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Review of Some Carnivora (Mammalia)
From the Thomas Farm Local Fauna
(Hemingfordian: Gilchrist County, Florida)

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ABSTRACT

Species of the carnivore genera *Cynelos* (Amphicyonidae), *Hemicyon* (Ursidae), and *Euoplocyon* (Canidae) are recognized in the medial Hemingfordian Thomas Farm Local Fauna. In addition early Mustelinae are indicated by the ramus referred to *Miomustela*(?) by Olsen. The record of the latter and that of *Hemicyon* and *Euoplocyon* represent the earliest occur- rences of each taxon in North America; all four records constitute the first recognized occurrence of each in eastern North America. The Thomas Farm *Cynelos*, *Hemicyon* and musteline are very closely related to European representatives of these taxa from the early Burdigalian, confirming previous correlations of the Burdigalian Age with at least part of the Hemingfordian "Age."

INTRODUCTION

Since its discovery in 1931, the Thomas Farm Quarry has remained the most productive Terti- ary locality in eastern North America and has yielded the largest sample of Hemingfordian vertebrates from this part of the continent. Various taxa of the local fauna have been de- scribed and complete faunal lists have been pub- lished (Ray, 1957; Olsen, 1962; Patton, 1967) that have established the Thomas Farm Local Fauna as a reference point for Miocene faunal comparisons between eastern and western North America. The recognition of *Cynelos* (Amphicyo- nidae), *Hemicyon* (Ursidae), and *Euoplocyon* (Canidae) in the Thomas Farm Local Fauna con- stitutes a refinement in our knowledge of this critical local fauna.

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INSTITUTIONAL ABBREVIATIONS

AMNH, Department of Vertebrate Paleontology, the American Museum of Natural History

F:AM, Frick Collection, the American Museum of Natural History

MCZ, Museum of Comparative Zoology, Harvard University

MNHN, Museum National d'Histoire Naturelle

SYSTEMATICS

FAMILY AMPHICYONIDAE TROUESSART, 1885

SUBFAMILY AMPHICYONINAE TROUESSART, 1885

GENUS *CYNELOS* JOURDAN, 1862

Cynelos caroniavorus (White, 1942)

Daphaenus caroniavorus White, 1942
Parictis bathygenus White, 1947
Absonodaphoenus bathygenus (White, 1942), Olsen, 1958

Revised Diagnosis. About the size of *C. schlosseri* (Dehm, 1950). M^1 triangular, crown constricted lingual to paracone and metacone; M^2 rectangular approximately 3/4 the width of M^1; M^3 oval, approximately half the width of M^2, with no distinct cusps. P_2-M_1 separated by diastemata approximately equal to half the length of P_3 (P_4-M_1 diastema may be absent). Talonid of M_2 very reduced with an indistinct hypoconid and no entoconid.

Discussion. The species of *D. caroniavorus* and *P. bathygenus* were defined on disparate elements (upper molars and a lower jaw fragment respectively), but Olsen (1958) recognized them as belonging to a single taxon for which he inadvertently used the wrong specific name. Both White and Olsen indicated that this taxon was distinct generically and Olsen formally recognized this in proposing the generic name *Absonodaphoenus* for the Thomas Farm material. In his discussion of the relationships of this form, he made what appears to us to be a prophetic remark in a comparison with the type specimen: "The upper molars of *A. bathygenus* compare well with the general form and structure of those found in *Amphicyon eseri* from the Miocene of Europe, but are not closely allied to any known genera from North America." Although the name "*Amphicyon eseri*" has been used for species of

at least three genera of amphicyonids (see Kuss, 1965), the type may belong to a species of *Cynelos* Jourdan, 1862, the genus to which we believe the Thomas Farm species should be assigned. There seems little doubt that *Absonodaphoenus* is an amphicyonine rather than an amphicynoidontine (as Olsen had concluded) because of its simple, transversely elongate, tribosphenic upper molars, presence of an M^3, strong hypoconid on M_1, and large protoconid on M_2. Its small size invites comparison with *Cynelos* and *Pseudarctos* Schlosser, 1899. It lacks the diagnostic wide, simple premolars, short trigonid, and broad talonid of M_1 and M_2 of *Pseudarctos* and agrees with the more primitive *Cynelos* in having a long, deep jaw with diastemata shorter than half the length of the premolars; elongate slender premolars with variable development of a posterior cusp on P_4; talonids narrower than trigonids on M_1-M_2; M_2 with short trigonid; M^1-M^2 relatively short and wide, often with concave anterior and posterior borders, in which the protocone forms part of a U-shaped crest with the variable present conules.

In his study of the genus, Kuss (1965) restricted *Cynelos* to two species groups that range from Aquitanian through Burdigalian time. Later Ginsburg (1966) relegated two Oligocene species to the genus, each of which appears to represent a member of the two groups present in the early Miocene. *Cynelos caroniavorus* closely resembles the *C. rugosidens* group and particularly the form *C. schlosseri* (Dehm, 1950), known from Burdigalian deposits in the Loire Basin in France (Ginsburg, 1974) and limestone fissure fillings at Wintershof-West, Bavaria (Dehm, 1950). The American and European forms resemble one another closely in size, in the degree of reduction of M^3, the small size of M_2^3 to M_1^1, the small size of P_4 in relationship to M_1, and the lack of defined conules on the upper molars (see data in Kuss, 1965). The Thomas Farm species differs very little from its European relative; in size it falls within the lower range of values for dimensions of the cheek teeth of *C. schlosseri*, but its lower premolars are relatively smaller and more widely spaced. Further material is needed before geography can be overcome as one of the prime considerations in separation of the American form.

Hunt (1972) has previously recognized the presence of *Cynelos* in North America, specifically the *Cynelos lemanensis* group, which ranges from late Arikareean through the medial Hemingfordian. It now appears that species closely allied to the *C. rugosidens* group were also present during part of medial Hemingfordian time in North America.

FAMILY URSIDAE GRAY, 1825

SUBFAMILY HEMICYONINAE FRICK, 1926

GENUS *HEMICYON* LARTET, 1851

Subgenus *Phoberocyon* (Ginsburg, 1955)
Hemicyon (Phoberocyon) johnhenryi
(White, 1947)

Aelurodon johnhenryi White, 1947

Revised Diagnosis. Relatively unreduced, narrow premolars with well-developed posterior accessory cusps on P_2-P_4; maximum width of M_1 across metaconid equal to or slightly exceeded by width of trigonid of M_2; narrow talonids on M_1 and M_2 with large hypoconids and shallow basins; small paraconid present on M_2; protoconid of M_2 higher than metaconid; mandible slender.

Description. Hemicyon johnhenryi from Thomas Farm was described as a new species of *Aelurodon* (White, 1947) using a ramus with lower dentition as the type specimen (MCZ 4059). No upper teeth have been referred to this species. Although the mandible and dentition of *H. johnhenryi* bear a superficial resemblance to that of *Aelurodon*, numerous features differentiate *Hemicyon* and *H. johnhenryi* from *Aelurodon*. These are as follows: (1) The mandible of *Hemicyon* has a premasseteric fossa not found in *Aelurodon* (or any other nonursid carnivore); (2) the lower premolars are much smaller in relation to M_1 than is seen in most *Aelurodon*; P_4, especially, is large and robust in *Aelurodon* in contrast to *Hemicyon*; (3) M_2 is larger, relative to M_1, than in *Aelurodon* (in *Aelurodon* the M_2 is smaller than P_4).

A second specimen of *Hemicyon johnhenryi*, a left ramus with P_1-M_2, is housed in the Frick Collection, the American Museum of Natural History (F:AM 98608, fig. 1). Although unquestionably of the same species, minor differences do exist between this referred specimen and the holotype of *H. johnhenryi* (MCZ 4059), which provide an indication of individual variation within this species. Also, P_1 is missing in the type specimen but present in the referred specimen and can be described for the first time, as can the relative placement and sizes of the incisor alveoli.

The lower incisor alveoli are crowded between the large root of the canine and the very rugose symphyseal suture. They form a triangular configuration with the I_2 root falling behind those of I_1 and I_3. The root of I_1 indicates that it was smaller than the subequal I_2-I_3. The P_1 of *H. johnhenryi* is relatively large and bladelike in appearance. The highest point of the crown is in the anterior part of the enamel crest although no cusp is readily apparent. All the teeth of the referred ramus are smaller and more slender than those of the holotype (table 1). The alveolus for M_3 is also smaller as was presumably M_3. The talonid of M_1 of the holotype has a small entoconid, whereas that of the referred specimen has two equal-sized but small cusps in the position of the entoconid. The protoconid and metaconid of M_2 are lower on the referred specimen than these cusps on the holotype, although the protoconid is the larger cusp as in the latter. The referred ramus appears to be shallower anteriorly than the holotype but this may be due only to breakage in the holotype. In both specimens the anterior edge of the masseteric fossa is bounded by a low ridge that passes posteroventrally toward the edge of the large muscle scar for the masseter medialis on the angular process. The premasseteric fossa is shallow and extends anteriorly to beneath the anterior part of M_2, and then forward as a shallow groove to the position of the mental foramina. The referred ramus of *H. johnhenryi* has two large mental foramina, one below P_2 and one below P_4. On the holotype ramus there are three mental foramina; two smaller foramina beneath P_4 in place of the large single foramen seen on the referred ramus. The condyle of the holotype is much heavier than that of the referred ramus and the height of the ascending ramus is less. The overall impression of the holotype is of a relatively heavier, more massive jaw.
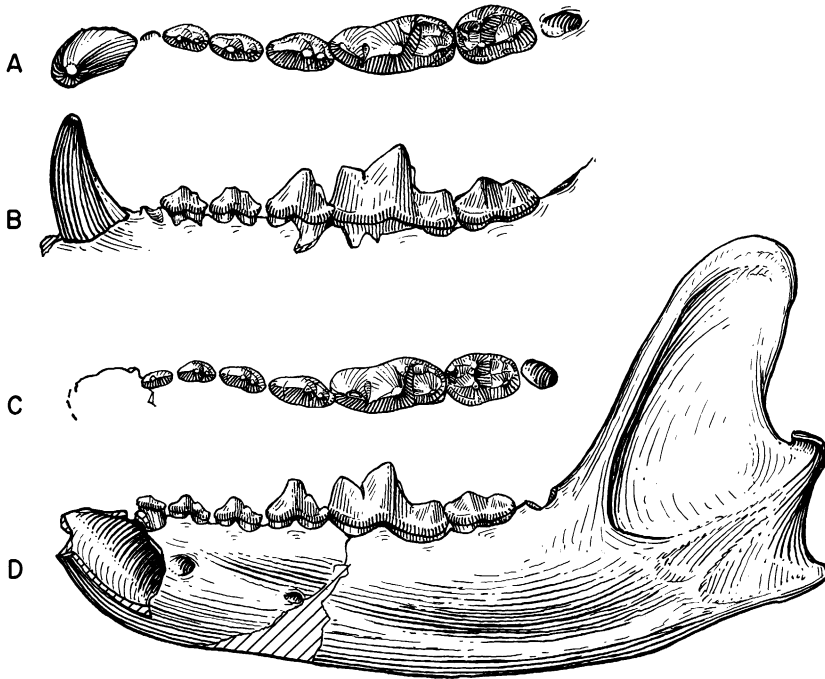
Discussion. Hemicyon johnhenryi is the

FIG. 1. *Hemicyon* (*Phoberocyon*) *johnhenryi* (White, 1947). Holotype, MCZ 4059, right (reversed, drawn from cast), C, P_1 alveolus, P_2-P_4, M_1-M_2, M_3 alveolus. A. Occlusal view. B. Lateral view. Referred specimen, F:AM 98608, left ramus, C alveolus, P_1-P_4, M_1-M_2, M_3 alveolus. C. Occlusal view. D. Lateral view. All ×1/2.

earliest occurring species of *Hemicyon* in North America, and, as might be expected, exhibits numerous features that may be considered primitive for the genus. These serve well to differentiate this species from the other North American species of *Hemicyon* whose features are more characteristic of the genus, i.e., demonstrate a greater emphasis on a massive, bearlike mandible and large, crushing M_1-M_2. The mandible of *Hemicyon johnhenryi* is relatively slender; the masseteric and premasseteric fossae are the shallowest among those known for species of *Hemicyon*. The teeth of *H. johnhenryi* are among the largest known for the species of *Hemicyon* but the mandible is much less deep. The premolar series is not so drastically reduced as it is in the other species nor are diastemata as apparent between them. The talonids of M_1 and M_2 of *H. johnhenryi* are much less basined than in most of the other species as the large hypoconid occupies most of the talonid. The entoconid is small and variable in expression. A small paraconid is retained on M_2.

In Europe where the record of *Hemicyon* extends from the Burdigalian to the Tortonian, species with the suite of morphological characters that typify *H. johnhenryi* are restricted to the Burdigalian. These species are the sole representatives of the genus *Phoberocyon* Ginsburg, 1955 [*P. aurelianensis* (Frick, 1926), and *P. huerzeleri* Ginsburg, 1955] distinguished by its author from *Hemicyon* Lartet, 1851, by the following features: P_3-P_4 with posterior accessory cusps; M_1 long and slender, talonid low and inclined forward; M_2 of the same width as M_1, massive, low, with strong trigonid cusps, including a strong paraconid, protoconid more elevated than metaconid, talonid as in M_1. As Ginsburg (1955, p. 89) pointed out, the species of *Phoberocyon* show a curious mixture of archaic and specialized features, however they are most easily distinguished from the species of *Hemicyon* (and *Plithocyon* Ginsburg, 1955) by primitive features. Consequently, we have chosen to regard *Phoberocyon* as a plesiomorphous sister group to *Hemicyon* and have therefore reduced

this taxon to the rank of a subgenus to show this relationship. We are aware of the fact that a group so distinguished may be paraphyletic, but a far richer record of these rare ursids is needed for useful phylogenetic analysis.

Hemicyon (*P.*) *johnhenryi* is closest in size to *H.* (*P.*) *aurelianensis*, but differs in that the paraconid on M_2 is smaller and there is no sharp groove separating it from the metaconid. Unfortunately, nothing is known of the premolars of *H.* (*P.*) *aurelianensis*, but the smaller *H.* (*P.*) *huerzeleri* has posterior cusps on P_3 and P_4 (but not P_2). *Hemicyon* (*P.*) *huerzeleri* has an M_2 trigonid more nearly resembling *H.* (*P.*) *johnhenryi*. Considering the great range in dental measurements shown by individuals of the sexually dimorphic species of ursids, it is possible that the two European *Phoberocyon* species lie near the extremes of variation for a single species (compare the ranges with comparable dimensions for single taxa of better represented hemicyonines in the data given by Hürzeler, 1944, and Ginsburg, 1955). If this is the case then *H.* (*P.*) *johnhenryi* would be weakly distinguished from the European forms only by having posterior accessory cusps on P_2 as well as P_3-P_4 and perhaps shorter diastemata between the premolars.

Hemicyon (*Phoberocyon*) *johnhenryi* is presently known only from the Thomas Farm deposit, but associated metacarpals IV-V (F:AM 68254) from the Hemingfordian Blick Local Fauna (Gawne, 1975, p. 2) of the Zia Sand records the presence of a long-footed *Hemicyon* in New Mexico that is comparable in size with the limbs expected of *H.* (*P.*) *johnhenryi*.

FAMILY CANIDAE GRAY, 1821

SUBFAMILY BOROPHAGINAE SIMPSON, 1945

GENUS *EUOPLOCYON* MATTHEW, 1924

Euoplocyon spissidens (White, 1947)

Aelurodon spissidens White, 1947
Enhydrocyon spissidens (White), Olsen, 1958

Revised Diagnosis. P_4 more slender than that of *E. praedator* Matthew, 1924. Talonids of M_1 and M_2 are longer and wider than in *E. praedator*. The protoconid and metaconid of M_2 are separate, distinct cusps. The lower tooth row of *E. spissidens* is less curved than that of *E. praedator*.

Discussion. *Euoplocyon spissidens* is known only from lower dentitions. Previous authors have primarily used the size and placement of the premolars, the trenchant talonid, and absence or near absence of a metaconid on M_1 in determining the generic affinities of this species. The

TABLE 1
Comparative Measurements of *Hemicyon johnhenryi* and *Hemicyon aurelianensis*
(Measurements in Millimeters; parentheses indicate an approximate measurement.)

	Hemicyon johnhenryi		*Hemicyon aurelianensis*
	F:AM 98607 (Cast of MCZ 4059, holotype)	F:AM 98608	MNHN 228 (Holotype)[a]
Length from canine to condyle	201.0	(198.0)	—
Depth of ramus between P_2 and P_3	36.6	31.8	—
Depth of ramus between M_2 and M_3	(42.0)	42.5	—
Depth of condyle at center	17.0	11.1	—
P_1 (length × width)	—	8.1 × 4.2	—
P_2 (length × width)	12.4 × 6.5	10.9 × 5.4	—
P_3 (length × width)	14.0 × 6.9	12.9 × 6.0	—
P_4 (length × width)	18.2 × 9.7	16.8 × 8.0	—
M_1 (length × width)	33.6 × 14.3	33.2 × 13.1	35.0 × 13.5
M_2 (length × width)	22.0 × 15.0	19.7 × 13.0	(21.0 × 13.5)
M_3 (alv.) (length × width)	15.0 × 6.9	(11.0 × 6.0)	—

[a]Measurements of M_1 from Hürzeler, 1944, p. 154; M_2 from Ginsburg, 1955, fig. 2.

problems inherent in working with limited material are apparent in the taxonomic history of *E. spissidens*. White (1947) diagnosed the species and referred it to *Aelurocyon*. Olsen (1958), using *Enhydrocyon crassidens* Matthew, 1907, for comparison, noted the less crowded tooth row and the less robust teeth of *Enhydrocyon*, also seen in *E. spissidens*, and the absence of the lingual flexure in the trigonid of M_1 of *Aelurocyon*, in contrast to *E. spissidens*, and transferred "*Aelurocyon*" *spissidens* to *Enhydrocyon* Cope, 1879. Olsen (1958) also noted that the small ridge which occupies the position of the metaconid on M_1 was present in *Enhydrocyon crassidens*, *E. spissidens*, and a referred specimen of *Euoplocyon praedator* (MCZ 17301) but felt that *E. spissidens* did not otherwise closely resemble *Euoplocyon praedator*.[1] For the following reasons, we believe that *Euoplocyon* is the more correct generic assignment for *E. spissidens*: (1) The teeth of *Euoplocyon* are less robust than those of *Enhydrocyon*; (2) P_4 has an anterior accessory cusp which is lacking in *Enhydrocyon*; (3) the talonids of M_1 and M_2 are larger than those of *Enhydrocyon*; (4) the hypoconid of M_1 in *Euoplocyon* is more labially placed and less bladelike, whereas that of *Enhydrocyon* occupies most of the talonid; (5) *Euoplocyon* has a P_1, whereas *Enhydrocyon* often lacks this tooth; and (6) the mandible of *Euoplocyon* increases in depth between P_3 and M_1; the opposite being true in *Enhydrocyon*.

Euoplocyon spissidens differs from *E. praedator*, the only other described species of *Euoplocyon*, in the reasons stated in the diagnosis. The referred ramus MCZ 7310 is compared in figure 2 with the type of *E. praedator* (here figured for the first time). The most obvious differences are the distinct cusps on the trigonid of M_2 in *E. spissidens*. In *E. praedator* the trigonid of M_2 is composed of a single crest in which the protoconid and metaconid cannot be differentiated.

The trenchant talonid and the absence of a metaconid on M_1 led Matthew (1924) to relate

Euoplocyon to the Simocyoninae Zittel, 1893. These features, however, are widely encountered among carnivores and for this and other reasons the Simocyoninae can be shown to be a highly polyphyletic group whose members can be allocated to the Amphicyonidae, Ursidae, and Canidae. The unusual presence of anterior and posterior cingular cusps and a posterior accessory cusp on all four premolars, used by Matthew (1924) in his diagnosis of *E. praedator*, are found only in the borophagine canids *Tomarctus* Cope, 1873, *Prohyaena* Schlosser, 1887, and *Aelurodon* Leidy, 1858. As these three genera have a number of features in common (such as a premaxillary-frontal bone contact, an enlarged I^3 with accessory cusps, a parastyle on P^4) and probably form a natural group, *Euoplocyon* could perhaps be better placed with these genera in the Borophaginae Simpson, 1945.

Euoplocyon is known from two species: *Euoplocyon spissidens* from the Thomas Farm Local Fauna (medial Hemingfordian) and *E. praedator* from the Lower Snake Creek Fauna (early Barstovian). Gazin (1932) referred a single M_1 from the Skull Spring Fauna (early Barstovian) of Oregon to ?*Euoplocyon*. This latter identification remains uncertain, but the genus is nonetheless widespread over North America.

FAMILY MUSTELIDAE SWAINSON, 1835

SUBFAMILY MUSTELINAE SWAINSON, 1835

Miomustela(?) sp. Olsen, 1956

The small mustelid referred to *Miomustela*(?)sp. by Olsen (1956) appears to represent a third carnivore from Thomas Farm belonging to a genus also present in the Old World Miocene. Olsen's queried reference to *Miomustela* Hall, 1930, must be rejected on the grounds of the distinctly different morphology of the carnassial and the large size of the crowded premolars as indicated by their alveoli. The carnassial has a very high compressed trigonid with a small low metaconid and a narrow trenchant talonid. The presence of an M_1 metaconid differentiates the Thomas Farm species from contemporary *Paleogale* Meyer, 1846. Comparable forms are known from the Runningwater Formation of Nebraska and among the various species assigned to the genus *Plesictis* Pomel, 1846, in Aquitanian and Burdigalian faunas of Europe. The latter differ so

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[1] The presence of a ridge in the position of the metaconid appears to be variable in *Euoplocyon*. The ridge is totally absent in the type specimen of *E. praedator* (AMNH 18261) but present as a different ridge in other specimens (F:AM 27314, 27315) referred to that species.
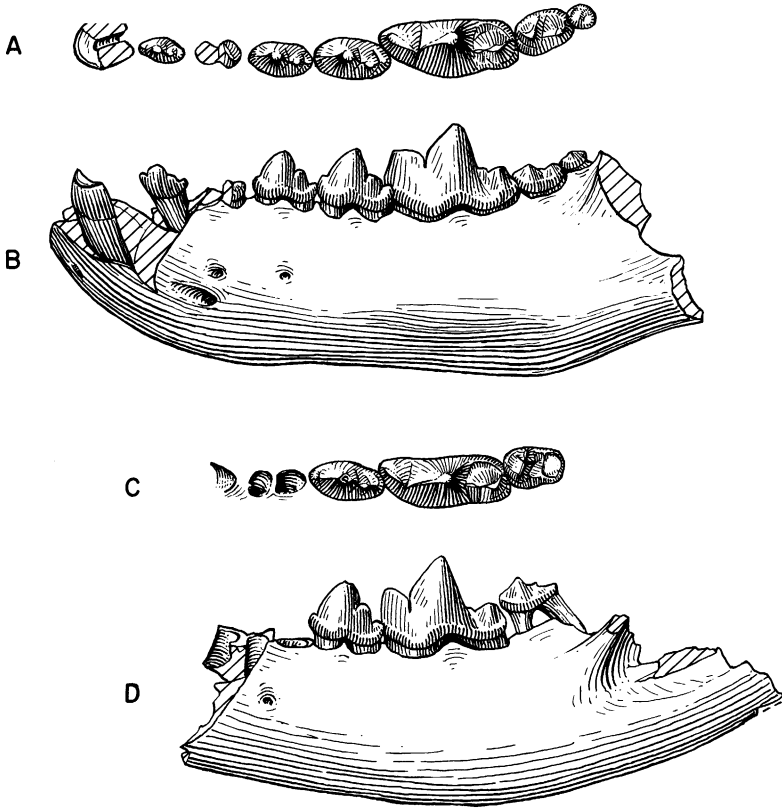
FIG. 2. *Euoplocyon praedator* Matthew, 1924. Holotype, AMNH 18261, left ramus, C broken, P_1, P_2 broken, P_3-P_4, M_1-M_3. A. Occlusal view. B. Lateral view. *E. spissidens* (White, 1947), referred, MCZ 7310, left ramus, P_2-P_3 alveoli, P_4, M_1-M_2. C. Occlusal view. D. Lateral view. All natural size.

TABLE 2

Comparative Measurements of *Euoplocyon spissidens* and *Euoplocyon praedator*

(Measurements are in Millimeters; parentheses indicate an approximate measurement.)

| | *Euoplocyon spissidens* | | *Euoplocyon praedator* |
	MCZ 4246[a] Type	MCZ 7310	AMNH 18261 Type
Depth of ramus at P_3	19.0	19.4	21.7
Depth of ramus at M_2	21.0	22.5	22.9
P_1 (length × width)	—	—	5.9 × 3.7
P_2 (length × width)	—	—	length alveolus (6)
P_3 (length × width)	—	Length alveolus (8)	8.4 × 4.8
P_4 (length × width)	10.0 × 5.0	10.0 × 5.2	10.0 × 5.7
M_1 (length × width)	17.0 × 7.0	17.0 × 7.0	18.2 × 7.7
M_2 (length × width)	—	7.8 × 5.1	6.8 × 5.3
M_3 (length × width)	—	—	3.4 × 3.2

[a]Measurements from White, 1947, p. 498.

radically from the holotype of the genotypic species (*P. genettoides* Pomel, 1846) that reference to that genus seems as unlikely as reference to *Miomustela*. Hough (1948) and de Beaumont (1968) have shown that *P. genettoides*, and the closely related *P. lemanensis* Pomel, 1853, are procyonids although musteloid in dental adaptation. The Thomas Farm form is closest to "*P.*" *julieni* Viret, 1929, and "*P.*" *sicaulensis* Viret, 1929, in size (see Dehm, 1950, fig. 78) and morphology. "*Plesictis*" *julieni* is known from a skull (the type, Viret, 1929) which shows the inflated bullae with strongly forward directed meati, and widely separated paroccipital and mastoid processes typical of mustelids and contrasting with contemporary *Plesictis*. These features and the parasagittal crests are matched in specimens from the Runningwater Formation. Mustelids such as these have many of the features of the later Cenozoic and living Mustelinae, and possibly represent the earliest occurrences of that subfamily in the New World.

SUMMARY

The presence of the Holarctic carnivore genera *Cynelos* and *Hemicyon* in the Thomas Farm Local Fauna and their very close morphological correspondence with European counterparts yields further data on the intercontinental correlation of these early Miocene mammal faunas. As the comparisons detailed above reveal, *Cynelos caroniavorus* and *Hemicyon* (*Phoberocyon*) *johnhenryi* closely resemble the exclusively Burdigalian *C. schlosseri* and *H.* (*P.*) *aurelianensis* respectively. These European species occur together in the Sables de l'Orléanais of the Loire Basin of France. *Cynelos schlosseri* (type) and *H.* (*P.*) *huerzeleri* [closely related to *H.* (*P.*) *aurelianensis*] occur in the fissure fills at Wintershof-West in Bavaria. Both assemblages are regarded as early Burdigalian Age following the concept of that Age held by European paleomammalogists.

Euoplocyon is recognized in the Thomas Farm Local Fauna extending both the temporal and geographic ranges of this genus from early Barstovian faunas in Oregon and Nebraska into the Hemingfordian of Florida.

The identification of *Miomustela*(?)sp. by Olsen (1956) is rejected. The mustelid in question is apparently a true musteline related to species that are now incorrectly included within the procyonid genus *Plesictis*. Such musteline species are known from Aquitanian and Burdigalian faunas of Europe and Hemingfordian faunas of North America.

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