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Taphonomy of mammalian fossil remains from Siwalik rocks of Pakistan

Catherine Badgley

Abstract.—Siwalik rocks of Pakistan are a virtually continuous, continental sedimentary sequence, extending in age from 18 to 1 ma B.P. This paper describes taphonomic features of late Miocene mammalian assemblages from a highly fossiliferous interval about 400 m thick, based on field documentation of sedimentary environments at 42 fossil localities and systematic fossil collection of 21 localities.

Within a broadly fluvial system, I recognize four sedimentary environments of bone accumulation, distinguished by lithology, unit-thickness, unit-geometry, contacts, sedimentary structures, and relationship to adjacent units. Each environment corresponds to an association of lithofacies. Facies Association I is interpreted as the persistent, major channel bodies of a meandering fluvial system; Facies Association II as coarse-grained flood deposits, such as crevasse splays, deposited beyond the main channels; Facies Association III as channel margins, including levees and swales; and Facies Association IV as predominantly subaerial floodplains.

Taphonomic features of bone assemblages from each facies association include skeletal-element composition, surface distribution of specimens, degree of articulation, hydraulic equivalence between organic and inorganic sedimentary particles, frequency of juvenile remains, size distribution of fauna, and an estimate of duration of accumulation of individual fossil localities. The distribution of these features among the four facies associations suggests that bone assemblages in Facies Associations I and II accumulated by the action of currents in river channels or floods, whereas bone assemblages in Facies Associations III and IV accumulated through concentration by biological agents and/or attrition at a repeatedly used site of predation.

Inclusion in fluvial accumulations depends on initial availability of skeletal remains and hydraulic characteristics of individual skeletal elements, but not taxonomic identity per se. For biological accumulations, however, taxonomic composition reflects the preferences of the individual agents of accumulation. The probability of preservation of taxa in fluvial accumulations is probably mainly a function of body size, as reflected in the sizes of isolated skeletal elements. Thus, in this Siwalik system, bone assemblages that experienced fluvial transport are better representations of original community composition than bone assemblages created by biological agents or passive accumulation.

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Introduction

Long fossiliferous sequences offer a unique perspective on evolutionary patterns within lineages and on changes in community organization. The duration of these historical records is itself uniquely valuable; modern communities represent only snapshots of complex, dynamic systems. But the information content of fossil assemblages is as diminished in quantity relative to the original system as modern ecosystems are limited in temporal perspective. Fossil assemblages are products both of once-active communities and of sampling processes that degrade, dissociate, and reassociate organic remains as fossil assemblages. Fossil assemblages are, therefore, most informative—in terms of original community composition, time span of the sample,

and environments represented—when natural sampling processes are made evident.

Here, I describe the sampling history of mammalian fossil assemblages from Middle Siwalik rocks of Pakistan. This sequence contains the richest and best-documented record of Neogene mammalian evolution in South Asia (Pilbeam et al. 1979; Barry et al. 1982). Sampling history refers to the agent of accumulation, criteria for selection, and time span of accumulation of mammal remains from Siwalik localities. These inferences are necessary although not sufficient to specify sampling distributions for the original community of Siwalik mammals. That is, taphonomic data presented here and in studies of modern mammalian death assemblages indicate that the probability of preservation varied among Siwalik taxa in relation to body size and other

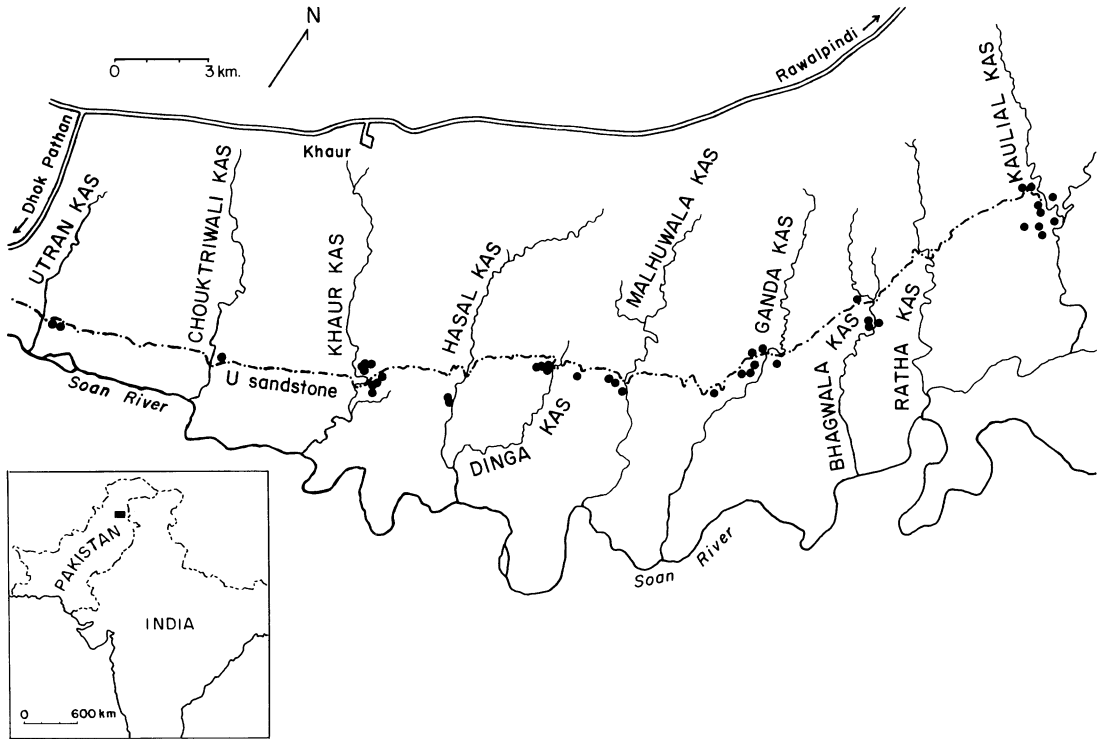


FIGURE 2. Map of the Khaur field area, Potwar Plateau, northern Pakistan. Lateral extent of Siwalik exposures is indicated by the outcrop pattern of the U-sandstone. Closed circles represent fossil localities with microstratigraphic documentation.

provides only limited evidence of sampling processes that is distinguishably independent of relative abundance of taxa in the parent populations. Figure 1 illustrates an inferential model of paleocommunity reconstruction. This paper covers steps 1 through 4; steps 5 and 6 are presented elsewhere (Badgley 1982). Other taphonomic models in the literature (e.g., Clark et al. 1967; Holtzman 1979) emphasize the processes of transformation from life assemblage to death assemblage and other intermediate stages to fossil collection. These models are useful for envisioning taphonomic histories from beginning to end. The emphasis in Fig. 1 is to demonstrate the explicit connection between evidence and inferences but not to reconstruct taphonomic histories in full detail. Figure 1 also indicates the order in which inferences must accrue. While the final step is dependent on the validity of the earlier ones, none represent a priori assumptions.

Siwalik sediments and faunas

The Siwalik Group is a Neogene, continental molasse that accumulated on the southern mar-

gin of the Himalayas. Siwalik rocks of the Potwar Plateau, northern Pakistan, constitute a relatively continuous record of terrestrial vertebrate faunas from over 18.0 to about 1.0 ma B.P. (Pilbeam et al. 1979; Johnson et al. 1985). Siwalik mammals are diverse taxonomically and ecologically. They include the youngest known creodonts and adapid primates, endemic radiations of murid and rhizomyid rodents, viverrid carnivores, tragulid and bovid artiodactyls, and hipparionine (equid) perissodactyls, as well as cosmopolitan taxa (Pilbeam et al. 1979; Barry et al. 1982). Recently recovered material of the hominoid primates *Sivapithecus* and *Ramapithecus* has played a critical role in revising views of hominoid phylogeny (Pilbeam et al. 1980; Pilbeam 1982; Lipson and Pilbeam 1982; Ward and Pilbeam 1983).

The taphonomic study reported here pertains to the "U-interval," a late Miocene portion of the Potwar Siwalik sequence near the town of Khaur. Named for a prominent marker sandstone (the U sandstone), the U-interval, as discussed here, is about 400 m thick and has been

TABLE 1. Siwalik mammalian fauna from the U-interval. Many groups are still under taxonomic revision. Information from Pilbeam et al. (1979), Barry et al. (1982), and J. Barry (pers. comm.).

| Insectivora | Tubulidentata | Artiodactyla |
|---|--|---|
| Erinaceidae | Orycteropodidae | Suidae |
| Soricidae | <i>Orycteropus browni</i> | <i>Tetraodonodon magnus</i> |
| Tupaïidae | Proboscidea | <i>Propotamochoerus hysudricus</i> |
| Primates | Gomphotheriidae | <i>Hippopotamodon sivalense</i> |
| Lorisidae | <i>Choerolophodon corrugatus</i> | Suidae <i>incerta sedis</i> |
| Ramapithecidae | <i>Stegolophodon</i> sp. | <i>Schizocoerus gandakasensis</i> |
| <i>Ramapithecus punjabicus</i> | cf. <i>Platybelodon</i> | Anthracotheiidae |
| <i>Sivapithecus indicus</i> | Deinotheriidae | " <i>Anthracotherium</i> " <i>punjabienne</i> |
| Rodentia | <i>Deinotherium indicum</i> | <i>Hemimeryx pusillus</i> |
| Sciuridae (2 taxa) | Perissodactyla | sp. nov. |
| Cricetidae | Equidae (3 taxa) | Tragulidae |
| <i>Democricetodon</i> | Chalicotheriidae | <i>Dorcabune nagrii</i> |
| Rhizomyidae | <i>Chalicotherium salinum</i> | <i>Dorcatherium majus</i> |
| <i>Kanisamys sivalensis</i> | Rhinocerotidae | <i>D.</i> cf. <i>nagrii</i> |
| <i>Brachyrhizomys</i> | <i>Gaiotherium browni</i> | <i>D.</i> sp. nov. |
| (<i>Rhizomyoides</i> ?) | <i>Aceratherium</i> cf. <i>A. simorrense</i> | Giraffidae |
| Muridae | <i>Brachypotherium perimense</i> | <i>Bramatherium megacephalum</i> |
| <i>Progonomys</i> sp. | <i>Chilotherium intermedium</i> | another sp. |
| <i>P. debruijini</i> | | Bovidae |
| <i>Karnimata darwini</i> | | <i>Miotragocerus punjabicus</i> |
| <i>Parapodemus</i> sp. | | <i>Elachistoceras kbauristani</i> |
| Gliridae | | <i>Gazella</i> sp. |
| Carnivora | | <i>Selenoportax vexillarius</i> |
| Amphicyonidae | | (<i>Protragelaphus</i> cf. <i>skouzesi</i>) |
| <i>Arctamphicyon lydekkeri</i> | | (<i>Protoryx</i> sp.) |
| Mustelidae | | |
| <i>Eomellivora</i> sp. | | |
| <i>Sivaonyx bathygnathus</i> | | |
| cf. <i>Ischyricis</i> | | |
| mustelid indet. (size of | | |
| <i>Martes americana</i>) | | |
| Viverridae | | |
| <i>Viverra chinjiensis</i> | | |
| viverrine, large sp. | | |
| <i>Herpestes</i> sp. | | |
| Hyaenidae | | |
| <i>Percrocuta grandis</i> | | |
| <i>Progenetta</i> sp. (<i>Thalysictis</i> ?) | | |
| <i>Palhyaena sivalensis</i> | | |
| Felidae | | |
| <i>Paramachaerodus</i> sp. | | |
| <i>Felis</i> cf. <i>sivaelurus</i> | | |

traced laterally for over 40 km (Fig. 2). This interval is the most productive part of the Khaur section, in terms of both the number of documented fossil localities and the number of collected specimens (Barry et al. 1980). Most of the Potwar Siwalik hominoid fossils come from the U-interval (Badgley et al. 1984). The age of the U sandstone is estimated at ca. 8.0 ma B.P. (Tauxe 1979; Tauxe and Opdyke 1982). The average sediment accumulation rate is calculated as about 0.5 m/1,000 yr by paleomagnetic correlation (Behrensmeyer and Tauxe 1982); hence, 400 m represents about 800,000

yr. On this basis, the U-interval represents the time span ca. 7.8–8.6 ma B.P.

The mammalian fauna of the U-interval is given in Table 1. About 60 taxa are recognized, with much material still under study. Other vertebrate remains—fish, reptile, and bird—are found infrequently by comparison with mammalian fossils and are not discussed here. Considering that the U-interval is the most densely sampled portion of the Potwar Siwalik sequence, there is surprisingly little change in faunal composition relative to other levels. There are two appearances (the murid *Karnimata* and the trag-

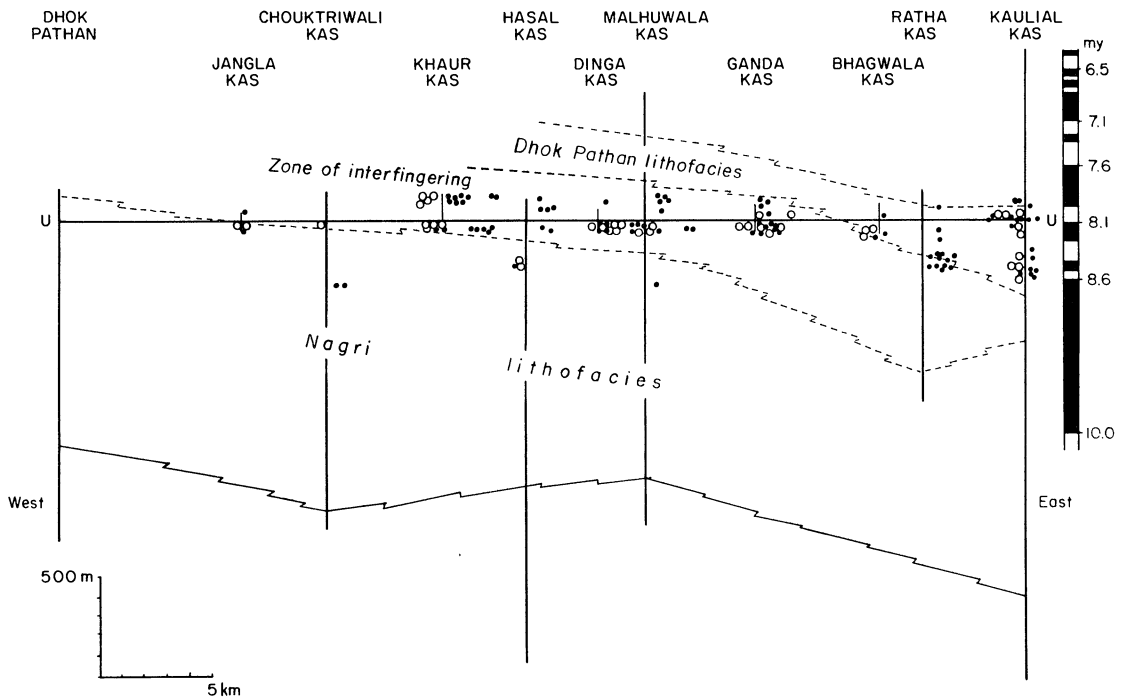


FIGURE 3. Cross-section of Middle Siwalik sediments in the Kaur area. Paleomagnetic stratigraphy of this sequence indicated on the right, with absolute dates from the magnetic polarity time scale. The boundary between the Nagri and Dhok Pathan lithofacies is time transgressive from east to west. Vertical lines indicate long measured sections in the Kaur area. Circles represent fossil localities that occur in the U-interval, as described in the text. Open circles indicate localities documented in this study. (Figure modified from Barry et al. 1980.)

ulid *Dorcatherium* cf. *D. nagrii*) and one disappearance (the suid *Tetraconodon*) at the base of the U-interval (Barry et al. 1982). Following these changes, mammalian composition remained constant, at the current level of taxonomic resolution. Thus, variation in the composition of fossil assemblages from the U-interval reflects mainly variability in sampling processes or in local population sizes but not long-term changes in taxonomic composition.

Siwalik sediments are predominantly fluvial, consisting of repetitive alternations of sandstones and finer-grained units (Pilbeam et al. 1979; Badgley and Behrensmeyer 1980). Much of the lateral exposure of the U-interval occurs in a time-transgressive zone of interfingering between two distinctive lithofacies (Fig. 3). To the west and in the lower portion of any vertical transect, thick (>30 m), blue-gray sheet sandstones predominate, extending laterally for 20 km or more. The proportion of silts and silty clays is relatively low and increases gradually in younger sediments. To the east and higher in any vertical

transect, silts and silty clays predominate with thin (3–10 m), buff sandstones that extend laterally for 0.5–4.0 km. These two facies are known formally as the Nagri lithofacies and Dhok Pathan lithofacies, respectively (Barry et al. 1980). They differ in paleocurrent directions, sandstone mineralogy, sandstone geometry, and sedimentary structures. Both are fluvial facies, but they differ in depositional mode (Badgley and Behrensmeyer 1980; Behrensmeyer and Tauxe 1982). Behrensmeyer and Tauxe (1982) interpret the Nagri sediments as the product of a braided river system and the Dhok Pathan sediments as the product of several meandering systems. Most vertebrate fossils from the U-interval have been found in sediments of the Dhok Pathan lithofacies and the zone of interfingering between the two facies (Badgley and Behrensmeyer 1980).

The focus of this study is the relationship between fossils and sediments of the U-interval. Specific goals include (1) interpretation of the sedimentary environments of fossil assemblages,

TABLE 2. Facies associations of Middle Siwalik fossil assemblages.

| Facies association | Observations | | | Interpretation |
|--------------------|--|--|--|---|
| | Predominant lithologies | Sedimentary structures | Post-depositional features | Circumstances of deposition |
| I | Sandstone; conglomerate | Trough cross beds; massive plane bedding; erosional base | Roots/burrows uncommon | Major channels of Dhok Pathan Fm. |
| II | Conglomerate; sandstone | Trough cross beds; sharp upper and lower contacts | Root horizons along top contacts | Flood deposits outside channels, e.g., crevasse splay |
| III | Silty sand; sandy silt; silt; sandy silty clay | Ripple bedding; plane lamination; sharp and gradational contacts | Roots/burrows; invertebrates; mottled horizons; nodules; disrupted bedding | Channel margin, swale or pond |
| IV | Silty clay; clayey silt | Occasional laminated bedding; gradational contacts | Roots/burrows; diverse nodules; mottled zones; slickensides; disrupted bedding | Floodplain land surfaces and paleosols |

(2) reconstruction of the circumstances of accumulation of skeletal remains, and (3) estimation of the relative amount of time represented by each fossil assemblage. The criterion for selection of mammal remains, the quantification method, and, ultimately, the sampling distribution are direct consequences of these assessments of preservational history.

Methods

Fieldwork consisted of microstratigraphic documentation and systematic collection of localities from the U-interval. In the Siwaliks, “localities” are surface concentrations from a restricted outcrop area (Barry et al. 1980). Sedimentary units were documented on a vertical scale of centimeters and a horizontal scale of meters. I recorded microstratigraphic data at 42 localities (Fig. 3), about one-third of the localities known from the U-interval. The lateral and vertical distribution of localities in this sample matched the distribution of all localities through the U-interval. I selected localities for study using the criteria that source horizons of fossils had to be identifiable and that the overall sample had to be representative of the occurrences of fossil assemblages in the major lithologies present. The most productive localities in each lithology were examined.

Microstratigraphic documentation of each locality consisted of descriptions based on field exposures and hand specimens of fossil-bearing and adjacent strata. Identification of fossiliferous horizons was based on fossil material in situ, matrix

present on surficial fossils, and the surficial distribution of fossil assemblages. Lithologic features for each horizon included grain size, color, an estimate of mineral composition, texture, sorting, rounding, and cementation. I noted both the nature of primary sedimentary structures, such as laminated bedding, ripple bedding, and cross bedding, and the absence of bedding. Contacts were designated as sharp, rapidly gradational (within a vertical span of 10 cm or less), or diffusely gradational (over a vertical span greater than 10 cm), and also as erosional or interfingering or neither. Postdepositional features included mottling, distortion of primary depositional features, textural heterogeneity, slickensides, autochthonous nodular precipitates, and trace fossils. I used these geologic data to classify localities among four facies associations (Table 2) that represent the major subenvironments of the fluvial systems in the Dhok Pathan lithofacies. Locality descriptions, consisting of microstratigraphic sections and verbal summaries, for all 42 localities are given in Badgley (1982). Each locality was classified according to the facies association considered to be the major fossil source.

Collection

I selected 21 localities for collection. The foremost priority in selecting localities was to have samples unbiased by collecting procedures for each facies association. I gave preference to localities with larger sample sizes and to localities that had not been previously collected. For five

TABLE 3. Stratigraphic data relevant to assessing duration of accumulation for fossil assemblages. (a) Estimate of the comparative time span represented by the bone accumulation relative to the time span represented by sediment for localities in each facies association. (b) Estimates of the number of years per meter of sediment for a range of sediment accumulation rates for each facies association. (c) Average stratigraphic thickness of localities from each facies association. "Stratigraphic thickness, whole locality" refers to the entire stratigraphic span from which fossils were collected, including possibly more than one facies association. "Stratigraphic thickness, productive FA" refers to the thickness of fossiliferous sequence from the primary facies association (FA). "Unit thickness" refers to the thickness of individual strata within the productive facies association. "Sequence thickness" refers to the thickness of the whole facies association, even when not fossiliferous throughout. (d) Estimate of duration of accumulation based on (b) and (c). Conversion factors in (b) were multiplied by the value of stratigraphic thickness for each locality individually; these results were then averaged. (e) Average sample size for localities in each facies association.

| | Facies association | | | |
|--|--------------------|---------------|----------------|--------------------|
| | I (N = 17) | II (N = 8) | III (N = 7) | IV (N = 9) |
| a) Duration of fossil accumulation vs. sediment accumulation | Same to greater | Greater | Same | Less to same |
| b) Duration-thickness conversion factor (yr/m) | | | | |
| High rate | 20 | 20 | 20 | 20 |
| Intermediate rate | 2,000 | — | — | 2,000 |
| Low rate | 12,000 | 1,000 | 1,000 | 12,000 |
| c) Av. stratigraphic thickness, whole locality | 4.9 m | 2.8 m | 2.7 m | 1.2 m |
| Av. stratigraphic thickness, productive FA | 2.9 m | 2.1 m | 2.2 m | 1.2 m |
| Av. unit thickness | 3.0 m | 0.9 m | 0.3 m | 0.9 m |
| Av. sequence thickness | 4.1 m | 0.9 m | 3.0 m | 9.5 m |
| d) Estimated duration of fossil accumulation, whole locality | 95–51,240 yr | 80–5,506 yr | 53–5,212 yr | 24–2,400–14,422 yr |
| Estimated duration of fossil accumulation, productive FA | 60–6,470–35,870 yr | 62–5,044 yr | 45–2,240 yr | 24–2,400–14,422 yr |
| e) Av. # of specimens, whole locality | 117 | 206 | 116 | 29 |
| Av. # of specimens, productive FA | 103 | 166 | 104 | 29 |

localities, my samples were secondary collections, following earlier "high-grade" collecting; I later combined the data from my samples with the data from the earlier collections.

Fossils were collected in a manner that recorded their approximate distribution on the surface. For most localities, I laid out a grid system of squares ranging in size from 2 m × 2 m to 10 m × 10 m, depending on the outcrop area of the locality. Fossils from each square were collected and recorded separately. Additional methods included collection of contiguous transects, collection of isolated concentrations of fossils, and excavation. The primary service of squares and transects was to facilitate a thorough search. These methods were adequate for finding the remains of mammals larger than 1 kg in estimated body weight, but not for smaller mammals.

I recorded each specimen to skeletal element and to the lowest taxonomic level attainable at

the time of collection, with levels ranging mainly from family to species. For many specimens identifiable to family, it was possible to distinguish size categories that probably correspond to genus or species. Further taxonomic resolution (particularly of postcranial elements) was not possible without the recovery of more associated skeletal material, an uncommon occurrence in Middle Siwalik sediments.

For localities that had been previously collected, it was possible only to match my collection with catalog records. The earlier collection included the more complete and taxonomically diagnostic material; relatively few incomplete catalogued specimens had possible matches in my collection. For fragments of skulls, pelves, scapulae, vertebrae, and teeth, I devised a correction factor: a fragmentation index, based on the ratio of the estimated minimum number of vertebrae to the total number of vertebral fragments in my surface collections. I based the frag-

mentation index on vertebrae because, except for first and second cervicals, vertebrae tend to be ignored in high-grade collections. The fragmentation index for vertebrae closely matched that for the other skeletal elements mentioned above, in samples from virgin localities (Badgley 1982). For limbs, metapodials, and phalanges, I counted complete specimens plus the number of either proximal or distal ends according to the larger number.

Duration of accumulation

The duration of accumulation (Table 3) represents the time span from which living assemblages have been sampled. This time span indicates the time resolution of the fossil assemblages. In theory, a fossil assemblage can represent less time, the same amount of time, or more time than the sediment that contains it. For example, the remains of a single carcass represent an instantaneous death event, but the sediment that buries the carcass may represent years or decades. On the other hand, a flood deposit may represent a depositional period of hours or days; but skeletal material contained within, if harvested from a land surface or reworked by erosion of floodwaters, may represent decades to centuries. For each facies association, I evaluated duration of accumulation on the basis of sedimentologic aspects of facies and the vertical distribution of fossils (Table 3a).

Since most fossils occurred as surface finds, it was necessary to take the entire vertical distribution of fossils as representative of the interval of accumulation. The source horizons for most fossils at each locality usually represented considerably less than the entire vertical distribution. Thus, I calculated two sets of estimates of the interval of accumulation, one for the entire vertical distribution and one for the stratigraphic span of most of the fossil sample (ca. 80%).

I calculated the duration of fossil accumulation as the sum of the products (stratigraphic thickness)*(duration-thickness conversion factor) for all facies associations in the productive stratigraphic interval. Each facies association has a set of conversion factors (Table 3b) for estimating duration of fossil accumulation from stratigraphic thickness. These numerical values are intended not to convey a false sense of precision but to combine plausible sediment accumulation rates

with taphonomic factors related to burial, factors such as hydraulic equivalence and the amount of association among specimens. Average, minimum, and maximum sedimentation rates are taken from Schindel's (1980) compilation of sedimentation rates for modern fluvial environments.

The low conversion factor of 20 yr/m for all facies associations incorporates Schindel's maximum sedimentation rate with the time represented in a land-surface bone assemblage (Hill 1975; Behrensmeyer 1978; Behrensmeyer and Dechant-Boaz 1980). The conversion factor of intermediate value (2,000 yr/m) for Facies Associations I and IV is the average sediment accumulation rate for the U-interval (Behrensmeyer and Tauxe 1982). The slowest sediment accumulation rates, corresponding to the high conversion factors for Facies Associations I and IV, are indicated by paleosol units. Zones of intensely developed pedogenic features represent depositional hiatuses estimated as ranging from 100 to 10,000 yr (Leeder 1975; Bown and Kraus 1981). Counting both the time of sediment accumulation (with the average rate of 2,000 yr/m) and the upper end of this range results in a high conversion factor of 12,000 yr/m. The value of 1,000 yr/m for the high conversion factor for Facies Associations II and III represents an intermediate sediment accumulation rate considered appropriate for these facies associations. Further details are given in the Appendix. Data for individual localities can be found in Badgley (1982). Average values for all localities in each facies association are given in Table 3d.

I combined taphonomic data for localities of the same facies-association, reasoning that within each facies-association, fossil assemblages experienced broadly similar sedimentary taphonomic histories. Taphonomic features of the four composite taphonomic assemblages are given in Table 4.

Hydraulic equivalence

Hydraulic equivalence refers to the "transportability" of individual skeletal elements compared to the sediment matrix. Two particles are considered hydraulically equivalent when they have the same settling velocity, the fall velocity in still water. Settling velocity is proportional to

TABLE 4. Taphonomic features of Siwalik fossil assemblages.

| Facies association | Element completeness in relation to size | Spatial distribution in sediment | Articulation | Hydraulic equivalence | % juvenile individuals |
|--------------------|---|-------------------------------------|--------------|-----------------------|------------------------|
| I (N = 7) | Large mammal: elements incomplete | Scattered | No | Approximately | 1 |
| II (N = 3) | Large mammal: few elements complete | Scattered | No | Approximately | 1 |
| III (N = 5) | Large mammal: most elements complete | Clustered | No | Greater | 12 |
| IV (N = 6) | Variable; partial remains of single individuals | Scattered; clustered; densely piled | Yes | Greater | 16 |

the square root of the radius of a spherical particle (Blatt et al. 1980). Transportability is a qualitative concept, having no reference to a specific hydraulic parameter or equation. In the context of this study, the best conceptual analogue in hydraulics is stream "competence," defined by the maximum size of sediment that flow can move (Blatt et al. 1980). The parameters of settling velocity are particle size, its specific weight in fluid, and the viscosity of the fluid. It is possible to calculate the diameter of an inorganic particle (e.g., quartz) that is hydraulically equivalent to a particular skeletal element.

Estimates of hydraulic equivalence through comparisons of settling velocities are taken as a rough indicator of stream competence with respect to vertebrate skeletal elements. For bones of modern mammals, settling velocities estimated from measurements of volume and density are within 43% of observed settling velocities (Behrensmeyer 1975). Similarly, diameters of quartz-equivalents are within 67% of diameters determined from observed settling velocities, with most deviations <50% (Badgley 1982). Thus, I consider the calculated estimates of settling velocities to lie within an order of magnitude of actual values.

Table 5 presents calculated hydraulic equivalents for clasts of quartz, clay, and calcite (the composition of most sedimentary particles in the Siwaliks), ranging in diameter from 0.5 to 6.0 cm. This range corresponds to the observed dimensions of approximately spherical clasts in conglomerates of the U-interval. Even these rough estimates provide useful insights into the transport history of Siwalik fossil assemblages. The purpose of calculating hydraulic equivalence is to assess the possibility that skeletal elements *could* have been transported along with the sed-

iments in which they occur. While hydraulic equivalence between skeletal elements and inorganic sedimentary particles does not prove that they had similar transport histories, a large discrepancy in settling velocities undermines the hypothesis that bones and sediment were delivered to a site by the same fluvial agent.

Results

The sedimentary environments recognized here represent adjacent but discrete depositional settings in a meandering fluvial system (Allen 1970a,b). The purpose of describing the facies associations is to provide field evidence for interpretations of depositional and postdepositional taphonomic influences on the fossil assemblage from each sedimentary environment.

Sedimentary environments

Facies Association I.—Facies Association I consists of buff sandstones that are fine- to medium-grained and moderately well sorted, with conglomerate lenses. Sandstone units average 3.0 m in thickness and persist laterally for up to several kilometers perpendicular to flow. These units have erosional bases and many exhibit cut banks. Trough cross-bedding is the most common sedimentary structure. These sandstones fine upwards into bioturbated silty sands and silts (Facies Association III). Postdepositional features are uncommon.

Conglomerate lenses occur at the base or in the middle of sandstone bodies. Conglomerates are intraformational, with clasts of calcareous nodules, clay and silt fragments, onkolites, ferruginous nodules, sand pebbles, and bones. The average clast size is 1–2 cm across, with large clasts rarely exceeding 5 cm across. Most conglomerates are trough-shaped, cross-bedded, and

TABLE 5. Estimates of hydraulic equivalence between inorganic sedimentary particles and skeletal elements. Three kinds of inorganic clasts are considered (quartz, clay, calcite), each with a characteristic density; inorganic clasts are assumed to be spherical. Three densities of skeletal elements are evaluated (vertebra, limb, tooth), representing a range of densities in bones of modern mammals (Behrensmeier 1975). Calculated hydraulic equivalents are reported as nominal diameters (diameter of a sphere with equivalent volume to an object of nonspherical shape) and as volumes. Diameters of inorganic clasts are in the pebble range of grain size. Measured volumes of Siwalik fossils include representative specimens from the largest mammals in the fauna.

| Density of inorganic clast | | Density of skeletal element | Diameter of inorganic clast | | | | | |
|---|-------|-----------------------------|-----------------------------|--------------|---------------|--------------------|--------------------|--------------------|
| | | | 0.5 cm | 1.0 cm | 2.0 cm | 4.0 cm | 5.0 cm | 6.0 cm |
| Nominal diameter (cm)/volume (cc) of skeletal element | | | | | | | | |
| $\rho_p = 2.65$ quartz | vert | 1.11 | 7.5/220.8 | 15.0/1,766.3 | 30.0/14,130.0 | 60.0/ 113,040.0 | 75.0/ 220,781.0 | 90.0/ 381,510.0 |
| | limb | 1.65 | 1.3/1.1 | 2.5/8.6 | 5.1/69.5 | 10.2/548.0 | 12.7/1,070.0 | 15.2/1,849.0 |
| | tooth | 1.96 | 0.8/0.3 | 1.7/2.7 | 3.4/21.3 | 6.9/170.1 | 8.6/332.1 | 10.3/574.0 |
| $\rho_p = 2.0$ clay | vert | 1.11 | | 9.1/393.2 | | 36.4/25,264.0 | 45.5/49,148.4 | |
| | limb | 1.65 | | 1.5/1.9 | | 6.2/122.0 | 7.7/238.2 | |
| | tooth | 1.96 | | 1.0/0.6 | | 4.2/37.9 | 5.2/73.9 | |
| $\rho_p = 2.7$ calcite | vert | 1.11 | | 15.5/1,931.7 | 30.9/15,453.9 | 61.8/ 123,630.8 | 77.3/ 241,466.0 | |
| | limb | 1.65 | | 2.6/9.4 | 5.2/74.9 | 10.5/599.2 | 13.1/1,170.3 | |
| | tooth | 1.96 | | 1.7/2.9 | 3.5/23.3 | 7.1/186.0 | 8.9/363.3 | |

Measured volumes of Siwalik fossils: molar crown (Proboscidea) 1,150 ± 50 cc, distal femur (Proboscidea) 1,140 ± 50 cc, proximal radius (Proboscidea) 650–700 cc, calcaneum (large rhino) 375 ± 20 cc, distal humerus (giraffid) 156 ± 10 cc, distal femur, epiphysis (giraffid) 140 ± 10 cc, molar crown (rhino) 120 ± 10 cc.

laterally restricted to a few meters across. They are usually <1 m thick. Fossil accumulations in Facies Association I are usually associated with conglomerate lenses.

The sandstones and sandstone-conglomerate complexes of this facies association were formed by the upper range of current velocities present in the fluvial system. Facies Association I corresponds to the active channels within meander belts that formed alluvial ridges by lateral and vertical accretion, followed by avulsion onto a different region of the floodplain (Behrensmeier and Tauxe 1982).

Facies Association II.—The lithologies of Facies Association II are conglomerate and sandstone, lithologically and texturally similar to those of Facies Association I. The distinguishing features are unit thickness, shape, and relationship to adjacent strata. The coarse-grained units are all relatively thin (Table 3c). Conglomerate when present is volumetrically predominant, whereas in Facies Association I, conglomerate lenses constitute a minor part of total unit volume. These units range from a few meters to <500 m across. They occur within otherwise long sequences of fine-grained deposits (Facies Association IV) full of pedogenic features. But these coarse units are not part of coarsening-upward or fining-upward sequences. Both upper and lower contacts are

sharp; that is, these units “interrupt” a fine-grained sequence, ending as abruptly as they start. In contrast, the coarse units of Facies Association I pass into fining-upward sequences up to several meters thick and are sometimes preceded by thin coarsening-upward sequences.

While basal contacts are sharp, they are not all distinctly erosional. Some are very irregular with about 20 cm of undulatory relief, suggestive of micro-topography on a stabilized land surface. Most conglomerates are extensively cross-bedded as are the associated sand lenses. Both single and multilayer units are present. Postdepositional features are uncommon, except for the occasional network of root casts on the top surfaces.

These sedimentologic features suggest that Facies Association II resulted from energetic, short-lived episodes with minimal internal reworking. I interpret these deposits as products of high-velocity floods which carried coarse material out of channels and onto floodplains. Both crevasse splays and ephemeral floodplain channels are included in this category. Many of the coarse clasts, including bones, may have been entrained during flooding and erosion of floodplain surfaces.

Facies Association III.—Facies Association III exhibits heterogeneous lithologies and wide-

spread bioturbation. These deposits overlie or pass laterally into thick sandstones of Facies Association I. The average sequence thickness is 3.0 m.

There are two sedimentary modes to this facies association. One mode is an alternation of thin beds (each 0.5 cm to 0.5 m thick) of poorly sorted sand and silt. These sequences contain as many as 20 distinct strata and fill an original topographic depression a few meters to tens of meters across. Contacts are mainly sharp and nonerosional. Internal bedding structures when present consist of laminated bedding and ripple bedding. Even when preserved, internal bedding is often disrupted. Burrow and root structures, mottled horizons, and textural inhomogeneities are common. The other expression of Facies Association III is a sequence of equivalent total thickness and lithology but with only two or three distinct units. Strata range from 0.4 to 1.8 m thick. Contacts are both gradational and sharp; none are erosional. No other sedimentary structures are present. Within each unit, there is considerable variability in sorting and texture that could only reflect postdepositional processes. Nodules and root/burrow casts are common. Both blue-gray and orange-brown mottling, presumably indicative of variable oxidation states, are extensive in some localities. Also, some localities contain abundant autochthonous molluscs.

These features suggest the portions of channel belts not occupied by active channels as the site of deposition. Micro-environments include levees, swales behind point bars and levees, and abandoned channels. Sediment deposition probably occurred both by primary fluvial deposition and by reworking of earlier deposits by wind, runoff, slumping, and trampling. Postdepositional features suggest that these sites were emergent for considerable periods.

Facies Association IV.—The sediments of Facies Association IV are predominantly fine-grained and form relatively thick sequences. Lithologies are mixtures of silt and clay with variable amounts of sand. Contacts between fine-grained units occur as diffuse transitions in color, texture, and lithology. This facies association forms sequences up to 80 m thick (M. Monaghan, pers. comm.). Most units exhibit no internal bedding structures. Occasional traces of

faint horizontal banding and patches of laminated bedding indicate that at least some of these deposits had original bedding structures. Mottling occurs widely in discrete horizons or as anastomosing networks, threadlike traces, circular spots, or patches. Autochthonous nodules are often present, either scattered through fine-grained units or in densely concentrated horizons, or, rarely, as discontinuous cemented layers. Root and burrow structures are abundant. Carbonized plant fragments occur sporadically.

Facies Association IV represents floodplains. Within the U-interval, floodplain sediments extend laterally for up to tens of kilometers (Behrensmeyer and Tauxe 1982). Where contemporaneous facies have been traced laterally, floodplain deposits begin 0.5–1.0 km from channel edges, except where cut banks occur. Most of the postdepositional features, including nodules, mottling, color transitions, root and burrow casts, and the generally mixed texture of the sediments, can be interpreted as products of soil formation (Bown and Kraus 1981; Retallack 1981).

In summary, channel deposits reflect the continual influence of flowing water, as indicated by pervasive cross-stratification and the rarity of bioturbation. Channel-margin deposits, with their alternations or mixtures of coarse- and fine-grained sediment, preservation of both small-scale sedimentary structures and abundant bioturbation features, indicate sites of episodic flowing water, standing water, and emergence. The textural heterogeneity and complex postdepositional features of floodplain sediments point to a predominantly subaerial history. Coarse-member flood deposits exhibit the lithologies and sedimentary structures of high current velocities across floodplain surfaces. From channel to channel-margin to floodplain deposits, there is a progressive decrease in grain size and frequency of primary sedimentary structures and an increase in the extent of bioturbation. This spectrum of depositional and postdepositional features is paralleled by taphonomic features of the fossil assemblages in these facies associations.

Duration of fossil accumulation

The average time span of fossil accumulation in each facies association is given in Table 3d.

I used long-term, short-term, and, in some instances, intermediate values of sedimentation rates (Table 3a) to estimate time represented by the fossil assemblage at each locality. For each facies association, depositional characteristics suggest which portion of the spectrum is most appropriate for the sediments and thus the fossil assemblages.

Bone assemblages from Facies Association I span a greater stratigraphic thickness than assemblages from any other facies association (Table 3c). Since both channel and floodplain deposits represent potentially low rates of net sediment accumulation, bone assemblages from Facies Association I probably represent the greatest temporal span. Bones of Facies Association II were probably harvested from more restricted spatial and temporal sources than the assemblages of Facies Association I. These fossil assemblages represent relatively short periods of bone accumulation. Fossil assemblages from channel margins also represent relatively short periods of accumulation. Floodplain assemblages represent potentially the shortest as well as quite long periods of accumulation, depending on taphonomic characteristics of individual localities.

The sedimentary environments most conducive to bone preservation were not those in which the predominantly terrestrial mammals lived or died. Facies Associations I and II, the coarse sediments, constitute about 20% (by thickness) of the U-interval. The sediments of Facies Association III comprise about 30% and those of Facies Association IV about 50% of the entire sequence (Badgley 1982; Behrensmeyer and Tauxe 1982). The distribution of fossils shows the opposite pattern: over 65% of all collected fossils come from Facies Association I and II; about 25% are from Facies Association III; and about 10% are from Facies Association IV (Badgley 1982). The most widespread, habitable environment is the least fossiliferous.

Fossil assemblages

Taphonomic features of the composite assemblages from each facies association (Table 4) include the size range of mammals, the completeness of specimens from mammals of different sizes, the spatial distribution of bones in relation to each other, the presence of articulated mate-

rial, and an estimate of hydraulic equivalence between bones and inorganic sedimentary particles. Although most fossils were found on the surface and not in situ, the surficial distribution of most assemblages permitted a fair assessment of spatial distribution and the possibility of articulation in bones of the original taphocoenose.

Taphonomic Assemblage I.—The fossil assemblages from Facies Association I include the largest samples in the U-interval. Fossils occurred as isolated specimens distributed randomly over the weathered surfaces of the source horizons. Clustering of specimens that would imply association of skeletal material occurred at only one locality. No articulated material was found on the surface or in situ. Most bones were broken with breaks ranging from fresh to very worn to bone pebbles. The full size spectrum of Siwalik mammals is represented; however, elements from mammals >500 kg tend to be the most incomplete. For example, proboscidean and rhino molar fragments are typically 10%–20% of the whole molar. The largest complete, isolated teeth are those of *Hipparion*. Such teeth are hydraulically equivalent to a quartz or calcite sphere 2–3 cm across (Behrensmeyer 1975), a size range corresponding to the larger clasts present in conglomerate lenses. Other large specimens include distal and proximal ends of rhino limbs, fragments of large-mammal vertebra, scapula, and pelvis. Table 5 indicates that such bone fragments are hydraulically equivalent to clast-sizes represented in the conglomerate lenses of Facies Association I. A proboscidean distal femur, with a measured volume of $1,140 \pm 50$ cc, corresponds to a calcite sphere 5.0 cm in diameter. Such a large clast is uncommon in conglomerates, representing the upper extreme of inorganic clast sizes; however, such a specimen is also at the upper extreme of organic clast sizes for this taphonomic assemblage.

Taphonomic Assemblage II.—Bones were also distributed randomly over the source horizons and exhibited no apparent clustering with one exception. At the edge of one locality (211) within an area of $\sim 10 \times 10$ m, there were several fragmentary limb and pelvic bones of rhino and proboscidean affinity. Most bones were incomplete, although the frequency of complete limb bones of small artiodactyls was higher than in Taphonomic Assemblage I. Wear on speci-

mens varied from fresh and unabraded to the presence of bone pebbles.

The full size range of Siwalik mammals is present. Specimens range in size from bone chips to complete but fragmented rhino and proboscidean limbs; the largest teeth are molars of these taxa. Measured volumes of selected fossils of large Siwalik mammals (Table 5) indicate that the largest postcranial elements and teeth exceed the largest inorganic clasts in hydraulic equivalence. But most specimens (>90%) correspond in approximate hydraulic equivalence to the size range of inorganic clasts in these conglomerates.

Taphonomic Assemblage III.—The localities of Taphonomic Assemblage III represent surface concentrations at least twice as dense as those of Taphonomic Assemblages I and II. There is considerable clustering of specimens with a relatively high density of scattered material between clusters. Although no specimens were found articulated, some of the adjacent limb and podial elements may have been articulated before weathering out. Most skeletal elements are incomplete, except for podials and phalanges. Surface wear ranges from fresh to very worn, with most specimens fresh.

Mammals of the entire size range are represented. The size range of specimens is broad, with more large elements present than in Taphonomic Assemblage I and Taphonomic Assemblage II. The larger elements include partial and complete gomphothere tusks, a rhino scapula, incomplete rhino and giraffe tibiae, and rhino and gomphothere molars. These elements are hydraulically equivalent to carbonate and quartz clasts more than an order of magnitude larger in diameter than the coarsest sand particles present in the source sediments. Individual skeletal elements hydraulically equivalent to coarse sand and finer-grained lithologies include postcranials and isolated teeth of mammals <5 kg and all body parts of mammals <1 kg (Behrensmeyer 1975; Korth 1979). Thus, most specimens of Taphonomic Assemblage III are well beyond the limits of hydraulic equivalence with inorganic particles of the source horizons.

Taphonomic Assemblage IV.—The six localities of Taphonomic Assemblage IV are variable in all taphonomic features discussed here. Four localities represented in whole or in part the partial remains of single individuals, as inferred from

either the presence of articulated material or the close fit of adjacent body parts. Two localities were dense piles of bone probably accumulated by a single agent. Two other localities contained both clusters of associated fossils and a scatter of fossils, a pattern that resembles an attritional surface skeletal assemblage (e.g., Behrensmeyer and Dechant-Boaz 1980). Much of the material of Taphonomic Assemblage IV was found in situ. The articulated units contained numerous complete elements, and the nonarticulated component consisted chiefly of fragmentary remains whether the material was found in place or on the surface.

Although the taxonomic diversity of individual localities tends to be much lower than in other sedimentary environments, the full size range of Siwalik mammals is represented in the composite assemblage. Individual specimens range in size from bone chips to gomphothere molars. As individual elements, virtually all recorded specimens are hydraulically equivalent to inorganic particles several orders of magnitude larger (in diameter) than the particles in the matrix surrounding the fossils. Articulated material cannot be considered comparable in transportability to individual elements and probably would present more resistance to hydraulic transport than would isolated elements (except for floating carcasses).

Faunal composition

The term "fossil assemblage composition," as used here, refers to the most basic taxonomic description for the composite assemblages—the distribution of fossil specimens among all taxonomic categories. This description does not recognize the distribution of *individuals* among taxonomic categories. For convenience, I call this feature "taxonomic abundance of the fossil assemblage." Estimation of the number of individuals from the number of specimens requires choice of a quantification method (discussed below).

The fossil-assemblage composition of the four taphonomic assemblages is given in Table 6a. Taphonomic Assemblage I has the largest composite sample size, reflecting both the actual productivity of this facies association and my deliberate collection of the richest localities. In both Taphonomic Assemblages I and II, bovids ex-

TABLE 6. Fossil-assemblage composition, documenting the distribution of fossil remains among taxa, mainly at the family level, in each taphonomic assemblage. (a) The number of specimens, with each element counted. (b) The number of individuals, computed according to the quantification method appropriate for each taphonomic assemblage (see text). RAM = Ramapithecidae, CARN = Carnivora, PROB = Proboscidea, EQUID = Equidae, CHAL = Chalicotheriidae, RHIN = Rhinocerotidae, SUID = Suidae, ANTH = Anthracotheriidae, TRAG = Tragulidae, GIR = Giraffidae, BOV = Bovidae.

| | | RAM | CARN | PROB | EQUID | CHAL | RHIN | SUID | ANTH | TRAG | GIR | BOV | Total |
|---------------------------|---|------|------|------|-------|------|------|------|------|------|-----|------|-------|
| (a) Number of specimens | | | | | | | | | | | | | |
| Taphonomic assemblage I | # | 6 | 46 | 29 | 166 | 3 | 54 | 40 | 18 | 39 | 41 | 378 | 820 |
| | % | 0.7 | 5.6 | 3.5 | 20.2 | 0.4 | 6.6 | 4.9 | 2.2 | 4.7 | 5.0 | 46.0 | |
| Taphonomic assemblage II | # | 1 | 4 | 20 | 52 | 0 | 32 | 26 | 4 | 10 | 25 | 97 | 271 |
| | % | 0.4 | 1.5 | 7.4 | 19.2 | 0.0 | 11.8 | 9.6 | 1.5 | 3.7 | 9.2 | 35.8 | |
| Taphonomic assemblage III | # | 20 | 20 | 23 | 99 | 7 | 49 | 49 | 5 | 15 | 11 | 70 | 368 |
| | % | 5.4 | 5.4 | 6.3 | 26.9 | 1.9 | 13.3 | 13.3 | 1.4 | 4.1 | 3.0 | 19.0 | |
| Taphonomic assemblage IV | # | 5 | 100 | 11 | 23 | 0 | 9 | 51 | 0 | 2 | 5 | 80 | 286 |
| | % | 1.7 | 35.0 | 3.9 | 8.0 | 0.0 | 3.2 | 17.8 | 0.0 | 0.7 | 1.7 | 28.0 | |
| (b) Number of individuals | | | | | | | | | | | | | |
| Taphonomic assemblage I | # | 6 | 46 | 29 | 166 | 3 | 54 | 40 | 18 | 39 | 41 | 378 | 820 |
| | % | 0.7 | 5.6 | 3.5 | 20.2 | 0.4 | 6.6 | 4.9 | 2.2 | 4.7 | 4.9 | 46.0 | |
| Taphonomic assemblage II | # | 1 | 4 | 20 | 52 | 0 | 32 | 26 | 4 | 10 | 25 | 97 | 271 |
| | % | 0.4 | 1.5 | 7.4 | 19.2 | 0.0 | 11.8 | 9.6 | 1.5 | 3.7 | 9.2 | 35.8 | |
| Taphonomic assemblage III | # | 8 | 9 | 4 | 8 | 2 | 6 | 10 | 3 | 7 | 3 | 16 | 76 |
| | % | 10.5 | 11.8 | 5.2 | 10.5 | 2.6 | 7.9 | 13.1 | 3.9 | 9.2 | 3.9 | 21.1 | |
| Taphonomic assemblage IV | # | 1 | 11 | 6 | 7 | 0 | 3 | 7 | 0 | 2 | 3 | 16 | 56 |
| | % | 1.7 | 19.6 | 10.7 | 12.5 | 0.0 | 5.4 | 12.5 | 0.0 | 3.6 | 5.4 | 28.6 | |

hibit the highest specimen frequency (36%–46%) and equids follow (19%–20%). Other taxa constitute 12% or less of the remaining fossil assemblage composition. In Taphonomic Assemblage III, equids are most abundant (27%) with bovids next (19%). In Taphonomic Assemblage IV, carnivores are most abundant (35%) with bovids next (28%).

Skeletal-part composition

The elements of the mammalian skeleton vary in physical properties such as density and vol-

ume, and exhibit corresponding variation in response to processes of dissociation and destruction. For example, vertebrae are the elements most transportable in moving water because of their low density and high surface-area-to-volume ratio (Behrensmeyer 1975, 1982). Skeletal-part frequency has been considered a potential indicator of the accumulation history of bone assemblages, particularly in identifying effects of fluvial transport and winnowing (Voorhies 1969; Behrensmeyer 1975, 1982; Brain 1981).

The skeletal-part composition of the four

TABLE 7. Skeletal element composition, documenting the distribution of mammalian remains among the common skeletal elements in each taphonomic assemblage. + means that element is present in frequency <0.5%. Tooth Is = isolated tooth, RT/TK = root/tusk, MX = maxilla, MD = mandible, SK = skull, HC = horncore, VT = vertebra, SCA = scapula, PEL = pelvis, HUM = humerus, FEM = femur, RAD = radius, TIB = tibia, UL = ulna, FIB = fibula, POD = podial, CAL = calcaneum, AST = astragalus, MT = metatarsal, MC = metacarpal, MPin = metapodial indeterminate, PH = phalanx, PAT = patella, SH = shaft.

| | | Tooth Is | RT/TK | MX | MD | SK | HC | VT | SCA | PEL | HUM | FEM |
|---------------------------|---|----------|-------|----|----|----|----|-----|-----|-----|-----|-----|
| Taphonomic assemblage I | # | 282 | 13 | 8 | 44 | 33 | 25 | 81 | 17 | 25 | 28 | 31 |
| | % | 22 | 01 | 01 | 04 | 03 | 02 | 06 | 01 | 02 | 02 | 02 |
| Taphonomic assemblage II | # | 131 | 10 | 6 | 20 | 11 | 9 | 43 | 9 | 10 | 10 | 19 |
| | % | 26 | 02 | 01 | 04 | 02 | 02 | 09 | 02 | 02 | 02 | 04 |
| Taphonomic assemblage III | # | 162 | 9 | 15 | 23 | 39 | 7 | 108 | 9 | 22 | 20 | 31 |
| | % | 17 | 01 | 02 | 02 | 04 | 01 | 12 | 01 | 02 | 02 | 03 |
| Taphonomic assemblage IV | # | 112 | 10 | 4 | 23 | 15 | 4 | 39 | 9 | 4 | 10 | 10 |
| | % | 31 | 03 | 01 | 06 | 04 | 01 | 11 | 02 | 01 | 03 | 02 |

FACIES ASSOCIATION

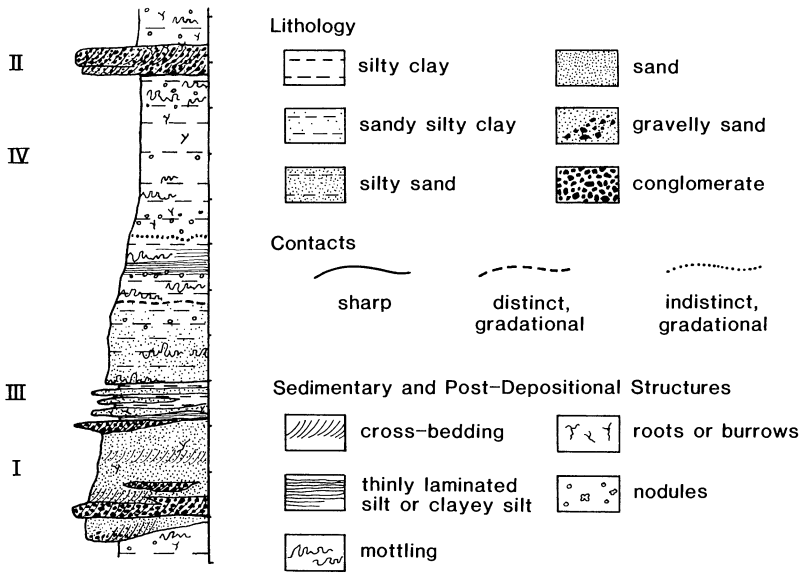


FIGURE 4. Generalized microstratigraphic section from Siwalik sediments of the U-interval. The four facies associations described in the text are indicated in their superjacent relationships.

taphonomic assemblages is given in Table 7. In Fig. 5, skeletal-part composition is compared to the relative frequency of skeletal elements in the average mammal skeleton. It is visually apparent that all four taphonomic assemblages depart markedly from the proportions of a whole mammal skeleton. In all assemblages, isolated teeth, skulls, mandibles, and limbs are overrepresented by 2%–17% (i.e., the percentage values in fossil assemblages are larger than in the original skeleton). Vertebrae and phalanges are underrepresented by 8%–16%. Elements that are neither depleted nor enriched include maxillae, scapulae,

pelves, ulnae, fibulae, and patellae. The other categories are more variable. A second quantitative comparison of skeletal-part composition is the application of Spearman's measure of rank-order correlation, r_s (Blalock 1972), to skeletal-part frequencies for pairs of taphonomic assemblages. Table 8 lists r_s for all possible pairwise comparisons of skeletal-part frequencies of the four taphonomic assemblages and the average mammal skeleton. On the basis of this statistic, the taphonomic assemblages are more similar to each other in skeletal-part composition than any assemblage is

TABLE 7. Extended.

| RAD | TIB | UL | FIB | POD | CAL | AST | MT | MC | MPin | PH | PAT | RIB | SH | Total |
|-----|-----|----|-----|-----|-----|-----|----|----|------|----|-----|-----|-----|-------|
| 39 | 41 | 14 | 5 | 67 | 57 | 16 | 11 | 18 | 78 | 96 | 19 | 99 | 110 | 1,257 |
| 03 | 03 | 01 | + | 05 | 05 | 01 | 01 | 01 | 06 | 08 | 02 | 08 | 09 | |
| 8 | 16 | 2 | 0 | 21 | 7 | 5 | 8 | 8 | 23 | 13 | 8 | 82 | 17 | 496 |
| 02 | 03 | + | 00 | 04 | 01 | 01 | 02 | 02 | 05 | 03 | 02 | 17 | 03 | |
| 21 | 22 | 7 | 3 | 33 | 16 | 12 | 4 | 5 | 36 | 31 | 2 | 197 | 92 | 926 |
| 02 | 02 | 01 | + | 04 | 02 | 01 | + | 01 | 04 | 03 | + | 21 | 10 | |
| 8 | 9 | 10 | 4 | 17 | 5 | 6 | 2 | 3 | 11 | 17 | 4 | 26 | 4 | 366 |
| 02 | 02 | 03 | 01 | 05 | 01 | 02 | 01 | 01 | 03 | 05 | 01 | 07 | 01 | |

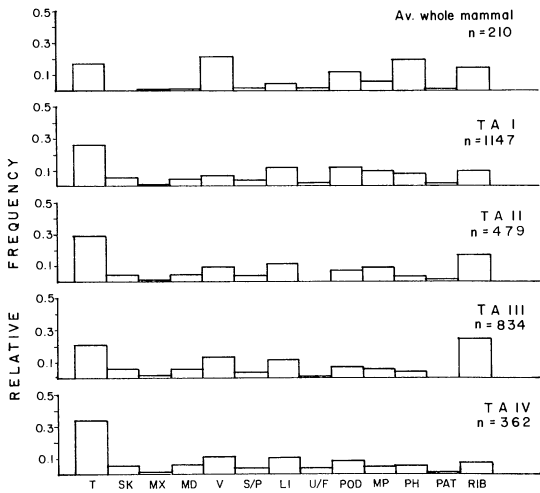


FIGURE 5. Relative frequency of skeletal elements from the average whole mammal and the four taphonomic assemblages; *n* represents the number of individual skeletal elements in each count. Note that the patterns of the four taphonomic assemblages resemble each other more than any does the pattern of the average whole mammal. Abbreviations: TA = Taphonomic Assemblage, T = tooth, SK = skull, MX = maxilla, MD = mandible, V = vertebra, S/P = scapula and/or pelvis, LI = limb (includes humerus, radius, femur, tibia), U/F = ulna and/or fibula, POD = podial, MP = metapodial, PH = phalanx, PAT = patella, RIB = rib.

to the average whole mammal. This pattern suggests that the major transformation of skeletal proportions occurred before final burial, during exposure to carnivory, scavenging, and weathering. Elements that are consistently lost in all Siwalik assemblages (vertebrae, podials, and phalanges) exhibit the lowest densities in modern mammals.

Distribution of fauna according to body size

Mammalian body size, as reflected in the volumes, surface areas, and weights of individual skeletal elements, has an important influence on the outcome of preservational processes. The rates of many degradative processes, such as carnivore damage, drying and cracking from exposure to strong sunlight, and acid etching by roots and fungi, would be expected to operate more rapidly on remains of smaller animals, in part because of higher surface-area-to-volume ratios (Behrensmeyer 1978). With respect to fluvial transport, larger particles require a higher critical shear stress than small particles (of the same density and shape) to become entrained by cur-

TABLE 8. Spearman's coefficient of rank-order correlation, *r_s*, comparing the skeletal element composition of the four taphonomic assemblages with each other and that of the average whole mammal. TA = taphonomic assemblage; MA = mammal.

| | Av. whole MA | TA I | TA II | TA III | TA IV |
|--------------|--------------------|--------|--------|--------|--------|
| Av. whole MA | (1.00) | — | — | — | — |
| TA I | .65 | (1.00) | — | — | — |
| TA II | .58 | .87 | (1.00) | — | — |
| TA III | .61 | .81 | .93 | (1.00) | — |
| TA IV | .63 | .78 | .81 | .85 | (1.00) |

rents. Hence, the sizes of individual skeletal elements and articulated units should be a critical factor in determining transportability. The estimations of hydraulic equivalence presented earlier suggest that skeletal remains of the largest Siwalik mammals had a lowered probability of preservation in fluvial bone concentrations.

I divided Siwalik mammal species of >1 kg (estimated adult weight) into four size groups: A, 1–15 kg (e.g., Mustelidae); B, 16–100 kg (e.g., Hominoidea); C, 101–250 kg (e.g., Equidae); D, >250 kg (e.g., Proboscidea). Some families (e.g., bovids, tragulids, suids) have species in more than one size group. This grouping reflects natural gaps in the spectrum of estimated species' weights for B–C and C–D. The break between A and B reflects other considerations. Much of the census information available for modern ecosystems of high mammalian species richness applies only to taxa >15 kg (e.g., Western 1973; Berwick 1974; Sinclair and Norton-Griffiths 1979). Also, the taphonomic study of the modern, terrestrial skeletal assemblage of mammalian remains at Amboseli Park, Kenya (Behrensmeyer and Dechant-Boaz 1980), indicates that, under these conditions of climate and vegetation, mammals <15 kg are depleted in the earliest stage of taphonomic history.

The estimated number of individuals of each size group is given for each taphonomic assemblage in Table 9. The frequency distributions of Taphonomic Assemblages III and IV are the more even distributions. In all assemblages, the highest proportion occurs in size-group B and the lowest in size-group A.

Discussion

The taphonomic data presented above form the basis for inferring the mode of accumulation,

TABLE 9. Frequency distribution of individuals from each taphonomic assemblage among four body-size categories. The number of individuals (N) reported here is smaller than in Table 6 because a small fraction of specimens was not readily assignable to size category.

| | A (1–15 kg) | B (16–100 kg) | C (101–250 kg) | D (>250 kg) | |
|---------------------------|----------------|------------------|-------------------|----------------|-----------|
| Taphonomic assemblage I | 4 | 52 | 27 | 17 | (N = 732) |
| Taphonomic assemblage II | 2 | 44 | 25 | 28 | (N = 272) |
| Taphonomic assemblage III | 16 | 49 | 25 | 19 | (N = 73) |
| Taphonomic assemblage IV | 12 | 44 | 21 | 24 | (N = 51) |

the method of quantification, and therefore, the taxonomic abundance of the fossil assemblages. Below, I discuss the mode of accumulation for each taphonomic assemblage, then consider the problem of quantification and the significance of taxonomic abundance, skeletal-part composition, and body-size distribution of the four taphonomic assemblages.

The agent of accumulation for each taphonomic assemblage is indicated largely by sedimentologic information. Taphonomic Assemblages I and II represent fluvial accumulations in channels and flood deposits, respectively. This interpretation is supported by the approximate hydraulic equivalence between the inorganic conglomerate clasts and the mammalian skeletal remains, the scatter of specimens through the source sediments, the dissociated nature of specimens, and the range of wear on specimens.

Taphonomic Assemblage I.—In Facies Association I, bones were probably derived from multiple sources—from remains of individuals that died in or near channels, from individuals whose remains were brought to the channel environment by biological agents, and by erosion of penecontemporaneous channel-margin and floodplain deposits. Taphonomic Assemblage I exhibits greater time averaging than the other assemblages because the fossiliferous conglomerate lenses may occur at several levels within thick sandstones. More than any other, this depositional environment represents the pooling of all possible modes of bone accumulation at early stages of taphonomic history—into a fluvial concentration. The actual pattern of concentration is presumably the same as for other coarse particles (e.g., as lag deposits of the coarsest particles in scour structures on the channel floor).

Taphonomic Assemblage II.—The potential sources of vertebrate remains are material already accumulated within the channel system, material buried in channel-margin or floodplain deposits

eroded during flooding, material on the floodplain surface, and living animals drowned by flood waters. No whole skeletons (or articulated material of any kind) are present in Taphonomic Assemblage II, so the role of floods as an agent of mortality is difficult to assess here. If floods contributed to the mortality of terrestrial vertebrates, their skeletal remains show largely the effects of subsequent taphonomic processes (disarticulation, scattering, and weathering of elements). The presence of these deposits within a sequence of floodplain sediments suggests that the flood streams had made their way some distance from their source channels. It is thus plausible that these sheets of coarse sediment entrained a considerable portion of their skeletal assemblage from land surfaces. In addition, Taphonomic Assemblage II contains a few notable specimens outside the range of hydraulic equivalence with the inorganic conglomerate clasts. These specimens suggest that a small fraction (~5%) of the skeletal assemblage was buried rather than transported by flood deposits. An alternative interpretation is that inorganic clasts comparable to the largest specimens were not available in this fluvial system. The episodic nature of crevasse splays and floodplain channels and the possible derivation of much skeletal material from the floodplain surface indicate that Taphonomic Assemblage II spans a time as short as decades. If considerable skeletal material was derived from the bedload of channels or from incisive erosion of floodplain deposits, then a greater time span is indicated. Both Taphonomic Assemblages I and II are attritional in the sense that the faunal samples represent moderate to long time spans (Voorhies 1969).

An alternative pattern of accumulation characterizes Taphonomic Assemblages III and IV. Both depositional environments can reasonably be considered subaerial for much of their existence. The disparity in hydraulic equivalence be-

tween sediment grain size and the size range of most skeletal remains excludes the hypothesis of fluvial accumulation. While complete or partial skeletal remains might have floated about on floodwaters, it seems unlikely that such remains would be finally deposited in concentration with remains of many other taxa. In addition, the high frequency of carnivore remains in Taphonomic Assemblages III and IV relative to I and II argues against floods as the mechanism of accumulation, since floodwaters would be expected to act as a mortality agent nonselective with respect to taxonomic identity. These circumstances suggest that these mammal remains accumulated through concentration by carnivores, scavengers, or bone collectors, or through attrition at sites repeatedly used for predation. This interpretation is supported also by the clustering of specimens and higher spatial density of skeletal material, the presence of articulated material in Taphonomic Assemblage IV, and the higher frequency of unworn specimens.

Taphonomic Assemblage III.—The predominant fluvial influence here was burial of skeletal remains in sluggish or still water. Pulses of sedimentation could have contributed a certain size range of skeletal elements but could not account for the clustering of material. The average time span of fossil accumulation is relatively short, comparable in its range to that of Taphonomic Assemblage II. Compared to the other taphonomic assemblages, Taphonomic Assemblage III is notably enriched in the larger skeletal elements of the largest Siwalik mammals, suggesting that sites of concentration may have formed around the remains of large mammals.

Taphonomic Assemblage IV.—This set of localities is the most heterogeneous for all taphonomic features discussed here. Floodplains were the most extensive of all depositional environments and presumably were continuously populated with abundant organic diversity. The very nature of this setting suggests that a variety of autochthonous bone assemblages would have been present at any time, including isolated skeletal elements, remains of single carcasses, and concentrated remains of multiple individuals. The predominant taphonomic feature of Facies Association IV, however, is its comparative barrenness of fossils. Thus, the documented instances of fossil concentration indicate unusual circum-

stances of preservation or concentration or both. Taphonomic Assemblage IV contains patterns representative both of single carcasses and of concentrated remains of several individuals. No localities can readily be viewed as results of long-term attrition along single land surfaces; the expected pattern in floodplain deposits would be laterally continuous fossiliferous horizons, a pattern that is not present here. Thus, Taphonomic Assemblage IV presumably represents a combination of partial carcasses and biological concentrations. The time span of fossil accumulation ranges from instantaneous to relatively short (up to decades) for concentrated remains of multiple individuals to relatively long for circumstances in which several independent occurrences of partial individuals occur in close stratigraphic proximity and are collected as one locality.

Two aspects of faunal composition support the view of Taphonomic Assemblages III and IV as biological accumulations. The frequency of juvenile individuals is bimodal among the four taphonomic assemblages (Table 4). Taphonomic Assemblages I and II contain extremely low proportions of juveniles (1%), whereas Taphonomic Assemblages III and IV contain 12% and 16%, respectively. The proportion of individual carnivores in each taphonomic assemblage displays a similar pattern (Table 6), that is, the frequency of carnivores is notably greater in the nonfluvial assemblages. If all four taphonomic assemblages were derived from the same original community, this pattern can be seen either as a selective elimination of juveniles from fluvial assemblages or a selective concentration of such remains in nonfluvial assemblages. Living mammalian carnivores are known to select juveniles as preferred prey (e.g., Kruuk 1972) and to kill and concentrate remains of other carnivores (Brain 1980; Scott and Klein 1981). Hence, it is more plausible that these proportions indicate selective concentration, probably by mammalian carnivores. Since carnivores also tend to destroy remains of juveniles more effectively than adult remains, the proportion of juveniles documented in Taphonomic Assemblages III and IV probably underestimates the frequency of juvenile prey.

Quantification

The problem of determining the number of individuals represented in a fossil assemblage rests

ultimately on the probability that two (or more) skeletal elements are derived from the same skeleton. Under some circumstances, taphonomic features indicate clearly how specimens should be counted as individual bodies—for example, articulated material indicates a count of one for that unit. More often, the situation is not clear. Nonetheless, the taphonomic history of a fossil assemblage provides essential guidelines in many instances. Taphonomic processes that concentrate complete or partial remains of individuals indicate that the probability that any two skeletal elements come from the same skeleton is relatively high. Taphonomic processes that disperse partial remains of individuals or isolated skeletal elements reduce the probability that any two skeletal elements come from the same skeleton.

When it is *known* that no two skeletal elements are from the same skeleton (even when all elements are from the same species), then the appropriate quantification method is to count each specimen as one individual. Then, the number of identified specimens per taxon (NISP) equals the number of individuals. On the other hand, when it is known that associated material is present, then a more appropriate quantification method is to determine the minimum number of individuals (MNI), taking into account frequency of skeletal parts, variation in size, and weathering condition. For most fossil assemblages, these conditions of association cannot be known, so no method of quantification can be expected to give certain results. But, pertinent information is often available in the taphonomic setting to indicate whether the probability of association of skeletal elements is low or high. Here, I propose that different quantification methods are appropriate for fluvial and biological accumulations (see also Badgley, 1986).

Bones from channel deposits were harvested from diverse spatial and temporal sources. Once in the channel system, skeletal material hydraulically equivalent to sand and conglomerate clasts probably experienced transport and reworking along with the rest of the sediment. Also, the stratigraphic span of fossils is large, indicating that bones were entrained over periods extremely long in relation to the durability of surface bone assemblages. It is unlikely that bones from the same individual would end up in the same fossil

concentration. Thus, the probability of association of skeletal elements in Taphonomic Assemblage I is low and the quantification method of choice is NISP.

Taphonomic Assemblage II represents a considerably shorter period of time than Taphonomic Assemblage I. Bones may have been drawn from diverse sources, including channels, channel banks, floodplain deposits, and land surfaces. Any of these entrainment processes involves dispersal of skeletal material from the original death sites, thereby reducing the probability that bones in the fossil assemblage were derived from the same individual. While the probability of association between bones may be slightly higher in Taphonomic Assemblage II than in Taphonomic Assemblage I, it is still quite low. Hence, the appropriate quantification method here is also NISP.

For Taphonomic Assemblages III and IV, skeletal elements have a relatively high probability of original association. Living bone accumulators usually transport parts of carcasses (not isolated bones) to sites of concentration (Hill 1979; Brain 1981). Thus, quantification by MNI is an appropriate method to account for the number of contributing carcasses. Two taphonomic factors reduce the accuracy of the estimate by MNI. Disarticulation, scattering, and destruction reduce the original association of skeletal elements. In addition, localities of Taphonomic Assemblages III and IV have in some instances more than one source horizon, and bones from different strata have vanishingly small probabilities of association. During collection, associated material could be recognized. Since most material was collected on the surface, it was not possible to resolve the locality sample completely into its appropriate subsamples from each horizon. Nonetheless, the probability of association of specimens remains stronger and the estimate by MNI is thus more accurate than by NISP.

The distribution of specimens and individuals among different taxonomic categories can be compared in Table 6. In Taphonomic Assemblages I and II, the number of specimens and individuals is the same. In both Taphonomic Assemblages III and IV, the number of individuals is about 20% of the number of specimens (although MNI was determined on a locality-

TABLE 10. Rank abundance of skeletal elements in the average mammal skeleton and the four taphonomic assemblages, showing change in skeletal element composition with increasing influence of fluvial transport. The order of increasing influence of fluvial transport and winnowing increases downward from assemblage IV to I. Abbreviations as in Table 7.

| Av. whole mammal | VT | PH | TEETH | RIB | POD | MP | LIMB | SCA/PEL | UL/FIB | MX | MD | PAT | SK |
|---------------------------|-------|-------|-------|------|-----|-----|------|---------|---------|---------|--------|--------|--------|
| Taphonomic assemblage IV | TEETH | VT | LIMB | POD | RIB | MD | SK | PH | SCA/PEL | UL/FIB | MP | MX | PAT |
| Taphonomic assemblage III | RIB | TEETH | VT | LIMB | POD | SK | MP | SCA/PEL | PH | MD | MX | UL/FIB | PAT |
| Taphonomic assemblage II | TEETH | RIB | LIMB | VT | MP | POD | MD | SK | SCA/PEL | PH | PAT | MX | UL/FIB |
| Taphonomic assemblage I | TEETH | LIMB | POD | MP | RIB | PH | VT | SK | MD | SCA/PEL | UL/FIB | PAT | MX |

by-locality basis). The effective sample size of individuals is thereby reduced such that Taphonomic Assemblages III and IV together comprise only 11% of the total faunal sample. It is all the more notable that the frequency of juveniles (all taxa) and carnivores is so high in these accumulations.

In faunal composition of the fossil assemblages, the two fluvial assemblages are more similar to each other than to either of the non-fluvial assemblages and vice versa. All assemblages are alike in the identity of the most abundant group (bovids) and of the least abundant groups (chalicotheriids). The middle ranks are more variable. The assemblages differ markedly in the frequencies of carnivores. In Taphonomic Assemblages III and IV especially, the frequencies of carnivores are high compared to the frequency (~1%) of carnivores among living mammals of a comparable size range in several modern East African ecosystems (Foster and Kearney 1967; Delany and Happold 1979). This pattern suggests that a high frequency of carnivore remains might be a general indication of biological concentration, again, probably by carnivores.

Skeletal-part composition

The taphonomic processes that characterize each facies association can be envisioned as episodes in the transformation of whole carcasses to an endpoint of miscellaneous elements that accumulated in channel scours. Fossils that were finally preserved in channel deposits could have been derived in part from earlier or contemporaneous floodplain or channel-margin assemblages (Behrensmeyer 1982). A plausible spectrum of transformation from no fluvial transport to prolonged transport and winnowing is whole mammal, Taphonomic Assemblage IV, Taphonomic Assemblage III, Taphonomic Assemblage II, Taphonomic Assemblage I. Directional changes in skeletal-part composition would be expected to track these successive taphonomic modifications. Table 10, in which skeletal-part categories are expressed as rank abundances, permits examination of this proposed transformation.

The transformation from average whole mammal to the untransported floodplain assemblage (IV) involves an initial marked depletion of phalanges and metapodials and a marked en-

richment of skulls, mandibles, and limbs. These changes can be proposed as the preburial, land-surface portion of the transformation of skeletal-part frequencies. Across the spectrum of fluvial transport, only vertebrae exhibit unidirectional depletion. This pattern matches the predicted and observed behavior of vertebrae in fluvial settings (Voorhies 1969; Behrensmeyer 1975, pers. comm. 1975). Podials and phalanges exhibit successive depletion from Taphonomic Assemblages IV to III to II and are then enriched in Taphonomic Assemblage I. Mandibles change irregularly. Patellae, ulnae, fibulae, and maxillae start and remain in low ranks.

With the exception of the pattern for vertebrae, these results do not support the concept of skeletal-part proportions that are generally diagnostic of sedimentary taphonomic histories. Vertebrae aside, the more common elements recur in each taphonomic assemblage, suggesting that rivers entrained and concentrated skeletal parts largely in proportion to their availability. The deviations of the four taphonomic assemblages from the average whole mammal are greater than that observed in the modern skeletal assemblage at Amboseli Park from the average whole mammal (Behrensmeyer and Dechant-Boaz 1980). Possibly, a specific suite of carnivores and scavengers imposes a distinctive alteration of original skeletal proportions in each community.

Body-size distribution

The distribution of individuals among the four size categories exhibits noteworthy variation in the smallest and largest size categories (Table 9). Taphonomic Assemblages I and II are similar in having an especially low representation of individuals from group A. This pattern may result from fluvial winnowing and abrasion; remains of smaller mammals were probably present initially but were selectively removed to be deposited elsewhere, probably not in concentration, or selectively destroyed by abrasion. Taphonomic Assemblages I and III have similar, low percentages of individuals from group D; both Taphonomic Assemblages II and IV have a slightly higher representation of large mammals. This pattern suggests a closer relationship between Taphonomic Assemblages I and III and between Taphonomic Assemblages II and IV

than has been indicated. If channel assemblages derived more skeletal material from channel margins than from floodplains and if flood deposits derived more material from floodplains than from other sources, then stronger resemblances should occur than are observed in the faunal composition of the relevant pairs of taphonomic assemblages. Above, I argued that many skeletal elements of mammals in group D were beyond the capability of extensive fluvial transport. This pattern may indicate that the original distribution of large-mammal remains increased with distance away from channels.

Conclusions

These preservational patterns, covering steps 1–4 of Fig. 1, have important implications for the reconstruction of original community composition. In order to specify original population sizes of Siwalik mammals, it is necessary to establish sampling distributions corresponding to taphonomic processes that shaped Siwalik fossil assemblages. It is useful to consider the criteria for selection of skeletal elements in this respect.

Taphonomic Assemblages I and II represent fluvial accumulations drawn from a broader temporal (and probably spatial) distribution than Taphonomic Assemblages III and IV. Probably all available habitats were sampled by Facies Association I, on the evidence of sedimentation patterns in a meandering fluvial system. The important characteristics of sedimentary particles in determining transportability are density, volume, and shape. It is unlikely that taxonomic identity per se exerted a direct influence on transportability. Rather, it is plausible that isolated skeletal elements or articulated sequences of elements of equivalent transportability were entrained according to their availability. If individuals contributed the same skeletal proportions to the death assemblages and if skeletal remains of all taxa were equally transportable, then fluvial assemblages could be considered without taxonomic bias in representing the original mammalian death assemblages.

On the basis of sedimentary context and patchy distribution, Taphonomic Assemblages III and IV are most plausibly interpreted as biological concentrations accumulated over relatively short time spans. These assemblages provide material of better quality than do

Taphonomic Assemblages I and II for taxonomic diagnosis of both cranial and postcranial elements. Even though the contribution of fossils from Taphonomic Assemblages III and IV to the total sample is low, certain taxa (e.g., some small carnivores) are known exclusively from these sedimentary contexts. If Taphonomic Assemblages III and IV were mainly the results of biological agents, then their taxonomic composition cannot be considered a reflection of the availability of living mammals but rather a reflection of the preferences of the agent(s) of accumulation. Modern bone concentrations that represent active accumulation by biological agents are primarily associated with predation and scavenging. Living predators and scavengers exhibit prey preferences on the basis of taxonomic identity, age, and health (Bertram 1979).

The predominant criterion for selection of skeletal remains in fluvial accumulations is probably body size, as reflected in the hydraulic characteristics of isolated skeletal elements. This criterion is indirectly related to taxonomic identity, in that taxa of different body sizes would have different probabilities of preservation in fluvial assemblages. The predominant criteria for selection of skeletal remains in biological accumulations are probably taxonomic identity and age of individual prey animals. Probabilities of preservation in these assemblages can only be estimated with information about the prey preferences of the different agents of accumulation and some ability to recognize fossil concentrations as products of specific agents—an unlikely prospect for Siwalik fossil assemblages.

In summary, the sedimentary environments of Siwalik fossil assemblages from the U-interval provide valuable information for paleocommunity reconstruction. Four sedimentary environments of bone accumulation are recognized. Taphonomic Assemblages I and II are hypothesized as fluvial accumulations on the basis of sedimentary environment per se and other taphonomic features. Taphonomic Assemblages III and IV are interpreted as largely biological accumulations, with carnivorous mammals as the most probable agents of accumulation. These assemblages contain the better material for taxonomic resolution. Given the criteria for selection outlined above, the fluvial accumulations con-

tain the better representations of original community composition, once the relationship between body size and probability of preservation can be specified (Badgley 1982). This is an unusual conclusion because transported assemblages have been traditionally considered poor sources of paleoecological information. It follows that community composition in the original Siwalik system can only be estimated at a relatively coarse level of taxonomic resolution. Nonetheless, even at a coarse level of taxonomic resolution, there is a critical difference between the taxonomic abundance of the fossil assemblage and original community composition whenever the probability of preservation varies among taxa on *any* basis.

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Appendix

Sediment Accumulation Rates for Estimating Time Span of Fossil Localities

For Facies Association I, the long-term sediment accumulation rates are most appropriate. The lateral and vertical extent of channel sandstones in combination with reactivation surfaces indicate persistence of channels with considerable internal reworking of sediments. I hypothesized that bone assemblages preserved in channel deposits were derived in part from bones already buried in channel-margin and floodplain deposits. If so, then vertebrate remains represent a time span proportional not only to the period of channel formation but also to the depth that channels have cut into floodplain deposits.

The bone assemblages of Facies Association II represent a longer time span than the period of deposition itself. Since Facies Association II represents flood deposits, the period of deposition may have ranged from a few hours to a few weeks. Bones entrained during passage of flood waters over channel-margin and floodplain surfaces would exhibit the time span of a land-surface assemblage, that is, on the order of decades (Hill 1975; Behrensmeyer and Dechant-Boaz 1980). If floodwaters derived material by erosion of floodplain deposits or carried bones from the bedload of channels, then the time represented by the final bone assemblage could increase by one or two orders of magnitude. Thus, I provided a temporal estimate independent of the thickness and inferred sedimentation rate of the source horizon. The estimate of 20–1,000 yr represents a range from the time span of a land surface assemblage to a generalized estimate of time

contained in <1 m of floodplain sediment (see below). For each locality, the overall estimate of duration reflects the number of coarse units present and the nature of intervening sediment.

For Facies Association III, deposition was episodic but without considerable erosion, nor are indications of long-term, stabilized surfaces present. Hence, the most appropriate sediment accumulation rates are those in the intermediate range for modern fluvial systems. Since such rates are quite variable (Schindel 1980), I used conversion factors spanning three orders of magnitude: 20–1,000 yr/m. The preservation of some primary depositional structures, the absence of erosional surfaces, and the absence of well-developed paleosols suggests that the lower end of this spectrum is most appropriate for individual fossiliferous layers.

Rates of floodplain sedimentation (Facies Association IV) varied widely. While sediment accumulation rates calculated for Siwalik sediments are about 1 m/2,000 yr (Behrensmeier and Tauxe 1982), there is evidence that local de-

position was both much slower and much faster. Rapid deposition is indicated by the very existence of certain fossil assemblages: the occurrence of partial skeletons of medium-sized mammals with uniform weathering characteristics suggests burial in <20 yr. Intermediate depositional rates are indicated by an unusual portion of the paleomagnetic record. An 11-m interval from Ganda Kas, sampled at 1-m intervals, contains a magnetic polarity reversal with transitional geomagnetic pole positions (Tauxe and Badgley 1984). Since geomagnetic reversals are considered to take a few thousand years, this sequence exhibits a pattern corresponding to about 500 yr/m. Hiatuses in sediment accumulation rates are indicated by some paleosol horizons. Zones of intensely developed pedogenic features represent inferred depositional hiatuses on the order of 1,000–10,000 yr (Leeder 1975; Bown and Kraus 1981). I used a range of conversion factors from 20–12,000 yr/m to encompass this variability.