ELSEVIER

Palaeogeography, Palaeoclimatology, Palaeoecology 115 (1995) 37-60

PALAEO

Floodplains and paleosols of Pakistan Neogene and Wyoming Paleogene deposits: a comparative study

Anna K. Behrensmeyer [a], Brian J. Willis [b], Jay Quade [c]

[a] *Department of Paleobiology, MRC NHB 121 Smithsonian Institution, Washington, DC 20560, USA*
[b] *Bureau of Economic Geology, The University of Texas, University Station, Box X, Austin, TX 78713-7508, USA*
[c] *Department of Geosciences, Building #77, Gould-Simpson Building, University of Arizona, Tucson, AZ 85721, USA*

Received 15 May 1993; revised and accepted 11 October 1994

Abstract

Comparative study of fossil-bearing fluvial deposits in the Eocene Willwood Formation of northern Wyoming and the Miocene Chinji Formation of northern Pakistan indicate how tectonic and climatic processes operating at different scales controlled physical and chemical features of floodplain environments and affected preservation of the paleontological record.

The architecture of Willwood Fm. floodplain deposits represents a combination of avulsion-belt sediment packages and overbank sediments that formed alluvial ridges. The architecture of the Chinji Fm. floodplain deposits was controlled by widely distributed crevasse-splay deposition and floodplain topography. Similarities in individual paleosol-bounded overbank sequences from the two formations indicates that the internal structure of such deposits can be independent of channel belt proximity to areas of aggradation. Chinji Fm. paleosols have little vertical zonation and show no consistent pattern of lateral change in relation to major channels, while overbank paleosols in the Willwood Fm. exhibit considerable soil horizon development and a pattern of increasing maturity from alluvial ridge to distal floodplain. The "pedofacies model" of Bown and Kraus (1987) based on such lateral trends in the Willwood paleosols is not applicable to the Chinji Fm.

Plant and animal fossils are abundant in the Willwood overbank deposits, with vertebrate remains concentrated in paleosol A horizons. Plant remains are rare in the Chinji Fm. and vertebrate fossils occur primarily in channel fills rather than in paleosols. These differences relate to contrasting patterns of floodplain deposition and to levels of oxidation that controlled penecontemporaneous recycling of organic material, particularly in paleosols. Different large-scale climatic and tectonic controls on temperature and rainfall, water table fluctuations, and soil biota are proposed to account for the differences in organic preservation. Large and small-scale environmental processes also affected spatial and temporal resolution of the organic record, resulting in important differences in the paleoecological and evolutionary information that can be reconstructed from the two sequences.

1. Introduction

The Miocene Chinji Formation in the Himalayan foredeep basin and the Eocene Willwood Formation in the intracratonic Bighorn Basin (Fig. 1) consist of alluvial deposits with strikingly similar appearance. Both formations record sediment aggradation in basins adjacent to rising mountain belts, both are dominated by red-hued fluvial overbank deposits with abundant paleosols, and both are richly fossiliferous. Despite broad similarities, these formations have many important differences in their paleoenvironmental and organic records. Previously published descrip-

0031-0182/95/$9.50

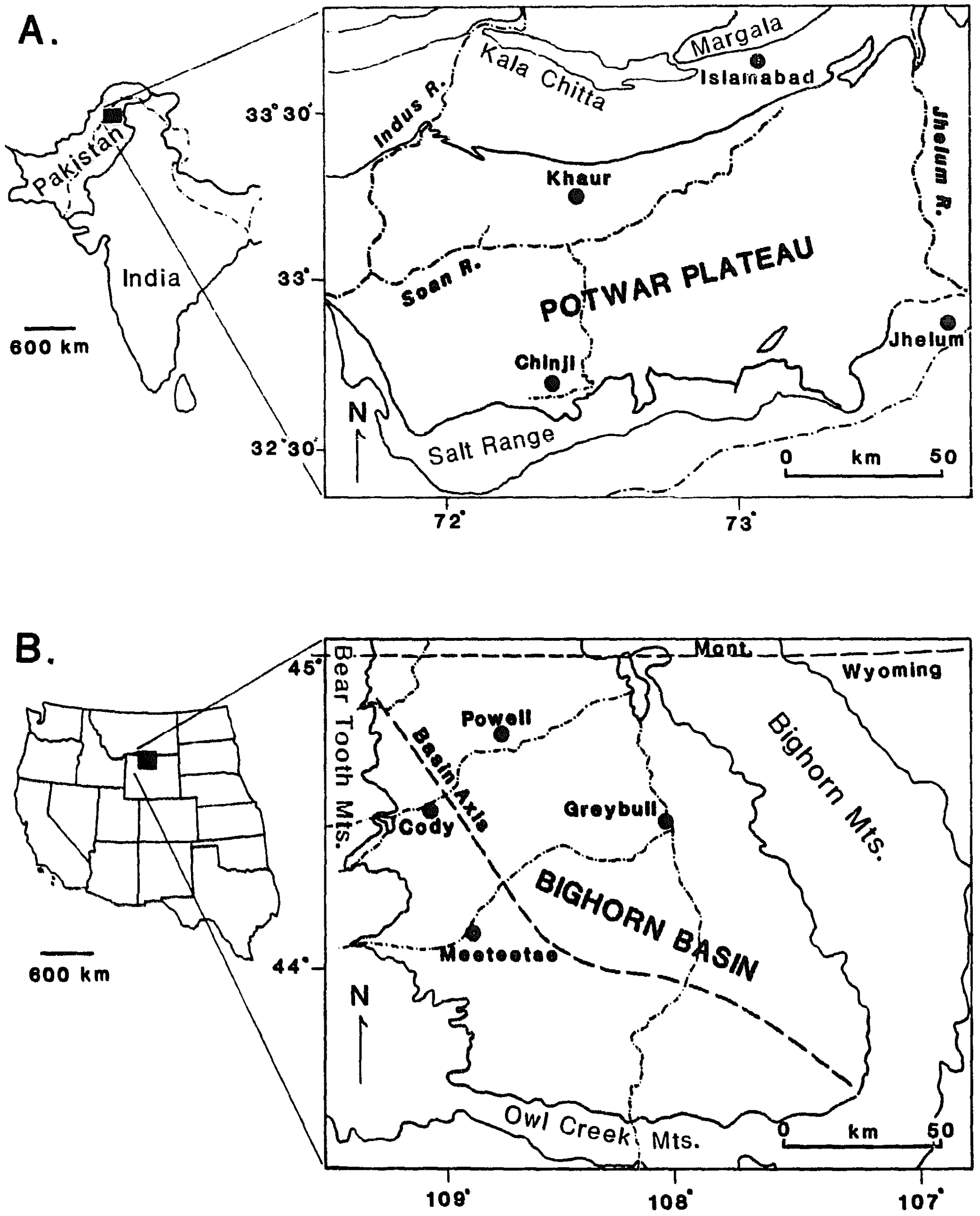

Fig. 1. Location maps for the Pakistan Neogene (A) and Wyoming Paleogene (B) sequences, drawn to the same scale. Shaded areas are the presently exposed areas of the sedimentary basins.

tions suggest that the two formations represent different styles of floodplain aggradation, with varying patterns of overbank sedimentation represented in the development of crevasse-splays, minor channels, levees and sheet flood deposits (Bown and Kraus, 1987; Kraus, 1987; Behrensmeyer, 1987; Willis, 1993a). The organic record differs as well; plant fossils are common in the Willwood Fm. and nearly absent from the Chinji Fm., and Willwood paleosols preserve abundant vertebrate remains while Chinji paleosols do not (Wing, 1984, 1987; Bown and Kraus, 1981b; Raza, 1983; Behrensmeyer, 1987; Badgley et al., 1992).

The purpose of this paper is to compare the two formations in order to better understand the relationship between fluvial depositional processes, fossil preservation, and the paleoecological record.

The Chinji Fm. and the Willwood Fm. share many features that make them appropriate for such a comparative study (Table 1). They are similar in thickness, span comparable time intervals of about 3 Ma, and both have fossil records that are well known in terms of taxonomic composition of faunas or floras, temporal framework, taphonomy, and sedimentological context. Moreover, in both examples, overbank strata include numerous, laterally continuous paleosol units representing temporarily stable land surfaces. The architecture of the overbank deposits, the physical and chemical characteristics of the paleosols, and the organic records of the two formations provide comparative paleoenvironmental and taphonomic evidence at different scales. Lateral and vertical facies characteristics document the spatial heterogeneity of floodplain sub-environments, including crevasse splays, minor channels, levees, and ponded areas and their relationship to major fluvial channels. At a finer scale, paleosol features provide evidence for habitats occupied by the floodplain biotas, and the sedimentary contexts of organic records within the overbank deposits indicate differences in time-averaging and other taphonomic features that affect paleoecological interpretations.

2. The Chinji Formation, northern Pakistan

2.1. Background

The Siwalik Group of Pakistan provides a record of fluvial deposition associated with continental collision, uplift of the Himalayas, and foredeep subsidence. Much of the sedimentological and taphonomic research reported here pertains to the Potwar Plateau of northern Pakistan, which is similar in size to the Bighorn Basin (Fig. 1). The Potwar exposures of the Siwalik Group thus provide a relatively small sample of a fluvial system that stretched along the entire Himalayan front.

Table 1

Summary of paleogeographic, chronostratigraphic, lithological, and paleontological features of the Chinji Fm. of the Pakistan Neogene sequence and the Willwood Fm. of the Big Horn Basin Paleogene sequence. Quantitative information from the Chinji Fm. is from Behrensmeyer, 1987; Barry et al., 1991; Willis, 1993b. Quantitative information for the Willwood Fm. is from Bown, 1980; Bown and Kraus, 1981a; Bown and Kraus, 1987; Kraus, 1987; Gingerich, 1982; Bown and Kraus, 1993; Kraus and Aslan, 1993

	Chinji Fm.	Willwood Fm.
General features		
Paleo-latitude	25–30°N	45–46°N
Age Range	3.2 m.y. (14—10.8 Ma)	3.0 m.y. (55—52 Ma) (southern BHB)
Thickness	665 m (Gabhir Kas)	770 m (south) 850 m (north)
Overall sediment accumulation rate	0.21 m/1000 yr	0.22 m/1000 yr (0.35 in north)
Estimated paleotemperature	not known, but latitude sub-tropical	10—15°C MAT (Lower) 15–18°C MAT (Upper)
Overbank deposits		
Color, primary deposits	gray, brown, red	green-gray, gray
Color, paleosols	red, orange, brown	gray, red, purple, orange
Dominant lithology	siltstone, sandy siltstone	mudstone, siltstone, claystone
Overbank sequence thickness (between paleosols)	7.3 ± 3.2 m	3–6 m (simple pedofacies sequence)
Thickness between major channel sandstones	37 m ± 29	15–40 m (compound pedofaciessequence)
Floodplain width	100 km between rivers	15–20 km = width of 1/2 alluvial ridge
Paleosol thickness	1–3 m	1.5 m (stage-1) to 3–5 m (stage-5)
Estimated maximum time for paleosol formation	13,000–23,000 yr	10,000–16,000 yr (15,300–25,600 for avulsion-belt deposits)

The Siwalik Group as a whole (Fig. 2A) is characterized by kilometer-scale alternations of coarse and fine-grained rocks. The Kamlial, Nagri, and Soan Formations are sand-dominated, while the Chinji and Dhok Pathan Formations are composed primarily of mudstone (Fatmi, 1973; Willis, 1993b; see also Willis and Behrensmeyer, this issue). These textural alternations represent long-term shifts in the positions and/or sizes of major channel belts within the basin (Willis, 1993a). Throughout the sequence, fossils are more common in the fine-grained formations and in mud-dominated portions of the coarse-grained formations (see Bartels et al., this issue). Rates of (compacted) sediment accumulation, which have been calculated using magnetostratigraphy, increase from 0.10–0.20 m/1000 yr in the Kamlial and Chinji Fms. to 0.30–0.50 m/1000 yr in the Nagri Fm. and above (Johnson et al., 1985; Behrensmeyer, 1987).

Early sedimentological work on the Potwar Plateau was aimed at providing stratigraphic and chronologic framework for the abundant vertebrate fossils (Pilbeam et al., 1979; Johnson et al., 1982), which include remains of the hominoid primate *Sivapithecus* (Pilbeam et al., 1977). Subsequent studies focussed on the broad lateral and vertical relationships of the fluvial channel and overbank facies of the Chinji, Nagri, and Dhok Pathan Fms. (Behrensmeyer and Tauxe, 1982; Behrensmeyer, 1987; Willis, 1992; Khan, 1993). Preliminary work on a limited sequence of paleosols provided a general interpretation of environmental conditions in the Dhok Pathan Fm. (Retallack, 1991). Carbon isotopic signals in pedogenic carbonate throughout the sequence show a marked change from C3- to C4-dominated vegetation between about 7 and 5 Ma. (Quade et al., 1989; Quade and Cerling, this issue). Over the past decade, detailed sedimentological research in the

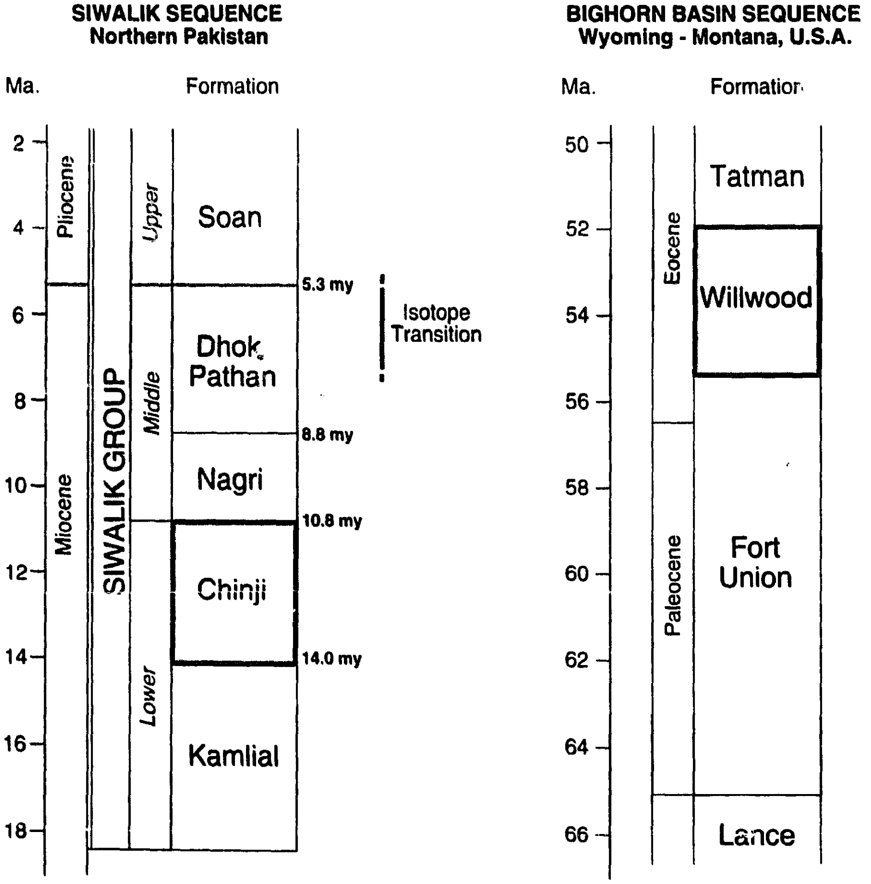

Fig. 2. Formations and ages of the Siwalik sequence and the Bighorn Basin sequence, showing the stratigraphic position of the Chinji and Willwood Formations.

Dhok Pathan and Nagri Fms. and especially in the Chinji Fm. has documented lateral facies associations and pedogenesis within the fine-grained, fossil-bearing floodplain deposits (Behrensmeyer, 1987, 1989; Willis, 1992; Behrensmeyer et al., 1992; Willis and Behrensmeyer, in press). This work plus previously unpublished information on the Chinji Fm. overbank facies provide the basis for the following discussion.

2.2. *Overbank deposits of the Chinji Formation*

The Chinji Fm. overbank deposits consist of three dominant lithofacies: (1) laterally extensive, bedded, calcareous mudstones with varying degrees of bioturbation, (2) ribbon, shoestring, and tabular sand bodies (following the terminology of Friend et al., 1979), and (3) leached, heavily bioturbated, massive silty-clay to silty-sand beds. Repeated sequences of these three facies occur every 5–10 m. A typical paleosol-bounded overbank sequence, as defined here, consists of well-bedded calcareous mudstones (facies 1) with laterally discontinuous sand bodies (facies 2) that directly overlie a paleosol and extend upward through the next well-developed paleosol (facies 3) (Fig. 3). The mudstones become increasingly bioturbated upward, with consequent loss of primary bedding structures. Zones of weak pedogenic modification may alternate with bedded sediments in the middle to upper part of the overbank sequence. The capping paleosol is unbedded, brown to red-orange in color (Munsell Hues 5-10R, 5-10YR), and may have some or all of the following features: clay cutans, slickensides, gray or red mottling, sesquioxide nodules, $CaCO_3$ nodules, and discrete burrow and root traces (Fig. 3). In contrast to the calcarous fine-grained sediments that represent unaltered parent alluvium in this fluvial system, the paleosols lack matrix carbonate for most of their thickness; we attribute this to pedogenic leaching of carbonate from the upper soil zone. The thickness of the leached zone is a measure of maturity in modern soils (Birkeland, 1984; Retallack, 1990) and is assumed to be a rough indicator of relative maturity in the Chinji paleosols. $CaCO_3$-cemented mudstones and concentrations of carbonate nodules often occur immediately below the leached zone, forming a resistent bench on the outcrop profile.

The features of Chinji paleosols are not easily matched with the standard soil groups (Soil Survey Staff, 1975) but have a number of features in common with modern soils of the Gangetic plain in eastern India (Agarwal and Mukerji, 1951). These soils, locally known as "bangar" soils, occur on areas of the alluvial plain where deposition has ceased. They are characterized by leaching of $CaCO_3$ from the upper solum, concentrations of semi-indurated to indurated $CaCO_3$ nodules in the lower solum, and some clay illuviation the middle or upper zones of the soil. On coarser, better drained substrates there may be complete leaching of calcium carbonate and no nodules. Iron occurs as nodules or dispersed within the upper parts of these soils, which generally are dark gray in color. Except for the color difference, bangar soils are reasonable modern analogues for at least some of the Chinji paleosols.

Petrographic evidence shows that carbonate nodules in the paleosols are diverse in shape, internal morphology, and relationship to the surrounding matrix. Irregular micritic nodules millimeters to a few centimeters in diameter that have diffuse boundaries and a granular or patchy internal fabric are assumed to be pedogenic. These often follow root traces or burrows. Other nodules of similar external morphology have distinct boundaries and clear internal lamination and appear to have formed from bioturbated carbonate-rich muds. These typically occur lower in the soil profile but are mixed with the pedogenic nodules, and the two nodule types are difficult to distinguish based on hand specimens.

The paleosol zone that lacks matrix $CaCO_3$ probably represents mineral A or B/Bt horizons as defined in modern soils (Birkeland, 1984), but there are no consistent patterns of mineral or clay translocation within the leached zone and the thickness of this zone is laterally variable (Behrensmeyer and Willis, 1992). Given disrupted internal fabrics and highly variable vertical distributions of sesquioxide and $CaCO_3$ nodules, it appears that intense bioturbation could be partly responsible for preventing the formation of clear soil horizons, other than the leached zone and the

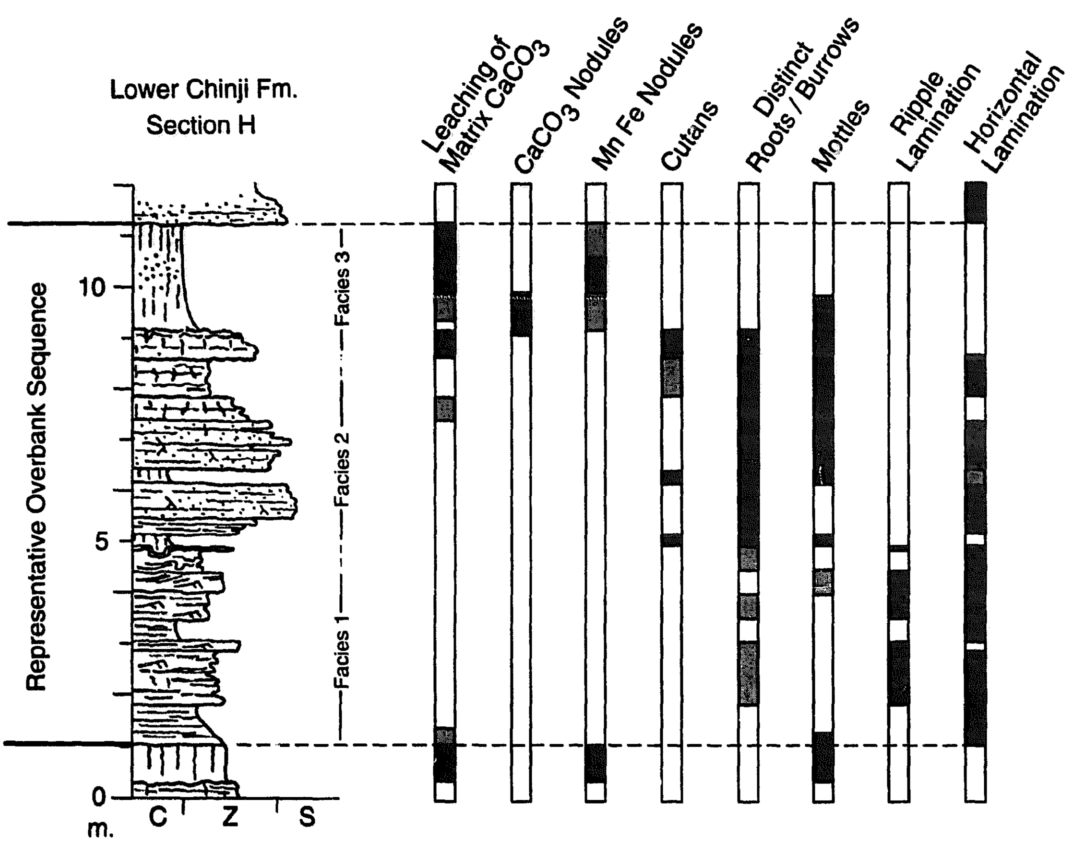

Fig. 3. A representative overbank sequence (Section LC-H) from the lower Chinji Fm. 1.0 km W of Gabhir Kas, Potwar Plateau, showing the vertical change in sedimentary features associated with the lower bedded facies (facies 1), the middle disrupted facies (facies 2), and the capping paleosol (facies 3). Black bars indicate that the feature is present, stippled bars indicate that it is uncommon, and white that it is absent.

underlying concentrations of pedogenic carbonate nodules (Bk). Lateral variation in the Bk horizons suggests that carbonate accumulation was controlled by local drainage conditions. As evidence for this, the Bk zone typically disappears when paleosols are traced laterally over a sandy channel fill and reappears where the substrate returns to silt or clayey silt. Petrographic evidence, magnetic mineralogy, and lateral tracing of paleomagnetic isochons (Tauxe and Badgley, 1984, 1988; McRae, 1989, 1990) indicate that much of the iron oxidation within paleosols occurred penecontemporaneously to within a few thousand years after burial.

Overbank sequences may fine or coarsen upward or show no clear vertical trend in texture. Sand bodies occur as laterally extensive tabular sheets or as wedges, ribbon or shoestring channel fills with clearly defined erosional margins, or as a combination of these patterns (e.g., incised channels with sandy lateral "wings") (Fig. 4A,B). Contacts between tabular sandstones and underlying paleosols often are horizontal (i.e., a relatively flat surface in the original depositional setting) and show little evidence of erosion, but ribbon and shoestring sand bodies may cut several meters into underlying deposits.

Abandoned channels (especially those over 1.0 km in width; Behrensmeyer, 1987) may contain all three overbank facies, although heavily bioturbated mudstones and paleosols (facies 3) are more common and bedded calcareous mudstones (facies 1) are less common than in typical floodplain situations. Inclined heterolithic stratification (IHS: Thomas et al., 1987), intraformational conglomerates with reworked iron oxide and $CaCO_3$ nodules, and vertebrate remains also are typical of fine-grained channel fills. Such features provide the most useful evidence for the channel-fill nature of these deposits, because channel edges are difficult to detect when mudstone fill abuts against an

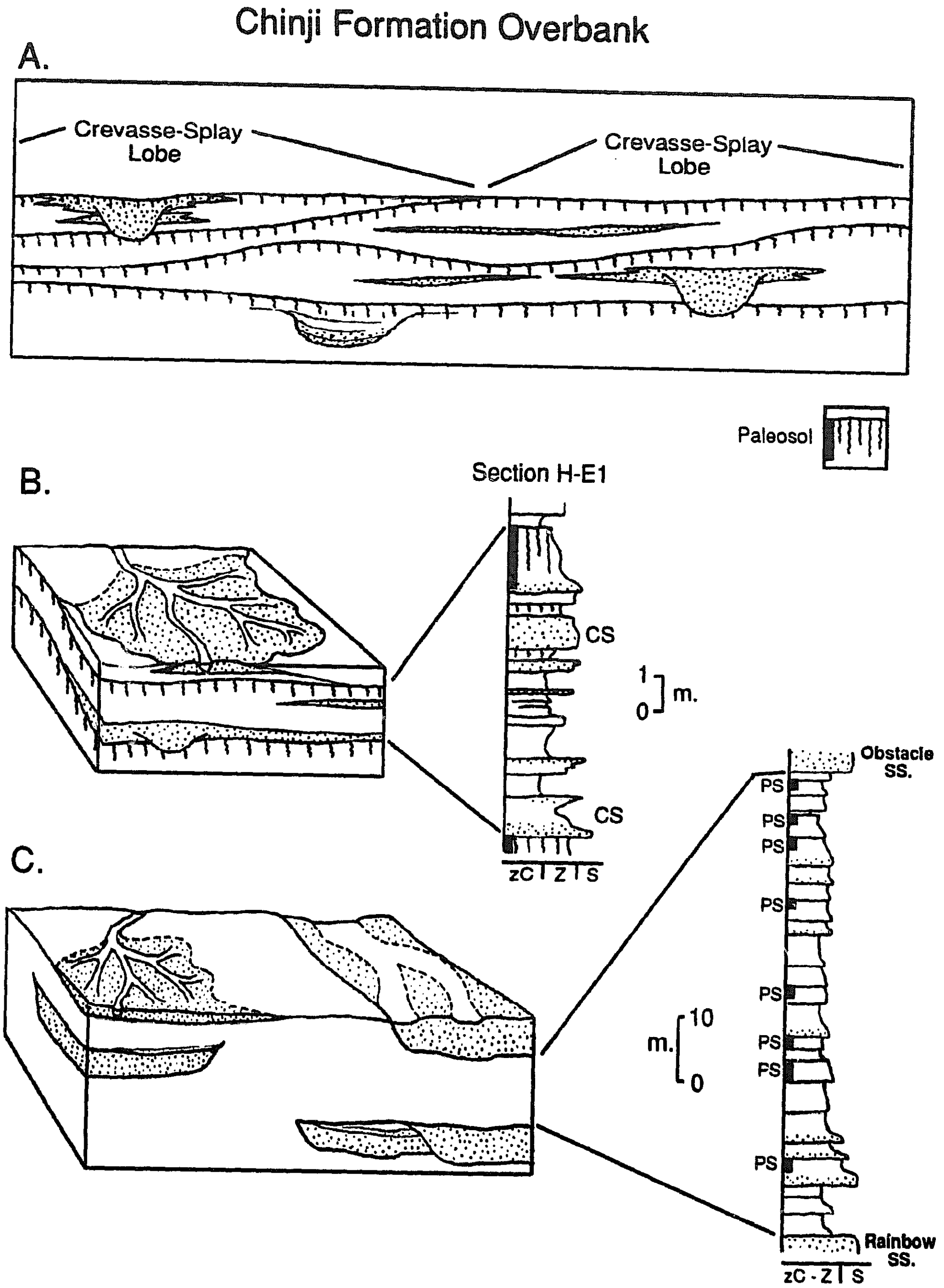

Fig. 4. A. Representative cross-section through Chinji Fm. overbank deposits, showing irregular, paleosol-bounded, overbank sequences. Sandstones are stippled, mudstones are white, and vertical tick-marks indicate major paleosols. B. A typical overbank sequence, measured 160 m E of the log shown in Fig. 3. *CS*= crevasse-splay, black vertical bar indicates leached zone. C. A representative log through superimposed overbank sequences between two major channel sand bodies in the lower Chinji Fm. (Willis, 1993b: Appendix, meter 290–370). *PS*= paleosol. Lithologic bar: *C*= clay, *Z*= silt, *S*= sand.

erosional bank formed of similar fine-grained overbank facies.

Individual overbank sequences can be traced laterally for several kilometers, and they gradually thin and end where bounding paleosols converge (Fig. 4A,B). Within an overbank sequence, minor sand sheets and sandy channel fills commonly (but not always) occur at the thickest point within the overbank sequence and grade laterally into thinner mudstones. Individual paleosols have been traced up to 15 km in continuous outcrops, and associated overbank deposits generally do not thicken or coarsen laterally toward major sand bodies., indicating that they were not formed by levee-topping sheet flood aggradation from the main channels ("true overbank" deposition of Kraus and Alsan, 1993). Over distances of a few kilometers, the leached zone of a Chinji paleosol may thin and its nodule content decrease until it pinches out in a stack of bedded, bioturbated mudstones. In situations where the upper contact is non-erosional, this trend can be interpreted as representing decreasing pedogenic maturity along a stable land surface that passed into a topographically lower area of active sedimentation. Cut-banks of major sand bodies may truncate up to 15 m of overbank deposits representing several overbank sequences (Fig. 4B). Careful documentation of over 50 paleosols shows that there is no trend toward decreased maturity near the paleochannels (in a vertical or lateral sense) or increasing maturity at considerable distances from these channels.

The architecture of the Chinji Fm. can be characterized three-dimensionally as a sequence of superimposed wedges or lobes formed by the overbank sequences, with minor sand bodies representing crevasse-splay channels and sheets, and larger sand bodies representing the major channel belts (Fig. 4) (Behrensmeyer, 1989; Willis, 1992, 1993a). It appears that the Chinji floodplains aggraded primarily during phases of crevasse-splay activity, which may or may not have accompanied avulsion of a major channel (e.g., Smith et al. 1989; Willis and Behrensmeyer, 1994). Initially, pulses of aggradation filled topographically low, perhaps seasonally flooded areas (Fig. 5). Laminated overbank sediments accumulated rapidly at first but then slowed, allowing increasing disruption of primary bedding and pedogenesis upward until the crevasse-splay lobe or lobes stablized above the local water table and a capping paleosol formed. This process resulted in a mosaic of floodplain environments, including permanent or seasonal swamps and lakes and topographically higher and drier land surfaces where soils were well-developed (Fig. 5). The components of this mosaic lack a consistent lateral relationship to the major channel belt deposits, i.e., dry and wet areas were not

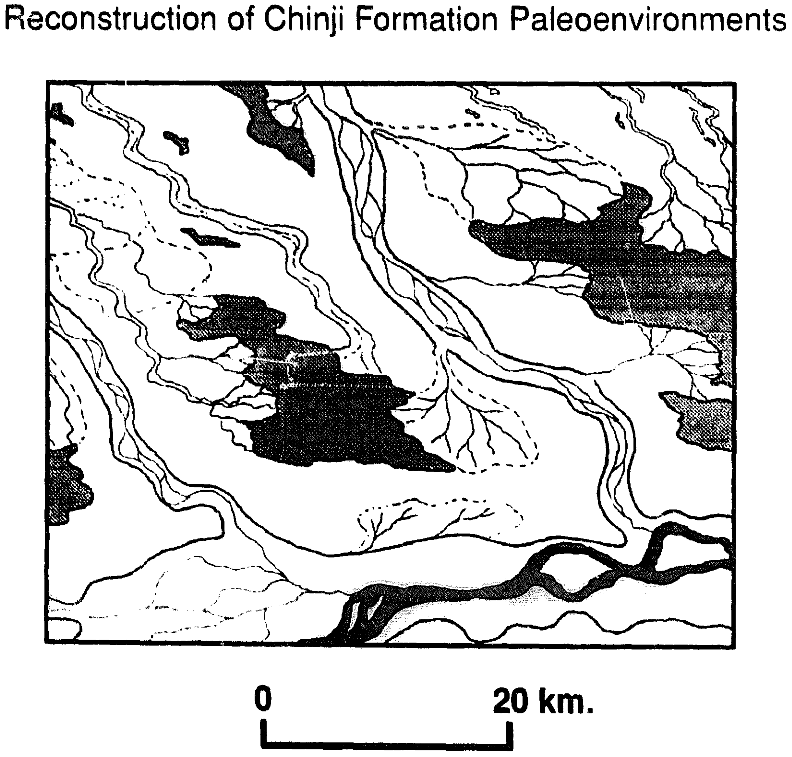

Fig. 5. Plan-view reconstruction of the Chinji Fm. alluvial plain. Ponded areas are shaded.

predictably near or far from the active channels. The thickness of an overbank sequence at any given site was controlled by topographic lows in the floodplain and by the level above which sediment no longer could accumulate, i.e., the point where avulsion shifted deposition to another area. We assume that, within the relatively short time intervals of 10^3–10^4 yr represented by each overbank sequence, basin subsidence did not vary enough spatially or temporally to have much influence on lateral differences in the thicknesses of these sequences.

2.3. The organic record

The vertebrate fossil record in the Chinji Fm. occurs primarily in overbank deposits, although some abraded remains have been recovered from the major channel sandstones. Both microvertebrates (<5 kg) and larger animals up to several thousand kg are represented, often in somewhat different depositional circumstances (see Bartels et al., this issue). In the overbank context, vertebrate fossils typically are within or on the margins of small-scale abandoned channels filled with fine to coarse-grained sediment (Table 2) (Raza, 1983; Behrensmeyer, 1987; Badgley et al., 1992). Fossil occurrences in paleosols are rare, consisting of isolated fragmentary remains and occasional dense patches of associated skeletal parts suggesting burrow fills. Small gastropods occasionally are preserved in the leached zones of Chinji paleosols, usually as internal molds (steinkerns), and bivalves occur uncommonly in channel fill deposits. Ostracods have been found in association with concentrations of micromammals (S.M. Raza, pers. comm., 1992). In general, however, the skeletal record for invertebrates is remarkably sparse.

Plant fossils are extremely rare in the Chinji Fm., consisting only of poorly preserved logs in the major sandstones and rare leaf impressions in fine-grained mudstones and calcareous siltstones. Preliminary palynological reconaissance indicates that there is little preserved pollen. Free carbon from degraded plant remains is rare in the paleosols, generally $<0.2\%$. In spite of the near-absence of a direct paleobotanical record, carbon isotopes in the paleosol carbonates and vertebrate teeth provide evidence that vegetation on the alluvial plain was predominantly of the C3 photosynthetic pathway (forested or wooded habitats, and perhaps some C3 grasslands; Quade et al., 1989; Quade et al., 1992; Morgan, 1994). Oncolites up to several cm in diameter occur in some of the larger channel fills, where they are concentrated by fluvial reworking in sandy lag deposits.

Table 2

Taphonomic contexts for organic preservation in the Chinji and Willwood Formations. Key: – = very rare to absent, (+) = uncommon, + = present, + + = common

	Macroplant	Microplant	Invertebrate	Vertebrate	Ichnofossil
Chinji Formation					
Channel lag + bar	(+)	–	–	+	+ +
Abandoned channel fill	(+)	–	(+)	+ +	+ +
Levee	–	–	–	(+)	+
Floodplain: poorly drained	–	–	–	(+)	+ +
Floodplain: well-drained	–	–	(+)	(+)	+ +
Crevasse-splay	–	–	(+)	(+)	+
Willwood Formation					
Channel lag + bar	+	–	–	(+)	+
Abandoned channel fill	+ +	+ +	(+)	(+)	+
Levee	+ +	+	(+)	(+)	+
Floodplain: poorly drained	+ +	+ +	(+)	+	+
Floodplain: well-drained	(+)	–	+	+ +	+ +
Crevasse-splay	?	?	+	+	+

Ichnofossils representing roots and invertebrate burrows are abundant in the overbank and channel deposits but have not yet been studied in detail.

Chinji Fm. bone accumulations in channel fills are interpreted as time-averaged, attritional accumulations (Raza, 1983; see Bartels et al., this issue). The evidence for this is partly sedimentological and partly taphonomic. Interbedded coarse bar deposits and fine-grained units with bioturbated zones indicate alternating periods of sedimentation and incipient soil development in many of the fossil-bearing channel fills. During pauses in sedimentation, autochthonous vertebrate remains could accumulate in the abandoned channel environment; these would be incorporated into the substrate or buried (with or without transport) when the channel was active or when overbank flooding introduced fine-grained sediments into the topographic depression formed by the channel. Reactivated channels were confined within preexisting channel belts and probably did not rework overbank sediments outside of this context. Hence there would have been minimal input of bones eroded from older overbank deposits. Most bones recovered from the channel fill deposits are minimally abraded, also indicating that they were not subjected to multiple cycles of reworking.

According to the above model, each episode of bone preservation in a channel fill would represent a relatively short time interval, on the order of 100's to 1000's of years. This estimate is supported by an overall rate of sediment accumulation for the Chinji Fm. of 0.14–0.19 m/1000 yr and the maximum period of time represented by each well-developed paleosol, which is calculated at 23,000–13,000 yr (Table 1; Behrensmeyer, 1987). This time span is derived by dividing the overall time interval for a particular thickness of strata, which is based on paleomagnetic correlations to the Global Polarity Time Scale, by the number of paleosols included in this sequence of strata. Actual time intervals represented by paleosols would be less than this, on average, because some time would be needed to accumulate the sediment upon which the soil is developed in each overbank sequence. The amount of time represented by most channel fill deposits, which are capped by well-developed paleosols, should be considerably less than the maximum estimate of 23,000 yrs for an entire overbank sequence.

The abundance of vertebrate fossils in abandoned channels may also relate to preferential use of such low-lying areas by living animals, especially during times of water scarcity (Behrensmeyer, 1987). Increased vertebrate mortality in and around waterholes is well-documented in recent ecosystems (Haynes, 1985a,b, 1988), and this can be caused by increased predator activity as well as deaths resulting directly from drought or starvation. In the Chinji Fm., there is no evidence for mass-mortality events other than occasional dense accumulations of fish remains in abandoned channels and in calcareous purple mudstones interpreted as hydromorphic soils. The latter may be analogous to calcareous "bhat" soils of low-lying areas of the Gangetic plain (Agarwal and Mukerji, 1951).

The scarcity of bones and invertebrate shells in the paleosols is probably the result of post-burial destruction rather than a low supply of such remains in the original ecosystem. Animal remains undoubtedly were buried in the substrates of the topograpically higher Chinji overbank environments, but most did not survive to become fossilized. Post-burial destruction could have been partly due to rapid oxidation of organic components combined with the pedogenic process of ferrolysis, in which alternating wet and dry conditions, plant decomposition, and iron oxidation result in the periodic release of hydrogen ions (Brinkman, 1970; Gerrard, 1987), leading to acidic conditions unfavorable for bone preservation. Intense bioturbation and recycling of nutrients also could have contributed to the destruction of skeletal remains.

3. The Willwood Formation of northern Wyoming

3.1. Background

The Pakistan Neogene deposits formed at the junction of colliding continents. In contrast, the Cretaceous to Eocene rocks of the Bighorn Basin resulted from the formation of a mid-continental basin between mountain ranges that arose during the latter part of the Laramide orogeny (Bown, 1980; Willis and Behrensmeyer, this issue). Stratigraphic and sedimentological research has covered most of the basin. As in the Pakistan Siwalik succession, much of the geologic work has been done in association with paleontological collecting.

The Bighorn and Clarks Fork Basins filled with several thousand meters of clastic sediments during the Paleocene and Eocene, after regression of the Cretaceous sea toward the southeast (Bown, 1980; Hickey, 1980) (Figs. 1B, 2B). The Paleocene Ft. Union Fm. consists of 600 m (southeast) to over 3000 m (northwest) of drab mudstones and sandstones with lignites and coals (Bown, 1980). Deposition occurred in a variety of fluvial and lacustrine environments. The overlying Willwood Fm., which varies in thickness from 880 m in the north to 770 m in the south, is predominantly fine-grained and is distinguished by bright red, orange and purple colors associated with pedogenically modified sediments. Average compacted sediment accumulation rates were originally reported at 0.22–0.35 $m/10^3$ yr but now have been recalculated at 0.3–0.6 $m/10^3$ yr (Table 1) (Gingerich, 1982; Kraus, 1987; Kraus and Aslan, 1993; Bown and Kraus, 1993).

Sedimentological study of Paleogene fossil-bearing strata in the Bighorn Basin has focused primarily on the Willwood Formation, which spans the time between about 55 and 52 Ma (Wing et al., 1991). In addition to research on the overall stratigraphy and tectonic setting (Neasham and Vondra, 1972; Hickey, 1980; Bown, 1980) and the channel deposits (Kraus, 1980; Kraus and Middleton, 1987), considerable work has been done on the overbank deposits. This includes investigations of the sedimentary context and floral record of plant-bearing carbonaceous shales (Wing, 1984; Farley, 1990) as well as sedimentological and taphonomic studies of vertebrate-bearing overbank deposits and paleosols (Bown and Kraus, 1981a,b, 1987; Winkler, 1983; Kraus, 1987; Kraus and Bown, 1988; Bown and Bear, 1991; Aslan, 1990; Bown and Kraus, 1993; Kraus and Aslan, 1993). Willwood Fm. paleosols of differing maturity and their associated deposits provide the basis for the Bown and Kraus "pedofacies model" for overbank deposits. The term "pedofacies" refers to "laterally contiguous bodies of sedimentary rock that differ in their contained laterally contiguous paleosols as a result of their distance (during formation) from areas of relatively high sediment accumulation" (Bown and Kraus, 1987: p. 599).

Recent work on oxygen isotopes from pedogenic carbonate nodules and vertebrate tooth enamel in the Wyoming Paleogene succession (Koch et al., 1992; Koch et al., this issue) indicate that the climate varied from warm in the late Paleocene to relatively cool (MAT 10–20°C) in latest Paleocene to earliest Eocene, to warm again in the late Early Eocene (Table 1). Leaf-margin analyses of paleotemperatures are consistent with this evidence, indicating relatively cool and equable climatic conditions in the earliest Eocene (i.e., for much of the Willwood Fm.) and warmer conditions for the rest of the early Eocene (Wing and Greenwood, 1993).

3.2. Overbank deposits of the Willwood Formation

Overbank deposits, which we regard as including crevasse-splay, levee, sheet-flood, pond, and minor channel deposits, in the Willwood Fm. consist of bedded mudstones and fine sandstones that alternate with intervals showing variable degrees of pedogenic modification. A series of five paleosol stages is used to characterize the continuum of features associated with increasing soil maturity (Bown and Kraus, 1987; Kraus and Bown, 1988) (Fig. 6a). These features include mottling (yellow, orange, red), development of clear A and B horizons and sub-horizons, $CaCO_3$ and sesquioxide glaebules or nodules, root traces, rhizoliths, and burrows. Chemical and textural analyses of vertical trends also show illuviation of clays, iron, and manganese in the B horizon (Bown and Kraus, 1981a). The combined thickness of the A and B horizons is of greatest importance in assigning a paleosol to a particular stage (Bown and Kraus, 1993). The least mature, stage-1 paleosols have mottling, incipient $CaCO_3$ glaebules, and no differentiation of soil horizons, while the most mature, stage-5 paleosols have thick, clearly differentiated Ae (a zone in A that is leached of iron and manganese), Ao (a zone in A with

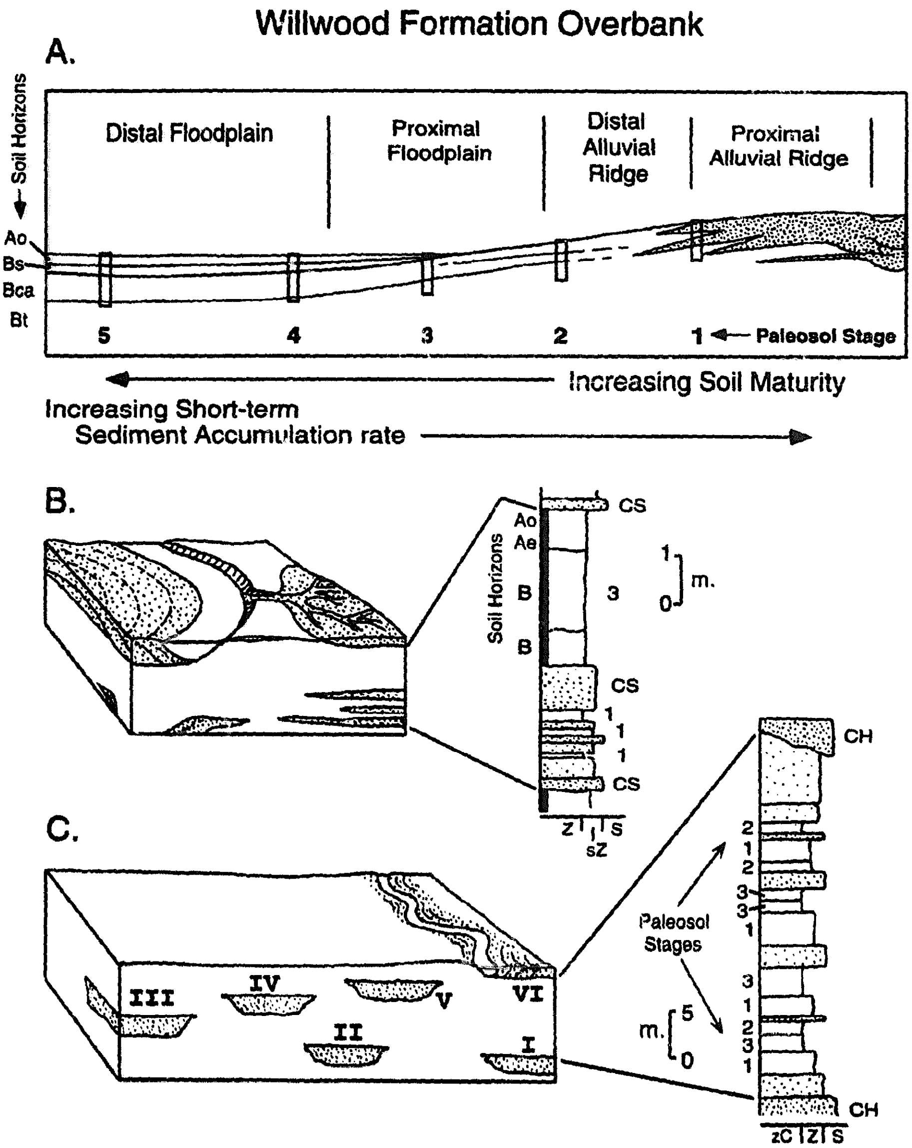

Fig. 6. A. Simplified diagram of pedofacies model for the Willwood Fm., modified from Bown and Kraus (1987). B. A representative simple pedofacies sequences (NE 1/4, NW 1/4, Sec. 15, T 56, R 101 W, Park County, Wyo.; Kraus, 1987: p. 604). Numbers indicate paleosol stages, other abbreviations as in Fig. 4. The lower part of this sequence meets stratigraphic criteria for an avulsion-belt deposit (Kraus and Aslan, 1993). C. A representative compound pedofacies sequence between major channel sandstones (NE 1/4, NE 1/4, SW 1/4, Sec. 20, T 56, R 101 W, Park County, Wyo.; Kraus, 1987: p. 608). Block diagram shows step-wise avulsion of the channel belt before it returns to the same position on the floodplain (modified from Kraus, 1987). Note: a Willwood Fm. paleosol-bounded "simple overbank sequence" of Bown and Kraus (1987) is equivalent to the paleosol-bounded overbank sequence of the Chinji Fm. described in this paper.

concentrated organic carbon) and B horizons. $CaCO_3$ and illuvial clay accumulations in the B horizon are most pronounced in stage-3 and decline in more advanced stages (Bown and Kraus, 1987).

The "simple pedofacies sequence" (Fig. 6b; Kraus, 1987; Kraus and Bown, 1988) is described as the most basic unit of the Willwood Fm. overbank deposits. These sequences are 3–6 m thick (Table 1) and consist of a bedded, sandy or silty basal unit 0.5–3 m thick, a variable middle zone that commonly has stage-1 or stage-2 paleosols alternating with bedded sediments, and a capping paleosol. This paleosol has a well-developed profile, usually stage-2 or stage-3 maturity but occasionally more advanced (stage 4–5).

The middle zone of the simple pedofacies sequence may be absent, in which case the basal coarse deposits are overlain by mudstones with a single, stage-2 to stage-3 paleosol profile. The next overbank cycle begins with another bedded, sandy unit, which often rests conformably on an organic A horizon at the top of the preceding cycle. The most mature soils are associated with "true" overbank deposits at some distance from the main channels, which were the source of incremental additions of fine-grained sediment (Kraus and Aslan, 1993). Overbank deposits proximal to paleochannels have more preserved bedding and less mature paleosols; pedogenic disruption of bedding and paleosol maturity increase away from channels toward the more distal floodplain settings (Fig. 6a), where some mature paleosols may have hydromorphic features (e.g., gleying) indicating water-logging, possibly associated with perched water-tables (Kraus and Aslan, 1993).

The architecture of the Willwood "true" overbank deposits (as defined by Kraus and Aslan, 1993) is formed by fine-grained sediment bodies that occur on both sides of major and tributary channel belts and that extend parallel to these belts. These sediment bodies thin and fine laterally away from the alluvial ridge, forming wedges in cross-sectional view (Fig. 6a; Bown and Kraus, 1987) as a result of overbank sedimentation events being more frequent proximal to the active channel. According to this model, stage-1 soils should occur primarily in proximal alluvial ridge settings and stage-5 soils in the distal floodplain, with other stages distributed sequentially inbetween over distances of approximately 20 km (Table 1). Although the entire pedofacies sequence has not been traced along one continuous horizon from stage-1 to stage-5 (Bown and Beard, 1990), lateral transitions between one stage and the next have been documented (Bown and Kraus, 1987: p. 598). Lateral patterns are complicated by local effects of substrate and floodplain topography (Bown and Beard, 1990; Aslan, 1990; Kraus, 1992) and by interbedded avulsion-belt deposits (Kraus and Aslan, 1993), and the pedofacies model is meant to apply at a scale of kilometers to 10's of kilometers within the "true" overbank deposits (Bown and Kraus, 1987; Kraus and Aslan, 1993).

Compound pedofacies sequences made up of 15–40 m of simple pedofacies sequences occur between channel sandstones (Fig. 6C) (Kraus, 1987). The compound sequences ideally show vertical change from low to high soil maturity, representing the transition from proximal alluvial ridge to distal floodplain, followed by continued change back to low soil maturity representing the return of proximal alluvial ridge deposits (Kraus, 1987). This relatively symmetric pattern results from "a river combing back and forth across its floodplain in discrete steps" (Kraus, 1987: p. 607; Fig. 6C). Variations in the pattern indicate that channels avulsed in both large and small lateral steps. Ribbon sandstones deposited by small tributary streams may directly overlie mature paleosols, while multistoried sheet sandstones representing large rivers typically overlie immature levee deposits, suggesting greater stability and longer avulsive steps for tributary versus major channel belts (Kraus, 1987). The documented stratigraphic intervals of 15–40 m for compound sequences imply 40,000 to 200,000 years for a channel to return to a given position, based on estimated rates of sediment accumulation (Table 1). Rapid deposition during avulsion events is thought to be responsible for some discrete packages of crevasse-splay units and immature paleosols (Kraus and Aslan, 1993). Intervening sequences of finer-grained sediments and more mature paleosols represent overbank sedimentation of well-established channels between avulsions.

Systematic changes in floodplain deposits and paleosols in the Willwood Fm. imply a relatively predictable distribution of overbank environments as a function of distance from the channels. Autocyclic fluvial processes (i.e., processes intrinsic to the fluvial system rather than external climatic or tectonic controls) are responsible for the vertical stratigraphic sequences over 10's of meters that record increasing and decreasing soil maturities associated with step-wise channel avulsion across the alluvial plain. In contrast, larger-scale vertical changes in paleosol maturity over hundreds of meters, or "pedofacies megasequences," are related primarily to tectonic processes affecting rates of basin filling. Slower rates mean more mature soils and vice versa (Kraus, 1987; Bown and Kraus, 1993). The position of the northern and southern study areas in relation to the basin's axis of subsidence also affected the composition of floodplain deposits. In the north, on the axis of subsidence for the early Eocene, sandstones are common and paleosols reach only moderate stages of maturity. In the south, approximately 50 km from the basin's axis, tributary channels are common and paleosols reach advanced stages of maturity (Kraus, 1987; Kraus and Bown, 1988).

Bown and Kraus (1981a) originally suggested that mature Willwood soils (stages 4 and 5) might be spodosols, based on comparisons of color and mineral zonation with modern soils (Soil Survey Staff, 1975). Like spodosols, the Willwood soils have an epipedon rich in organic carbon and aluminum and iron oxides in the lower solum, but the presence of calcrete glaebules in the lower solum is unusual for this soil type, which forms under acidic conditions in modern environments. Carbonate translocation and precipitation is attributed to alternating wet and dry conditions early in pedogenesis (Bown and Kraus, 1987). Regardless of which modern soil type they might represent, Willwood soils are thought to have formed in an equable sub-temperate to sub-tropical climate, with initial pedogenesis taking place on land surfaces with moderate to good drainage and alternating wet and dry conditions controlled by fluctuating water tables (Bown and Kraus, 1981a). The preservation of gray, carbon-rich A horizons in the Willwood paleosols, the dominantly gray hues of the primary overbank deposits, and the presence of beds with carbonized plant remains indicate that oxidation was not intense enough to remove organic carbon in the later phase of pedogenesis. This could relate to cool and equable temperatures (i.e., no hot-dry season) (Wing and Greenwood, 1993), a water-table with only moderate seasonal fluctuations or locally perched watertables where clay translocation impeded drainage, a relatively equable rainfall regime, or a combination of all these variables. Paleobotanical evidence indicates that prolonged periods of frost or drought were not part of the Willwood climatic regime in spite of the evidence for relatively cool mean annual temperatures (Wing and Greenwood, 1993).

3.3. The organic record

Many types of organic remains are preserved in the Willwood Fm. (Table 2). Macroplant fossils and palynomorphs occur in gray carbonaceous shales associated with fine-grained overbank deposits that formed in abandoned channel and wet floodbasin environments (Wing, 1984; Farley, 1989, 1990). The flora represents forest and swamp communities. The plant record occurs throughout the Willwood Fm. and is present though not equally well preserved in all parts of the basin (Wing, 1984; Farley, 1989). Much of the vertebrate fossil record occurs in the A horizons of the Willwood paleosols (Bown and Kraus, 1981a,b; Winkler, 1983; Badgley and Gingerich, 1988). Bones and teeth, mostly of mammals less than 10 kg body weight, are abundant and well-preserved in this context. Willwood paleosols also preserve snails and calcified *Celtis* seeds (Winkler, 1983; Badgley and Gingerich, 1988), as well as a diverse assemblage of ichnofossils attributed to oligochaete worms, insects or spiders, and vertebrates (Bown and Kraus, 1983). Oncolites and stromatolites have not been reported in the Willwood Fm. Unionid pelecypods occur in crevasse splay sandstones (C. Badgley, pers. comm., 1993). Further discussion of the taphonomy of the Willwood Fm. is given in Bartels et al. (this issue).

Skeletal remains are widely distributed laterally along individual Willwood paleosols (Bown and Kraus, 1981b), implying that a considerable number of animals died over a wide area on successive land surfaces. There is no evidence for mass mortality events, and the skeletal assemblages are interpreted as resulting from attritional deaths over extended periods of time. Remains that survived early post-mortem destructive processes (e.g., carnivory, scavenging, trampling, weathering) were buried in the upper soil zone by bioturbation or the addition of small increments of sediment to the floodplain surface (Bown and Kraus, 1981b) and persisted there, apparently in spite of continuing pedogenesis. Early permineralization and encrustation by iron and carbonate deposits could have contributed to the survival of the skeletal remains (Aslan, pers. comm., 1993). Willwood vertebrate fossils are thought to have accumulated over much of the time of soil formation (Bown and Kraus, 1981b; Bown and Beard, 1990), and therefore could represent time-averaging for periods up to 10^4 years in stage 4–5 paleosols.

4. Comparison of overbank deposits

4.1. Paleosol-bounded overbank sequences

The paleosol-bounded overbank sequences in the Willwood and Chinji Formations are broadly similar. Both begin vertically with bedded mudstones or sandstones and grade upward into more bioturbated, pedogenically modified sediments capped by a well-developed paleosol. Silt-grade siliciclastic material dominates the overbank deposits in both formations, although available textural analyses indicate that the Willwood sediments include more clay (Bown and Kraus, 1981a; Aslan, 1990; Kraus and Aslan, 1993). The range of thicknesses of overbank sequences overlaps, but these are somewhat thinner in the Willwood Fm. (3–6 m) than in the Chinji Fm. (4–11 m) (Table 1). Mature paleosol thickness is slightly greater in the Willwood Fm. (3–5 m) compared with the Chinji Fm. (2–3 m). In both formations, the lower contacts of the overbank sequences are primarily nonerosional and represent crevasse-splay deposition. Overall rates of sediment accumulation are similar for the Willwood Fm. in the southern Bighorn Basin and the Chinji Fm. (Table 1), implying that overbank sequences represent about 10,000–50,000 years in both cases. Although the sedimentary successions indicate that the Paleocene–Eocene basin was generally underfilled, while the Neogene basin was overfilled (Willis and Behrensmeyer, this issue), during the times of active aggradation it appears that both areas were close to an even balance between these two states. When the rate of basin filling balanced or slightly exceeded subsidence, some areas of the alluvial plain were elevated enough above the water table to develop well-drained paleosols. The Chinji bedded mudstones are less pedogenically modified than those of the Willwood, however, with fine lamination and minimal evidence of bioturbation characterizing the lower part of each overbank sequence. Willwood mudstones retain less primary stratification (Kraus, 1987), indicating a different balance in the rate and periodicity of sediment accumulation versus the intensity of biological activity and other soil-forming processes. The vertical distance between paleosols is less in the Willwood, suggesting that lower rates of accumulation allowed more thorough pedogenic modification of each overbank sequence. The estimated amount of time for mature paleosol development is less in the Willwood Fm. than in the Chinji Fm. (10–16 kyr vs. 13–23 kyr: Table 1), however, implying that the physical and chemical effects of the soil-forming processes relate more directly to the nature and intensity of these processes than the time period over which they operated.

Some of the differences between the overbank deposits of the two formations can be related to the scale and sedimentation style of the two fluvial systems. The drainage area and major channels of the Siwalik system (both main and tributary channels) were larger (Willis and Behrensmeyer, this issue), and thicker individual overbank sequences (up to 11 m) suggest that there were deeper topographic depressions on the Siwalik floodplain than in the Bighorn Basin system. Flood events carried large volumes of sediment via crevasse splays into low-lying areas of the Chinji floodplain, and initial filling of floodplain depressions was rapid enough to prevent significant bioturbation (Willis and Behrensmeyer, 1994). Sediment input rates may have been slightly lower than subsidence rates during these periods of aggradation, contributing to channel instability and the dominance of crevasse-splay sedimentation. In contrast to the Chinji floodplain setting, situations in which 5–10 m of fine-grained sediment accumulated rapidly in topographic lows were less common on the Willwood floodplain, although avulsion-belt sequences are now thought to represent such deposits (Kraus, 1992; Kraus and Aslan, 1993). Floodplain sedimentation in the Willwood alluvial system included significant aggradation during large-scale crevasse-splay events, but between such events, alluvial ridges were formed through levee aggradation and crevasse-splay activity proximal to the major channels. Overbank sedimentation events associated with alluvial ridge formation typically resulted in decimeter- to meter-thick beds separated by periods of subaerial exposure with root penetration and incipient soil formation (Bown and Kraus, 1981a; Kraus, 1987). Floodplain sedimentation therefore appears to have differed in the two systems because Willwood channels were stable enough between times of avulsion for crevasse-splay activity to build alluvial ridges, while Chinji channels apparently shifted too frequently to allow significant alluvial ridge formation.

4.2. Paleosols

The most obvious difference in the overbank sequences from the two areas is the development of the capping paleosols. Progressive stages of pedogenic development are recognized in the Willwood Fm., but a similar sequence of immature to mature paleosols is not obvious in the Chinji Fm. Moreover, Chinji paleosols have fewer clear diagnostic soil horizons. This plus the lack of organic matter makes assignment of the paleosols to modern soil types difficult. The features of modern "bangar" and "bhat" soils of the Gangetic plain (Agarwal and Mukerji, 1951) suggest these modern soils may serve as analogues for some of the Chinji paleosols. Lateral changes occur in Chinji paleosols from the central parts of large crevasse-splay lobes to their margins, but these changes take place over distances of a few kilometers and are small compared with documented lateral trends in the Willwood paleosols (Bown and Beard, 1990). Neither the vertical or the lateral patterns in paleosol development in the Chinji Fm. match the pedofacies model for the Willwood Fm.

The differences in paleosol development can be examined in terms of fluvial setting, climate, vegetation, and local drainage conditions. The Willwood Fm. formed approximately 20° latitude farther north than the Chinji Fm. in what is now the temperate zone. Soil features and paleontological evidence in the Willwood indicate that the paleoclimate was humid sub-tropical (Bown and Kraus, 1981a; Wing et al., 1991), and the mean temperature probably was similar to or slightly cooler than that for the Chinji Fm. (Wing et al. 1991; Wing and Greenwood, 1993; see also Wing and Hickey, this issue; Koch et al., this issue). The modern alluvial soils that appear similar to those of the Chinji Fm. occur in areas with about 140 cm annual rainfall and a MAT of 25°C (Agarwal and Mukerji, 1951). The moisture regime in both basins would have been affected by the amount of discharge from the source areas and by direct precipitation on the floodplains. Rainfall apparently was sufficient in both cases to sustain permanent woodlands or forests over much of the floodplain (Wing, 1987; Quade et al., 1989; Quade and Cerling, this issue; Wing and Hickey, this issue).

In the Chinji Fm., the red color, scarcity of free carbon, and magnetic mineralogy indicate that paleosols were subject to periods of intense oxidation, most of which appears to have occurred during or shortly after soil formation. Monsoonal conditions in the sub-Himalayan belt would have caused seasonal fluctuations in the water tables of the alluvial plain and intense evapotranspiration in the sedimentary basin during the dry season. A prolonged dry season would have helped to promote oxidation of organic materials, and the periods of intense flooding would have contributed to channel instability. Buildup of overbank sequences occurred primarily during flood cycles. Paleosols that developed on crevasse-splay surfaces would have changed as these surfaces became more emergent relative to seasonal high stands of the water table, with decreased production of iron sequioxide nodules and increased flushing of carbonate from the upper soil profiles. Drainage continued to be good throughout the period of soil development, perhaps in part because clay was not abundant in the Chinji sediments and illuviation in the Bt horizon was insufficient to cause perched water tables.

In contrast, the preservation of gray, carbon-rich A horizons in the Willwood paleosols, the dominantly gray hues of the primary overbank deposits, and the presence of beds with carbonized plant remains indicate substantially less oxidation in the Bighorn Basin overbank environment. A climate promoting equable temperature and moisture conditions in the Willwood environment would have led to more moderate levels of oxidation favorable for the preservation of organic carbon (Retallack, 1984, 1990). Relatively equable rainfall directly affecting the Willwood alluvial plain could have buffered fluctuations in source-area discharge and prevented long periods of drying of the land surfaces; perched water tables and generally subdued topography on the Willwood floodplains also could have contributed to equable moisture conditions in the soils.

If these hypotheses are correct, then climate, tectonics, and to a lesser extent sediment texture acted together to control organic preservation in the two sequences. Tectonic processes set the relative height of the basin-wide water tables, while temperature and rainfall regimes as well as drainage conditions in the soils controlled levels of oxidation and other surficial processes that affected organic remains in the overbank environments.

5. Taphonomic and paleoecologic implications

5.1. *Taphonomic comparisons*

Vertebrate remains are abundant in the organic A horizons of the Willwood paleosols but rare to absent in the Chinji paleosols. Given the amount of ion translocation needed to form the mature paleosols in the Willwood Fm., it is unclear how the abundant bones preserved in the Ao horizons of these soils survived destruction by acid dissolution and bioturbation. If bones accumulated in the Ao horizon throughout the period of pedogenesis (Bown and Kraus, 1981b; Bown and Beard, 1990), then this implies that these remains were not adversely affected by the pedogenic leaching that mobilized soil cations and clay particles, perhaps because conditions were favorable for early permineralization. Explaining the near-absence of skeletal remain in the Chinji paleosols is somewhat easier. High levels of biological activity in the Chinji soils would have helped to destroy bones through recycling of their organic and inorganic components and through physical disruption and mixing of the soil matrix. Acidic conditions in the upper zone that was leached of carbonate could have contributed to bone destruction, and alternating wet and dry conditions associated with ferrolysis (Brinkman, 1970; Gerrard, 1987) also could have promoted oxidation of organic carbon and acid dissolution of vertebrate remains. Moreover, the preservation of fossils in the Chinji abandoned channels, where the moisture regime would have been relatively stable and oxidation rates lower, and where sediment accumulation was rapid, indicates that survival of bones depended on their being protected from the zones of greatest pedogenic activity (chemical or biological) (Behrensmeyer, 1988).

There may also be pre-death biases reflected in the abundance and distribution of fossil remains in the Willwood versus the Chinji Fm. Since many of the Willwood species were smaller in body size than those of the Chinji, it is possible that the overall production of skeletal remains was greater because annual mortality rates are higher for smaller animals (Western, 1980; Behrensmeyer, 1982) and population sizes usually are larger as well. Whether this had any significant effect on the abundances of preserved bones in paleosols would depend, however, on vertebrate population densities on the two alluvial plains and the relative intensity of pre-burial destructive processes such as carnivory and weathering in the two systems. There also may have been a greater tendency for animals to congregate and to die around remaining sources of water and forage during dry seasons in the Chinji ecosystem, i.e., near large- and small-scale abandoned channels where most of their remains are preserved.

5.2. *Temporal resolution and completeness*

The paleosol versus channel-fill taphonomic modes for vertebrate preservation represent different types of time-averaging and stratigraphic completeness within the overbank sequences. In the Chinji Fm., channel fills represent sporadic episodes of accumulation, transport, and burial of skeletal remains derived mainly from the abandoned channel sub-environments. If each episode occurred with minimal reworking of older bones from pre-existing deposits, time-averaging would be on the order of 100's to 1000's of years (Fig. 7A). The preserved faunas thus could repre-

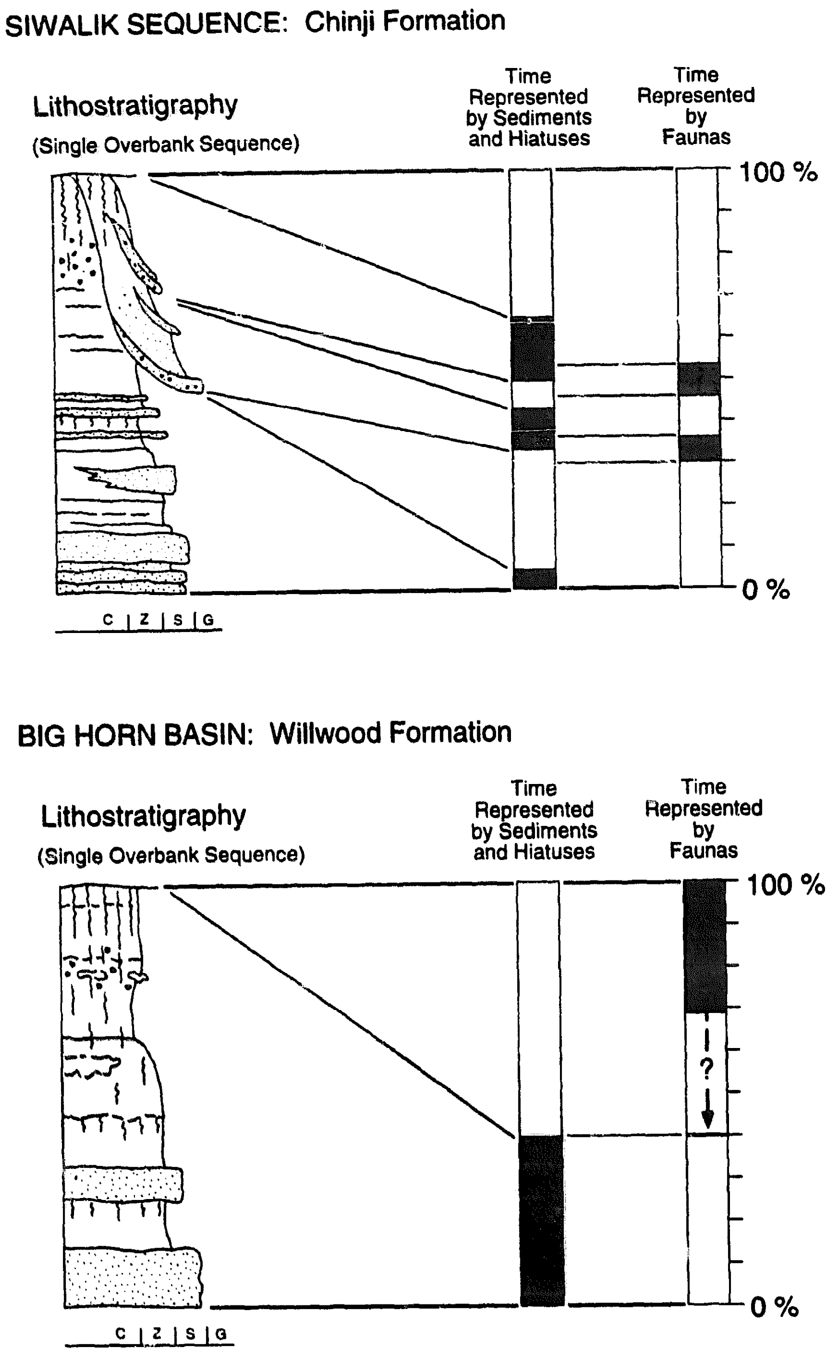

Fig. 7. Comparative schematic diagram showing overbank sequences and paleosols of the Chinji and Willwood Fms. in relation to the hypothesized completeness of the sedimentological and paleontological record. Black bars indicate the interval over which sediment or fossils accumulated. The total time spanned by each sequence is estimated at 10,000 to 23,000 yr (see text, Table 1). For discussion of relative completeness in text, each interval on the right hand scale represents 1000 yr, for a total time span of 10,000 yr. Key to scale at base of columns: *g* = gravel, *s* = sand, *z* = silt, *c* = clay.

sent whatever ecological conditions occurred in the abandoned channel setting over such time intervals. In the Willwood Fm., faunal remains are thought to have been continuously time-averaged in soils representing up to 10^4 years (stage 4–5 paleosols) (Bown and Kraus, 1981b; Bown and Beard, 1990), and thus would reflect changes in the local ecology during the progression of a soil from stage 1 to the most mature stage achieved in a particular fossiliferous stratum. The ecological signature in the preserved fauna should be strongest for habitats associated with the most mature paleosol stage, since this stage presumably would represent the longest period of time both for soil development and bone accumulation. It is possible, however, that diagenetic processes were more effective at preserving bones in earlier phases of soil formation.

Based on Sadler's original definition of stratigraphic completeness (Sadler, 1981) and the interpretations given above, the overbank sequences of the Willwood Fm. should be more complete at the 10^3 yr level than those of the Chinji, because the Willwood sequences sample a greater percentage of 10^3 yr time intervals represented by periods of initial sediment accumulation (40% of the 10^3 yr intervals compared with 10% in the example in Fig. 7). This is a consequence of somewhat slower and more sporadic aggradation in the Willwood overbank environment, as evidenced by more frequent early-stage paleosols in a typical overbank sequence. However, floodplain channels such as those in the Chinji Fm. provided renewed opportunities for sedimentation during the time interval spanned by an overbank sequence, potentially resulting in greater completeness at the 10^3 yr level (e.g., 50% of the 10^3 yr intervals could be represented; Fig. 7A). The higher freqency of channel fill deposits in the Chinji Fm. implies that stratigraphic completeness at this level of resolution could exceed that of overbank sequences in the Willwood Fm. (Fig. 7).

Completeness of the fossil record differs markedly from that of the stratigraphic record in the Willwood Fm. but not in the Chinji Fm. This is because fossil accumulation in the Willwood occurred mainly during long time intervals of paleosol formation when sedimentation had slowed or ceased altogether. Paleontological completeness at the 10^3 yr level thus could exceed stratigraphic completeness for the Willwood Fm. (40–60%; Fig. 7B). In contrast, the preservation of fossils in the Chinji Fm. depended mainly on episodes of sedimentation in channel fills, and the 10^3 yr level of paleontological completeness is less than or comparable to stratigraphic completeness (e.g., 30% vs. 50%; Fig. 7A).

5.3. *Paleoecological comparisons*

Given the differences between the architecture of the two formations' overbank sequences, it is reasonable to reconstruct the Chinji alluvial plain as a complex mosaic of low and high areas that did not closely parallel the active channels. In contrast, the Willwood alluvial plain appears to have been a dominated by linear alluvial ridges that paralleled the channels. According to the Willwood pedofacies model, there was a unidirectional trend of increasingly mature paleosols, with some variation depending on local drainage conditions, over the 15–20 km distance from a major alluvial ridge to the distal floodplain. This undoubtedly provided important ecological gradients that affected the spatial distributions of many Eocene plants and animals. Different habitats represented by the Willwood sediments and faunas (Bown and Beard, 1990) might have been more continuously interconnected along the systems of alluvial ridges, helping to promote greater overall stability of plant and animal populations through time intervals of 10^2–10^4 yrs. In contrast, over the 100 km distance between major channels on the Chinji alluvial plain (equivalent to a floodplain width of 50 km), the lack of marked alluvial ridges and the patchwork of low and high areas would have provided a more spatially variable (patchy) ecosystem for the Neogene biota. Marked seasonal fluctuations in the water table also would have made the temporal distribution of resources in this environment less predictable. Although both the Eocene and Neogene faunas would have been displaced to some extent by seasonal flooding, it is possible that the Chinji floodplain was subject to more long-distance migrations of animals and also to colonization by plants that could thrive in frequently disturbed habitats.

The differing patterns of preservation for vertebrate fossils in the Willwood and Chinji Fms. have important implications for the paleoecological significance of the preserved faunas. The Willwood paleosol faunas represent samples of the communities that existed on floodplain surfaces at varying distances from the alluvial ridges (Bown and Kraus, 1981; Bown and Beard, 1990). The fossil bones and teeth are autochthonous, or nearly so, and should accurately represent the spatial distribution of the original populations unless these distributions are blurred by the effects of time-averaging. In contrast, fossil remains in the Chinji Fm. preferentially sample animals that frequented small-scale or abandoned floodplain channels and other low areas, as well as those that died there during times of ecological stress. Although the abandoned channels were characterized by relatively low-energy or intermittent flow, many of the skeletal remains were transported short distances prior to burial (See Bartels et al., this issue). The fossil record of the Chinji Fm. therefore provides a parauthochthonous or allochthonous record that is biased toward greater representation of animal species that frequented specific areas of the overbank environment.

Habitats associated with Chinji abandoned channels could have changed during the 10^2-10^3 yr intervals of time-averaging, causing faunal mixing because of vegetational shifts in the depositional site, e.g., a succession from wetter to drier-adapted plants or from more to less disturbed conditions, with associated animal species, as the channel depressions filled with sediment. In the Willwood, changes in habitat boundaries during the 10^3 10^4 yr interval of soil formation also could have caused mixing of faunal remains from different sub-communities. Eocene habitat boundaries were stable enough during the periods of fossil accumulation, however, that some differences in original species distributions apparently were preserved (Bown and Beard, 1990).

6. Conclusion

The comparative analysis of the Willwood and Chinji Fms. clarifies similarities and differences in two terrestrial fossil-bearing sequences and demonstrates how different processes of overbank sedimentation and pedogenesis affect fossil preservation and paleoecological information.

Preservational differences between the Willwood and Chinji Fms. resulted from physical and biological processes operating at different scales. Large-scale climatic controls on temperature, rainfall, and water-table fluctuations were important in pedogenesis and the destruction or preservation of organic materials, and large-scale tectonic processes affected the sizes and stability of major channels as well as water table fluctuations. Smaller-scale processes of floodplain aggradation were responsible for the frequency and distribution of overbank channels, areas of active deposition, and emergent areas of soil formation on the alluvial plain, thereby controlling the specific sites where fossils accumulated and were buried. The Willwood and Chinji Fms. have generally comparable overbank sequences, apparently because of similarities in the way floodplain deposition occurs in episodes of crevasse-splay or avulsion-belt activity combined with varying proportions of levee progradation and sheet flooding. However, because of differences in soil moisture and permeability, oxidation rates, and perhaps also soil biota, the Willwood Fm. has a rich fossil record preserved in carbonaceous mudstones and paleosols that cap the overbank sequences, while the Chinji Fm. has abundant fossils only in environments such as abandoned channels that were not subject to intense penecontemporaneous recycling of organic materials.

The Chinji fossil record is primarily associated with abandoned channel fills, but many of the preserved organisms probably did not spend most of their lives in this environment. Paleoecological information such as species richness, which is based on the vertebrate assemblages, is "decoupled" from paleoenvironmental information that can be inferred from Chinji Fm. paleosols and their isotopic record. This means that although we can reconstruct the scale and lateral variability of the Chinji Fm. overbank environment and show that it was vegetated by forest or woodland, we cannot show how the animals were distributed across the land surface because of the taphonomic bias against preservation of vertebrates in the paleosols. This contrasts with the paleontological record of the Willwood Fm., where autochthonous fossil assemblages are preserved in the paleosols and are associated with paleoenvironmental information that can be derived from these paleosols.

In this instance, it appears that original ecological gradients for different vertebrate species are indeed preserved (Bown and Beard, 1990). This does not mean that information on spatial paleoecology is entirely lacking in the Chinji Fm., however, because it is possible to compare faunas in different types of channel fills or from place to place across the basin as a whole.

The final issue to consider is what effects differing taphonomic and paleoecological circumstances might have on the evolutionary record of faunas in the two sequences. Willwood paleosols provide a time-averaged sample of populations that would combine specimens representing short-term morphological changes over 10^3–10^4 yrs, so variability in quantitative features such as molar length might be somewhat greater than for a population representing any given point in time. The Willwood fossil assemblages should be comparable in this respect, however, and because they occur throughout the formation, they provide samples well-suited for documenting long-term morphological trends (Gingerich, 1980, 1982; Rea et al., 1990; Behrensmeyer, 1982; Badgley and Gingerich, 1988). Such samples also are appropriate for recording extinction and immigration events within the habitats represented by the faunal assemblages. Because of this fine-scale association of faunas and habitats, however, individual assemblages might not record immigration or speciation events occurring in habitats that are not well-represented by the paleosol assemblages. In the Chinji Fm., potential effects of habitat specificity in the faunas are at least somewhat countered by taphonomic processes that mixed species from different habitats, and perhaps also by ecological processes such as migrations that redistributed faunas over the floodplain. This spatial and temporal mixing should make Chinji fossil assemblages more suitable for recording basin-scale immigration and extinction events (Barry et al., 1990, 1991). The smaller population samples provided by the Chinji channel-fill assemblages and the somewhat unpredictable stratigraphic occurrence of this context makes them less ideal for following detailed evolutionary trends in vertebrate lineages.

The emphasis in the preceding discussions has been on preservational and environmental differences within particular sedimentary basins, as represented by the Willwood and Chinji Formations. There is, however, a broader ecological component that may be reflected in these differences. The combined evidence suggests that the Eocene overbank environments were relatively stable during periods of fossil accumulation, as were the associated vegetational habitats and faunas, whereas the Chinji overbank environments and biotas were subject to a less equable temperature and water table regime. This could have resulted soley from differences in basin-scale tectonics and climate, but it might also reflect global-scale differences in the climates of the Eocene versus the Miocene. Further comparative work on the paleoenvironments and taphonomy of other Paleogene and Neogene fossil-bearing sequences will be necessary to test this hypothesis.

Acknowledgments

We thank Scott Lidgard and Peter Crane, chief organizers of the Fifth North American Paleontological Convention, and Catherine Badgley, co-organizer and co-editor of the symposium on Long Records of Land Biotas, for their roles in generating the exchange of ideas that is reflected in this paper. Scott Wing contributed valuable information on Eocene paleoclimates, and John Barry helped with data on Chinji faunas. Andres Aslan, Catherine Badgley, David Fastovsky, and Mary Kraus provided helpful reviews of the manuscript. The Siwalik research was supported by the Smithsonian Foreign Currency Program (#7087120000-04), NSF Grants EAR 8720713 and EAR 9004057, and ACS/PRF #20169-AC8 to J.S. Bridge and A.K. Behrensmeyer. This is the National Museum of Natural History's Evolution of Terrestrial Ecosystems Program Publication no. 16.

References

Aslan, A., 1990. Paleotopographic controls on hydromorphic paleosol development in the Willwood Formation, Bighorn Basin, Wyoming. Thesis. Univ. Colorado, Boulder, CO, 139 pp. (unpublished).

Agarwal, R.R. and Mukerji, S.K., 1951. Gangetic alluvium of India: pedochemical characters of the genetic soil types of Gorakhpur District in the United Provinces. Soil Sci., 72: 21-33.

Badgley, C.E. and Gingerich, P.D., 1988. Sampling and faunal turnover in early Eocene mammals. Palaeogeogr. Palaeoclimatol. Palaeoecol., 63: 141-157.

Badgley, C.E., Behrensmeyer, A.K. and Morgan, M.E., 1992. Patterns in vertebrate taphonomy over four Siwalik formations. J. Vertebr. Paleontol., 12, p. 17A (suppl. to no. 3).

Barry, J.C., Flynn, L.J. and Pilbeam, D.R., 1990. Faunal diversity and turnover in a Miocene terrestrial sequence. In: R. Ross and W. Almon (Editors), Causes of Evolution: A Paleontological Perspective. Univ. Chicago Press, pp. 381-421.

Barry, J.C., Morgan, M.E., Winkler, A.J., Flynn, L.J., Lindsay, E.H., Jacobs, L.L. and Pilbeam, D., 1991. Faunal interchange and Miocene terrestrial vertebrates of southern Asia. Paleobiology, 17: 231-245.

Behrensmeyer, A.K., 1982. Time resolution in fluvial vertebrate assemblages. Paleobiology, 8: 211-227.

Behrensmeyer, A.K., 1987. Miocene fluvial facies and vertebrate taphonomy in northern Pakistan. In: F.G. Ethridge, R.M. Flores and M.D. Harvey (Editors), Recent Developments in Fluvial Sedimentology. SEPM Spec. Publ., 39: 169-176.

Behrensmeyer, A.K., 1989. Overbank facies and paleosols of the Chinji Formation, northern Pakistan. In: Progr. Abstr. 4th Int. Conf. Fluvial Sedimentol., Barcelona, p. 72.

Behrensmeyer, A.K., 1988. Vertebrate preservation in fluvial channels. Palaeogeogr. Palaeoclimatol. Palaeoecol., 63: 183-199.

Behrensmeyer, A.K. and Hook, R.S., 1992. Paleoenvironments and taphonomy. In: A.K. Behrensmeyer, J.D. Damuth, W.A. DiMichele, R. Potts, H.-D. Sues and S.L. Wing (Editors), The Evolutionary Paleoecology of Terrestrial Plants and Animals. Univ. Chicago Press, pp. 15-136.

Behrensmeyer, A.K. and Tauxe, L., 1982. Isochronous fluvial systems in Miocene deposits of Northern Pakistan. Sedimentology, 29: 331-352.

Behrensmeyer, A.K., Quade, J. and Willis, B.J., 1992. Floodplains and paleosols in the Siwalik Miocene sequence: implications for taphonomy and paleoecology of faunas. In: Abstr. Progr. 5th North Am. Paleontol. Conv., p. 22.

Behrensmeyer, A.K. and Willis, B.J., 1992. Lateral change in paleosols of the Chinji Fm., northern Pakistan. Geol. Soc. Am. Abstr. with Program, 24, p. 7.

Birkeland, P.W., 1984. Soils and Geomorphology. Oxford Univ. Press, New York.

Bown, T.M., 1980. Summary of latest Cretaceous and Cenozoic sedimentary, tectonic, and erosional events, Bighorn Basin, Wyoming. In: P.D. Gingerich (Editor), Early Cenozoic Paleontology and Stratigraphy of the Bighorn Basin, Wyoming. Univ. Mich. Pap. Paleontol., 24: 5-32.

Bown, T.M. and Beard, K.C., 1990. Systematic lateral variation in the distribution of fossil mammals in alluvial paleosols, lower Eocene Willwood Formation, Wyoming. Geol. Soc. Am. Spec. Pap., 243: 35-151.

Bown, T.M. and Kraus, M.J., 1981a. Lower Eocene alluvial paleosols (Willwood Formation, northwest Wyoming, U.S.A.) and their significance for paleoecology, paleoclimatology, and basin analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol., 34: 1-30.

Bown, T.M. and Kraus, M.J., 1981b. Vertebrate fossil-bearing paleosol units (Willwood Formation, Lower Eocene, northwest Wyoming, U.S.A.): Implications for taphonomy, biostratigraphy, and assemblage analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol., 34: 31-56.

Bown, T.M. and Kraus, M.J., 1983. Ichnofossils of the alluvial Willwood Formation (lower Eocene), Bighorn Basin, northwest Wyoming. Palaeogeogr. Palaeoclimatol. Palaeoecol., 43: 95-128.

Bown, T.M. and Kraus, M.J., 1987. Integration of channel and floodplain suites, I. Developmental sequence and lateral relations of alluvial paleosols. J. Sediment. Petrol., 57: 587-601.

Bown, T.M. and Kraus, M.J., 1993. Time-stratigraphic reconstruction and integration of paleopedologic, sedimentologic, and biotic events (Willwood Formation, Lower Eocene, northwest Wyoming. Palaios, 8: 68-80.

Bown, T.M., Kraus, M.J. and Rose, K.D., 1991. Temporal holostrome reconstruction of the Willwood Formation and the reapportionment of paleopedologic, sedimentologic, and paleobiotic events in time. J. Vertebr. Paleontol., 11, p. 17A (suppl. to no. 3).

Brinkman, D., 1970. Ferrolysis, a hydromorphic soil forming process. Geoderma, 3: 199-206.

Cerling, T.E. and Quade, J., 1992. Isotope evidence for climatic, ecologic and faunal change in the Siwaliks of Pakistan. In: 5th North Am. Paleontol. Conv. Abstr. Progr., p. 54.

Farley, M.B., 1989. Palynological facies fossils in nonmarine environments in the Paleogene of the Bighorn Basin. Palaios, 4: 565-73.

Farley, M.B., 1990. Vegetation distribution across the early Eocene depositional landscape from palynological analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol., 79: 11-27.

Fatmi, A.N., 1973. Lithostratigraphic units of the Kohat-Potwar Province, Indus Basin, Pakistan. Mem. Geol. Surv. Pakistan, 10: 1-80.

Friend, P.F., Slater, M.J. and Williams, R.C., 1979. Vertical and lateral building of river sandstone bodies, Ebro Basin, Spain. J. Geol. Soc. London, 136: 39-46.

Gerard, J., 1987. Alluvial Soils. Van Nostrand Reinhold, New York, 305 pp.

Gingerich, P.D., 1980. History of early Cenozoic vertebrate paleontology in the Bighorn Basin. In: P.D. Gingerich (Editor), Early Cenozoic Paleontology and Stratigraphy of the Bighorn Basin, Wyoming. Univ. Mich. Pap. Paleontol., 24: 1-24.

Gingerich, P.D., 1982. Time resolution in mammalian evolution: sampling, lineages, and faunal turnover. In: Proc. 3rd North Am. Paleontol. Conv., 1: 205-210.

Haynes, G., 1985a. Taphonomic studies of elephant mortality in Zimbabwe. Elephant, 2: 57-59.

Haynes, G., 1985b. Age profiles in elephant and mammoth bone assemblages. Quat. Res., 24: 333–345.

Haynes, G., 1988. Mass deaths and serial predation: comparative taphonomic studies of modern large mammal death sites. J. Archaeol. Sci., 15: 219–235.

Hickey, L.J., 1980. Paleocene stratigraphy and flora of the Clark's Fork Basin. In: P.D. Gingerich (Editor), Early Cenozoic Paleontology and Stratigraphy of the Bighorn Basin, Wyoming. Univ. Mich. Pap. Paleontol., 24: 33–49.

Johnson, N.M., Stix, J., Tauxe, L., Cerveny, P.F. and Tahirkheli, R.A.K., 1985. Palaeomagnetic chronology, fluvial processes and tectonic implications of the Siwalik deposits near Chinji Village, Pakistan. J. Geol., 93: 27–40.

Khan, I.A., 1993. Evolution of Miocene–Pliocene fluvial paleoenvironments in eastern Potwar Plateau, northern Pakistan. Thesis. State Univ. New York, Binghamton, NY.

Kraus, M.J., 1987. Integration of channel and floodplain suites, II. Vertical relations of alluvial paleosols. J. Sediment. Petrol., 57: 602–612.

Kraus, M.J. and Aslan, A., 1993. Eocene hydromorphic paleosols: significance for interpreting ancient floodplain processes. J. Sediment. Petrol., 63: 453–463.

Kraus, M.J. and Bown, T.M., 1988. Pedofacies analysis: a new approach to reconstructing ancient fluvial sequences. Geol. Soc. Am. Spec. Pap., 216: 143–152.

Kraus, M.J. and Middleton, L.T., 1987. Contrasting architecture of two alluvial suites in different structural settings. In: F.G. Ethridge, R.M. Flores and M.D. Harvey (Editors), Recent Developments in Fluvial Sedimentology. SEPM Spec. Publ., 39: 253–262.

McRae, L.E., 1989. Chronostratigraphic variability in fluvial sequences as revealed by paleomagnetic isochrons. Thesis. Dartmouth College, Hanover, NH (unpublished).

McRae, L.E., 1990. Paleomagnetic isochrons, unsteadiness, and non-uniformity of sedimentation in Miocene fluvial strata of the Siwalik Group, northern Pakistan. J. Geol., 98: 433–456.

Mohindra, R., Parkash, B. and Prasad, J., 1992. Historical geomorphology and pedology of the Gandak megafan, middle Gangetic plains, India. Earth Surf. Proc. Landforms, 17: 643–662.

Neasham, J.W. and Vondra, C.F., 1972. Stratigraphy and petrology of the Lower Eocene Willwood Formation, Bighorn Basin, Wyoming. Geol. Soc. Am. Bull., 83: 2167–2180.

Quade, J., Cerling, T.E. and Bowman, J.R., 1989. Development of Asian monsoon revealed by marked ecological shift during the latest Miocene in northern Pakistan. Nature, 34: 163–166.

Quade, J., Cerling, T.E., Morgan, M.M., Pilbeam, D.R., Barry, J., Chivas, A.R., Lee-Thorp, J.A. and Van der Merwe, N.J., 1992. The carbon and oxygen isotopic composition of carbonate in fossil tooth enamel: is it altered? Chem. Geol., 94: 183–194.

Pilbeam, D., Barry, J., Meyer, G.E., Shah, S.M.I., Pickford, M.H.L., Bishop, W.W., Thomas, H. and Jacobs, L.L., 1977. Geology and palaeontology of Neogene strata of Pakistan. Nature, 270: 684–689.

Raza, S.M., 1983. Taphonomy and paleoecology of middle Miocene vertebrate assemblages, southern Potwar Plateau, Pakistan. Thesis. Dep. Geol. Geophys. Yale Univ.

Rea, D.K., Zachos, J.C., Owen, R.M. and Gingerich, P.D., 1990. Global change at the Paleocene–Eocene boundary: climatic and evolutionary consequences of tectonic events. Palaeogeogr. Palaeoclimatol. Palaeoecol., 79: 117–128.

Retallack, G.J., 1990. Soils of the Past. Unwin-Hyman, London, 520 pp.

Retallack, G.J., 1991. Miocene paleosols and ape habitats of Pakistan and Kenya (Oxford Monogr. Geol. Geophys., 19). Oxford Univ. Press, Oxford, 346 pp.

Sadler, P.M., 1981. Sediment accumulation rates and the completeness of stratigraphic sections. J. Geol., 89: 569–584.

Smith, N.D., Cross, T.A., Dufficy, J.P. and Clough, S.R., 1989. Anatomy of an avulsion. Sedimentology, 36: 1–23.

Soil Survey Staff. 1975. Soil taxonomy, a basic system of soil classification for making and interpreting soil surveys. Handbook U.S. Dep. Agric., 436: 1–754.

Tauxe, L. and Badgley, C.E., 1984. Transition stratigraphy and the problem of remanence lock-in times in the Siwalik red beds. Geophys. Res. Lett., 11: 611–613.

Tauxe, L. and Badgley, C.E., 1988. Stratigraphy and remanence acquisition of a paleomagnetic reversal in alluvial Siwalik rocks of Pakistan. Sedimentology, 35: 697–715.

Thomas, R.G., Smith, D.G., Wood, J.M., Visser, J., Calverley-Range, E.A. and Koster, E.M., 1987. Inclined heterolithic stratification—terminology, description, interpretation and significance. Sediment. Geol., 53: 123–179.

Western, D., 1980. Linking the ecology of past and present mammal communities. In: A.K. Behrensmeyer and A.P. Hill (Editors), Fossils in the Making. Univ. Chicago Press, pp. 41–54.

Willis, B.J., 1993a. Ancient river systems in the Himalayan Foredeep, Chinji Village area, northern Pakistan. Sediment. Geol., 88: 1–76.

Willis, B.J., 1993b. Evolution of Miocene Fluvial systems through a kilometer-thick coarsening-upwards succession, Siwalik Group, northern Pakistan. Sediment. Geol., 88: 77–121.

Willis, B.J. and Behrensmeyer, A.K., 1992a. Morphology of Siwalik paleosols exposed in northern Pakistan. Geol. Soc. Am. Abstr. Program, 24, p. 7.

Willis, B.J. and Behrensmeyer, A.K., 1992b. Relationship of overbank deposition and pedogenesis within the Chinji Formation. Geol. Soc. Am. Abstr. Program, 24, p. 7.

Willis, B.J. and Behrensmeyer, A.K., 1994. Architecture of Miocene overbank deposits in northern Pakistan. J. Sediment. Res., B64: 60–67.

Wing, S.L., 1984. Relation of paleovegetation to geometry and cyclicity of some fluvial carbonaceous deposits. J. Sedimentary Petrol., 54: 52–66.

Wing, S.L., 1987. Eocene and Oligocene floras and vegetation of the Rocky Mountains. Ann. Mo. Bot. Garden, 74: 748–784.

Wing, S.L., Bown, T.M. and Obradovich, J.D., 1991. Early

Eocene biotic and climatic change in interior western North America. Geology, 19: 1189–1192.

Wing, S.L. and Greenwood, D., 1993. Fossils and fossil climate: the case for equable continental interiors in the Eocene. In: J.R.L. Allen, B.J. Hoskins, B.W. Sellwood and R.A. Spicer (Editors), Palaeoclimates and their Modelling with Special Reference to the Mesozoic Era. Philos. Trans. R. Soc. London B, 341: 243–252.

Winkler, D.A., 1983. Paleoecology of an early Eocene mammalian fauna from paleosols in the Clark's Fork Basin, northwestern Wyoming (U.S.A.). Palaeogeogr. Palaeoclimatol. Palaeoecol., 43: 261–298.