

Faunal stability during the Early Oligocene climatic crash

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Abstract

Traditional Neo-Darwinism views species as highly flexible entities which adapt to climatic change by gradually evolving new morphologies. Of the 177 species of mammals from the upper Eocene–lower Oligocene (37–30 Ma) White River Group in the High Plains, most species are static for 2.4 million years on average, and some persist much longer. Only three examples of gradualism can be documented in the entire fauna, and these are mostly size changes. Contrary to expectations, most mammalian species show no change during the earliest Oligocene climatic crash (33.2 Ma), in spite of the fact that the vegetation changed from dense forests to open forested grassland, mean annual temperatures dropped 13°C, and conditions got much drier and more seasonal. Only a few mammalian lineages speciated, a few more went extinct, and the vast majority (62 out of 70) persisted through this climatic event with no observable response whatsoever. This evidence shows that organisms are much less responsive to the environment than short-term neontological studies suggest.

Keywords: Eocene; Oligocene; mammal; evolution; climate

1. Introduction

In the 24 years since the original publication of the “punctuated equilibrium” model (Eldredge and Gould, 1972), many scientists have examined tempos and modes of evolution. Some early studies were flawed because they examined a single morphological character (neglecting all other variability) in a single lineage (rather than the entire fauna) over a restricted geographic range (neglecting the possibility of migrating

clines) at the wrong scale and with inadequate temporal control (Gould and Eldredge, 1977). In recent years, however, more rigorous analyses across entire faunas have begun to accumulate (summarized in Barnosky, 1987; Gould, 1992; Stanley, 1992; Prothero, 1992b; Eldredge, 1995; and the papers in Martin and Barnosky, 1993, and Erwin and Anstey, 1995). For example, Stanley and Yang (1987) and Jackson and Cheetham (1995) examined all the available lineages in their respective groups (Atlantic Coast bivalves and cheilostome bryozoans) and found that most species were static through millions of years. The debate is no longer whether punctuated equilibrium or gradualism can be demonstrated (they both occur), but which is more prevalent.

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With the exception of protists (which are partly or completely asexual, and do not fit Mayr's model of allopatric speciation — see Lazarus, 1983), the pattern of punctuation and stasis seems to prevail among most marine metazoan taxa that have been rigorously examined.

Among terrestrial vertebrates, only fossil mammals offer the dense and continuous fossil record with large population samples that are necessary to evaluate tempos and modes of evolution. The patterns of evolution reported so far have been mixed. Gingerich (1976, 1980, 1985, 1987, 1993) has been one of the foremost proponents of gradualism, based on his studies of mammals from the lower Eocene beds of the northern Bighorn Basin of Wyoming and Montana. However, this research has been criticized on a number of grounds (Gould and Eldredge, 1977; Eldredge, 1995). The alleged gradualism in *Hyopsodus*, *Cantius* (formerly *Pelycodus*), *Plesiadapis*, *Carpolestes*, *Haplomylus*, and a few other taxa are just part of a fauna of over a hundred genera. Detailed monographs by Bown (1979), Schankler (1980), and Gingerich (1989) have shown that stasis is prevalent among most of the taxa not featured by Gingerich (1976, 1980, 1987). In addition, the patterns reported by Gingerich for a single sequence in the northern Bighorn Basin do not take geographic variability into account. This is especially critical with size changes, which could be due to migrating clines. Schankler (1981) found that some of Gingerich's patterns do not hold up even in the southern Bighorn Basin, only 50 miles to the south. Finally, as Lande (1976) and Gould and Eldredge (1977) pointed out, the rates of evolution reported in the gradual transformations of Gingerich are so slow that they could be due to genetic drift rather than to natural selection.

Krishtalka and Stucky (1985, 1986) reported a gradualistic transformation in the early Eocene artiodactyl *Diacodexis*. However, this is a single lineage from the same faunas described by Schankler, Gingerich, and Bown, so these studies do not address the overall prevalence of gradualism versus stasis. Flynn (1986) reported on the species of rhizomyid rodents from the Miocene Siwalik deposits of Pakistan. Most species show prolonged stasis over millions of years, with rapid "stairstep" evolution between species. One group became fos-

social and had much shorter species duration, possibly because the isolation of burrowing habitats increases the rate of speciation.

Vrba (1980, 1985) reported patterns of evolution in antelopes from the late Neogene of Africa. Her studies demonstrated stasis punctuated by multiple speciation events, and much of the speciation was concentrated at the late Pliocene (2.8 Ma) climatic change that signaled the beginning of the ice ages. However, these studies do not address the patterns of evolution within the entire fauna, or even the entire family Bovidae.

Barnosky (1987) summarized studies of Pleistocene mammals by a number of authors. Depending upon what criteria were used, examples of stasis and punctuation outnumbered examples of gradualism by about 2:1. More recently, a number of detailed studies on Pleistocene mammals were reported in the volume edited by Martin and Barnosky (1993). Again, examples of stasis and punctuation far outnumbered cases of gradualism (even in the six studies summarized by Gingerich, 1993, in that same volume).

In the research reported below, we have conducted an unbiased survey of all fossil mammal lineages across the Eocene–Oligocene transition (Chadronian through Whitneyan North American land mammal "ages") which have large enough sample sizes and recent systematic revision. Preliminary results of this study have been reported several times over the last decade (Prothero and Shubin, 1983; Prothero, 1992a,b, 1994a,b), but publication of this research was delayed until systematic revisions of the key mammalian groups could be completed and published. Unlike most of the previous examples, this study considers geographic variation over a wide area (from western Montana and North Dakota in the north and west, to Colorado in the south), with very fine-scale chronostratigraphic control from magnetic stratigraphy and $^{40}\text{Ar}/^{39}\text{Ar}$ dating (Prothero and Swisher, 1992; Evanoff et al., 1992; Prothero, 1996a; Prothero and Whittlesey, 1997). Finally, recent studies of the Eocene–Oligocene transition (summarized in Prothero, 1992b, 1994a) provide independent direct evidence of the timing and magnitude of climatic changes that occurred during this time interval. Thus, it is possible to

address the response of these mammals to a well documented episode of global climate change.

In addressing modes of evolution of lineages, we use species names only as labels for identifying segments of lineages. We discuss changes both within those segments, and between the segments, so far as change has been documented. As in many parts of the fossil record, it is not uncommon for a species to appear suddenly from an unknown ancestry, persist for a time with little or no change, and then disappear, apparently extinct. In some sequences, this is the rule rather than the exception. This makes evolution hard to study and leaves many questions about evolution and biogeography unanswered. If such taxa persist for millions of years without change (stasis), this can be seen as evidence for punctuated equilibrium, which predicts that stasis is the norm. So even poorly-documented or poorly-studied species can provide us with some useful information if they persist long enough time that a significant change would be predicted in the gradualistic model.

2. The White River Chronofauna

One of the densest and most complete records of mammalian evolution anywhere in the world is preserved in the White River Group of the High Plains. The spectacularly stark and beautiful outcrops of the Big Badlands of South Dakota have been a Mecca for fossil collectors ever since the first fossils were described in 1846. In fact, these were the first fossil vertebrates reported from west of the Mississippi. In the 150 years since, enormous collections have accumulated, and White River fossils are found in nearly every rock shop and mineral show across the country. However, most of these collections had little or no stratigraphic data, so detailed biostratigraphy and examination of changing lineages through time could not be studied.

Fortunately, Morris Skinner and other collectors of the Frick Collection (now stored in the American Museum of Natural History in New York) were careful about the stratigraphy of the deposits and their fossils. Nearly every Frick specimen was zoned to the nearest foot from known

marker beds, and the data was recorded right on the specimen. Some White River fossils in the Smithsonian Institution and the University of Nebraska State Museum are also well zoned. This makes it possible to do detailed biostratigraphy for the first time (e.g., Emry, 1992; Prothero and Emry, 1996; Prothero and Whittlesey, 1997; Prothero, 1996a). In addition, the fine stratigraphic detail and large sample sizes in the Frick Collection allows us to examine large populations of certain lineages on a foot-by-foot basis in key areas. Combined with the high-resolution chronostratigraphy now in place, it is possible to estimate durations of species and rates of change with fairly high precision and confidence.

For a long time, however, the systematic data base for these mammals was not so well resolved. The last complete review of the White River fauna was over fifty years ago by Scott et al. (1937). Since those monographs, one of the most abundant and important groups, the oreodonts, were grossly oversplit by Schultz and Falkenbach (1956, 1968), based on invalid criteria such as post-mortem deformation (see Stevens and Stevens, 1996). Fortunately, most of the common groups of White River mammals have now been restudied, so a modern, rigorous systematic framework is now in place on which we can base our analyses.

As recognized by Emry (1981) and Emry et al. (1987), the mammals of the White River Group were part of a coherent longer-term assemblage known as the "White River Chronofauna". Most of the families and many of the genera first appeared in the late middle Eocene (Duchesnean), and by the late Eocene (Chadronian) nearly all the typical groups were in place. The main components of the White River Chronofauna persisted through the Orellan and Whitneyan (early Oligocene), and even through much of the early Arikareean (late Oligocene). In the late Arikareean (early Miocene), the White River Chronofauna was replaced by typically Miocene immigrant groups, which eventually formed a long-lived "Clarendonian chronofauna" of the middle and late Miocene (Webb, 1977, 1983; Tedford et al., 1987).

In the sections that follow, we report on the latest systematic and stratigraphic studies of the most abundant groups of mammals in the White

River Chronofauna. Not every group has been recently revised, but these groups are relatively rare and would not have influenced our overall conclusions. Many of the taxa discussed below are known from less than a dozen specimens from a restricted stratigraphic interval, so it is not possible to analyze their shape change through time. However, these occurrences are sufficient to document stasis, as reported in the literature. Where enough specimens (typically more than 100) occur over enough temporal duration, then analyses of size and shape change have been undertaken (unless the most recent reviser has reported no change through the duration of the species).

Not every species from the White River Chronofauna is discussed below. Only those which occur from more than one level and more than a few specimens in the middle–late Chadronian or Orellan are relevant to the main topic of the paper. Several rare species which occur in isolated early Chadronian localities have been left out to save space, as have a few rare Whitneyan taxa. However, the census for late Chadronian and Orellan mammals is nearly complete, so reliable estimates of percentage faunal change and durations of species can be generated.

2.1. Artiodactyls

Among larger mammals, the most abundant in the Chadronian through Whitneyan are even-toed ungulates, or artiodactyls. Three families are particularly common: the oreodonts, leptomerycids, and camelids.

Oreodonts: Scott et al. (1937) recognized only three genera and less than a dozen species from the White River Group, and Thorpe (1937) was similarly conservative. Unfortunately, the Schultz and Falkenbach (1956, 1968) monographs threw the taxonomy of oreodonts into total chaos. These authors oversplit the family into dozens of invalid species, genera, and even subfamilies based on features due to post-mortem deformation (for example, “*Platychoerus*” or “flat pig” was a dorsoventrally crushed *Miniochoerus*, and “*Stenopsochoerus*” or “narrow pig” was a laterally crushed *Miniochoerus*). Their work is also plagued by inadequate statistical comparisons; their taxo-

nomic definitions were often based on stratigraphic boundaries with no observable morphological change. The problems with their taxonomy have been widely recognized within the profession for years (e.g., Harksen and Macdonald, 1969, p. 13; Lander, 1977; Savage and Russell, 1983, p. 195, footnote 2; Gustafson, 1986, p. 16; Emry et al., 1987, p. 140). Fortunately, Stevens and Stevens (1996) and CoBabe (1996) have brought some semblance of order to the group.

From the multiple subfamilial lineages of Schultz and Falkenbach (1956, 1968), Stevens and Stevens (1996) have reduced the group to two main lineages in the late Eocene and early Oligocene. The main lineage is the most common of all Badlands fossils, the larger oreodont *Merycoiododon* (incorrectly referred to “*Prodesmatochoerus*” by Lander, 1977, 1997). Although this genus was grossly oversplit by Schultz and Falkenbach (mostly because they are so common, and intraspecific variability is high), Stevens and Stevens (1996) recognize only *Merycoiododon culbertsoni* in the late Chadronian and early Orellan (34.7–32.8 Ma). Despite the variability of the thousands of known specimens, there are no discernible size changes or consistent morphological changes through this entire interval (Fig. 1).

In the late early Orellan (early Chron C12r, 32.8 Ma), most *Merycoiododon* specimens exhibit inflated auditory bullae. This change is the basis of *Merycoiododon bullatus* of Stevens and Stevens (1996), known as *Eporeodon bullatus* in the older literature (e.g., Thorpe, 1937; Scott et al., 1937). It was erroneously referred to “*Eucrotaphus*” by Lander (1977, 1997), and it is equivalent to numerous Schultz and Falkenbach (1968) taxa. Bullar inflation occurs abruptly over the entire population, with no gradual inflation in specimens from intermediate levels (Fig. 1). In fact, there are a few specimens from the lower levels that have inflated bullae, and a few from the upper levels which do not, suggesting that bullar inflation was an all-or-nothing, abruptly changing character state. The mean size of the bullae remains constant as size increases in *Merycoiododon* throughout the late Orellan and Whitneyan.

In the late Whitneyan (late Chron C12r, 31.3–29.0 Ma), large oreodonts referable to

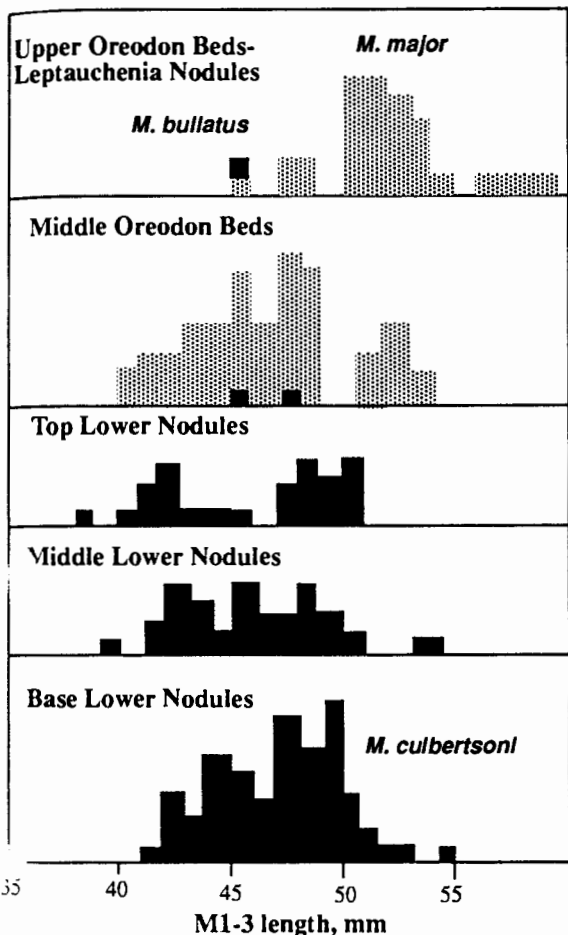


Fig. 1. Size distributions of Frick *Merycoiododon* specimens from the Cottonwood Pass area of the Big Badlands. Black boxes indicate specimens with no bullae, stippled boxes denote specimens with inflated bullae. Specimens from the different levels in the lower nodules (early Orellan, Chron C13n, about 32.8–33.2 Ma) are all *Merycoiododon culbertsoni* according to Stevens and Stevens (1996) and show no net size change; nor there any bimodality that might indicate more than one species (contra Schultz and Falkenbach, 1968). Specimens from the Middle Oreodon beds ("Upper Nodules") are latest Orellan (mid Chron C12r, about 32.2 Ma), and are referable to *Merycoiododon bullatus* according to Stevens and Stevens (1996). All but two of these specimens (indicated by black boxes) have inflated auditory bullae (mean bullar width = 18.3 ± 4.6 mm; mean bullar length = 21.0 ± 2.8 mm; $n=26$). Whitneyan specimens from the Upper Oreodon beds and *Leptauchenia* nodules (Chrons C12n–late C12r, 30.7–31.7 Ma) are referred to *Merycoiododon bullatus* and *M. major* by Stevens and Stevens (1996). These are noticeably larger animals, and all but one specimen has inflated bullae. However, the mean dimensions of these bullae (mean bullar width = 17.5 ± 5.0 mm; mean bullar length = 21.7 ± 1.5 mm; $n=9$) are not statistically different from those of *M. bullatus*, so there is no gradual size change in bullae.

Merycoiododon major appear. These are disjunctly larger in size than early Whitneyan *Merycoiododon bullatus*, and persist almost unchanged for about 2 m.y. (Fig. 1).

One of the few possible examples of gradualism in the entire White River fauna is the smaller lineage of oreodonts. Long known as "*Merycoiododon gracilis*" in the older literature (e.g., Thorpe, 1937; Scott et al., 1937), this same lineage was split into multiple genera and dozens of species by Schultz and Falkenbach (1956, 1968) and incorrectly referred to *Oreonetes* by Lander (1977, 1997). Stevens and Stevens (1996) refer all these taxa to *Miniochoerus*. Late Chadronian *Miniochoerus chadronensis* is only slightly smaller and difficult to distinguish from contemporary *Merycoiododon culbertsoni*. But in the early Orellan, *Miniochoerus* undergoes a dwarfing trend (30% size reduction in about a million years), with concomitant reduction in the proportions of the premolar row relative to the molars (Fig. 2). Although the apparent gradual size reduction may appear to validate the gradualistic model, it should be noted that size is much more labile than shape (Stanley and Yang, 1987). In fact, Gould and Eldredge (1977) excluded simple size change from the concept of punctuated equilibrium, since changes in shape are much more important in understanding the origin of new species.

Stevens and Stevens (1996) referred specimens from just below the marker ash known as the Persistent White Layer ("PWL," dated at 34.4 Ma, according to Obradovich et al., 1995) to about 50 feet above the PWL at Lusk, Wyoming, to the taxon *Miniochoerus chadronensis* (mean M^{1-3} length = 47 mm; observed range = 44–50 mm). Specimens that are intermediate in size (mean M^{1-3} length = 42 mm; observed range = 39–45 mm) occur between 0–50 feet above the PWL at Lusk. The smaller miniochoeres (from the late early Orellan) were referred to *M. gracilis* (mean M^{1-3} length = 34 mm; observed range = 31–37 mm) and *M. affinis* (mean M^{1-3} length = 38 mm; observed range = 36–41 mm). *M. affinis* first appears about 50 feet above the PWL at Lusk, Wyoming (mid Chron C13n, 33.3 Ma), and *M. gracilis* first appears about 100 feet above the PWL at Lusk (early Chron C12r, 32.8 Ma). Both species

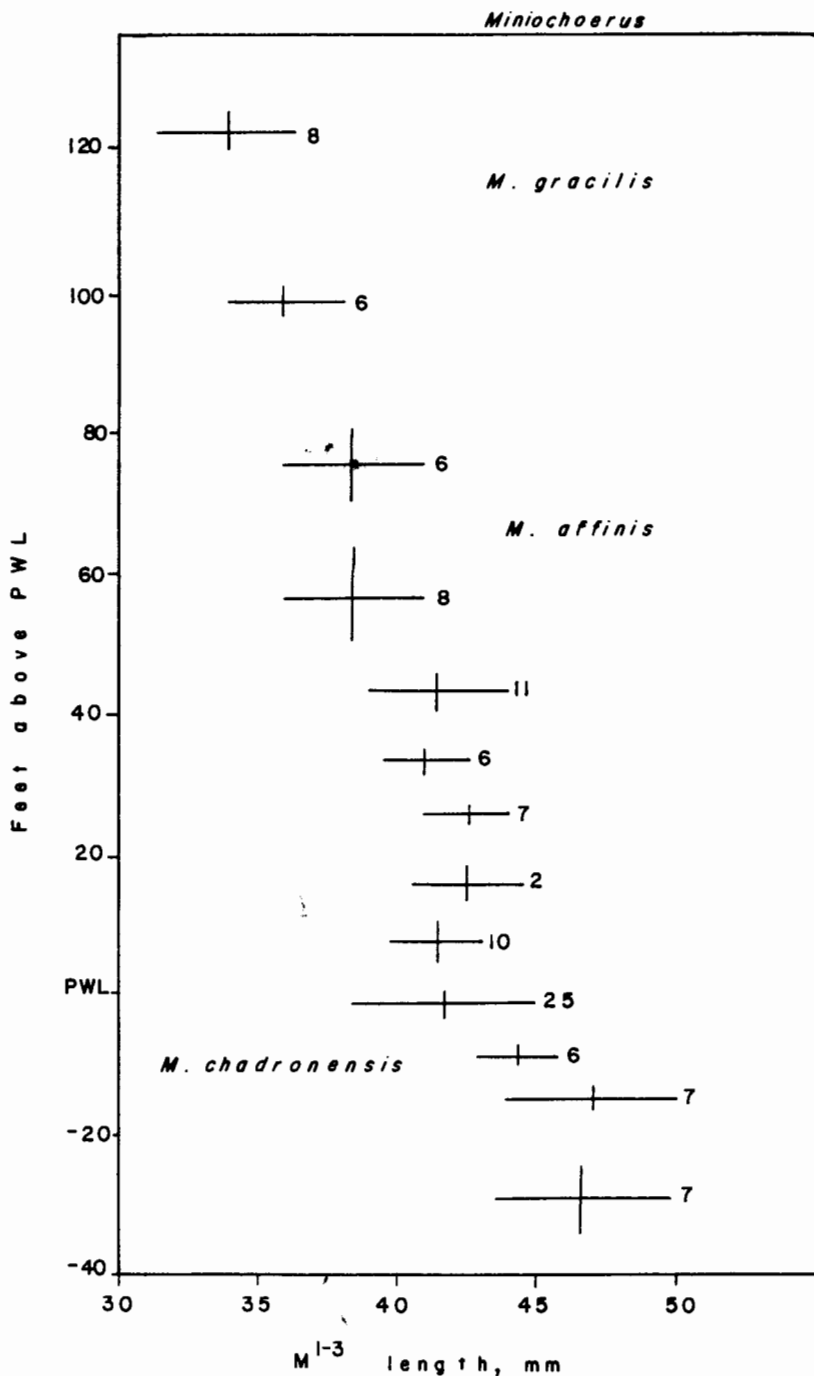


Fig. 2. Size change in Frick *Miniochoerus* from the Lusk area, Wyoming. Horizontal bar gives the standard deviation around the mean; vertical bar gives the stratigraphic range of the sample; number indicates sample size. PWL is dated at 34.36 ± 0.11 Ma; base of Chron C13n (33.5 Ma) occurs at 40 ft above the PWL; top of Chron C13n (33.0 Ma) occurs at 80 ft above PWL. Taxonomy after Stevens and Stevens (1996) or Stevens (1977 MS). Although there appears to be a gradual size change through this interval. *M. chadronensis* actually ranges back to 35 Ma without change. Both *M. gracilis* and *M. affinis* persist to about 32 Ma without further change in size. The late early Orellan climatic change takes place at about the 60 foot level in Lusk, so the dwarfing was already underway a million years before the climate changed.

range through the early Orellan without further change. In the late Orellan (mid Chron C12r, 32.2 Ma), a slightly larger but more advanced species, *M. starkensis*, appears (Stevens and Stevens, 1996). This is the last species of *Miniochoerus*, persisting until the middle Whitneyan (late Chron C12r, 31.2 Ma).

In addition to merycoidodontines, a second subfamily of oreodonts, the leptaucheninines, are so abundant in the Whitneyan that they were the original indicator of that age. CoBabe (1996) reduced 7 genera and 31 species recognized by Schultz and Falkenbach (1968) to only two genera (*Leptauchenia*, *Sespia*) with three species. *Leptauchenia decora* (the oldest specimens were called "*Pseudocyclopidus orellaensis*" and "*Hadroleptauchenia eiseleyi*" by Schultz and Falkenbach, 1968) first appears in the early Orellan (latest Chron C13r, 33.6 Ma) and is found in beds as young as the Monroe Creek Formation (about 25 Ma). The larger taxon, *Leptauchenia major* (usually referred to "*Cyclopidius*"), first appears in the late Whitneyan (late Chron C12r, about 31.2 Ma) and also ranges up into the Monroe Creek Formation. Thus, the durations of these two species are about 8.5 and 6.2 m.y., respectively. Although both species are highly variable, most of this variability can be attributed to post-mortem deformation. CoBabe (1997) found no size or morphological characters that varied consistently during the long ranges of these species.

Lander (1997) summarized the occurrences of the primitive oreodonts known as agriocherers. *Agriocherus maximus* is an extremely long-ranging species, known from the early Chadronian (37 Ma) to the early Arikareean (28 Ma), or about 9 m.y. in duration with no visible change.

Ruminants: After oreodonts, the most abundant artiodactyl in the White River Group is the tiny deerlike ruminant *Leptomeryx*. Heaton and Emry (1996) have summarized recent studies of leptomerycids and conducted a detailed analysis of the group. In the earliest Chadronian (Quarry A level at Flagstaff Rim, Chron C16n2, 35.7 Ma), only *Leptomeryx yoderi* is present. In the middle Chadronian, the genus splits into two species: the larger, primitive *L. mammifer* (derived by a gradual anagenetic size increase from *L. yoderi*) and *L.*

speciosus (similar in size to *L. yoderi*, but distinguished by the entoconulid on the last lower molar). *L. speciosus* is static until the end of the Chadronian, when it evolved into *L. evansi*, the only leptomerycid of the Orellan. According to Heaton and Emry (1996) this later transformation is marked by the subtle, gradual change in a number of characters (labial ridge behind the p3 protoconid, *Palaeomeryx* fold on molars, slight size reduction, and a few other features). *Leptomeryx evansi* then persists without further change or speciation through the early Whitneyan (mid Chron C12r, about 31.7 Ma). While the transition from *L. speciosus* to *L. evansi* is not stratigraphically instantaneous, it occurs in a relatively short time compared to the long durations of both species.

The deerlike ruminant *Hypertragulus calcaratus* is also common in Orellan deposits. Prothero and Whittlesey (1997) recommended its first appearance as the defining criterion for the beginning of the Orellan. It persists through the Orellan and early Whitneyan without observable morphological change.

The tiny hypsodont ruminant *Hypisodus minimus* has not been revised recently, but Haake and Galbreath (1979) could find no consistent morphological changes in specimens from the early Chadronian through early Whitneyan.

Tylopods: Prothero (1996b) has recently reviewed the camelids from the White River Group. The primitive species *Poebrotherium eximium* is found from the early Chadronian through the earliest Orellan (latest Chron C13r, 40 feet above PWL at Lusk, Wyoming) without observable change. In the late Chadronian, *Poebrotherium wilsoni* arises by abrupt lengthening of the p1-2 diastema, and persists unchanged until the early Whitneyan (mid Chron C12r, about 31.7 Ma). The larger species, *Paratylopus labiatus*, also appears abruptly in the earliest Orellan, and persists without change through the Orellan. It is succeeded by *Paratylopus primaevus*, which is found throughout the Whitneyan. In addition, *Paralabis cedrensis* persists through the entire Whitneyan without visible change.

Several different lineages of stenomyline camels appear in the Whitneyan or Arikareean, and they

range throughout the entire Arikareean without noticeable change. These include *Pseudolabis dakotensis* (late Whitneyan to late Arikareean, 31.3–20 Ma), *Miotylopus gibbi* (early to late Arikareean), *Miotylopus leonardi* (early to late Arikareean, 28–20 Ma), and *Miotylopus taylori* (early to middle Arikareean, 28–25 Ma). Indeed, many of the larger mammals of the Arikareean (such as the rhinoceroses — see below) show remarkable persistence without change through almost the entire 8 m.y. interval.

The Oromerycidae (Prothero, 1997a) were tylopod artiodactyls that have long been mistaken for primitive camels. Only *Eotylopus reedi* is known from more than one place in the White River Group. It ranges from the middle Chadronian at Flagstaff Rim, Wyoming (Emry, 1992), to the very latest Chadronian in eastern Wyoming (Evanoff et al., 1992) with no apparent change.

The Protoceratidae have long been associated with ruminants, but recent work has established that they were also tylopods (Prothero, 1997b). *Poabromylus minor* ranges from the late Duchesnean (about 39 Ma) to the end of the Chadronian (33.8 Ma — Evanoff et al., 1992). *Heteromeryx dispar* and *Pseudoprotoceras longinarius* range through the middle and late Chadronian. *Protoceras celer*, however, is restricted to the middle–late Whitneyan of South Dakota.

Other artiodactyls: Compared to oreodonts, camels, and leptomerycids, other artiodactyls are relatively rare in the White River Chronofauna (Fig. 3). Specimens of the large, piglike entelodont *Archaeotherium* are the most abundant non-selenodont artiodactyls. Effinger (1997) recognizes only one species in the Chadronian, *A. coarctatum*, and one in the Orellan, *A. mortoni*. Each persists without change through several million years.

The piglike peccaries are very rare. Wright (1997) found that *Perchoerus probus* ranges through the entire Chadronian through Whitneyan, and *Thinohyus lentus* through the Chadronian and Orellan.

The anthracotheres are also rare, and have not been revised since Macdonald (1956) and Russell (1978). Most taxa are known from only a few specimens at a single locality, so they are irrelevant

to discussions of change. Only *Heptacodon curtus* is known from multiple localities and it appears to range through the Orellan and Whitneyan.

Although there are few specimens of the primitive artiodactyls known as leptocherids, Edwards (1976) found that the species are very long-ranging. *Stibarus obtusilobus* ranges from the middle Chadronian through the late Whitneyan; *Stibarus quadricuspis* from the middle Chadronian through the Orellan. *Leptochoerus spectabilis* ranges from the early Orellan to the late Whitneyan; *Leptochoerus elegans* from the early Chadronian through middle Whitneyan; and *L. emilyae* from the early to late Orellan.

2.2. Perissodactyls

Horses: Contrary to the common orthogenetic notion that only one lineage of horse was present in the Oligocene, gradually evolving from *Mesohippus* to *Miohippus*, Prothero and Shubin (1989) found that White River horses were very speciose (Fig. 4). *Mesohippus bairdi* and *M. exoletus* range from the late Chadronian to late Orellan; *M. westoni* from the early Chadronian to late Orellan; *M. barbouri* from the early Orellan to late Orellan. *Miohippus* is not the anagenetic successor of *Mesohippus*, but overlapped the latter genus through much of the Chadronian and Orellan. *Miohippus obliquidens* is an extremely long-ranging species, found from the late Chadronian to late Whitneyan. *Miohippus grandis* (referred to *M. "assiniboensis"* by Prothero and Shubin, 1989, but corrected by Storer and Bryant, 1993) ranges through the middle to late Chadronian. *Miohippus intermedius* and *M. gidleyi* are restricted to the late Whitneyan. *Miohippus annectens* and *M. equinanus* range from the late Whitneyan into the early Arikareean.

Ceratomorphs: In the past, rhinos have been greatly oversplit due to minor differences in molarization of premolars. Recent taxonomy (Prothero et al., 1989) has de-emphasized these features, since they can be shown to be highly variable within single populations. For example, *Hyracodon* was split into numerous invalid species, each based on slightly differences in the molarization of premolars. Prothero (1996c) recognized *Hyracodon*

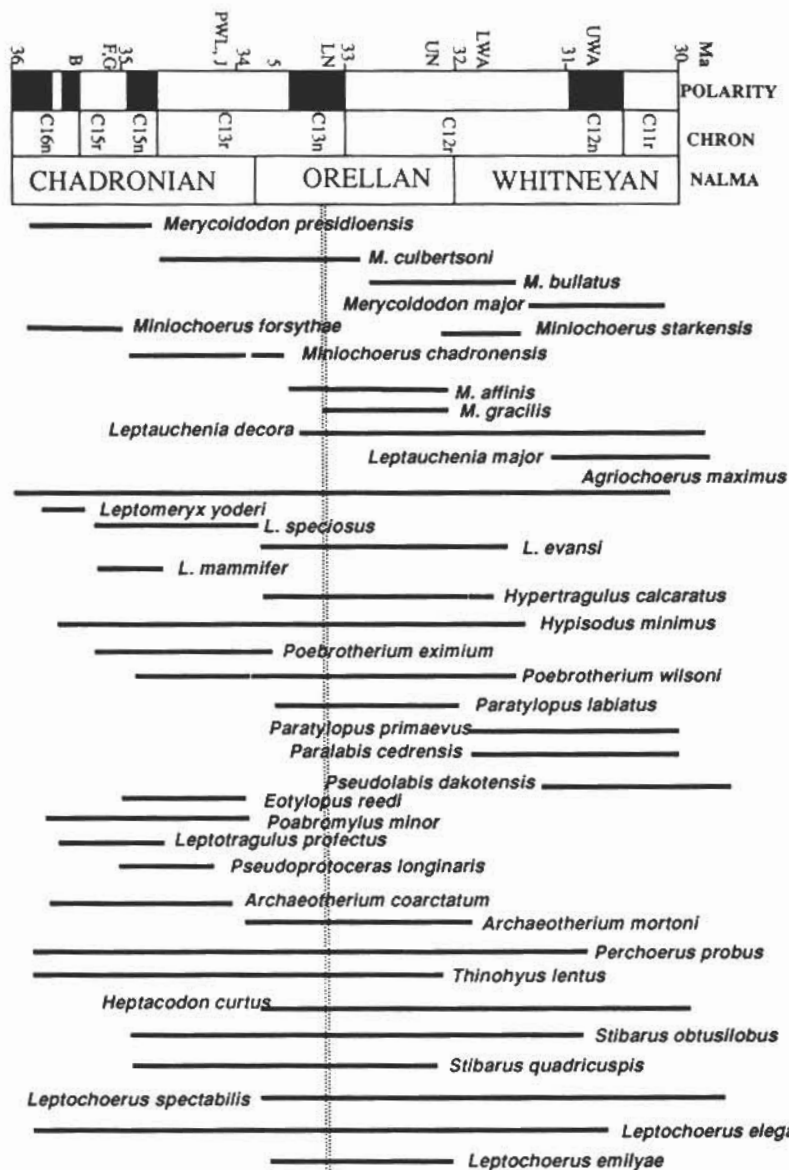


Fig. 3. Temporal durations of valid species of artiodactyls from the White River Group. Time scale after Prothero and Swisher (1992), Prothero (1996a), Prothero and Whittlesley (1997), Berggren et al. (1995), with modifications from Úbradovich et al. (1995). Eocene/Oligocene boundary coincides with the Chadronian/Orellan boundary within the precision of the dating. The earliest Oligocene (mid-Orellan, Chron C13n) climatic event is shown by the stippled bar. NALMA = North American land mammal "ages." Abbreviations of dated marker ashes and important stratigraphic horizons as follows: B, F, G, J = dated ashes at Flagstaff Rim, Wyoming; PWL = Persistent White Layer at Lusk, Wyoming, or "Purplish White Layer" in Sioux County, Nebraska (= Flagstaff Rim Ash J, according to Evanoff, pers. comm.); S = 5 tuff at Douglas, Wyoming (Evanoff et al., 1992; Obradovich et al., 1995); LN, UN = Lower and Upper Nodular Zones in Big Badlands, South Dakota; LWA, UWA = Lower and Upper Whitney Ashes, western Nebraska.

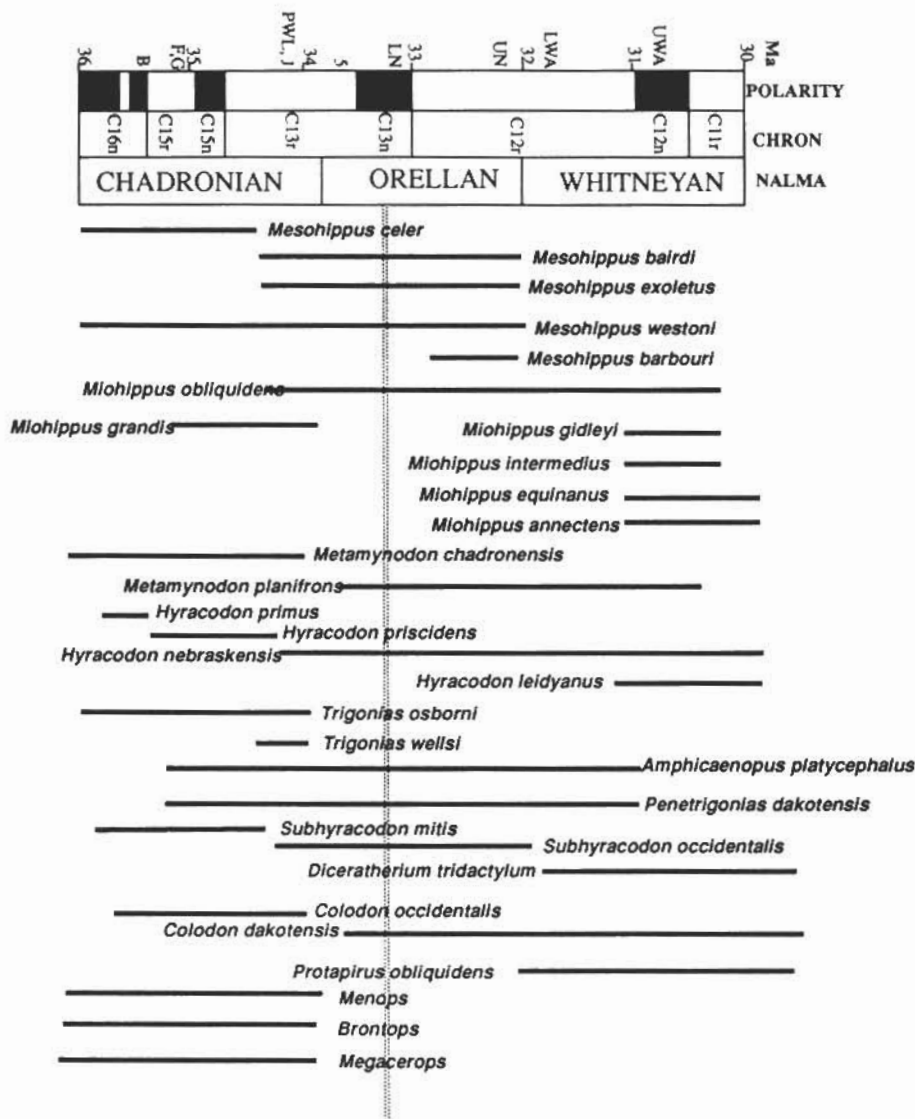


Fig. 4. Temporal durations of valid species of perissodactyls in the White River Group. All conventions as in Fig. 3.

priscidens through most of the Chadronian, *Hyracodon nebraskensis* through the late Chadronian, Orellan, and Whitneyan, and a larger, more advanced lineage, *Hyracodon leidyanus*, which also ranges through the middle and late Whitneyan.

Among the true rhinoceroses (family Rhinocerotidae), *Trigonias osborni* ranges through the entire Chadronian. *Subhyracodon mitis* occurs in the early and middle Chadronian, and

Subhyracodon occidentalis through the latest Chadronian and Orellan. The Whitneyan member of this lineage, *Diceratherium tridactylum*, is slightly larger in size, and some specimens show incipient rugosities for horns on the nasal ridges that characterize its Arikareean descendant, *Diceratherium armatum*. Two species, *D. armatum* and *D. annectens*, span almost the entire Arikareean (28-21 Ma) without noticeable change. *Amphicaenopus platycephalus* occurs in the

Chadronian and Whitneyan (but not the intervening Orellan); the same peculiar disjunct range characterizes *Penetrigonias dakotensis*.

Amyrodonts are less common than other rhinocerotoids, but *Metamynodon chadronensis* occurs throughout the Chadronian, and *Metamynodon planifrons* is found from the early Orellan to the late Whitneyan.

Tapiroids (Radinsky, 1963) are extremely rare in the White River Group, but *Colodon occidentalis* ranges through the Chadronian, and *Colodon otensis* through the Orellan and Whitneyan. *Protapirus obliquidens* ranges through the late Orellan and Whitneyan.

Brontotheres: Osborn (1929) grossly oversplit this group, based on small intrapopulational differences and supposed stratigraphic sequence within the Chadronian. Scott et al. (1937, p. 905), Clark et al. (1967), and most other authors have rejected his taxonomy, but no complete species-level revision has yet replaced it. Of the 7 genera and 37 species that Osborn (1929) listed in Chadronian deposits, Mader (1989) recognizes just 3 genera (*Menops*, *Brontops*, and *Megacerops*), but he has not resolved the species-level taxonomy. Such a revision will have to await the preparation of numerous brontothere skulls from the Frick Collection that are still in their original plaster jackets (some for more than 50 years). This collection has a clear stratigraphic succession (especially at Flagstaff Rim, Wyoming) with several large quarry samples that would demonstrate intrapopulational variability. For the present, however, it is impossible to determine the species-level diversity of brontotheres.

2.3. Carnivorans and creodonts

As would be expected, predatory mammals are much less common than their prey. Only a few carnivorous mammals are known from large sample sizes at more than a few stratigraphic levels, so it is impossible to look at fine-scale variation through time. However, recent systematic revisions of the most important groups has demonstrated stasis in nearly every group, with some extremely long-ranging species (Fig. 5).

Canidae: Wang (1994) and Wang and Tedford

(1996) have recently revised the early North American canids. They have shown the group to be much more diverse than previously reported, and a number of species occur in the Orellan and Whitneyan. The most common canid is *Hesperocyon gregarius*, which ranges from the Duchesnean through Whitneyan without any morphological change that could be documented in the large sample size catalogued by Wang (1994, appendix I). Other canids are much rarer, but some show long species durations. "*Hesperocyon*" *coloradensis* is restricted to the Orellan. "*Mesocyon*" *temnodon* and *Osbornodon renjie* occur in the Orellan and Whitneyan. *Osbornodon sesnoni*, *Parahydrocyon josephi*, *Ectopocynus antiquus*, *Oxyetocyon cuspidatus*, and *Cynodesmus thoooides* are known from the Whitneyan, and some of these taxa range into the Arikareean. The small, primitive borophagine *Cormocyon pavidus* occurs in the Orellan and Whitneyan.

Amphicyonidae: The amphicyonids, or "bear-dogs," have been updated by Hunt (1996). *Daphoenus vetus* and *D. hartshornianus* range from the Chadronian through early Arikareean. *Brachyrhynchocyon dodgei* occurs throughout the middle and late Chadronian, and possibly into the earliest Orellan. *Daphoenictis tedfordi* ranges through most of the Chadronian. *Paradaphoenus minimus* first appears in the earliest Orellan and ranges into the middle Arikareean.

Nimravidae: Considerably more common in the White River Group are the cat-like nimravids, which have been recently reviewed by Bryant (1996). *Dinictis felina* ranges from the mid-Chadronian to the late Whitneyan. *Pogonodon platycopis* occurs in the Orellan and the Whitneyan. *Hoplophoneus mentalis* ranges through the middle and late Chadronian. *Hoplophoneus primaevus* occurs throughout the Orellan and Whitneyan (and may range into the Chadronian). *Hoplophoneus occidentalis* occurs in the late early Orellan and the Whitneyan. *Hoplophoneus sicarius* is known from three specimens, one from the lower nodules in the Badlands, and two from unknown levels in Wyoming. *Hoplophoneus dakotensis*, *Eusmilus cerebrealis*, and *Nimravus brachyops* first occur in the late Whitneyan, and range into the middle Arikareean.



Fig. 5. Temporal durations of valid species of carnivorans and creodonts in the White River Group. All conventions as in Fig. 3.

Other carnivorans: In addition to amphicyonids, canids, and nimravids, there are a number of smaller White River carnivorans which were reviewed by Baskin and Tedford (1996). Most are known from only a few specimens, so their biostratigraphic utility is limited. For example, *Drassonax harpagops* is known from two specimens, one from the Scenic Member in the Big Badlands and one from the Orella Member in

Nebraska; both are from unknown levels. *Palaeogale lagophaga* occurs in the Orellan of Colorado, Montana, and South Dakota. The majority of the taxa discussed by Baskin and Tedford (1996), however, are from the Chadronian. They are known from so few levels that their sample size is inadequate even to document stasis.

Creodonts: Mellett (1977) reviewed the common

White River creodont *Hyaenodon* (Fig. 5). A number of rare species have short ranges within the Chadronian: *H. montanus* (early–middle Chadronian); *H. megaloides* (middle Chadronian); *H. mustelinus* (early–late Chadronian); and *H. microdon* (early Chadronian). However, the common species have long ranges. *Hyaenodon horridus* (the largest species) ranges from the early Chadronian to the end of the Orellan. *Hyaenodon crucians* occurs from the early Chadronian to the early late Orellan. *Hyaenodon brevirostris* occurs in the Whitneyan and early Arikarean.

2.4. Rodents

Ischyromyids: The most abundant of all White River rodents are the squirrel-like ischyromyids, which were revised by Heaton (1988, 1993, 1996). He found that *Ischyromys* (*Titanotheriomys*) *veterior* ranges through the early and middle Chadronian (Fig. 6). *I. (T.) douglasssi*, *I. (T.) relictus*, and several large unnamed species are known from single localities of Chadronian age. Specimens referable to *Ischyromys typus* occur in the late Chadronian and range to the end of the Orellan. The smaller species *I. (I.) parvidens* is restricted to the late Chadronian and early Orellan. As Heaton (1993) points out, this research invalidates the traditional idea (Howe, 1966; Wood, 1980) that a single gradually evolving anagenetic lineage of *Ischyromys* increased in size progressively from the late Chadronian through the early Whitneyan. Instead of three successive species (*I. parvidens*–*I. typus*–*I. pliatus*), there are two different-sized lineages, both exhibiting stasis, that coexist through the early Orellan (*I. typus* and *I. parvidens*). The sudden increase in mean size in middle Orellan ischyromyid samples is due to the reduction in numbers or extinction of the small species, *I. parvidens*, leaving only the larger species, *I. typus*.

Cylindrodonts: Emry and Korth (1996) reviewed the abundant Chadronian rodents known as cylindrodonts (Fig. 6). *Pseudocylindrodon neglectus* ranges from the early to middle Chadronian. *Cylindrodon nebrascensis* is found in the middle and late Chadronian. *C. natronensis* occurs in the early and middle Chadronian. *C. solarborus* is found in the middle and early late Chadronian.

Several other species of cylindrodonts were recognized by Emry and Korth (1996), but they are restricted to a few specimens from single localities.

Aplodontids: Wood (1980), Korth (1981a,b, 1986, 1989a,c, 1994b), and Emry (1992) gave the stratigraphic distribution of the aplodontid rodents (the living species are known as “mountain beavers” or sewellels) of the White River Group (Fig. 6). *Prosciurus vetustus* is restricted to the middle Chadronian; *P. relictus* and *P. parvus* range through the entire Orellan; *P. magnus* is from the late Orellan and Whitneyan. *Pelycomys rugosus* occurs in the late Chadronian; *P. placidus* occurs throughout the Orellan; *P. brulanus* is restricted to the early Orellan (Orella A–B). The only specimen of *Oropyctis pediasius* occurs in the early Whitneyan. The only specimen of *Epeiomys spanius* comes from an unknown level in the Orellan. *Campestralomys annectens* is restricted to Orella D; *C. siouxensis* ranges from the middle Whitneyan to early Arikarean.

Sciurids: Wood (1980), Korth (1987, 1989a), Korth and Emry (1991), and Emry (1992) gave the stratigraphic distribution of the White River squirrels (Fig. 6). *Protosciurus jeffersoni* occurs in the middle Chadronian, and *P. mengi* in the late Orellan. *Oligospermophilus douglassi* ranges from the latest Chadronian through the entire Orellan. *Cedromus wardi* ranges from Orella B–D; *C. wilsoni* occurs in the latest Orellan or earliest Whitneyan.

Castorids and eutypomyids: According to Wood (1980), *Eutypomys thomsoni* occurs in the late Orellan; *E. inexpectatus* and *E. parvus* are restricted to the early Chadronian; *E. magnus* occurs through the Chadronian and Orellan (Fig. 6). According to Wood (1980), Emry (1992), Korth (1988, 1989a), and Xu (1996), the only beaver in the White River Group is *Agnotocastor*. *Agnotocastor galushai* occurs in the middle Chadronian; *A. readingi* from Orella C; *A. coloradensis* from the late Orellan to early Arikarean; *A. praetereadens* from the early Whitneyan. The castorids diversified greatly in the Arikarean (Xu, 1996), but that radiation is beyond the scope of our study.

Eomyids: Wood (1980), Korth (1980, 1981a,b, 1989a,b), Emry and Korth (1993), and Storer (1987) reviewed the common White River rodents of the family Eomyidae (Fig. 6). *Adjidaumo mini-*

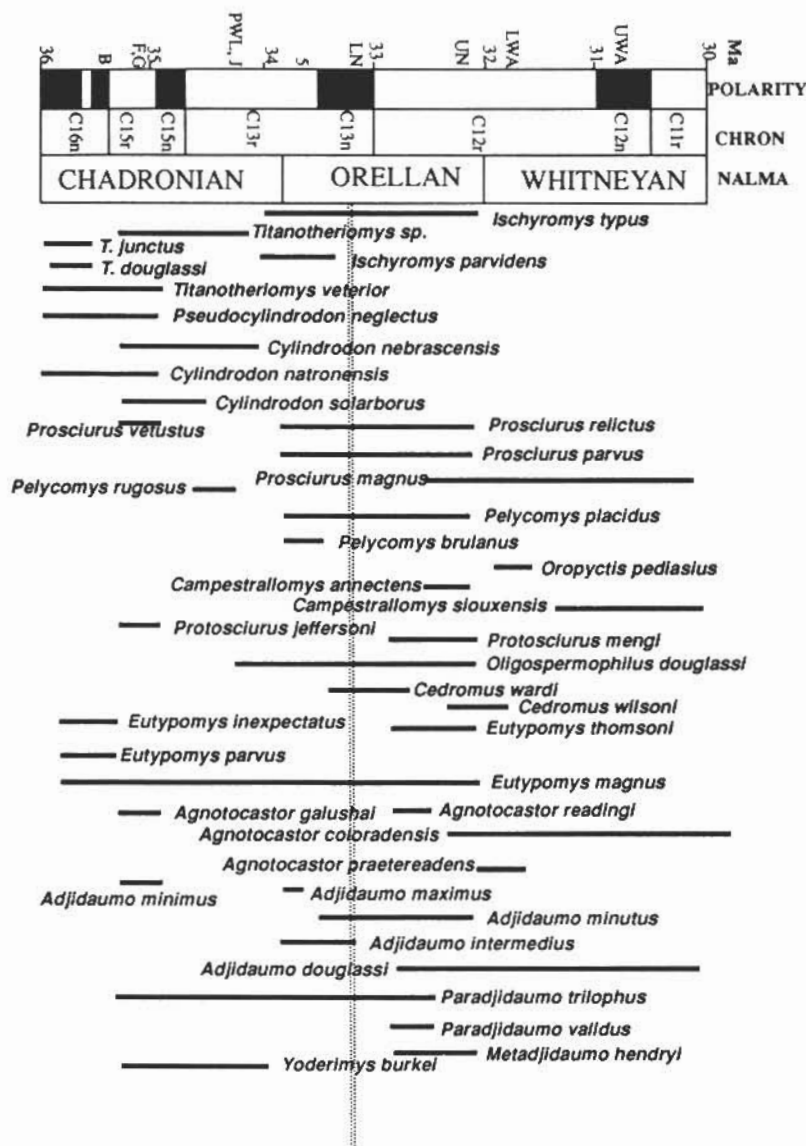


Fig. 6. Temporal durations of most of the valid species of rodents in the White River Group. All conventions as in Fig. 3.

mus occurs in the middle Chadronian, *A. maximus* in Orella A, *A. minutus* in Orella B–D, *A. intermedius* in Orella A–B, and *A. douglassi* in the late Orellan–Whitneyan. *Orelladjidaumo xylodes* is known from one specimen from Orella B. *Paradjidaumo trilophus* ranges from the middle Chadronian to the Orella C; Korth (1989b, p. 43) remarks that despite the large samples, there are no changes in size or morphology in this long-

ranging species. *Paradjidaumo validus* is restricted to Orella C; *P. hypsodus* is probably late Orellan in age. *Metadjidaumo hendryi* is restricted to the late Orellan.

A number of new species of yoderimyines were reported from the early Chadronian by Emry and Korth (1993), and *Yoderimys burkei* ranges into the middle Chadronian. Evanoff et al. (1992) reported *Yoderimys* sp. from the latest Chadronian

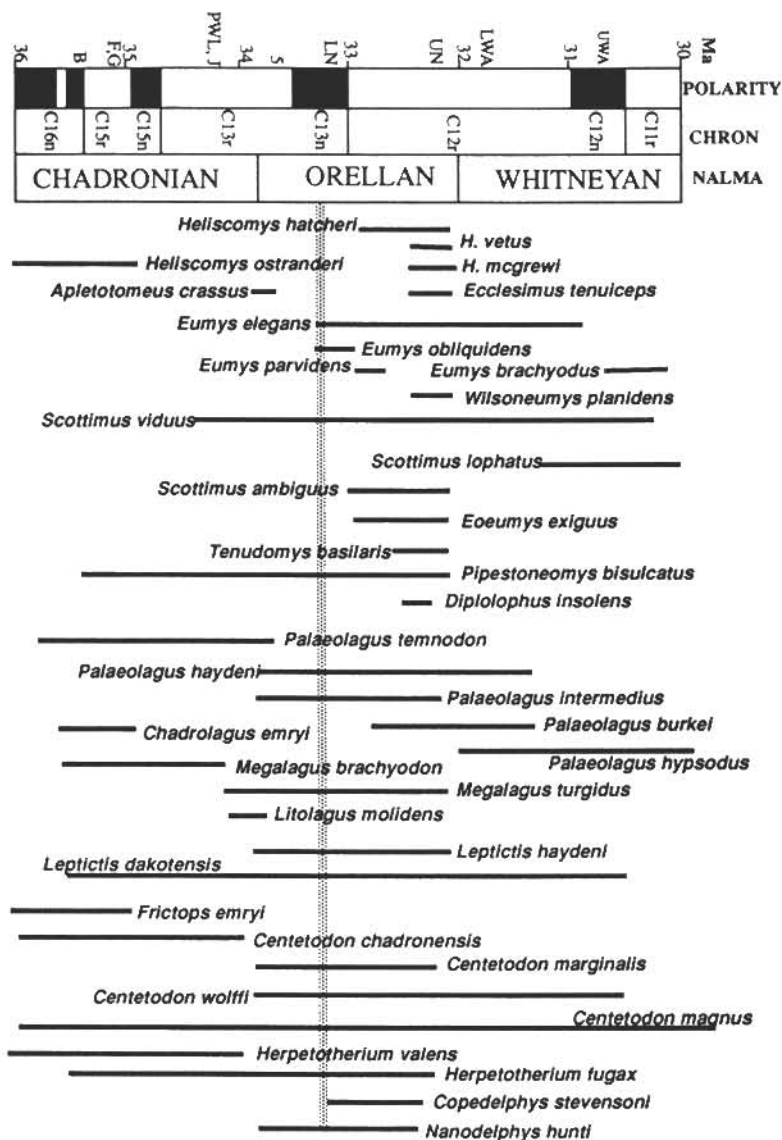


Fig. 7. Temporal durations of the rest of the valid species of rodents, plus rabbits, insectivorans, and marsupials in the White River Group. All conventions as in Fig. 3.

and Hageman (1988), but at each level, they can be assigned to *P. haydeni* or *P. temnodon* based on size and the presence or absence of roots on their upper cheek teeth, according to Gawne's identifications. We suspect that *Palaeolagus hemirhizis* is an artificial composite of two different species of rabbits (*P. temnodon* and *P. haydeni*) which overlap in range during the earliest Orellan.

They were lumped together because of the poor stratigraphic resolution of the University of Nebraska State Museum collections from Orella A.

Undisputed *Palaeolagus haydeni* specimens occur throughout the middle Orellan (Orella B-D in Toadstool Park, Nebraska) in great abundance. Korth and Hageman (1988) showed that this species increases slightly in size through the

Orellan, but no other morphological changes are apparent. The last *P. haydeni* occur in the early Whitneyan.

Palaeolagus intermedius is much rarer, but apparently ranges from Orella A to Orella D without any noticeable changes (Prothero and Whittlesey, 1997). The distinctively small species *Palaeolagus burkei* first occurs in mid Chron C12r (at the base of the upper nodules in the Badlands and in Orella C at Toadstool Park), and decreases slightly in size during the late Orellan (Orella D); it ranges into the early Whitneyan. *Palaeolagus hypsodus* first occurs in the early Whitneyan (mid Chron C12r, base of Whitney A, base of Poleslide Member), and ranges into the Arikareean.

In summary, Chadronian *Palaeolagus* shows about 2 m.y. of stasis, followed by gradual reduction in size and development of rootless upper molar during the early Orellan. From Orella B onward, several species of *Palaeolagus* are present, and except for slight size changes, they are static for several million years (until the middle Whitneyan).

According to Emry and Gawne (1986), *Chadrolagus emryi* is restricted to the middle Chadronian. Korth and Hageman (1988) reported that the rare rabbit *Megalagus turgidus* ranged through the entire Orellan, and point out that it increases slightly in size through the Orellan. In the Frick Collections, *M. turgidus* first appears 30 feet below the PWL at Lusk, Wyoming, so it could be used as an indicator of the latest Chadronian. However, it is difficult to distinguish from the typical Chadronian species *M. brachyodon*, which is characteristic of the middle Chadronian (Emry and Gawne, 1986), and may occur in the late Chadronian (Evanoff et al., 1992).

Litolagus molidens is an extremely rare rabbit. Four specimens are known between 40–90 feet above the PWL at Lusk (late C13r–early C13n) and one specimen from 30 feet below the 5 tuff at Douglas (late C13r). Its rarity makes this range discrepancy less surprising, but its range appears to span the latest Chadronian–earliest Orellan.

2.6. Insectivorous mammals

Compared to other mammalian groups, the insectivores have been relatively unstudied. Many

of the taxa are so tiny that they are rarely found during surface prospecting, and must be recovered by screen-washing. Consequently, their reported occurrences are restricted to localities and levels where extensive screen-washing has occurred, so that most of the reported stratigraphic ranges are probably underestimates. Still, for the sake of completeness, we will review what is known about White River insectivores (Fig. 7).

Novacek (1997) has studied the largest and most abundant of insectivores, the leptictids. *Leptictis haydeni* ranges through the entire Orellan. *Leptictis dakotensis* ranges from the Chadronian through Whitneyan. *Frictops emryi* is found in the early and middle Chadronian (Emry, 1992).

Lillegraven et al. (1981) reported the known occurrences of the geolabidine insectivore *Centetodon*. *C. chadronensis* is known from the early to late Chadronian. *C. marginalis* is known from the earliest to latest Orellan. The two specimens of *C. wolffi* are known from the early Orellan and late Whitneyan. *C. magnus* has an extraordinarily long range — from the late Uintan (43 Ma) to the latest Arikareean (21 Ma) — or about 22 m.y.

A number of species in several genera of insectivores, including *Apternodus*, *Clinopternodus*, *Micropternodus*, *Oligoryctes*, *Domnina*, *Cryptoryctes*, *Proterix*, *Ankyledon*, and *Oligoscalops*, were reported from the White River Group (Savage and Russell, 1983), but no Chadronian species are presently recognized in the Orellan or Whitneyan. Until more specimens are studied and their systematics are updated, it is impossible to tell how long-ranging most of these species are.

Besides insectivorans, there are a number of very rare taxa whose limited occurrence prevents much evolutionary analysis. These include the Chadronian pantolestid *Chadronia margaretae*, the Chadronian–Orellan apatemyid *Sinclairiella*, the early–middle Chadronian pangolin *Patriomanis americanus*, and the bizarre mole-like epiotheres, including the Chadronian *Epoicotherium unicum* and *Xenocranium* sp. (Emry, 1992) and the Orellan *Xenocranium pileorivale*. None of these taxa is known from more than a few specimens spanning

much time, so it is impossible to comment on their evolutionary patterns.

2.7. Marsupials

Marsupials are also very rare, but Korth (1994c) has recently summarized their occurrences in the White River Group (Fig. 7). *Herpetotherium valens* is known from the Chadronian, and *H. fugax* occurs in the middle Chadronian Pipestone Springs locality in Montana, and in the Orellan of Nebraska and Colorado. *Copedelphys stevensoni* ranges through the Orellan in Colorado and Wyoming. *Nanodelphys hunti* occurs in the Orellan of Nebraska, Colorado, and Wyoming. The distribution of marsupials is so spotty that none has yet been reported from the Whitneyan, yet they are well known from the Arikarean.

2.8. Summary

From the above discussion, it is obvious that stasis is the norm among the mammals of the White River Chronofauna. A century of paleontological research has revealed very few examples of gradual transformations in the 177 species lineages summarized here. Only the dwarfing in early Orellan *Miniochoerus*, the transformation from *Leptomeryx speciosus* to *L. evansi*, and possibly the changes in size and upper cheek tooth roots in early Orellan *Palaeolagus* might qualify as examples of gradualism. Since Gould and Eldredge (1977) and Stanley and Yang (1987) excluded size change from the concept of gradualism, there are even fewer examples of gradual morphological transformations.

Except for these three lineages, all other White River species that have any duration at all show stasis throughout their existence. When transformations between species occur, they are very rapid compared to the duration of the species that existed before and after the transformation. Although the sample in Figs. 3–7 is not complete, the mean duration of species ranges for the entire White River Chronofauna is 2.37 ± 2.2 m.y. (Table 1). Some groups have much shorter average durations (rodents average 1.14 ± 1.1 m.y.), while others were much longer-lived (such as carnivorous

Table 1
Species longevities of White River mammals

Order	N	Mean(m.y.)	Standard dev.
Artiodactyls	41	2.91	5.0
Perissodactyls	29	2.20	1.2
Carnivorans/creodonts	32	4.60	3.4
Rodents	58	1.14	1.1
Rabbits	8	1.58	0.7
Insectivores	5	6.70	7.7
Marsupials	4	2.10	1.2
Total	177	2.37	2.2

mammals, which average 4.6 ± 3.4 m.y., or insectivores, which average 6.7 ± 7.7 m.y.). In short, most species lasted at least 2–3 m.y., several ranged through the entire 7 m.y. of the White River Group, and some species (such as *Centetodon magnus*) persisted as long as 22 m.y.

Stanley (1978, 1979) estimated the mean duration of Pleistocene mammalian species at about 1.0 m.y., and Eocene mammalian species at 2.6 m.y. Gingerich (1980, 1985), however, estimated the duration of Eocene mammalian species at 0.8–1.0 m.y. Our results are more in line with the longer estimates and with the estimates of species durations among marine invertebrates, which range from 2.0 to 4.4 m.y. (Gingerich, 1985).

Of course, this study is hampered by the fact that not all species are represented in the large numbers that make detailed evolutionary studies possible. Those which have received such study have been addressed in detail. For other taxa, only species ranges are available. While some cases of minor anagenesis may be missed for such taxa, the fact is that these species exhibit an enormous amount of morphological stability in comparison to their seemingly abrupt origination events.

Among well-documented taxa, we find that gradual changes in morphology are rare. Species may change slightly in mean size, but other than that they tend to remain unchanged for long intervals before disappearing or giving rise to descendants. Even in these well-documented taxa, as with poorly-documented taxa, it is often impossible to establish ancestor-descendant relationships. This fits well with the punctuated

equilibrium model. Of course, it is assumed under the concept of evolution that all species are related, but if the major transitions occurred rapidly in restricted geographical areas, then they tend not to be documented. Under the gradualistic model, we would expect major changes to be documented in every lineage, since the White River sequence provides continuous coverage for almost 7 m.y.

The patterns seen in the White River Chronofauna (sudden appearances, stasis, sudden disappearances or species transitions) are the most common pattern throughout the fossil record. What makes it more striking in the White River sequence is the completeness of the record. Patterns that a gradualist might have dismissed as a result of gaps in the stratigraphic sequence or unfossiliferous zones cannot be so easily dismissed here. This is particularly true of the critical interval in the early and middle Orellan, when several areas (especially Lusk, Wyoming) produce almost continuous records of fossils across the early Oligocene climatic crash, with no gaps or barren intervals. The sample density shown in Fig. 2 is representative, so the abruptness of appearance of many species cannot be attributed to gaps in the record.

Critics might suggest that the investigators of the White River Chronofauna are biased in favor of static species definitions. Nothing could be further from the truth. Many of the early investigators, such as Osborn and Scott, were firm believers in gradual orthogenetic changes in horses and brontotheres. Howe (1966) attempted to demonstrate anagenetic change in *Ischyromys*, and Schultz and Falkenbach (1968) believed in the gradual transformations among their oversplit rodent taxa.

Unlike many invertebrate paleontologists and micropaleontologists, mammalian paleontologists have historically not been particularly interested in precise range-zone biostratigraphy, so they were not unconsciously biasing their species definitions to make them easier for zonation. In fact, they were so uninterested in biostratigraphy that they seldom bothered to collect adequate stratigraphic data on most specimens. Until Morris Skinner and the collectors of the Frick Laboratory made the effort to record stratigraphic data with the Frick

Collections, there was no such data base, so biostratigraphy is just emerging for the White River Group after 150 years of study. In spite of all these biases in favor of gradualism, very few examples of gradual transformation have ever been documented among the dozens of lineages in this richly fossiliferous interval.

3. Diversity analyses

The temporal ranges of species shown in Figs. 3–7 can also be summarized in terms of diversity statistics. This was attempted at the generic level by Prothero (1985) and Stucky (1992), but the chronostratigraphic precision and systematic quality of the data base has improved considerably since then. For this study, the middle Chadronian–late Whitneyan was divided into million-year increments, and each taxon present in the increment, as well as each origination and extinction, were tallied.

The results are shown in Table 2. Standing diversity reaches a peak of 90 species in the late Orellan, and then declines in the Whitneyan. This decline, however, may be partly an artifact of the limited outcrops of Whitneyan strata (found mostly in the Big Badlands of South Dakota and in western Nebraska), compared to the abundantly fossiliferous Chadronian and Orellan strata found in several states (Emry et al., 1987). However, this result is consistent with the peak in generic diversity in the Orellan reported by Stucky (1992) (fig. 24.4), followed by a decline in generic diversity in the Whitneyan. However, Stucky's data did not have the species-level resolution, nor temporal resolution within the Orellan or Whitneyan, that our study does.

Origination and extinction rates can also be calculated from these data. Again, the late Orellan was the period of highest extinction, primarily because many of the taxa characteristic of the Orellan do not persist to the Whitneyan. Remarkably, the Chadronian/Orellan (=Eocene/Oligocene) boundary, and the mid-Orellan climatic event (both during the 33–34 Ma time interval), were periods of remarkably low extinction.

Table 2
Diversity data for the White River Chronofauna (given in species per m.y. time increment)

	34–35 Ma	33–34 Ma	32–33 Ma	31–32 Ma	30–31 Ma
Diversity	77	83	90	59	57
Extinctions	28	17	45	13	21
Originations	15	38	26	18	4

However, the Chadronian–Orellan transition was the interval of highest origination rate.

Alroy (this volume), using an entirely different method, compared diversity calculated from sequential faunal lists. Unfortunately, his method tends to ignore rare taxa that may not occur in his faunal lists but are known for the time interval, and much of his data base did not have the advantage of the up-to-date systematic studies that were available to us. (As much as possible, we have freely shared these unpublished papers with him). His generic diversity curve (this volume, fig. 4) shows a sharp drop at the Chadronian–Orellan transition, which is opposite to the results obtained by our data or by Stucky (1992). Alroy (this volume) claims that this is due to depression of origination rate during the early Orellan, but our more complete data base yields the highest origination rate during the late Chadronian–early Orellan.

Alroy (this volume) criticizes our study for focusing on extinction rates during the Chadronian–Orellan transition, rather than origination rates. However, his observation of low origination rate is a comparison between late Chadronian and early Orellan faunal lists, but we are comparing early and middle Orellan faunas which span the climatic event discussed below. Indeed, Alroy's data set shows that there is no difference in diversity between the early and late Orellan, which is precisely our point.

4. Discussion

The tremendous stability demonstrated by species in the fossil record raises larger questions about the nature of species. Traditional Neo-Darwinism has typically treated species as arbi-

trary slices of continuously evolving lineages (see discussion in Eldredge, 1995). Natural selection was thought to be constantly acting on every tiny feature of an organism, weeding out even the smallest imperfection. Species were thought to continuously respond to changes in their environment, adapting to every small climatic fluctuation as studies on the Galapagos finches (see Weiner, 1994) so vividly demonstrated. A popular metaphor was the "adaptive landscape" originally introduced by Sewall Wright (1931). Species were always trying to reach the "adaptive peaks" of the "landscape" and were continually changing in response to the shifting of the peaks beneath them. In another popular metaphor, species were seen as infinitely flexible "rolling balls" which constantly tracked environmental change. Lest anyone doubt this characterization of Neo-Darwinian concepts of species flexibility, the recent textbooks by Minkoff (1983), Strickberger (1990), and Ridley (1993), or Weiner's summary of recent evolutionary research (Weiner, 1994), all promote this perspective.

However, as the studies which document stasis in the fossil record continue to accumulate, Neo-Darwinists have been forced to reassess the nature of species. As Eldredge (1995, p. 64) points out, this dynamic concept of species clashes with common sense and experience. Naturalists have long known that when organisms encounter changing environments, the typical response is not to gradually evolve and adapt, but to move to more favorable habitats. The rapid environmental changes during the Ice Age cycles of the Pleistocene did not cause much gradual evolutionary transformation. Instead, the majority of Pleistocene mammals remained unchanged, but moved in response to their changing habitats (White and Harris, 1977; Barnosky, 1987; Vrba, 1980, 1985).

A similar response was reported by Cronin (1985, 1987) for marine ostracodes, and the habitat-tracking response of most marine microfossils is so well known that they have been used as temperature indicators for migrating water masses.

In the White River Group, there is independent evidence of environmental deterioration. Recent research (summarized in Prothero, 1994a) has shown that the Eocene–Oligocene transition was probably the most fundamental climatic change in the last 65 m.y., with the tropical “greenhouse” world of the Mesozoic and Paleocene–early Eocene being replaced by the modern “icehouse” world. Oxygen isotopes show that global cooling began in the middle Eocene, and the major cooling event (marked by the biggest marine extinction of the entire interval) took place at the end of the middle Eocene (about 37 Ma, or near the beginning of the Chadronian). Unfortunately, the fossil record of the Duchesnean–Chadronian transition is so poor that we cannot conduct the kind of detailed analysis outlined above. However, it is interesting to note that most Duchesnean taxa persist into the Chadronian, and there are relatively few extinctions at the end of the Duchesnean. In fact, the beginning of the Chadronian is marked primarily by first appearances rather than by a mass extinction event (Emry et al., 1987; Lucas, 1992).

Through the late Eocene, there was relatively little climatic change. Miller et al. (1992) documented four separate impact horizons (dated from 35.4–36 Ma) which apparently had no effect on faunas, either on land or in the marine realm (Prothero, 1994a). The actual Eocene/Oligocene boundary (as recognized by the extinction of the spiny planktonic foraminiferan *Hantkenina*) occurs late in Chron C13r, about 33.7 Ma, or very close to the Chadronian/Orellan boundary as currently calibrated (Berggren et al., 1995; Prothero and Whittlesey, 1997). However, as numerous paleontologists (e.g., Corliss et al., 1984; Snyder et al., 1984; Aubry, 1992) have shown, the boundary itself is not a major mass extinction event worthy of the grandiose title “Terminal Eocene Event,” but is marked by extinction of just a few foraminifers and coccoliths (see Prothero, 1994a).

All of the recent evidence points to major cli-

matic change in the earliest Oligocene (mid Chron C13n, about 33.2 Ma). This is the biggest shift in the oxygen isotopes, and may indicate a drop in mean global temperatures by 2–3°C (Miller et al., 1987; Miller, 1992). Miller et al. (1991) summarized the evidence for a major growth of Antarctic ice sheets in the earliest Oligocene, which was the primary trigger of this climatic change. Different causes have been given for this pulse of Antarctic glaciation, but it was probably due to the expansion of circum-Antarctic circulation between Australia and Antarctica, combined with the development of the North Atlantic Deep Water (Prothero, 1994a).

In North America, the response was dramatic. Using land floras from Alaska and the Pacific Northwest to the Gulf of Mexico, Wolfe (1978, 1992, 1994) showed that mean annual temperature in North America declined almost 13°C in North America in less than a million years. This is more than three times the temperature change between Pleistocene glacials and interglacials. More important was the increase in seasonality. According to Wolfe (1978), the mean annual range of temperature increased dramatically from about 5°C to almost 25°C. In botanical terms, most of North America went from subtropical vegetation typical of Central America today, to highly seasonal deciduous vegetation typical of the northeastern United States today.

Although plant fossils and pollen are not well preserved in the White River Group, Retallack (1983, 1992) has interpreted climatic changes from changes in paleosols. The Chadron Formation paleosols of the Big Badlands (which are as young as Chron C13n in the Cottonwood Pass and Pinnacles areas of the Badlands — Prothero and Swisher, 1992; Prothero and Whittlesey, 1997) were produced in a dense woodland with greater than 1000 mm annual precipitation. Lower Scenic Member paleosols (early Orellan, late Chron C13n) were formed in a more open, mixed woodland–grassland, with less than 500 mm annual precipitation. Sedimentological evidence from Douglas, Wyoming (Evanoff et al., 1992) shows an abrupt transition early in Chron C13n from moist floodplains to semi-arid landscapes with abundant dune deposits of volcanic dust.

What about the non-mammalian fauna? Climatically sensitive land snails (Evanoff et al., 1992) are particularly good environmental indicators. Latest Chadronian land snails were large-shelled subtropical taxa now found in central Mexico, and indicate a mean annual temperature of 16.5°C and an annual precipitation of 450 mm. Late early Orellan (Chron C13n in Douglas) land snails are drought-tolerant, small-shelled taxa indicative of a warm-temperate open woodland with a pronounced dry season, such as is found in Baja California today. Reptiles and amphibians strongly suggest cooling and drying (Hutchison, 1982, 1992), with aquatic forms (crocodilians, freshwater turtles, and salamanders) disappearing in the Orellan, replaced by land tortoises. Size reduction in turtles (Hutchison, 1992) also indicates increased aridity.

All of these climatic changes are concentrated in the late early Orellan, in the middle of Chron C13n, about 33.2 Ma (stippled bar across Figs. 3–7). A brief scan of Figs. 3–7 quickly shows that this was *not* a period of major faunal turnover or a mass extinction event in the mammals. Most of the characteristic Chadronian taxa, such as the brontotheres, oromerycids, cylindrodonts, and yoderimyines had already become extinct in the latest Chadronian or earliest Orellan (late Chron C13r). The dwarfing trend in miniochoeres and rabbits also takes place in the earliest Orellan, and is already completed by the late early Orellan. A few taxa (such as *Eumys elegans* and a few other rodents, and *Miniochoerus gracilis*, the most dwarfed of the miniochoeres) first appear in Chron C13n, but most of the Orellan species had already appeared in the earliest Orellan. Even more striking is the number of lineages which showed no evolution whatsoever in the late early Orellan. At least 62 out of 70 lineages pass through this climatic crisis with no change that would allow a systematist to recognize a different species.

The only sign in the mammalian faunas that climatic change might have taken place in the late early Orellan is the greater abundance of eumyine cricetid rodents, and the first appearance of rare leptachenine oreodonts, both of which had higher-crowned teeth that might be better adapted to tougher vegetation. Likewise, the disappearance

of *Ischyromys parvidens* appears to coincide with the late early Orellan. But the overall Orellan fauna remained essentially unchanged through the interval, composed of the same few dominant taxa (Emry et al., 1987; Clark et al., 1967): *Merycoiodon culbertsoni*, *Miniochoerus gracilis*, *Leptomeryx evansi*, *Poebrotherium wilsoni*, *Archaeotherium mortoni*, *Meshippus bairdi*, *Hyracodon nebraskensis*, *Subhyracodon occidentalis*, *Ischyromys typus*, and *Palaeolagus haydeni*. These dominant groups persisted through the entire early Orellan (32.6–33.8 Ma), and only a few new taxa (such as *Palaeolagus burkei* and *Merycoiodon bullatus*) augment or replace them in the late Orellan. The next significant turnover event occurs at the Orellan–Whitneyan boundary, when eolian deposits dominate, and leptachenine oreodonts become the most common mammals (Emry et al., 1987).

The nearly complete lack of response to this well documented climatic change raises interesting questions about the nature of species. The studies of fruit flies and Galapagos finches seem to show that organisms can evolve rapidly in response to environmental pressure. Yet these changes must not amount to much long-term change or to new species very often, because the prevalence of stasis in the fossil record shows that most species persist for millions of years in spite of environmental change. The data discussed above are the most clear-cut example yet of a complete mammalian fauna which does not track the environment, but virtually ignores radical shifts in vegetation, temperature, and seasonality. Unlike Ice Age organisms, these mammals do not even migrate in response to the climate change. The faunas of the earliest, early late, and late Orellan remain virtually identical from the north (North Dakota) to the south (Colorado).

This conclusion is in striking contrast to Vrba's (Vrba, 1985) turnover pulse hypothesis, which postulates that most faunal change occurs during climatic change. Even though recent work by DeMenocal (1995) has provided new evidence for climatic changes in the Plio-Pleistocene of Africa, the climatic evidence in our study is equally strong. Instead, our result contradicts the widespread

notion that climatic change is the driving force in evolution.

Some reviewers have suggested that the lack of response of early Orellan mammals was due to the fact that they were survivors of several mass extinctions, starting in the middle Eocene. However, the White River Chronofauna in no way resembles the ice-adapted Pleistocene mammalian faunas; most of the taxa are similar to those that were very successful in the deep forests of the Duchesnean and Chadronian. It is possible to imagine that a few taxa might be extreme generalists who could live on any vegetation that came along (like living goats, for example), but not the entire White River Chronofauna.

We do not have a simple solution to the puzzle of the lack of response by Orellan mammals to environmental change. Clearly, the attempt by Neo-Darwinists (Charlesworth et al., 1982; Levinton, 1983; Lande, 1985) to explain stasis by stabilizing selection is wrong in this case, because the environmental changes in the late early Orellan must have been very destabilizing. The usual alternative is to argue that species are complex, integrated entities, which have developmental constraints that prevent them from changing in any direction (Maynard-Smith, 1983; Kauffman, 1983; Mayr, 1992; Gould, 1980, 1992). These ideas are very promising, but it is not possible to evaluate them in the extinct White River Chronofauna. Unlike Pleistocene life, the White River mammals have few modern counterparts or living descendants, and even when there are living relatives (horses, camels, rhinos, dogs, rabbits, beavers, and squirrels, for example), they are so different from their early Oligocene ancestors that any such comparison would be suspect.

Evolutionary theory has come a long way since Eldredge and Gould (1972) first pointed out that stasis is the norm in the fossil record, and the data cannot be simply dismissed or explained away. As the other papers in this symposium demonstrate, the prevalence of stasis and the apparent coincidences of episodes of stasis and faunal turnover are macroevolutionary phenomena that cannot be explained by processes seen in a fruit-fly jar. In fact, stasis and resistance to change is so ingrained that species can actually pass through the most

significant climatic change of the last 65 million years as if nothing happened.

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