Palaeogeography, Palaeoclimatology, Palaeoecology, 30(1980): 133—155

PALEOECOLOGY OF MIDDLE SIWALIK SEDIMENTS AND FAUNAS, NORTHERN PAKISTAN

CATHERINE BADGLEY and ANNA K. BEHRENSMEYER

Biology Department, Yale University, New Haven, Conn. 06520 (U.S.A.), and Duke Marine Lab, Beaufort, N.C. 28516 (U.S.A.)
Peabody Museum, Yale University, New Haven, Conn. 06520 (U.S.A.)

(Received August 1, 1979; revised version accepted October 30, 1979)

ABSTRACT

Badgley, C. and Behrensmeyer, A. K., 1980. Paleoecology of Middle Siwalik sediments and faunas, northern Pakistan. Palaeogeogr., Palaeoclimatol., Palaeoecol., 30: 133—155.

The Siwalik deposits of northern Pakistan are distinctive for their excellent sedimentary record and Neogene mammal faunas that include a family of hominoids, the Ramapithecidae. A 160-m interval was chosen from 3500 m of local section for study of lateral lithofacies variation, microstratigraphy and taphonomy of selected fossil localities. Field data consist of: (1) stratigraphic sections that span 30 km of lateral exposure, (2) microstratigraphic sections of fossil localities in representative depositional environments, and (3) taphonomic sampling of a subset of these localities. These data form the basis for landscape, habitat, and community reconstruction. The physiography of the paleoenvironment was determined by braided and meandering river channels. Lateral distribution of channel and floodplain deposits suggests that a mosaic of vegetation types covered the entire drainage basin, including constantly renewed plant successions along channel margins and more stable associations on floodplains. Vertebrate fossils occur in three major depositional settings: channel-lag, channel-margin swales, and floodplain land surfaces. Most collected fossils come from channel-lag conglomerates. The predominant taphonomic influence on the overall fossil assemblage from this interval has been fluvial transport and sorting resulting in a sampling bias toward medium-sized taxa. However, rank abundances from the fossil samples may be valid for these taxa. Fluvial processes probably harvested bones from all habitats present, but no habitat associations of major taxa are detectable. A relatively high species richness of small to medium ungulate herbivores suggests the presence of diverse vegetation types that probably included forest, woodland, and grassland. The ramapithecids were uncommon, medium-sized members of this community.

INTRODUCTION

Since 1973, a joint Yale Peabody Museum-Geological Survey of Pakistan (Y-GSP) Expedition has annually worked in fossiliferous sediments of the Siwalik Group in the Potwar Plateau of northern Pakistan (Fig.1). Preliminary reports from this expedition on paleontological, geological, and primatological results are in print (Pilbeam et al., 1977 a, b, 1979).

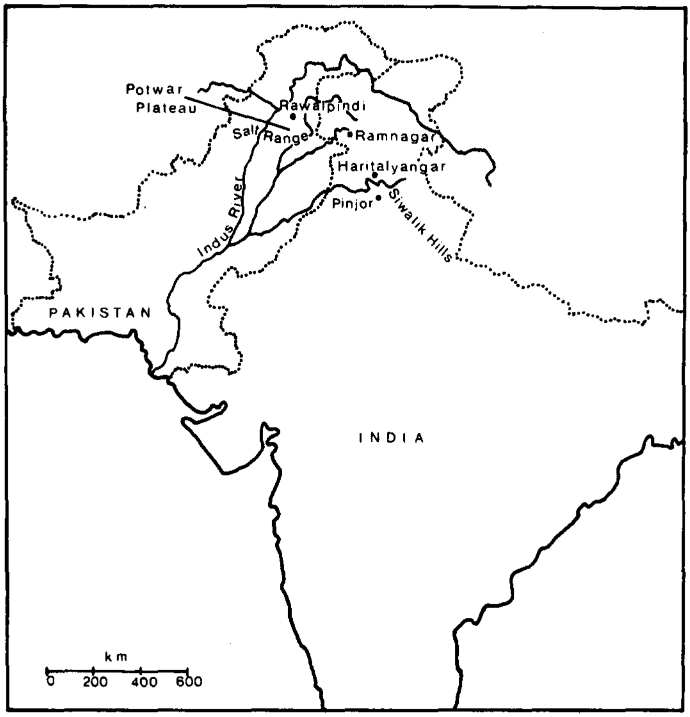

Fig.1. Map showing the relationship of the Potwar Plateau, which includes the Khaur study area, to the physiography of India and Pakistan.

One of several aims of the expedition is to reconstruct environments and communities for the mammalian fauna that includes *Ramapithecus* and other hominoid primates.

In the Potwar Plateau, southwest of Rawalpindi, over 3000 m of middle Miocene to Pleistocene, Siwalik sediments are exposed in recent river valleys that cut through a mantle of later Pleistocene alluvium. This area has been mapped and collected by vertebrate paleontologists for more than a century (e.g., Pilgrim, 1910, 1913; Lewis, 1937; Cotter, 1933; Gill, 1951). The sediments are primarily fluvial and consist of alternating sandstones and finer-grained lithologies ranging from clay to sandy silt. Both coarse and fine-grained lithofacies vary markedly in lateral and vertical distribution. The major fossil vertebrate groups present are turtles, fish, crocodilians, birds, and mammals: bovids, equids, suids, giraffes, gomphotheres, deinotheres, rhinos, tragulids, carnivores, rodents, chalicotheres, anthracotheres, and primates (Table I). Fossil plants are scarce, consisting of rare pieces of lithified wood, a few leaf impressions and carbonized fragments of vascular tissue. The status of pollen in these highly oxidized sediments is currently under investigation.

Previous interpretations of the broad physical and biotic environment

TABLE I

Faunal list of mammals occurring in the U sandstone interval compiled from lists of taxa documented in zones 5 and 6 of the Khaur area biostratigraphic succession (Pilbeam et al., 1979, J. C. Barry, L. L. Jacobs and B. J. MacFadden, pers. comm.) (The list is subject to revision)

- Primates
  - Lorisidae cf. *Galago*
  - Ramapithecidae
    - *Gigantopithecus* cf. *bilaspurensis*
    - *Sivapithecus indicus*
    - *Ramapithecus punjabicus*

- Insectivora
  - Erinaceidae
  - Soricidae
  - Tupaiidae

- Tubulidentata
  - Orycteropodidae
    - *Orycteropus browni*

- Rodentia
  - Sciuridae (4 taxa)
  - Gliridae
  - Ctenodactylidae
    - *Sayimys sivalensis*
  - Muridae
    - *Progonomys* sp.
    - *P. debruijm*
    - *Karnimata darwini*
    - *Parapodemus* sp.
  - Rhizomyidae
    - *Kanisamys sivalensis*
    - *Rhizomyoides* cf. *R. nagrii*

- Creodonta
    - *Metapterodon* sp. nov.

- Carnivora
  - Amphycyonidae
    - *Amphicyon* sp.
    - *Agnotherium* sp. nov.
  - Hyenidae
    - *Percrocuta carnifex*
    - *P. grandis*
    - *Progenetta* (2 species)
  - Felidae
    - *Paramachaerodus* sp.
  - Mustelidae
    - *Eomellivora* sp.
    - *Sivaonyx* sp.
    - cf. *Ischyrictis*
  - Viverridae
    - *Viverra chinjiensis*
    - Paradoxurinae
    - Herpestinae
    - Gen. nov.

- Proboscidea
  - *Gomphotheriidae*
    - *Choerolophodon corrugatus*
    - *Stegolophodon* sp.
  - Deinotheriidae

- Perissodactyla
  - Chalicotheriidae
    - *Chalicotherium salinum*
  - Rhinocerotidae
    - *Brachypotherium perimense*
    - *Chilotherium intermedium*
    - *Gandaitherium browni*
  - Equidae
    - *Cormohipparion theobaldi*
    - *"Hipparion" antilopinum*
    - ?*Hipparion* sp.

- Artiodactyla
  - Tragulidae
    - *Dorcabune nagrii*
    - *Dorcatherium majus*
    - *D.* sp. indet. (small)
  - Giraffidae
    - *Bramatherium megacephalum*
    - *Giraffokeryx punjabicus*
  - Anthracotheriidae
    - *Anthracotherium punjabiense*
    - *Merycopotamus dissimilis*
  - Suidae
    - *Tetraconodon magnus*
    - *Hippopotamodon sivalense*
    - *Lophochoerus nagrii*
    - *Propotamochoerus hysudricus*
    - *Schizochoerus gandakasensis*
  - Bovidae
    - *Miotragocerus punjabicus*
    - *Selenoportax vexillarius*
    - ?*Pseudotragus* sp.
    - *Elachistoceras khauristani*
    - *Gazella* sp.

have been based on published reports of fossil faunas and floras or on museum collections of sediment samples (Krynine, 1937) and fossils (e.g. Tattersall, 1969a, b; Prasad, 1971; Varishat et al., 1978), and not on paleoecologically oriented field studies. Both floras and faunas serving as the bases for these paleoecological reconstructions of the Miocene "Nagri" and "Dhok Pathan" faunas covered stratigraphic ranges of many hundreds of meters and several large collecting areas separated by hundreds of kilometers. Reconstructions of overall habitat were based primarily on the functional anatomy and presumed habitat of certain key taxa such as *Hipparion* (Tattersall, 1969a) or Aardvark (Lewis, cited in Krynine, 1937).

An ideal paleoecological reconstruction for terrestrial deposits would encompass geomorphic, edaphic (soil), floral, and faunal relationships through time. With such evidence, landforms could be inferred from sedimentation patterns; climatic regimes from geochemical and floral data; vegetation from pollen, cuticles and plant macrofossils; and faunal communities from large fossil samples, widely distributed through time and space. These data would serve as the basis for assessing species richness and relative abundance, environmental heterogeneity, ecological associations between animals and vegetation, and between animal taxa, and the consistency of these patterns through time.

These ideal conditions are not met in the Siwalik system, nor, in all probability, in any terrestrial deposit. In our Siwalik deposits, fossil plant remains are very rare, and attempts to recover plant remains (pollen, grass cuticles) have been unsuccessful; thus one of the most important paleoecological indicators is as yet inaccessible. Fossil animal remains occur in relatively small samples, although these are widely distributed through a thick sedimentary sequence. Geochemical work that might have climatic implications has not yet been done. There is however a great deal of information contained in the physical characteristics of the sediments and in the taphonomy of the fossil faunas. In this paper, we investigate how far such information can take us in interpreting middle Siwalik paleoecology.

We have examined the overall sedimentation across part of a large paleodrainage basin and detailed patterns of deposition and taphonomy of fossiliferous facies within this basin. Our work has focused on localities and sediments within a stratigraphic interval 160 m thick, laterally continuous over 30 km. The fauna listed in Table I occurs throughout this interval and is correlated with late Vallesian—early Turolian faunas of Eurasia (Pilbeam et al., 1977a; Pilbeam et al., 1979). Both fauna and strata represent, within a total local Siwalik section of 3500 m, a relatively small increment of time. Using paleomagnetic correlations, this interval is now estimated to be about 8.0 m.y. old (Tauxe, 1979).

Our reconstructions involve several assumptions that relate field data to interpretations. We assume that the depositional and distributional characteristics of the diverse lithofacies reflect the nature of fluvial systems from which they were derived, as well as morphological and hydrological characteristics of the drainage basin in which they accumulated. In the taphonomic properties of bone concentrations, we aim to identify some of the processes by which once-living animals have been selected to become fossils; this represents an attempt to define the limits of the faunal data-base for paleoecological reconstruction. In paleoecological reconstruction, we emphasize species richness, body-size distributions within trophic levels, relative abundance of taxa, and animal-habitat associations as important community descriptors.

Ultimately, we will address the following paleoecological questions:

(1) What taphonomic sampling biases have acted upon the original middle Siwalik community through processes of death, burial, and fossilization?

(2) What physical and vegetational habitats were present in the overall fluvial system?

(3) How can we characterize the mammalian community?

(4) Do mammalian taxa exhibit habitat preferences that are evident from the fossil record?

(5) What were the habitat preferences and community roles of specific taxa such as the ramapithecids?

LITHOFACIES

The goal of this component of the paleoecological investigation is to define the paleoenvironments in the drainage basin where middle Siwalik sediments and fossils were deposited. Evidence is drawn primarily from a series of fifteen correlated stratigraphic sections spanning 60 to over 100 vertical meters each and covering 30 km of nearly continuous lateral exposures. This portion of the middle Siwalik sequence occurs within the upper half of the total measured thickness of approximately 3500 m between Khaur Village and the Soan River (Fig.2). The stratigraphic interval used for detailed paleoenvironmental study lies in a transition zone between Nagri and Dhok Pathan facies, where it is not possible to map a distinct boundary based on published definitions of these formations (Fatmi, 1973). The stratigraphic relationships of the middle Siwalik formations are discussed in other publications (Pilbeam et al., 1977a; Pilbeam et al., 1979).

The portion of the Siwalik sequence discussed in this paper includes a distinctive marker horizon, the "U" sandstone. The U sandstone itself is a typical "blue-gray" sandstone (see below for characterization of these sandstones), with an extensive outcrop in the Khaur area. It has been a convenient reference horizon for many productive fossil localities, including the bulk of the primate localities in the Khaur area. In addition, a paleomagnetic isochron has been documented just below the U sandstone along much of its outcrop (Fig.3) (Behrensmeyer and Tauxe, in prep.). Thus, the U sandstone is minimally time transgressive along its lateral extent. We will refer to the sediments of a stratigraphic level which includes strata from

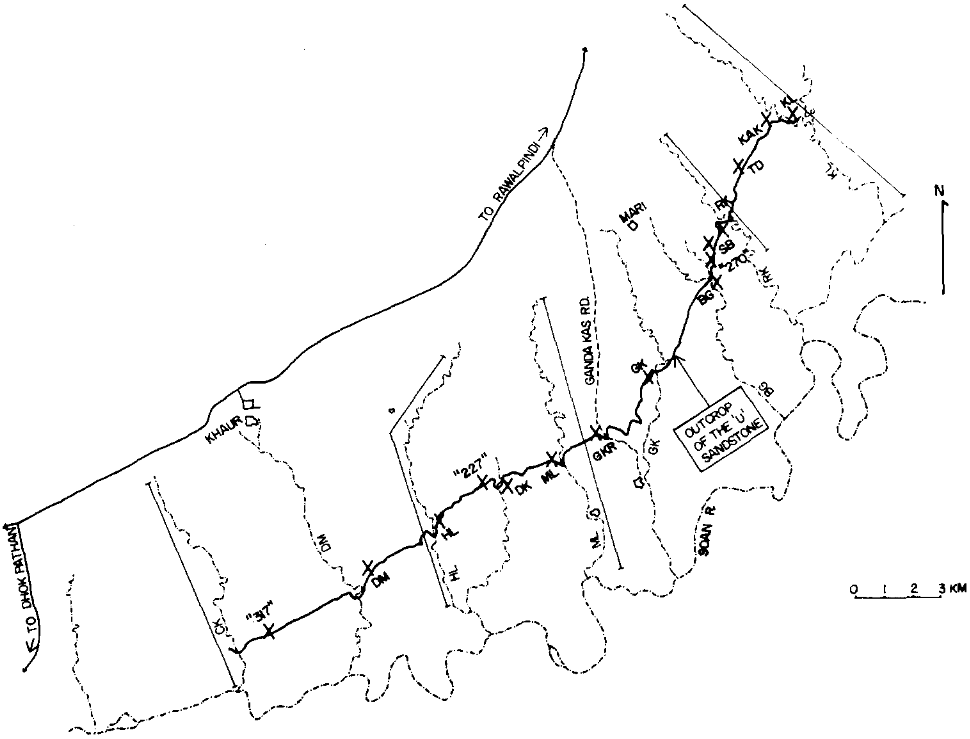

Fig.2. Map of the Khaur area, showing part of the north limb of the Soan synclinorium within which the middle Siwalik sediments are exposed. Straight lines indicate positions of long stratigraphic sections, and *X*'s mark the positions of the fifteen short sections through the U sandstone interval which were used for the lateral lithofacies study. In Figs. 2 and 3, lettered symbols are abbreviations for local valley names.

100 m below to 60 m above the U sandstone as the "U sandstone interval". This interval is representative of sedimentation patterns throughout much of the Khaur area sequence.

Lithological data consist primarily of field observations, with supplementary information from thin sections of selected sandstones. Observed sedimentary characters for both macro- and microstratigraphy include: texture, color, bedding characteristics and three-dimensional sedimentary-unit shape, rounding, mineralogy, evidence for bioturbation, diagenetic minerals (e.g. soil carbonates) and fossil content (vertebrate and non-vertebrate).

Sediments of the U sandstone interval consist primarily of sands and silts that occur either in discrete, well sorted units or in poorly sorted mixed lithologies. There are two common types of sandstone, designated informally as the "blue-gray" and "buff" sandstones. These differ markedly in composition as well as color, and each can be characterized by distinctive

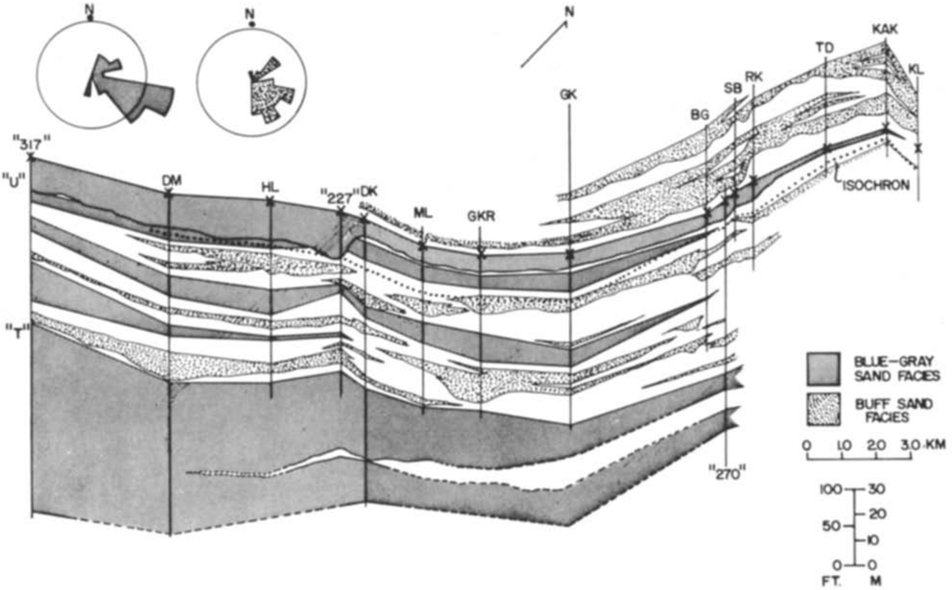

Fig.3. Fence diagram of strata within the U sandstone interval, constructed from stratigraphic sections measured along outcrops of the U sandstone. *X*'s refer to map points shown in Fig.2. The U sandstone is indicated at the left side of the figure. The isochron is a paleomagnetic datum that has been traced beneath the U sandstone. Rose diagrams summarize current directions measured on large scale (at least 2 m across) trough axes for blue-gray (27 averaged measurements) and buff-sand facies (21 averaged measurements) within the U sandstone interval. Note geographic separation and interfingering of the two facies.

sedimentary features. The blue-gray sands are typically coarse- to medium-grained, angular, clean, immature in composition with abundant, unweathered feldspars, ferro-magnesium minerals and metamorphic rock fragments. The buff sands are coarse- to fine-grained, with both rounded and angular grains, weathered feldspars, relatively few ferro-magnesium minerals and rock fragments, and typically poor sorting, with hematitic grain coatings and silty matrix.

Silts and silty clays are usually poorly sorted and indistinctly bedded. They range in color from drab gray to buff, brown, dark gray, yellow, red and red-orange. Primary limestones occur but are rare: laterally continuous, micritic units 10—20 cm thick are occasionally interbedded in the finer clastic sediments and marls are sometimes associated with the blue-gray facies. However, zones of carbonate nodules of varying diameters are relatively common in the silty lithologies, and reworked nodule-clasts are important components of some sand-gravel units.

The U interval sediments can thus be grouped into three broad lithofacies: the blue-gray sand facies, the buff sand facies and the silt—clay facies. Following paleoenvironmental interpretations are based on the vertical and horizontal relationships among these three lithofacies.

The blue-gray sands occur as discrete, laterally extensive, homogeneous units 10—50 m thick that interfinger with gray and red silts and consistently thin and pinch out toward the east and northeast (Fig.3). Mega-ripple structures (trough cross-stratifications up to 15 m across and up to 1.5 m thick) are common, and a sample of 27 current directions measured on the downstream directions of trough axes are dominantly oriented ESE (107°). This orientation is nearly perpendicular to the direction of maximum thinning (south to northeast, east of Ganda Kas, see Figs. 2 and 3), indicating that the blue-gray sands were laid down by a river system flowing from northwest to southeast. The river lay to the south of the Khaur area and periodically spread its deposits into this area. The sands occasionally include large-scale silt partings (meters to tens of meters in length) and lenses of mudclast conglomerate, but generally lack substantial cut-bank features. Well-defined fining-upward bedding sequences are absent. These characteristics indicate large-scale braided channels rather than meandering ones. Mineralogy and textural features of the sands indicate that the river drained areas with metamorphic basement rocks and high rates of physical erosion, as does the modern Indus River (personal observation). Causes of the periodic lateral spread of the sands are not yet understood, but may involve tectonic or climatic events in the upper part of the paleo-drainage system.

In contrast to the blue-gray sand bodies, the buff sands are generally not laterally persistent and show no tendency to pinch out in any particular direction. Most buff-sand units are 2—5 m thick, but some are up to 15 m. They are often complexly interbedded with silts, sandy clays and lenses of carbonate-nodule conglomerate. Laterally, buff-sand units are usually less than 2—3 km in width and often end abruptly with erosional cut-banks several meters in height. They also pass laterally into interbedded sand and silt over distances of several tens of meters. Sand bodies often show increased silt and clay content upward, but few instances of classical upward-fining, point-bar sequences (Allen, 1965; Leopold and Wolman, 1960) are present. Small-scale silt lenses and clay drapes (1—10 cm thick) are common and generally show deformation attributed to bioturbation. The sands are usually massive in outcrop, but weathered dipslopes reveal trough cross-stratified units 0.5—2.0 m thick and up to 10 m across. Twenty-one measurements of trough axes in the larger buff sand bodies show a dominant SE current direction (126°) with greater variability than in the blue-gray sands.

The characteristics of the buff-sand facies indicate that both meandering and braided channels were responsible for deposition, suggesting moderately sinuous rivers with fluctuating (e.g. seasonal) flow. There are numerous instances of apparent channel cut-off, but abandoned channels are filled with fine sand and silt and there is little evidence for deposition in bodies of standing water such as back-levee ponds or ox-bow lakes. The absence of pond deposits implies good sub-surface drainage of overbank areas, periodic (perhaps seasonal) lowering of the watertable, and rapid clastic filling of the abandoned channel troughs. Along any given horizon, channel lenses tens to hundreds of meters in width are typically separated by finer-grained overbank deposits for 1—2 km laterally, suggesting multiple contemporaneous channelways.

The silt-clay facies typically consists of units 1—5 m thick which can be traced laterally using color, texture and carbonate-nodule content for distances of up to several kilometers. Fine laminae are sometimes present in the better sorted silts and silty clays but usually are all but obliterated by bioturbation. Evidence for the latter consists of rootcasts and burrow-fills as well as disrupted laminae and non-homogeneous mixing of sediment textures. Nodules occur both dispersed through the fine-grained units and in distinct layers up to 1 m thick. They are generally composed of $CaCO_3$, but some spherically concentric examples appear to be dominantly hydrous iron oxides. Nodule sizes vary from less than 1 cm to about 5 cm in diameter. Beds of linked nodules or massive carbonate that can be identified as caliche or groundwater carbonate are rare and very local in extent.

The silt-clay facies clearly represents a fluvial overbank environment which must have included a variety of floodplain, swale and levee subenvironments. Nodule horizons and bioturbation indicate soil-forming processes, and the dominantly oxidized sediments imply relatively well-drained land surfaces. Successive silt—clay units appear to be conformable except where buff-sand channels cut into them locally.

The buff-sand and silt—clay facies are intimately associated in an interfingering and interbedded complex of vertical accretion deposits. Some large-scale buff sand channels apparently moved laterally across the floodbasin, removing previous sediments, but the overall pattern is dominated by smaller channels (tens to hundreds of meters across), of variable sinuosity and flow, that formed and were abandoned to reform elsewhere. The buff sand rivers bore large amounts of fine sediment which formed floodplain deposits. Overbank sedimentation was episodic enough to permit some incipient soils to form.

These interpretations are based on the U sandstone interval, but can be extended to much of the Khaur area sequence. Sedimentary episodes marked by widespread blue-gray facies occur throughout the lower 2500 m of the section. Episodes with alternating blue-gray and buff sand represent a long-term interfingering of two (or more) major fluvial regimes. The buff river system, with its generally thicker deposits, appears to have been more persistently present in the Khaur region. It is also more dominant toward the northeast, while the blue-gray facies is dominant toward the southwest — further evidence for the broad geographic relationships between the two river systems.

The paleoenvironments of Siwalik land surfaces in the Khaur area were thus primarily controlled by the buff river system(s). Multiple channels, swales formed in abandoned channels, and intervening areas of relatively flat floodplains characterized the topography inhabited by the Miocene faunas.

Shifting channels probably helped to create a pattern of heterogeneous environments and constantly renewed plant successions, including areas of relatively open ground along newly abandoned channelways or where flooding prevented vegetation other than grass from becoming well established. During the periodic spread of the blue-gray sands into the Khaur area, environments must have changed temporarily to a pattern of greater homogeneity, perhaps to broad plains of open grassland or swamp. The internal homogeneity and lateral extent of these sands also suggest that the river was not obstructed by dense vegetation (e.g. forests) while spreading sand over a conformable contact with the buff-sand and silt—clay facies.

MICROSTRATIGRAPHY

The aims of the microstratigraphic and taphonomic studies of selected late Miocene fossil localities are to determine the patterns of fossil accumulation, depositional environments associated with bone concentrations, and preservation biases affecting taxa and skeletal parts under different circumstances of accumulation. "Microstratigraphy" refers to the detailed field study of sediments on a small scale. Here the purpose of microstratigraphy is to interpret the depositional environments of specific fossil accumulations from sedimentary and stratigraphic features of these localities.

Detailed microstratigraphy was studied at 27 localities from the U sandstone interval. The number of collected fossil specimens from these localities ranges from 16 to 500, with an average of 133 specimens per locality. For each locality, the sedimentary and stratigraphic data include: identification of the fossiliferous units; lithology, geometry and sedimentary structures of fossiliferous layers and adjacent units, and post-depositional features such as carbonate nodules, trace fossils and other forms of bioturbation.

The results of the microstratigraphic study indicate that, while isolated fossil specimens (single bones or teeth) occur at low density throughout the sediments, fossil concentrations (defined as including more than one individual and/or ten or more identifiable specimens) are regularly associated with a subset of the many lithologies present. In the Khaur area, fossil concentrations are abundant in the buff-sand system and rare in the blue-gray sand system. In the buff-sand system they occur in all three major depositional settings: channels, channel margins and floodplains. Some localities, especially the richer ones, include more than one fossiliferous layer representing more than one depositional environment or sedimentation event.

The fossiliferous channel deposits, referred to as Type I fossil-bearing facies, are conglomerates within, or associated with, a cross-bedded sandstone unit (Fig.4). Conglomerates consist of variable mixtures of carbonate and/or ferruginous nodules, silt and clay pellets, algal onkolites, sand pebbles, bones, and occasional extra-formational pebbles. The source of

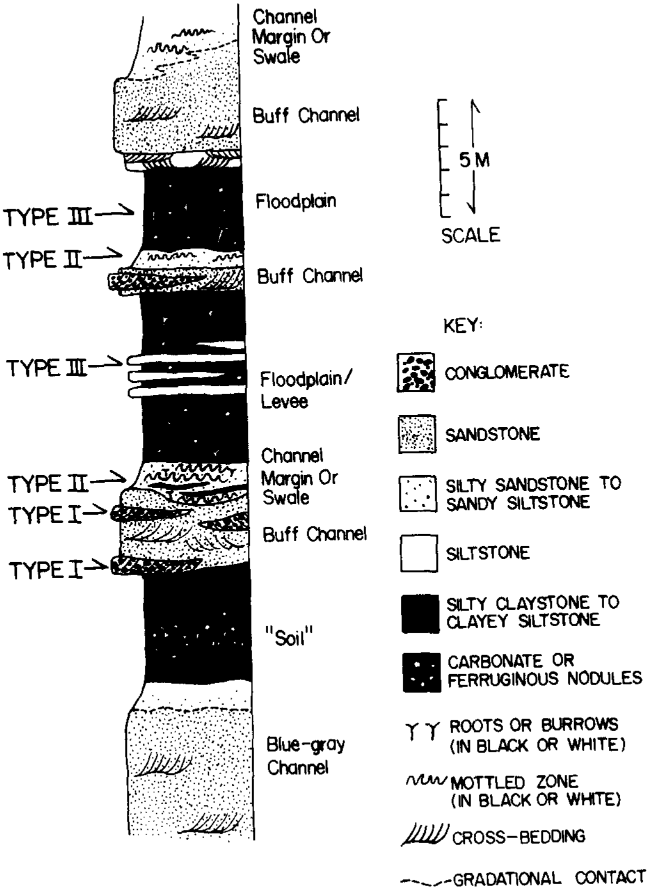

Fig.4. Schematic section showing the typical characteristics and relationships of Types I, II and III fossiliferous facies in the U sandstone interval.

most of the clasts is older sediments of the same fluvial system. The algal onkolites and onkolitic crusts probably are of quiet-water, fluvial origin (S. Golubic, pers. comm.). Both intraformational conglomerates and associated sandstones show well-developed cross-bedding and often distinct cut-and-fill trough structures and size-sorting of clasts. The fossiliferous layers vary from 0.2—2.0 m in thickness. Conglomerates are interpreted as channel-base or channel-bar lag deposits, formed primarily by erosion of penecontemporaneous, nodule-bearing, floodplain sediments.

The Type II fossil-bearing facies is lithologically complex and laterally variable over distances of only a few meters. The predominant lithology is silty sand to sandy silt, typically overlying a cross-bedded, buff sandstone. The sandy-silty layer is very heterogeneous in texture with extensive post-depositional bioturbation. Thin lenses of red-brown silty clay, extending laterally for several square meters, and contorted smaller mud drapes are common. Bioturbation features, consisting of mottled areas, burrow traces, footprints, and root casts suggest that these sediments were subjected to subaerial or very shallow water conditions permitting plant growth and animal habitation. The deposits are 1—2 m thick and pass upwards into finer-grained, more homogeneous silts and clays. Sometimes, these silty—sandy sediments lie within an original, topographic depression in the underlying channel sandstone. The fossil localities in such sedimentary contexts are interpreted as channel-margin swale or channel-fill sites.

The Type III fossil-bearing facies occurs in fine-grained lithologies that bear no regular stratigraphic relationship to sandstone units. The lithologies vary from silt to silty clay. While some of these units have finely laminated bedding, generally no bedding is evident in the fossil localities, and the predominant features are poor sorting, mottling, slickensides, carbonate nodules, root casts, and burrow traces. The carbonate nodules, bioturbation, and lack of primary depositional features indicate strong modification of the original sediment by subaerial processes, including plant and animal habitation and soil development. Type III fossiliferous sites are very localized spatially, encompassing a few square meters horizontally and usually about 0.5 m vertically. We infer that these localities formed on land surfaces that may represent local hiatuses in the vertical aggradation of the floodplains.

Among the 27 localities studied, 63% occur in the Type I channel facies, 22% in the Type II channel-margin facies, and 15% in the Type III floodplain facies. This pattern is also generally representative of over 100 other localities in the Khaur area. The channel localities (Type I) are usually the largest in terms of numbers of specimens, and the floodplain localities are typically the smallest — reflecting different processes of bone accumulation. Most of the collected Y-GSP specimens in this region thus bear the preservational biases associated with the Type I channel facies.

TAPHONOMIC FEATURES

The vast majority of Y-GSP expedition localities are characterized by surface fossil concentrations, and few are suitable for quarrying. We have taphonomically sampled twelve localities (Table II) from the U sandstone interval, collecting within measured squares or along transects all surface fossils identifiable to skeletal part or taxon. From these localities, we have the following information: (1) the sedimentary characteristics of the source strata for the fossils; (2) faunal composition for all elements identifiable to taxon (taxonomic level ranges from species to sub-order); (3) skeletal-part composition for all fossils identifiable to skeletal part; (4) matrix attached to fossils, evidence for primary weathering, breakage patterns, and signs of chewing; (5) occurrences of articulated parts; (6) generalized spatial distributions of bones. From these primary data, we have calculated the minimum numbers of individuals per taxon, based on teeth, postcranial

TABLE II

Taphonomic features of localities in different sedimentary environments

Loc.	Predominant sed. env.	Number of elements id. to taxon	Number of major groups present	MNI	Average number of elements/ individual	Range average number of elements/ind.
350	Type I	65	10	26	2.5	1—4
261	Type I	53	10	16	3.3	1—6
211	Type I	257	10	21	12.24	1—22.5
359	Type I	39	9	13	3.0	1—7
362	Type I	29	5	8	3.6	1—11.5
269	Type II	106	10	26	4.1	1—7.7
260	Type II	95	9	17	5.6	1—22
224	Type II	69	9	14	4.9	1—10
330	Type II	126	10	13	9.7	1—30
351	Type III*	15	1	1	15.0	15
270	Type III	114	6	13	8.8	1—20
262a	Type III*	40	1	1	40.0	40

Summary of certain taphonomic features from twelve taphonomically sampled localities within the U sandstone interval.
Taxonomic levels range from genus to order. "Major Groups" are as indicated in Table III. MNI, the minimum number of individuals, was determined for each locality on the basis of taxonomic affinity, body parts, and body size. The average number of elements/ individual = number of elements ID to taxon/MNI. In the last column, the average number of elements/individual (= number of ident. elements/MNI) was calculated for each major group separately, to show the variation in number of specimens/individual in relation to sedimentary environment. All localities are fossil "concentrations" except those marked by *, which are designated as "occurrences" (refer to text for definitions).

remains, and considerations of body size (using size estimates determined by comparing body parts such as teeth and limb ends of the fossil taxa with analogous modern taxa).

The taphonomic features of the localities studied can be discussed in relation to the three fossil-bearing facies. Localities occurring in Type I channel facies generally contain a wide array of taxa and skeletal parts. Skeletal-part composition is altered from the proportions present in average complete skeletons by a relative increase in teeth, long bones, metapodials, and mandibles, and a decrease in scapulae, skulls, vertebrae, podials (including astragali, calcanea), and phalanges. The condition of fossils varies from very weathered and abraded to fresh and complete. Many bones are broken, particularly those whose original shapes were long or platy; some of the breaks occurred before fossilization and some appear to be diagenetic. Generally, many of the major faunal groups are represented, spanning a body-size range from small carnivore to gomphothere. Overall, the number of bones per individual is influenced by sample size, as noted by Grayson (1978); however, for similar-sized samples, Type I localities consistently have relatively few bones (3—4) per individual. These features taken together indicate a mixture of transport histories and removal of more transportable bones, in accordance with sorting patterns determined by Voorhies (1969) and Behrensmeyer (1975).

Fossil concentrations in Type II facies (bioturbated, sandy silts) also exhibit a range of weathering states and taxa. Many bones are broken, and primary breaks that can be observed under matrix are both fresh and weathered. In some instances, signs of carnivory are notable, including tooth marks and very irregularly damaged, apparently gnawed, limb ends. Generally, the same major terrestrial vertebrate groups are represented as in the Type I facies, but the proportions differ somewhat. Groups that are consistently intermediate or low in abundance (e.g., carnivores, primates) in the channel facies may be abundant in Type II facies. Skeletal-part representation is similar to that of channel localities, but generally the number of specimens representing each individual is greater and has a wider range than in the channel localities, indicating differences in the amount of transport or winnowing between these two sedimentary environments. These numerical differences are related in part to the sample size at each locality (Table II).

The taphonomic features of the Type II channel-margin localities probably reflect a combination of fluvial and non-fluvial processes (e.g., predator accumulation); this interpretation is consistent with sedimentologic and geometric evidence indicating a bioturbated, topographic depression. Temporary shallow ponds and abandoned channels, perhaps some distance from a larger, permanently flowing channel, are possible reconstructions for this taphonomic setting.

Fossils found in the Type III floodplain facies have distinct preservation features that suggest lack of fluvial transport. This is the only facies in which skeletal parts are found clearly articulated. Some of these localities consist of associated skeletal material from one individual ("occurrences") and some are associations of single bones and partial skeletons, representing two or more individuals ("concentrations"). The skeletal-part composition per individual is variable, typically higher than in the previously described assemblages, and approaches that of articulated units in the original skeletons. Bones are often complete, and breakage can usually be clearly ascribed to diagenesis or original carnivore damage. Crushing and tooth marks may occur on several bones from one skeleton. Sometimes single bones and partial skeletons form a pile, suggesting accumulation by a predator, scavenger, or collector (e.g., porcupine), and not by water. These localities occur with both low and high taxonomic diversity. They are the source of several taxa that are rare or absent in coarser facies (e.g., lorisids, a tupaiid, a pangolin, and a number of small viverrids), a pattern that may result from the mode of death, preservation, or more directly from the habitats associated with the floodplain facies. Our present sample size of these localities is too small to allow us to choose between these alternatives.

Some general geological and biological processes can be inferred from the observed patterns of fossil accumulation. For the Type III localities, the bone-concentrating processes are interpreted as predominantly biological.

While the low-density "background" scatter of bones in Siwalik silt—clay facies probably reflects random processes of disarticulation and scattering of carcasses (Hill, 1979), concentrations of more than one individual on a land surface have a high probability of being non-random, i.e., due to a bone collector. Concentrations attributable to modern vertebrate collectors can often be distinguished on the basis of bone-breakage patterns, skeletal-part differences, and taxonomic composition (e.g., Brain, 1980 and in press; Hill, 1975, 1979). With further work, it should be possible to distinguish broadly between collecting agents (e.g., carnivores, rodents, birds of prey) in the Siwalik floodplain concentrations.

We feel that most channel-deposited bones were derived from floodplain land surfaces; thus, Type III localities represent potential pre-transport channel material. Recent work on modern surface skeletal assemblages (Behrensmeyer et al., 1979) suggests however that the more randomly dispersed bones on land surfaces (e.g. the Type III "occurrences" vs. "concentrations") are the major constituents of pre-transport, death assemblages. In the channel and channel-margin localities geological processes have obscured biological effects on the original death assemblage to varying degrees. Fluvial transport has sorted the death assemblage into lag-element concentrations of bones within a certain size range. The lag concentrations may have come about through the kinematic wave effect (Langbein and Leopold, 1968), by which large particles — bones, carbonate clasts, mud clasts — create local flow conditions that tend to concentrate other similar particles in bars along the channels.

FAUNAL COMPOSITION

The representation of major mammalian groups in ten channel and channel-margin localities is statistically (Mann Whitney U Test) rather homogeneous (Table III). In terms of ranking by minimum numbers of individuals, bovids usually predominate, equids often rank second, and other major groups — suids, elephants, rhinos, tragulids, giraffes — are subequally abundant. The rare elements are ramapithecids, anthracotheres, and chalicotheres. Carnivores are intermediate in abundance. The "common" taxa range in body size from about 5 to 3000 kg (small bovid to gomphothere), with ungulates in the size range 20—1500 kg represented by the greatest diversity of skeletal elements. Within this range, animals larger than about 200 kg tend to be represented only by teeth, fragments of teeth, podials, and fragments of large bones. Recovery of numerous very small (2 mm diameter) bone fragments in these localities indicates that the under-representation of small mammals is not solely an artefact of our surface-collecting technique but represents an actual preservational size bias against smaller species in these sedimentary facies or their low original abundances in the paleocommunity.

TABLE III

Rank abundances of major mammalian groups

Rank major group	1	2	3	4	5	6	Tot. loc.
Bovid	9(2)	1(1)					10
Equid	2(2)	4(4)	3(3)	1(1)			10
Suid		6(6)	3(2)	1(1)			10
Giraffe	1(1)	3(3)	4(4)		1(1)	1(1)	10
Rhino		3(3)	4(4)	1(1)	1(1)	1(1)	10
Tragulid		3(3)	3(3)	2(2)	1(1)		9
Proboscid.		2(2)	5(3)	1(1)		1(1)	9
Carnivore		6(5)	2(2)				8
Anthracoth.		2(2)	3(3)	1(1)	2(1)		8
Primate	1(0)	1(0)	2(2)	2(2)			6
Chalicoth.		1(1)	1(1)			1(1)	3

Rank abundances, in terms of minimum number of individuals, for 10 localities from Types I and II sedimentary environments. Bovids were most common (Rank 1) at 9 out of 10 localities and ranked second at one locality. Numbers in parentheses indicate the number of ties for rank that the specified taxon had with other major groups. The last column indicates the number of localities at which each group was present.

HOMINOIDS

Following the 1978 field season, the expedition had collected 103 hominoid (ramapithecid) specimens from twenty localities, all of which occur in channel and channel-margin facies (Types I and II). Typically, 1—3 specimens of hominoids represent 1—2 individuals at localities which have produced a large number of other specimens and taxa. Thus their presence is partly a function of sample size, as is true for other "rare" taxa over 5 kg in body size. Four localities have yielded five or more hominoid individuals, and at two localities of moderately large sample size (locs. 182 and 260: between 200 and 300 specimens identifiable to taxon), hominoids outnumber all other major groups in terms of minimum numbers of individuals. These two localities represent unusual taphonomic circumstances which are not yet clear. In general, patterns of occurrence and taphonomic features of hominoid remains in our present sample of fossil localities are similar to those of other uncommon taxa, and there is no suggestion of paleoecological or preservational biases associated exclusively with the hominoids.

DISCUSSION

Based on the evidence presented above, we offer the following discussion of the paleoecological questions specified in the introduction.

(1) What taphonomic sampling biases have acted upon the original middle Siwalik community through processes of death, burial and fossilization?

Both the largest and the most common fossil concentrations occur in channel-related deposits, the Types I and II contexts. We conclude from the characteristics of the sediments and fossils that the predominant biases in the fossilized death assemblages result from fluvial transport, sorting and accumulation. Such processes can explain the rarity of certain skeletal parts such as skulls and scapulae and of articulated material, the high percentage of fossils that are broken, and the representation of most individuals by very few bones. In these assemblages (and therefore in much of the Y-GSP collection), bones probably were harvested from an extensive catchment area that included many different habitats.

In the buff-sand system, lithological features indicate that conglomerates derived their clasts from contemporaneous floodplain deposits. Reconstruction of lateral paleogeography suggests that inter-channel distances were not great relative to channel widths; if so, then bank erosion and sheetwash during flood periods would have led to bone entrainment. Resulting bone accumulations would be likely to consist of transportable elements from all available floodplain and channel-margin habitats.

The largest "common" mammals from the U sandstone interval, rhino, giraffe, gomphothere and deinothere, are typically represented by relatively small fragments of bone and teeth and not by the larger bones in their skeletons. Animals less than 5 kg body weight are not common in any sedimentary environment (except in highly localized microfauna sites), probably due in part to selective, pre-burial destruction of small-animal remains (Behrensmeyer et al., 1979). Medium-sized animals between 5 and 200 kg predominate. One explanation of this pattern is that medium-sized animals were numerically dominant in the paleocommunity and provided most of the carcasses available for fluvial transport and burial. Alternatively, the skeletal remains of these mammals may have been hydraulically equivalent to the carbonate and mud clasts of the intra-formational conglomerates and therefore of optimal size to accumulate in the lag deposits of the fluvial system. Smaller bones were not deposited in these concentrations, and bones of the large animals either were not moved at all or were not trapped as lag. In this case, the fossil sample of the living community would be biased toward higher representation of medium-sized taxa. But *within* this size group, relative abundances of these taxa would more closely reflect original abundances of their skeletons. At present we feel that fluvial biasing processes relating to bone size were of considerable importance in creating the assemblages of medium-sized taxa. Any discussion of original relative population sizes must first consider the limitations imposed by this taphonomic factor.

(2) What physical environments and vegetational habitats were present in the overall fluvial system?

With specific reference to the U sandstone interval, the fluvial system that deposited the buff sands and associated silt—clay facies was characterized by low-relief floodplains and multiple shallow channels. Overall, the channels were probably braided, with meandering stretches where gradients were lower. Variation between braided and meandering patterns occurred both spatially and through time. Inter-channel areas included channel bars and islands of various sizes as well as larger floodplains with incipient to well-developed soils. Distances between major channel complexes probably did not exceed 5 km. During periods of high flow, most of the channels were active, with considerable sheetwash, bank erosion and channel-switching leading to rapid changes in local environments. These would have included, in addition to the major open channels and the broader floodplain areas, a mosaic of swales, levees, abandoned channels, and channel bars. Low areas probably were at least seasonally swampy but permanent ponds and lakes were uncommon.

The fluvial environments reconstructed above would determine general characteristics of vegetation and habitats available to the faunal community. Broader floodplain areas could have developed relatively mature plant communities adapted to the seasonal fluctuations in the water table, including periodic floods. The mosaic of environments associated with the channels probably would not have been conducive to continuous riparion forest; rather, this zone would have been characterized by patches of vegetation, perhaps representing a spectrum from forest and woodland—savanna to open grassy areas and seasonally vegetated mudflats. Without further information on the composition of the plant community, we cannot categorize the ecosystem as "predominantly forest, savanna, bush, etc." However, based on the physical components of the system, we do feel the evidence favors a mosaic of floral associations rather than a single dominant one.

The environments associated with the blue-gray sand system were relatively simple: broad areas of shallow, braided sandy channels with occasional mud-capped bars or mud-filled pools. Laterally, the channel system passed into low-relief levees and extensive back-levee ponds or swamps. The blue-gray river system in general seems to have been characterized by more continuous sediment movement and a more stable and higher water table than the buff-river system. Constantly shifting, sandy substrates and water-logged floodplains were probably not inhabited by a *complex* plant community during the periods of blue-gray sand deposition. Consequently, these areas probably supported less diverse, less abundant faunas than areas dominated by the buff-sand system.

(3) How can we characterize the mammalian community?

For the Miocene ecosystem represented by the U-interval fauna and geology, the vertebrate paleocommunity can most reasonably be defined as all species that inhabited the drainage system of the buff river paleo-channels in the Khaur Siwalik sequence. The area covered is broad, probably on the order of thousands of square kilometers, but any smaller divisions of the paleocommunity cannot be justified at present.

The mammalian paleocommunity of this drainage system included a minimum of 36 genera and 39 species > 5 kg and at least 20 smaller taxa (carnivores, primates, insectivores, rodents, etc.) (Table I). These taxa can all be considered "contemporaneous" in a geological or biostratigraphic sense, and most were probably ecologically contemporaneous as well, i.e., interacting members of the drainage-basin community at any given point in time. However, it is possible that ecological fluctuations with periods of tens, hundreds or thousands of years occurred, with attendant changes in the taxa that made up the vertebrate community. Such fluctuations are not discernible in the bone assemblages or their contexts, and some channel-lag fossil concentrations may represent time-averaging of tens to hundreds of years. Characterization of the paleocommunity therefore must encompass a relatively long period of time as well as a large area of land surface. It is difficult to compare the species richness of such a paleocommunity to that of a modern, time-specific community. However, the significance of the time-averaged fauna is that it consists of the sum of taxa adapted to the Siwalik fluvial system through the time period of the U sandstone interval.

On geological evidence, some fossil localities appear to represent short-term bone accumulations ($\leqslant$ several years). Taxa that repeatedly co-occur at these fossil localities can more surely be related to a contemporaneous community in the more time-specific, ecological sense; these include about fifteen species of ungulate between 5 and 3000 kg. Schaller (1967) records that in the Kanha National Park in India, eleven or more co-existing ungulate species were common in 1900, although only three are abundant now. The time-specific, ungulate, species richness of the Siwalik paleocommunity was probably higher than the highest recorded, recent ungulate species richness in the Indian subcontinent.

The herbivore fossil sample (excluding microfauna) can be characterized in terms of relative abundances and body sizes represented. We have suggested that the overall fossil sample is biased toward preservation of medium-sized animals by fluvial taphonomic processes. *Within* the medium-size category (5—200 kg), approximately 15 out of 19 ungulate species weighed less than 100 kg. The number of relatively small ungulates was thus considerably greater than in many modern savanna communities, particularly in comparison with those in East Africa (Lamprey, 1964; Coe et al., 1976).

The predominance of small- to medium-sized ungulates in the Siwalik fauna implies diverse vegetational niches suitable for such animals. This in turn points to a relatively complex habitat mosaic with abundant browse and cover, since smaller ungulates (at least bovids) tend to be more dependent on these resources than do larger ungulates (Jarman, 1974).

(4) Do mammalian taxa exhibit habitat preferences that are evident from the fossil record?

The reconstruction of paleoenvironments associated with the U interval indicates the possibility that clearly demarcated habitats existed, such as areas of continual fluvial disturbance along channel margins versus the more stable floodplains that might have supported more permanent vegetation. In addition, the dental morphologies of the mammalian herbivores suggest availability of diverse vegetation, including grasses for the high-crowned hipparions and browse for the rhinos, tragulids, and suids.

We have suggested that the channel-related fossil concentrations have harvested bones from all available habitats on channel margins and floodplains. The taxonomic co-occurrences in our present sample of localities do not indicate a preservation pattern representing distinct habitats; i.e., there are not "forest-fauna" localities or "grassland-fauna" localities. Rather, when several ungulates are present, grazers and browsers consistently occur together. This mixing of feeding types stands in contrast to a regular association of specific feeding and habitat types with a specific sedimentary environment, such as occurs in Plio-Pleistocene faunas of the Koobi Fora Formation, east of Lake Turkana. There, a dominantly browsing fauna was found associated with lake margin environments and a grazing assemblage with channels (Behrensmeyer, 1975).

The Middle Siwalik pattern of co-occurring grazers and browsers has several interpretations, some of which are mutually exclusive: (1) the co-occurrences may reflect fluvial mixing of death assemblages from distinctly separate habitats along a gradient from channel to floodplain, such as from open grassland along channel margins to closed-canopy forests on floodplains; (2) the mixing may reflect the original patchiness of vegetation, with canopied and open areas distributed unevenly over the land surfaces, and with areas sampled by bone-preserving, fluvial events being much larger than the size of any habitat patch; (3) there may have been one large, undifferentiated habitat that accommodated all the herbivorous feeding types, such as shrubland, open woodland, or wooded grassland. The paleoenvironmental evidence, on the basis of lateral variations in lithology, original drainage characteristics, and bioturbation, supports the second interpretation: a mosaic of vegetation types covering a multi-channeled alluvial plain.

The bone concentrations in floodplain deposits appear to represent nonfluvial accumulations, and occurrences of single skeletons or parts thereof may be the death sites of those individuals. Insofar as death sites reflect habitat preferences, these occurrences could represent animal-environment associations, but our sample is too small to detect ecological patterns. The floodplain localities with remains of several individuals probably reflect the preferences of the accumulating agent(s) rather than any original habitat associations.

(5) What were the habitat preferences and community roles of specific taxa such as the ramapithecids?

There are three lines of evidence that might elucidate the autecology of specific taxa in the middle Siwalik fauna. These emphasize more or less independent methods of paleoecological reconstruction that can be used in conjunction with evidence based on functional anatomy.

The first type of evidence is based on repeated associations between the taxon under study and a particular sedimentary context. If a significant pattern of association can be demonstrated, then this may be good evidence for habitat specificity, if taphonomic biases can be excluded. For the Siwalik mammals, we have shown that none of the taxa at present reveal such patterns, and that the habitat of each must be broadly defined as the drainage system of the buff-sand rivers. Within this broad habitat, ramapithecids were relatively uncommon components of the mammal community, judging from their low abundance as fossils in assemblages dominated by similar-sized taxa.

A second line of evidence lies in repeated associations between a given taxon and others with habitat requirements that can be interpreted from anatomical considerations. We have not yet fully explored such evidence for Siwalik taxa. It appears that hominoids may be more frequently associated with carnivores in the sample of fossil localities, but this is partly a consequence of the large sample size required for representation of both of these rare taxa. Of greater significance is the broad-scale association of the ramapithecids with a community characterized by many species of small ungulates. The ecological implications of this invite further investigation. In their co-occurrences with ungulates of different food preferences, the ramapithecids provide no specific clues concerning their own diet or habitat.

A third line of evidence lies in broad-scale comparisons through time of the faunal assemblages that include a taxon of interest with those that do not. This biostratigraphic approach is underway. We will be able to compare the U sandstone interval, in which hominoids are present, with other stratigraphic intervals where they are absent, for clues to indicate why they appeared and disappeared (e.g., changes in preservational biases, or changes in body-size distributions in the paleocommunities).

None of these lines of reasoning are likely to provide answers to specific questions such as whether *Ramapithecus* lived in the forest, the woodland, and/or the grassland. It is likely that the answers to these questions would not be simple even if fossil hominoids were alive today. Species habitat preferences and tolerances may fluctuate diurnally, seasonally, or change in response to environmental or community changes over a longer time. The fluvial taphonomic biases do not permit a clear resolution of the habitats of any middle Siwalik taxa. The same biases do not necessarily characterize paleocommunities elsewhere. Ultimately, understanding the structure of the overall paleocommunity will provide the most informative perspective on the roles of specific taxa such as the early hominoids. Approaches such as that of Andrews and Evans (1979), using ecological diversity spectra, may indicate valid modern analogues.

CONCLUSION

The fossil assemblages of the U sandstone interval have been strongly modified by fluvial processes which probably have caused an overall sampling bias toward better preservation of medium-sized taxa. These fluvial processes also served to "harvest" bones from a wide area, so that the fossil assemblages taken together are representative of the species that made up the overall community in the drainage basin through time. Relative abundances, at least by rank order, are probably valid for medium-sized taxa, but not for those outside this size range. The members of the community inhabited a diverse set of fluvial environments, probably characterized by a mosaic of vegetation types from forest to woodland to open grassland. The mammal community was dominated by medium to small herbivore species with a wide range of dietary preferences. The ramapithecids, herbivores near the lower end of this size range, were uncommon but persistent members of the community at least throughout deposition of the U sandstone interval, a time period perhaps on the order of a few hundred thousand years.

This is a preliminary report. Study of Siwalik paleoecology continues and is the focus of doctoral dissertation research by CB.

ACKNOWLEDGEMENTS

We thank all members of the joint Yale University-Geological Survey of Pakistan research group for their advice, support and cooperation, especially our co-leaders, David R. Pilbeam and Ibrahim Shah. Our taphonomical field work was ably assisted by John Barry, John Damuth, Mahmood-ul-Hassan, Andrew Hill, Bonnie Lipschutz, Mahmood Raza and Lisa Tauxe. We thank David Pilbeam, Lou Jacobs and Bruce MacFadden for comments on early drafts of this paper. The work has been supported throughout by the National Science Foundation and the Smithsonian Foreign Currency Program: current grants are NSF BNS 5984 and SFCP FC80254100.

REFERENCES

Allen, J. R. L., 1965. A review of the origin and characteristics of recent alluvial sediments. Sedimentology, 2: 93—114.

Andrews, P. and Evans, E. N., 1979. The environment of *Ramapithecus* in Africa. Paleobiology, 5: 22—30.

Behrensmeyer, A. K., 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. Bull. Mus. Comp. Zool., 146: 473—578.

Behrensmeyer, A. K. and Dechant, D. E., 1980. The recent bones of Amboseli Park, Kenya, in relation to East African paleoecology. In: A. K. Behrensmeyer and A. Hill (Editors), Fossils in the Making. University of Chicago Press, Chicago, Ill., 330 pp.

Behrensmeyer, A. K. and Tauxe, L., in prep. Isochronous fluvial paleoenvironments in Miocene Siwalik deposits of northern Pakistan.

Behrensmeyer, A. K., Western, D. and Dechant Boaz, D. E., 1979. New perspectives on paleoecology from a recent bone assemblage. Paleobiology, 5(1): 12—21.

Brain, C. K., 1980. Some criteria for the recognition of bone-collecting agencies in African caves. In: A. K. Behrensmeyer and A. Hill (Editors), Fossils in the Making. University of Chicago Press, Chicago, Ill., 330 pp.

Brain, C. K., in press. The Hunters of the Hunted: an Introduction to African Cave Taphonomy. University of Chicago Press, Chicago, Ill.

Cotter, G. de P., 1933. The geology of the part of the Attock District west of longitude 72° 45′ E. Geol. Surv. India Mem., 55: 63—161.

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

Gill, W. D., 1951. The stratigraphy of Siwalik series in the northern Potwar, Punjab, Pakistan. Q. J. Geol. Soc. Lond., 107: 375—394.

Grayson, D. K., 1978. Reconstructing mammalian communities: a discussion of Shotwell's method of paleoecological analysis. Paleobiology, 4(1): 77—81.

Hill, A., 1975. Taphonomy of Contemporary and Late Cenozoic East African Vertebrates. Thesis, University of London, London, 331 pp. (unpublished).

Hill, A., 1979. Disarticulation and scattering of mammal skeletons. Paleobiology, 5(3): 261—274.

Jarman, P. J., 1974. The social organization of antelope in relation to their ecology. Behavior, 58(3, 4): 215—267.

Krynine, P. D., 1937. Petrography and genesis of the Siwalik series. Am. J. Sci., 34: 422—446.

Lamprey, H. F., 1964. Estimation of large mammal densities, biomass and energy exchange in Tanargire Game Reserve and the Masai Steppe in Tanzania. E. Afr. Wildl. J., 2: 1—46.

Langbein, W. B. and Leopold, L. B., 1968. River channel bars and dunes — theory of kinematic waves. U.S.G.S. Prof. Pap., 422-L: 1—20.

Leopold, L. and Wolman, M. G., 1960. River meanders. Bull. Geol. Soc. Am., 71: 769—794.

Lewis, G. E., 1937. A new Siwalik correlation (India). Am. J. Sci., Ser. 5, 33: 191—204.

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

Pilbeam, D., Meyer, G. E., Badgley, C., Rose, M. D., Pickford, M. H. L., Behrensmeyer, A. K. and Shah, S. M. I., 1977b. New hominoid primates from the Siwaliks of Pakistan and their bearing on hominoid evolution. Nature, 279: 689—695.

Pilbeam, D. R., Behrensmeyer, A. K., Barry, J. C. and Shah, S. M. Ibrahim, 1979. Miocene sediments and faunas of Pakistan. Postilla, 179: 45 pp.

Pilgrim, G. E., 1910. The correlation of the Siwaliks with mammal horizons of Europe. Geol. Surv. India Rec., 40: 185—205.

Pilgrim, G. E., 1913. The correlation of the Siwaliks with mammal horizons of Europe. Geol. Surv. India Rec., 43: 264—326.

Prasad, K. N., 1971. Ecology of the fossil hominoidea from the Siwaliks of India. Nature, 232: 413—414.

Schaller, G. B., 1967. The Deer and the Tiger. University of Chicago Press, Chicago, Ill., 370 pp.

Tattersall, I., 1969a. Ecology of North Indian *Ramapithecus*. Nature, 221: 451—452.

Tattersall, I., 1969b. More on the ecology of North Indian *Ramapithecus*. Nature, 224: 821—822.

Tauxe, L., 1979. A new date for *Ramapithecus*. Nature, 282: 399—401.

Varishat, R. N., Gaur, R. and Chopra, S. R. K., 1978. Community structure of middle Sivalik vertebrates from Haritalyangar (H. P.), India. Palaeogeogr., Palaeoclimatol., Palaeoecol., 23: 131—140.

Voorhies, M., 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. Contrib. Geol. Univ. Wyo., Spec. Pap., No. 2: 69 pp.