine, FAM 61678; zygomatic arch, FAM 61674a; right ramus with M_1, FAM 61673; right ramal fragment with M_2, FAM 61674; and lower canine, FAM 61673h.

DIAGNOSIS.—Close to *O. cyonoides* in size and other features P_1 present; anterior premolars widely spaced. Differs from *O. cyonoides* in the higher cusp on P^2 and the higher cusps and distinct heels on P_2 and P_3; P_4 with slender upright principal cusp and strong posterior accessory cusp. M_2 elongate and strongly cuspidate as in *O. cyonoides.*

DESCRIPTION.—The single rooted first premolars are represented by alveoli in the mandible. They are separated from the canines by diastemata of 2 mm. The succeeding premolars are loosely spaced, not

FIGURE 5. Mandible of *Osteoborus galushai* new species. Holotype, FAM 61671 and 61672. Occlusal and left lateral views. Natural Size.

crowded or overlapping as in advanced species of *Osteoborus*. Though P_2 and P_3 lack distinct accessory cuspids, the principal cusp is high and slender, not bluntly rounded as in *O. secundus*. A distinct posterior heel remains in each tooth. In P_4 the principal cusp is slender and nearly vertical as compared with the bulbous backswept cusp in *O. secundus* and other more borophagine species. A sharp crest marks its anterior slope. The posterior accessory cusp is high and not compressed against the posterior cingulum. A lingual cingulum is continuous.

M_1 agrees closely with the same tooth in *O. cyonoides*. The metaconid is strong and the talonid relatively long. The talonid basin is divided by a low hypholophid into a large anterior and a smaller posterior basin. M_2 is relatively long and thus agrees with *O. cyonoides* and differs from more advanced species such as *O. secundus*. It bears

Table 7. MEASUREMENTS OF DENTITION OF *Osteoborus galushai* (in mm)

Upper Dentition	FAM 61676	FAM 61675	FAM 61677
P^2 length × width		9.5 x 5.9	
P^3 length × width	11.9 x 5.8		
P^4 length × width	23.5 x 10.7	24.8 x 12.6	
M^1 length × width	16.3 x 19.2		16.5 x 19.7
M^2 . length × width	9.1 x 13.7		11.2 x 13.6
P^1-P^4 length	51.8	52.3	
P^1-M^2 length	69.5		

Lower Dentition	FAM 61671	FAM 61672	FAM 61673	FAM 61674
P_2 length × width	8.2 x 4.7	8.3 x 4.7		
P_3 length × width	9.6 x 5.4	9.6 x 5.4		
P_4 length × width	15.9 x 9.3	15.9 x 9.3		
M_1 length × width		25.6 x 9.5	25.9 x 10.7	
M_1 Trigonid x Talonid		19.4 x 6.4	17.6 x 8.0	
M_2 length × width	12.3 x 7.9			13.9 x 8.3
P_{2-4} length	35.4	35.1		
P_4-M_2 length	52.7		ca. 57	
Depth jaw below P_4	29	28		

a distinct trigonid and a longer basined talonid as in *O. cyonoides*. M_3 is represented by a single elongate alveolus.

Two mental foramina occur on the labial side of the jaw about 12 mm below the anterior ends of P_4 and P_3 respectively.

The upper premolars of *O. galushai* are not so closely spaced as in many species of *Osteoborus*. P^1 is relatively large, but single rooted. The alveolar diameter in FAM 61675 measures 5 mm. P^2 and P^3 are double-rooted elongate teeth. No anterior accessory cusp is evident in P^2, whereas in P^3 it is a distinct cusp nearly as large as the posterior accessory cusp. The principal cusp in P^2 is higher than in *O. cyonoides* and bears stronger anteroposterior crests. Its unworn height in FAM 61675 is 5.7 mm. P^3 agrees closely with that in *O. cyonoides*.

Two of the three upper carnassials of *O. galushai* differ little from those of *O. cyonoides*. The third (FAM 61675) differs markedly in the structure of the protocone. In it the protocone forms a relatively bulbous protuberance from the anterolingual corner of the tooth. Three distinct cuspules descend one beneath another in the protoconal area; the largest is lowermost and touches the parastyle. This character must be regarded as an atavistic peculiarity of one specimen, rather than a diagnostic feature of the species.

M^1 does not differ significantly from those of *O. cyonoides*. In one specimen of M^2 (FAM 61677) the labial moiety is wider and the metacone is relatively larger than in observed specimens of *O. cyonoides*. However a second specimen (FAM 61676) agrees in every detail with specimens of *O. cyonoides*.

RELATIONSHIPS.-*Osteoborus galushai* from Mixson's most nearly resembles *O. cyonoides* from the Edson Beds in Kansas. The principal differences are the presence of P_1 and the widely spaced premolars. Further differences appear in the more slender, higher cusped, less borophagine structure of the premolars, and suggest a slightly earlier stage of evolution than *O. cyonoides*.

Osteoborus cf. *O. galushai*

Figure 6, Table 8

MATERIAL.—UF 12304, right mandibular ramus with M_2 and roots or alveoli for C through M_1, UF 12312, RM_1; UF 12307, LC^1; UF 12305, RP^4; UF 12306, LM^1; UF 15129, RM_3; UF 12309, thoracic vertebra. UF 12310, left metacarpal V; UF 12311 left metacarpal II; and

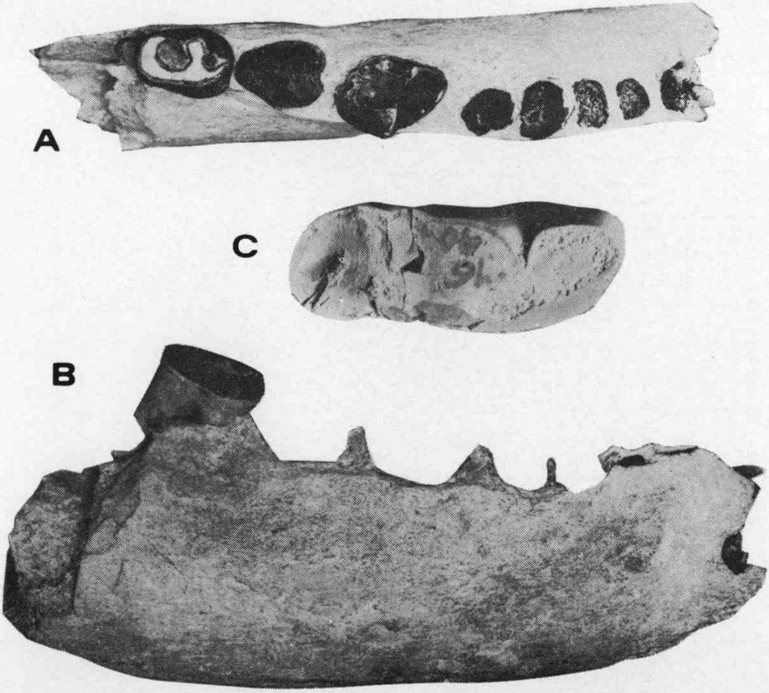

FIGURE 6. Mandible of *Osteoborus* cf. *O. galushai*. A. and B. Occlusal and lateral views, UF 12304, right mandible with M_2. C. UF 12312, right M_1, × 1½. All natural size.

Table 8. COMPARATIVE MEASUREMENTS OF DENTITION OF *Osteoborus* cf. *galushai* (in mm)

Upper Dentition	UF 12305 McGehee	UF 12402 Hogtown
P^4 length x width	28[1] x 14.2	
M^1 length		17.8[1]
M^2 width		24.2

Lower Dentition	*O.* cf. *galushai*		*O. dudleyi*	*Osteoborus hilli*		
	UF 12304	UF 12312	FGS V5644	CWT 2419	CWT 1558	CWT 1643
P_3 length	11.5[1]					
P_4 length x width	16.5[1]		17.8 x 12.8	18.4 x 12.8	17.2 x 12.0	19.3 x 14.1
M_1 length x width	29.7[1]	32.8 x 12.8	30.9 x 12.6	30.1 x 12.6	30.5 x 12.8	32.1 x 13.6
M_2 length x width	14.3 x 10.1					
Length between C and P_4	19.0		13.9	15.6	19.5	18.0
Length between C and M_2	68		61			
Depth Jaw Below P_4	30.5		34.5			
Depth Jaw Below M_1	31.5		33.0			

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[1] Approximate

UF 10990, left calcaneum, all from McGehee Farm Locality, and UF 12402 RM^1 from Hogtown Creek II Locality.

HORIZONS AND LOCALITIES.—McGehee Farm Locality, 5 miles north of Newberry, Alachua County, Florida. In fluviatile clay, sand, and gravel deposits of the Alachua "Formation." Early Hemphillian age (Webb, 1964; Hirschfeld and Webb, 1968). Hogtown Creek II Locality on western edge of the city of Gainesville, Alachua County, Florida; Hemphillian fossils, including *Geochelone alleni* described by Auffenberg (1966), occur in fluviatile phosphatic sands and gravels.

DESCRIPTION.—The McGehee jaw is slender and tapers in the symphyseal region, thus contrasting with the Bone Valley jaw of massive ramus and deep symphysis. Such differences may be taxonomically significant, but they may also correlate with individual differences in size, sex, and age.

No alveolus for P_1 appears in the jaw of *O.* cf *galushai* from McGehee. P_2 was evidently single-rooted with an alveolus about 5 mm in diameter. P_3 was double-rooted and about two-thirds the size of P_4. Such a large P_3 suggests a rather primitive stage of *Osteoborus* evolution. On the other hand, one of the Hemphill (Coffee Ranch) jaws of *O. cyonoides* (UCMP 30113) has a P_3 proportionally as large as the McGehee form. P_4 is set well labial to M_1, and the jaw is bowed labially in the manner characteristic of *Osteoborus*. Unfortunately the crown of P_4 is not represented.

The lower carnassial tooth, UF 12313, agrees in size with the roots in the jaw of UF 12304 and presumably represents the same species. It is rather well worn, but still retains a distinct broadening at the metaconid. The carnassial cusps are worn flat as in borophagines generally.

In the McGehee mandible M_2 is well developed. A distinct paralophid occurs, and the metaconid lies opposite the protoconid. The cusps of the talonid are no longer distinct, but rather a well developed lophid encircles the heel and joins the protoconid. The tooth closely resembles M_2 of *O. cyonoides*, except that it is larger. There is no alveolus for M_3 in this specimen.

The first upper molars from Hogtown Creek and McGehee are heavily built in characteristic borophagine fashion. Adaptation to bone crushing is emphasized in the McGehee specimen by the presence of an unusually broad, rounded protoconal shelf, but this character shows great variation in M^1 in large samples of *Osteoborus*.

RELATIONSHIP.—In most features the sample of *Osteoborus* from McGehee and Hogtown resembles that from the Hemphill Fauna in

Texas referred to *O. cyonoides*. However the measurements of the McGehee specimens fall above or at the upper edge of the range of the Hemphill sample and the premolars are larger and more widely spaced. The same differences distinguish the McGehee-Hogtown form from the type of *O. cyonoides* (Martin) from the Edson fauna of Kansas. In the larger anterior premolars, the McGehee-Hogtown sample resembles *O. galushai* from Mixson's Bone Bed.

In size the specimens from McGehee and Hogtown Creek agree more closely with the somewhat larger *O. hilli* and *O. dudleyi*. However the Florida specimens are clearly more primitive on the basis of the relatively long slender jaw, the relatively large P_3, and the strong metaconid on the lower carnassial. The first two characters also suggest a possible relationship to the California species, *O. littoralis* (Vanderhoof), though M^1, the only directly comparable element, is nearly square in *O. littoralis* and transversely elongate in the McGehee and Hogtown populations. Possibly this material represents a larger, perhaps earlier, sample of *Osteoborus galushai*. Final determination must await better specimens.

Osteoborus validus (Matthew and Cook)

Figure 7, Table 9

MATERIAL.—Right mandibular ramus with alveoli for C through M_1, UF 12308; left metacarpal II, UF 12403; both from the fluvio-estuarine gravels, McGehee Farm Locality, 5 miles north of Newberry, Alachua County, Florida, early Hemphillian Age (Webb, 1964). RP_4, FAM 61556, from Mixson's Bone Bed, Williston, Levy County, Florida.

DESCRIPTION.—This new material adds little to our knowledge of *O. validus* but it does indicate the presence of that very large species in eastern United States during Hemphillian time.

The approximate lengths of the lower teeth in the edentulous jaw are given in Table 9. The canine alveolus shows that it was a very large tooth, but the dimensions cannot be measured accurately. The premolars are considerably reduced as compared with the lower carnassial. Those anterior to P_4 are obliquely oriented, with the anterior end of each tooth overlapping the posterior end of each preceding tooth on the labial side. P_1 is represented by a large single rooted alveolus; the other premolars are double rooted.

The bottom edge of the ramus was sheared away in the McGehee jaw, but there can be no doubt that the mandible was very heavily constructed, with the maximum width of 26 mm just posterior to the

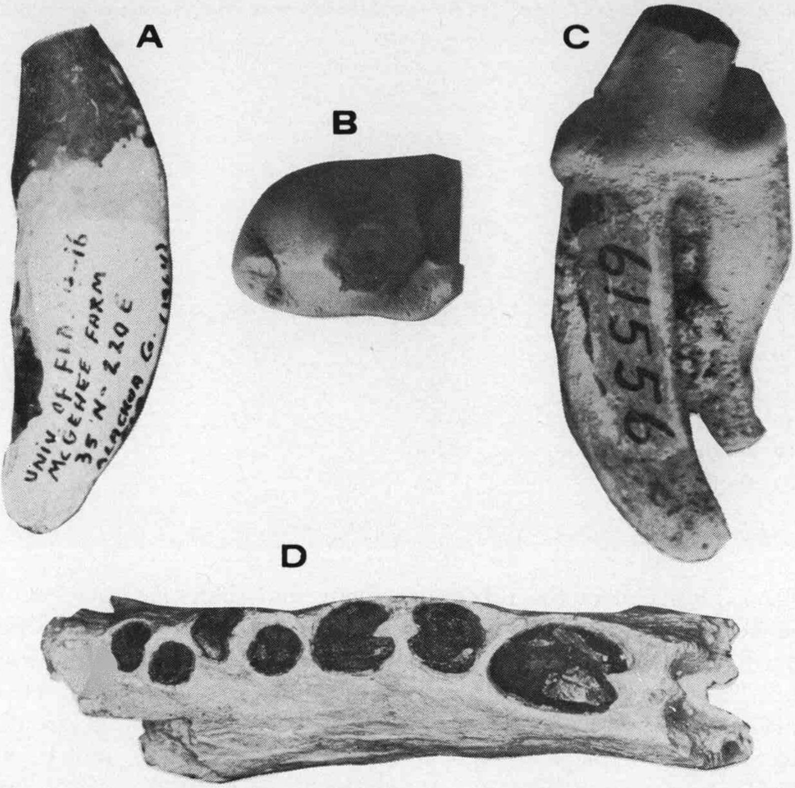

FIGURE 7. Mandible of *Osteoborus validus*. A. UF 12307, lower canine. B. and C. FAM 61556, right P_4, × 1½. D. UF 12304, mandible with alveoli for P_1-M_1. All natural size.

symphysis and a depth below M_1 of about 57 mm. The positions of the two mental foramina agree with those in the type of *O. validus* and in the referred jaw from the Higgins Fauna (Hesse, 1940). They lie about 21 mm below the alveolar border, one directly below the posterior root of P_3, and the other below the posterior root of P_2. The isolated P_4 from Mixson's Bone Bed has two closely appressed roots, a low anterior cingular cusp, and a heavy principal cusp. Although the posterior portion of the tooth is broken, it evidently consisted of a heavy posterior accessory cuspid and a broad posterior cingulum. The roots of the tooth have a vertical dimension of 33 mm.

RELATIONSHIPS.—In their original description Matthew and Cook (1909) regarded *validus* as a subspecies of *Aelurodon haydeni* that differed from the type "in the shorter and more crowded premolar

Table 9. MEASUREMENTS OF TEETH AND METACARPAL OF *Osteoborus cf. validus* (in mm).

Teeth	UF 12308	FAM 61556
P^1 length	6[1]	
P^2 length	11.5[1]	
P^3 length	15[1]	
P_4 length x width	21[1]	ca. 23[1] x 14.2
M^1 length	42[1]	
Metacarpal	UF 12403	
Max. length	87.7	
Prox. width	16.0	
Prox. depth	20.5	
Dist. width	16.5	
Dist. depth	15.5	

[1] Approximate

region, reduction of the tubercular teeth, and slight enlargement of the carnassial." In their study of the Coffee Ranch sample (now referred to *Osteoborus cyonoides*) Matthew and Stirton (1930) continued to regard *validus* as a subspecies of *Aelurodon haydeni.* Then Stirton and Vanderhoof (1933) intimated that *validus* was specifically distinct from *A. haydeni* and referable to *Osteoborus*, and Hesse (1940), Johnston (1939a), and Vanderhoof and Gregory (1940) supported this view. The principal basis for this generic transfer is the reduction and crowding of the premolars in *O. validus.* This feature is clearly shown in the type specimen as originally noted by Matthew and Cook. This condition is not exhibited so convincingly in the Higgins Fauna sample, referred to *validus* by both Johnston and Hesse. In a skull Johnston (1939a) notes that "there is no crowding of the teeth, and there are short spaces between the premolars." Likewise in the mandible figured by Hesse (1940) the premolars are in anteroposterior alignment and are separated by small gaps, although Hesse described them as "crowded together."

With respect to premolar spacing, the McGehee jaw agrees much more closely with the type of *O. validus.* It also agrees with the type in being slightly smaller than the jaws from Higgins.

In the type of *Aelurodon haydeni* the length of P_3 is more than 70% of the length of P_4, whereas in the Higgins, Snake Creek, and McGehee jaws, it is 60% or less. Premolar spacing is a highly variable character, and one that is particularly affected by ontogenetic change. Evidently reduction in premolar size is a more reliable feature, and on this basis all the above samples are referred to *validus* and that species placed in *Osteoborus*.

Diversity of Canidae in the Pliocene of Florida

The diversity of *Osteoborus* species in Hemphillian deposits of Florida seems remarkable, especially if one accepts the traditional view that the land surface of peninsular Florida was restricted to a small archipelago during the Pliocene. Recent evidence shows that during some parts of the Hemphillian, the sea lay at least as low as its present level (Webb and Tessman, 1968). Even so, four or five

	COASTAL	INLAND
	Bone Valley	Withlacoochee 4 A
LATE HEMPHILLIAN	*Carpocyon limosus* *Osteoborus dudleyi*	*Osteoborus orc*
EARLY HEMPHILLIAN	*Osteoborus cf. galushai* *Osteoborus validus*	*Osteoborus galushai* *Osteoborus validus*
	Mc Gehee – Hogtown	Mixson's Bone Bed

FIGURE 8. Age and distribution of Canidae in Florida.

species in a single genus of canids is twice what is observed today in Florida, or even in North America. Nor is such localized intrageneric diversity found in any fossil canids during the Miocene.

Two alternative explanations for the Hemphillian diversity within *Osteoborus* may be advanced:

1) The Hemphillian included sufficient time for a major faunal overturn, and we are sampling two or more faunal strata, or

2) the genus *Osteoborus* is so broadly defined that it includes several adaptively distinct lineages, and we are sampling diverse ecologies.

The evidence summarized in Figure 8 suggests that, at least with respect to *Osteoborus,* two temporally distinct faunal strata occupied Florida during Hemphillian time, an interval of about 6 million years. This does not mean that the later stratum evolved from the earlier, in fact this view is strongly opposed by comparisons between the known species. Rather in the later Hemphillian new immigrant species appeared as ecological replacements of the early Hemphillian species. The explanations for such faunal turnover lie beyond the scope of this paper. It is sufficient here to note the occurrence.

The second explanation for the diversity of Hemphillian *Osteoborus* in Florida also warrants some consideration. The morphological separation between certain species pairs is vast. Including little *Osteoborus orc* in the same genus as the great species of *Osteoborus* strains the definition of that genus. *O. orc* evidently occurs in an inland situation, whereas the Bone Valley species is clearly coastal. When only the early Hemphillian canid fauna is considered, the situation is less complex. Only two species are known, both of the genus *Osteoborus,* a large one, *O. validus,* and a medium-sized one, *O. galushai.* Similar species occur together at both McGehee and Mixson's, even though the ecologies appear to be considerably different at these sites. Thus, the early Hemphillian diversity of *Osteoborus* may be compared readily to that of *Canis* today.

LITERATURE CITED

Auffenberg, Walter. 1966. A new species of Pliocene tortoise, genus *Geochelone,* from Florida. J. Paleontol. 40: 877-882.

de Beaumont, Gerard. 1964. Essai sur la position taxonomique des genres *Alopecocyon* Viret et *Simocyon* Wagner (Carnivora). Eclogae Geol. Helvetiae, 57: 829-836.

Brodkorb, Pierce. 1963. Fossil birds from the Alachua Clay of Florida. Florida Geol. Surv., Spec. Publ. No. 2, (4): 1-17.

Camp, C. L. and V. L. Vanderhoof. 1940. Bibliography of fossil vertebrates 1928-1933. Geol. Soc. Amer., Spec. Paper, 27, pp. 1-503.

Cook, Harold J. and J. R. Macdonald. 1962. New Carnivora from the Miocene and Pliocene of western Nebraska. J. Paleontol. 36: 560-567.

Dahr, Elias. 1948. On the systematic position of *Phlaocyon leucosteus* Matthew and some related forms. Arkiv fur Zoologi. 41: 1-15.

Downs, Theodore. 1956. The Mascall fauna from the Miocene of Oregon. Univ. California Publ. Geol. Sci. 31: 199-354.

Galbreath, E. C. 1956. Remarks on *Cynarctoides arcidens* from the Miocene of Northeastern Colorado. Trans. Kansas Acad. Sci. 59: 373-378.

Gazin, C. Lewis. 1932. A Miocene mammalian fauna from southeastern Oregon. Carn. Inst. Washington Publ. (418): 37-86.

Green, Morton. 1948. A new species of dog from the Lower Pliocene of California. Univ. California Publs., Dept. Geol. Sci., 28: 81-90.

Hall, E. R. and W. W. Dalquest. 1962. A new doglike carnivore, genus *Cynarctus*, from the Clarendonian, Pliocene, of Texas. Univ. Kansas Publs., Mus. Nat. Hist., 14: 135-138.

Hesse, Curtis J. 1940. A Pliocene vertebrate fauna from Higgins, Lipscomb County, Texas. Univ. Texas Publ., (3945): 671-689.

Hibbard, Claude W. 1944. Two new mammals from the Middle Pliocene of Seward County, Kansas. Univ. Kansas Sci. Bull. 30: 107-114.

Hirschfeld, Sue E. and S. David Webb. 1968. Plio-Pleistocene megalonychid sloths of North America. Bull. Florida State Mus. 12: 213-295.

Hough, Jean R. 1948. The auditory region in some members of the Procyonidae, Canidae and Ursidae. Bull. Amer. Mus. Nat. Hist., 92: 67-118.

Johnston, C. Stuart. 1939a. A skull of *Osteoborus validus* from the early Middle Pliocene of Texas. J. Paleontol. 13: 526-530.

———. 1939b. Preliminary report on the late Middle Pliocene, Axtel Locality, and the description of a new member of the genus *Osteoborus*. Amer. J. Sci. 237: 895-898.

Leidy, J. and F. A. Lucas. 1896. Fossil vertebrates from the Alachua Clays of Florida. Trans. Wagner Free Inst. Science, 4: 1-61.

Macdonald, J. R. 1948. The Pliocene carnivores of the Black Hawk Ranch Fauna. Univ. California Publs., Dept. Geol. Sci., 28: 53-80.

———. 1963. The Miocene faunas from the Wounded Knee Area of Western South Dakota. Bull. Amer. Mus. Nat. Hist. 125: 143-238.

McGrew, P. O. 1935. A new *Cynodesmus* from the Lower Pliocene of Nebraska with notes on the phylogeny of the dogs. Univ. California Publs., Dept. Geol. Sci., 23: 305-312.

———. 1937. The genus *Cynarctus*. J. Paleontol. 11: 444-449.

———. 1938. Dental morphology of the Procyonidae with a description of *Cynarctoides*, gen. nov. Field Mus. Nat. Hist., Geol. Ser., 6: 323-339.

Martin, H. T. 1930. Two new carnivores from the Pliocene of Kansas. J. Mammal. 9: 233-238.

Matthew, W. D. and Harold J. Cook. 1909. A Pliocene fauna from western Nebraska. Bull. Amer. Mus. Nat. Hist. 26: 361-414.

———, and R. A. Stirton. 1930. Osteology and affinities of *Borophagus*. Univ. California Publs., Bull. Dept. Geol. Sci., 19: 21-34.

Olsen, S. J. 1956a. The Caninae of the Thomas Farm Miocene. Breviora, (66): 1-12.

———. 1956b. A new species of *Osteoborus* from the Bone Valley Formation of Florida. Florida Geol. Surv., Spec. Publ. (2): 1-5.

Rose, F. L. and W. G. Weaver. 1966. Two new species of *Chrysemys* (=*Pseudemys*) from the Florida Pliocene. Tulane Studies Geol. 5: 41-48.

Simpson, G. G. 1930. Tertiary land mammals of Florida. Bull. Amer. Mus. Nat. Hist., 59: 149-211.

———. 1932. Miocene land mammals from Florida. Bull. Florida Geol Surv., 10: 9-41.

Skinner, M. F., S. M. Skinner, and R. J. Gooris. 1968. Cenozoic rocks and faunas of turtle butte, south central South Dakota. Bull. Amer. Mus. Nat. Hist. 138: 379-436.

Stirton, R. A. and V. L. Vanderhoof. 1933. *Osteoborus,* a new genus of dogs, and its relations to *Borophagus* Cope. Univ. California Publs., Bull. Dept. Geol. Sci. 23: 175-182.

Stock, Chester. 1947. A peculiar new carnivore from the Cuyama Miocene, California. Bull. So. California Acad. Sci. 46: 84-89.

Thorpe, Malcolm R. 1922. Some Tertiary Carnivora in the Marsh collection, with description of new forms. Amer. J. Sci. 3: 423-455.

Tolkien, J. R. R. 1965. The Lord of the Rings. 3 vols. New York: Ballantine Books.

Vanderhoof, V. L. 1931. *Borophagus littoralis* from the marine Tertiary of California. Univ. California Publs., Dept. Geol. Sci., 21: 15-24.

———. and J. T. Gregory. 1940. A review of the genus *Aelurodon.* Univ. California Publs., Dept. Geol. Sci., 25: 143-164.

Viret, Jean. 1933. Contribution a l'etude des carnassiers miocenes de la Grive St. Alban. Trav. Lab. Geol. Univ. Lyon, 21: 1-30.

Weaver, W. G. and J. S. Robertson. 1967. A re-evaluation of fossil turtles of the *Chrysemys scripta* group. Tulane Studies Geol., 5: 53-66.

Webb, S. D. 1964. The Alachua Formation. *In* Guidebook, 1964 Field Trip, Soc. Vert. Paleo., Gainesville, Florida, pp. 22-29.

———. 1966. A relict species of the burrowing rodent *Mylagaulus* from the Pliocene of Florida. J. Mammal. 47: 401-412.

———. and Norm Tessman. 1968. A Pliocene vertebrate fauna from low elevation in Manatee County, Florida. Amer. J. Sci. 266: 777-811.

White, T. E. 1941. Additions to the fauna of the Florida Pliocene. Proc. New England Zool. Club, 18: 67-70.

———. 1942. The Lower Miocene mammal fauna of Florida. Bull. Mus. Comp. Zool. 92: 1-49.

Wilson, J. A. 1960. Miocene carnivores, Texas Coastal Plain. J. Paleontol. 34: 983-1000.

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