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BIOSTRATIGRAPHIC SURVEYS IN THE SIWALIKS OF PAKISTAN: A METHOD FOR STANDARDIZED SURFACE SAMPLING OF THE VERTEBRATE FOSSIL RECORD

Anna K. Behrensmeyer and John C. Barry

ABSTRACT

Much of the vertebrate fossil record consists of fragmentary specimens that are widely dispersed across eroding outcrops. This paper describes a method of standardized surface surveying that samples fragmentary surface fossil assemblages for information relating to biostratigraphy, taphonomy, and paleoecology that is not usually available from more traditional approaches to paleontological collecting. Biostratigraphic surveys have been used in the Miocene Siwalik sequence of northern Pakistan since 1979 to better define important faunal appearance and extinction events and to learn more about the taphonomy and overall productivity of the highly fossiliferous fluvial deposits. The surveys record all bones encountered during walking transects in specified stratigraphic intervals, which are well exposed and delimited by strike valleys between tilted sandstones. High quality or informative specimens are collected, and dense patches of fossils are designated as formal localities and treated separately. The resulting survey data permits analysis through time of variables such as fossil productivity per search hour, proportions of different skeletal parts and vertebrate groups, and ratios of abundant mammal families such as Equidae and Bovidae, as well as tests for correlations between these and other variables. Biostratigraphic survey data compliment other types of paleontological information about faunal evolution in the Siwalik sequence and provide new insights on biotic versus environmental correlates of changes in the abundances of particular groups through time. The methodology can be adapted and used for other fossiliferous sequences throughout the vertebrate record.

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INTRODUCTION

Field paleontologists are often at their best (and happiest) when free to roam over promising exposures, letting experience and instinct lead them to the places where fossils occur. Will Downs (Figure 1) was a master of this approach, and the field of vertebrate paleontology benefited greatly from his talents at locating and collecting highly productive fossil sites. However, areas where fossils are relatively abundant and dispersed over the outcrops also lend themselves to a different collecting strategy, one in which controlled surface surveys enhance the traditional focus on the discovery of richly productive sites or unusual fossils. This methodology, which will be described below, was developed by the Harvard – Geological Survey of Pakistan – Smithsonian research team in the 1970s (Barry et al. 1980) and was used initially to document biostratigraphic changes through time in the Miocene Siwaliks. It is a tribute to Will that in spite of his aversion to “controls” of any kind, he participated in these surveys and contributed to the development of the methodology. Fundamentally, he was interested in the science and what the team could learn with new approaches, even when these might put a damper on his preferred way of doing things.

The basic goal of controlled surface sampling of the vertebrate record is to document, in a manner as free of collecting biases as possible, the fossil assemblage that occurs on the ground surface at a particular stratigraphic level. Documentation targets any remains that have been naturally exposed and are visible on outcrop surfaces – from whole bones and teeth to scraps of bone, as well as coprolites or other trace fossils. Identification at any level of taxonomic resolution is potentially useful, and the resulting data can address questions such as the proportion of fish versus reptile versus mammal, the frequency of tooth versus limb and vertebra fragments, or the relative abundance of equid versus bovid teeth. The controlled surface surveys provide information that usually cannot be recovered from museum catalogues or traditional, taxon- or body-part specific collecting strategies, and the two approaches are complimentary when applied to the same strata. The surface surveys have their own sets of biases, which will be discussed below, but these biases differ from those in collections oriented toward the recovery of the more complete and identifiable specimens. Perhaps the most important benefit of controlled surface surveys is that they can be repeated at different stratigraphic intervals, as was done in the Siwaliks, thereby providing information on changes in the taxonomic composition of the fossil assemblages through time, i.e., biostratigraphic trends. The same methods can also be used for comparisons of contemporaneous faunas and skeletal part assemblages in different areas or lithofacies. The key is to eliminate noise from inconsistent collecting strategies so that such comparisons result in reliable information about the bone assemblages themselves.

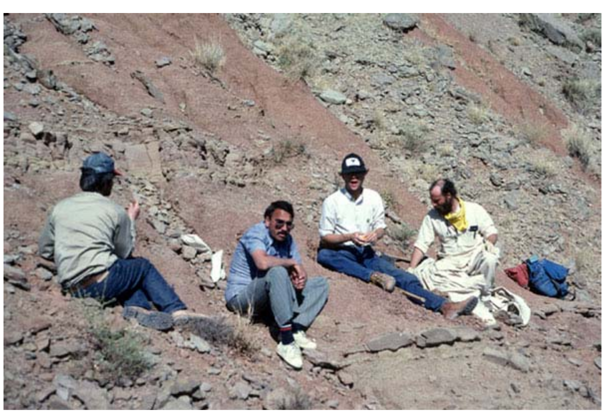


Figure 1. The “rodent boys” at Chinji Locality Y640 in 1984; from left: Larry Flynn, Iqbal Cheema, Louis Jacobs, and Will Downs.

In this paper, we describe the methods that were developed by the Siwalik research team to investigate biostratigraphic change through time in the vertebrate paleocommunity. We also provide examples of some of the results of these sampling methods and guidelines for using them in other regions and time intervals.

BACKGROUND

The Siwalik sequence has been recognized for its rich terrestrial vertebrate record since the 1830's, and the extensive Potwar Plateau exposures in northern Pakistan (Figure 2) have been under investigation by the Harvard - Geological Survey of Pakistan - Smithsonian team since the early 1970's. This project, headed by David Pil-

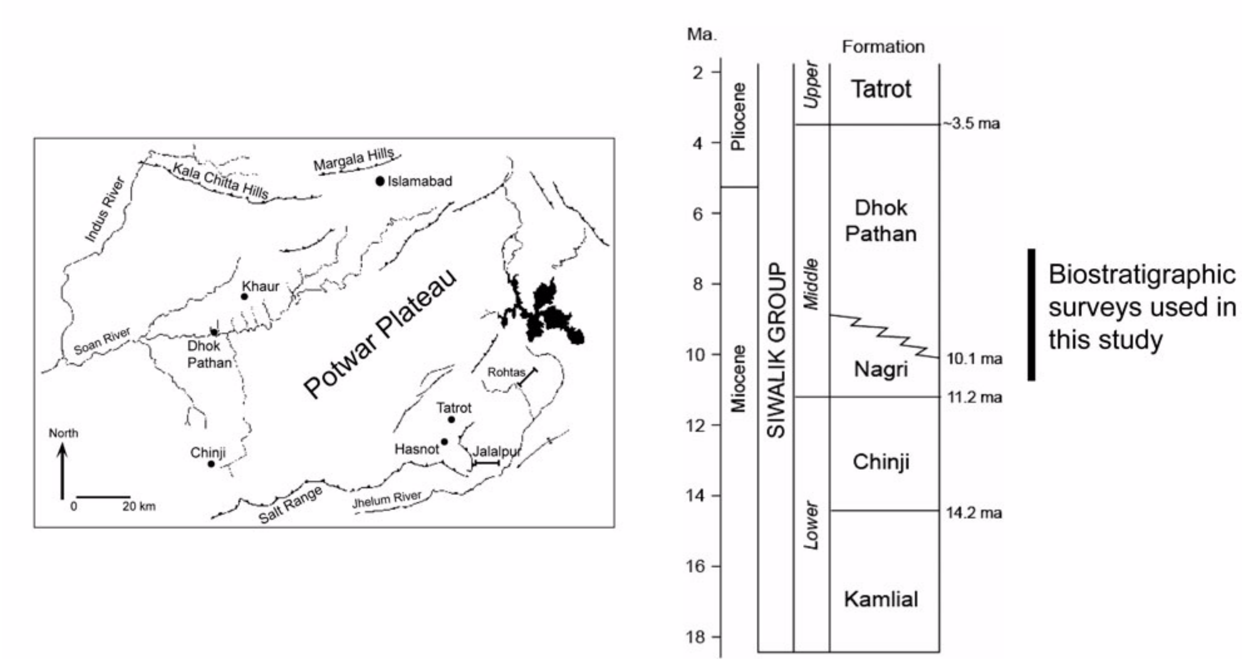


Figure 2. Map of the Potwark Plateau showing important place names and a generalized stratigraphic section with chronstratigraphy for the major Siwalik formations. Boundary dates are from Barry et al. 2002.

beam, S. Ibrahim Shah, S. Mahmood Raza and J. C. Barry, has been multidisciplinary in scope and has yielded a wealth of geochronological, sedimentological and paleontological information for over 5000 m of fluvial deposits spanning the time period between about 18 and 5 Ma (Johnson et al., 1985; recent summary in Barry et al. 2002). The Miocene–Pliocene strata have traditionally been divided into the Kamlial, Chinji, Nagri, and Dhok Pathan Formations (Figure 2). In all of these formations, exposures typically consist of gently tilted strata that form shallow strike-valleys and higher ridges as the surface expression of the large structural synclinorium underlying the Potwar Plateau. The ridges are formed by laterally extensive channel sandstones and the valleys by more easily eroded floodplain mudstones and siltstones (Willis and Behrensmeyer 1994). Fossils weather out of these strata and accumulate on the outcrop surfaces between the ridges, providing ideal conditions for controlled sampling within well-defined stratigraphic intervals (Figure 3). The Potwar Plateau is capped by late Pleistocene silts and gravels (the Potwar Silts), which buried an erosional unconformity on Mio-Pliocene sediments. In many areas these overlying deposits have been removed by erosion, but in others they cover the older sediments with silts or coarse gravels that limit recovery of the Mio-Pliocene fossils.

The biostratigraphic surveys of Siwalik strata were done in many different areas of the Potwar Plateau; these areas are named for the modern drainages or 'kas' that typically cut through the exposures perpendicular to regional strike. In the Khaur region, located in the north-central Potwar, these include the following kas: Kaulial, Malhuwala, Dinga, Dhok Mila, Ganda, and Ratha (map positions provided in Barry et al. 1980). Surveys also were done in the Rhotas area near the city of Jhelum and in the lower Chinji, upper Chinji/lower-Nagri, and Kamlial Formations in the southern portion of the Potwar. Kaulial Kas, in particular, was a focal area for pinning down the level of first appearance of a "big bovid" using controlled surface surveying methods. The surveyed portion of the Kaulial Kas section consists of about 2100 m (6930 feet) spanning the time interval from 10.9 to about 7.1 Ma and is one of the few areas in the northern Potwar where the later part of this interval is well enough exposed to produce a reasonable fossil record. In both the Khaur and Chinji areas this approach also was used to define the "*Hipparion*" appearance level, and the resulting data support the assertion that equids do not occur lower than this level (Barry et al. 2002)

METHODS

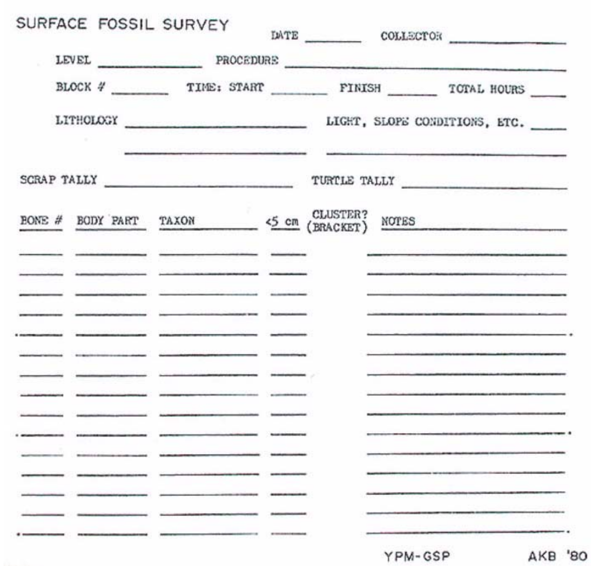
The first requirement for standardized surface sampling is to have a clear research goal in mind, because this affects the type of data recorded and the deployment of people doing the recording. In the case of the Siwalik surveys, we were interested

Figure 3. Photo of typical strike valley in the Dhok Pathan Fm. near Kaulial Kas. Biostratigraphic survey KL11 was done in this area, between the flat patches with bushes near the center of the photograph to below the ridge-capping sandstone, a thickness of approximately 100 m.

in delimiting a number of biostratigraphic events that were suggested by more traditional survey and collection methods, i.e., the level of disappearance (LAD) of *Sivapithecus*, the decline and extinction of the Tragulidae, the regional appearance datum for "*Hipparion*" and a large genus of bovid, and the overall faunal response to changes in fluvial systems and climate between ~8.0 Ma and 6.0 Ma. Thus, we designed our sampling strategies to cover sequences of exposures in several different areas that fell within this time range, with correlations between areas based on the well-documented Siwalik magnetostratigraphic record (Tauxe and Opdyke 1982; Johnson et al. 1985; Barry et al. 2002). We were also interested in assessing fossil productivity of different stratigraphic levels throughout the Potwar sequence, as we knew from more traditional collecting that it was likely to vary considerably and was undoubtedly important in considerations of biostratigraphy of these intervals. We thus broadened sampling to include fragmentary fossil debris ("scrap"), even if unidentifiable except as vertebrate remains.

In addition to providing data relating to our primary goals, the biostratigraphic surveys also can address questions such as: 1) the effect of different outcrop slopes and lighting (bright sun, overcast, etc.) on fossil collecting, 2) variation among different individuals in finding fossils, 3) variation in skeletal parts preserved in different lithofacies and stratigraphic intervals, 4) ratios of "good" fossils (i.e., identifiable to major group, etc.) to scrap, 5) variation through time and by facies of aquatic versus non-aquatic vertebrates, and 6) relative frequency of recovery of small mammals on walking surface surveys (as opposed to crawling the outcrops). We do not attempt to treat all of these questions here but point them out as possibilities for future research.

As erosion proceeds along the Potwar Plateau strike valleys, resistant lags of carbonate nodules, gravels, and fossil bones tend to be dispersed widely over the ground surface. Occasionally there are patches of more abundant fossils weathering out from particular lithofacies, and these are treated separately as localities (Barry et al. 1980; Behrensmeyer and Raza 1984). The biostratigraphic surveys target the scatter of fossils between the richer patches, although many of the more evenly dispersed remains may ultimately have been derived from spatially circumscribed concentrations. Relatively few Siwalik fossils are found in situ, and the fragmentary remains recorded on the surveys represent the net result of original (pre-fossilization) taphonomic processes combined with erosion and fragmentation on the modern outcrop surfaces. Nevertheless, there is little chance that fossils from higher or lower levels contaminate the level being sampled, given the continuous strike ridges that separate these levels (Figure 3). The areas used for the biostratigraphic surveys either had not been previously searched or


SURFACE FOSSIL SURVEY

DATE ______ COLLECTOR ______

LEVEL ______ PROCEDURE ______

BLOCK # ______ TIME: START ______ FINISH ______ TOTAL HOURS ______

LITHOLOGY ______ LIGHT, SLOPE CONDITIONS, ETC. ______

SCRAP TALLY ______ TURTLE TALLY ______

BONE #	BODY PART	TAXON	<5 cm	CLUSTER? (BRACKET)	NOTES

YPM-GSP AKB '80

Figure 4. Data card format used for Siwalik biostratigraphic surveys.

were documented only on the basis of spatially circumscribed fossil localities.

Survey parties usually consist of three to six individuals, each of whom is given a biostratigraphic survey card to fill out (Figure 4) as he or she covers the assigned area of outcrops. Well-defined blocks of exposures are typically surveyed by several individuals together, evening out differences in experience between individuals. One individual is responsible for assigning the search area and for keeping people on more-or-less parallel tracks along the outcrops, for noting light and substrate/slope conditions, outlining the area on air-photo overlays, and collecting the cards at the end of each survey. Individuals vary in their ability to identify fossils, so the more experienced typically assisted the less experienced. In practice, most of the surface fossils can only be identified to major vertebrate or mammal group, which is relatively easy even for inexperienced collectors.

For each biostratigraphic survey block, the surveying team typically spends several hours walking along a dissected, low-relief strike valley or proceeding carefully across the steeper slopes below a capping sandstone looking for fossils. When a team member finds a fossil, decisions must be made during the recording process about the identity and size of the bone or tooth fragment (Figure 4). A number of rules were developed to standardize recording and collecting of some of the materials encountered on the surveys.

1. At the start of each biostratigraphic survey block, the surveyor fills out the top portion of the card, and at the end of the block notes the finish time and total hours. Individuals were asked to stop the clock during any significant rest-breaks during the surveys.
2. All bones are recorded, either tallied as "scrap" if unidentifiable or "turtle scrap" if identifiable as such, or as separate items numbered sequentially and identified to body part and taxon. Body part can be as non-specific as "limb fragment - mammal," or as specific as "upper right premolar - *Hipparion*."
3. Patches of multiple fragments of bones or teeth that have recently broken up on the eroded surfaces are counted as single occurrences.
4. Each bone is scored as either larger or smaller than 5 cm maximum dimension, to keep track of the degree of fragmentation in a survey block and also the observation capabilities of different surveyors.
5. Two or more identifiable and separately recorded bones from the same or different individuals that occur in a small area (e.g., ~1-10 square meters) are noted as "clusters" by brackets on the survey card (Figure 4). Some of these were later designated as localities and given a locality number.
6. If a surveyor is stuck on fossil identification, he/she calls in another surveyor for a second opinion, or in some cases collects the specimen for later identification. We often convened periodically to go over identifications, and in practice, most people kept close enough together that it was easy to check an identification without stopping the survey.
7. The group leader(s) are called in to collect particularly good or informative specimens, which are documented on air photos or, in some cases, simply to survey level and block. Surveyors are instructed to leave such specimens in place and to put a cairn at the discovery site, then get the assistance of other team members. If air photographs and/or a GPS are available, map position and GIS coordinates should also be recorded.
8. At a particularly rich patch of fossils, i.e., a locality, the survey clock is stopped and the team gathers to collect the patch and document it as a locality. Once this is done, the clock starts again, and the survey continues.

This procedure can result in a lot of information in a relatively short period of time, depending of course on the density of surface fossils and the size of the survey team. It can also result in the discovery of high-quality specimens (Figure 5) as well

Figure 5. Locality Y410, site of the *Sivapithecus* face (GSP 15000), which was found by Mark Soloman during a biostratigraphic survey (KL03). These surveys encouraged people to search difficult outcrops and normally unproductive lithologies. A mass of bone that turned out to be part of the cranium of the specimen was just emerging near the base of the outcrops of floodplain silts (circle where people are clustered); another year of gully erosion would have made recovery of the intact specimen impossible.

as the collection of additional identifiable material to supplement formal localities (Barry et al. 1980, 2002). The standardized methodology allows various kinds of analyses that are not possible with more free-form paleontological surveying. In the examples to follow, we focus on measures of fossil productivity – identifiable bones and teeth per search hour, ratios of different taxa or body parts – e.g., bovid versus equid and teeth versus axial remains, abundance of a particular taxon relative to total identifiable sample, etc. The fossil productivity measures can be used in conjunction with geological data to investigate how sedimentary environments or stratigraphic intervals vary in fossil richness. Taxonomic data, even at very coarse levels of identification (e.g., mammal versus reptile) can provide evidence for questions such as the abundance of aquatic components in the fauna. The value of such information is most apparent when the data are compared through time or across different areas representing the same time.

RESULTS

There are many ways to use data from controlled surveys to explore patterns across space or through time in the fossil assemblages themselves, or to test hypotheses concerning relationships of paleontological trends to geological or geochemical evidence for paleoenvironmental characteristics of the ancient landscapes and faunas. The examples below are primarily exploratory in nature and are used to demonstrate the potential benefits of standardized sampling. The results of these initial analyses raise many questions that can be pursued in subsequent studies.

In the following sections, we use tallies and proportions of the basic data collected for the biostratigraphic surveys, which consist of identified specimens and tallies of turtle fragments and unidentifiable scraps. Because specimens that were found in several or many recently broken fragments were counted as one, the total number of specimens should be a good approximation of the actual number of separate fossils for each survey

Table 1. A. Biostratigraphic survey data, with levels of approximately the same age combined; these data are used for secular trend analyses (Figure 6). Age and duration information from Barry et al. 2002. Turtle tallies were kept separately on the cards after the first year of surveying, and the total reptile counts combine numbered records and turtle tallies. $NISP_V$ is the sum of Fish, Mammal, and Total Reptile columns, representing the total number of specimens that could be identified at least to major vertebrate group. **B.** Raw data by survey level, showing the more detailed breakdown of the 24 levels, some of which are combined in A. **C.** Reptile data showing proportions of Chelonia, crocodyloids, and a few rare taxa.

Survey Level	**Age (Ma)**	**Duration**	**Search Hours**	**Numbered Records**			**Turtle Tally**	**Total Reptile**	**NISPV**	**Scrap**	**NISPV / Search Hour**
				Fish	Mammal	Reptile					
KL07	7.289	0.324	10.25	0	35	0	15	15	50	111	4.88
KL09+KL10	7.561	0.292	7.80	0	27	0	4	4	31	94	3.97
KL08	7.719	0.125	13.30	0	68	8	24	32	100	181	7.52
KL11+KL21	7.949	0.344	18.24	0	157	7	34	41	198	226	10.86
KL12	8.485	0.149	10.42	0	113	3	38	41	154	201	14.78
ML05	8.658	0.123	5.91	0	73	25	0	25	98	187	16.58
KL16	8.733	0.137	10.50	1	79	0	25	25	105	154	10.00
ML06	8.787	0.246	8.34	0	35	9	0	9	44	102	5.28
KL02+KL14	8.840	0.126	10.67	1	82	5	22	27	110	180	10.31
DK01+KL13	9.001	0.155	14.75	0	83	2	26	28	111	224	7.53
KL01	9.184	0.043	9.49	0	100	9	18	27	127	180	13.38
KL03	9.270	0.062	12.92	4	57	15	44	59	120	184	9.29
KL05+06	9.543	0.126	12.84	0	105	18	23	41	146	201	11.37
KL04	9.703	0.109	13.57	0	153	19	23	42	195	301	14.37
KL20	9.784	0.139	11.61	0	37	2	19	21	58	72	5.00
RK01+DH01-2	10.300	0.114	18.89	0	101	14	58	72	177	358	9.37
RK02	10.385	0.124	6.74	2	28	6	17	23	53	48	7.86
Totals			196.24	8	1333	142	390	532	1877	3004	9.56
Total NISPID plus Scrap										4881	

block or interval. We refer to this as NISP (number of identifiable specimens; Badgley 1986a). The sample that was identifiable to taxon is $NISP_V$ (identifiable at least to major vertebrate class) or $NISP_F$ (for family or order), and the sample identifiable to skeletal region is $NISP_{SK}$, or $NISP_{SKM}$ for mammals only. In both cases, NISP probably is fairly close to MNI, minimum number of individuals, or MNE, minimum number of elements, respectively, given the wide dispersal of most of the specimens across the surveyed outcrops (Badgley 1986a). However, we retain NISP as our basic unit of analysis since we cannot test for MNI and MNE using data recorded on the survey cards. A total of 121 survey blocks combined into 24 separate numbered surveys (levels) were used in this analysis.

Fossil Productivity

The number of fossil bones that were identified at least to major vertebrate class (mammal, reptile, fish, bird) and/or to skeletal element provides the basic data used for analysis of overall fossil productivity. This combines the numbered specimens on the survey cards and the “turtle tally,” which was used as a quick way to keep track of small fragments of fossil turtle shell. The number of identified specimens ($NISP_V$) divided by the total number of search hours for each survey level (i.e., the total for all surveyors who searched that level)

Table 1 (continued).

Table 1B.

Survey Level	Age (Ma)	Duration	Search Hours	All Major Groups Numbered Records Fish	Mammal	Reptile	Turtle Tally	Total Reptile	NISPV	Scrap
KL07	7.289	0.324	10.25		35		15	15	50	111
KL09	7.561	0.292	4.50		10		2	2	12	39
KL10	7.561	0.292	3.30		17		2	2	19	55
KL08	7.719	0.125	13.30		68	8	24	32	100	181
KL11	7.949	0.344	11.74		116	2	23	25	141	137
KL21	7.949	0.344	6.50		41	5	11	16	57	89
KL12	8.485	0.149	10.42		113	3	38	41	154	201
ML05	8.658	0.123	5.91		73	25	0	25	98	187
KL16	8.733	0.137	10.50	1	79		25	25	105	154
ML06	8.787	0.246	8.34		35	9	0	9	44	102
KL02	8.840	0.126	2.75		21	3	0	3	24	34
KL14	8.840	0.126	7.92	1	61	2	22	24	86	146
DK01	9.001	0.155	4.84		10		11	11	21	54
KL13	9.001	0.155	9.91		73	2	15	17	90	170
KL01	9.184	0.043	9.49		100	9	18	27	127	180
KL03	9.270	0.062	12.92	4	57	15	44	59	120	184
KL05	9.543	0.126	7.34		24	11	0	11	35	62
KL06	9.543	0.126	5.50		81	7	23	30	111	139
KL04	9.703	0.109	13.57		153	19	23	42	195	301
KL20	9.784	0.139	11.61		37	2	19	21	58	72
DH01	10.300	0.114	7.07		30	2	29	31	61	159
DH02	10.300	0.114	2.33		5	2	10	12	17	17
RK01	10.307	0.114	9.49	4	66	10	19	29	99	182
RK02	10.385	0.124	6.74	2	28	6	17	23	53	48
Total			196.24	12	1333	142	390	532	1877	3004
Proportion of Total				0.006	0.710			0.283		

gives a standardized measure of its fossil productivity (P_f; Table 1, Figure 6A), with the mean value for all survey levels of about 10 identifiable fossils per hour. Alternatively, we could have used the area of outcrop covered in each survey to standardize search effort; this was recorded on air photographs, but digitized information for outcrop area is not yet available.

We can make the assumption that the $NISP_V$ / Hour (P_f) accurately represents the underlying fossil productivity of each interval, but other variables may also affect the pattern of temporal variation in productivity shown in Figure 6A. One of these is the thickness (duration) of the stratigraphic interval being surveyed, which was variable depending on search conditions. We tended to range vertically through thicker intervals for surveys that were relatively unproductive but followed productive strata laterally as far as possible, typically remaining within a relatively thin stratigraphic interval. Dividing P_f by interval duration gives a measure of productivity per 100 kyr (Table 1, Figure 6B), which highlights the narrow zone of exceptionally high productivity at KL01 and also the marked drop-off in productivity upward in the sequence, after 7.6 Ma.

Unidentifiable scrap was tallied for each survey interval, partly as a measure of the preservational state of surface fossils, and partly to encourage surveyors to pick up and examine every fossil they encountered. Not surprisingly, there is a high correlation between the number of identifiable

Table 1 (continued).

Table 1C. Reptiles Survey Level	Age (Ma)	Turtle Tally	ID Turtle	Total Chelonia	Lizard	Snake	Crocodylo id	Reptile Indet.	Total Reptile
KL07	7.289	15	0	15					15
KL09	7.561	2	0	2					2
KL10	7.561	2	0	2					2
KL08	7.719	24	2	26		1	4	1	32
KL11	7.949	23	1	24			1		25
KL21	7.949	11	0	11			5		16
KL12	8.485	38	2	40			1		41
ML05	8.658	0	20	20			3	2	25
KL16	8.733	25	0	25					25
ML06	8.787	0	8	8			1		9
KL02	8.840	0	15	15					15
KL14	8.840	22	0	22			2		24
DK01	9.001	11	0	11					11
KL13	9.001	15	0	15			2		17
KL01	9.184	18	6	24			3		27
KL03	9.270	44	3	47					47
KL05	9.543	0	11	11					11
KL06	9.543	23	6	29			1		30
KL04	9.703	23	15	38			4		42
KL20	9.784	19	0	19			2		21
DH01	10.300	29	1	30	1				31
DH02	10.300	10	0	10			2		12
RK01	10.307	19	1	20			9	1	30
RK02	10.385	17	0	17			5		22
Total		390	91	481	1	1	45	4	532
Proportion of Total				0.904	0.002	0.002	0.085	0.008	

bones ($NISP_V$) and scrap (Figure 7, Table 1B). The ratio is remarkably consistent throughout the survey samples, and we assume that this reflects a combination of taphonomic processes operating prior to deposition as well as fragmentation on the modern outcrop surfaces. In future analyses it should be possible to test the role of modern outcrop topography on the proportion of unidentifiable scrap using notes on the terrain and photographs for each of the surveys. On average, for the portion of the Siwalik sequence sampled using the surveys, one can expect to find a minimally identifiable fossil for every 1.6 unidentifiable scraps, and a mammal specimen identifiable at least to family for every 5 unidentifiable scraps. This metric is a good indicator of the abundance of information for higher taxonomic levels that is available in the eroded surface fossil assemblages of this fluvial sequence. The proportion of museum-quality, collectible specimens found on these surveys is much lower, compared to the high-density patches that constitute formal localities.

Fossil productivity (P_f) based on biostratigraphic survey data can be compared with productivity based on number of localities for approximately the same intervals (Figure 8, Table 2). The regression coefficient is positive but insignificant (R^2 = 0.11), and when the two obvious outliers are removed, it is also insignificant (R^2 = 0.35). The productivity of a biostratigraphic survey thus is not a good predictor of whether the interval will have rich concentrations of fossils, indicating a partial disconnect between the presence of such patches and the scatter of vertebrate remains between them. Interestingly, this suggests some degree of continuity through time in the back-

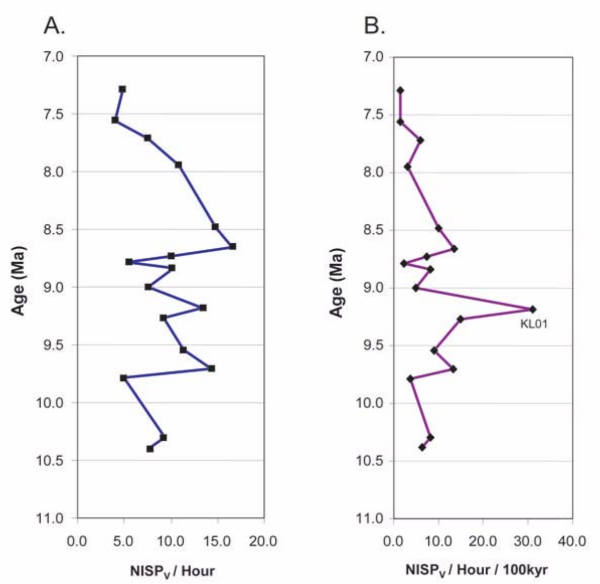


Figure 6. A. Plot of average number of vertebrate remains per search hour that are identifiable at least to major taxon and/or body part, relative to the median age of successive biostratigraphic surveys. This shows variation in the fossil productivity (P_f = $NISP_V$/hour)through time, from the upper part of the Nagri Fm. through part of the Dhok Pathan Fm. **B.** Data from A divided by the duration of the interval sampled for the biostratigraphic survey, which provides a measure of average productivity per hundred thousand years. The peak at about 9.2 Ma is survey KL01, which is a buff sandstone dipslope and overlying finer-grained deposits above the 'U' sandstone level. This level also includes a large number of productive localities and many *Sivapithecus* specimens. Data in Table 1.

ground of isolated fossil vertebrate occurrences in the Siwalik deposits, contrasting with strong fluvial and/or taphonomic controls on the presence or absence of notable bone concentrations.

Skeletal Parts

The proportions of different skeletal parts in a fossil assemblage can be used to infer the impact of taphonomic processes such as transport and density-dependent destruction on the remains prior to burial (Voorhies 1969; Behrensmeyer 1991). The biostratigraphic surveys provide standardized data for examining patterns through time in the representation of different skeletal elements. Here we focus on teeth and axial elements (vertebrae plus ribs), which represent the most and least dense elements in a complete skeleton, respectively (Voorhies 1969; Behrensmeyer 1975, 1988). Teeth are generally regarded as the most "preservable" elements in the vertebrate body, based on their density and mineralogy, which are particularly resistant to chemical and biological break-down. Teeth average 37% and axial parts 19% of the total sample of 1282 mammalian records identifiable to body part (Figure 9, Table 3), whereas they are 27% and 39%, respectively (excluding caudal vertebrae), in the skeleton of a living ungulate (combination of bovid and equid). Relative to this standard, the Siwalik fossil assemblage is shifted toward the denser, more preservable (and identifiable) elements. However, variations through time show that some survey intervals preserved a much higher proportion of teeth than others, suggesting differences in the taphonomic filter(s) that controlled the preservation of vertebrae and ribs versus teeth.

Based on studies in modern ecosystems and laboratories, non-random variations through time in axial versus tooth frequencies shown in Figure 9 could result from changes in: 1) levels of pre-burial biotic processing of skeletons, i.e., carnivore and scavenger pressure (Behrensmeyer 1993, 2002); 2) degrees of fluvial reworking of the original bone assemblages, with increased reworking resulting in proportionately fewer axial elements (Voorhies 1969; Behrensmeyer 1991); 3) contributions of channel versus floodplain deposits to the surface fossil assemblages recorded in the biostratigraphic surveys; more durable body parts, especially teeth, would be expected if channel deposits are the primary source of the fossils for any given level. In the biostratigraphic survey data, teeth are consistently dominant through the sequence, except for three intervals where they drop close to a 1:1 ratio relative to axial elements. There is an unusual dominance of teeth at about 8.8 Ma (survey ML06), followed by a drop to an unusually low proportion at 8.7 Ma (ML05). Both of these extremes are in the Malhuwala Kas area, ~15 km southwest of Kaulial and Ratha Kas where most of the surveys were done. It is possible that variations in search conditions or original position on the alluvial plain contribute to the differences in the ML samples. If we ignore these two points, the ratio in Figure 9B shows a slight trend toward increased tooth dominance upward in time, which corresponds to the sedimentological shift toward more mountain-proximal (buff), higher energy fluvial systems in the Dhok Pathan Fm. of the Kaulial Kas section (Behrensmeyer and Tauxe 1982). This suggests that the overall tooth versus axial pattern reflects degree of fluvial reworking rather than other possible causes listed above, but further work is needed to test this hypothesis.

Major Vertebrate Groups

Most paleontological collecting efforts focus on one vertebrate class or size category (e.g., macro-mammals) and pay less attention to associ-

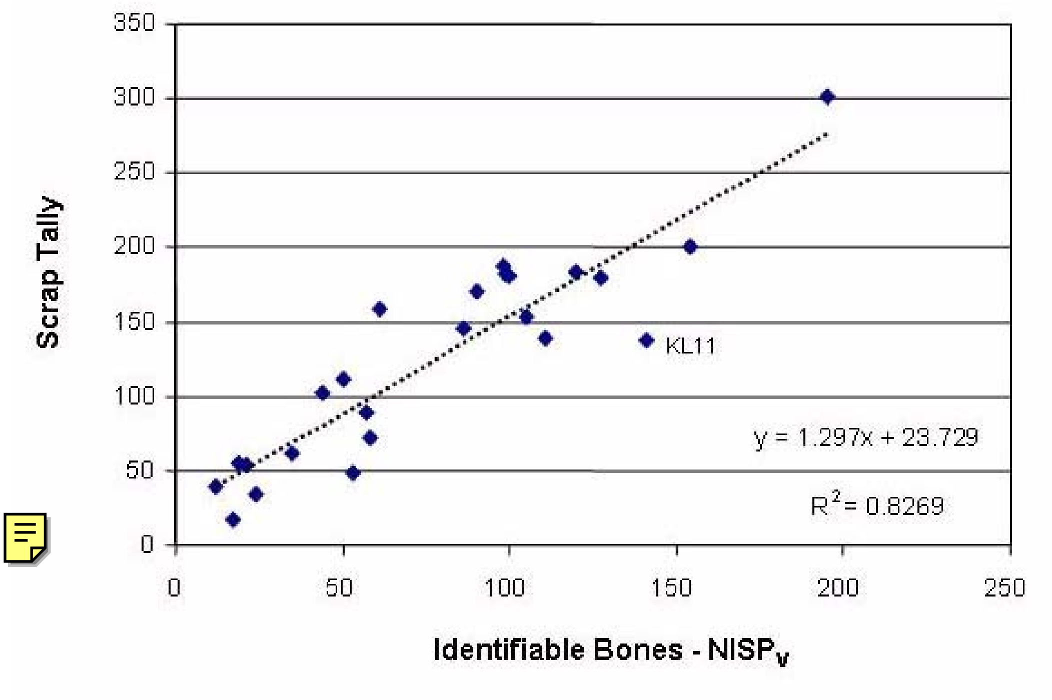


Figure 7. Relationship of identifiable bones to unidentifiable scrap, i.e., fossil fragments that are not certainly identifiable either to major vertebrate group or body segment. Total $NISP_V$ (identifiable bones) = 1877; Total N(scrap) = 3004 from 33 biostratigraphic surveys (all blocks and individual collectors combined for each numbered survey). Survey KL11 is an outlier that has an unusual number of identifiable bones relative to scrap, which may relate to relatively fresh eroding outcrop surfaces (see photograph in Figure 4).

ated fossils from other groups such as fish and reptiles. Therefore, the proportions of major vertebrate groups in most catalogued inventories are biased by collecting practices and cannot be used to examine the proportions of these groups in the source assemblages. Such information can be important, however, for instance as a general indicator of aquatic versus terrestrial habitats in fossil-preserving environments and overall taphonomic (and potentially ecological) dominance of the different types of vertebrates. Standardized sampling also provides a means of examining and comparing these variables at different times and places in the vertebrate record.

In the Siwalik biostratigraphic survey data, mammal remains average 71% and reptiles 28% of the recorded sample, whereas fish are very rare (0.4%; Figure 10, Tables 1 and 4). The near absence of fish is unexpected, since many of the depositional environments were clearly aquatic and occasional beds of abundant fish remains occur throughout the sequence. It is probable that this pattern represents a taphonomic bias against the preservation of fish remains in the Siwalik fluvial system. Apparently there were few robust forms, such as armored catfish, whose remains would likely survive as fossils and also be recognized on the biostratigraphic surveys. Of the documented reptilian remains, 88% are chelonian, 8% crocodyloid, and the remainder snake, lizard, and unidentifiable reptile. Most of the chelonian remains are ornamented shell fragments from the family Trionychidae, which are the common "soft-shelled" aquatic turtles, but tortoise and other smooth-shelled fragments also occur.

The relative abundance of reptiles versus mammals through time (Figure 10) shows an initial decline from RH02 through KL04, which coincides with the transition from the channel-dominated blue-gray fluvial system of the Nagri Fm. to the more floodplain-dominated buff fluvial system of the Dhok Pathan Fm. (Behrensmeyer and Tauxe 1982; Barry et al. 2002). The anomalous peak in reptile versus mammal in KL03 is followed by a fairly constant reptile abundance of around 20%. In both RK02 and KL03, the high relative abundance of reptiles is accompanied by fish remains, suggesting that these two levels sample more aquatic environments than the other levels, and also that the decline in the reptiles in the early part of the sequence reflects a shift to less aquatic conditions

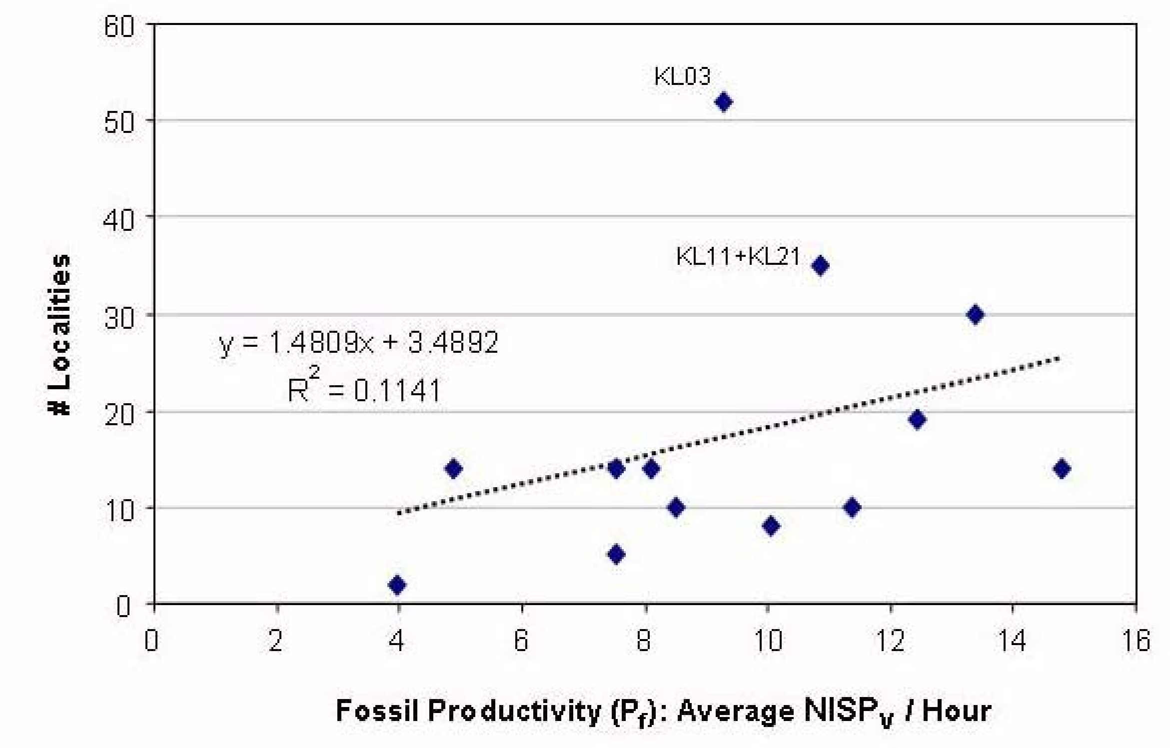


Figure 8. Comparison of fossil productivity based on biostratigraphic surveys versus formal localities (data from Table 2). The weak positive relationship shows a slight tendency for rich patches of bones to occur in generally fossiliferous intervals, but a high P_f is not a particularly good predictor of bone concentrations (i.e., localities) in the same interval. Data in Table 2.

Table 2. Comparison of fossil productivity (P_f), based on biostratigraphic survey data, and numbers of localities. Data from Table 1A were consolidated into 13 100 kyr time intervals to match the data for localities (Barry et al. 2002). See also Figure 8.

Survey Level	Age (Ma)	NISPV / Search Hour	Formal Localitie s
KL07	7.3	4.88	14
KL09+KL10	7.6	3.97	2
KL08	7.7	7.52	5
KL11+KL21	7.9	10.86	35
KL12	8.5	14.78	14
ML05+KL16	8.7	12.43	19
KL02+KL14+ML06	8.8	8.10	14
DK01+KL13	9.0	7.53	14
KL01	9.2	13.38	30
KL03	9.3	9.29	52
KL05+06	9.5	11.37	10
KL04+KL20	9.7	10.05	8
RK01-2+DH01-2	10.3	8.50	10
Total			227

in the source deposits of the surface fossil assemblages.

Only one bird was recorded in the entire biostratigraphic survey sample (on ML06). Since it is unlikely that we would have missed many identifiable avian remains in the nearly 5000 bones examined during the surveys, this indicates a strong taphonomic bias against the preservation of such remains in the Siwalik fluvial system.

Equidae versus Bovidae

An initial motivation for doing biostratigraphic surveys was to increase the temporal resolution on important biostratigraphic events, such as the appearance of "*Hipparion*" and the shift from equid to bovid dominance through the Siwalik sequence. Biostratigraphic surveys in the northern Potwar Plateau record the regional "*Hipparion*" appearance datum as shown in Figure 11. About two-thirds of the remains consist of teeth or tooth fragments (Table 5), which should be similar in terms of the impact of fluvial processes on their taphonomic histories. These remains also should be equally identifiable to family. Equid molars are generally larger than bovid molars, however, thus their abun-

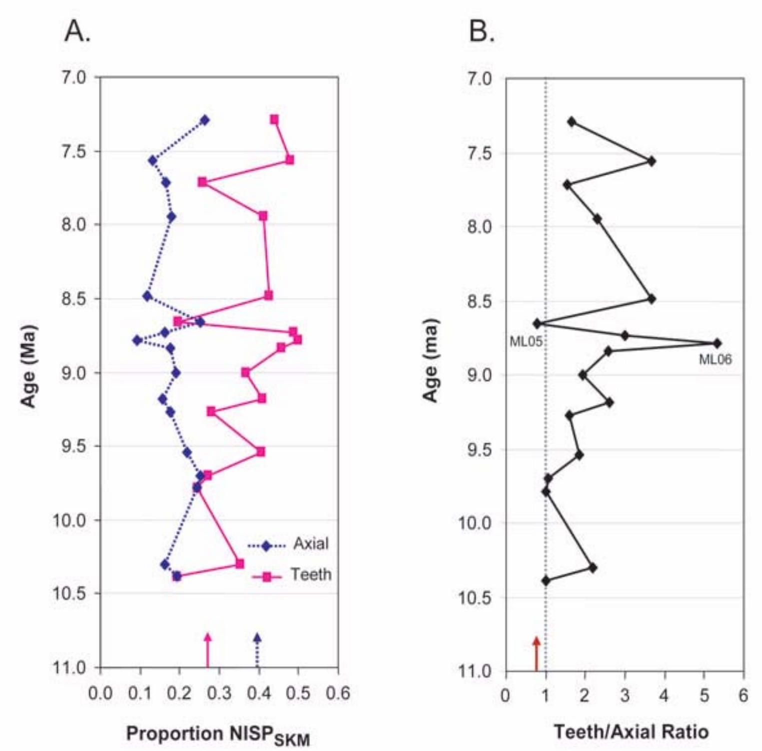


Figure 9. Comparison of biostratigraphic survey results for mammalian skeletal parts, teeth and axial post-cranial (vertebrae and ribs), based on the total number of records that could be identified to body part ($NISP_{SKM}$, Table 3). A. Proportions of axial parts and teeth relative to total numbers of specimens identifiable to body part ($NISP_{SKM}$), plotted by stratigraphic level. Pink and blue arrows indicate proportions in a complete equid-bovid skeleton. B. Ratio of teeth to axial parts; axial parts are more abundant than teeth in only a few levels (i.e., left of the dotted line; red arrow indicates ratio in a complete equid-bovid skeleton). Teeth average 37% and axial parts 19% of the total sample of 1282 records.

dance may be somewhat inflated in the preserved remains and recorded samples. Overall, however, we regard the survey data for equids and bovids as more or less isotaphonomic. Any biases in relative abundance should be equivalent from level to level, and changes through time are likely to reflect underlying ecological shifts in the diversity and/or abundance of these two groups.

The biostratigraphic survey data begin close to the "*Hipparion*" datum. There is an estimated 85 kyr between RK01, which has no equid (i.e., species of the genus "*Hipparion*") specimens, and RK02+DH01+DH02 with five equid specimens. Biostratigraphic surveys in other regions plus the locality data provide further support for a first appearance datum (FAD) at 10.3 Ma (Barry et al. 2002). Based on their frequency in the sample identifiable to mammalian family, the abundance of equid remains rises while bovid abundance falls sharply between 10.3 and 9.8 Ma. Equids continue to dominate the mammalian macro-fauna until shortly before 8.5 Ma (Figures 11A, 12A), when bovids become more abundant. The ratio of equids to bovids shows that equids reached their peak relative to bovids between 9.5 and 9.0 Ma (Figure 12A). The same overall pattern is preserved in the teeth-only analysis (Figures 11B, 12B), except that the two lines are farther apart and equids are more common than bovids until 7.7 Ma. We suggest that this results primarily from higher survival and visibility of equid teeth on outcrop surface. Using all documented skeletal remains (primarily appendicular) helps to boost tallies of bovids relative to equids, perhaps because of more equivalent survival and visibility levels for these post-cranial parts. Our working hypothesis, therefore, is that the differences between Figures 11-12 A and 11-12 B are a measure of durability and collecting bias between these two families rather than a pre-burial taphonomic or ecological signal.

The overall pattern through time in Equidae versus Bovidae, plus some of the shorter-term fluctuations in the sampled abundances not related to teeth versus all identifiable parts, may indicate shifts in the ecology of the alluvial plain favoring greater original abundance of one or the other. There is no obvious environmental event at the "*Hipparion*" appearance datum, and Barry et al.

Table 3. A. Tallies of skeletal parts for all vertebrates on the 24 biostratigraphic surveys, with some similar-age surveys combined. Teeth include both complete and fragmentary specimens; other categories were mostly fragmentary. Appendicular elements were identifiable as humerus, femur, phalanx, etc., while limb frags were only identifiable as such; these could also be included with appendicular. **B.** Mammalian skeletal parts only. Lower two rows provide comparable data for a complete skeleton, averaged for a combined bovid and equid (wildebeest and zebra). Caudals (N=15) are excluded from the axial category because they so rarely survive pre-burial taphonomic processes (Behrensmeyer and Dechant 1980). See also Figure 9.

		All Vertebrates									
Survey Level	**Age (Ma)**	**Teeth**	**Skull**	**Mandible**	**Axial**	**Appendicular**	**Limb Frags**	**Total NISPSK**	**Teeth/Total NISPSK**	**Axial/Total NISPSK**	**Teeth/Axial Ratio**
KL07	7.289	15	1	3	9	3	3	34	0.44	0.26	1.67
KL09+KL10	7.561	11	1	0	3	7	1	23	0.48	0.13	3.67
KL08	7.719	17	1	4	13	25	8	68	0.25	0.19	1.31
KL11+KL21	7.949	65	8	7	29	39	10	158	0.41	0.18	2.24
KL12	8.485	45	4	9	12	23	12	105	0.43	0.11	3.75
ML05	8.658	14	2	1	20	14	22	73	0.19	0.27	0.70
KL16	8.733	36	2	5	12	16	4	75	0.48	0.16	3.00
ML06	8.787	16	3	1	3	7	3	33	0.48	0.09	5.33
KL02+KL14	8.840	36	1	6	14	22	2	81	0.44	0.17	2.57
DK01+KL13	9.001	30	3	4	15	21	7	80	0.38	0.19	2.00
KL01	9.184	39	3	9	16	27	4	98	0.40	0.16	2.44
KL03	9.270	16	1	3	10	17	11	58	0.28	0.17	1.60
KL05+06	9.543	42	4	4	22	23	11	106	0.40	0.21	1.91
KL04	9.703	41	6	8	38	47	11	151	0.27	0.25	1.08
KL20	9.784	11	2		12	8	9	42	0.26	0.29	0.92
RK01+DH01-2	10.300	35	7	2	17	25	16	102	0.34	0.17	2.06
RK02	10.385	5	3		9	12	3	32	0.16	0.28	0.56
NISPSK		474	52	66	254	336	137	1319			
Proportion of Total		0.359	0.039	0.050	0.193	0.255	0.104				

(2002) suggest that the faunal turnover at around that time reflects biotic processes (e.g., competition). Our data support this hypothesis, because partial competitive exclusion could explain the reciprocal relationship of bovids versus equids shortly after 10.3 Ma, as well as the low levels of bovid abundance for several million years thereafter. The switch in abundance around 8.5 Ma also is not closely correlated with environmental change, although there is evidence that patches of C_4 vegetation may have been present at this time (Morgan 1994; Barry et al. 2002). Turnover events at 7.8 Ma and 7.3-7.0 Ma, which are based on the overall Siwalik faunal record and linked to environmental changes, are not obviously correlated with the equid versus bovid trends in Figures 11-12.

Mammalian Families

Eight major groups of macro-mammals dominate the Siwalik paleocommunity. Their relative abundances in the biostratigraphic survey sample are represented in Figure 13 (Tables 6 and 7). Although most of these taxa have been identified based on teeth, they are not necessarily as isotaphonomic as bovids and equids. For example, a single proboscidean or rhinoceros tooth can produce a large number of identifiable fragments, especially compared with smaller artiodactyl teeth. Thus, the proportions of the different groups in the survey samples are not a fair representation of their original relative abundances. As in the case of the plots of equid versus bovid abundance, however, these biases should be relatively constant

Table 3 (continued).

Table 3B.

Mammals Only

Survey Level	Age (Ma)	Tooth	Skull	Mandible	Axial	Appendicular	Limb Frags	Total NISPSKM	Teeth/Total NISPSKM	Axial/Total NISPSKM	Teeth/Axial Ratio
KL07	7.289	15	1	3	9	3	3	34	0.44	0.26	1.67
KL09+KL10	7.561	11	1		3	7	1	23	0.48	0.13	3.67
KL08	7.719	17	1	4	11	25	8	66	0.26	0.17	1.55
KL11+KL21	7.949	64	7	7	28	39	10	155	0.41	0.18	2.29
KL12	8.485	44	3	9	12	23	12	103	0.43	0.12	3.67
ML05	8.658	14	2	1	18	14	22	71	0.20	0.25	0.78
KL16	8.733	36	2	5	12	16	3	74	0.49	0.16	3.00
ML06	8.787	16	2	1	3	7	3	32	0.50	0.09	5.33
KL02+KL14	8.84	36	1	5	14	21	2	79	0.46	0.18	2.57
DK01+KL13	9.001	29	3	4	15	21	7	79	0.37	0.19	1.93
KL01	9.184	39	2	8	15	27	4	95	0.41	0.16	2.60
KL03	9.27	16	1	2	10	17	11	57	0.28	0.18	1.60
KL05+06	9.543	41	3	4	22	20	11	101	0.41	0.22	1.86
KL04	9.703	41	6	8	38	47	11	151	0.27	0.25	1.08
KL20	9.784	9	2		9	8	9	37	0.24	0.24	1.00
RK01+DH01-2	10.3	35	5	2	16	25	16	99	0.35	0.16	2.19
RK02	10.385	5	3		5	11	2	26	0.19	0.19	1.00
		468	45	63	240	331	135	1282	0.37	0.19	1.95
		0.365	0.035	0.049	0.187	0.258	0.105				
Modern Ungulate		38	1	2	56	45		142			
Proportion of Total		0.268	0.007	0.014	0.394	0.317			0.27	0.39	0.68

from interval to interval. The rare mammalian taxa found on the surveys include aardvark, primate, chalicothere, carnivore (including hyena) and rodent, which are grouped as “other” in Figure 13.

Overall there is moderate consistency in the proportions of the eight major groups, and nearly all continue in the paleocommunity through a time span of 3 Ma. Giraffes disappear from the sample between 8.0 and 7.7 Ma, and equids become dominant, mostly at the expense of bovids, shortly after their appearance (see also Figure 11). There is an interesting peak in giraffe abundance at 9.3 Ma (KL03), which coincides with the period of maximum equid dominance, as well as unusual numbers of turtles (Figure 11, Table 1). There also are a large number of fossil localities at this level (Table 2), including the *Sivapithecus* face site. This suggests that KL03 had somewhat different fluvial conditions and perhaps less seasonally dry habitats than other intervals. Another intriguing pattern is the increase of tragulids and suids in the youngest intervals (after 7.9 Ma), coinciding with the decline of giraffes and equids. Stable isotopes indicate an important transition toward more intensely monsoonal climate and C_4 vegetation starting around 7.3 Ma (Quade et al. 1989), and tragulid extinctions were part of the major faunal turnover between 7.3 and 7.0 Ma (Barry et al. 2002). It is interesting that shortly before that time, tragulids were still prominent members of the Siwalik paleocommunity.

DISCUSSION

The biostratigraphic surveys provide new information about the taphonomy and paleoecology of the Siwalik faunas and suggest many avenues for further investigation. Although additional

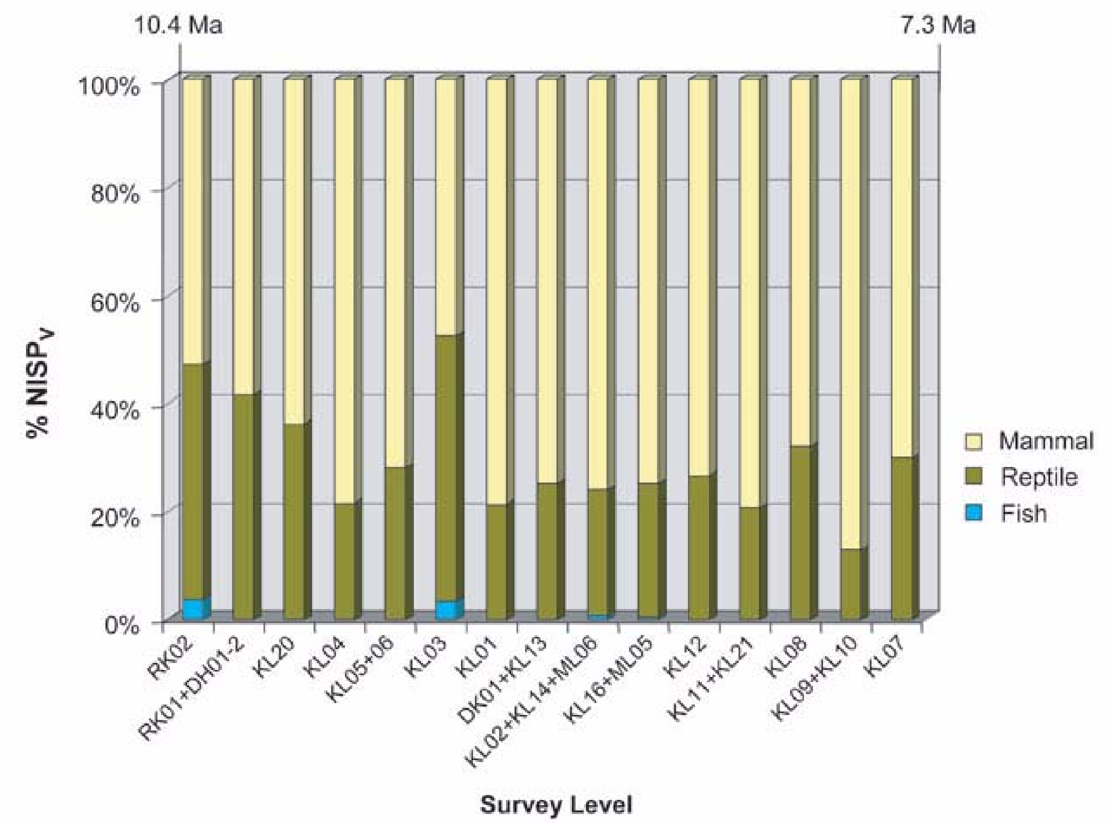


Figure 10. Major vertebrate groups through time, based on proportion of the identifiable samples for each biostratigraphic survey level ($NISP_V$, N=1877; Tables 1 and 4), arranged from oldest to youngest, left to right. A single bird occurrence on ML06 is not plotted. KL03 is unusual for its large number of records of Chelonia, including many remains of the family Trionychidae.

Table 4. Relative proportions of three major vertebrate groups in 15 time intervals, based on data from Table 1. Time intervals represent approximately 100 kyr each. See also Figure 10.

Survey Level	Age (Ma)	Fish	Reptile	Mammal
KL07	7.3	0.000	0.300	0.700
KL09+KL10	7.6	0.000	0.129	0.871
KL08	7.7	0.000	0.320	0.680
KL11+KL21	7.9	0.000	0.207	0.793
KL12	8.5	0.000	0.266	0.734
KL16+ML05	8.7	0.005	0.246	0.749
KL02+KL14+ML06	8.8	0.006	0.234	0.760
DK01+KL13	9.0	0.000	0.252	0.748
KL01	9.2	0.000	0.213	0.787
KL03	9.3	0.033	0.492	0.475
KL05+06	9.5	0.000	0.281	0.719
KL04	9.7	0.000	0.215	0.785
KL20	9.8	0.000	0.362	0.638
RK01+DH01-2	10.3	0.000	0.416	0.584
RK02	10.4	0.038	0.434	0.528

multivariate analysis and statistical treatments of our datasets are beyond the scope of this paper, there are a number of issues raised by these preliminary analyses, which we enumerate briefly below as points of departure for future research.

Biases in the Survey Data

The survey data have possible sampling biases that could affect our results, including inconsistent or incorrect identification, variability in surveyor ability to see small versus large bones, and the effects of sunny versus overcast days and outcrop conditions on fossil visibility. Also, samples size varies considerably in the different survey blocks and intervals, affecting the consistency of our secular patterns. It will be possible in future research to examine the above variables by analyzing the records of particular surveyors, light and slope conditions, area sampled, and the size of fragments recorded (greater than or smaller than 5 cm). We can remove skeletal elements that may be problematic (e.g., humeri and femora, which may not have been correctly attributed to equid versus bovid) and re-analyze the dataset to calibrate the

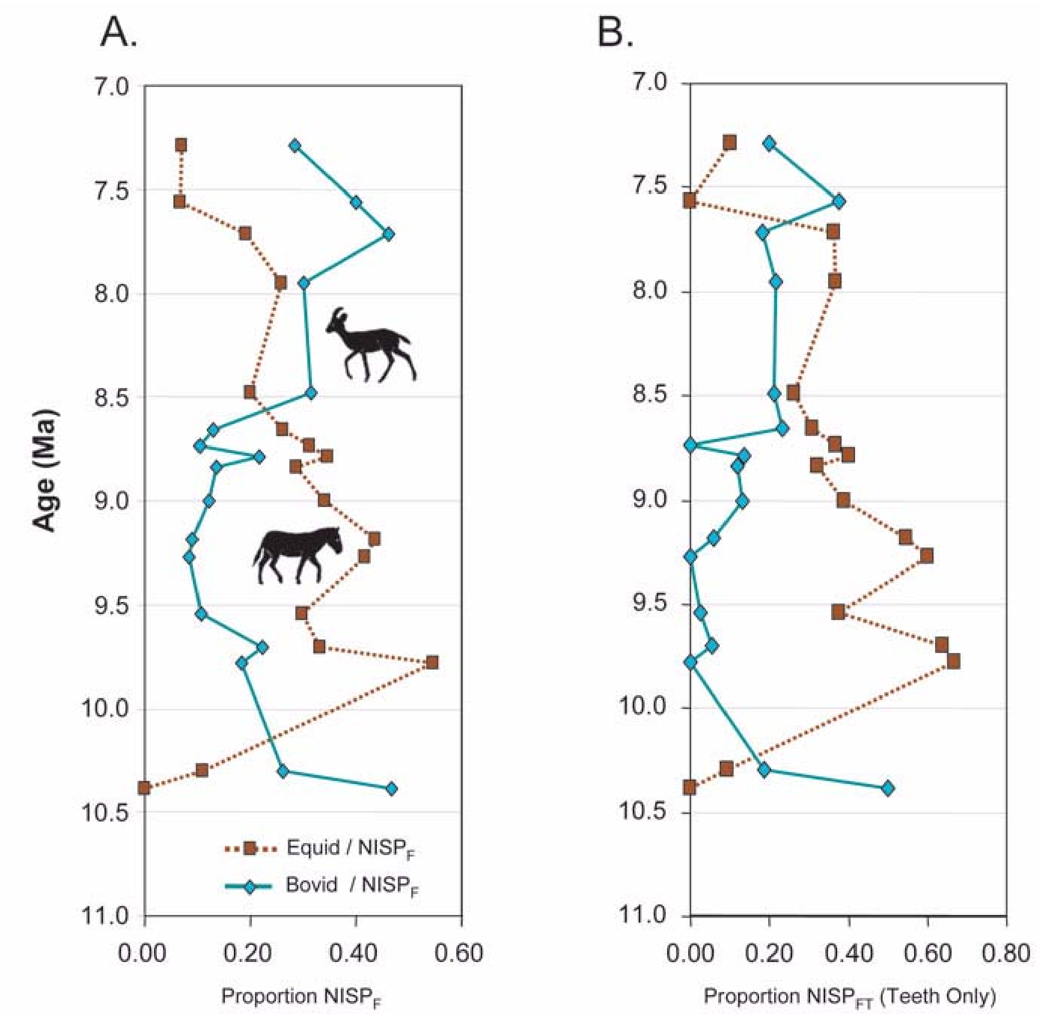


Figure 11. A. Plot of proportion of bovid versus equid specimens through time, based on the sample of all skeletal parts identifiable to mammal family at each survey level. Equids are dominant from soon after their FAD at about 10.3 Ma until about 8.6 Ma, when bovids become more numerous. **B.** Proportions of equids versus bovids through time, based on teeth only; differences from A likely reflect a taphonomic bias favoring the preservation and discovery of equid teeth, which generally are larger and more robust than bovid teeth. Data from Table 5.

impact of inconsistent identification. We can also analyze blocks within the same survey level and calculate error bars based on sample size for the trends through time. Additional survey data from the Chinji Fm. and parts of the Potwar Plateau will also strengthen our analysis, once it can be put in digital format.

On the plus side, there should be no systematic biases in the types of vertebrate remains recorded through the survey levels. We did not have any particular expectation of what we would find, or search images for specific taxa, that could influence the types of trends portrayed in Figures 6, 9, 11-13. The surveys were not done in stratigraphic order; we jumped around to different parts of the sequence, thus the sampling was "blind" in the sense that individuals did not have any prior knowledge of what the trends would be in the compiled data.

Taphonomic versus Paleoecological Signals

In spite of possible sampling biases discussed above, the results of this study show that significant taphonomic and paleoecologic information is preserved in the biostratigraphic survey data. This phenomenon is most apparent in the trends through time in skeletal parts (Figure 6), major vertebrate groups (Figure 10), and equid versus bovid patterns (Figures 11, 12). The overall characterization of the mammalian families in Figure 13 also contains ecological information, in spite of acknowledged problems with preservation biases of larger versus smaller taxa. The challenge is to figure out ways of distinguishing taphonomic ver-

Table 5. Survey data for Equidae and Bovidae, based on number of specimens identifiable to family ($NISP_F$). See also Table 6 and Figures 11-12.

Table 5A. All identifiable elements

Survey Level	Age (Ma)	Equidae NISP	Equidae/NISPF	Bovidae NISP	Bovidae/NISPF	Equid/Bovid	Total NISPF
KL07	7.289	1	0.07	4	0.29	0.25	14
KL09+KL10	7.561	1	0.07	6	0.40	0.17	15
KL08	7.719	5	0.19	12	0.46	0.42	26
KL11+KL21	7.949	24	0.26	28	0.30	0.86	93
KL12	8.485	11	0.20	19	0.32	0.58	60
ML05	8.658	6	0.26	3	0.13	2.00	23
KL16	8.733	15	0.31	5	0.10	3.00	48
ML06	8.787	8	0.35	5	0.22	1.60	23
KL02+KL14	8.840	15	0.29	7	0.13	2.14	52
DK01+KL13	9.001	14	0.34	5	0.12	2.80	41
KL01	9.184	24	0.44	5	0.09	4.80	55
KL03	9.270	10	0.42	2	0.08	5.00	24
KL05+06	9.543	14	0.30	5	0.11	2.80	47
KL04	9.703	24	0.33	16	0.22	1.50	72
KL20	9.784	6	0.55	2	0.18	3.00	11
RK01+DH01-2	10.300	5	0.11	12	0.26	0.42	46
RK02	10.385	0	0.00	7	0.47	0.00	15
		183	0.28	143	0.22		665

Table 5B. Teeth only

Survey Level	Age (Ma)	Equidae $NISP_{FT}$	Equidae/ $NISP_{FT}$	Bovidae $NISP_{FT}$	Bovidae/ $NISP_{FT}$	Equid/ Bovid	Total $NISP_{FT}$
KL07	7.289	1	0.10	2	0.20	0.50	10
KL09+KL10	7.561	0	0.00	3	0.38	0.00	8
KL08	7.719	4	0.36	2	0.18	2.00	11
KL11+KL21	7.949	22	0.37	13	0.22	1.69	60
KL12	8.485	10	0.26	8	0.21	1.25	38
ML05	8.658	4	0.31	3	0.23	1.33	13
KL16	8.733	11	0.37	0	0.00		30
ML06	8.787	6	0.40	2	0.13	3.00	15
KL02+KL14	8.84	11	0.32	4	0.12	2.75	34
DK01+KL13	9.001	9	0.39	3	0.13	3.00	23
KL01	9.184	18	0.55	2	0.06	9.00	33
KL03	9.27	9	0.60	0	0.00		15
KL05+06	9.543	14	0.38	1	0.03	14.00	37
KL04	9.703	23	0.64	2	0.06	11.50	36
KL20	9.784	6	0.67	0	0.00		9
RK01+DH01-2	10.3	3	0.09	6	0.19	0.50	32
RK02	10.385	0	0.00	1	0.50	0.00	2
		151	0.37	52	0.13		406

sus ecological signals when we have no direct information on original population sizes of the component taxa, and only a limited basis for assessing the impact of differential skeletal part preservation/ visibility on taxonomic representation (e.g., the example of equid versus bovid based on all skeletal parts versus teeth-only). Nevertheless, it should be possible to marshal multiple lines of evidence to test the relationships of these biostratigraphic patterns to sedimentological, geochemical, and other paleontological trends. If we can eliminate or control for taphonomic trends using this approach, we will be able to better justify any patterns that remain as paleoecological in origin. The taphonomic patterns have their own value as well, and it would be interesting if the increasing proportion of teeth upward in the Dhok Pathan could indeed be

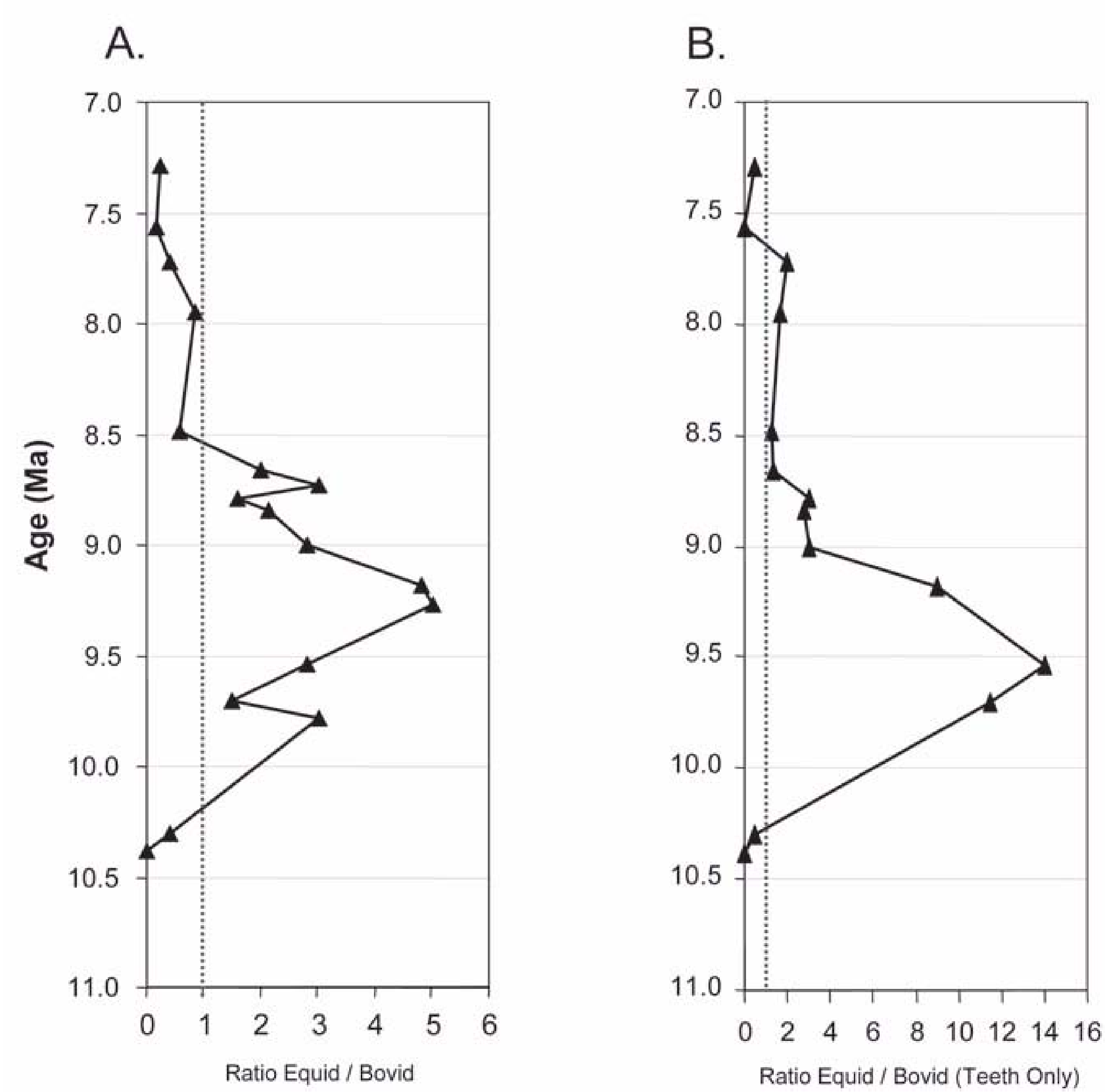


Figure 12. A. Equid to bovid ratio, based on all specimens identifiable to these two groups (Table 5A), showing a peak for equids between 9.5 and 9.0 Ma. Dotted line indicates a 1:1 ratio. **B.** Equid to bovid ratio, based on teeth only (Table 5B), with some intervals missing due to absence of bovids (denominator = 0).

linked with the tectonic evolution of the sub-Himalayan foreland basin.

Comparisons with Other Standardized Surveys

In general, standardized surveys in the vertebrate fossil record are relatively uncommon, perhaps because so much of the field effort in vertebrate paleontology has been to locate and collect "good specimens," which usually are rare. Yet such surveys can provide large samples and valuable information in addition to collectible specimens, as demonstrated by a number of previous and ongoing studies (e.g., Behrensmeyer 1975; Badgley 1986b; Smith 1980, 1993; Eberth 1990; Morgan 1994; Bobe and Eck 2001; Bobe et al. 2002; Blumenschine et al. 2003; Behrensmeyer et al. 2004) that have gathered data to address questions about associations of particular types of taphonomic assemblages with different lithofacies or paleoenvironments. Such research then is used as a foundation for exploring various aspects of the paleoecology of the preserved faunas. Many of these studies focus on developing multi-locality datasets of fossils for specific facies where bones are concentrated. Others are tapping into the scatter of bones between the patches, examining distributions and trends in relation to fluvial architecture (Smith 1980, 1993; Bobe et al. 2002; Campisano et al. 2004), tracing single productive levels in the approach labeled "landscape paleontology" (Potts

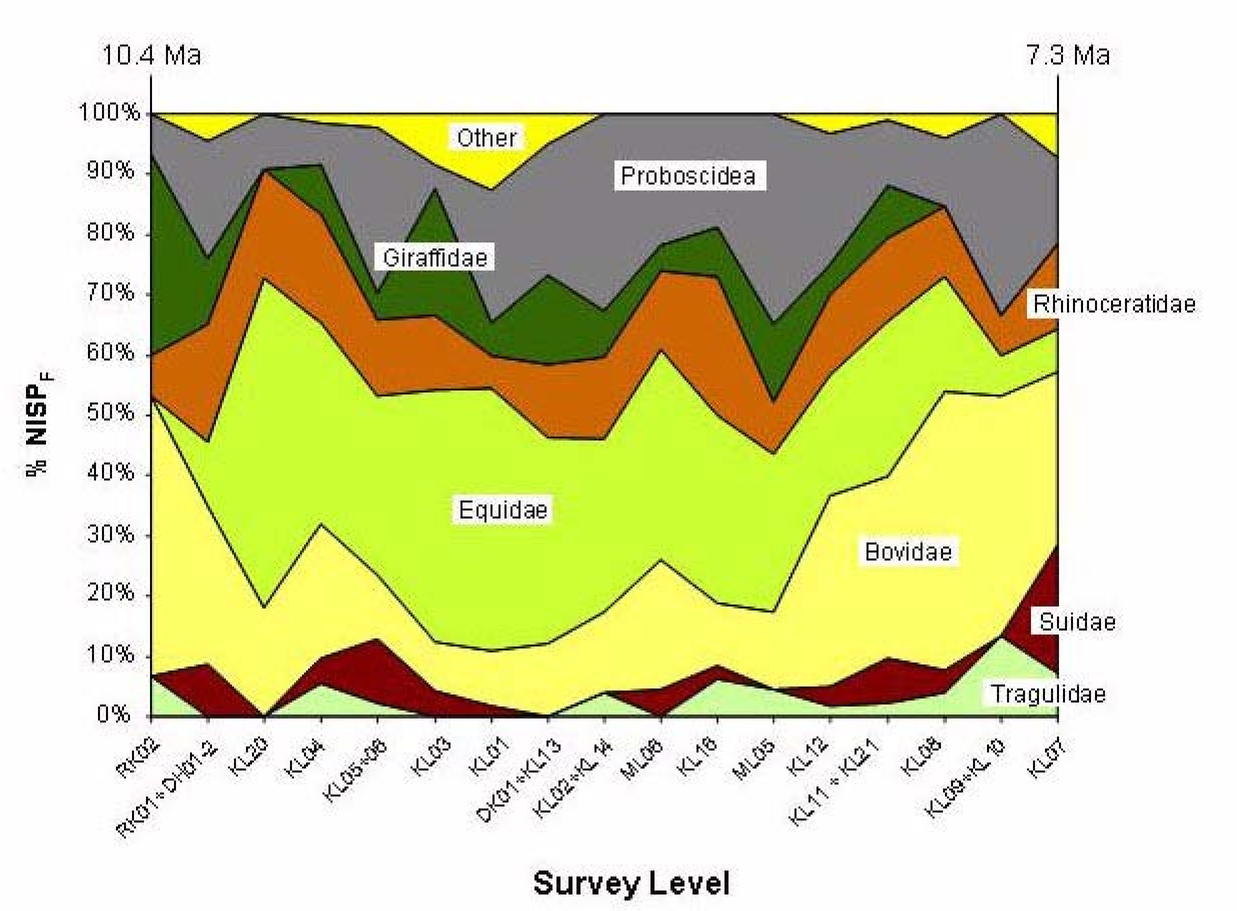


Figure 13. Area plot of the mammalian families represented in the biostratigraphic survey data, based on proportion of specimens that could be identified at least to family ($NISP_F$) or order, in the case of Proboscidea. Surveys are arranged from oldest to youngest, left to right. “Other” includes aardvark, carnivore, chalicothere, rodent, and primate. Equidae includes only species of the genus *Hipparion*. Data in Table 7.

et al. 1999; Blumenschine et al. 2003) and documenting fossil occurrences across large areas of exposures using GIS-based technology (Sagebiel et al. 2004; Straight 2004).

There have been few attempts, however, to apply standardized methods to specific biostratigraphic problems such as illustrated in this paper. One such approach tested for dinosaur diversity and hypothesized decline prior to the bolide impact at the Cretaceous – Tertiary boundary (Sheehan et al. 1991). A large group of field workers was organized to systematically census a sequence of fossiliferous strata in the uppermost Cretaceous Hell Creek Fm. of Montana and North Dakota. The censuses logged 15,000 search hours and recorded only in situ fossils, documenting map location, skeletal part, taxon, stratigraphic level, and lithofacies. This resulted in 556 specimens (MNI) from 8 different dinosaur families. Based on this sample, there was no decline in ecological diversity through three successive stratigraphic intervals for three different fossiliferous facies in two collecting areas, providing support for abrupt rather than gradual extinction of the dinosaurs. That study differed from the Siwalik biostratrigraphic surveys because it was limited to in situ specimens, but it is similar in the use of standardized search and recording procedures to investigate biostratigraphic patterns through time.

Applying the Biostratigraphic Survey Approach to Other Sequences

The Siwalik sequence of the Potwar Plateau was an ideal context in which to develop and test the methods outlined in this paper. The 10-15º tilt of the strata, laterally continuous strike-valley exposures between sandstone ridges, thick, continuous fluvial sequence, and the availability of willing surveyors all contributed to the success of this approach. However, the biostratigraphic survey methodology can be adapted to other, perhaps less ideal geological and paleontological circum-

Table 6. Raw data for $NISP_F$ for mammalian families (plus Order Proboscidea, which are mainly Gomphotheriidae) recorded on the 29 biostratigraphic surveys used for this study. "Other" sums the rare taxa to the right of the double line.

											Other				
Survey Level	**Age (Ma)**	**Tragulidae**	**Suidae**	**Bovidae**	**Equidae**	**Rhinoceratidae**	**Giraffidae**	**Proboscidea**	**Other**	**Total**	**Carnivora**	**Primate**	**Aardvark**	**Chalicothere**	**Rodent**
KL07	7.289	1	3	4	1	2		2	1	14					1
KL09	7.561	2		2	1	1		1		7					
KL10	7.561			4				4		8					
KL08	7.719	1	1	12	5	3		3	1	26					1
KL11	7.949	2	5	25	17	8	6	7	1	71	1				
KL21	7.949		2	3	7	5	2	3		22					
KL12	8.485	1	2	19	12	8	3	13	2	60	1	1			
ML05	8.658	1		3	6	2	3	8		23					
KL16	8.733	3	1	5	15	11	4	9		48					
ML06	8.787		1	5	8	3	1	5		23					
KL02	8.840					2	1	5		8					
KL14	8.840	2		7	15	5	3	12		44					
DK01	9.001			2			2			4					
KL13	9.001			3	14	5	4	9	2	37	2				
KL01	9.184		1	5	24	3	3	12	7	55	3	2			
KL03	9.270		1	2	10	3	5	1	2	24	1	1			2
KL05	9.543		3	1	6			2	0	12					
KL06	9.543	1	2	4	8	6	2	11	1	35	1				
KL04	9.703	4	3	16	24	13	6	5	1	72	1				
KL20	9.784			2	6	2		1		11					
DH01	10.300		4	7		2	2	2	1	18			1		
DH02	10.300							1		1					
RK01	10.307			5	5	7	3	6	1	27				1	
RK02	10.385	1		7		1	5	1		15					
Total NISPF		19	29	143	184	92	55	123	20	665	10	4	1	1	4
Proportion of Total		0.029	0.044	0.215	0.277	0.138	0.083	0.185	0.030						
Teeth only		0	17	52	151	17	65	101	3	406					
Proportion of Total		0.000	0.042	0.128	0.372	0.042	0.160	0.249	0.007						
Not used															
ML02	8.570	1		2	1			2		6					
ML01	8.636			3	1	2	2	5		13					
DM03	8.831		1	1	3	1	8	3		17					
GK01	8.927				1					1					
DM02	8.969				1					1					
UT01										0					
UT02					1	1				2					
UT03					3	1				4					

stances to address similar or other types of questions. Potentially serious problems, especially in horizontal or faulted fossil-bearing deposits, include: 1) mixing on outcrop surfaces of fossils from many different stratigraphic sources; and 2) difficulty in identifying and following specific strata or intervals that are producing the lags of surface fossils. Careful use of topography and marker

Table 7. Proportions of mammalian families (and one order-Proboscidea) for each of 17 survey intervals. See also Figures 11-13.

Survey Level	Age (Ma)	Tragulidae	Suidae	Bovidae	Equidae	Rhinoceratidae	Giraffidae	Proboscidea	Other	Total NISPF
KL07	7.289	0.07	0.21	0.29	0.07	0.14	0.00	0.14	0.07	14
KL09+KL10	7.561	0.13	0.00	0.40	0.07	0.07	0.00	0.33	0.00	15
KL08	7.719	0.04	0.04	0.46	0.19	0.12	0.00	0.12	0.04	26
KL11+KL21	7.949	0.02	0.08	0.30	0.26	0.14	0.09	0.11	0.01	93
KL12	8.485	0.02	0.03	0.32	0.20	0.13	0.05	0.22	0.03	60
ML05	8.658	0.04	0.00	0.13	0.26	0.09	0.13	0.35	0.00	23
KL16	8.733	0.06	0.02	0.10	0.31	0.23	0.08	0.19	0.00	48
ML06	8.787	0.00	0.04	0.22	0.35	0.13	0.04	0.22	0.00	23
KL02+KL14	8.840	0.04	0.00	0.13	0.29	0.13	0.08	0.33	0.00	52
DK01+KL13	9.001	0.00	0.00	0.12	0.34	0.12	0.15	0.22	0.05	41
KL01	9.184	0.00	0.02	0.09	0.44	0.05	0.05	0.22	0.13	55
KL03	9.270	0.00	0.04	0.08	0.42	0.13	0.21	0.04	0.08	24
KL05+06	9.543	0.02	0.11	0.11	0.30	0.13	0.04	0.28	0.02	47
KL04	9.703	0.06	0.04	0.22	0.33	0.18	0.08	0.07	0.01	72
KL20	9.784	0.00	0.00	0.18	0.55	0.18	0.00	0.09	0.00	11
RK01+DH01-2	10.300	0.00	0.09	0.26	0.11	0.20	0.11	0.20	0.04	46
RK02	10.385	0.07	0.00	0.47	0.00	0.07	0.33	0.07	0.00	15
Proportion of Total		0.03	0.04	0.22	0.28	0.14	0.08	0.18	0.03	665

beds, as well as documentation of in situ fossils, can help to control the problem of mixed source levels. It is often possible to select a particularly favorable combination of topography and lithology, such as a plateau-forming sandstone or a laterally continuous gravel that forms a marked break in slope, and restrict surveying to these situations. The condition of the fossils themselves (e.g., fresh versus highly abraded or fragmented) also can be a useful indicator of post-exposure history.

Of course, documenting only in situ fossils is the most conservative and accurate approach to establishing biostratigraphic trends through time (Sheehan et al. 1991), but usually this requires a large amount of effort and results in limited samples. Paleontologists learn to gauge whether surface fossils are derived from a particular source bed or stratigraphic interval, thus enabling them to exploit rich accumulations of naturally excavated specimens. The biostratigraphic survey approach seeks to harness and standardize this expertise in order to recover more information from the fossil record relating to ecological and taphonomic changes across space or time. The nature of the fossil-bearing deposits and the question(s) being addressed must ultimately determine survey design. Whatever this design, it is very important to record the details of the field approach so that the strengths and limitations of the samples are clear to other researchers.

CONCLUSION

Standardized sampling of the vertebrate fossil record holds great promise for increasing the quantity and quality of information about taphonomy, paleoecology, and faunal change through time. Large samples are available in fragmentary surface materials that can be identified at taxonomic levels above genus and species, and such data can be recorded efficiently during walking surveys that also result in the discovery of rich bone concentrations and anatomically complete specimens. The methods used for the Siwalik biostratigraphic surveys provide an example of this approach, but for other places, field practices will need to be tailored to particular geological contexts, outcrop topographies, and fossil frequencies. The increased application of this overall approach, aided by GPS and GIS technology, could contribute substantially to understanding of depositional systems, taphonomic processes, faunal evolution, and environmental change in the vertebrate record. The biostratigraphic survey method also provides a basis for comparing fossil productivity, skeletal part ratios, and faunal patterns in widely different fossiliferous sequences and time periods throughout the Phanerozoic.

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