PALAEO

Taphonomy of vertebrate assemblages from the Paleogene of northwestern Wyoming and the Neogene of northern Pakistan

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Abstract

We compare the taphonomy of vertebrate assemblages from two long continental records—the early Paleogene of the Bighorn Basin, Wyoming, and the Neogene Siwalik sequence of northern Pakistan. Both sequences contain a similar array of fluvial facies, and the abundance of these facies differs among formations. We document environments of preservation of vertebrate localities over time to determine comparability of fossil assemblages within and between sequences. Changes in sample size and species richness are noted to reveal potential sampling effects on patterns of faunal turnover. Preservational history determined the environment, sample size, quality of specimens, taxonomic composition, and spatial and temporal resolution of fossil assemblages and thereby the quality of the fossil record and its suitability for further analyses.

In both sequences, changes in prevailing taphonomic processes reflect changes in lithofacies and habitat distribution. Correlated changes are found in fossil productivity, species richness, and faunal composition. Both sequences contain some episodes of apparent faunal change in which appearances and disappearances of rare taxa can be attributed principally to changes in sample size. The Paleogene record has high taxonomic resolution (i.e., to genus or species) for most mammalian fossil remains. Temporal and spatial averaging of Paleogene fossil assemblages changes with lithofacies. The Neogene record has higher taxonomic resolution for remains of small mammals (<2 kg) than of large mammals. All formations have several fossiliferous facies, with moderate to high degrees of temporal averaging and low to high degrees of spatial averaging.

Different preservational circumstances impose different constraints on paleocological and evolutionary analyses. The best opportunities for paleocommunity reconstruction are provided by high taxonomic resolution, large samples, and varied environments of preservation. These circumstances are found in limited portions of each record. The best opportunities for documenting evolution within lineages and species-replacement patterns are provided by high taxonomic resolution, high temporal resolution, and consistent preservational context. These taphonomic attributes pertain to the more common Paleogene mammals, particularly from the rich paleosol localities of the Willwood Formation, and to the more common Neogene small mammals from abandoned-channel fills of the Siwalik record.

1. Introduction

Processes of preservation determine the nature of the fossil record at different scales. At a global scale, only depositional environments contribute to the long-term fossil record. Their ecology and geology constitute the environmental record of the history of life, and their distribution is controlled by plate tectonics, sea level, and climate. At the scale of a depositional system, the spatial distribution of local environments determines the habitats available to organisms; the rates and processes of preservation may vary greatly among these environments in relation to physical aspects of environment and biological attributes of inhabitants. At the scale of a fossil assemblage, taphonomic processes influence the taxonomic composition, the taxonomic, temporal, and spatial resolution, and the abundance of preserved material.

Taphonomic features of fossil assemblages provide a basis for assessing the quality of the fossil record and the nature of evolutionary and ecological questions that can be addressed with the available data. Differences in the lateral distribution of sedimentary facies, in associated habitats and processes of mortality, and in post-mortem alteration, transport, and burial may substantially change the amount, quality, and identifiability of preserved material. In turn, these aspects of fossil assemblages (and collections made from them) determine the reliability of inferences about original faunal composition, associations among taxa, rates of morphological evolution within lineages, and patterns of immigration and extinction. Changes in preservational bias may reflect significant environmental changes that are correlated with changes in biotic composition or fossil productivity (e.g., Behrensmeyer, 1988; Kidwell, 1988). Recognition of changes in taphonomic selectivity facilitates the distinction between apparent and real changes in original biotas (e.g., Koch, 1987; Badgley and Gingerich, 1988). Relevant data include patterns of covariation among biotic composition, taphonomic attributes of fossil assemblages, and sedimentary facies.

Sedimentary facies strongly influence the fossil collections that they yield. These influences stem from the combined effects of depositional environ-

ments on the distribution of living organisms, the manner in which biotic remains are preserved as fossil assemblages, and the techniques used in recovering fossils as collections. The wider the variety of sedimentary facies represented at a given stratigraphic interval, the greater the potential that the aggregate fossil assemblage will closely reflect the original biota. If complementary collecting techniques are employed, the greater the potential that collections will accurately reflect the fossil assemblages.

The long continental sequences of the early Paleogene of Wyoming and the Neogene Siwalik rocks of northern Pakistan contain a rich vertebrate record in predominantly fluvial deposits. Both sequences contain a broadly similar array of fluvial facies, and the frequency of facies changes markedly over time and space (see Willis and Behrensmeyer, this issue; Behrensmeyer et al., this issue). In addition, fossil productivity and assemblage composition vary among facies and within the same facies over time. Comparison of vertebrate taphonomy in these two long records focuses on four subjects: (1) changes over time in fossil productivity in relation to facies and inferred environments, (2) changes in fossil productivity (sample size) in relation to species richness to reveal potential sampling effects on patterns of faunal turnover, (3) the consequences of different taphonomic histories for taxonomic, temporal, and spatial resolution of vertebrate remains, and (4) causes of enhanced preservation of selected vertebrates in particular depositional environments – in terms of life-habitats, habitat-specific mortality, and post-mortem processes of accumulation. From these results, we discuss how preservational circumstances constrain reconstruction of paleocommunities and patterns of faunal change in each sequence. Our coverage is restricted to vertebrate remains, especially mammals, with some data presented for reptiles and fishes. Bird fossils are known from both sequences (Bartels, 1980; Harrison and Walker, 1982) but are quite rare. Invertebrates, especially gastropods and pelecypods, are present in both sequences but have not been studied in this respect. Wing et al. (this issue) document the distribution of macrofloral remains

in relation to depositional environments for the Bighorn Basin.

The paper is organized by subject, compared and contrasted for each field area. First, we review the nature of fossil assemblages in each area. Then taphonomic data from each sequence are presented for fossil productivity in relation to facies and taxonomic richness in relation to sample size. Next, we evaluate the taxonomic, temporal, and spatial resolution of fossil assemblages and selective preservation of taxa in relation to depositional environment. We distinguish between *fauna* – as the vertebrate portion of the original biota, *fossil assemblage* – as the preserved record of the original fauna, and *collection*–as the samples collected from fossil localities. Also, we present the effects of different collecting techniques when relevant.

2. The nature of vertebrate fossil assemblages

2.1. Wyoming Paleogene

The Bighorn Basin (including the northern part, the Clarks Fork Basin) of northwestern Wyoming contains abundant remains of Paleocene to early Eocene vertebrates from the Fort Union and Willwood formations. Taphonomic research to date has focused on processes and rates of bone accumulation and taphonomic biases for surface-collected vertebrate assemblages in paleosols of the Willwood Formation (Bown and Kraus, 1981a,b; Winkler, 1983; Bown and Beard, 1990) and for selected quarry sites, mainly from the Fort Union Formation (e.g., Alexander, 1982; Bartels, 1987; Leite, 1992). Winkler (1983) evaluated the role of collecting method on faunal composition.

Fossil assemblages

Fossil assemblages are mainly of three kinds: (1) spatially restricted concentrations in coarse lithologies, (2) laterally extensive fossiliferous mudstones, and (3) dense concentrations of small vertebrates in lenses of limestone. Sample sizes range from one to thousands of specimens, with many localities containing more than 100 recorded specimens (Rose, 1981). Teeth and jaws are generally well preserved, but many postcranials are

fragmented or crushed, presumably from compaction or recent weathering.

The spatially and stratigraphically restricted concentrations in coarser lithologies extend over tens to a few hundred square meters laterally and 0.5–2 m vertically (Alexander, 1982; Bartels, 1987). Vertebrate remains are disarticulated and dispersed within the sediment matrix. Many of these concentrations occur in muddy sandstone or intraformational conglomerate lenses within purer channel-sandstone deposits of the Fort Union Formation. Bones and teeth are matrix-supported and generally show little abrasion or other surface damage.

Fossil assemblages in mudstones are stratigraphically restricted to units that are usually <1 m in thickness but extend laterally for up to kilometers (Bown and Kraus, 1981b). Vertebrate remains are generally disarticulated with a moderate frequency of associated gnathic, dental, and postcranial remains (see also Winkler, 1983; Bown and Beard, 1990). These fossiliferous mudstone units are paleosol horizons of varying maturities (Neasham and Vondra, 1972; Bown and Kraus, 1981a, 1987; Bown and Beard, 1990) and are the primary source of vertebrate remains from the Willwood Formation. Vertebrate concentrations from carbonaceous mudstones or sandstones are rare in the Willwood Formation (Bown and Kraus, 1981b).

The third context for vertebrate remains is small lenses and pods of limestones (Gingerich, 1987). These vary widely in size and shape; some are interpreted as fillings of hollow trees, while others are interpreted as small ponded areas. A wide variety of fossils has been recovered, including snails, clams, plant debris, burrows, amphibians, lizards, mammals, and birds.

Collecting methods

Three collecting methods have been employed for these Paleogene fossil assemblages. Quarrying (excavation) has been the method of choice for the richest Paleocene concentrations of the Fort Union Formation. This method is well suited to the concentrated remains from discrete beds with relatively little exposed surface. Also, the generally coarse, unweathered matrix makes screen washing difficult until the matrix has been exposed and

reduced to small pieces. Quarrying has yielded vertebrate remains of all sizes (Alexander, 1982).

Surface collecting has been the primary method for the vertebrate concentrations in paleosols, because these units have insufficient fossil concentrations to warrant quarrying and they have extensive exposed surfaces (generally subvertical) that are continually renewed by natural erosion. This method tends to under-represent remains of the smallest vertebrates, especially in terms of relative abundance (Winkler, 1983). But surface collecting of these concentrations yields a high return in fossils for the time expended.

The third method is screen-washing. Fossiliferous matrix is collected, dried, washed with water, acid, or kerosene, and sorted. This labor-intensive method is typically employed to recover remains of the smallest vertebrates from particularly productive matrix; fragile material may be damaged in this process. Screen washing has been used to supplement surface collecting and quarrying for selected localities from the Fort Union and Willwood formations.

2.2. Siwalik Neogene

The Siwalik Group of the Potwar Plateau, northern Pakistan, contains a rich vertebrate record that spans much of the Neogene. Taphonomic research to date has focused on the distribution of fossil localities among depositional environments, inferring circumstances of mortality and accumulation, and reconstructing abundance of taxa in the original community (Badgley and Behrensmeyer, 1980; Badgley, 1982, 1986a,b; Raza, 1983; Behrensmeyer, 1988; Badgley et al., 1992).

Fossil assemblages

Siwalik localities are typically scatters of vertebrate bones and teeth from a restricted stratigraphic interval and areal distribution. The scale of most localities is 0.5 to several meters thick and a few to tens of square meters in area. On rare occasions, a fossiliferous unit extends for tens to hundreds of meters. No complete skeletons have been found, and articulated remains are rare. Sample size ranges from one to thousands of

specimens, with most localities represented by less than 100 recorded specimens.

Collecting methods

Different collecting methods have been employed for recovering remains of large versus small mammals. Surface collecting has been the primary means of collecting remains of large-mammals, those taxa with original body mass of >2 kg. This practice has ranged from selective collection of taxonomically diagnostic material at most localities to systematic collection of all material from a gridded area for a subset of localities (Badgley, 1982; Raza, 1983). Also, excavations have been conducted at a small number of localities where dense concentrations occur in situ. While surface collecting sometimes has yielded remains of rodents, insectivores, bats, and the smallest primates and carnivores, the primary method of recovering small-mammal material has been screen washing. This method has yielded a rich record of small mammals throughout the Siwalik sequence (e.g., Jacobs et al., 1989; Flynn et al., this issue). In most instances, remains of large and small mammals are preserved at the same locality—with small-mammal remains concentrated in spatially restricted layers and large-mammal remains more broadly dispersed. Since the record of large and small mammals has resulted from different collecting methods, we report the long-term trends in Siwalik fossil productivity, species richness, and faunal turnover separately for these two size groups.

3. Fossil productivity in relation to sedimentary facies

In both the Paleogene and Neogene sequences, fossil productivity, as indicated by the number of localities or the number of catalogued specimens of mammals, varies in relation to lithofacies, both at the scale of formations and at the scale of depositional environments within each formation. In each sequence, formations differ in dominant lithology and sediment accumulation rate (Table 1). While the relationship between dominant lithology and sediment accumulation rate is

Table 1

Geological and paleontological attributes of formations as generalized from sources mentioned in text; also, see Figs. 1 and 3. Rates of sediment accumulation vary about 5-fold at the scale of formations. Number of localities varies by about an order of magnitude from few to many. Taxonomic richness varies by a factor of about 2 from low to high. Since formation boundaries are time-transgressive, age estimates are representative

Formation	Age (Ma)	Dominant lithology	Sed. accum. rate	Number of localities	Taxonomic richness
Bighorn and Clarks Fork basins, northwestern Wyoming					
	50				
Willwood		mudstone	high to low	many	med-high
	56.5				
Fort Union		mudstone+	low to high	few	low-med
	65		sandstone		
Siwalik formations, Potwar Plateau, northern Pakistan					
	5.3				
Dhok Pathan		mudstone	high	many	high
	8.8				
Nagri		sandstone	high	few	med-high
	10.8				
Chinji		mudstone	low	many	high
	14.0				
Kamlial		sandstone	low	few	low
	18.3				

variable, there is a consistent relationship between dominant lithology and mammalian fossil productivity: mudstone-dominated formations have more localities and higher taxonomic richness than sandstone-dominated formations. This difference probably reflects the overall prevalence of terrestrial habitats suitable for mammals in fluvial systems with larger floodplains and fewer or smaller channel belts.

3.1. Wyoming Paleogene

The Paleogene formations span about 15 m.y. The Fort Union Formation typically consists of closely spaced, thick sandstones and minor carbonaceous mudstones and lignites in the lower part and more widely separated sandstones interbedded with better drained mudstones in the upper part. There are lateral and regional deviations from this pattern. Fossils are rare throughout. Vertebrate concentrations occur mainly in intraformational conglomerates at the bases of sandstone channel deposits in the lower Fort Union and in a wider range of contexts in the upper part (Bartels, 1987; Bartels et al., 1992; Leite, 1992). The Willwood

Formation contains thick sequences of mudstone with well-developed, laterally extensive paleosols and minor sandstone units (Kraus, 1980). Vertebrate fossils occur primarily in the paleosol units, with minor occurrences in swamp, crevasse-splay, channel, and abandoned-channel deposits (Bown and Kraus, 1981b; Bartels, 1987; Bown and Beard, 1990) and in freshwater limestones (Gingerich, 1987).

Fossil productivity for localities in the Clarks Fork Basin is higher for the Willwood than for the Fort Union Formation. (The Fort Union is not well exposed in the central Bighorn Basin). Figure 1a depicts the number of localities and records for mammalian remains; the data are changed little by including remains of other vertebrates. The correlation coefficient between number of localities and number of catalog records is 0.4. For three of the Paleocene zones, between 90–100% of the records come from a single rich quarry, decreasing the potentially higher correlation. In this local sequence, the boundary between the Fort Union and Willwood formations lies near the base of zone Cf-2 (Gingerich, 1976; Rose, 1981). The outcrop area of the upper Fort Union
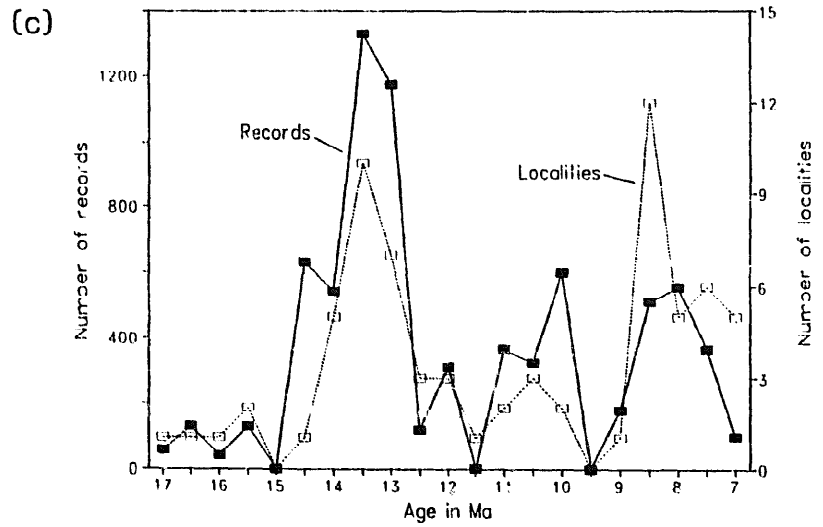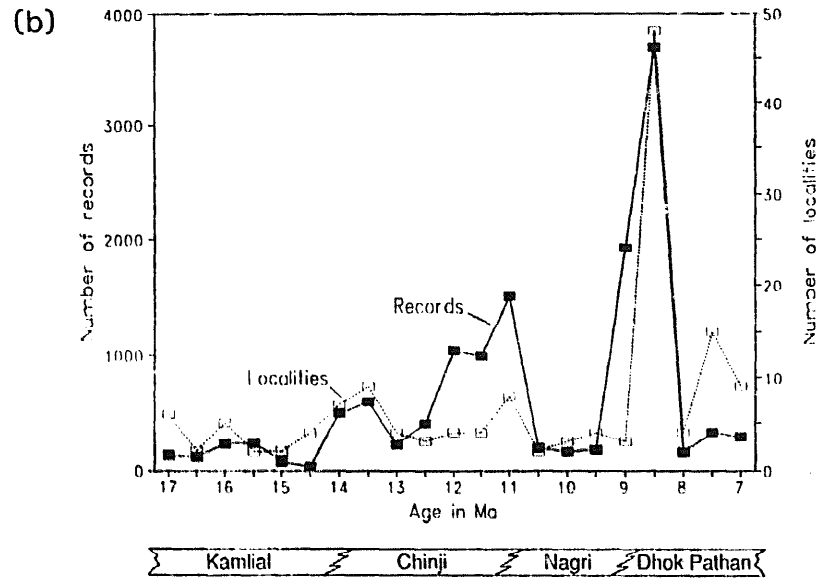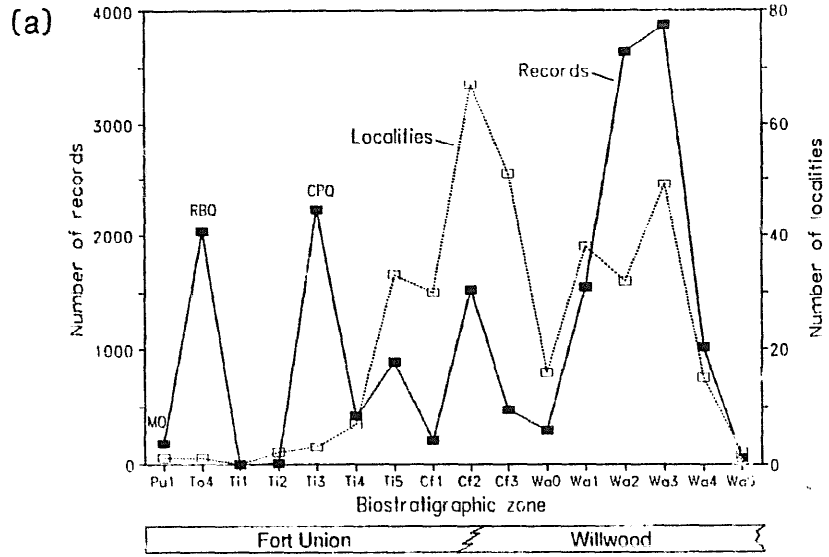
(a)

Number of records

Number of localities

MO
RBO
CPO
Records
Localities

Pu1 To4 Ti1 Ti2 Ti3 Ti4 Ti5 Cf1 Cf2 Cf3 Wa0 Wa1 Wa2 Wa3 Wa4 Wa5
Biostratigraphic zone

Fort Union   Willwood

(b)

Number of records

Number of localities

Records
Localities

17 16 15 14 13 12 11 10 9 8 7
Age in Ma

Kamlial   Chinji   Nagri   Dhok Pathan

(c)

Number of records

Number of localities

Records
Localities

17 16 15 14 13 12 11 10 9 8 7
Age in Ma

Table 2

Distribution of vertebrate localities among fluvial environments. + means present but not abundant. + + means abundant. means absent

Formation	Depositional context				
	Channel lag	Abandoned channel	Splay	Swamp	Floodplain/ paleosol
Paleogene record, Bighorn and Clarks Fork basins					
Willwood	+	+	+	+	+ +
Fort Union					
upper	+	+	+	+	+
lower	+ +	+	–	+	—

	Major channel		Secondary channel		Splay	Floodplain palaeosol
	Lag	Fill	Lag	Fill		
Neogene large-mammal record, Siwalik Group of Potwar Plateau, Pakistan						
Dhok Pathan						
Number	0	2	19	8	12	13
% (n=54)	0	4	35	15	22	24
Nagri						
Number	4	3	1	4	0	4
% (n=16)	25	19	6	25	0	25
Chinji						
Number	4	14	26	19	1	13
% (n=77)	5	18	34	25	1	17
Kamlial						
Number	4	5	2	2	2	2
% (n=17)	22	28	11	11	11	11

Formation is roughly similar to that of the Willwood Formation in the Clarks Fork Basin (Gingerich, 1983; Gingerich and Klitz, 1985), so the difference in productivity cannot be attributed to area of exposure. But for the lower Fort Union Formation, restricted outcrop area probably is a significant factor. Also, the stratigraphic thickness, duration, and outcrop area of biostratigraphic zones vary markedly within formations; and these factors probably do influence fossil productivity. For example, the zone Wa-0 is represented by a narrow strip of section, much in subvertical outcrop, only 5–37 m thick (Gingerich, 1989),

while zones Wa-1 and Wa-2 are over 100 m thick with a much larger outcrop area (Gingerich and Klitz, 1985). High in the local section (Wa-4, Wa-5), outcrop area declines due to the pattern of badland erosion.

The distribution of fossil localities among sedimentary environments changes from lower Fort Union to upper Fort Union to Willwood. Table 2a indicates the range of productive sedimentary environments in the Bighorn Basin. Overall, poorly to moderately drained mudstones are the dominant facies in the Fort Union Formation. Sandstones are thicker and more prevalent in the lower Fort

Fig. 1. Fossil productivity over time, as indicated by number of catalogued localities and number of catalogued specimens (records). Position of formation boundaries indicated in each sequence. (a) Early Paleogene of Clarks Fork Basin, Wyoming, with data compiled for mammalian biostratigraphic zones; Pu = Puercan, To = Torrejonian, Ti = Tiffanian, Cf = Clarkforkian, Wa = Wasatchian; MQ = Mantua Quarry, RBQ = Rock Bench Quarry, CPQ = Cedar Point Quarry. Information provided by P.D. Gingerich. (b) Neogene Siwalik record for large mammals (>2 kg), with data compiled for 0.5-m.y. intervals. (c) Siwalik record for small mammals (<2 kg), with data compiled for 0.5-m.y. intervals.

Union than in the upper Fort Union. In the lower Fort Union, fossil concentrations occur primarily in channel deposits. Individual fossiliferous units occur in basal conglomerates of active channels, as transported bedload in crevasse-splay deposits at the base of avulsion sequences, and as minimally transported concentrations that accumulated during channel abandonment (Bartels, 198 , Leite, 1992). Hence, the most productive fossiliferous facies is not the dominant one (mudstone). In the upper Fort Union, fossil localities occur in a broad range of environments (Table 2a), including abandoned channels, splay deposits, swamps, and floodplain (Bartels, 1987; Leite, 1992). In the Willwood Formation–dominated by moderately to well drained mudstones, most localities occur in paleosol units formed on floodplain mudstones, with occasional localities in other depositional contexts (Bown and Kraus, 1981b). Hence, the most productive facies is also the dominant one (mudstone).

3.2. Siwalik Neogene

The distribution of Siwalik vertebrate localities among sedimentary environments has been documented for four formations that span about 13 m.y. Siwalik formations vary in lithofacies, sediment accumulation rate, and fossil productivity (Table 1b). The Kamlial and Nagri formations are dominated by coarser lithologies (>50% sandstone) and larger channel belts, while the Chinji and Dhok Pathan formations are dominated by fine-grained lithologies (>50% mudstone) and smaller channels (see Willis and Behrensmeyer, this issue). The net sediment accumulation rate is lower for the two older formations and increases sharply at the Chinji-Nagri boundary (Johnson et al., 1985).

Mammalian fossil productivity is significantly higher in the Chinji and Dhok Pathan formations than in the Kamlial and Nagri formations (Fig. 1b,c; Badgley et al., 1992). The number of records and the number of localities are well correlated (r=0.8) for large-mammal remains. In Fig. 1b, notable increases and decreases in fossil productivity occur at formation boundaries (with

some imprecision because formation boundaries are time-transgressive by up to 1 m.y. over lateral distances of 30–40 km (Barry et al., 1980)). While the Kamlial and Nagri formations are consistently low in productivity, the Chinji and Dhok Pathan Formations exhibit intervals of both high and low productivity. For small-mammal remains (Fig. 1c), the correlation between the number of records and the number of localities is slightly weaker (r=0.7) than for large mammals. The most productive intervals occur in the Chinji and Dhok Pathan formations, as is similar for the large-mammal record.

The pattern of fossil productivity in relation to depositional environments within formations is more variable than in the Paleogene record. Vertebrate fossils occur principally in four kinds of fluvial deposits—large (major) channel complexes, secondary (floodplain) channel complexes, crevasse splays, and well-drained floodplains. The only major environment without vertebrate fossils is marly floodplain lakes. The frequency of fluvial environments changes across formations, with large channel complexes dominating the coarser-grained Kamlial and Nagri formations and floodplains dominating the finer-grained Chinji and Dhok Pathan formations. Fig. 2 illustrates the frequency of fossil localities (n = 164) in the principal fossiliferous environments over four formations. Fossil productivity varies among fluvial environments within formations, with the major and secondary channel environments containing most localities for each formation. In the Kamlial and Nagri formations (Fig. 2a), more localities occur in the most prevalent environment—the major channel complexes—than in other depositional environments. In the Chinji and Dhok Pathan formations (Fig. 2b), more localities occur in secondary channels than in other environments, even though floodplains are the most prevalent environment. Hence, for these two formations, fossil preservation does not track the most prevalent depositional environment. In contrast to the Bighorn Basin, the voluminous Siwalik floodplain paleosols preserve fossils in low frequency across all formations. Causes of change in productivity across formations and environments in both
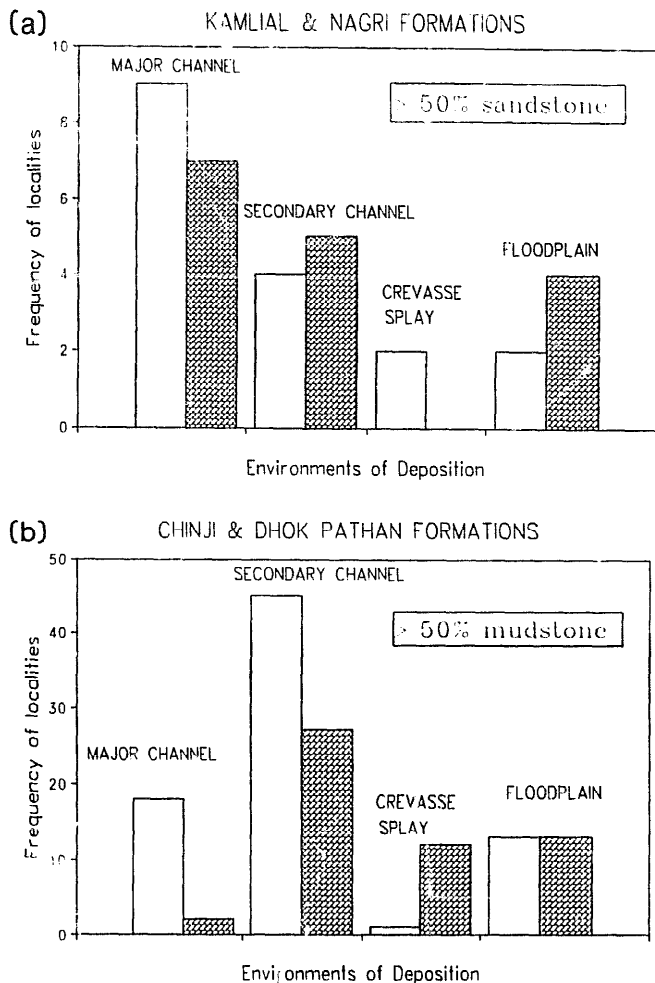
(a)

(b)

Fig. 2. Siwalik fossil productivity (number of localities with documented fluvial facies, among four depositional environments from (a) the sandstone-dominated Kamlial (light stipple) and Nagri (dark hatching) formations compared to (b) the mudstone-dominated Chinji (light stipple) and Dhok Pathan (dark hatching) formations. The sample of fossil localities (n = 164) is a representative subset selected for taphonomic study from about 850 localities.

sequences are considered below. (See also Behrensmeyer et al., this issue.)

4. Species richness and sample size

Changes in sample size are important to monitor because they are usually highly correlated with changes in species richness. Generally, larger samples taken from the same distribution of species abundances exhibit higher taxonomic richness. Common taxa are less sensitive than rare ones to

varying sample sizes. Increases in sample size alone may result in apparent new appearances in a particular collection and decreases may result in disappearances. For example, over 2000 mammalian specimens had been collected from Cedar Point Quarry up to 1981; then two new species of mammals were found in subsequent excavation. Changes in sample size over time may lead to artificial truncation of species ranges or to apparent peaks of appearances and disappearances (e.g., Badgley and Gingerich, 1988; Stucky, 1990).

4.1. Wyoming Paleogene

For localities from the Clarks Fork Basin, sample size and species richness are highly correlated ($r = 0.9$ for square root of sample size v. species number). Fig. 3a indicates that sample size and species richness rise and fall in concert. Also, comparison of Figs. 1a and 3a indicates that biostratigraphic zones in the Willwood Formation are on average more speciose than those in the Fort Union Formation, an expected consequence of generally greater sample sizes per zone. This "typical" pattern of covariation indicates that episodes of species disappearances at the end of Ti-3, Ti-5, Cf-2, Wa-3, and Wa-4 and episodes of appearances at the beginning of Ti-3, Cf-2, and Wa-1 should be interpreted with caution, since the observed changes in sample size could be the cause of some of these apparent events. In their study of Paleogene faunal turnover, Maas et al. (this issue) identified some of the same intervals as inadequately sampled.

4.2. Siwalik Neogene

For the Siwalik record, this relationship is evaluated for rodents, the most speciose group of small mammals, and for artiodactyls, the most speciose group of large mammals. Sample size is highly correlated with the number of species per interval for rodents (Fig. 3b, $r = 0.9$ for square root of sample size versus number of species found) and slightly less for artiodactyls (Fig. 3c, $r = 0.7$). This difference probably reflects less resolved taxonomy for the artiodactyls and the likelihood that many of the originally common species were artiodactyls.

(a) Bighorn Basin mammals

(b) Siwalik artiodactyls

(c) Siwalik rodents
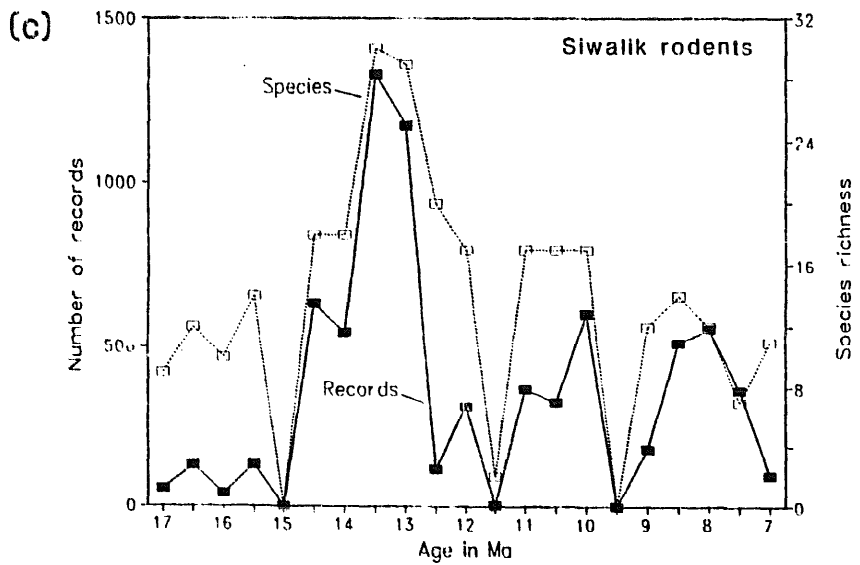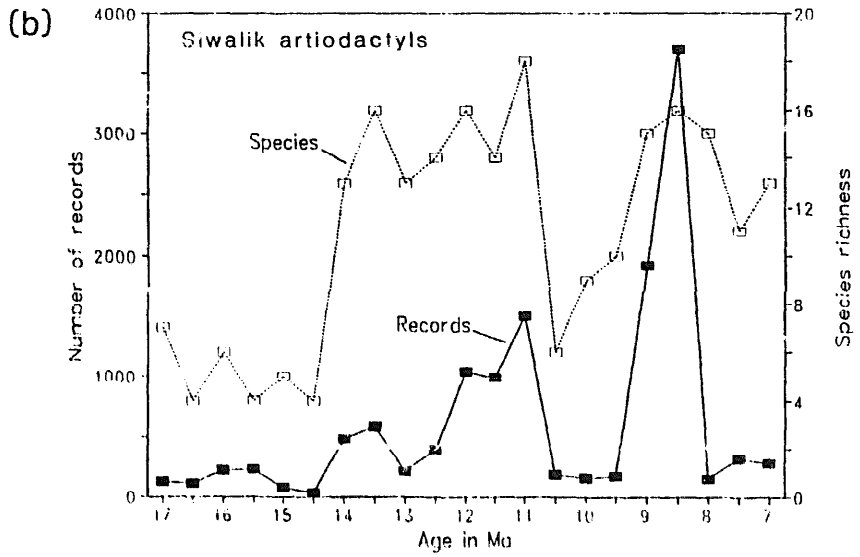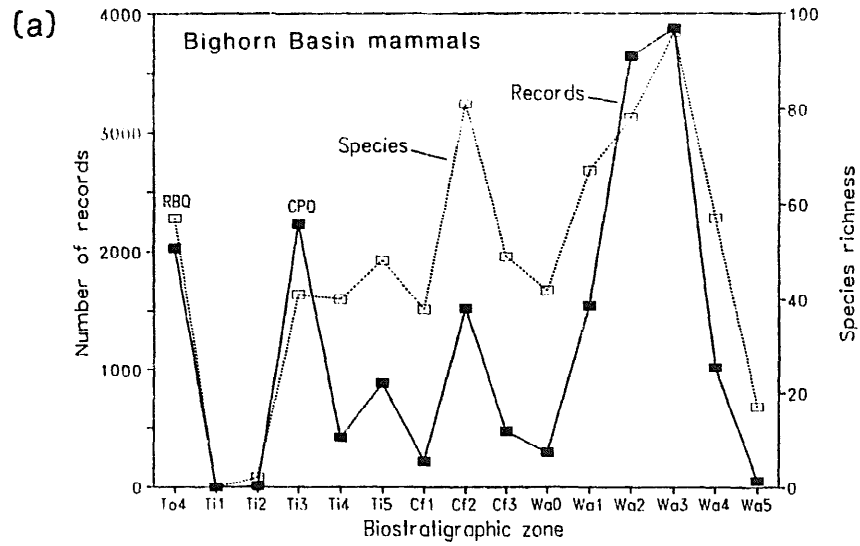
Consequently, changes in fossil productivity upsection, such as those near some formation boundaries, should influence the apparent timing of appearances and disappearances as well as overall species richness for the small-mammal record. Episodes of appearances close to the Kamlial-Chinji boundary and the Dhok Pathan-Nagri boundary and of disappearances in the upper Chinji, upper Nagri, and in the highest part of the documented section (ca. 7 Ma) should be interpreted with caution. An increase in large-mammal species, especially in those that are typically rare at best, should occur in association with the peak of sample size at 8.5–9.0 Ma (lower Dhok Pathan Formation).

5. Taxonomic, temporal, and spatial resolution

Different processes of mortality and accumulation may result in widely varying degrees of taxonomic, temporal, and spatial resolution in vertebrate fossil assemblages (Badgley, 1986a; Behrensmeyer, 1991). Taxonomic resolution depends on the diagnostic utility of preserved remains; some elements are much more diagnostic—especially in isolation—than others. Evidence for taxonomic resolution lies with the skeletal-element composition of fossil assemblages and the degree of association of skeletal remains (since for associated remains, the diagnostic aspect of one element may be extended to other elements). The potential range of taxonomic resolution is from subspecific variant (very high) to vertebrate class (low). Temporal resolution depends on the form of mortality and the mode of accumulation—processes that may occur prior to final burial of a bone assemblage. Evidence for degree of temporal resolution includes the nature of bone damage—weathering stage, signs of predation or scavenging, and abrasion, the degree of association of skeletal

remains, the relationship of bones to sedimentary matrix, and general characteristics of the depositional environment. Temporal resolution varies from virtually instantaneous (very high) to millions of years (very low) if reworking of bone is involved (Behrensmeyer, 1982; Behrensmeyer and Chapman, 1993). While the ends of the spectrum are fairly readily identified, there is considerable uncertainty in placing assemblages between the extremes. Spatial resolution depends on processes of mortality, accumulation, and transport. Evidence for spatial resolution includes the areal extent of the assemblage, bone damage, degree of association, the relationship of bones to sedimentary matrix, and the depositional processes that affected the sediment. Spatial resolution ranges from the locus of death of individuals (high) to much of the depositional basin (low). Here, we summarize resolution in qualitative terms for fossil assemblages from the more productive environments in each paleontological record.

5.1. Wyoming Paleogene

For the Bighorn Basin, we contrast fossil assemblages from channel deposits of the Fort Union Formation with assemblages from paleosols of the Willwood Formation. Collections from both formations are heavily dominated (>80%) by dental and gnathic elements (Table 3b,c), resulting in a high degree of taxonomic resolution, since these elements are diagnostic to the species level. Even in some quarried samples, collecting bias for dental and gnathic elements has contributed to these high proportions from the Fort Union Formation: from 10 to 20% of all excavated material from Rock Bench and Cedar Point quarries consisted of dental, gnathic, and cranial material, while typically 70–80% of catalogued specimens consisted of these skeletal parts (Bartels, 1987). In the Willwood Formation, collections of all fossil

Fig. 3. Sample size (number of catalogued specimens) versus species richness for the Paleogene Clarks Fork Basin, Wyoming, and Siwalik Neogene of northern Pakistan. Data compiled for mammalian biostratigraphic zones for (a) the Paleogene record; abbreviations as in Fig. 1a. Data compiled for 0.5-m.y. intervals for (b) Siwalik artiodactyls and for (c) Siwalik small mammals. In each graph, the dotted line with open squares represents number of species found, the solid line with solid squares the number of catalogued records.

Table 3
Skeletal-element frequencies (%) of mammalian fossil assemblages from different depositional environments, compared to values for the average whole mammal. MDX = mandible + maxilla, T = isolated teeth, SK = skull, S/P = scapula + pelvis, LB = limb, MP = metapodial, POD = podial, PH = phalanx, VT = vertebra, RIB+ = ribs and other elements, n = number of specimens from pooled fossil localities for each depositional environment. Status: + means fossil assemblages enriched (double or more) on average, - means depleted (half or less) on average, - means neither enriched nor depleted on average. (a) Skeletal-element proportions for average whole mammal. (b) Skeletal-element proportions from a quarried, screen-washed locality in the upper Fort Union Formation; data from Alexander (1982). (c) Skeletal-element proportions for 46 localities in 9 class A gray mudstones, Sand Creek Facies of Willwood Formation; data from Table 2 of Bown and Kraus (1981b). (d) Skeletal-element proportions for several environments in the Chinji Formation; 1° channel = major channel, 2° channel = secondary or floodplain channel. (e) Skeletal-element proportions for several environments in the Dhok Pathan Formation; data from Badgley (1986b)

| Skeletal part(s) | | | | | | | | | | |
MDX	T	SK	S/P	LB	MP	POD	PH	VT	RIB+	n
(a)										
Average mammal										
2	17	0.5	2	6	6	12	19	21	14.5	210
(b)										
Fort Union channel										
5	82	0.2	0	3	2 = MP + POD		5	3	1	516
Status										
+	+	-	-	-	-		-	-	-	
(c)										
Willwood paleosol										
22	66	0.1	0.3	4	3 = MP + POD		3	2	0.1	13,248
Status										
+	+	-	-	-	-		-	-	—	
(d)										
Chinji Fm										
1° channel lag	4	22	2	0	10	5	10	6	41 = VT + RIB+		107
1° channel fill	18	21	3	1	12	6	10	8	21 = VT + RIB+		228
2° channel lag	7	21	1	2	11	7	19	10	24 = VT + RIB+		934
2° channel fill	4	21	2	2	16	5	15	11	24 = VT + RIB+		273
Floodplain	11	38	4	0	7	0	7	3	30 = VT + RIB+		90
Status	+	+	+	-/-	+	-/-		-	?		
(e)										
Dhok Pathan Fm										
Channel lag	5	26	5	4	14	9	12	8	7	10	1,147
Crevasse splay	5	29	4	4	11	8	7	3	9	20	479
Channel margin	5	21	6	4	12	5	7	4	13	24	834
Floodplain	7	34	5	4	14	4	8	5	11	8	362
Status	+	+	+	+	+		-	-	—		

material yielded almost 70% dental and gnathic elements (Winkler, 1983).

The strong departure in these fossil assemblages from the skeletal-element composition of the original skeleton (Table 3a) must reflect predation, scavenging, and surficial weathering, rather than fluvial transport. While fossil assemblages in channel deposits of the Fort Union Formation show evidence of hydraulic transport from the sediment matrix and stratigraphic context, there is little

hydraulic sorting or abrasion of skeletal elements (Table 4; Alexander, 1982; Bartels, 1987). The skeletal-element composition is very similar to that of fossil assemblages from paleosol units (Table 3) interpreted as untransported by fluvial agents (Bown and Kraus, 1981b). For one Fort Union quarry site, Alexander (1982) proposed that the fossil assemblage originated in floodplain proximal to the channel. For other Fort Union quarry sites, Bartels (1987) interpreted the fossil assemblages as attritional/predator accumulations that arose during episodic channel abandonment. The dense concentration of vertebrate remains and generally fresh quality of bone suggest a short-term episode of intense mortality, an interval long enough for disarticulation but not substantial weathering, then minor transport and burial. Thus, taphonomic

data for these localities (Table 4) suggest that temporal and particularly spatial averaging of the fossil assemblages is low, and resolution is high.

The Willwood Formation presents a different pattern. Paleosol units are estimated to have formed over 10^3–10^4 years (Kraus and Bown, 1986; also, see Behrensmeyer et al., this issue). Vertebrate remains accumulated by attrition over a substantial period of soil formation (Bown and Kraus, 1981b). Thus, temporal averaging is moderate to high. Bown and Beard (1990) documented a gradient in skeletal-element completeness that is inversely related to paleosol maturity and positively correlated with sediment accumulation rate; hence, temporal resolution varies laterally along "pedofacies." Fossiliferous horizons may extend over a great area, but at the scale of a few square

Table 4

Taphonomic features of fossil assemblages from the major depositional environments of the Fort Union and Willwood formations (Paleogene of Wyoming) and of the Chinji and Dhok Pathan formations (Neogene Siwalik record). These taphonomic data are basis for estimating degrees of temporal and spatial averaging in fossil assemblages. For temporal averaging, "low" is on the order of one year or less, while "high" is on the order of 10^2–10^3 yr. For spatial averaging, "low" is on the order of 10–100 m², while "high" is on the order of >100 km². Fort Union Formation, channel deposits: information from Alexander (1982) and Bartels (1987). Willwood Formation, floodplain paleosols: information from Bown and Kraus (1981b) and Badgley (unpub. data). Chinji Formation, secondary channels: information from Morgan, Behrensmeyer and Raza (unpub. data). Dhok Pathan Formation, secondary channels: information from Badgley (1986b)

Taphonomic feature	Fort Union channel	Willwood paleosol	Chinji lag	fill	Dhok Pathan lag	fill
Association	rare	occ, common	rare	occ	none	occ, common
Bone damage						
Breakage	high	high	high	med–hi	high	medium
Punctures, gnaws	rare	occ	occ	occ	few	common
Weathering	fresh–slight	fresh–great	sl–fr	fr–sl	sl–fr	fr–sl
Abrasion	little–med	none	fr–peb	fr–sl	fr–peb	little
Hydraulic sorting	little	none	yes	little	yes	little
Sediment accumulation	bedload, sheetwash	suspension	bedload	bedload, suspension	bedload	bedload, suspension
Timespan of accumulation (fossils, F vs. sediment, S)	F > S	S ≥ F	F > S	F > S	F > S	F > S
Temporal averaging	low	med–hi	med–hi	med	med–hi	med
Spatial averaging	low	low–med	med–hi	low–med	med–hi	low–med

Abbreviations: occ = occasional, med = medium, hi = high, fr = fresh, sl = slight, peb = bone pebble.

meters, vertebrate remains occur in discrete clusters often of associated elements. Individual clusters show low spatial averaging, but as a whole, paleosol assemblages show moderate spatial averaging.

5.2. Siwalik Neogene

Taphonomic features are examined for assemblages of large mammals from the productive environments of the Chinji and Dhok Pathan formations. These assemblages are more similar to each other in skeletal-element composition than to the original mammal skeleton (Table 3a,d,e). They are slightly enriched in teeth, skull fragments. mandibles, and limb elements and slightly depleted in vertebrae and phalanges. Teeth (including isolated teeth) and jaws constitute 21–49% of the assemblages, with the highest frequencies in the floodplain environment (in the direction of Willwood values). Much of these departures from element frequencies in the original mammal skeleton represents processes such as predation, scavenging, and weathering that preceded fluvial transport, winnowing, and accumulation, since the untransported floodplain and channel-margin assemblages show alterations of the same kind as the transported channel-lag and splay assemblages (Badgley, 1986b). Differences in skeletal-element composition among the assemblages are greatest for floodplain versus all other environments. This contrast probably reflects the influence of winnowing and fluvial transport in the assemblages from channel and splay deposits.

Siwalik assemblages have a lower degree of taxonomic resolution than assemblages from the Bighorn Basin, because a smaller fraction of Siwalik assemblages consists of jaws, teeth, and skulls. For the most common group of Siwalik large mammals (bovid artiodactyls), the elements most diagnostic at the species level are horn cores, and these are rare. Assemblages from abandoned-channel fills and floodplains typically have more associated remains as well as a higher proportion of taxonomically diagnostic elements. Hence, these assemblages have higher taxonomic resolution than those from channel-lag and splay deposits.

Siwalik channel environments can be subdivided

into the lag and fill (abandoned channel) components. These divisions represent quite different processes of accumulation and different degrees of spatial and temporal averaging (Badgley, 1986b; Behrensmeyer, 1988). The lag component consists of material which was transported as bedload during the more active phase of the channel and occurs in the lower part of channel units. The overlying fill component typically contains an alternation of bedload and suspended-load sediments and often passes upward into a paleosol (see Behrensmeyer et al., this issue). Both parts of the channel may contain fossil concentrations. Fossil assemblages from the lag facies exhibit many features indicative of fluvial transport (Table 4), including abraded bones, bones dispersed through the sediment matrix, bone sizes that are roughly hydraulically equivalent to the matrix grains, lack of single-individual skeletal association, and under-representation of the more transportable elements such as vertebrae. Reworking of penecontemporaneous sediment and vertebrate material was likely, since channel geometries and clast composition indicate harvesting of floodplain sediments. Temporal averaging should range from short to potentially quite long, and spatial averaging from local to very broad. Assemblages from the fill facies exhibit features suggesting autochthonous accumulation (Table 4), including unabraded bones, clusters of bones in the sediment matrix, bone sizes that are not hydraulically equivalent with the sediment matrix, associated and sometimes articulated elements, and a less sorted array of skeletal elements. Temporal and spatial averaging should be predominantly low, with the possible addition of transported material increasing the range of each.

6. Selective preservation of taxa in relation to facies

Faunal composition of fossil assemblages varies among depositional environments, and certain taxa occur predominantly in a subset of environments. Variation in fossil-assemblage composition among depositional environments may reflect original habitat preferences of taxa, selective mortality in certain habitats, enhanced preservation in cer-

tain habitats, or a combination of factors. Choosing among these alternatives involves a consideration of the life-habits of the relevant organisms, plausible hypotheses of mortality, and comparative taphonomic data for a range of taxa and environments in the depositional system. Taxonomic composition, abundance of taxa, and frequency of depositional environments change upsection in the Paleogene and Neogene sequences under consideration here. Below we evaluate causes of varying abundance of selected taxa in relation to depositional environments.

6.1. Wyoming Paleogene

We review three cases from the vertebrate record of the Bighorn Basin: (1) reptiles, (2) phenacodontids, and (3) selected mammals from individual pedofacies.

Reptilian vertebrates (here including turtles, crocodilians, champsosaurs, and lizards) are useful indicators of habitat because aquatic, semi-aquatic, and terrestrial forms are discernible. Also, for some aquatic taxa, body size is correlated with habitat size (Neill, 1971; Ernst and Barbour, 1989). Changes in proportions (and abundance) of species with different habitat affinities should reflect changes in the distribution and size of aquatic versus terrestrial habitat. The herpetofauna changes through the Paleogene record in a manner that reflects increasing prevalence of subaerial habitat (Bartels, 1987). In habitat affinities, some species were highly aquatic (aquatic turtles, champsosaurs, and the crocodilian Leidyosuchus), some turtles and the crocodilian Allognathosuchus were semi-aquatic, and other forms were terrestrial (including terrestrial turtles and lizards).

Data on relative abundance of all vertebrate taxa are not widely available. Table 5a presents the proportion of major vertebrate groups at one thoroughly collected locality from each formation. Notable differences are the higher proportions of crocodilians and turtles (aquatic forms) from the upper Fort Union locality and the higher proportions of mammals (terrestrial forms) from the Willwood locality. These differences follow the prevalence of channel facies in the Fort Union Formation and the prevalence of well-drained

floodplain in the Willwood Formation. Fish remains vary in abundance by an order of magnitude among several Willwood paleosol units sampled (Smith et al., 1988); the abundance of fish remains suggests that fish mortality was higher in the floodplains, where fish could have been stranded after the flood season. Based on inferred species size and habitat, the crocodilians and turtles indicate a wide variety of permanent aquatic habitats in the lower Fort Union Formation; these habitats diminished in the upper Fort Union and Willwood (Bartels, 1987).

The number of reptile species per biostratigraphic zone ranged from 11 to 22 (Table 5b). Major trends include (1) abundant remains of large crocodilians and large aquatic turtles in the lower Fort Union Formation, (2) decrease in abundance and size of large crocodylids and some aquatic turtles in the upper Fort Union and into the Willwood, and (3) increase of semi-aquatic and terrestrial turtles, small alligatorids, and terrestrial lizards in the Willwood. The greatest taxonomic turnover among reptiles—including the extinction of champsosaurs—occurred at the Clarkforkian–Wasatchian boundary, somewhat higher than the change (during Cf-2) from Fort Union to Willwood facies (Bartels, 1987). Bartels interpreted the changes in the herpetofauna as reflecting decrease in size and frequency of permanent aquatic habitats, increase in amount of terrestrial habitat from Fort Union to Willwood formations, enhanced preservation of terrestrial forms, selective extinction (champsosaurs, some alligatorids, and some turtles), and evolutionary trends within several groups. The abundance and taxonomic richness of large aquatic forms in the Fort Union Formation and their diminished presence in the Willwood Formation are consistent with habitat preference, selective mortality in the preferred habitat (many of these aquatic reptiles are predators on each other), and enhanced preservation in the Fort Union channel deposits (Willwood channel deposits produce fewer fossils of any kind).

The second Paleogene example involves phenacodontids, the largest of the herbivorous condylarths, from the Bighorn Basin. Contemporaneous species of Phenacodus and Ectocion occur in con-

Table 5
Faunal composition of vertebrate remains in relation to depositional environment and for re[...] the groups in Palaeogene biostratigraphic zones. (a) Faunal composition (% of specimens) in relation to facies for two well-samp[l]d localities, one from the Fort Union Formation (FG-6, data from Alexander, 1982), one from the Willwood Formation (SC-67, data from Gingerich, 1989). (b) Species richness of reptiles from the Paleocene to early Eocene of the Bighorn and Clarks Fork basins. Modified from Bartels (1987), with information about Wasatchian 0 from Gingerich (1989). (c) Relative frequency (%) of major vertebrate groups from depositional environments of the Siwalik Chinji Formation. Numbers in parentheses refer to number of localities and number of specimens.

Vertebrate group					
Mammal	Crocodile	Turtle	Fish	Lizard	Anuran

(a) Depositional environment	Mammal	Crocodile	Turtle	Fish	Lizard	Anuran
Fort Union Fm., CI-2 channel deposit (n = 864)	60	24	5	0	11	0.3
Willwood Fm., Wa-0 paleosol (n = 249)	18	3	2	10	3	0

(b) Biostratigraphic zone	Champsosaur	Crocodilian	Aquatic turtle	Semi-aquatic turtle	Terrestrial turtle	Lizard
Puercan 1	1	4	6	1	0	0
Torrejonian 4	1	4	7	1	0	5
Tiffanian 3	2	5	8	1	0	2
Tiffanian 4	2	4	5	1	0	2
Tiffanian 5	2	4	4	1	0	6
Clarkforkian 1	2	3	1	1	1	2
Clarkforkian 2	2	3	5	1	1	6
Clarkforkian 3	1	5	5	1	1	3
Wasatchian 0	0	3	2	0	0	2
Wasatchian 1-2	0	3	4	4	2	6
Wasatchian 3	0	5	4	4	2	7

(c) Depositional environment	Mammal	Crocodile	Turtle	Fish	Snake
Major channel lag (2,78)	41	35	19	3	0
Major channel fill (4,246)	23	42	27	8	0
2 channel lag (7,209)	39	34	14	11	0.5
2 channel fill (8,300)	35	26	24	13	1
Floodplain (5,110)	66	1	0	0	0
Floodplain fish loc (1,53)	2	2	6	87	0

trasting abundance from different sedimentary environments (Thewissen, 1990). In the mid-Tiffanian (Ti-3), *Phenacodus grangeri* was fairly common in both channel and floodplain localities. *P. magnus* appeared in Ti-4, with greater abundance in channel than in floodplain localities, and *P. grangeri* became rare in channel localities and more abundant in floodplain localities. Tiffanian *Ectocion* was represented by the *collinus-mediotuber-osbornianus* lineage, known only from floodplain localities, and by *E. cedrus*, known only from channel localities. In the Clarkforkian and early Wasatchian, *E. osbornianus* was the most abundant phenacodontid, and *Phenacodus intermedius* (the probable continuation of the *P. grangeri* lineage) became the most abundant species of *Phenacodus*, while *P. magnus* became extinct. Concurrently, the floodplain habitat increased at the expense of channel habitats in the transition from Fort Union to Willwood facies. For these phenacodontids, the species associated with floodplain in older strata became the dominant species in younger strata, in which the floodplain habitat had expanded greatly. Habitat preference or habitat-specific mortality are the likely causes of differential abundance of these lineages in the Tiffanian. Enhanced preservation is unlikely, since preservation of closely related species of fairly similar size occurred in both channel and floodplain deposits. For occurrences in Willwood rocks, enhanced preservation could also have had an impact. Schankler (1981) interpreted biostratigraphic changes in abundance of Wasatchian phenacodontids from the central Bighorn Basin in terms of interspecific competition and environmental changes, but his data were not explicitly linked to facies.

The third case concerns lateral changes in faunal composition along a pedofacies unit. A pedofacies is a laterally continuous paleosol that varies in soil maturity (Bown and Kraus, 1987). Bown and Beard (1990) documented changes in abundance of mammal species along a spectrum from immature to very mature, laterally continuous paleosols in the central Bighorn Basin. For example, two species of the hyopsodontid condylarth *Hyopsodus* and two species of the adapid primate *Cantius* occurred in inverse proportions from immature to

mature paleosols: *Cantius frugivorous* and *Hyopsodus* cf. *H. minor* were abundant in mature paleosols located distal to the channel belt, while *Cantius* sp. nov. and *Hyopsodus* cf. *H. miticulus* were abundant in the laterally equivalent, immature paleosols close to the channel belt. Enhanced preservation cannot be the main cause, since preservation of mammalian remains was high across the entire pedofacies unit. Habitat preference or habitat-specific mortality could account for these gradients in species abundance. Bown and Beard presented additional examples of lateral changes in faunal composition and correlated changes in taphonomic completeness of skeletal elements. Winkler (1983) documented distinctive differences in faunal composition of assemblages from different kinds of paleosol horizons in the Clarks Fork Basin. Bown and Kraus (1993) related faunal turnovers in the Willwood Formation of the central Bighorn Basin to periods of decreased paleosol maturity and inferred floodplain instability.

6.2. Siwalik Neogene

The abundance of certain taxa varies strikingly among depositional environments within formations, while other taxa are preserved fairly evenly across all productive environments. The Chinji and Dhok Pathan formations best illustrate these trends, with larger samples of localities and specimens than from the Kamlial and Nagri formations. Here we note differences in abundance for three categories of vertebrate remains: (1) aquatic vertebrates, (2) small mammals, and (3) large mammals.

Aquatic vertebrates in the Siwalik record include fishes, crocodilians, and turtles. Remains of these groups are persistent but rarely abundant through the sequence. Fragmentary fish remains are often abundant in the concentrate from screen-washing of bulk sediment (W. Downs, pers. comm., 1993). Aquatic-vertebrate remains are typically associated with channel deposits and are usually rare to absent from floodplain deposits (Table 5c). One notable exception is a floodplain locality consisting predominantly of several partial fish skeletons (last entry, Table 5c). In life, aquatic vertebrates would have ranged throughout the floodbasin during

flood stage when the entire area was predominantly aquatic. During low-water season, both active and abandoned channels would have been suitable habitats. The selective representation of aquatic vertebrates in channel deposits probably represents the conjunction of appropriate habitat and enhanced preservation due to rapid burial.

The second Siwalik example concerns small mammals. A taphonomic survey of Siwalik small-mammal localities indicates that more localities and larger samples come from abandoned-channel fills – especially associated with secondary flood-plain channels – than from any other fluvial environment (Badgley, unpublished data; Badgley et al., 1992). The most striking example occurs in the lower Chinji Formation: along 10 km of laterally continuous exposures, an interval about 20 m thick contained nine concentrations of small-mammal remains, yielding over 700 teeth assigned to 30 species. Yields were as high as 30 teeth per 45 kg (one bag) of sediment matrix (Will Downs, pers. comm., 1988). All these small-mammal concentrations occur in abandoned-channel fills. In life, the small mammals—which included tree shrews, adapid primates, hedgehogs, squirrels, true mice, and bamboo rats—would have occupied a

range of terrestrial, arboreal, and possibly subterranean habitats. The original populations should have ranged into the floodplains as well as proximal to channels, in response to seasonal changes in the flood cycle. The frequency of small-mammal remains in abandoned-channel fills suggests a mechanism of concentration in mortality—such as predator accumulation, as well as enhanced preservation due to the episodic, rapid sedimentation evident in this environment. The changes in frequency of localities and to a lesser degree of specimens across formations (Fig. 1c) follows the changes in the frequency of floodplains and floodplain channels across formations.

Large mammals are the most abundant component of the Siwalik fossil record. Most were terrestrial, and the few semi-aquatic species (such as otters, anthracotheres) are relatively rare as fossils. Table 2 indicates the frequency of localities within each depositional environment, while Fig. 4 presents the frequency of large-mammal remains associated with productive environments of the Dhok Pathan Formation. Spearman rank-order correlation (Snedecor and Cochran, 1980) gives a nonparametric measure of similarity of assemblage composition of the four productive environments
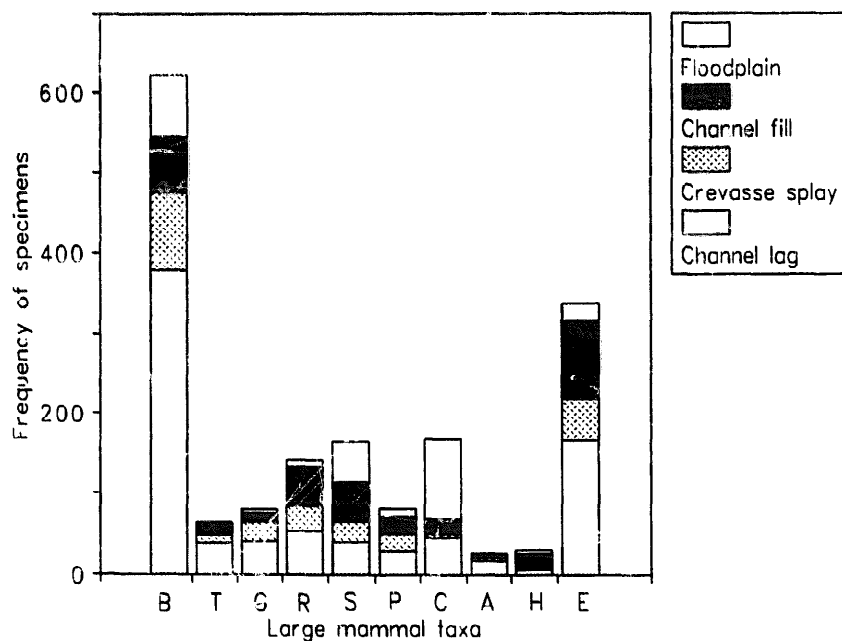

Fig. 4. Frequency of mammalian specimens for ten groups of large mammals from four fluvial environments, Dhok Pathan Formation, late Miocene. B = bovid, T = tragulid, G = giraffid, R = rhinocerotid, S = suid, P = proboscidean, C = carnivore, A = anthracothere, H = hominoid, E = equid. Data from Badgley (1986b).

of the Dhok Pathan Formation (Table 6). The statistical procedure measures the similarity of depositional environments by their rank order of taxa, based on the number of specimens per higher taxon (data in Fig. 4). Cluster analysis of these values results in the pattern (floodplain [channel fill (channel lag + crevasse splay)]). Thus, based on the rank-order of mammalian taxa, assemblages from channel lags and crevasse splays are most similar and channel-fill assemblages are more similar to channel-lag and crevasse-splay assemblages than to floodplain assemblages. Recall from above that floodplain assemblages also differed from those in other environments in skeletal-element frequencies.

The large-mammal assemblages from channel-lag and crevasse-splay deposits are predominantly fluvial accumulations, but the channel context does not represent the life habitat of most of the preserved fauna. Enhanced preservation of large-mammal remains entrained by channels is a likely factor, perhaps due to high short-term rates of sedimentation. Habitat preference or selective mortality in near-channel habitats is also likely, since channel-lag and crevasse-splay assemblages are more similar in faunal composition to channel-fill assemblages than either is to floodplain assemblages (Fig. 4, Table 6).

Assemblages from the channel-fill localities are predominantly autochthonous accumulations with slight to moderate fluvial reworking. This environment alternated between aquatic and terrestrial, and, judging from modern fluvial habitats, would have had high primary productivity (e.g., Sheppe, 1972). Hence, the large mammals preserved probably foraged and died there from a range of largely biotic causes.

Dhok Pathan floodplain assemblages exhibit taphonomic features—such as clustered associated remains, a higher proportion of juvenile large mammals and carnivore species, and unabraded bones—indicative of biological rather than hydraulic accumulation (Badgley, 1986b). The relatively high frequency of both juveniles and carnivores suggests that selective mortality was an important factor in the existence of these fossil remains.

In comparison with the Willwood Formation, the question arises—why are mammalian remains not more common from Siwalik floodplain deposits? Behrensmeyer et al. (this issue) suggested that greater climatic seasonality in the Miocene of northern Pakistan diminished the preservation potential of floodplain paleosols for vertebrate remains. But since paleosol features of the two stratigraphic sequences have much in common, an ecological consequence of climatic seasonality may be more significant. If rainfall was strongly seasonal—as both paleosol leaching depths (Quade and Cerling, this issue) and size-structure of Siwalik mammalian faunas (Morgan et al., this issue) suggest, then the floodplains would have had reduced primary productivity for a substantial portion of the period when the floodbasin was predominantly a subaerial habitat. From the standpoint of food resources, the more habitable areas during the dry season may have been channel margins, where channels and groundwater could have supported year-round vegetation in greater abundance. A general analogue for the pattern of seasonal mammal movements is the Okavango Delta, Botswana, where a permanent system of rivers and lakes serves as a retreat from the floodplain for most large mammals during the dry

Table 6

Spearman rank-order correlations for number of specimens (n) of ten mammalian higher taxa distributed among four depositional environments from the Dhok Pathan Formation. Data depicted in Fig. 4

	Channel lag (n = 817)	Crevasse splay (n = 271)	Channel fill (n = 361)	Floodplain (n = 286)
Channel lag	1.00			
Crevasse splay	0.83	1.00		
Channel fill	0.67	0.76	1.00	
Floodplain	0.64	0.45	0.69	1.00

season (Ross, 1987). Thus, habitat avoidance may be as strong as preservation as a factor in explaining the low frequency of mammalian remains in floodplain deposits.

It is also noteworthy that channel deposits of the Willwood Formation preserve little fossil material. This feature may follow from the geometry and reactivation history of Willwood channels. Alluvial ridges of the Willwood were probably higher than those of the Fort Union Formation, and, once abandoned, they were not commonly reactivated but rather were buried by floodplain deposits. The circumstances for temporary abandonment, reactivation and rapid burial of vertebrate remains—circumstances that were common during Fort Union and Siwalik deposition—rarely occurred in Willwood fluvial systems.

6.3. Taxonomic richness in relation to variety of facies

Since certain taxa are predominantly found in particular facies, it follows that taxonomic richness for a particular stratigraphic interval should increase if a greater variety of sedimentary facies is sampled. Examples from each record illustrate this relationship.

In the Paleogene of Wyoming, the middle Clarkforkian (Cf-2) represents a time when typical Fort Union deposition (large channels, poorly drained floodplains) interfingered with typical Willwood deposition (small channels, well drained floodplains). A Willwood-facies quarry site within Locality SC-188, interpreted as representing predator accumulations along an oxbow (Bartels, 1990), yielded 167 specimens attributed to 24 species of mammals. When surface-collected remains (85 specimens representing 14 species) from paleosol units of the same locality were added to the quarry sample, taxonomic richness rose to 30 species ($n = 252$). When this collection was added to a quarry sample derived from a Fort Union-facies channel deposit (locality FG-6, 881 specimens, 26 species), the total richness rose to 42 species ($n = 1133$). If nearby, middle Clarkforkian, surface-collected localities (representing both Fort Union and Willwood facies) were added, the aggregate sample increased to 52 mammalian species based on 2026

specimens. Middle Clarkforkian reptile diversity follows a similar pattern. SC-188 has produced seven reptile species. When the sample from FG-6 was added, the number rose to 10 species, and when other middle Clarkforkian, surface-collected localities were added, the total diversity rose to 19 species. Some of the increased diversity may result from an increase in sample size alone. But the presence of five mammals and one reptile exclusively in the channel deposit (FG-6), four mammals and one reptile exclusively in the oxbow/paleosol deposit (SC-188), and 10 mammal and three reptile species only in the surface-collected localities suggests that a wide variety of environments must be sampled in order to obtain accurate estimates of original faunal composition.

A similar pattern occurs for Siwalik assemblages from different sedimentary facies. Since in Siwalik assemblages taxonomic resolution is lower for many specimens, this pattern is reported at a higher taxonomic level for a stratigraphic interval within the Dhok Pathan Formation (Badgley, 1986b). Localities from channel-lag deposits tend to have the greatest taxonomic richness of large mammals, but the greatest taxonomic richness of small mammals occurs in abandoned-channel deposits. Certain taxa, including tragulids, chalicotheres, and anthracotheres, are virtually unknown from floodplain localities, but most remains of hyaenids are from floodplain localities. The best estimate of original taxonomic richness entails fossil assemblages from the broadest range of coeval depositional environments.

7. Discussion

This survey of taphonomic data from the Paleogene record of northwestern Wyoming and the Neogene Siwaliks of Pakistan serves as a basis for evaluating the influence of preservation on the apparent faunal composition of localities and selected stratigraphic intervals, on taxonomic resolution, faunal turnover, and evolutionary rates and patterns of mammalian lineages, and on community reconstruction.

Fossil-assemblage composition results from original faunal composition, sampling biases that arose

during preservation and collection, sample size, and taxonomic resolution of recovered material. In both the Paleogene and Neogene sequences, predepositional processes established the major aspects of skeletal-element composition (since fluvially transported assemblages were fairly similar to non-transported assemblages) and thereby the taxonomic resolution of assemblages. Taxonomic resolution is generally greater for Paleogene than for Neogene assemblages because of the higher proportion of elements diagnostic to the species level in the former. For localities of the same sample size from each sequence, the number of specimens diagnosed to species level is much greater for the Paleogene record.

Collecting method strongly influences the potential recovery of small-vertebrate remains. For the Bighorn Basin and the Pakistan Siwaliks, localities with the richest faunal composition are those where surface collecting or excavating was supplemented with screen washing. The richest localities from each record—with sample sizes of hundreds to thousands of specimens—contain 50–60 species of mammals and 10–25 non-mammalian vertebrates. The most meaningful estimates of original faunal composition for a given stratigraphic interval are obtained from a set of localities representing a variety of depositional environments. Collections from intervals of substantially different sedimentary facies must be compared with caution, since the original environments also differed.

Both sequences contain evidence of some facies control of fossil-assemblage composition and turnover at the scale of formations and of depositional environments within formations. This control operated through habitat availability in some instances (e.g., aquatic vertebrates) and through taphonomic processes in other instances (e.g., Siwalik small mammals). In evaluating changes in assemblage composition over time, the most taphonomically consistent practice is to compare assemblages from the same taphonomic context (e.g., abandoned-channel fills) from interval to interval. This practice is more feasible in the Siwalik record than in the Paleogene record of Wyoming. In the Siwaliks, the same depositional environments remain productive across formations, whereas in the Paleogene, one dominant productive environ-

ment is replaced by another. In both sequences, further study of assemblage composition in interfingering or transitional zones between formations would permit documentation of time-equivalent assemblages in different fluvial environments. Also, since notable changes in fossil productivity occur near formation boundaries in both sequences, the potential sampling effects on faunal turnover require appraisal.

Community reconstruction involves data about taxonomic composition and abundance of fossil assemblages and sedimentary context as a basis for inferring original abundances of taxa and habitat associations. The most detailed reconstructions result when taxonomic resolution is high, temporal and spatial averaging are low, samples are large, and fossil assemblages are preserved in a variety of environments across the depositional system. The closest match to these ideal circumstances in the Paleogene record of the Bighorn Basin is the zone of interfingering between Fort Union and Willwood formations (as mentioned above for the middle Clarkforkian), where fossil assemblages occur in channel deposits, abandoned channels, and paleosols. In the Siwalik record of the Potwar Plateau, the most productive intervals of the Chinji and Dhok Pathan formations provide rich or numerous localities from a range of environments and variable temporal and spatial averaging (Table 4). But taxonomic resolution is not currently as high as in the Paleogene record.

Study of evolutionary change within lineages and of species-replacement patterns requires consistently high taxonomic resolution; high temporal resolution and consistency of preservational context contribute further resolution to the pattern. The Paleogene record has consistently high taxonomic resolution for many taxa, while temporal averaging ranges from low in the Fort Union to medium-high in Willwood paleosols (Table 4) and the preservational context changes substantially. The Siwalik record has better taxonomic resolution for small mammals than for large mammals throughout the sequence. For small mammals, the preservational context appears to remain the same (abandoned-channel fills) over four formations, and temporal averaging is generally low to medium for the small-mammal com-

ponent of these assemblages. From the standpoint of preservation, the best opportunities for documenting patterns of evolution are with the more common species from floodplain paleosols of the Willwood Formation (large samples, high taxonomic resolution, consistent preservational context) and with the more abundant small mammals of the Siwalik record (large samples, high taxonomic resolution, consistent preservational context, and high temporal resolution).

8. Conclusion

The early Paleogene of northwestern Wyoming and the Siwalik Neogene of northern Pakistan exhibit similarities and differences in taphonomy of vertebrate remains. The sequences are similar in that changes over time in formations are correlated with changes in fossil productivity and species richness. Mudstone-dominated formations have more localities, more fossil vertebrates, and more vertebrate taxa (especially of mammals) than do sandstone-dominated formations. The sequences differ in the specific fluvial environments that preserve most vertebrate material. In the Paleogene record, the dominant environment of preservation shifts from fluvial channels in the Fort Union to floodplain paleosols in the Willwood. In the Siwaliks, several environments consistently preserve fossils throughout the sequence, but the most productive environments across four formations are channel-lag deposits and abandoned-channel fills. Certain vertebrate groups are found predominantly in a subset of depositional environments. The causes of this differential abundance include habitat preference, habitat-specific mortality, and enhanced preservation. Differences in pre-burial taphonomic processes resulted in greater taxonomic resolution in the Paleogene record and in a greater range of temporal and spatial averaging over most of the Siwalik record than from the Paleogene record. These differences in the preservational features of each record impose different opportunities and constraints on paleocommunity reconstruction and analysis of mammalian evolution.

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