

Evolution's Tempo and Mode during the Eocene Epoch: comparison of two long contemporaneous records of the fossil mammal *Hyopsodus* in the American West.

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Abstract

The spatial and temporal record of the early Eocene mammal *Hyopsodus* exemplifies the complex and sinuous nature of evolution. I transform the dualism of punctuated equilibrium and phyletic gradualism patterns into a discussion of regional and local evolutionary patterns. In this paper, I show that evolution follows a gradual pattern at the local level, while punctuated changes occur through migration, climate change and ecological shifts at the regional level. These conclusions are demonstrated by comparing two long fossil records of the small mammal *Hyopsodus* from the Bighorn Basin of northern Wyoming and the Piceance Creek Basin of western Colorado. Separated by a large geographic distance and the high Rocky Mountains, the two sedimentary basins preserve a long record of evolutionary change during the Wasatchian Land Mammal Age (55 to 50 million years ago). In both basins *Hyopsodus* diversifies into a number of different sized species during the late Wasatchian. Northward migration played an important role in the diversification of *Hyopsodus*. The large species *H. powellianus* appears earlier in the Piceance Creek Basin and expanded northward into the Bighorn Basin as global temperatures warmed during the early Eocene. Gradual *in situ* changes, such as the gradual transformation of *H. simplex* into *H. minor* in the Bighorn Basin, are not witnessed in the Piceance Creek Basin. Additional fossils may prove *H. minor* migrated into the Piceance Creek Basin only after originating from the Bighorn Basin. There currently is a stratigraphic gap between the last appearance of *H. simplex* and first appearance of *H. minor* in the Piceance Creek Basin. This paper draws attention to the dense fossil record of the Eocene and the value it serves as a window into understanding evolutionary patterns spanning millions of years.

Introduction

No other theory in paleontology has garnished the amount of fame than Eldredge and Gould's theory of punctuated equilibrium has (Eldredge and Gould, 1972). Since its proposal in 1972, numerous paleontologists set out to test the theory. In order to rule out punctuated equilibrium, paleontologists must demonstrate each of the tenets of the alternative theory – phyletic gradualism. According to Eldredge and Gould, phyletic gradualism must stand upon the following principles. First, new species must arise from the transformation of an ancestral population into its modified descendants. Second, this process of transformation is even and slow. Third the transformation between ancestor and descent involves the entire population. And fourth, the transformation between one species into another species is played out over the entire geographic range of the ancestral species. Needless to say, the tenets of phyletic gradualism could only be proven from an immense fossil record spanning an exceptionally long period of time and extending across vast geographic distances. Outside of the marine realm, one of the very few places in the world such studies can be conducted is the fossil rich deposits of Eocene age in the basins scattered between the high mountain ranges of the Rocky Mountains (Figure 1).

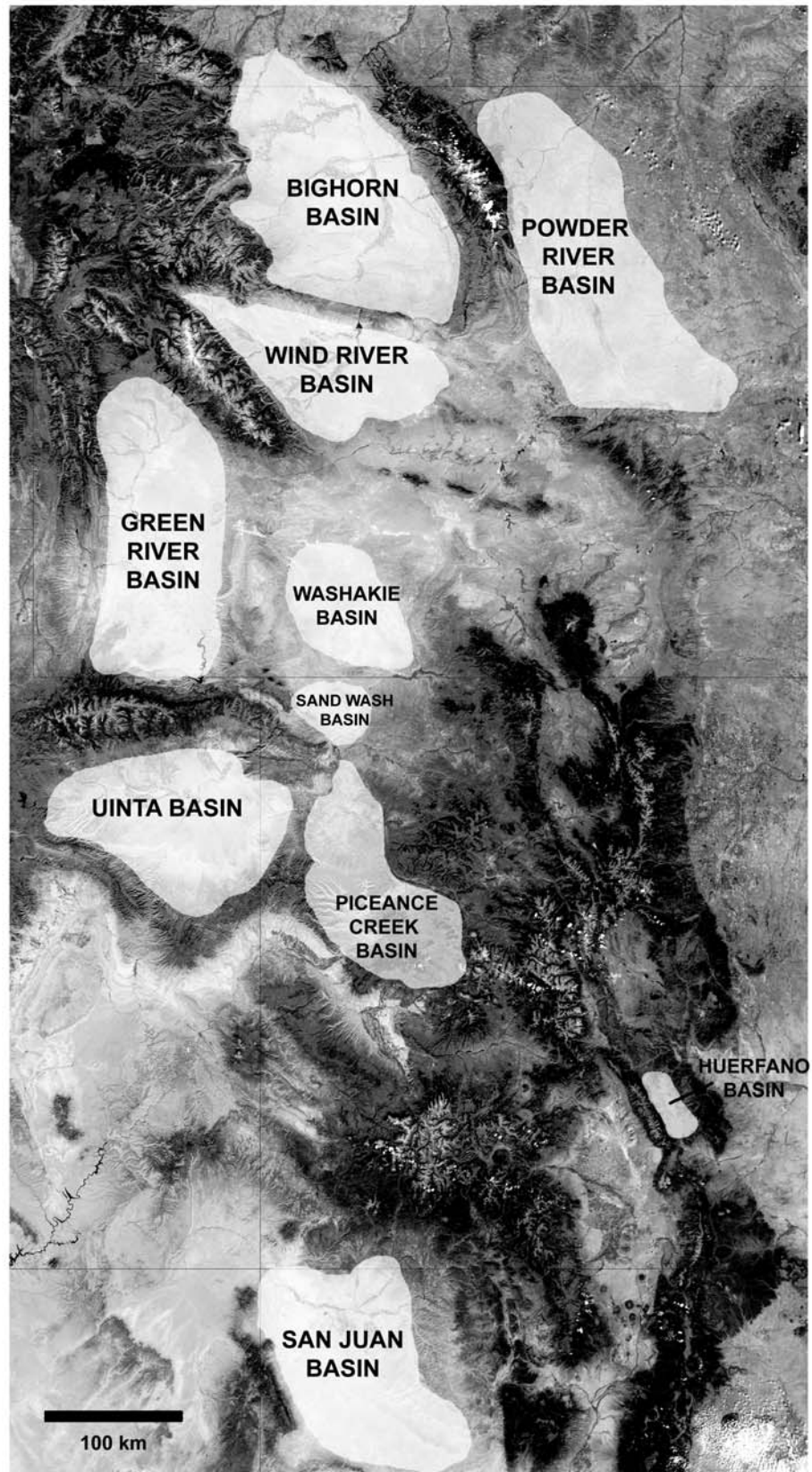


Figure 1. Major Eocene sedimentary basins of the American west.

During the latest Cretaceous and throughout the Paleocene, the initial uplift of the Rocky Mountains formed a series of large sedimentary basins. These sedimentary basins accumulated immense amounts of eroded sediment from the newly uplifted mountains, establishing a long and extensive record of rocks during the Paleogene Period.

Depending on how these basins are subdivided, 15 to 20 basins are currently recognized in the literature (Figure 1). Ten of these basins preserve a rich record of Eocene aged rocks with abundant fossil mammals. These fossil mammals facilitate correlating Eocene deposits between basins. By stitching each basin's fossil record together, mammalian paleontologists have produced an extensive record of mammalian evolution across the early to middle Eocene, an interval of nearly 15 million years (Table 1). However, each basin does not record the same length of time, and the overlap is somewhat meager for some of the basins. Furthermore, each basin differs in the density of its fossil record. During the last century, one basin rose to prominence for its exceptional fossils—the Bighorn Basin in northern Wyoming.

BASIN	Early Eocene								Middle Eocene						
	Wa0	Wa1	Wa2	Wasatchian				Wa7	Bridgerian				Uintan		
				Wa3	Wa4	Wa5	Wa6		Br0	Br1	Br2	Br3	Ui1	Ui2	Ui3
SAN JUAN BASIN						X	X								
HUERFANO BASIN						X	X	X	X	X					
PICEANCE CREEK BASIN		X	X	X	X	X	X	X	?	?					
SAND WASH BASIN		X	X												
WASHAKIE BASIN				X	X	X	X	X				X	X	X	
UINTA BASIN							X	X	X	X	X	X	X	X	X
GREEN RIVER BASIN						X	X	X	X	X	X				
WIND RIVER BASIN			X	X			X	X	X	X	X		X	X	X
BIGHORN BASIN	X	X	X	X	X	X	X	X	?	?	?				
POWER RIVER BASIN	X	X	X	X											

Table 1: Temporal overlap of Eocene sediments between large sedimentary basins in the American West. Shaded cells indicate temporal overlap between Piceance Creek and Bighorn Basins. Biochrons defined in Robinson et al. 2004, and in table 2.

The Bighorn Basin of northern Wyoming preserves an extremely dense record of fossil mammals during the early Eocene. In particular it is the fossilized teeth that provide such an extensive record. Fossil teeth are important because researchers can distinguish teeth of differing species. Each species is recognized from the unique arrangement of cusps and crests displayed on each tooth. Remarkably, paleontologists do not need to possess a complete skeleton in order to identify the specimen to a species; often a single isolated tooth will suffice.

The extensive record of fossil mammal teeth from the Bighorn Basin enabled paleontologists to study evolutionary rates during the early Eocene, and scrutinize Eldredge and Gould's theory of punctuated equilibrium. Using these teeth, mammalian paleontologists plotted morphological change (often as a measurement of tooth size) against the stratigraphic position in the rock formation. The methodology is somewhat similar to what Eldredge used on the Devonian trilobite *Phacops* and Gould used on the Pleistocene snail *Poecilozonites* that initially lead them to propose the theory of punctuated equilibrium. However, the same methodology applied to the small Eocene mammal *Hyopsodus* from the Bighorn Basin resulted in an observed gradual transformation of a single small species into a diversity of small, medium, and large species (Gingerich, 1974). Other examples of gradual evolution among various groups of fossil mammals from the Bighorn Basin were proposed, illustrating slow and even change in the size of the teeth (Gingerich, 1976). Criticism came from every direction, even among mammalian paleontologists working on Eocene mammals in neighboring basins (McKenna et al. 1977, West, 1979). The harshest criticism came from McKenna et al (1977), who likened these studies to "connect-the-dots" art (McKenna et al. 1977). In

contrast to Gingerich's studies, West (1979) interpreted evolutionary stasis in later middle Eocene specimens of *Hyopsodus* in the Bridger Basin. Indeed stratigraphic discontinuity existed between each of the localities leading to various interpretations of the data. Gingerich (1985) presented a larger data set of nearly 900 specimens of *Hyopsodus*, but it failed to extinguish the critics' fire. It would take considerable time before a large enough sample of fossil mammals was accumulated from the Bighorn Basin to plug all the stratigraphic gaps. In 1994, the measurements of 2055 first molars of *Hyopsodus* were plotted against their stratigraphic position (Bown et al. 1994a; Figure 2). This study differed from the earlier studies. First, the oldest species (*Hyopsodus loomisi*) did not change in size during the early Eocene (Wa-1 through Wa-2 Biozones). A punctuated change occurred later (at the Wa-2/Wa-3 boundary) resulting in the sudden appearance of a slightly large species (*Hyopsodus simplex*) that again did not change in size during middle early Eocene (Wa-3 through Wa-4 Biozones). Indeed the evolutionary pattern of these two species conforms to the punctuated equilibrium model as proposed by Eldredge and Gould (1972). In contrast, younger specimens (from the Wa-5 through Wa-6 Biozones) show a gradual diversification into four contemporary species of different sizes. This more densely packed sample does not require any "connecting the dots" because the dots are so numerous they have become a line (Bown et al. 1994a fig. 1). The question I ask is: does *Hyopsodus* undergo phyletic gradualism during the later Wasatchian time period?

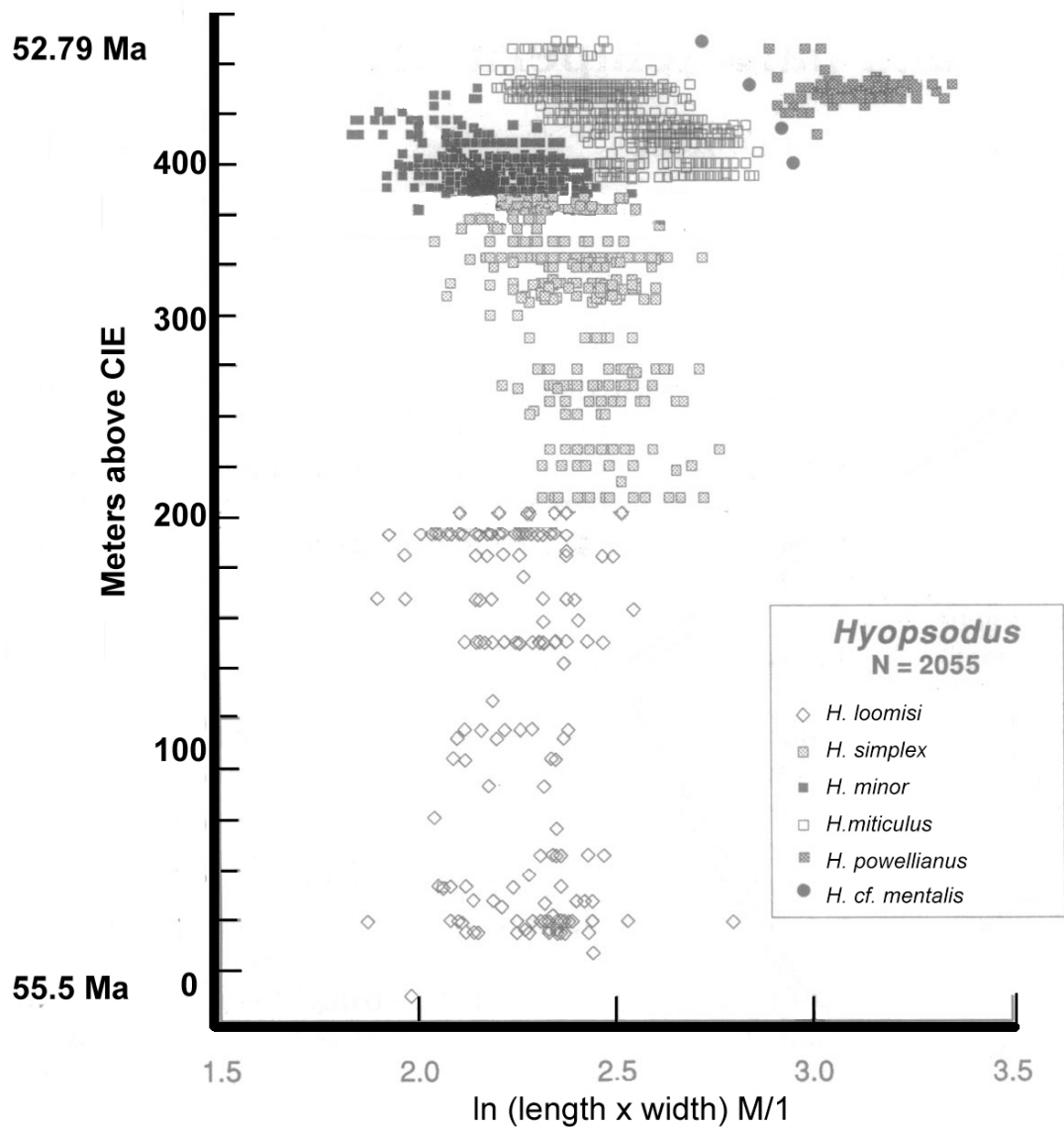


Figure 2. Stratigraphic position and measurements of the lower first molar area for 2055 specimens of *Hyopsodus* from the southern Bighorn Basin. From Bown et al. 1994 fig. 1.

Eldredge et al. (2005) offered an explanation related to the fact that the fourth principle of phyletic gradualism, transformation between one species into another species is played out over the entire geographic range of the ancestral species, was never demonstrated for these localized populations of fossil mammals in the Bighorn Basin.

Paraphrasing Eldredge et al. (2005), “local populations... can be expected to develop more substantial amounts of morphological change in the short term ...[and] the patterns of generally fluctuating change documented... in Eocene mammals... reflect the evolutionary histories of geographically localized populations... [The] meticulously collected time series from the Bighorn Basin of Wyoming is only a localized subset of the region over which *Hyopsodus* and other species have been documented to have lived.” In other words, the evolutionary pattern of *Hyopsodus* will be localized to each sedimentary basin. To investigate this assertion, I compare the extensive *Hyopsodus* fossil record of the Bighorn Basin with another basin— the Piceance Creek Basin in western Colorado.

The Piceance Creek Basin differs fundamentally in two ways from the Bighorn Basin. First, the Piceance Creek Basin differs in its southern location. The center of the Piceance Creek Basin is located 490 miles (788 km) south of the center of the Bighorn Basin. Even today the Piceance Creek Basin hosts 30% more mammal species than the more northern Bighorn Basin (Badgley and Fox, 2000). Second, the main body of the Rocky Mountains, with towering peaks 14,000 feet high, stands between the two basins; the Bighorn Basin exists on the eastern slope of the Rocky Mountains, while the Piceance Creek Basin exists on the western slope of the Rocky Mountains. With a large mountain range separating the two basins, each basin was likely subjected to different climatic regimes during the Eocene, as they are today. Without a doubt, *Hyopsodus*, found in both basins, enjoyed a wide geographic distribution during the Eocene. Indeed any shared

evolutionary pattern found between the two basins incontrovertibly extended across a large extent of the true geographic range of *Hyopsodus*.

If the Eldredge et al (2005) explanation is correct, and phyletic gradualism in the Bighorn Basin results from a localized pattern, there should be a different pattern in the evolutionary tempo and mode of *Hyopsodus* and other small mammals in the Piceance Creek Basin. If there is a similar pattern in the evolutionary tempo and mode between the two basins, then all four principles of phyletic gradualism established by Eldredge and Gould over thirty years ago will have finally been reached.

Methods

Biostratigraphic Correlation

Clyde et al. (2007) recently summarized the magnetostratigraphic framework of the Bighorn Basin. A similar magnetostratigraphic framework for the Piceance Creek Basin is currently lacking. However, the recent discovery of the Paleocene-Eocene boundary defining carbon isotopic excursion in the Piceance Creek Basin, allows for a non-biological correlation to the carbon isotopic excursion to the Bighorn Basin (Koch et al. 1992; Burger, 2007). Although no other non-biological calibration point is shared between the two basins at this time, the mammalian biostratigraphic zonation is well documented (Robinson et al. 2004). The Wasatchian North American Land Mammal Age is divided into a number of subdivisions: the Sandcouleean, Graybullian, Lysitean and Lostcabinian. The Wasatchian is also divided into numerical biochrons (Wa-0 to Wa-7). The numerical biochrons provide a means to correlate between the two basins, and are established from first appearances of mammalian species (Table 2). Difficulties arise in

the heterogeneous nature of sedimentary rates. In the Bighorn Basin, sedimentary accumulation rates were higher in the northern portion of the Basin (Clarksfork Basin) (Bown et al. 1994b; Clyde et al. 2007). Within the Piceance Creek Basin, sedimentary rates are less well constrained, but appear uniform, based on biostratigraphic relationships between the upper and lower formational contacts of the Wasatch Formation. In this study, I used stratigraphic levels for first appearances from the southern Bighorn Basin based on the Elk Creek Section (Bown et al. 1994b; Clyde et al. 2007). Bown et al. (1994a) utilized the Elk Creek stratigraphic section in their illumination of gradual change of *Hyopsodus* during the Wa-5 to Wa-6 biozones. To insure that sedimentary rates remained relatively constant I use the graphic correlation method to compare the two basins, based on the first appearances of 9 genera. Graphic correlation method is used to detect variable sedimentary rates between two geographically separated sections. (Shaw, 1964; Miller, 1977), but it can also illustrate the migration patterns of organisms over time. For example, *Xenicohippus* appears below the trend line, indicating that *Xenicohippus* first appeared in the Piceance Creek Basin, before being observed in the Bighorn Basin. In fact, the geographic range of *Xenicohippus* never extended into the northern portion of the Bighorn Basin (Bown and Kihm, 1981). The greatest benefit of graphic correlation is that stratigraphic levels between the Bighorn and Piceance Creek Basins can be directly compared. The linear formula for converting stratigraphic meter level positions of each basin is given in figure 3.

FAD Biochron	Genus	Stratigraphic level above P-E boundary	
		Bighorn Basin	Piceance Creek Basin
Wa-0	<i>Hyopsodus</i>	0 m	20 m
Wa-0	<i>Diacodexis</i>	0 m	20 m
Wa-0	<i>Eohippus</i> (<i>Hyracotherium</i>)	0 m	20 m
Wa-0	<i>Cantius</i>	0 m	20 m
Wa-3	<i>Homogalax</i>	200 m	400 m
Wa-5	<i>Bunophorus</i>	365 m	575 m
Wa-6	<i>Heptodon</i>	430 m	950 m
Wa-7	<i>Lambdaotherium</i>	636 m	1100 m
Wa-6/5	<i>Xenicohippus</i>	425 m	480 m

Table 2: Stratigraphic position of first appearances of key index fossils.
Bighorn Basin stratigraphic levels from Bown et al. 1994b.

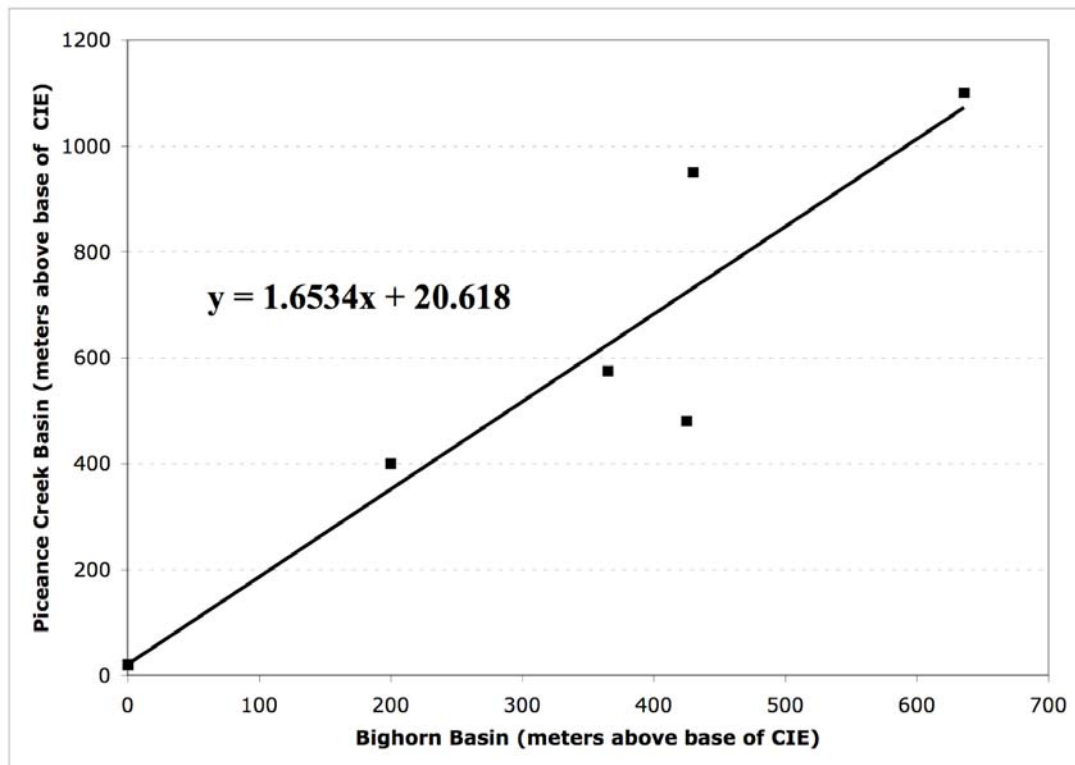


Figure 3. Graphic correlation between the southern Bighorn Basin (Elk Creek Section) and the Piceance Creek Basin based on stratigraphic positions listed in table 2. The resulting linear equation was used to convert actual meter levels from the Piceance Creek Basin, into equivalent meter levels with the Bighorn Basin.

Measurement

Far fewer fossils of *Hyopsodus* have been recovered from the Piceance Creek Basin, than the Bighorn Basin. Measurements of only 56 lower first molars and 66 lower second molars were plotted against the equivalent stratigraphic position in the Bighorn Basin, calculated from the stratigraphic conversion formula (Figure 3). The natural log was taken of the area (length x width) measured using digital calipers. Thus figure 4 and figure 2 can be directly compared for similarities knowing that the stratigraphic positions are equivalent to each other.

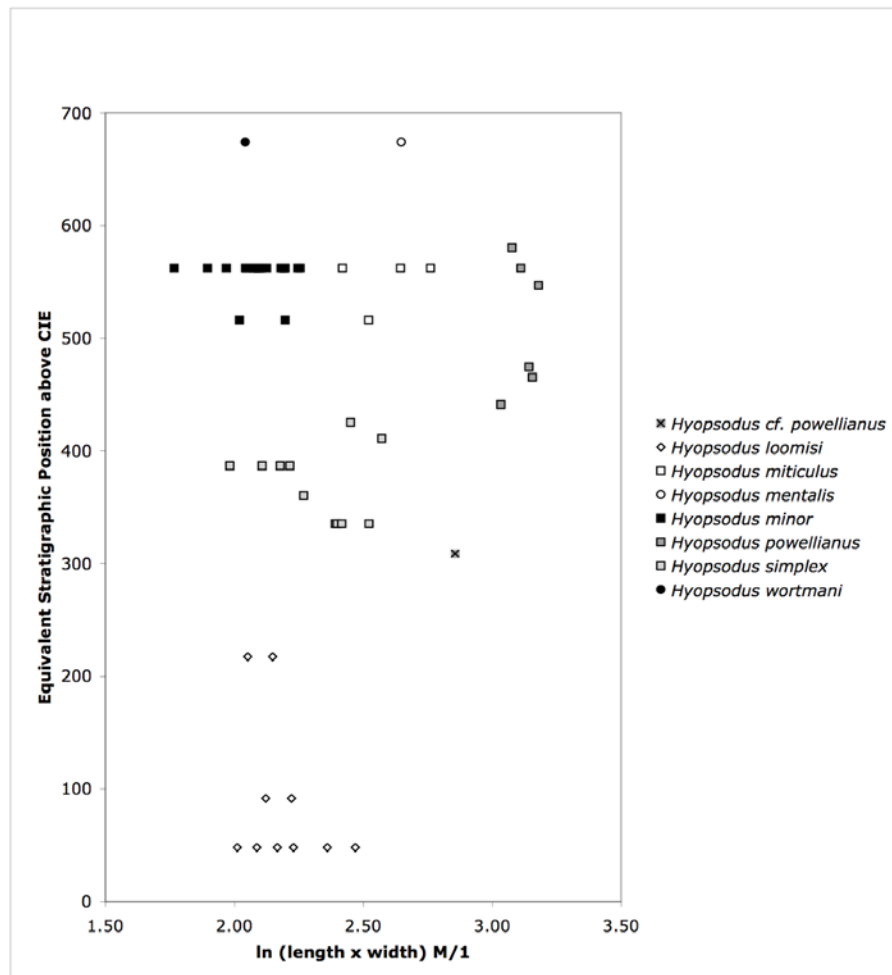


Figure 4. Stratigraphic position and measurements of the lower first molar area for 56 specimens of *Hyopsodus* from the Piceance Creek Basin.

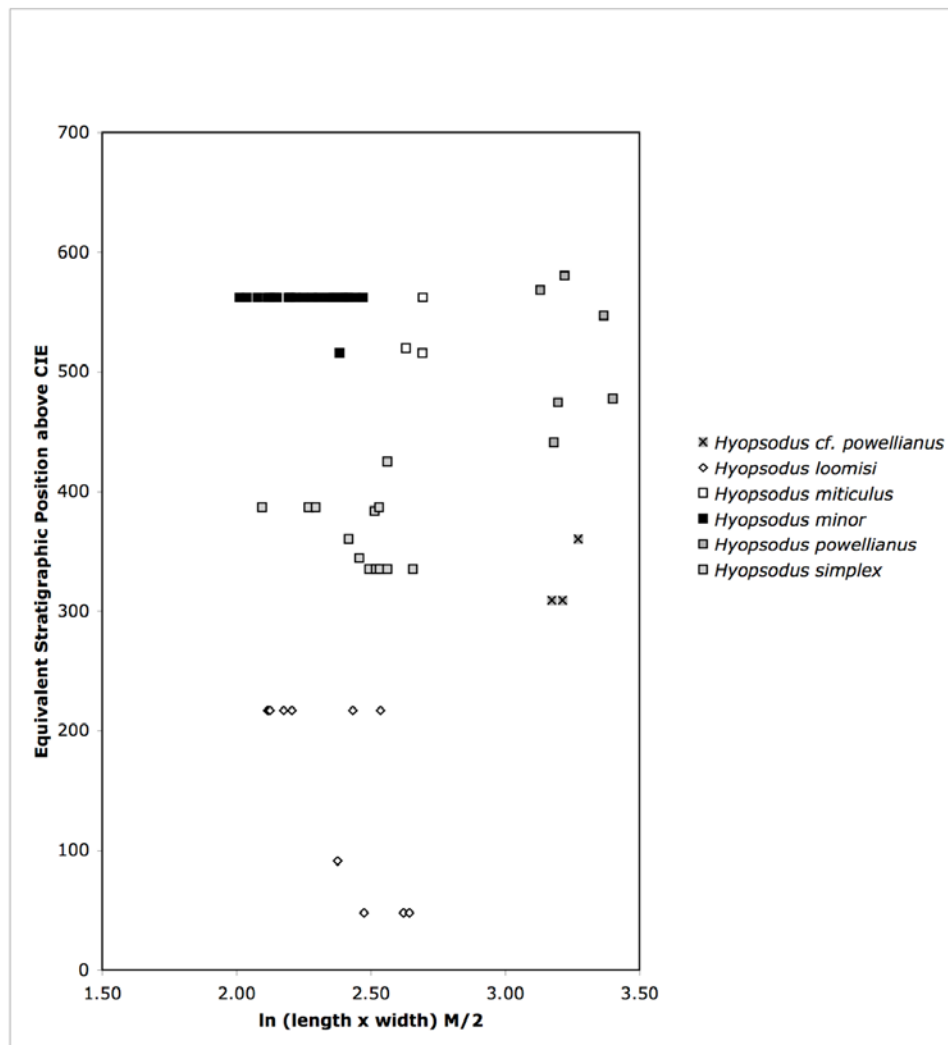


Figure 5. Stratigraphic position and measurements of the lower second molar area for 66 specimens of *Hyopsodus* from the Piceance Creek Basin.

Results

In general the two basins depict similar patterns; a single lineage diversifying into a number of species (Figure 3 compare with Figure 4 & 5). For example, during the earliest Wasatchian time *Hyopsodus loomisi* extends to about the 217 equivalent meter level in the Piceance Creek Basin, and the 200 meter level in the Bighorn Basin, demonstrating an equilibrium state. At some point during the 217 to 335 equivalent meter level in the Piceance Creek Basin the slightly larger *Hyopsodus simplex* first appears and

extends to the equivalent 425 meter level in a similar size range as specimens from the Bighorn Basin. The major difference between the two basins is the unusually early occurrence of large specimens labeled *Hyopsodus cf. powellianus* in the Piceance Creek Basin. Indeed, slightly larger specimens indicate a third species below the 400 equivalent meter level. These specimens likely extend the temporal range of the large species *H. powellianus* below the 400 equivalent meter level in the Piceance Creek Basin. Larger specimens from this interval were not found among the 2055 specimens measured by Bown et al. (1994). *H. powellianus* only appears in the Bighorn Basin above the 441 meter level. During this time there is a gap in the presence of smaller species in the Piceance Creek Basin, with the species *H. minor* and *H. miticulus* appearing only after the 515 equivalent meter level. The observed gradual transition between *H. simplex* and *H. minor* in the Bighorn Basin is not well demonstrated with the fossil specimens from the Piceance Creek Basin. Above the 500 equivalent meter level three species coexisted in the Piceance Creek Basin— the small sized *H. minor*, medium sized *H. miticulus*, and the larger sized *H. powellianus*. This is identical to the pattern observed in units between the 400 to 500 meter levels in the Bighorn Basin (Figure 2). The fossil record in the Piceance Creek Basin extends for a greater amount of time, preserving the late Wasatchian species *H. wortmani* and *H. mentalis*.

Discussion

The general pattern of evolutionary change is similar between the two basins; a general diversification over time. However, slow and even transformation observed in the Bighorn Basin, for example the transition between *H. simplex* and *H. minor*, are not observed in the Piceance Creek Basin. Furthermore, shared trends within each species are

not apparent; perhaps a result of smaller samples sizes from the Piceance Creek Basin, or localized trends within a limited population, as mentioned previously.

More important, however, is the timing of the diversification of *Hyopsodus*. Large aberrant specimens of *Hyopsodus* (*H. cf. powellianus*) appear in the Piceance Creek Basin earlier than the Bighorn Basin. These specimens undeniably indicate northward migration of *H. powellianus* from the Piceance Creek Basin into the Bighorn Basin during the Lysitean (Wa-6). Rather than *in situ* evolutionary diversification, the major diversification during the Lysitean (Wa-6) resulted from stepwise immigration of more southern distributed species northward. This stepwise immigration of species is linked to rising global temperatures during the early Eocene, which culminated in the late Wasatchian/ early Bridgerian with the Early Eocene Climatic Optimum (EECO). After peaking, global temperature decreased throughout the rest of Earth's 50 million year history.

With regard to evolutionary rates, species of *Hyopsodus* do not share phyletic gradual transformation across a wide geographic region. Consequently, the fourth tenet of phyletic gradual evolution does not play out. We are left to conclude that punctuated equilibrium describes even the most cited example of phyletic gradualism, the diversification of *Hyopsodus* during the early Eocene.

The true meaning of punctuated equilibrium is that evolution works at the local level on the periphery of geographic ranges. Diversification results from allopatric

speciation (a geographically isolated population evolves into a new species) or parapatric speciation (a peripheral population evolves into a new species). Once evolved, species track their optimal habitat. As the Earth changes, species move around the geographic landscape. Species seek the best home suited for their particular adaptations. They come and go from the fossil record.

The triumph of punctuated equilibrium does not diminish the importance of localized changes. In fact, species originate in local settings. For example, the gradual transition of *H. simplex* into *H. minor* observed in the Bighorn Basin may be a local gradual trend, however if the appearance of *H. minor* into the Piceance Creek Basin is sudden (based on the few fossil we have) then we are witnessing the birth of a new species in a geographically isolated population of *Hyopsodus* in the Bighorn Basin that later extends its range into the Piceance Creek Basin.

Conclusions

In this paper I showcase the superb fossil record of the early Eocene in Rocky Mountain region by investigating the evolutionary tempo and mode of a single small mammal, *Hyopsodus*, across several million years of history in two geographically distinct basins. I scrutinize Eldridge and Gould's theory of punctuated equilibrium showing that the theory triumphs even within the dense fossil record of the Eocene. The success of their theory is really on the technicality that evolution works on the local level. Evolution is played out on the periphery of a species geographic range. The local nature of gradual change does not relegate its importance. In documenting local changes we are

more likely to document the birth of new species. Once born, these new species are free to migrate into whatever habitat suits them best— coming and going across the landscape as the ecology and climate of the planet changes.

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