Advances in Vertebrate Paleontology and Geochronology, edited by Y. Tomida, L. J. Flynn, and L. L. Jacobs, pp. 145–166. National Science Museum Monographs, No. 14, Tokyo, 1998

TAPHONOMY OF SMALL-MAMMAL FOSSIL ASSEMBLAGES FROM THE MIDDLE MIOCENE CHINJI FORMATION, SIWALIK GROUP, PAKISTAN

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Abstract This study focuses on taphonomy of small-mammal remains from the Lower Siwalik Chinji Formation in the stratotype area. From a stratigraphic interval about 20 m thick that extends laterally for 12 km, we prospected in all sedimentary facies for small-vertebrate concentrations. Thirteen sites were documented, most from facies representing abandoned floodplain channels. Screen-washed samples varied in richness, with sites yielding 0–256 identifiable small-mammal teeth. The sediment matrix ranged from fine conglomerate to silty clay. Based on sedimentological and taphonomic criteria, we propose that all concentrations were primary biological accumulations, in some instances with secondary fluvial reworking. Vertebrate predators were the probable agents of accumulation. The taxonomic composition of small-mammal assemblages varied little among sites; variation in lithology had no effect on the frequency of specimens at the family level. A mixture of arboreal, burrowing, and terrestrial small mammals was present; most species were terrestrial herbivores. Based on large and small mammals from the lower Chinji Formation, a seasonal woodland with riparian areas of forest was the likely vegetation.

Introduction

Species of small mammals (those less than ~1 kg in body weight) comprise at least half of the mammalian biodiversity of most modern terrestrial ecosystems, and rich mammalian fossil assemblages document this pattern throughout the history of mammals. In this study, we survey the depositional environments and taxonomic composition of small-mammal fossil assemblages from Neogene Siwalik fluvial sequences of Pakistan. The goals of the study are to characterize the taphonomy of small-mammal fossil assemblages, to evaluate variability in taxonomic composition of contemporaneous small-mammal assemblages from the paleoenvironments represented, and to infer ecological and taphonomic factors that created the patterns of preservation observed in this Siwalik sequence.

Sediments of the Siwalik Group (Fatmi, 1973; Shah, 1977; Willis and Behrensmeyer, 1995) form a thick Neogene molasse that accumulated on the southern margin of the

Himalayas and outcrop today in extensive but discontinuous exposures from Afghanistan to Burma (Myanmar). Locally, Siwalik sequences represent virtually uninterrupted deposition from the early Miocene to mid-Pleistocene. Siwalik vertebrate fossils have been documented since the nineteenth century. Siwalik sediments vary greatly in fossil productivity; the most fossiliferous areas studied to date are the Siwalik Hills, near Haritalyangar, India, and the Potwar Plateau of northern Pakistan (Pilbeam *et al.,* 1977). An outline of Siwalik mammalian biochronology was developed early in the twentieth century by Pilgrim (1910, 1913), Lewis (1937), and Colbert (1935a, b, c).

Since the mid-1970's, there has been renewed interest in Siwalik sediments as a record of fluvial response to Himalayan uplift and in Siwalik faunas as a South Asian theater of mammalian evolution. Siwalik sediments of the Potwar Plateau (Fig. 1) have been documented in terms of changes in sedimentary facies corresponding to Siwalik formations (Shah, 1977), lateral and vertical changes in the fluvial systems that produced the large-scale facies (Willis, 1983b), geochronology through paleomagnetic stratigraphy (e.g., N. M. Johnson *et al.,* 1982) and fission-track dating of ash layers (G. D. Johnson *et al.,* 1982), and stable-isotope geochemistry of paleosol carbonates and their paleoclimatic implications (Quade *et al.,* 1995). Siwalik faunas of the Potwar Plateau have been documented in terms of mammalian biochronology and evolution (e.g., Barry *et al.,* 1982; Flynn *et al.,* 1995), taphonomy and paleoecology of mammalian fossil assemblages (e.g., Badgley *et al.,* 1995), and faunal turnover in relation to paleoenvironmental change (Badgley and Behrensmeyer, 1995). Much of this work is still ongoing. Everett Lindsay was a major contributor to constructing paleomagnetic reference sections of the Potwar Plateau

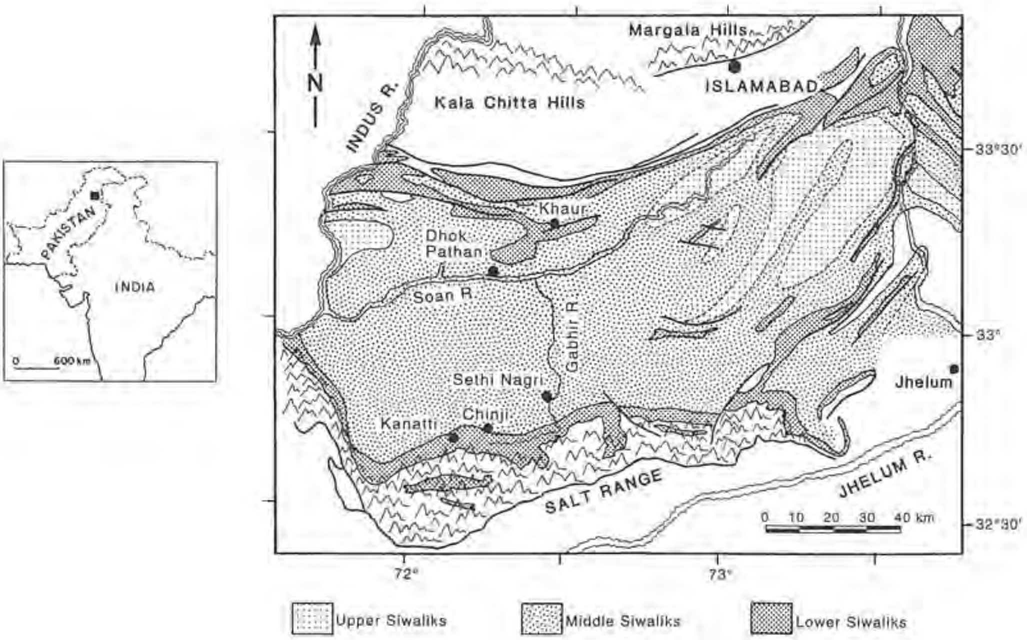

Fig. 1. Map of the Potwar Plateau with the distribution of Siwalik Group sediments. The study interval is southeast of Chinji village in the Lower Siwalik Chinji Formation.

(e.g., N. M. Johnson *et al.*, 1982) and establishing the taxonomy and biostratigraphy of Siwalik small mammals (e.g., Lindsay *et al.*, 1980; Barry *et al.*, 1982; Lindsay, 1988).

The earliest Siwalik biochronologies were based primarily upon large mammals (e.g., Pilgrim, 1913; Colbert, 1935b), because surface-collecting focused on them. Only when Lindsay and several of his students conducted intensive screen-washing campaigns did small primates, tree shrews, rodents, and insectivores emerge in large numbers from Siwalik fossil localities. A detailed picture of small-mammal systematics and biochronology followed (e.g., Jacobs, 1978; Flynn, 1982; Jacobs *et al.*, 1989; Lindsay, 1988; see also Flynn *et al.* (this volume)). Now, mammalian biochronology and faunal turnover from the Potwar Plateau are based equally on records of large and small mammals (Barry *et al.*, 1982, 1995).

Siwalik taphonomy has focused primarily on large-mammal remains (Badgley and Behrensmeyer, 1980; Raza, 1983; Badgley, 1986; Badgley *et al.*, 1995). This study is the first

Table 1. Small mammals known from the Chinji Formation, Potwar Plateau, Pakistan. All taxa listed have been recovered by us and our colleagues over the last 20 years, with the exception of *Sivacanthion*, reported by Colbert (1935c).

- Insectivora
  - Erinaceidae
    - *Galerix rutlandae*
    - cf. *Echinosorex* sp.
    - *Amphechinus kreuzae*
  - Soricidae
    - Large, gen. et sp. indet.
    - Crocidurinae, gen. & sp. indet. A
    - Crocidurinae, gen. & sp. indet. B
- Chiroptera
  - Small gen. & sp. indet.
- Scandentia
  - Tupaiidae
    - Gen. & sp. indet. A
    - Gen. & sp. indet. B
- Primates
  - Adapidae
    - *Sivaladapis* sp.
  - Lorisidae
    - Gen. & sp. indet.
- Rodentia
  - Sciuridae
    - Large Sciurinae, gen. & sp. indet.
    - *Eutamias urialis*
    - *Ratufa* sp.
    - *Heteroxerus* sp.
    - Petauristinae, gen. & sp. indet.
    - cf. *Hylopetes* sp.
  - Gliridae
    - cf. *Myomimus* sp.
  - Ctenodacytlidae
    - *Sayimys sivalensis*
    - *Sayimys chinjiensis*
    - *Sayimys* sp. B[1]
  - Thryonomyidae
    - *Kochalia geespei*
    - *Paraulacodus indicus*
  - Rhizomyidae
    - *Prokanisamys* cf. *P. benjavuni*
    - *Kanisamys indicus*
    - *Kanisamys nagrii*
    - *Kanisamys potwarensis*
  - Muridae
    - *Antemus chinjiensis*
    - *Progonomys* sp.
  - Cricetidae
    - *Dakkamys barryi*
    - *Dakkamys asiaticus*
    - *Paradakkamys chinjiensis*
    - *Dakkamyoides lavocati*
    - *Dakkamyoides perplexus*
    - *Punjabemys mikros*
    - *Punjabemys downsi*
    - *Megacricetodon aguilari*
    - *Megacricetodon sivalensis*
    - *Megacricetodon mythikos*
    - *Megacricetodon daamsi*
    - *Myocricetodon* sp.
    - *Democricetodon* A[2]
    - *Democricetodon* B-C
    - *Democricetodon kohatensis*
    - *Democricetodon* E
    - *Democricetodon* F
    - *Democricetodon* G
    - *Democricetodon* H
  - Hystricidae
    - *Sivacanthion complicatus*

Notes: [1]terminology of Baskin (1996); [2]*Democricetodon* species from Lindsay (1996).

to focus on small-mammal taphonomy. We examined a narrow stratigraphic interval from the Lower Siwalik Chinji Formation for both empirical and logistical reasons. First, small-mammals from the Chinji Formation have been collected from numerous stratigraphic levels, and the taxonomy of small-mammals is well established for most groups (Table 1). From the study interval, several rich fossil localities were known to have yielded large samples of both large- and small-mammal fossils before our study began. Second, paleomagnetic reversal boundaries and marker sandstones have been traced laterally for over 10 km within this part of the Chinji Formation (Sheikh, 1984; Johnson *et al.,* 1988). Also, a detailed lateral facies study focused on the distribution of paleosols in relation to channels and floodplains (Behrensmeyer, 1987; Behrensmeyer *et al.,* 1995).

The study interval lies in the lower third of the type section of the Chinji Formation (Fig. 2). Magnetic reversal boundaries, documented in multiple short stratigraphic sections, are tied into the Siwalik paleomagnetic reference section (Fig. 3; Johnson *et al.,* 1988). Correlation to the geomagnetic polarity timescale of Cande and Kent (1995) results in an age estimate of 13.7–13.4 Ma for the study interval.

Four sets of research questions guided this study. (1) In which facies are small-mammal assemblages found? How do the environments of fossil preservation compare to the range of originally habitable environments represented? (2) What agent(s) of accumulation created the small-mammal fossil assemblages? What kinds of preservation bias were introduced by these agents? (3) Is variability in the taxonomic composition and

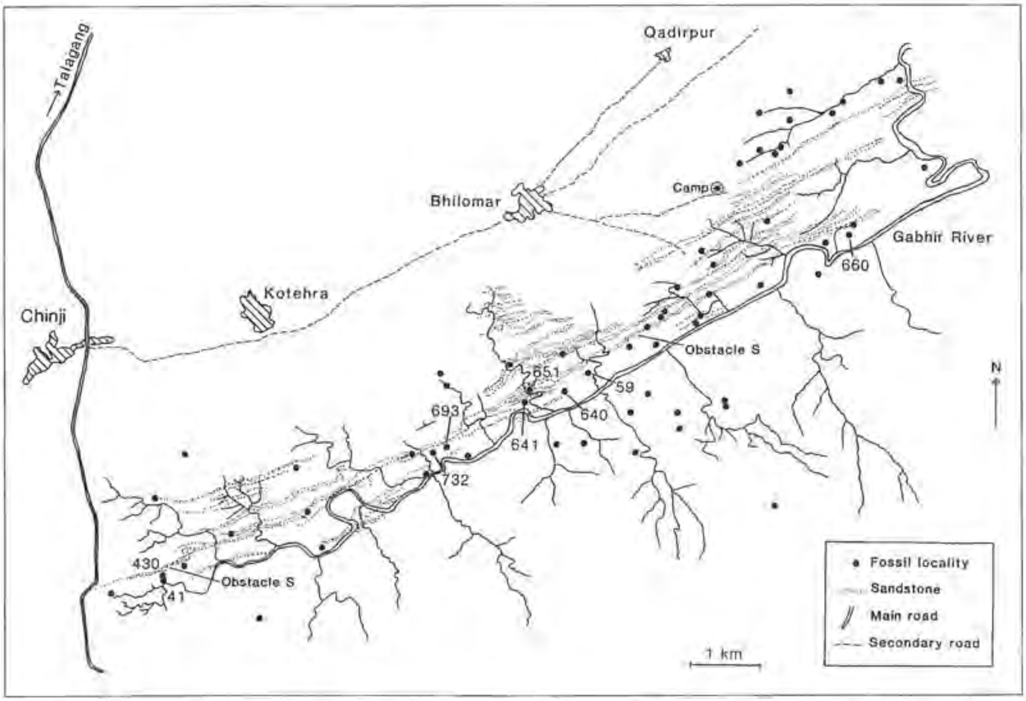

Fig. 2. Stratotype area for the Chinji Formation. The study interval extends from Locality 430 in the southwest to Locality 660 in the northeast. Only those localities sampled for this study are numbered.

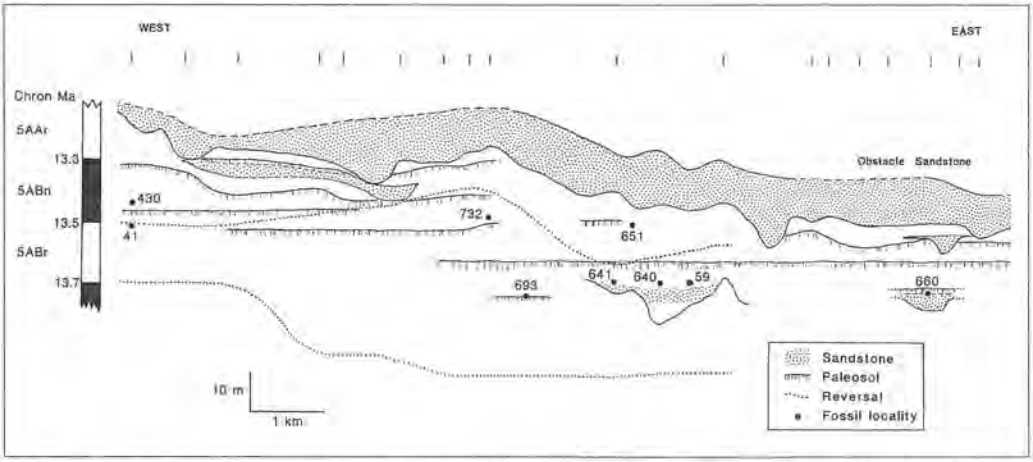

Fig. 3. Cross-section of the lower Chinji study interval. Small vertical ticks along the top indicate placement of stratigraphic sections for paleomagnetic sampling or lateral facies analysis. Lateral distribution of the Obstacle Sandstone and paleosols is based partly on the work of Sheikh (1984) and Behrensmeyer (1987). Geomagnetic timescale of Cande and Kent (1995).

abundance of small-mammal assemblages correlated with lithology? (4) What ecological diversity is represented in the small-mammal assemblages?

Methods

Methods include field work, identification, and analysis. Field work included the location of new collecting sites, collecting and processing matrix for fossil remains, and documentation of sedimentary environment(s) of each site. Downs completed the processing of matrix and preparation of fossils at the Bilby Research Center. Fossil specimens were identified by specialists working on the systematics of various small-mammal groups. Analysis focused on testing the statistical significance of variation in taxonomic composition among collecting sites.

Field work in Pakistan involved locating sites within the study interval, collecting sedimentary matrix, screen-washing bulk sediment samples, and preparing detailed stratigraphic sections for each collecting site. Sites were identified by resampling already known, productive localities with greater stratigraphic resolution and by finding new localities in different sedimentary facies. The study interval (Fig. 3) was selected to be about 20 meters thick and to extend laterally for about 12 km; these choices reflected a compromise between identifying a relatively narrow time interval and finding multiple samples from a range of sedimentary environments. Two lithological marker units, a thick sandstone known as the Obstacle Sandstone, which could be followed laterally for many kilometers (Fig. 2), and atprominent orange-brown paleosol, which could be traced laterally for at least 8 km, facilitated identification of the study interval. We prospected intensively the exposures of the study interval for localized concentrations of fossil vertebrate material, giving special attention to lithologies that were not well represented in earlier collections. In this manner, we identified nine localities with one or more strata containing small-vertebrate remains. Seven localities were situated within ~10 m above or below the orange-brown paleosol, and two more western localities were associated with a different, stratigraphically higher paleosol (Fig. 3).

Siwalik fossil localities are spatially discrete concentrations of fossil material, often with several laterally adjacent or superjacent strata containing concentrations (Raza, 1983; Badgley, 1986). When we found strata with promising matrix for screen-washing, we carefully traced out the productive layer and collected only matrix from that layer. From one to three productive strata occurred at each locality; each productive unit was treated as a separate sample during screen-washing and analysis. From nine localities, we collected 13 samples (Table 2). The amount of matrix collected for each sample depended primarily upon the density of fossil material and the extent of the productive unit. Our goal was to collect about 50–100 specimens (individual teeth or jaws) in each sample. Therefore, we collected more matrix from less productive sites and vice versa. In some cases, we collected the entire productive lens. Overall, the samples ranged from about 45 to about 1500 kg of matrix from the collecting units (Table 2).

Screen-washing of bulk sediment samples was conducted at the base camp in Pakistan. The wet-screening procedure was that described by McKenna (1962) and modified by Lindsay to use tandem screen boxes in order to separate coarse from fine concentrate. The finest mesh size was 0.7 mm. All matrix was washed twice. If the sediment was calcareous, it was soaked prior to one or both washings in a dilute solution of acetic acid (~20% of liquid volume). If the matrix contained a high quantity of clay, then concentrate from the first washing was secondarily disaggregated after soaking it in kerosene. The fine and coarse concentrates produced by two washings were returned to the laboratory of Downs. There, separation of particles by size was accomplished by immersing the coarse concentrate in

Table 2. Lithology, amount of matrix processed, and fossil productivity of collecting sites sampled for small mammals, lower Chinji Formation. Yield refers to the number of small-mammal cheek teeth recovered through screen-washing.

Collecting site	Lithology	Kg matrix processed*	Yield	Yield/kg matrix
41	Sandy silt and silty clay	1,485	16	0.01
59	Conglomerate	315	103	0.33
59a	Silty sand	225	79	0.35
430	Sandy silt + conglomerate	1,035	256	0.25
640b	Sandy silt + silty sand	585	64	0.11
640c	Silt + silty sand	68	10	0.15
641a	Sandy clayey silt + conglomerate	338	106	0.31
641c	Sand + sandy conglomerate	45	5	0.11
641d	Sandy clayey silt	45	0	0
651	Sandy clayey silt	1,305	150	0.11
660	Clayey sandy silt	225	6	0.03
693	Clayey sandy silt	90	1	0.01
732	Clayey silt	270	0	0
		Total: 6,031	796	

*assumes that one bag of matrix weighs about 45 kg heavy liquid (1, 1, 2, 2-tetrabromoethane), as described in Lees (1964) and Hauss and Airey (1980). Currently we use sodium polytungstate for heavy liquid separation. To remove the heavy liquids, the sorted concentrate was washed in acetone, dried under a fume hood, washed in ether, and dried in a vaccum oven. The final concentrate was examined for fossil content under a binocular microscope.

Fossil material from each collecting site, including mammalian teeth, mammalian postcranial material, and non-mammalian material, was sorted by Downs, who organized the mammalian teeth at the family level. Erinaceids were identified by Downs, soricids, chiropterans, sciurids, and glirids by us, ctenodactylids by Baskin (1996), thryonomyoids following Flynn and Winkler (1994), rhizomyids by Flynn, murids following Jacobs (1978) and Jacobs and Downs (1994), and cricetids (including dendromurines) by Lindsay (1988, 1996). We report family-level taxonomic composition of all the small-mammal assemblages and species composition for the sites with large samples.

Evaluation of the sedimentary facies at each collecting site involved preparation of a detailed stratigraphic reference section and documentation of the productive unit(s) within the lateral and vertical context of the larger-scale fluvial facies. The sedimentological and stratigraphic data recorded include lithology (grain size, sorting, texture, color), sedimentary structures such as cross-bedding, post-depositional structures such as bioturbation or nodule formation, the nature of contacts, the thickness and lateral extent of individual units, fossil content, orientation of fossils in the sediment, surface-damage patterns on fossils such as breakage or weathering, and lateral variation in these features. Figure 4a-g depicts stratigraphic sections for the 13 collecting units at nine localities. The sections themselves document much of the vertical dimension of the larger-scale context. Each sequence was traced laterally to determine the spatial scale and lateral variation of individual beds, as well as sequences of beds with a shared environmental context, such as channel-fill or floodplain paleosol. In the central third of the study area, we integrated our sections with those of the lateral facies study of Behrensmeyer (1987).

Analysis of the taxonomic composition of the small-mammal assemblages recovered from individual collecting units focused on two goals. First, we evaluated whether the taxonomic composition differed significantly among samples preserved in different lithologies, using an analysis of variance. This test can reveal differences in the habitats being sampled or in the effects of agents of accumulation that are correlated with lithology, such as fluvial transport. Second, we examined the relationship between sample size (number of identifiable teeth recovered) and taxonomic richness (number of families represented). This relationship can indicate whether differences in taxonomic diversity among samples could be due to sample size alone, compared with ecological or taphonomic factors.

Sedimentary Environments of Fossil Assemblages

The Chinji Formation consists of thick (~10-20 m), light gray, multi-storied sandstones that are separated by 30-40 m of maroon and red-brown mudstones (Willis, 1993a). Major sandstone sequences extend laterally for tens of kilometers and are interpreted as the major trunk channel of a braided fluvial system, comparable in scale to the modern Indus River. Flow directions are generally southeast, whereas the strike of the outcrops is northeast, so that exposures are nearly perpendicular to the average current direction of the major sandstones. Smaller-scale sandstones occur within the mudstone sequences; the latter are interpreted as the interfluve, floodplain deposits that include shallow lakes and subaerial regions. Pedogenic overprinting is common. The smaller-scale sandstones are considered to be floodplain tributary and distributary channels, on the order of tens of meters across (Willis, 1993a). In the study interval (Fig. 3), the Obstacle Sandstone is one of the major sandstone sequences of the lower Chinji Formation. The smaller-scale channels of Fig. 3 are floodplain channels. Below and above them are the mudstones and marls of the floodplain. Paleosols range from less than one to several kilometers in lateral extent; several kinds of paleosols can be recognized (Retallack, 1991; Behrensmeyer *et al.,* 1995; Quade *et al.,* 1995).

Table 3 and Figure 4 summarize the stratigraphy and interpretation of depositional environments of the 13 collecting sites. Interpretation of the sedimentary matrix took into consideration both the deposition of the individual bed and the broader stratigraphic context. Ten of the 13 collecting sites were from beds of mixed lithology within a heterogeneous sequence of silty sand, thin spatially restricted conglomerate lenses, and

Table 3. Lithology and environment of deposition of collecting sites, listed in order of occurrence from west to east in Figure 2. Environment of deposition is inferred from stratigraphic sections in Figure 4 and other information presented in text.

Collecting site	Lithology	Environment of deposition
41	sandy silt + silty clay	Channel fill with suspended sediment after channel abandonment; bioturbated
430	sandy silt + conglomerate	Small floodplain channel fill after abandonment; bioturbated
732	clayey silt + fine sand	Floodplain pond, fill from crevasse splay or sheetwash, followed by suspended sediment
693	clayey-sandy silt	Floodplain, suspended sediment; pedogenic overprint
641a	sandy-clayey silt + conglomerate	Abandoned-channel fill, mostly with suspended sediment; pedogenic overprint
641c	sand + sandy conglomerate	Sheetwash storm/flood deposit in abandoned channel
641d	sandy-clayey silt	Abandoned-channel fill with suspended sediment; pedogenic overprint
651	sandy-clayey silt	Pond with fine-grained fill from suspended sediment after channel abandonment
640b	silty sand + sandy silt	Sheetwash storm/flood deposit in abandoned channel; fine-grained fill from suspension
640c	silty sand + silt	Sheetwash storm/flood deposit in abandoned channel; fine-grained fill from suspension
59	conglomerate	Sheetwash storm/flood deposit in abandoned channel
59a	silty sand	Oxbow; storm/flood deposit in fine-grained fill from suspended sediment
660	clayey-sandy silt	Abandoned-channel fill with suspended sediment; pedogenic overprint

sandy-clayey silt above cross-bedded or massively bedded sandstones (Fig. 4a, c-g). These occurrences are all interpreted as part of the episodic filling of abandoned channels. The channels were the smaller floodplain tributary or distributary channels, not those of the main trunk river. In some instances (Localities 430, 651, 660), the channel was on the order of tens of meters across. In other instances (Localities 41, 641, 640, and 59), the overall channel belt was 2–3 km across. Localities 641, 640, and 59 occurred near the top of a large-scale landscape feature that extends laterally for several kilometers (middle of Fig. 3). This feature consists of a complex scoured surface, filled with gravelly sandstone and sandy silt overlain by mudstone containing small-scale scours with coarse- to fine-grained fill. A well-developed paleosol caps the sequence. Behrensmeyer (1987) interpreted this sequence as resulting from avulsion of the main river channel, scour of the floodplain surface, then relocation of the channel elsewhere on the floodplain. Subsequent channelized flow was intermittent and resulted in rapid aggradation with sand, sandy silt, and thin gravel layers. Figure 4e illustrates the channel-fill sequence. The intermittent nature of sediment accumulation is indicated by the numerous sharp contacts and abrupt changes in lithology upsection. Rapid accumulation is suggested by the preservation of small-scale sedimentary structures and very little bioturbation until fairly high in the sequence. (Most Siwalik sediments of mixed lithology are substantially bioturbated.) Other areas within the same scour feature show up to several vertical meters of accumulation of cross-bedded sandstone and conglomerate (Fig. 4d, f). As a low area on the floodplain, this abandoned-channel feature would have been a shallow floodplain lake for much of its existence. The presence of bivalves in some of the mudstone units near the top of the fill sequence (Fig. 4c, d) attests to the aquatic habitat. Paleosol overprinting of the fill sequence generally begins in the upper third of the sequence (Fig, 4a, e, f) but can extend lower (Fig. 4c, d). Capping the channel-fill sequence is typically a mature paleosol, indicating prolonged subaerial exposure of the surface.

Two additional depositional settings are represented at the collecting sites. Localities 732 and 693 occur in mudstone units within thick, fine-grained sequences (Fig. 4b). Neither site is in close proximity, laterally or vertically, to a floodplain channel. These environments are interpreted as interfluvial, periodically flooded land surfaces with most sediment settling from suspension. Locality 59a (Fig. 4f) is from a thin, laterally restricted sandy lens within a mudstone deposit near the top of a coarser-grained channel sequence. The mudstone deposit is quite localized and is interpreted as an oxbow or channel cutoff, temporarily isolated from the locus of channelized flow with bedload transport. The entire sequence (of Locality 59a and 59) is part of the fill of the large-scale scour described above.

In summary, most of the collecting sites were in the upper part of the fill sequence of small to large abandoned channels. Two sites were in floodplain mudstone deposits. One was in a channel cutoff or oxbow within an abandoned-channel fill sequence. Of the two floodplain sites, one yielded no identifiable small-mammal remains and the other only one (Table 2). Consequently, nearly the entire collection of small-mammal teeth from the study interval comes from abandoned channels. This skewed pattern of preservation does not result from failure to search other sedimentary facies extensively. We were aware that many of our sites were in abandoned-channel fills at an early point in our fieldwork and

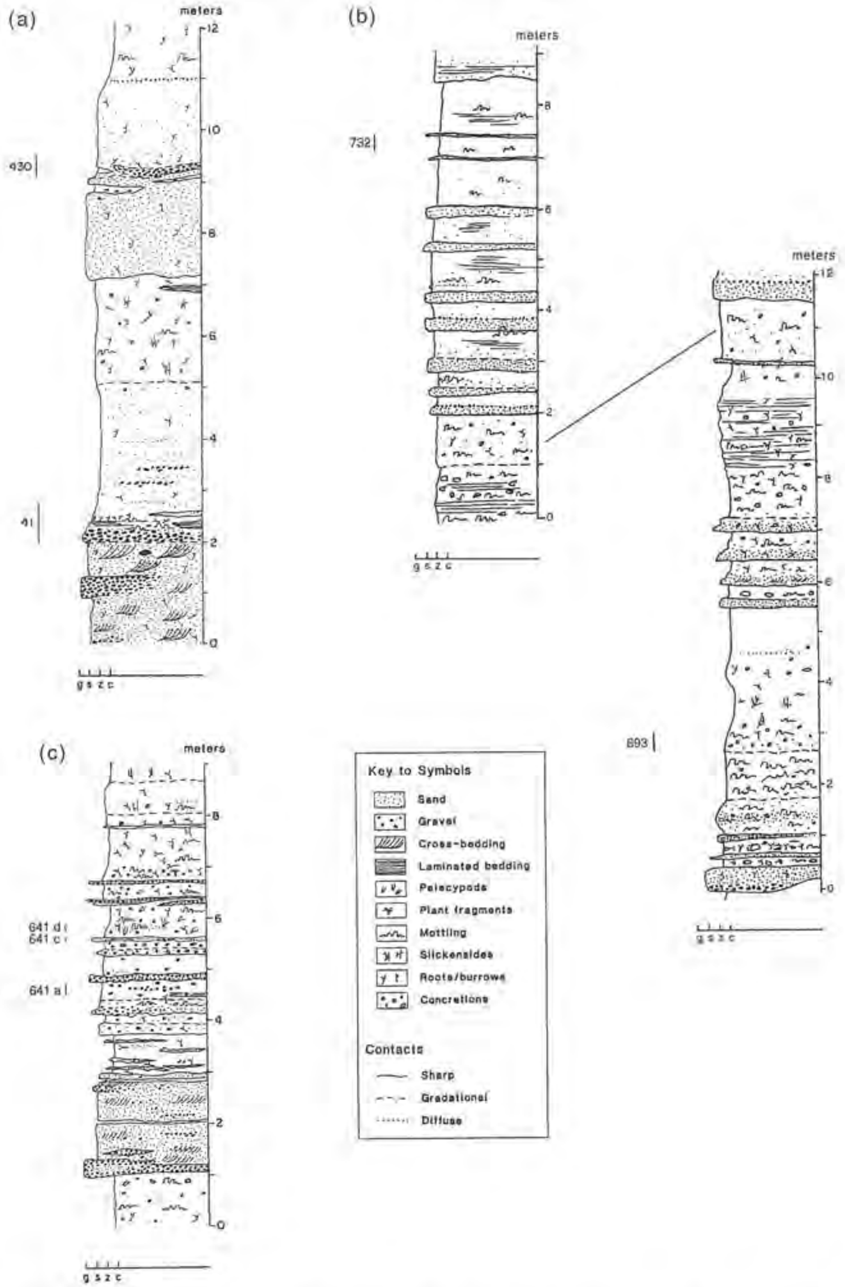

Fig. 4. Stratigraphic sections documenting depositional and post-depositional attributes of each collecting site. (a) Localities 41 and 430. (b) Localities 732 and 693. (c) Locality 641, with collecting sites 641a, 641c, and 641d. (d) Locality 651. (e) Locality 640, with collecting sites 640b and 640c. (f) Locality 59, with collecting sites 59a and 59. (g) Locality 660. Grain size scale is at the base of each section; g = conglomerate, s = sandstone, z = siltstone, c = claystone.

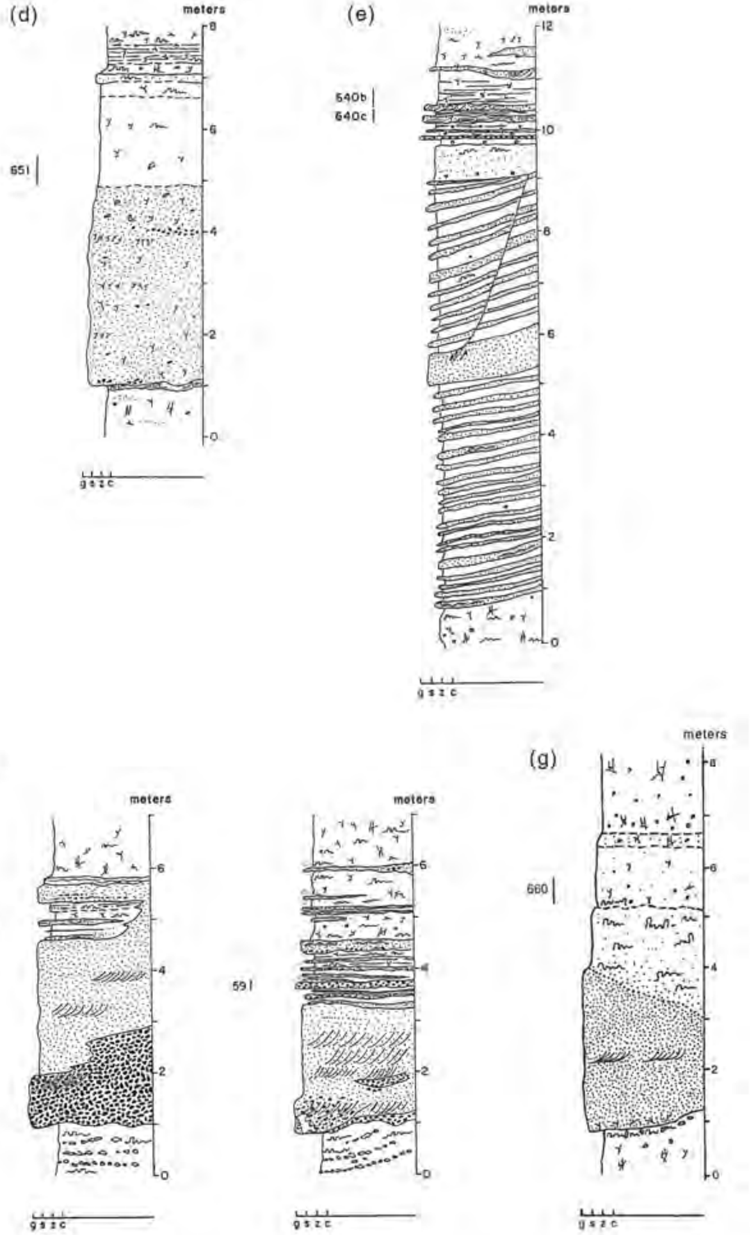

Fig. 4. Cont'd.

consequently devoted many hours to searching for fossil concentrations in other settings.

Several prevalent facies consistently lacked small-vertebrate concentrations. Thick, cross-bedded sandstones and conglomerates, interpreted as large- or small-scale channels, constitute about 30% of the section (Willis, 1993a). Thinly bedded marl units up to several meters thick, interpreted as shallow floodplain ponds and lakes, comprise about 10% of the section. Floodplain mudstones with pedogenic overprinting comprise about 60% of the section. In the study interval, we found no small-vertebrate concentrations in thick sandstone/conglomerates or in marls. We found two concentrations in floodplain mudstones (Localities 693, 732) but they yielded little. This pattern of small-vertebrate concentrations in abandoned-channel fill sequences may apply to the entire Chinji Formation in the stratotype area, since most of the small-vertebrate collecting sites fit a similar pattern as the one presented here. But there has been no attempt to survey systematically all sedimentary facies in other parts of the formation.

How does this restricted pattern of fossil preservation compare to the original range of habitable environments for terrestrial mammals? Some sedimentary facies represent depositional habitats that would not have supported terrestrial mammals, whereas other facies represent habitats that would have supported terrestrial species, at least during the low stage of the flood cycle. Table 4 enumerates the six major sedimentary environments of the Chinji Formation and their status as possible life habitats for terrestrial organisms. Depositional processes could have moved terrestrial organic remains from a habitat occupied in life to a habitat unoccupied in life. Just this kind of transfer characterizes many of the fossil assemblages of the Middle Siwalik Dhok Pathan Formation (Badgley, 1986). Table 4 also lists the habitats that could be represented through fluvial transport of organic remains to each of the six environments. The life habitats represented in autochthonous fossil assemblages are the environments themselves and potentially the edges of adjacent environments. Three of the six environments are potential life habitats for terrestrial organisms for a considerable part of the year. (All environments become aquatic during the flood season, Sheppe and Osborne, 1971). These three environments are levees, abandoned channels, and floodplain land surfaces. All three exist mainly as subaerial habitats and should sustain abundant terrestrial vegetation in multiple successional stages (Salo *et al.*, 1986). In the Chinji Formation, these environments preserve remains of small and large terrestrial mammals, although with unequal frequency – localities in levee and floodplain surface deposits are uncommon (Raza, 1983; Badgley *et al.*, 1995).

Fluvial transport can create fossil assemblages of allochthonous material or mixed allochthonous and autochthonous fossils in depositional environments that are not life habitats for the species preserved. In the Chinji Formation, mammalian fossil assemblages occur in channel and splay deposits by transport from other environments (Table 4). Remains of large mammals and large aquatic vertebrates dominate these assemblages. Deposits representing long-lasting, shallow floodplain ponds or lakes rarely contain fossils, and the scant fossil remains are generally those of aquantic vertebrates.

In summary, vertebrate fossil assemblages of the Chinji Formation occur in a wide range of sedimentary environments, although only two environments are highly productive (Table 4). Some represent the life habitats of terrestrial mammals and should contain autochthonous mammalian remains. Small-mammal fossil concentrations occur predominantly in this context. Other environments do not represent the life habitats of terrestrial vertebrates but are potential life habitats for aquatic vertebrates. Fossils of aquatic vertebrates in these habitats could be autochthonous, whereas mammalian fossils would be transported from other environments.

Table 4. Sedimentary environments, potential life habitats, and potential mixing of life habitats in fossil assemblages, Chinji Formation. Asterisks (*) indicate the most productive environments for vertebrate fossil assemblages.

Sedimentary environment	Potential habitat for terrestrial organisms	Habitats sampled in autochthonous assemblage	Other habitats sampled by fluvial transport	Fossil vertebrate assemblages of Chinji Formation
Active channel	no	aquatic, lotic; reworking of older sediments	Levee, oxbow, reworking of older sediments	T, A*
Splay	no	levee, floodplain	channel, levee, floodplain	T, A
Levee	yes	channel margin, edge of floodplain	channel, reworking of older sediments	T, t, A, a
Abandoned channel	yes	edge of pond, floodplain surface	ephemeral channel, oxbow, floodplain	T, t, A, a**
Floodplain land surface	yes	vegetated land surfaces	floodplain pond or lake	T, t (rare)
Floodplain pond or lake	no	shallow aquatic, lentic	floodplain land surfaces	A, a (rare)

T = large terrestrial mammals (>> 1 kg; bovids, suids, tragulids, proboscideans, carnivores, etc.)
t = small terresltrial mammals (< 1 kg; insectivores, rodents, small primates, etc.)
A = large aquatic vertebrates (crocodiles, turtles, large fish)
a = small aquatic vertebrates (frogs, small fish)

Agents of Accumulation

To assess the agent of accumulation of a fossil assemblage, we consider (1) whether fluvial transport is a likely factor, (2) whether fluvial transport is sufficient to explain the presence of a concentration, and (3) what the alternative agents of accumulation could be. Fluvial transport may be a factor when the fossils are of a size, shape, and density comparable to those of the particles in the sediment matrix. Fluvial transport is considered a sufficient explanation for the agent of accumulation when there is evidence that fossils have been gathered from different spatial sources and concentrated primarily by fluvial transport and sorting. Alternative circumstances of accumulation are biological and include mass death, burrows or nest sites, and predator activities.

The principal environment of preservation for productive small-mammal remains is abandoned floodplain channels (Tables 3-4). This environment is characterized by intermittent flow from temporary reactivation of the channel, sheetwash flooding after storms, and high water during the flood season. The microstratigraphy of this environment illustrates this variable flow (Fig. 4), with distinct thin layers that are laterally restricted and heterogenous in vertical sequence. Lithology changes over a wide range of grain sizes within individual units and abruptly between superjacent units. The lithologies of strata with small-mammal remains range from silty clay to conglomerate; and many strata contain mixed lithologies. In some instances, productive units of quite different lithology are superposed (e.g., 641c, d in Fig. 4c).

Samples from coarser lithologies yielded richer concentrations of small-mammal remains than from finer-grained lithologies (see yield/kg in Table 2). For the samples from conglomerates (59, 430, 641a, and 641c), the small-mammal teeth are within the grain-size range of other sedimentary particles, which include mudstone clasts and minor components of pedogenic nodules and bone fragments. Korth (1979) showed that the bones and teeth from a variety of rodents were hydraulically equivalent to quartz grain sizes ranging from fine to very coarse sand. The bone fragments and small teeth were dispersed within a silty-sand matrix, as were the inorganic clasts. Also, small-mammal teeth show no indication of abrasion, although a few are etched by acid. Hence, it appears that the organic and inorganic clasts were swept along together and that the final transport event was a surge of flowing water. However, the lateral extent of these conglomerate units and their stratigraphic context suggest that they contain material transported only a short distance. The lateral extent ranges from a few square meters to a few tens of square meters, and the maximum thickness ranges between 5 and 20 cm. There is no scour at the base of these units. Each is overlain by or mixed with a finer-grained lithology. At Locality 641a, the conglomerate is mixed with sandy-clayey silt through bioturbation (Fig. 4c). These features suggest that the conglomerates resulted from short-lived, highly localized pulses of fast-moving water. A possible scenario is that the beginning of the flood season or an intense rainstorm caused reactivation of flowing water in the abandoned channel; the first surge of water swept along debris (mainly mud chips, nodules from an eroding bank, plant and bone fragments) for a short distance (tens to hundreds of meters) and dropped the coarse sediment at a place where the water velocity fell (e.g., at an impediment or a bend in the abandoned channel). The key point here is that the small size of these units and their context outside of continuously active channel indicate a local source for the coarse sedimentary particles, including the small-mammal teeth. (In contrast, conglomerates within active channels are thicker, more laterally extensive, and situated within sandstones ≥ 2 m thick, as represented by the sandstone-conglomerate sequence from 0–2 m in Fig. 4a or from 1–3 m in Fig. 4f. Fossil assemblages from active channels are more likely to contain material harvested widely from the floodbasin, Badgley, 1986.)

It follows that the small-mammal remains from coarse units probably have not been transported very long or very far. Hence, it is likely that fluvial transport assimilated one or more pre-existing concentrations of small-mammal (and other organic) remains. Moreover, extended fluvial transport would more likely disperse pre-existing concentrations rather than maintain them (Hanson, 1980). If so, then other agents of accumulation were contributing to these concentrations. For insight into these other agents, we turn to the remaining localities.

In the other nine sampling units, the predominant lithology is silt with varying amounts of clay or sand (Table 3, Fig. 4). In these settings, the cheek teeth and occasional jaw fragments of small-mammals, as well as other small-vertebrate remains, mainly represent larger grain sizes than the range represented in the sediment matrix and are not likely to have experienced fluvial transport to the site. Rather, the organic remains were added as sediment accumulated or were added later and mixed in through bioturbation. Since the general environment of deposition alternated as an aquatic and subaerial habitat, biological agents could have contributed skeletel remains in several ways.

A mass death would have created a large array of many species. Depending upon the cause, carcasses would have been distributed over a wide area and would have included large as well as small-mammals. For the localities in the lower Chinji study interval, there is not a single land surface along which many fossils are distributed, although there is a narrow interval at the top of the large abandoned channel (Fig. 3, extending from Localities 641 to 59) that contains an unusually high density of fossils reprenting many species of large and small-mammals. Individuals are not represented by articulated carcasses, although there are articulated segments of some large mammals. Carcasses could have been in advanced stages of disarticulation before burial. The main discrepancy with this hypothesis is the localized nature of most fossil concentrations, especially for small-mammals. The productive stratigraphic units are usually only a few square meters in area, whereas a mass death that affected many individulas should have effect over a much larger area. The taphonomic data are not strongly consistent with this mechanism, but we cannot conclusively reject it.

A second way in which the localities could represent primary biological accumulations is through nesting sites on the ground, in burrows, or in trees. Most small-mammals have a focal area where young are born or food is stored. Most species of small-mammals are not social and do not live in multi-species groups, so that such sites, if preserved through sudden burial, would not result in multi-species fossil assemblages. The data for lower Chinji small-mammal assemblages are not consistent with this mechanism.

A third way in which biological processes could create small-mammal concentrations is through predation. Predators on small mammals from this ecosystem could have been avian, mammalian, or reptilian. Individual predators tend to concentrate on a subset of the species available and revisit feeding areas often. For example, a predatory bird may catch small prey from a wide area but revisit a perch or nest to consume the catch. Another way in which predators concentrate small-mammal remains is through defecation or regurgitation. For example, owl pellets and mammal scats are well-known sources of small-vertebrate remains and often contain parts from several individuals. Mammalian carnivores often have regular defecation areas as territorial markers, and birds of prey often use long-term feeding areas (Andrews, 1990). The composition and spatial distribution of small-mammal fossil assemblages from the lower Chinji Formation are consistent with this mechanism. The patchy distribution of remains, each patch occupying a very small area, the multi-species nature of each assemblage, and the fragmented nature of the fossil remains are all consistent with this mechanism of accumulation. In addition, some teeth show signs of etching by digestive acids. The main discrepancy with this hypothesis is that postcranial remains are relatively uncommon. Our experience suggests that their rarity does not result from destruction during the screen-washing process, since other quite delicate microvertebrate remains are numerous in the concentrate. Possibly, most of the postcranial elements were dispersed by water, harvested by other organisms, or differentially lost by weathering.

Two kinds of preservation bias are likely to result from predator accumulation. First is the general bias against smaller organisms because biological and physical processes destroy their remains more readily than remains of larger organisms. Second, individual predator species tend to be selective in the prey species taken (Andrews, 1990). A single species of predator is likely to have captured small-mammal prey from a subset of the species present. If several predatory species contributed to the small-mammal concentrations, then a greater diversity should be represented. We do not have information about the identity of the predator species. Regardless, if predators were the agents of accumulation, then the samples should be heavily dominated by the preferred prey species but not include all the species of small-mammals originally present. Both kinds of bias may explain why shrews and bats, groups that tend to be abundant where they occur, are poorly represented in the samples (Table 5, see below).

In summary, it is likely that all the concentrations examined in this study represent primary biological accumulations, some secondarily reworked by fluvial transport. For those rich concentrations from coarse lithologies, remains of several biological accumulations were probably mixed together during transport. The most likely biological agents to create these mixed-species concentrations are predators. Under this interpretation, some sites

Table 5. (a) Number of identifiable teeth for each family of small mammals from collecting sites included in this study). Sites with < 5 identifiable teeth (641d, 693, 732) omitted. For lithology, C=coarse (sandstone or conglomerate), F=fine (siltstone or claystone), M=mixed coarse and fine.

Site	41	59	59a	430	640b	640c	641a	641c	651	660
Lithology	F	C	F	M	M	M	M	C	F	F
Family										
Erinaceidae	0	12	9	6	7	2	21	0	7	2
Soricidae	0	3	0	1	1	0	1	1	0	0
Chiroptera	1	1	2	0	0	0	0	0	0	0
Adapidae	0	1	0	0	0	0	1	0	1	0
Sciuridae	0	14	4	11	5	1	7	1	9	0
Gliridae	0	5	1	1	1	0	1	0	0	1
Cricetidae	10	43	31	152	25	4	41	2	67	2
Rhizomyidae	1	15	7	36	12	2	5	1	39	0
Muridae	4	17	12	42	11	1	27	0	23	0
Ctenodactylidae	0	1	0	6	0	0	0	0	3	0
Thryonomyidae	0	0	1	1	0	0	1	0	1	1

(b) Results of analysis of variance of the effect of lithology (coarse, fine, mixed) on frequency of specimens in each of five families. (Six families omitted because of low overall frequencies) For all faunal variables, the degrees of freedom for main effect are 2 and for error are 7. Since the variance due to sampling error is greater than the variance due to the main effect, the F-ratio is low for all taxa. We cannot reject the null hypothesis that there is no effect of lithology on frequency of specimens at each site.

Faunal variable	SUM OF SQ EFFECT	SUM OF SQ ERROR	MEAN SQ EFFECT	MEAN SQ ERROR	F-RATIO	P-LEVEL
Erinaceidae	41.4	331.0	20.70	47.29	0.44	0.66
Sciuridae	28.4	191.2	14.18	27.32	0.52	0.62
Cricetidae	2,145.6	16,474.5	1,072.80	2,353.50	0.46	0.65
Rhizomyidae	44.1	1,829.5	22.05	261.36	0.08	0.92
Muridae	288.1	1,428.0	144.05	204.00	0.71	0.53

SQ=squares

represent feeding areas or territorial marking areas. We have not speculated on the identity of the predators. This would entail much larger samples and detailed examination of the fossils in the sediment matrix in order to document association, body parts, and bone-damage patterns; such data often permit recognition of certain classes of predators (e.g., Andrews, 1990). But this time-consuming procedure was not part of our sampling design.

Taxonomic Composition and Ecological Character

The taxonomic composition of the screen-washed samples, as represented by teeth identified to the family level, is summarized in Table 5a. Six of the eleven families are both uncommon in individual samples and absent from many of the samples. The five more abundant and widely distributed groups are erinaceids (hedgehogs), sciurids (squirrels), cricetids (hamsters), rhizomyids (bamboo rats), and murids (mice). In all but one sample, cricetids rank first in abundance. Murids and rhizomyids rank second or third at most localities. These counts should not be interpreted as a measure of the number of individuals in the samples at present.

Using an analysis of variance, we evaluated whether the lithology of the sample had an effect on taxonomic composition at the family level. This method partitions the variance in the data of Table 5a into that which can be ascribed to the main "effect" (lithology of the sampling unit) and that which results from unmeasured effects, including sampling error (Simpson *et al.*, 1960). Here, we are evaluating the effect of lithology on the frequency of specimens in different taxonomic groups. We omitted from this analysis the six most poorly represented groups. Lithologies were scored as coarse, fine, or mixed, based on the information in Table 3. The result (Table 5b) is that lithology has no significant effect on taxonomic composition at the family level. This finding is consistent with the interpretation that all the concentrations result from one mechanism of accumulation.

Sample size has the expected effect on taxonomic composition (Fig. 5): the correlation

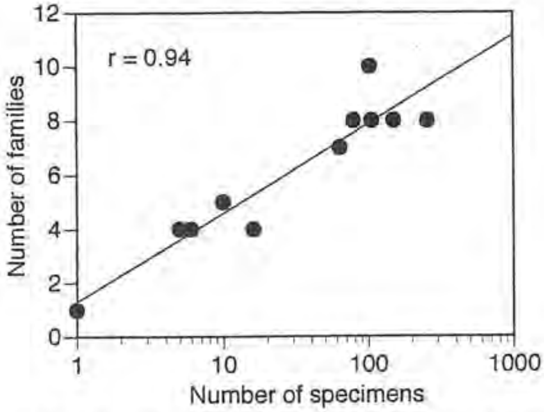

Fig. 5. Number of families of small mammals versus $\log_{10}$ of number of identifiable specimens (cheek teeth), based on data in Tables 2 and 5a. Pearson's correlation coefficient ($r = 0.94$) indicates a high correlation.

between $\log_{10}$ sample size and number of families is 0.94. Other than the sampling effect, there is relatively little variability in taxonomic composition at the family level among localities. At the species level for rodents only (Table 6), the five localities with the largest sample size record between 11 and 17 species. (Subsamples of some localities have been lumped in Table 6.) Fifteen of the 25 species listed occur at three or more localities. Hence, the taxonomic composition of rodent species is fairly consistent from samples distributed across the study interval.

Ecological attributes of the small-mammals can be inferred from dental morphology

Table 6. Taxonomic composition at the species level for rodents from five localities. "×" means present. We only list species present at one or more of the localities. "*n*" refers to the sample size of identifiable rodent teeth.

Locality *n*	59 154	430 243	640 64	641 78	651 142
Sciuridae					
Sciurid	×		×	×	
Eutamias urialis	×	×	×	×	×
Ratufa sp.					×
cf. *Hylopetes* sp.		×			
Gliridae					
cf. *Myomimus* sp.	×	×	×	×	
Ctenodactylidae					
Sayimys sivalensis	×	×			×
Thryonomyidae					
Kochalia geespei		×		×	
Rhizomyidae					
Kanisamys indicus	×	×	×	×	×
Kanisamys potwarensis	×	×		×	×
Muridae					
Antemus chinjiensis	×	×	×	×	×
Cricetidae					
Dakkamys barryi	×	×		×	
Dakkamyoides lavocati		×			
Punjabemys downsi	×	×	×	×	×
Punjabemys mikros		×	×	×	
Megacricetodon aguilari			×	×	
Megacricetodon sivalensis	×	×	×	×	×
Megacricetodon daamsi	×			×	
Myocricetodon sp.	×			×	
Democricetodon A	×				
Democricetodon B	×		×	×	
Democricetodon kohatensis	×	×		×	×
Democricetodon E	×	×			×
Democricetodon G		×	×		
Democricetodon H		×		×	×

and the habits of living relatives. The feeding habits represented include insectivory (hedgehogs, shrews, bats), frugivory-omnivory (small primates), and herbivory to granivory (rodents). The rodents all have low-crowned cheek teeth, although some lineages developed hypsodonty in the late Miocene (Flynn and Jacobs, 1982). In the lower Chinji (middle Miocene) assemblages, there are no conspicuous adaptations for heavy reliance on arid-season grasses. Based on the locomotor habits of modern representatives of each group, the small-mammals are primarily an assemblage of ground-dwelling species (although all small-mammals are scansorial in their locomotor capabilities). Arboreal species include the bat, small primates, and some of the squirrels. One of the squirrels was an Asian flying squirrel (cf. *Hylopetes*) and one was a giant squirrel (*Ratufa* sp.); extant species in these genera live in dense forest. All extant dormice are arboreal except species of *Myomimus* (Nowak, 1991), represented here. Some rhizomyids are burrowers and consume roots as a mainstay of their diets. Most extant murids and Old World cricetids are terrestrial (Nowak, 1991). Large mammals of the lower Chinji Formation include a few arboreal species (some of the small carnivores), but most of the diversity is in medium to large ungulates and proboscideans. Cenogram analysis of the body-size distribution of the entire mammalian assemblage from the lower Chinji Formation suggested seasonal woodland as the general vegetation type (Morgan *et al.,* 1995). Among both small and large mammals, fossil remains of the inferred arboreal species are rare, suggesting that areas of dense forest were restricted on the floodplain.

Conclusion

This is the first study of Siwalik small-mammals to focus on taphonomic issues. Intensive sampling of all fluvial environments within the lower Chinji Formation has documented concentrations of small-mammal remains primarily from only one of the six environments present (Tables 3–4). This environment is abandoned floodplain channels. Samples were taken from suitable matrix in floodplain mudstones, but these samples yielded no more than one identifiable fossil of small-mammals. In contrast, concentrated remains of large mammals are preserved in most of the environments present (Table 4).

This apparent restriction of small-mammal remains to one class of depositional environments surprised us. It is likely that small-mammals were widely distributed across the floodplain in the original ecosystem; if so, then processes of mortality, accumulation, and preservation were effective only in one depositional context. Abandoned channels have intermittent flow but fairly rapid rates of sediment accumulation. Possibly, it was the combined effects of biological accumulation and rapid fluvial deposition that resulted in this skewed pattern of preservation. Small-mammal remains in floodplain mudstones may also have been degraded by pedogenic processes.

All the small-mammal concentrations are likely to represent primary biological accumulations. A few assemblages experienced secondary fluvial mixing and transport. Vertebrate predators were the most likely agents of accumulation, and several individual sites probably represented long-term feeding areas or territorial marking areas. We do not know how many species of predator were involved, but likely there was more than one. The samples created in this manner should be dominated by the preferred prey species of the individual predators and are not likely to represent the full diversity of small-mammals in the original ecosystem.

The taxonomic composition of the small-mammal assemblages varied little among sites. The lithology of the concentration had no effect on taxonomic composition. As expected, there was a high correlation between sample size and taxonomic richness.

Ecological attributes of the small-mammals indicate a mixture of arboreal, terrestrial, and burrowing species. Most species were terrestrial herbivores. A seasonal woodland with riparian areas of dense forest would readily accommodate the small-mammals and the contemporaneous large mammals.

Future work in small-mammal taphonomy and paleoecology should include surveys of the depositional environments of fossil concentrations at older and younger stratigraphic intervals in the Siwalik sequence, study of skeletal elements and bone-damage patterns as a means of evaluating the predators that created the concentrations, isotopic analysis of enamel from selected rodents to evaluate C_3 versus C_4 grass consumption, and patterns of immigration, speciation, and extinction through the Siwalik sequence in relation to ecological attributes of small-mammals.

Acknowledgments

For help with fieldwork, we thank many members of the Harvard-Geological Survey of Pakistan Research Project. We especially thank those who contributed to screen-washing, including the donkeys who carried water to the wash sites, their drivers (pani-wallas), and the other "buckettes" (Alisa Winkler and Michèle Morgan) who helped to process many kilos of matrix. We also thank Everett Linfdsy for his contributions to our research. Kay Behrensmeyer provided a helpful review of the manuscript. This work was supported in part by grants from the Smithsonian Foreign Currency Program and the U.S. National Science Foundation.

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