Hyaeodonidae (Creodonta, Mammalia) from the Early Eocene Four Mile Fauna and Their Biostratigraphic Implications

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ABSTRACT

Hyaeodonid creodonts from the Four Mile Local Fauna of northwestern Colorado are re-examined in light of recent work in the Bighorn and Clarks Fork Basins. Prototomus phobos, P. martis, P. secundarius, P. robustus, P. deimos, Arfia opisthotoma, A. shoshoniensis, Prolimnocyon haematus, and Acarictis ryanii are now known from Four Mile. Acarictis, previously known only from lower teeth, is now known from an upper molar. These taxa suggest that the Four Mile Fauna is early Wasatchian in age and corroborate a Wa2 or Wa3 biochronologic age assignment. The species Prototomus secundarius and P. robustus initially suggest a Wa3 age for the Sand Quarry locality, but evidence provided by Gunnell (1989) suggests that this locality is actually Wa2 or Wa3 in age and the presence of these two species at Sand Quarry represents a biostratigraphic range extension. It is possible that the two species, which are significantly larger than other species of Prototomus, may have been in competition or ecologically partitioned from the similar sized species Arfia shoshoniensis and A. opisthotoma. The former two species do not co-occur with the latter two species at any locality. The presence of Arfia in Wa2 and Wa3 at localities in the Bighorn Basin may explain the absence of Prototomus robustus and P. secundarius there.

INTRODUCTION

The Four Mile Local Fauna is one of the largest early Wasatchian faunas outside the classic Wyoming and New Mexican Early Eocene basins. The fauna comes from exposures of the Wasatch Formation along Four Mile and Timberlake Creeks in Moffat County, northwest Colorado. At one time the area was considered unfossiliferous, but collecting by screenwashing resulted in a diverse collection largely composed of isolated teeth from 30 localities. McKenna (1954a, 1954b, 1955, 1960) studied the Four Mile fauna and assigned it an early Graybullian age, roughly equivalent to the age of the Sand Coulee beds in Bighorn Basin, Wyoming. More detailed information about the location of Four Mile sites, the history of work there, and a description of the entire Four Mile Fauna can be found in the papers by McKenna cited above, particularly 1960. The material McKenna (1960) described is housed in the University of California Museum of Paleontology and there is another, larger but undescribed collection from Four Mile housed in the American Museum of Natural History. Several authors have included material from the Four Mile Fauna in their revisions of specific taxonomic groups since McKenna’s work. Szalay (1969) analyzed microsopicids from Four Mile. Bown (1979) compared the mammalian diversity of the Four Mile Fauna with that of the Sand Creek Facies of the Willwood Formation. Krause (1982) described Four Mile multituberculates. More recently, Gunnell (1989) incuded Four Mile material in his study of Microsyopoidae (Mammalia, ?Primates) and Thewissen (1990) included Phenacodontidae (Mammalia, Condylarthra). Both of these authors also discussed the age of Four Mile localities. This topic is examined below.

The purpose of the present paper is, primarily, to revise the hyaeodonid creodonts from Four Mile and, secondarily, to use the creodonts to test the biostratigraphic ranges of hyaeodonids in the Clarks Fork and Bighorn Basins (e.g. Gingerich, 1983) and to provisionally assign Four Mile localities to specific Wasatchian biochronologic zones.
All hyaenodontid specimens from the Four Mile were referred by McKenna (1960) to either Sinopa sp. or to Protolomus viverrinus. He stated on page 92 that

...eventually it will be possible to treat Sinopa in much the same way as Simpson's (1943) revision of Granger's vertical taxonomy of Ectocyon, but at the present nothing is known of variation in Sinopa... Eventually, therefore, it may develop that the Four Mile species of Sinopa belongs to or is most closely related to an undescribed horizontal taxon from the early Wasatchian...

Since the time of McKenna's statement, early Wasatchian creodonts (Gingerich and Deutsch, 1989) have been extensively revised and many new species described. It is now possible to assign Four Mile creodonts to nine different species in four genera.

MATERIALS AND METHODS

Four Mile collections in the University of California Museum of Paleontology and the American Museum of Natural History were examined for this paper. The UCMP collection was previously described by McKenna (1960). The AMNH collection has not been systematically described and is much larger than the UCMP collection, although fewer localities are represented in it. Both of these collections were searched for material that could unambiguously be referred to hyaenodontid species. Some material, such as some isolated premolars, canines, and molar trigonids, is impossible to accurately assign to a species, or even an order. These specimens are not treated here.

Specimens were identified based on descriptions in the literature, particularly Gingerich and Deutsch (1989) and by comparison with material in the University of Michigan Museum of Paleontology from the Bighorn and Clarks Fork Basins. Gingerich and Deutsch primarily described and figured lower dentitions of hyaenodontid species, but there is referred material in the UMMP of other parts of the dentition that has been unambiguously assigned to species described from lower molars. In many cases, the upper dentitions are more easily diagnosed than lowers based on purely morphological considerations. Lower dentitions, especially of species of Prototomus, can usually only be distinguished by their relative sizes. The identifications in this paper were based on careful comparison with the referred material except where indicated below. All measurements were made with Mitutoyo digital calipers. The measurements used are the same as those described in Figure 1 of Gingerich and Deutsch, 1989.

The following localities have produced hyaenodontid specimens and are discussed in this paper: East Alheit Pocket, UCMP locality V67181, S25, T12N, R92W. West Alheit Pocket, UCMP locality V5357, S25, T12N, R92W. Despair Quarry, UCMP locality V5352, S12, T11N, R91W. McKenna's 5, UCMP locality V5353, S12, T11N, R91W. Sand Quarry, UCMP locality V5421, S24, T12N, R91W. All of the localities are in Moffat County, Colorado.

The following abbreviations are used in this paper:

AMNH=American Museum of Natural History
UCMP=University of California Museum of Paleontology
UM=University of Michigan Museum of Paleontology
L=length
W=width
TRL=trigonid length
TRW=trigonid width

SYSTEMATIC PALEONTOLOGY

CREODONTA Cope, 1875a
HYAENODONTIDAE Leidy, 1869
PROVIVERRINAE Schlosser, 1886

Acarictis Gingerich and Deutsch, 1989
Cf. Acarictis ryani Gingerich and Deutsch, 1989

Referred specimen. West Alheit Pocket: UCMP 44302, right M1.

Description. UCMP 44302 is a right M1 (Fig. 1, a-b) that has a pronounced metastylar blade with a very distinct carnassial notch in it. The blade is relatively longer than that found in Didelphodus, although it is shorter than those found in more derived hyaenodonts such as Prototomus. The paracone and metacone are fused at the base and the metacone is somewhat shorter than the paracone. The stylar shelf is fairly narrow and has a labial cingulum running from the anterior point of the parastyle to the posterior point of the metastyle, and has tiny cuspsules along its length. The parastyle is quite small and projects anteriorly. The postmetaconule crista
extends out onto the metastylar blade along the base of the tooth. There are poorly developed pre-and postcingulalae at the base of the protocone. The tooth is 3.6 mm long and 3.5 mm wide.

Discussion. Upper teeth of *Acaritis ryani* were previously unknown. This tooth can be referred to *Hyaenodontidae* because of the elongate metastylar blade and basally fused paracone and metacone. The fact that the metastylar blade is relatively shorter than in other *Hyaenodontidae* such as *Prototomus* matches expectations for *A. ryani* since the prevallid blade, which is the lower complement of the metastylar blade, is relatively short in this species. This and the size of the tooth, which is the size expected for upper molars of *A. ryani*, justify the assignment of this specimen.

*Acaritis ryani* was previously known from the middle and late Sanouleean subage of the Wasatchian Land Mammal Age from the Clarks Fork Basin, Wyoming (Gingerich and Deutsch, 1989). This specimen represents an extension in the known geographic range of this species.

*Arfia* Van Valen, 1965

*Arfia opisthotoma* (Matthew, 1901)

**Referred specimens.** East Alheit Pocket: UCMP 44346, right P₄. AMNH 129320, right M₃. AMNH 129328, left M₃ trigonid. AMNH 129330, right M₂ trigonid.

**Description.** UCMP 44346 is a fragmentary lower right fourth premolar. The anterior part is broken and the apex of the main cusp is worn. It has a width of 4.9 mm and an unbroken length of slightly more than 8.1 mm. The enamel of the tooth is finely crenulated. AMNH 129320 is a right M₃ that has a finely crenulated surface characteristic of *Arfia* and a trigonid that is relatively longer than found in *Arfia shoshoniensis*. The specimen has a length of 10.8 mm, a width of 5.9 mm, and a trigonid length of 6.7 mm. AMNH 129330 is a trigonid of right M₂. It has a length of 4.8 mm and a width of 4.9 mm.

**Discussion.** *Arfia opisthotoma* is primarily known from the Bighorn and Clarks Fork Basins, where it occurs only in the Wa₃ interval of the Wasatchian Land Mammal Age. Gingerich and Deutsch (1989) maintained that *Arfia opisthotoma* is distinct from *A. shoshoniensis* based on the size and shape of the trigonid and carnassial blade on M² and M₃. This difference is observable in specimens from Four Mile, but its exact significance is uncertain. Gingerich and Deutsch (1989) provided measurements of the dentitions of both species and these were used, where they were diagnostic, to assign Four Mile specimens to a particular species.

*Arfia shoshoniensis* (Matthew, 1915)

**Referred specimen.** East Alheit Pocket AMNH 129327, left M₃.

**Description.** This specimen is a trigonid of the lower left M₃. It is 6.0 mm long and 5.2 mm wide.

**Discussion.** See discussion of *Arfia opisthotoma* for the criteria used to assign specimens of *Arfia* to particular species. In the Bighorn and Clarks Fork Basins of Wyoming, *Arfia shoshoniensis* is known primarily from the Wa₂ zone of the Wasatchian Land Mammal Age. It is also known, however, from the very beginning of the Wa₃ and the end of the Wa₁ zones. In Wyoming, it is not known to co-occur with *Arfia opisthotoma*, but in East Alheit Pocket of Four Mile both species are present. This raises the possibility that the two species are a single species lineage and a transitional population with both variants lived in the Four Mile area. This might indicate that East Alheit Quarry represents a transitional time period in the early part of Wa₃. Due to the small sample of *Arfia* at Four Mile and the fragmentary nature of the specimens, a more definitive statement on this problem is impossible.

*Arfia* sp.

**Referred specimens.** East Alheit Pocket: AMNH 129326, left P₃; AMNH 129336, left M¹ fragment.

**Description.** AMNH 129326 is a left P₃ that is 8.7 mm long and 4.2 mm wide. It has a large posterior basin, but no anterior cusp. Its surface has the distinctive crenulated enamel surface of *Arfia*. AMNH 129336 is a fragment of a left M¹. It is missing the parasymphal region and most of the metastyle. It also has the finely crenulated surface characteristic of *Arfia*.

**Discussion.** These two specimens are definitely referable to *Arfia* based on their morphology and enamel texture, but they do not contain any of the subtle characteristics necessary to refer them to either *A. opisthotoma* or *A. shoshoniensis*. They do, however, belong to one of
these two species because their size rules out other species of *Arfia*, such as *A. zele* or *A. junnei.

*Protoctomus* Cope, 1874

*Protoctomus deimos* Gingerich and Deutsch, 1989

**Referred specimens.** Despair Quarry: UCMP 46642, right M1. East Alheit Pocket: AMNH 129324, right M2 fragment; AMNH 129325, right M1; AMNH 129338, left M1.

**Description.** UCMP 46642 is an isolated right M1 (Fig. 1, b-c). The paracone and metacone are fused at the base and the latter is slightly shorter than the former. The parastyle is relatively small compared to *Protoctomus secundarius* or *P. robustus*. There is a cingulum that runs from the anterior corner of the paracone to the posterior corner of the metastyle. The conules are both well developed and the postmetaconule cristae run onto the metastylar blade along its base. There are poorly developed pre- and postcingulae at the base of the protocone. The tooth is 4.6 mm long and 5.0 mm wide. AMNH 129325 is a right M1 like UCMP 46642 and is 4.3 mm long and 4.9 mm wide. AMNH 129338 is a left M1 4.9 mm long and 5.5 mm wide. AMNH 129324 is a fragment of a right M2 that is missing the protocone region and is badly corroded. It has a moderately long metastyle; shorter than that of *Protoctomus phobos*, *P. martis* or *P. robustus*, but longer than that of *P. secundarius* or *Prolimnocyon*. The size of the metastyle and its small size make this specimen referable to *Protoctomus deimos*.

**Discussion.** The three M1's from Four Mile agree almost perfectly in general morphology with an M1 referred to *P. deimos* (UM 79602), except that the pre- and postcingulae are better developed and have tiny cuspules along their length on the Michigan specimen. These cingulae are less developed on the Four Mile specimens and do not have cuspules. There is a small difference in the length/width ratio of the tooth (0.88-0.92 in the Four Mile specimens and 0.86-0.88 in the Michigan specimens published by Gingerich and Deutsch, 1989), but this is so slight that it may simply be a result of either the small size of the Michigan M1 sample (n=2) or of measurement error. It seems unlikely that the Four Mile material represents a new species. More likely, it is a geographic or stratigraphic variant of *P. deimos* from Wyoming. UCMP 46642 specimen was referred to *Protoctomus viverrinus* by McKenna (1960).

This species was previously known from the Bighorn and Clarks Fork Basins. *P. deimos* is known from the Wa1 and early Wa3 zones of the Wasatchian Land Mammal Age of the Bighorn and Clarks Fork Basins.

There is some controversy over the genus *Protoctomus* which is summarized in Gingerich and Deutsch, 1989. For practical reasons I have chosen to follow these authors in their usage of *Protoctomus* because it contains a group of closely related and morphologically similar species, all of which are distinguishable from other contemporary genera. The genus may prove to be paraphyletic on further analysis, but this does not necessarily negate its usefulness. Gingerich and Deutsch (1989) provided a comprehensive review, diagnosis, and discussion of the genus and its included species, and the reader is referred to that paper for more detailed information. In spite of the fact that the genus and all of its included species are readily distinguishable from other Wasatchian genera if relatively complete material is available, individual teeth may be more difficult to assign. Upper molars are the most distinctive and accurately assigned teeth. Lower molars are often distinguishable based on size using the measurements published by Gingerich and Deutsch (1989), but there is some overlap between small species of *Protoctomus* and *Prolimnocyon*. Anterior premolars are especially difficult to distinguish, not only between genera, but between orders (e.g. Carnivora) as well. Only those specimens that can be confidently assigned to a species are described in this paper.

*Protoctomus phobos* Gingerich and Deutsch, 1989

**Referred specimens.** East Alheit Pocket: AMNH 129332, left M1 fragment. McKenna’s 5: UCMP 43957, left and right dentary fragments.

**Description.** AMNH 129332 is a fragment of a left M1 missing the protocone area. It has a very short metastyle and narrow stylar shelf characteristic of *Protoctomus phobos*. It is 6.3 mm long. UCMP 43957 consists of the posterior portions of both the left and right dentaries of a single individual. The left is crushed and edentulous, but has the dentary condyle preserved. The right dentary contains the talonid of M1 and M2.3. The tips of the protoconids are broken on the last two molars, but they are otherwise relatively unworn. Measurements are presented in Table 1.
TABLE 1: Measurements of Prototomus phobos, UCMP 43957 (in mm)

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Discussion. UCMP 43957 was figured by McKenna (1960, p. 92) as Sinopa sp., but it can now be referred to Prototomus phobos. This species was previously known only from the Bighorn and Clarks Fork Basins during the Wa₁-Wa₃ zones.

Prototomus martis Gingerich and Deutsch, 1989

Referred specimens. Despair Quarry: AMNH 129342, left P₂₄, M₁ trigonid and right M₂₃; AMNH 129345, right M₂. East Alieht Pocket: AMNH 129329, right M₁; AMNH 129334, right M¹ fragment; AMNH 129335, right M₁ trigonid; AMNH 129341, right P₄. West Alieht Pocket: UCMP 44304, fragment of left M².

Description. AMNH 129342 is a fragmentary specimen with the left P₂₄ and M₁ trigonid and right M₂₃ preserved. The left P₂ is 5.4 mm long and 2.6 mm wide. P₃ is 6.3 mm by 2.9 mm. P₄ is 7.8 mm by 3.3 mm. The right M₂ is 7.4 mm long and 4.7 mm wide. AMNH 129329 and 129334 are both right M¹s. The former is 6.5 mm long and 7.1 mm wide and exhibits significant postmortem wear. The latter is only a fragment of the metastyle with the paracone and metacone attached. UCMP 44304 is a left M² with the protocone broken off. The paracone and metacone are fused at the base and the metacone is slightly shorter than the paracone, as is the case with all species of Prototomus. The paraestyle is larger than in P. deimos, but smaller than P. secundarius or P. robustus. The postmetaconule cristal extends onto the metastyle along its base, also as in other Prototomus species. The labial cingulum begins at the anterior corner of the paraestyle, but does not continue all the way to the posterior corner of the metastyle. Instead it tapers out and ends about 1.5 mm anterior to the corner of the metastyle. The tooth is 6.9 mm long. Its width cannot be measured due to the breakage of the protocone.

Discussion. This species is the most abundant hyaenodontid species in the Four Mile Fauna based on specimen counts. There is a minimum number of five individuals represented. UCMP 44304 was referred to Sinopa sp. by McKenna (1960). The previously known geographic range of Prototomus martis was limited to the Bighorn and Clarks Fork Basins, where it is known from the Wa₂ and Wa₃ zones of the Wasatchian Land Mammal Age.

Prototomus secundarius Cope, 1875b

Referred specimen. Sand Quarry: AMNH 80036, left M¹.

Description. This specimen is a left M¹ with a length of 6.7 mm and a width of 7.1 mm (Fig. 1, e-f). It has a relatively short paraestyle and a closely appressed metacone and paracone.

Discussion. This specimen is approximately the same size as Prototomus martis, but differs from that species in having a short paraestyle. This species was previously known from Wa₅ and Wa₆.

Prototomus robustus (Matthew, 1915)

Referred specimen. Sand Quarry: UCMP 44839, right M².

Description. This is a large right M² with a partially broken protocone (Fig. 1, g-h). It is 7.5 mm long and approximately 9 mm wide. The paracone and metacone are fused at the base and the metacone is the shorter of the two cusps. The paraestyle is very large, approaching the size of that found in Triemnodon. The labial cingulum ends posterior to the end of the metaestyle as in P. martis.

Discussion. This specimen was referred to Sinopa sp. by McKenna (1960). Prototomus robustus is the largest species of Prototomus and was previously known from only the Bighorn and Clarks Fork Basins, where it occurs in zones Wa₄ and Wa₅ of the Wasatchian Land Mammal Age.

LIMNOCYONINAE Wortman, 1902

Prolimnocyon Matthew, 1915
Prolimnocyon haematus Gingerich and Deutsch, 1989

Referred specimens. Despair Quarry: AMNH 129343, left M¹. East Alieht Pocket: AMNH 129322, left P₄.

Description. AMNH 129343 is a left M¹ that is missing part of the paraestyle. It is 5.0 mm wide and differs from Prototomus deimos, which is approximately the same size, in having a more concave ectoflexus and a relatively longer metastyle. AMNH 129322 is a left P₄ that is 4.8 mm long and 2.2 mm wide. It has a small anterior accessory cusp and a large talonid with two lateral
cusps. The main cusp is very tall and is more anteroposteriorly symmetrical than lower fourth premolars of other Wasatchian hyaenodontids.

Discussion. This species was previously known from the late Wa$_1$ through the early Wa$_3$ biochronologic zones in the Bighorn and Clarks Fork Basins.

THE FOUR MILE FAUNA AND WASATCHIAN BIOSTRATIGRAPHIC ZONATION

The Wasatchian is one of the most homogenous and easily recognizable of all of the Paleogene North American Land Mammal Ages. It has historically been divided into the Graybullian, Lysitean, and Lostcabinian subages based on faunas from Wyoming. Work in the last few decades in the Bighorn and Clarks Fork Basins of Wyoming has resulted in a large collection of mammals with tight stratigraphic control which have been used as a base for further subdivision of the Wasatchian into eight biochronologic zones. Gingerich and Simon's (1977) initially proposed a subdivision of five zones based on species of the adapid primate Cantius. Gingerich (1983) proposed a refined subdivision of seven zones (Wa$_1$-Wa$_7$) based on adapids, perissodactyls, and artiodactyls, and later (Gingerich, 1989) added an eighth zone (Wa$_8$). These zones were reviewed and refined by Gunnell (1989).

The Wyoming zonations provide a basic hypothesis of biostratigraphic ranges and age determinations for the Wasatchian Land Mammal Age. Most of the localities in the Bighorn and Clarks Fork Basins have careful stratigraphic control and have been well sampled and studied. The biochronologic zones are delimited by the ranges of common groups in the Wyoming faunas: primates, perissodactyls, artiodactyls, and carnivores. Other less common groups have known biochronologic ranges in the Bighorn and Clarks Fork Basins within these zonations.

Gingerich and Deutsch (1989), in their review of hyaenodontid systematics, summarized the ranges of hyaenodontid species in the Wyoming sections. The biochronologic ranges of several hyaenodontid species from the Clarks Fork and Bighorn Basins are summarized on the left side of Figure 2. These ranges form a hypothesis that can be tested by comparing the distribution of hyaenodontid species in Four Mile localities. There is no stratigraphic control at Four Mile because the localities are isolated and there is extensive faulting in the region (McKenna, 1960 and pers. comm.). The individual Four Mile localities are not thought to represent extensive periods of time, however, because they occur in localized concentrations from very thin rock units. Even though the Four Mile localities cannot be arranged superpositionally, they may serve as a test of the Wyoming biochronologic ranges because species that do not co-occur in one zone in the Bighorn and Clarks Fork Basins may co-occur in single Four Mile localities.

The five hyaenodontid bearing localities in the Four Mile have the following distribution of species:

Despair Quarry: Prototomus deimos, P. martis, Prolimnocyton haematus.

McKenna’s 5: Prototomus phobos.

West Alheit Pocket: Prototomus martis, Acarictis ryani.

Sand Quarry: Prototomus secundarius, P. robustus.

East Alheit Pocket: Arfia shoshoniensis, A. opisthotoma, Prototomus deimos, P. martis, P. phobos, Prolimnocyton haematus.

The three species from Despair Quarry are all known from the early part of Wa$_3$ in the Bighorn and Clarks Fork Basins. Both Prototomus martis and Prolimnocyton haematus are known from Wa$_2$ as well. Prototomus deimos is not known from Wa$_2$ in Wyoming, but it is known from Wa$_1$ and Wa$_3$. This suggests that it is likely to have lived during Wa$_2$, but has not been sampled or did not live in the Bighorn or Clarks Fork Basin areas. A correlation of Despair Quarry with Wa$_2$ or early Wa$_3$ zones would be consistent with the hyaenodontids found there (Fig. 2).

The McKenna’s 5 locality has produced only a single species, Prototomus phobos. Falsification of Wyoming ranges is impossible if only one species is present. A correlation of this locality with Wa$_1$, Wa$_2$, or Wa$_3$ would be consistent with this specimen (Fig. 2).

West Alheit Pocket has produced the species Prototomus martis and Acarictis ryani. These species are both present during the Wa$_2$ biochronologic zone in the Bighorn and Clarks Fork Basins. A correlation of West Alheit with this zone is consistent with known hyaenodontid biostratigraphic ranges (Fig. 2).

Sand Quarry has yielded Prototomus secundarius and P. robustus. These two species co-occur during the late part of the Wa$_5$ zone in Bighorn and Clarks Fork Basins. This is inconsistent with previous age assessments of the
previously assessed age of Sand Quarry as discussed below. The hyaenodontids by themselves suggest a Wa3 age for this locality (Fig. 2), but this is not advocated in this paper for reasons discussed below.

East Alheid Pocket has produced specimens of *Arfia shoshoniensis*, *A. opisthotoma*, *Prototomus deimos*, *P. martis*, *P. phobos* and *Protomynogyn haematus*. This locality has by far the greatest hyaenodontid diversity at Four Mile. All of these species except *Arfia opisthotoma* occur in the early part of Wa3. The two species of *Arfia* are not known to co-occur anywhere in the Bighorn or Clarks Fork Basins so their co-occurrence in the East Alheid Pocket locality is anomalous. The two species are often difficult to distinguish given only isolated teeth, but the third lower molars are quite distinctive in that *A. shoshoniensis* has a relatively shorter trigonid than *A. opisthotoma* (Gingerich and Deutch, 1989). The East Alheid material contains two lower third molars that clearly indicate the presence of both species as they are currently recognized. This co-occurrence has several possible explanations. The first is that the locality is time transgressive and spans the ranges of the two species. This is unlikely given that the locality is from a localized deposit in a thin stratigraphic unit. The second possibility is that the stratigraphic ranges from the Wyoming sections are incomplete. If that is the case, the most parsimonious explanation is that the range of *Arfia opisthotoma* should be extended down to overlap with that of *A. shoshoniensis*. This is because the other three species, *Arfia shoshoniensis*, *Prototomus deimos* and *Protomynogyn haematus* all have last occurrences in the early Wa3 zone and all three would have to be extended upward to overlap with the known range of *Arfia opisthotoma*. Given the lack of other information, the extension of a single range would seem more appropriate than an extension of three ranges. A third possible explanation is that the distinction between *Arfia shoshoniensis* and *A. opisthotoma* is artificial. The two species are approximately the same size and may represent an evolutionary continuum. The Four Mile sample may be intermediate to the Wyoming samples and may contain a transitional population where the two forms were both present. Given the small sample of material from Four Mile and its incomplete nature it is impossible to choose between these alternative explanations. An early Wa3 age assignment for this locality is most probable based on the available information (Fig. 2).

Several authors have considered the age of the Four Mile localities since McKenna's work. Szalay (1969) suggested that East Alheid Pocket might be older than other Four Mile localities based on his analysis of microsyopsids. Gunnell's (1989) reanalysis of microsyopsids did not substantiate this observation and neither do the hyaenodontids. Krause (1982) stated that the multituberculate fauna suggests an ecologic or temporal difference between Despair and Kent Quarries and other Four Mile localities. There are no hyaenodontids from Kent Quarry, but those from Despair Quarry suggest a similar age to West Alheid and East Alheid and do not suggest any ecologic differences.

Gunnell (1989) stated that Anthill Quarry, Kent Quarry, Despair Quarry, East Alheid, West Alheid, Sand Quarry, Timberlake Creek, and Timberlake Quarry have ages corresponding roughly to the boundary between Wa2 and Wa3. Thewissen (1990) corroborated this age using phenacomodontids. There are no hyaenodontids from Anthill Quarry, Kent Quarry, Timberlake Creek, or Timberlake Quarry. The hyaenodontids present in Despair Quarry, East Alheid Pocket, and West Alheid Pocket corroborate Gunnell's assessment except for the presence of *Arfia opisthotoma* in East Alheid noted above. The two hyaenodontid species present in Sand Quarry (*Prototomus robustus* and *P. secundarius*) are not consistent with a Wa2 or Wa3 biochronologic age. These two species only co-occur in the late Wa5 zone and neither occurs in Wa2 or Wa3. Both Four Mile species are represented by very diagnostic specimens and neither species is readily confusable with earlier hyaenodontid species. Since these species are significantly larger than other species of *Prototomus* and are easily distinguishable from other large hyaenodontids like *Arfia* it seems unlikely that they would have been missed or improperly identified in the Bighorn and Clarks Fork Basin collections. This suggests either that Sand Quarry has a later age than previously thought or that these two species had a longer stratigraphic range than was previously thought based solely on the Bighorn and Clarks Fork Basin deposits and there was a geographic or ecologic factor influencing the distribution of these species so they appeared later in the Wyoming sections than at Four Mile. The first possibility is unlikely because Gunnell based his age assessment on nine different species, all of which are fairly common both at Four Mile and in the Bighorn and Clarks Fork Basins.
It seems more likely that the geographic distribution of these two species was controlled in some way, perhaps by competition with *Arfia*. *Prototomus secundarius* and *P. robustus* are both about the same size as *Arfia shoshoniensis* and *A. opisthotoma* and the former two species do not have a known co-occurrence with the latter two, either in Wyoming or at Four Mile. There are no specimens of *Arfia* known from Sand Quarry, even though they would be readily identifiable even with very fragmentary material. It seems likely, based on Gunnell’s evidence, that this locality is approximately the same age as the other localities, but that some ecologic difference allowed the two large *Prototomus* species to be present rather than the *Arfia* species. There is not enough postcrania available to determine what sort of locomotory style the two *Prototomus* species had or whether it was similar to *Arfia*. If it is the case that the two species of *Prototomus* were ecologically partitioned from the two species of *Arfia*, then the logical conclusion would be that *Prototomus robustus* and *P. secundarius* have a stratigraphic range beginning in Wa2 or Wa3 and their late appearance in the Bighorn and Clarks Fork Basins was related to the disappearance of *Arfia* rather than the evolutionary origin of the two *Prototomus* species.

CONCLUSION

The diversity of hyaenodontid creodonts in the Four Mile fauna is much higher than previously thought. At least nine species representing four genera were present in the area. These are *Prototomus martis*, *P. phobos*, *P. secundarius*, *P. robustus*, *P. deimos*, *Arfia opisthotoma*, *A. shoshoniensis*, cf. *Acarictis ryani*, and *Prolimnocyon haematus*.

These species indicate that the Four Mile Fauna is Wa2 or Wa3 in age. A possible exception is Sand Quarry, which contains hyaenodontid species previously only known from the Wa4 and Wa5 zones in the Bighorn and Clarks Fork Basins. A range extension for these species and a biologic explanation for their absence in early levels of the Wyoming sections is advocated rather than a late age assignment for the Sand Creek locality.

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Figure 2: Stratigraphic ranges of hyaenodontid creodonts and the biochronologic correlations of Four Mile localities. On the left, represented by the solid vertical lines, are previously reported biochronologic ranges of hyaenodontid species from the Bighorn and Clarks Fork Basins. Note that Prototomus deimos is known from Wa1 and Wa2 zones, but not Wa2. On the right Four Mile localities are correlated with biochronologic zones by their hyaenodontid species to known ranges from the Bighorn and Clarks Fork Basins. The possible biochronologic placement of these localities is represented by the vertical, arrow-tipped dashed lines. Despair Quarry can be unquestionably correlated with Wa2 if Prototomus deimos is inferred to have lived during that zone on the basis of its first and last appearances in the Bighorn and Clarks Fork Basins. The Sand Quarry locality is shown in the late Wa5 zone based on its hyaenodontids, but an earlier age is advocated based on other evidence presented in the text.