TURTLE DIVERSITY AND ABUNDANCE THROUGH THE LOWER EOCENE WILLWOOD FORMATION OF THE SOUTHERN BIGHORN BASIN

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Abstract. — The early Eocene is a period of significant change in the composition of North American turtle faunas. Over the first 2.2 million years of the Eocene, the fossil record documents several immigrations into depositional basins of the Western Interior and an expansion in the ecological niches of turtles toward herbivory. Focusing on the Willwood Formation, we document change in generic and species richness in greater detail than previously available and place this in a better-constrained temporal framework, confirming that the two major episodes of change in the turtle faunas coincide with the appearance of Wasatchian mammals and with an interval of climate change at biohorizon B-C within the Wasatchian land-mammal age. We report changes in relative abundances of turtles and discuss possible explanations for these changes. Climate change (at least as estimated by proxies for mean annual rainfall or temperature) does not provide an adequate explanation for the observed changes. Rather, we think that changes in habitat heterogeneity may be a better explanation and that changes in the turtle fauna can best be understood by examining how change in climate, in combination with effects of local tectonic controls on floodplain development, affected the availability and preservation of diverse habitats.

INTRODUCTION

The mammalian portion of the terrestrial early Eocene vertebrate fauna has attracted much attention, but an understanding of the herpetofauna (amphibians and reptiles) is essential for evaluating and testing scenarios of coevolution of early Eocene climates and biotas. Testudines are the best represented order of the ancient herpetofauna. Turtles are preserved in great numbers in a variety of lithologies and depositional settings, and even isolated elements of the shell are readily recognizable and identifiable. The Bighorn Basin record of turtles studied here (Fig. 1), is significant in being one of the longest (approximately 2.2 million years) and most complete records of a local fauna in the Western Interior and because it is currently the only record of faunal change that can be correlated with similarly detailed studies of local changes in other aspects of the fauna (e. g., Gunnell, 1998; Hartman and Roth, 1998), climate (Wing et al., 2000) and hydrology (Bown and Kraus, 1993).

The Bighorn Basin testudine record was originally and preliminarily summarized by Hutchison (1980), who first recognized this major reorganization of the ecologic and taxonomic composition of turtle fauna. Subsequently, Hutchison (1982, 1992) explored the relationship between reptile diversity and climate change through the Paleogene, identifying the linked roles that climate and hydrology have in affecting changes in diversity and herpetofaunal composition. Systematic work on Bighorn Basin turtles in the last twenty years is somewhat more limited. Gingerich (1989) reported the earliest records of the immigrant *Echmatemys* from Wa-0 localities in the Clarks Fork Basin. Hutchison (1991) described the Kinosternidae (mud turtles) of the Bighorn Basin. Hutchison (1998) summarized
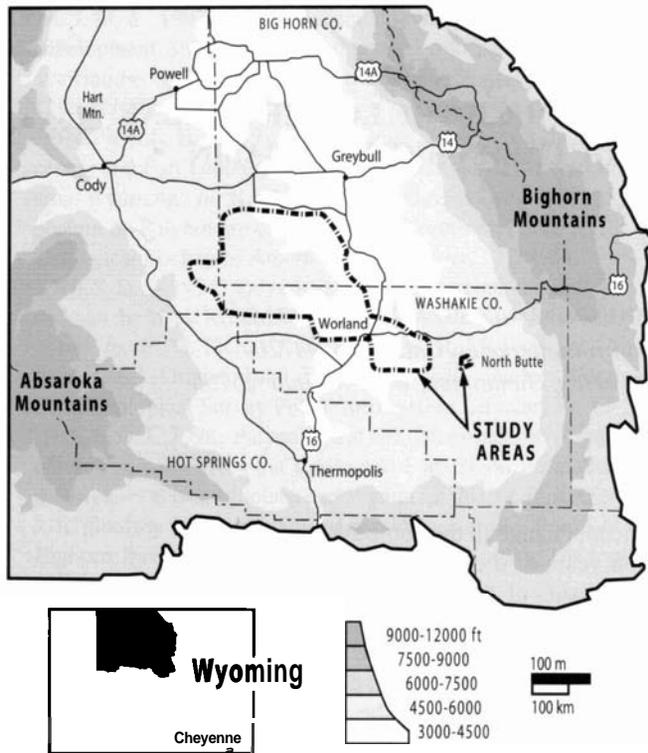
FIGURE 1 — Map of the Bighorn Basin, Wyoming, showing the distribution of turtle-bearing localities considered here.

the Paleocene-Eocene record of turtles in North America on a regional scale, observing two general patterns:

1. Across the Clarkforkian to Wasatchian North American Land-Mammal Age (NALMA) boundary, Clarkforkian taxa persist, and several new taxa appear (two genera of Kinosternidae, *Echmatemys* and Emydid P). These immigrants are relatively small in body size, represent both carnivores and omnivores, and are a mix of Asian and southern North American immigrants. Their first appearances are essentially synchronous across basins and correlate with mammalian immigrations (Hutchison, 1980; Holroyd and Hutchison, 2000).

A second major rearrangement of turtle faunas occurs in the mid-Wasatchian with the appearance and comparatively rapid increase in abundance of testudinids and dermatemydids (both large herbivorous turtles). This event is coincident with much increased warming, the local appearance of "megathermal" flora (Wing, 1998), and within a period of mammalian turnover called "Biohorizon B-C" (see Schankler, 1980; Bown et al., 1994). The late Wasatchian (late early Eocene) is marked by the last occurrences in the northern Rockies of the most common

Paleocene taxa (Emydid C and ***Planetochelys)*** as well as the smallest emydid (Emydid P). In the case of Emydid C and Emydid P, these are their last known occurrences anywhere; *Planetochelys* or a form similar to it appears to persist into the Uintan of Texas (Hutchison, unpubl. data).

Holroyd and Hutchison (2000), based on preliminary analysis of records of local faunas from several Wyoming basins, observed that taxonomic turnover during the Eocene is concentrated in the omnivorous to herbivorous turtles, both aquatic and terrestrial. Among the omnivore-herbivores, first appearances across basins are essentially synchronous, but last appearances (local extinctions) are not correlated across or within basins and are not readily correlatable to global climate trends, suggesting a different or more complex set of controls on their presence-absence. Carnivorous turtles, exclusively aquatic during this time, show no marked turnover at the regional scale, but do evince increasing diversity with the addition of kinosternids at the beginning of the Eocene and the local first appearance of additional trionychid genera in the mid-Wasatchian. However, the late Paleocene to early Eocene record of carnivorous turtles (particularly trionychids and baenids) is also more difficult to interpret than that of herbivorous taxa. Because many parts of the trionychid shell are morphologically conservative, isolated trionychid elements are difficult to assign below family level. Similarly, baenids (comparatively rare in any case) can only be assigned to genus when certain diagnostic elements are recovered. Consequently, it is very difficult to examine genus-level diversity patterns in these two groups in the absence of a more complete record. The problem is compounded in the Bighorn Basin record because only a handful of localities have produced sufficiently complete representatives of these groups to enable identification to genus. Thus, significant patterns of change may exist among carnivorous turtles through this interval, but they are still masked by an inadequate record of the groups.

Here we provide an updated summary of the Wasatchian Willwood Fm. turtle record based on more than 300 localities in the southern Bighorn Basin composite stratigraphic section (Bown et al., 1994), detail changes in the omnivorous-herbivorous turtle fauna, and examine how these relate to changes in climate and landscape through the period of greatest change, the early and middle early Eocene (basal to mid-Wasatchian).

THE TESTUDINE FAUNA

Thirteen genera in eight families are currently known from the Wasatchian of the Willwood Formation (Table 1). The number of species represented is still under study, but most genera appear to be monotypic through the Willwood Formation. An exception is the batagurid *Echmatemys,* which may show species changes through the section and include more than one lineage (Hutchison, pers. obs.). In terms of species richness, the numbers of species found throughout Willwood time are comparable to those observed in modern tropical to warm

TABLE 1 — Testudines of the Willwood Formation, with voucher specimens documenting the stratigraphic range of each genus in the southern Bighorn Basin stratigraphic sections. All specimens and localities are University of California Museum of Paleontology (UCMP). Locality equivalencies to US Geological Survey or Yale localities are noted as appropriate.

Baenidae
    Baena, 364 *m* , V81093: 173699
    Chisternon, 546 m, V96102 [=USGS D1212]: 173530
    Palatobaena, 364 m, V81093: 173700

Chelydridae
    Protochelydra, 343 m, V81071 [=Yale 135]: 136099; 481 m, V81170: 173526

Dermatemydidae
    Baptemys, ca. 420 m, V98097 [10 m below Yale 271]: 173815; 601 m, V96073 [=Yale 33]: 173529

Bataguridae
    Echmatemys, < 30 m, V99019 [=USGS D2018]: 212845; 601 m, V96073: 173713

Emydidae
    Emydid C, 30 m, V96118 [=USGS D1296]: 173533; 511 m, V81178: 126466
    Emydid P, 30 m, V96118 [=USGS D1296]: 173531; 435 m, V82201: 170567 and V82200: 170555

Family incertae sedis
    Planetochelys, 34 m, V97014: 173534; 446 m, V96190: 173761; 516 m, V96124: 173812

Kinosternidae
    Baltemys, 34 m, V97014: 173542; 546 m, V81182 [=Yale 192]: 127249

Testudinidae
    Hadrianus, 392 m, V82346 [=USGS D1413]: 154505; 636 m, V96148 [=USGS D1651]: 173695

Trionychidae
    Plastomenus, 380 m, V81043 [=Yale 67]: 154122; 505 m, V96045 [=USGS D1609]: 170351; cf.
    Plastomenus, 559 m, V99207 [=USGS D1622]: 173716
    Aspiderites (not shown), 465 m, V96159 [=USGS D1737]: 156078

temperate turtle faunas in much of Asia, the Amazon, or the southeastern United States. Generic richness of Bighorn Basin turtles, however, is greater than in many of these faunas. Despite its high diversity, the Willwood turtle fauna is still less rich than the most diverse modern faunas found in the Ganges River drainage (Iverson, 1992) or than in the latest Cretaceous to early Paleocene of North America (Hutchison and Archibald, 1986).

Turtles of the Willwood Formation display a wide range of shell shapes and sizes (Fig. 2), indicating the range of aquatic and terrestrial habitats they occupied. Baenidae is an extinct group of bottom-walking turtles that appear to have preferred river channels. Here Baenidae includes *Baena, Palatobaena,* and *Chisternon. Palatobaena* and *Chisternon* have not previously been reported from the Willwood Formation, but constitute the youngest known record of *Palatobaena* and the oldest

known record of *Chisternon* (Hutchison, 1998). For Chelydridae (snapping turtles), *Protochelydra* is the only described Wasatchian taxon, although another genus may be present (Hutchison, pers. obs.). Similarly, *Baptemys* is the sole early Eocene representative of the family Dermatemydidae, a family of large aquatic turtles endemic to North America.

Pond turtles of the Emydidae *sensu lato* (including both the Bataguridae and Emydidae *sensu stricto)* are the most diverse group of Willwood turtles, with a minimum of three genera. Records of "Emydidae indet." are probably poorly-preserved or pathologic *Echmatemys* specimens, but some may document another, undescribed genus ("Emydid E" of Hutchison, 1992, table 23.2). *Planetochelys,* of unclear phylogenetic affinities, is a highly specialized box turtle, possibly related to trionychoids (Hutchison, 1998). *Planetochelys* superficially resembles emydids and was originally discussed as a member of that family
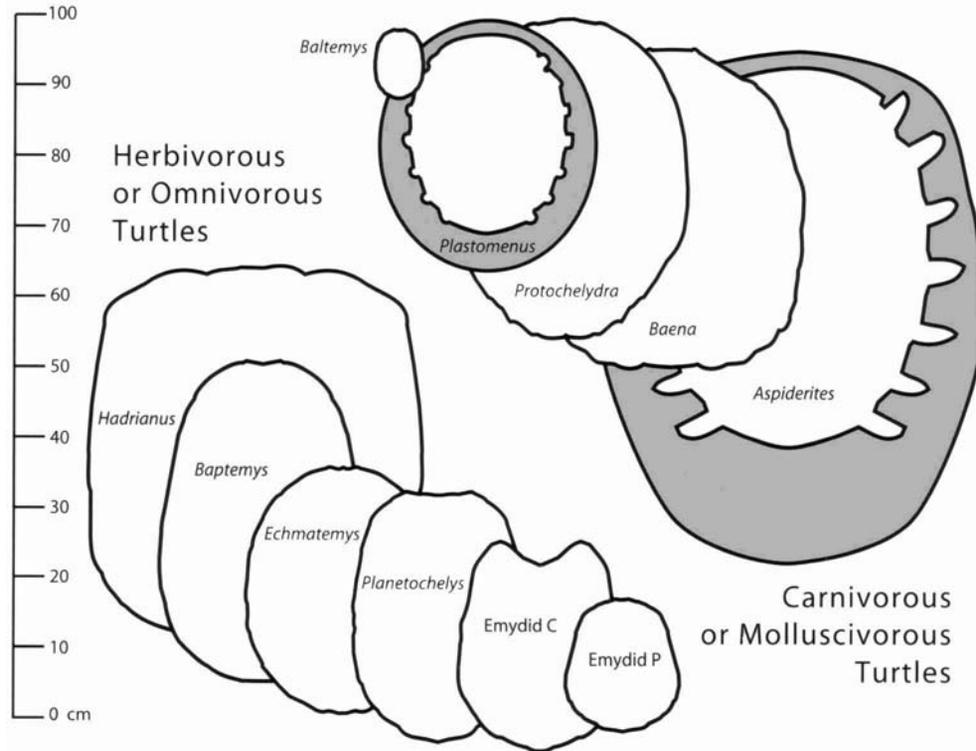
FIGURE 2 — Diagram showing maximum known shell size for representative Wasatchian turtles.
   Black outlines indicate the limits of the bony carapace; approximate extent of fleshy carapace of
   trionychids shown in gray.

(Emydid K of Hutchison, 1980). *Baltemys* is the sole representative of kinosternids (mud turtles) in the Willwood Fm., although *Xenochelys* is known from contemporaneous strata in the Wind River and Greater Green River Basins (Hutchison, 1991) where the two co-occur. Testudinidae (tortoises) are represented by *Hadrianus*, a large turtle of Old World origin. Trionychids (soft-shelled turtles) are common as fossils in the upper part of the Willwood Formation and two subfamilies, Trionychinae and Plastomeninae, are present. Unfortunately, fragmentary trionychids are difficult to classify and specimens identified only as Trionychinae may represent records of *Apalone* or the form-genus *Aspiderites*, which is also known from the Clarkforkian (Hutchison, 1998).

Ecologically, the majority of Willwood taxa are aquatic; only *Planetochelys* and *Hadrianus* show morphological features associated with terrestrial habits (Hutchison, 1998) and can be regarded as being at least partially terrestrial. *Planetochelys* is unique among early Eocene turtles in possessing a kinetic plastron similar to that of the extant emydoids *Cuora, Terrapene*, and *Emydoidea*. Specifically, the suture between the hyo- and hypoplastra remains unfused and is modified as a hinge that allows the anterior and posterior halves of the plastron to be closed to protect the head and tail when retracted. Among aquatic turtles, trionychids and baenids appear to favor chan-

nels, particularly those with sandy substrates. In the case of trionychids, we can make this inference based on analogy with modern taxa; in the case of baenids, we draw this inference from the disproportionate representation of complete specimens in channel deposits (Hutchison, 1984). By contrast, modern dermatemydids prefer more quiet, open water such as that found in large rivers, lakes, and ponds. Emydids sensu lato appear to be more catholic in their use of aquatic habitats, a fact reflected in their widespread distribution in many types of sediments. Dietarily, testudine diversity is fairly evenly split between carnivorous taxa and herbivorous to omnivirous taxa, and Willwood turtles show a considerable range of variation in adult body size among both carnivorous and herbivorous turtles (Fig. 2). Carnivorous turtles (based on cranial morphology and by analogy with modern relatives) displayed a range of habits from ambush predators (trionychids, chelydrids) to molluscivory (baenids, kinosternids).

The rise of a diverse herbivorous turtle fauna in North America is one of the hallmarks of the early Eocene and represents a significant shift in the ecological niche that turtles occupied in Western Interior faunas. Throughout the Cretaceous most of the turtles are inferred to be aquatic carnivores. Only one terrestrial herbivore (*Basilemys*) and two aquatic omnivore-herbivores (*Adocus,* and a macrobaenid), are present in

the eastern Rocky Mountain areas at the end of the Cretaceous. *Basilemys* became extinct at the end of the Cretaceous, although the two aquatic omnivore-herbivores persist into the Paleocene (Hutchison and Archibald, 1986). *Adocus* persists into the Torrejonian of northern areas (Montana, Wyoming, Colorado) and Clarkforkian of Texas (Hutchison, 1998), but is unreported in the Tiffanian or Clarkforkian of the northern Rockies. Macrobaenids are rare through the Paleocene (McKenna et al., 1987) and are last known in the Clarkforkian of Wyoming (Hutchison, unpubl. data). The first Paleogene probable omnivore may be Emydid C, which makes its appearance in the Torrejonian (e. g., in the upper Nacirniento Formation and in the Lebo Formation of Montana, Hutchison, pers. obs.), becomes the most common turtle in the Tiffanian and Clarkforkian (based on UCMP collections from Bison Basin and Greater Green River Basin), and persists into the Wasatchian in Wyoming. [Estes (1975) noted the presence of the European emydid *Ptychogaster* in the Tiffanian of the Clarks Fork Basin. As reported by Bartels (1980), this identification is suspect, and we now recognize these specimens and others from the Tiffanian of the Clarks Fork Basin to be Emydid C.] The jaws possess triturating surfaces (ridges associated with shearing surfaces on the overlying keratinous covering) that are relatively simple-suggesting a mixed diet.

The omnivorous-herbivorous family Dermatemydidae first appears in the Tiffanian of Texas in the form of a genus closely-related or ancestral to *Bapternys* (Hutchison, 1998), but representatives of this family do not appear in the northern Rockies until the mid-Wasatchian when *Bapternys garrnanii* appears (Hutchison, 1980). The peculiar eastern Paleocene genus *Planetochelys* (Weems, 1988, Hutchison and Weems, 1999), appears in the Clarkforkian and persists into the Wasatchian of Wyoming (Lysitean or Wa-6). Although absent from Wyoming thereafter, it persists into the middle Eocene (Uintan NALMA) in Texas (Hutchison, pers. obs.). The simple triturating apparatus suggests an omnivorous diet as in the other terrestrial or semi-terrestrial box turtles.

At the beginning of the Wasatchian, other omnivorous to herbivorous turtles begin to appear, all part of the testudinoid clade. The first is the batagurid *Echrnaternys* which appears at the beginning of the Wasatchian land-mammal age (Wa-0; Gingerich, 1989), persists throughout the Eocene, and is generally the most common turtle. *Echmaternys'* dietary preference based on the simple construction of the triturating surfaces of the jaws (resembling the extant *Clemmys, Terrapene, Ernydoidea),* was omnivorous or more likely herbivorous. Emydid P first appears shortly after *Echmaternys* and appears to be related to the Emydidae *sensu stricto,* generally resembling the extant omnivorouc *Clernrnys* and *Chrysemys picta* in shell shape. The jaw morphology of this form is unknown but its otherwise strong resemblance and probable relationship to the latter modem taxa suggests an omnivorous diet. One of the last but significant appearances of herbivorous turtles is the arrival of the tortoises (Testudinidae) of the genus *Hadrianus.* Based on the complexity of its triturating surfaces, it is the most herbivorous of the Willwood turtles.

LOCALITIES AND STRATIGRAPHIC SETTING

Our data set expands on the record of Wasatchian age turtles from the Willwood Formation in the southern Bighorn Basin (Hutchison, 1980). In discucion of their biostratigraphic context, both Schankler's (1980) range zone scheme and Gingerich's (1983, 1989) numbered interval scheme will be used to the extent that this is possible. Assignment to Wasatchian range zones (Schankler, 1980) is based on stratigraphic position as discussed in Bown et al. (1994) and Wing et al. (2000). Gingerich's (1983, 1989) Wa-0 through Wa-7 biozones are temporally more refined than Schankler's (1980) biostratigraphic scheme, but have not yet been adequately tested in the lower part of the Willwood section in the southern Bighorn Basin. The use of the numbered Wasatchian subzones in this paper is based on the correlations between Schankler's (1980) and Gingerich's (1983, 1989) zones as suggested in Clyde et al. (1994), Clyde (1997), and Wing et al. (2000; see also Gingerich, 1991, 2000).

In addition to numerous additional collections that fill gaps and stratigraphically refine the record of early and mid-Wasatchian turtles, a significant expansion of the data set is the incorporation of southern Bighorn Basin localities from the base of the Willwood Formation that are assigned to the Wa-0 biozone (see Wing, 1998; Strait, this volume). Since 1992, collecting in the Wa-0 interval in the southern Bighorn Basin has concentrated on localities in the North Butte area (Fig. **3).** Here earliest Wasatchian vertebrates have been recovered from a number of localities that occur within an approximately 40 meter thick interval containing one or two bright red, deeply weathered paleosols called the 'Wa-0 red bed' (Wing, 1998). Isotopic studies of carbonates from this interval record a negative carbon excursion (Koch et al., 1992, 1995, Wing et al., 2000). Several localities (in sections 30 and 31, T46N, R98W, Washakie County, Wyoming) occur within these red beds (Wing, 1998). Localities in section 18, T46N, R98W (see Wing, 1998, Sec. 94-5), occur approximately 11 meters below the 'Wa-0 red bed' (Wing, written comm., 2000). The latter local section has not yet been analyzed isotopically, so the position of these localities relative to the Wa-0 carbon isotope excursion is not known. None of the localities from the North Butte area are tied to the Willwood Formation section of Bown et al. (1994). However, all North Butte localities are stratigraphically lower than the lowest localities (at the 30 m level in exposures east of Worland) in the southern Bighorn Basin composite section. For the purposes of this paper, localities from the North Butte Wa-0 interval are treated as less than 30 meters without further refinement.

The turtle record of the Willwood Formation in the central Bighorn Basin is based on more than 300 localities in measured sections in the southern Bighorn Basin. Stratigraphic levels for these localities are documented by Bown et al. (1994) or estimated based on topographic position and proximity to localities in the Bown et al. composite section. All localities taken together span the interval from earliest Wasatchian (Wa-0) through the middle Wasatchian (Lysitean or Wa-6), and record
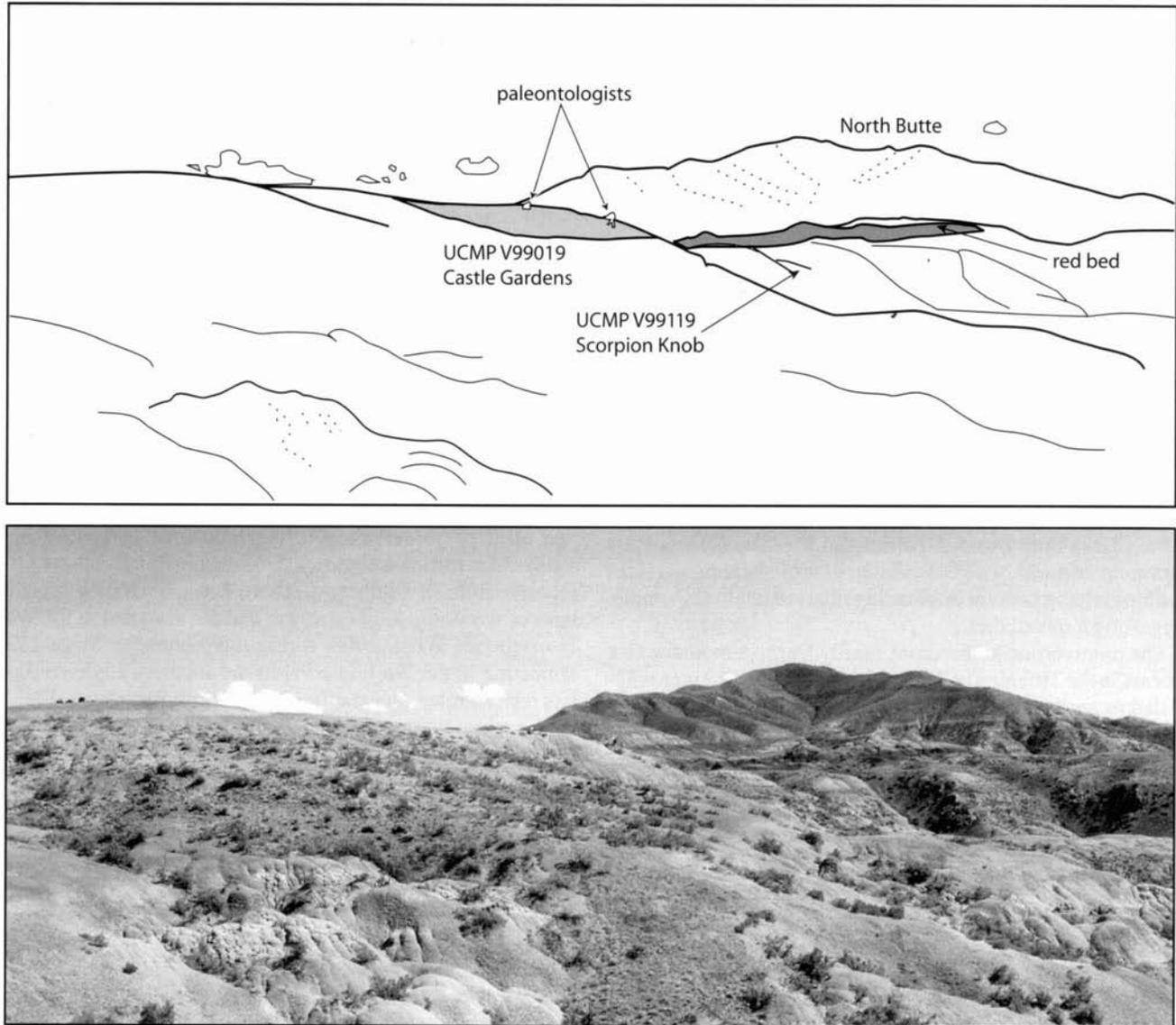
FIGURE 3 — Photograph looking southward toward North Butte, showing the position of the bed containing UCMP localities V99019 (Castle Gardens) and V99119 (Scorpion Knob). Although UCMP V99019 forms the cap of the small hill in the foreground, the bed can be traced laterally to a point where it is overlain by the "Wa-0 red bed" (Wing, 1998), a bright red, deeply-weathered paleosol.

changes in the fauna through several important climatic changes: the Wa-0 warm interval (Koch et al., 1992, 1995; Clyde and Gingerich, 1998), the 'early Eocene cool period' (Wing et al., 2000), and renewed warming coincident with a period of mammalian faunal turnover at "Biohorizon B-C" (approximately equal to Wa-5 or the Bunophorus interval zone; Schankler,1980; Bown et al., 1994; Wing, 1999). Sampling through the section is uneven. This is in part due to depositional biases, and, to a lesser extent, to artifacts of post-1980 collecting efforts.

CHANGES IN THE TESTUDINE FAUNA THROUGH THE WILLWOOD FORMATION

The Wa-0 North Butte localities have to date produced an abundance of the batagurid turtle *Echmatemys* (UCMP V94082: 173506; V94083: 173501; V99019: 212835-212846,212853, 212857; UCMP V99207: 173724-25), and less common and more fragmentary trionychids (UCMP V94083: 173502, 173507; V99019: 212847-212848, 212854, 212858; UCMP
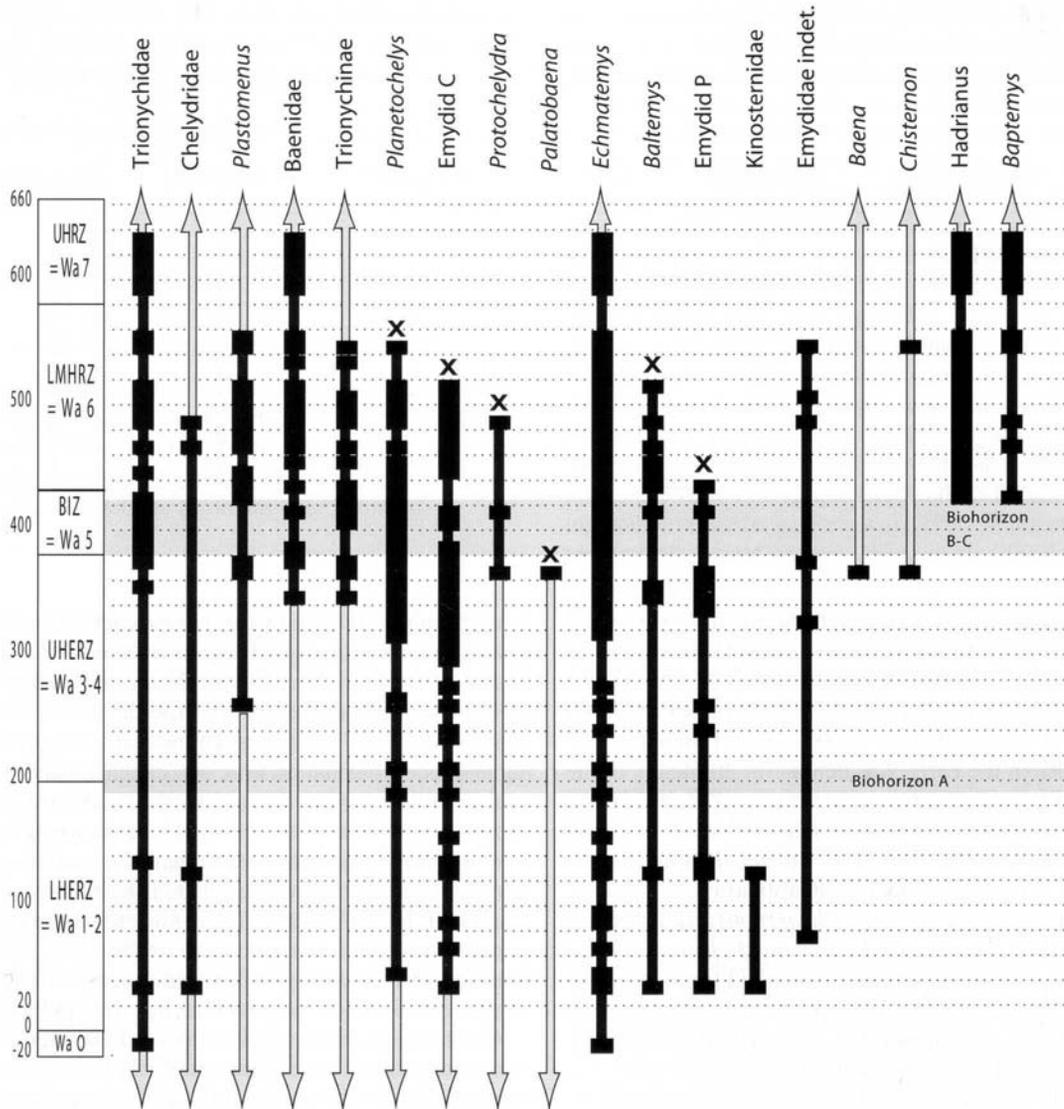
FIGURE 4 — Stratigraphic occurrences of turtle taxa in the Willwood Formation. Black bars indicate occurrences; narrower gray lines indicate ghost lineages; *x* indicates that the last occurrence shown represents a local last appearance. Abbreviations of biozones as follows: LHERZ, lower Haplomylus-Ectocion Range Zone; UHERZ, upper Haplomylus-Ectocion Range Zone; BIZ-Bunophorus Interval Zone; LMHRZ, Lower and Middle Heptodon Range Zone; UHRZ, Upper Heptodon Range Zone.

V99207: 173726). The only other reptiles recovered from these localities are sparse crocodilian bones representing the alligatoroid *Borealosuchus* (UCMP V94082: 173504; V94084: 173510; V99019: 212850), and osteoderms of glyptosaurine iguanid lizards (UCMP V94084: 173512). The abundance of *Echmatemys* in Wa-0 localities marks a dramatic change from older Clarkforkian faunas in the Bighorn Basin (documented in the University of Michigan collections), which are dominated by *Planetochelys* and Emydid C, with *Echmatemys* being absent. The reptile fauna is not particularly diverse, in contrast to the high diversity reported for the mammalian fauna

(Gingerich, 1989; Clyde and Gingerich, 1998; Strait, this volume). The low reptile diversity reflects, at least in part, sampling bias. Relatively few localities are known from the Wa-0 biozone. On average, a locality in the Willwood Formation produces only two turtle taxa; hence, in the absence of more localities or those with exceptional preservation, we should expect few taxa. Ghost lineages inferred for taxa known above and below but not in the Wa-0 interval in the Bighorn Basin would lead us to expect that at least one genus each of Baenidae and Chelydridae, plus *Planetochelys* and Emydid C, might have been present in the basin through Wa-0. However, even with

TABLE 2 — Counts of locality occurrences for the most common omnivorous-herbivorous turtle taxa, showing changes in relative abundance through time as depicted in Figure 5. Conversion of meter levels to absolute ages follows Wing et al., 2000: Age Model 1. Each stratigraphic grouping equals approximately 250,000 years. Localities provides the total number of localities present in the interval.

Meter level	*Planetochelys*	*Hadrianus*	*Baptemys*	Emydid P	*Echmatemys*	Emydid C	Locs.
480-590	10	36	7	0	53	8	75
375-480	36	33	4	4	69	18	114
310-375	29	0	0	6	24	36	56
250-310	4	0	0	2	14	12	18
190-250	1	0	0	0	3	6	8
120-190	2	0	0	2	10	18	16
60-120	0	0	0	0	3	4	7
< 60	1	0	0	1	7	1	10

the addition of these ghost lineages, testudine diversity is not as high in Wa-0 as it is throughout the remainder of Willwood time.

As the stratigraphic record shows (Fig. 4), preserved turtle diversity is at its lowest during Wa-0 time and increases approximately 50% in the early Wasatchian (at 30 meters in the composite section) with the first appearances of *Baltemys* and Emydid P. There is no substantial change in diversity until the interval represented by the 343 to 430 meter interval, during which several taxa make local first appearances (*Baena, Palatobaena, Hadrianus, Baptemys, Chistemon*) and disappearances (Emydid P). This interval corresponds to that termed Biohorizon B-C, during which there is marked turnover in the mammalian fauna (Schankler, 1980; Bown and Kraus, 1993; Bown et al., 1994). The episode of mammalian faunal turnover in the lower Willwood Formation termed Biohorizon A (Schankler, 1980) does not appear to have a corresponding turnover in the turtle fauna.

Analysis of occurrences (presence vs. absence) reveals that although the taxonomic composition is homogeneous within the study area, there are differences in relative abundance within the local stratigraphic sequence (Table 2; Fig. 5). Hutchison (1998) and Holroyd and Hutchison (2000) suggested that through the early Eocene, Paleocene holdover taxa slowly diminish in abundance as the abundance of immigrants rises. While this is true on a broad, regional scale (particularly when the Lostcabinian or Wa-7 is considered and the data are analysed based on biozones), the more detailed analysis presented here shows that while Emydid C and *Planetochelys* are somewhat reduced in abundance after the arrival of *Echmatemys* and Emydid P, both taxa persisted as a significant portion of the Willwood fauna. Both of these Paleocene holdovers (as well as Emydid P) only disappeared from the record after *Baptemys* and *Hadrianus* appeared. The possibility that immigrant taxa may have resulted in competitive displacement of endemic taxa

is really only suggested by the inverse correlation seen between the relative abundance of *Planetochelys* and *Hadrianus*.

An alternative climatic hypothesis may better explain observed changes in diversity and the demise of *Planetochelys* and Emydid C. The greatest abundance of the latter taxa during Willwood Formation time occurs during the 'early Eocene cool period.' At this time, climatic conditions most closely approximate those of the late Paleocene, when both of these taxa flourished. Renewed warming in the mid-Wasatchian may have been an important factor in their local disappearance; farther south in the Washakie Basin (where conditions were presumably somewhat warmer; Wilf, 2000), both taxa disappeared from the record at least 0.75 million years earlier than in the Bighorn Basin (Holroyd and Hutchison, unpubl. data).

Clear explanations for the observed changes in local richness and relative abundance are difficult to provide, in part because little is known about the climatic and ecologic correlates of these diversity measures in modem turtle populations. Of many temperature and rainfall variables, species richness in extant turtles is only significantly correlated with total annual rainfall and driest month rainfall (Iverson, 1992). However, paleobotanical measures of mean annual rainfall indicate that mean annual rainfall decreased through the early Eocene (Wilf, 2000), while turtle diversity increased through the same interval. Thus, rainfall amount alone is not an adequate explanation for observed patterns. The manner in which rainfall affects floodplain and wetland environments may be more critical for determining diversity. Bodie et al. (2000) identified a number of wetland characteristics that correlate with high species richness. They identified low annual duration of drying as the most important feature, and other additional variables affected relative abundance of turtle taxa. In their study, high abundance of species that preferred slow-moving aquatic environments correlated with connectedness of scours and frequent flooding while species preferring faster moving aquatic
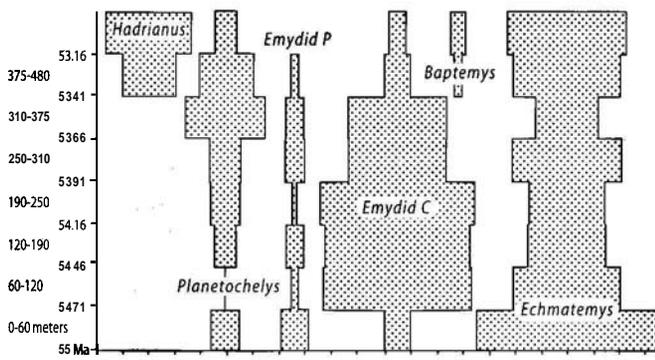
FIGURE 5 — Spindle diagram of omnivorous-herbivorous turtle occurrences, showing changes in the relative abundance as approximated by the number of locality occurrences. The width of each spindle represents the proportion of all localities within each interval at which the taxon has been recorded.

environments were more abundant in turbid wetlands close to the river. High regional diversity is apparently best achieved when heterogenous, favorable habitats are present.

Changes in habitat heterogeneity through time is a possible, and plausible, explanation for the changes in generic and species richness seen through Willwood Formation time. Certainly, the absence of baenids and the comparative rarity of trionychids, both of which appear to favor riverine areas with sand bottoms, below approximately 350 meters elevation, is an indication of the absence of suitable habitats present (or at least preserved) in the basin. As has been noted by Bown (1979) and Bown and Kraus (1993), the lower part of the Willwood Formation in the southern Bighorn Basin is dominated by mature paleosols that developed in distal floodplain settings. A greater variety of architectural elements is only present in the upper Willwood Formation, with increasing seasonality and the possible development of monsoonal conditions (Bown and Kraus, 1981; Kraus and Bown, 1993). The possibility of seasonally more arid conditions (Bown and Kraus, 1981) as a cause for changes in mammalian faunas at Biohorizon B-C coincides with the highest diversity of aquatic turtles, so we find it unlikely that drying *per se* was responsible for the changes in the vertebrate fauna.

Differences in relative abundance within omnivorous-herbivorous turtles may reflect floral abundances or facies differences, reflective of local habitat differences. Certainly, among extant turtle taxa, many exhibit distinct habitat preferences that have been anecdotally related to numerous factors such as water depth, turbidity, and availability of basking or nesting areas. Unfortunately, floral data through the lower part of the section are not as refined as that of the vertebrate record, so the possible role of local habitat differences cannot be evaluated in a direct fashion. Based on the available botanical evidence, Wing et al. (1995) and Davies-Vollum and Wing (1998) suggested that the Willwood Formation possessed a mosaic of conditions in the wet floodplain backswamp. Changes in sedi-

mentological regime through the Willwood Formation, particularly with respect to soil wetness (as reflected by hydromorphic paleosols) and floodplain instability (reflected in channel and paleosol development), have been investigated in some detail (Bown and Kraus, 1981,1993; Kraus and Bown, 1986, 1993; Wing and Bown, 1985). These changes are not yet tied directly to vertebrate localities throughout the section but should prove a fertile avenue for future inquiry.

In sum, the analysis of occurrences of Willwood turtles shows marked changes in the early Eocene turtle fauna, changes that are reflective of several episodes of faunal reorganization through a period of significant climatic change. However, attempts to unravel the causes and correlates of these changes in community structure highlight how little we know about the interaction of climate and biota effecting the changes, and how these are expressed in the preserved fossil record. For the most part, we have sought simple explanations for change, highlighting temperature (e. g., Rea et al.,1990; Wing et al., 1995), the rapidity of climate change (Wing et al., 2000), or seasonality (Bown and Kraus, 1981). However, these simple explanations are seemingly unsatisfactory, not only for the early Eocene, but for broader studies as well (e.g., Alroy et al., 2000). Understanding how climate has affected vertebrate diversity on the time scales considered here clearly requires a more complex explanation. In order to find that explanation, it will require a better understanding of how climatic factors affect modem diversity as well as a better idea of how local conditions affect our recovery of that record of change.

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