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The biostratigraphy and magnetic polarity zonation of the Pabbi Hills, northern Pakistan: An Upper Siwalik (Pinjor Stage) Upper Pliocene–Lower Pleistocene fluvial sequence

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Abstract

The Pabbi Hills, northern Pakistan, comprise an Upper Siwalik fluvial sequence spanning 3.2–0.5 Ma. The portion 2.2–0.9 Ma encompasses most of the Pinjor Faunal Stage (ca. 2.5–0.6 Ma) of India, and was extensively sampled for vertebrate fossil remains, with particular attention to recording spatial and vertical provenance. Detailed palaeomagnetic sampling confirms earlier investigations in the Pabbi Hills, and allows fossil material to be grouped within time-bands of 200–300 kyr. Over 40,000 vertebrate fossil specimens were found, of which ca. 10% were diagnostic to taxon and skeletal part. The distribution of fossil material was non-random, and over half came from 20 localities. We propose here a mammalian biostratigraphy for the Upper Pliocene to Upper Lower Pleistocene (2.2–0.9 Ma) of northern Pakistan that expands and revises earlier work. The *Elephas hysudricus* faunal interval zone (ca. 2.7–0.8 Ma) can be usefully divided into an earlier and a later component. The earlier part prior to 1.7 Ma includes taxa such as *Sivatherium*, *Canis cautleyi*, *Hyaenictis* or *Lycyaena*, anthracotheres, and hippopotamids, all of which were probably regionally extinct by 1.4 Ma. Taxa seen after but not before 1.4 Ma include *Crocuta*, *Panthera*, an ursid and a herpestid. These changes may indicate that dry-season grasslands expanded at the expense of woodland habitats after the Early Pleistocene, thereby reducing arboreal habitats and browsing opportunities.
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Keywords: Upper Siwaliks; Pinjor Stage; Biostratigraphy; Upper Pliocene; Lower Pleistocene; Grasslands

1. Introduction

The Upper Siwaliks of the Indian subcontinent span the Late Pliocene to Middle Pleistocene, ca. 3.3–0.6 Ma, thus making them one of the longest fluvial sequences of their age in the world. Since Pilgrim's (1910, 1913) classic studies, they have been subdivided into three lithological and faunal stages: the Tatrot, Pinjor and Boulder Conglomerate. Researchers in India (e.g., Azzaroli and Napoleone, 1982; Ranga Rao et al., 1988), and Nepal (e.g., Corvinus and Nanda, 1994) have maintained these divisions, and refined Pilgrim's scheme by using magnetic polarity zonation. As a result, they place the Tatrot–Pinjor boundary at the Gauss–Matuyama boundary, 2.58 Ma (Cande and Kent, 1995), and the end of the Pinjor Stage at <0.78 Ma, just above the Brunhes–Matuyama boundary. The "Boulder Conglomerate Stage" that follows is defined by coarse and often conglomeratic

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deposits, and marks the end of the Upper Siwalik series. (It should be noted, however, that because of tectonic disruption and foredeep sedimentation, the timing of the end of the Pinjor Stage and the inception of conglomeratic deposition varies considerably between drainage basins (see Opdyke et al., 1979, p. 32; Rendell et al., 1989, p. 41), and thus the "Boulder Conglomerate Stage" is not synchronous across the top of the Upper Siwalik series).

A rather different approach has been followed in Pakistan. Barry et al. (1980) pointed out that Pilgrim's scheme was open to confusion, since his stages were defined lithologically but used also in a faunal sense. The Nagri Faunal Stage (Lower Siwaliks), as example, could mean i) only those animals represented at the Nagri type-site; ii) those animals at the Nagri type-site as well as in nearby deposits that could confidently be correlated to that particular locality; or iii) all those animals represented in deposits attributed to the (lithologically-defined) Nagri Formation. In the inter-war years, researchers such as Pilgrim, Colbert and Lewis used the last-listed criterion, and consequently, the "Nagri Fauna" came to contain many older and younger taxa that have never been found at the type-site itself (see Barry et al., 1982, p. 97 for fuller details). To avoid such confusions, they proposed that faunal stages should be defined independently of lithological criteria by establishing "faunal interval zones", defined by "the stratigraphic interval between two distinctive biostratigraphical events" (Barry et al., 1982, p. 98); the boundaries of these "interval-zones" may of course change in the light of new discoveries, especially for those stratigraphic intervals that are poorly sampled. They additionally suggested that the faunal equivalent of the beginning of the (lithologically-defined) Upper Siwaliks was defined by the first appearance of *Elephas planifrons* ca. 2.9 Ma. A little later, around the Gauss–Matuyama boundary ca. 2.58 Ma, *Equus* and cervids with antlers arrived in the sub-continent (Barry, 1995, p. 118). Hussain et al. (1992) clarified the faunal changes that occurred between 3.5 and 1.8 Ma. Their data from the Mangla–Samwal anticline near Mirpur, Pakistan, comprise fossil specimens that can be securely linked to a carefully-mapped series of sections that were dated on the basis of magnetic polarity zonation to between 3.4 to 1.1 Ma, with additional support from fission-track dating of a volcanic ash at ca. 2.5 Ma. Fossil specimens were found in deposits from 3.4 to ca. 1.8 Ma. Hussain et al. (1992) propose that the lower limit of "*E. planifrons* Interval Zone" of Barry et al. should be revised downwards, from 2.9 to 3.3 Ma. They also provide an upper limit at 2.7 Ma,

instead of leaving it open-ended, and propose an additional interval-zone defined by the presence of cervids and *Elephas hysudricus*, which are first evidenced in the Samwal sections at 2.7 Ma (when *E. planifrons* and *E. hysudricus* were briefly contemporary). At around the same time, or perhaps a little later, *Equus* makes its first appearance in the area. As *E. hysudricus* is present throughout the remainder of the fossiliferous part of the Samwal sections (i.e., up to 1.8 Ma), the upper limit of this "*E. hysudricus* interval zone" was left open-ended pending further research (see Fig. 1).

Most research, whether in India, Pakistan or Nepal has concentrated on defining the Tatrot–Pinjor boundaries, or their equivalents in the type of "faunal interval zones" defined by Barry et al. (1982) and Hussain et al. (1992). The Pinjor Stage itself has been seen by Indian researchers (e.g., Nanda, 1997) as largely undifferentiated throughout its long existence, from ca. 2.5 to 0. 6 Ma. In Pakistan, the regional pattern of magnetic polarity zonation of the Upper Siwalik deposits was established by the early 1980s (Johnson et al., 1986). The framework for dating these sequences was based upon fission track dating of zircon grains from volcanic ash horizons that were present in several of the sampled sections (Johnson et al., 1982). Opdyke et al. (1979) documented the time span of several mammalian taxa by linking identified specimens to several Pliocene and Pleistocene palaeomagnetic sections across northern Pakistan. Here, we present new data from the Pabbi Hills, northern Pakistan (see Fig. 2), which add to and modify their results, and suggest that subtle but important changes occurred during the Olduvai subchron (ca. 1.77–1.95 Ma). These changes enable the Pinjor Stage in India and Nepal- or the broadly equivalent *E. hysudricus* interval zone in Pakistan- to be sub-divided into a lower and upper component.

2. The Pabbi Hills

The Pabbi Hills comprise an anticline of fluvial deposits with a total sediment thickness of ca. 1000 m that were laid down by a precursor of the present day Jhelum River. Fluvial deposition was cyclical, with an average duration of 30–50 kyr (Raynolds and Johnson, 1985, p. 310), and each cycle of sands, silts and clays is capped by a sandstone. Because of uplift and their greater resistance to erosion, these sandstones often form prominent escarpments that can be traced over several kilometres, thus forming key marker horizons for stratigraphic correlation. Two were particularly useful. The first was the one numbered by Keller et al. (1977) as
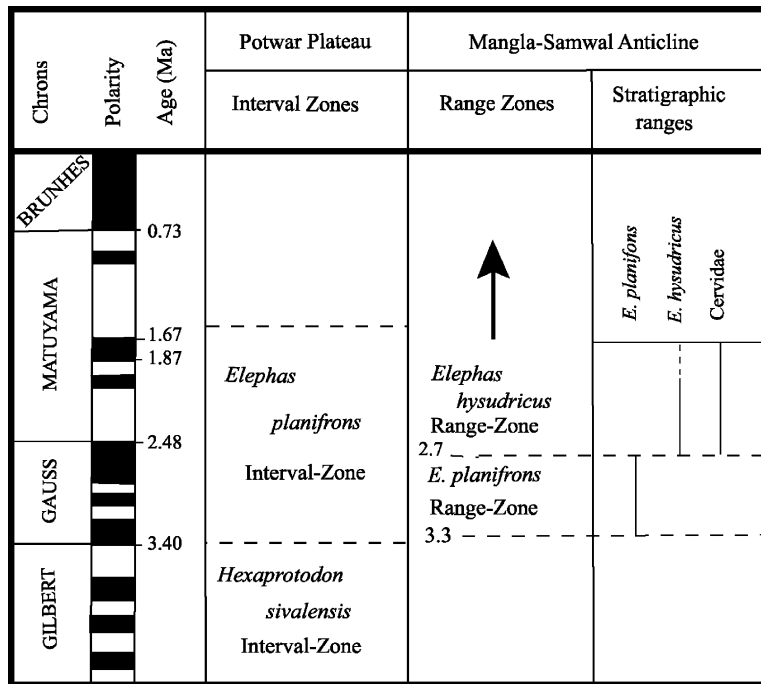
Fig. 1. Correlations of the Faunal Interval Zones of Barry et al. (1982) with those proposed by Hussain et al. (1992) for the Mangla–Samwal anticline. Note the replacement of the *E. planifrons* interval zone with a restricted *E. planifrons* zone, followed by an open-ended one based on *E. hysudricus*. Redrawn from Hussain et al., 1992, Fig. 6.

Sandstone (SST) 12, which is a particularly prominent sandstone that can be traced on both sides of the anticline over several kilometres; the second was Sandstone 3 (mapped in this study as Sandstone 5), which was present in three of the sections of Keller et al. (1977), as well as Choawala Kas (see Fig. 3).
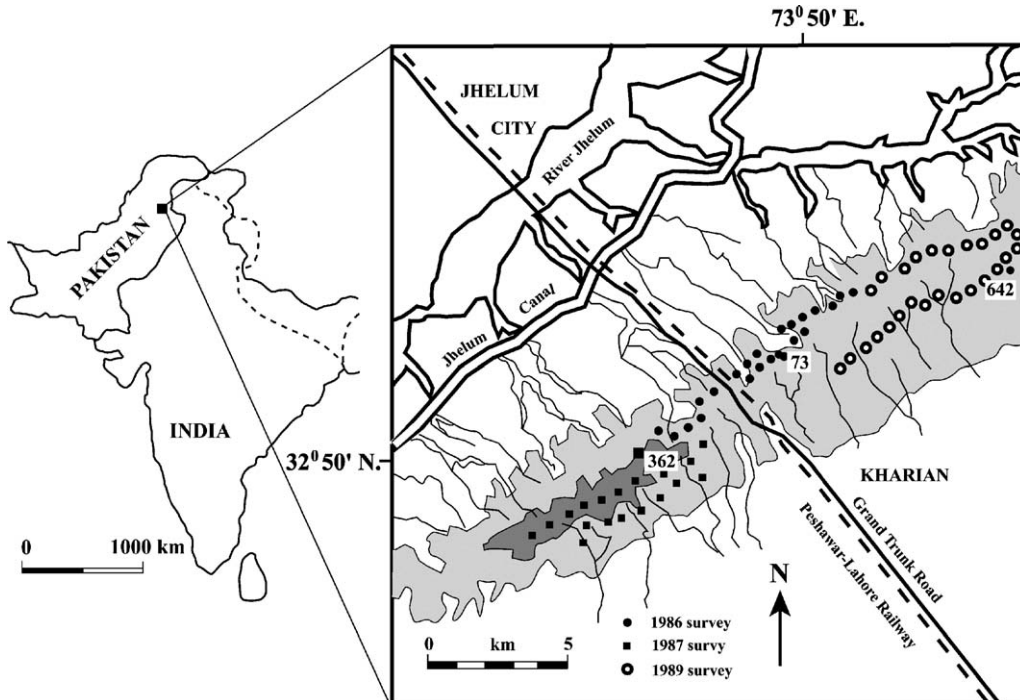

Fig. 2. The areas surveyed and localities excavated in the Pabbi Hills, 1986–1989.
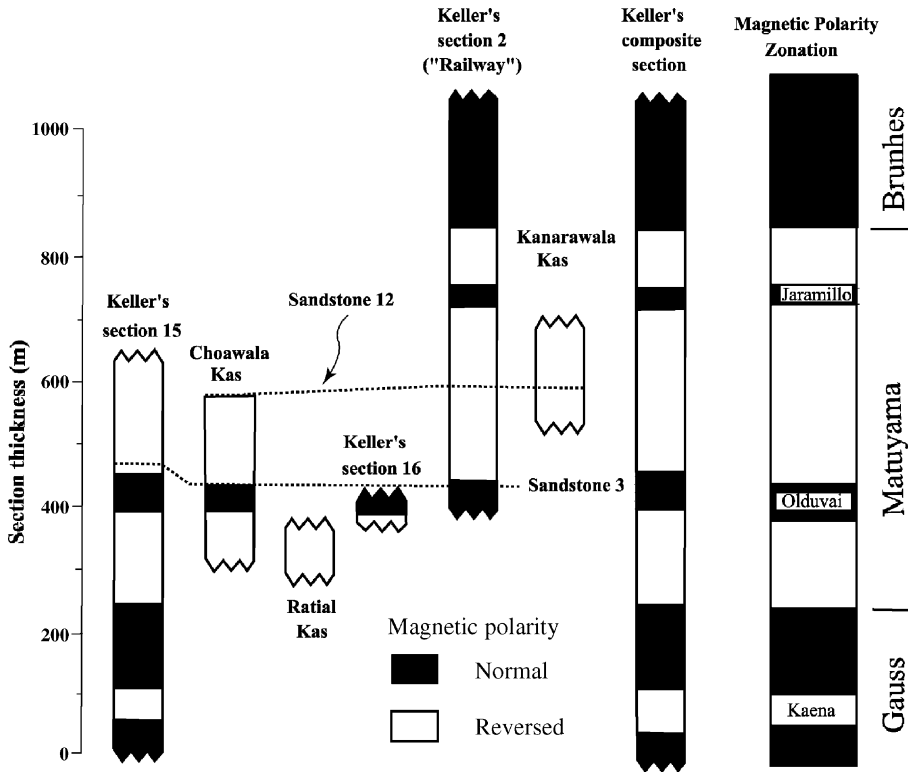
Fig. 3. Magnetic polarity zonation of sections in the Pabbi Hills. Source: Dennell (2004a,b, Fig. 3.3), Keller et al. (1977, Fig. 12) and Rendell (2004, Fig. 4.1).

2.1. Palaeomagnetic dating

The framework for dating the deposits in the Pabbi Hills was established by Keller et al. (1977), who took palaeomagnetic samples from a long section along the railway cutting that bisects the Pabbi Hills, and others along Khoharawala Kas (at the western end of the

anticline), and the headwaters of Kotha Kas on the southern limb of the anticline (see Fig. 4). These sections were used to create a composite section for the Pabbi Hills that could be correlated (see Fig. 3) with the magnetic polarity time scale of Opdyke (1972). This composite section showed a long reversed polarity zone that lay between two long zones of normal polarity and
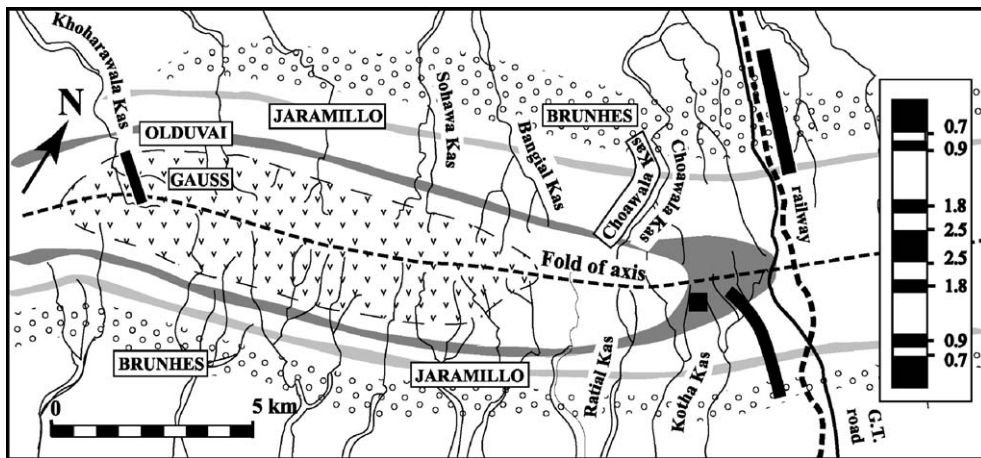

Fig. 4. Palaeomagnetic zonation of Keller et al. (1977) of the Pabbi Hills. The solid bars show the location of their main sections. Redrawn from Keller et al. (1977, Fig. 14).

which was interrupted by two short periods of normal polarity. As there are no volcanic ashes in the Pabbi Hills sequence that could be dated radiometrically, faunal remains were used to provide an indication of the probable age of these deposits. Keller et al. (1977, p.199) showed that the earliest remains of *Equus* were found 12 m above the base of the lower short event of normal polarity. In North America, the earliest remains of *Equus* were dated at ca. 3.5 Ma, and in the Old World, the earliest were ca. 2.5 Ma. On this basis, they suggested that the strata containing *Equus* remains had to be younger than 3.5 Ma. (Lindsay et al. (1980) subsequently showed that *Equus* first appeared in south Asia ca. 2.5 Ma). On this basis, they assigned the long interval of reversed magnetic polarity to the Matuyama Chron, and the short period of normal polarity that contained the oldest evidence of *Equus* in the Pabbi Hills to the Olduvai subchron. The younger short period of normal polarity was identified as the Jaramillo subchron. Keller et al. (1977) also referred the earliest deposits with normal polarity in the interior of Pabbi Hills to the Gauss Chron, and the youngest ones along both flanks of the anticline to the Brunhes Chron (see Fig. 4). As the Pabbi Hills sequence was terminated by uplift ca. 500 kyr, the Pabbi Hills are also one of the youngest anticlines in the world.

Rendell (2004) extended the palaeomagnetic sampling of Keller et al. (1977) to include Choawala Kas and Ratial Kas on the northern and southern limbs of the anticline in the central section of the Pabbi Hills southwest of Keller's 'railway section', and Kanarawala Kas 4 km northwest of the railway section. The sections in Choawala Kas and Kanarawala Kas, together with the 'railway section' of Keller et al. (1977), contain Sandstone 12 as a marker horizon that outcrops for at least 15 km along the strike on the northern limb of the anticline. As shown in Fig. 3, Rendell's (2004) interpretation of the magnetic polarity zonation was that the Choawala Kas section encompassed the Olduvai subchron, and the much shorter Ratial Kas section with reversed polarity was earlier than the Olduvai subchron, but still within the Matuyama Chron. On the basis of its reversed polarity and relative stratigraphic position, the Kanarawala Kas section can be placed in that part of the Matuyama Chron between the Olduvai and Jaramillo subchrons. This section includes Sandstone 12, which can be dated by interpolation between the Olduvai and Jaramillo subchrons to ca. 1.2–1.4 Ma (Rendell, 2004, p. 36). The absence of the Jaramillo subchron of normal polarity at the top of the section along Kanarawala Kas raised some issues concerning the comparability of measured sections, although Rendell (2004, p. 34)

noted that a difference of only 30 m over a total strata thickness of 1 km would have been sufficient to account for 'missing' this subchron even though it was identified 4 km away in section 2 of Keller et al. (1977) along the railway.

As seen in Fig. 3, the Choawala, Ratial and Kanarawala Kas sections can be incorporated into the geochronological framework developed by Keller et al. (1977), and the new data reinforce the framework for dating the vertebrate fossil finds. Rendell's data also clarified the extent to which the main sand units were time-transgressive. Keller et al. (1977, pp. 196–197) showed that Sandstone 3, in their nomenclature, appeared to be slightly diachronous, as it showed normal polarity in sections 2 and 16 but reversed polarity in section 15. They commented (Keller et al., 1977) that "*the discrepancy can be attributed to error in strike-mapping the ridge on the aerial photo and/or to the time-transgression of the strata*". In Choawala Kas, Sandstone 5 (which is equivalent to Keller's Sandstone 3) is a major ridge-forming sandstone ca. 21 m thick which has silts with normal polarity immediately beneath, and a silty-sand lens with reversed polarity magnetisation 6 m from the top of this unit. In section 2 ('railway section') of Keller et al. (1977, Fig. 9) this sandstone is shown within a normal polarity zone. The Choawala Kas data therefore support the suggestion of Keller et al. (1977) that Sandstone 3 is time-transgressive. However, if the average sedimentation rate is assumed to have been ca. 0.37 m/1000 yr (Keller et al., 1977, p. 198), the age of Sandstone 3 at section 15 can be estimated as 1.733 Ma, and as 1.802 Ma at section 2. The difference in age of 70,000 yr introduces an uncertainty of only $\pm 2\%$ of the average age of 1.77 Ma for these two sections. Given the low magnitude of this uncertainty, the sandstone horizons can still be used as stratigraphic markers for correlating the vertebrate faunas (see Rendell, 2004, pp. 34–36).

2.2. Stratigraphic correlation of fossil material

The palaeomagnetic zonation established by Keller et al. (1977) and Rendell (2004) provide a framework for placing most of the fossil material found in the Pabbi Hills between 1986–1990 within time bands of 200–300 kyr (see Table 1). Given the poor dating of fossil material from many Upper Siwalik sections, this marks a significant advance in establishing the time range of Upper Siwalik vertebrate taxa. As noted already, in India, for example, the Pinjor Faunal Stage (or *Equus sivalensis* Interval-Zone) is still treated as a single unit that lasts without internal subdivisions

Table 1
The Pabbi Hills fossil material in terms of provenance, dating and grading

Barry et al. (1980) criteria		Location known to within 10 m spatially and 3 m stratigraphically	Known to within <100–200 m spatially and 3–15 m stratigraphically		Total	Very limited stratigraphic value
Grading system of Barry et al. (1980)		Grade 1	Grades 2–4			Grades 5–6
Age (Ma)	Time-span (kyr)	Localities	Scatters	General collections		Gullies
Pabbi Hills survey evidence:						
0.9 – 1.2	300	–	882	255	1137	270
1.2 – 1.4	200	13,521	7002	2160	22,683	
1.4 – 1.7	300	–	384	672	1056	
1.7 – 1.9	200	4330	2356	2677	9363	
1.9 – 2.2	300	2423	4016	3121	9560	
Total		20,274	14,640	8885	43,799	

The excavated specimens from localities 73, 362 and 642, and a few find-spots (all of which correspond to the Grade 1 of Barry et al., 1980) are excluded. Most scatters and general collections can be tied to sediments between major sandstone units.

from 2.6–0.6 Ma. During the field surveys, fossil occurrences were recorded in relation to the major sandstone "marker" horizons described in this study. Most of those found in 1987 southwest of the GT (Grand Trunk) road in Kotha, Ratial, Choawala and Sohawa Kas could thus be dated as earlier than, contemporaneous with, or later than the Olduvai Event but still older than Sandstone 12. The oldest material (ca. 25% of total) came from deposits immediately below the Olduvai subchron, and is dated to ca. 1.95–2.2 Ma. Approximately the same total was collected from deposits dating to the Olduvai subchron (ca. 1.77–1.95 Ma), and most of the remainder was collected from the Sandstone 12 sequence (1.2–1.4 Ma). A small amount of material (1056 specimens) came from deposits between the Olduvai subchron and Sandstone 12; i.e., between 1.77 and 1.4 Ma. Attempts to collect material from deposits younger than Sandstone 12 proved disappointing, as only 1137 specimens were found along Sandstone 14 (0.9–1.2 Ma).

2.3. The survey and excavations

The areas surveyed in the Pabbi Hills are shown in Fig. 2, which also shows the location of the excavated localities. Three main types of fossil occurrences were noted during the surveys. The first were localities, or very dense occurrences of fossils over a small area (typically 10–100 specimens/m^2), and derived from one sedimentary layer. The second were scatters, or smaller "patches" of fossil that were less densely concentrated than in localities. The third were general collections; these typically covered a large area (up to several thousand m^2), over which fossils were present, but at low densities, and probably derived from more than one sedimentary unit. (Our "general collections"

correspond to the "survey blocks" used by Barry et al. (2002, p. 5) in their discussion of Siwalik Miocene material). Some specimens were collected in gullies, but these have little stratigraphic significance. There were also a few find-spots, of individual specimens that were still in their original context (as in a section, for example). Overall, over 40,000 specimens were collected (including undiagnostics) from over 670 fossil occurrences. Ca. 10% of the total could be identified to skeletal element and taxon at the family or generic level. Many of the most useful specimens for biostratigraphic purposes came from the three excavated localities. Two of these (localities 73 and 642) were within the Sandstone 12 sequence and are thus 1.2–1.4 Ma; the other (locality 362) lay within deposits attributed to the Olduvai subchron (1.77–1.95 Ma).

2.4. Stratigraphic context and spatial distribution

Almost all fossil specimens were found weathering out from or in situ within fine-grained yellow-buff sands and silts. The remainder were found in clays/fine silts (typically pink), or, in a few cases, a sandstone unit. Fossils were generally very well preserved. Most of the specimens from the three excavated localities were assigned to weathering stages 1–3 on Behrensmeyer's (1978) scheme, indicating little surface damage, and rapid burial. The specimens excavated from these localities were generally in excellent condition, with very little surface damage, often complete, and sometimes in articulation or anatomically adjacent to other specimens. Most specimens found on erosional surfaces were also well preserved, particularly those that had not been exposed for long, as on steep, actively eroding slopes. Specimens from the general collections

and from level surfaces (and thus fully exposed to sun and rain) tended to be less well preserved. The spatial distribution of fossil material was non-random. Over 60% came from 20 localities, the largest of which (locality 642) had over 4000 fossils on its surface when discovered. Although the average number of fossils per occurrence was 70, >75% of all occurrences had <25 specimens. This pattern seems typical of the Siwaliks. Raza et al. (2002) commented, for example, that most of the Miocene fossils they studied in the Sulaiman Range came from 12 rich localities, and Gaur (1987, p. 31) noted that fossils were typically found in pockets in the Indian Upper Siwaliks.

3. Vertebrate palaeontology

The commonest mammalian families represented were bovids, cervids, equids and elephantids. Other taxa were indicated by <150 specimens each. Each group can be taken in turn, starting with the commonest.

3.1. Bovidae

The surveys produced numerous specimens (2443) of bovid teeth, post-cranial elements, and horn-core fragments, most of which came from medium-sized animals. Fortunately, the excavations of localities 362 and particularly 642 produced good cranial specimens with both horn cores and maxillary teeth that permit more detailed identifications of some taxa. Overall, six types of bovids were recognised. The main medium-sized bovid was identified as *Damalops palaeindicus*. This type was initially identified as *Proamphibos lachrymans*, which was also the main type of bovid recognised in the analysis of Opdyke et al. (1979) of their material from the Pabbi Hills. This identification was revised following the discovery of a near-complete cranium (642EX1417), two near-complete mandibles (642EX1700 and 642EX1119) and good horn-core specimens (642EX1146, 642EX1377, 642EX1389 and 642EX1417) from locality 642, and comparisons with specimens from Tajikistan (Dmitrieva, 1977) and in the Natural History Museum, London. In the opinion of Gentry (1978, p. 557), *D. palaeindicus* is most likely related to the *Alcelaphus–Rabaticeras–Damaliscus* group of alcelaphines, with hartebeest as a modern representative. It is medium-sized in comparison to other bovids in the Pabbi Hills collections. The M_3 is usually ca. 25–30 mm long. There is no cingulum; the lateral lobes are slightly concave, and the medial lobes slightly convex. The infundibula are shallow, the central cavities are complicated, and the crowns are strongly

hypsodont. In occlusal view the molars are rather selonodont. The crown enamel is smooth and thin (ca. 0.6–0.8 mm). A moderate anterobuccal pillar is present on unworn lower molars, and a moderate basal pillar is present on worn molars. Goat folds are absent in the lower molars, and the M_3 is widest anteriorly in a mediolateral direction. The premolar rows are short. The horns have a circular or slightly oval cross-section, and show some outward torsion at the tip. A simple indicator of the degree of torsion is the ratio of total length along the horn to the direct length from tip to base. In this case, it is 1.22.

A second type of medium-sized bovid from locality 610 was tentatively identified as an alcelaphine. The teeth were similar to those of *D. palaeindicus*, but the medial and lateral lobes are rounder on the molars, less bunched-up mesodistally, and with no basal pillars. They are also slightly less hypsodont, the M_3 is anteriorly less wide but otherwise, the crown length and width are similar to those of *D. palaeindicus.*

A third type had horns that were larger than those of *D. palaeindicus,* and with less torsion. Its affiliation is unknown, but superficially it resembles one of the Tragelaphines, or bush-buck/kudu tribe. The best example was 362X12 from the excavation of locality 362. The horns are 4 cm apart at the base, slightly twisted, circular or slightly elliptical in cross-section, and without a keel. In the specimen from locality 362, the tapelength from tip to base is 25 cm, but 24 cm if measured directly; i.e., the twisting ratio is 1.04. This specimen can probably be associated with two mandibles from locality 362, one (362GB65) right with a moderately worn M_3, 38 mm long and 12 mm wide, and the other (362E GB2), also right, with the dp_4 and M_1, erupting. The dp_4 is 34.8 mm long and 10 mm wide. Other specimens with similar horns were found at several fossil occurrences ranging in age from 2.2–1.9 to 1.2–0.9 Ma.

The fourth type of bovid was identified as *Hemibos triqueticornis* (Rütimeyer). This type is large, and similar in size to a modern eland or African buffalo, with teeth that are strongly hypsodont and selenodont. The best specimens were 628GB1, a left maxilla, and 630GB33, a left mandible. The enamel is slightly rugose and usually ca 0.8–1.0 mm thick, and there is no cingulum. The cusps are strongly folded on the lateral lobes and basal pillars are present between each lobe. The average size of the M_3 was 40×15 mm. The specific identification of *Hemibos* as *H. triqueticornis* is on the basis of its probable horn morphology. Pilgrim (1939, pp. 259–269) recognised three types of *Hemibos–H. triqueticornis, H. acuticornis* and *H. antelopi-*

nus — and provided detailed descriptions. Each was distinguished primarily by the angle at which the horns diverge outwards and backwards. (Given the amount of intra-specific variation in bovid horn morphology, it is perhaps doubtful whether these groups represent distinct palaeo-species). In *H. triqueticornis*, the horns diverge at $>90°$, and are tilted back considerably above the plane of the face, following criteria set out in Nanda (1979). The best examples from the Pabbi Hills of this type of horncore were 642EX1164 and 642EX1181, excavated from locality 642. There is also a superlative cranium (H-GSP 16859), found by the Howard University-Dutch-GSP group at Mangla–Samwal, Mirpur, and identified as *Hemibos* (de Vos, pers. com.). This specimen is especially important it comprises the complete cranium, including the entire maxillary dentition as well as both horns. These are straight, triangular in cross-section, with the keel at the back.

The fifth type of bovid was very small, comparable in size to a modern dik-dik or small gazelle, and is identified as a gazelle. The best examples are a right mandible 642GB2112 from the surface of locality 642 and 610GB41, an M_3 from locality 610 (both 1.2–1.4 Ma). A few other similar dental specimens were also found during the field surveys. The length of the M_3 (17.5 mm) from localities 610 and 642 are identical to those listed by Pilgrim (1937, p. 809) for *Gazella lydekkeri* from the Dhok Pathan Formation, and considerably smaller than that of the Pinjor Stage *Antilope subtorta* Pilgrim (1937, p. 815; length 24.5 mm). An M_2 from occurrence 489, zone J, is also identical in size (11.8 mm) to that of a modern gazelle listed by Gaur (1987, Table 3.27). Several post-cranial specimens (mainly lower limb fragments) were found at locality 642 and a few other occurrences, but no horn-cores were found that could be attributed to this type.

The sixth and final type of bovid was very large. Only three examples were found. The first was 481E GB39, an M_3 (1.7–1.9 Ma), broken across the anterior lobe, with an estimated length of 65 mm. The crown width was 23 mm, and the enamel was 2–3 mm thick. The second specimen (1.2–1.4 Ma) was 125GB2, a right mandible with the M_3; the enamel is smooth; the crowns are selenodont, with the protoconid and hypoconid slightly lower than the metaconid and entoconid. The M_3 is 59 mm long, and 23 mm wide. The third specimen (1.2–1.4 Ma) comprised two pieces (668GB1 and 668GB6) of a right mandible, with a broken M_3. The mandible is very robust, and 36 mm wide at the exposed root of the M_3. This type does not seem to be derived from *Sivatherium* or (according to the criteria set out by Nanda, 1978a) from *Camelus*.

3.2. Cervidae

A large amount of dental, antler and post-cranial material (760 specimens) was classed as cervid. Almost all was found in surface collections, and it was not possible to link different types of antler to either post-cranial or dental material. As the taxonomy of Siwalik cervids is both complex and probably in need of revision (Opdyke et al., 1979, p.29), identifications of the Pabbi Hills cervid material beyond the family level were not attempted. The teeth attributed to cervids are hypsodont, have a pronounced cingulum, and slightly rugose enamel ca. 1.5–2.0 mm. thick. On the basis of size, these teeth can be interpreted as showing one type of cervid, albeit of fairly varying size. There were, however, two types of antler. One is branched at the pedicel, with at least one smaller branch near the tip of the main beam; the antler itself has a roughly circular cross-section. The best example is specimen 695GB1, likely to be earlier than the Olduvai subchron (i.e., >1.95 Ma), and broadly similar to one of *Cervus simplicidens* shown by Sahni and Khan (1988, Fig. 168) from the Tatrot–Pinjor zones (see Fig. 5). The other is more palmate at the pedicel, with a more oval cross-section, and similar in form to *Dama*.

3.3. Artiodactyla (bovid/cervid) post-cranial remains

A large amount of post-cranial material was found that could be classed as bovid or cervid, and most of the remains identified as Artiodactyl were probably bovid or cervid. Although few of the post-cranial bovid and cervid remains could be linked to specific types of dentitions, horns and antler, they were nevertheless useful in showing likely body size and range as well as the likely community structure. As example, the size range of elements such as the distal metapodia and
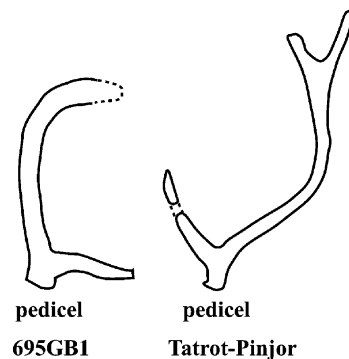

Fig. 5. Cervid antler, specimen 695GB1. The Tatrot–Pinjor example is from Sahni and Kahn (1988, Fig. 168).
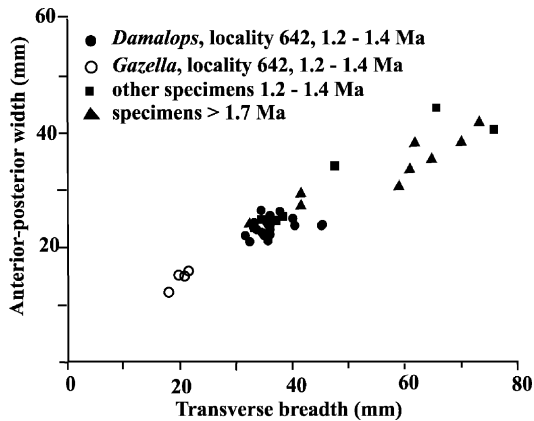
Fig. 6. Scattergram of bovid distal metacarpals.

astragali can provide some indication of the probable ratio of large- to medium- to small-bovids and cervids (see Figs. 6 and 7). Although these ratios are subject to a variety of distorting factors — such as the predatory preferences of *Pachycrocuta*, or differential taphonomic histories — these may be averaged in samples as large and diverse as those from the Pabbi Hills.

3.4. Giraffidae (Sivatherium giganteum)

Nine teeth and 16 post-cranial (mainly fore-limb) specimens were identified as *S. giganteum*, a large, 4-horned and probably short-necked giraffe. All specimens were found on or in deposits attributed to the Olduvai subchron or earlier (i.e., >1.7 Ma); none was found in the younger and equally large data set from Sandstone 12. One of the best examples was specimen 378GB1 (1.7–1.9 Ma), an M^1 or M^2, 51 × 49 mm, which compares well with 50 × 50 mm for an M^1 and 55 × 52 mm for a M^2, listed in Colbert (1935, p. 345). Locality 362 contained several sivathere remains, including a humerus, radius, ulna (362X19, 362X25, 362X27 and 362X136), and also a distal metacarpal (362B1) and a 1st phalange (362X100).

3.5. Suidae

Suid remains are not plentiful in Upper Siwalik deposits, but there was some useful additional new material among the 71 specimens found. These include two crania found eroding from the surface (fossil occurrences 525 and 343), a pair of mandibles (73EX314), an articulated rear leg (73EX196, 73EX322-327, and 73EX852-856) excavated at locality 73, and several dentitions. There appear to be two types on the basis of the size of teeth. However, there are major size differences in suids between males and females, young and old, and so the observed differences may be due to age and sex. If there are indeed two types, previous studies suggest that they should be attributable to *Sus falconeri*, and *Potamochoerus palaeindicus* (Colbert, 1935, pp. 256–266).

3.6. Perissodactyla

Although rare, 87 specimens were identified as *Rhinoceros sivalensis*. These include a complete cranium (642EX1602) from locality 642, two mandibles (341GB33 and 642EX1062), a scapula (73EX5) and numerous limb and teeth specimens. Interestingly, rhinoceros was represented in two of the hyaenid localities (73 and 642) that were excavated, indicating that it was vulnerable to predation or scavenging.

Substantial equid remains (296 specimens) were found during the surveys, and the excavations of localities 73 and 642. The excavated localities contained the remains of several horses, and provide useful information on the size of fore- and hind-limbs as well as dentitions. A complete cranium (642EX1609) and two mandibles (642EX1215 and 642EX1532) were excavated at locality 642 (1.2–1.4 Ma), and three complete pairs of mandibles were found at fossil occurrences 109 (1.2–1.4 Ma), 689 (1.4–1.7 Ma) and 693 (1.9–2.2 Ma). All of this material was attributed to *E. sivalensis*. Two issues need to be considered: i) the relationship of the equids from the Pabbi Hills to earlier Upper Siwalik ones from Mangla–Samwal; and ii) the last appearance datum (LAD) of *Hipparion* in South Asia.

3.6.1. The equids from Mangla–Samwal in comparison to those from the Pabbi Hills

Hussain et al. (1992) recognised two types of *Equus* in their Upper Siwalik section at Mangla–Samwal, ca.
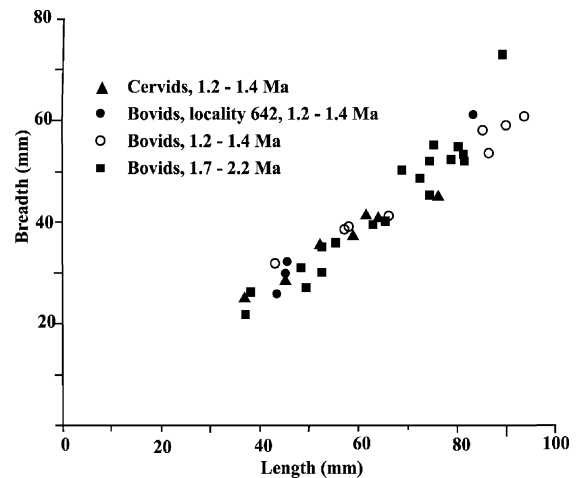

Fig. 7. Scattergram of bovid and cervid astraguli.

30 km from the Pabbi Hills. Most were identified as *E. sivalensis* on the basis of size and morphology. A smaller type was also recognised at locality H-GSP 8460, and provisionally called *Equus* species A. Interestingly, the equid post-cranial material from the Pabbi Hills is distinctly smaller than those remains identified at Mirpur as *E. sivalensis*, but also slightly smaller and more gracile than that called *Equus* species A. by Hussain et al. (1992) (See Fig. 8). This issue cannot be resolved at present, but various explanations can be offered. One is that *E. sivalensis* sensu strictu has a short time-range and was later replaced by an equid that was smaller post-cranially. Alternatively, *E. sivalensis* may have become smaller during the Late Pliocene and Early Pleistocene. Another (and probably remote) possibility is that other Upper Siwalik equid material that is normally classified on dental grounds as *E. sivalensis* may belong to a smaller species not yet formally designated. Finally, the larger type of equid at Mirpur might derive from *E. cautleyi*, which Sahni and Khan (1988, p. 51) state is larger than *E. sivalensis*. (Basu (2004, p. 112) also notes that a larger type of equid than *E. sivalensis* may be present in the upper part of the Nagrota Formation (Pinjor Stage)).

3.6.2. The last appearance datum of Hipparion in South Asia

One of the key issues in studies of Upper Siwalik biostratigraphy concerns the timing of the first appearance of *Equus*, and the last appearance of *Hipparion*, the tridactyl (3-toed) horse. Lindsay et al. (1980) showed that *Equus* first appeared in South Asia ca. 2.5 Ma, most probably from North America. According to Barry et al. (1982), the earliest specimen of *Equus* in

Fig. 8. Scattergram of equid distal metapodia from the Pabbi Hills and Mangla–Samwal.

the Upper Siwaliks is from locality D68 at Hasnot, just below the Gauss–Matuyama palaeomagnetic boundary at 2.58 Ma. At Mangla–Samwal, Mirpur, *Equus* also appears at around this time (Hussain et al., 1992). Its first appearance in Europe and East Africa was placed somewhat later, at ca. 1.8–2.3 Ma. The appearance of *Equus* is thought to coincide with the immigration of new taxa, notably *Elephas* and *Leptobos* (Barry et al. (1982) *Elephas–Leptobos–Equus* horizon).

The date at which *Hipparion* becomes extinct remains problematic. According to Barry et al. (1982) its last appearance was during the *Elephas planifrons* Interval-Zone (3.3–2.7 Ma). Opdyke et al. (1979, p. 27) however claimed that the last appearance of *Hipparion* was in the middle part of the Matuyama Chron (i.e., above the Olduvai subchron), ca. 1.5 Ma, on the basis of a specimen from DP33 in the Pabbi Hills. This find is very anomalous, as *Hipparion* is not evidenced at Mangla–Samwal, Jalalapur, Rohtas, or any other Upper Siwalik section that covers the period between 1.5 and 2.5 Ma. In India, *Hipparion* is not thought to extend into the Pinjor Zone, i.e., beyond 2.5 Ma (see Nanda, 1997, pp. 182–3). One possibility is that the Pabbi Hills specimen was reworked, or misidentified. Given the large number of equid remains from the Pabbi Hills, the absence of *Hipparion* in earlier sections is unlikely to be an artefact of inadequate sampling.

The main criterion for distinguishing *Hipparion* from *Equus* is dental rather than pedal. In *Hipparion*, the protocone of the molars and premolars is separate from the main cusp, whereas it is joined in *Equus* (see Fig. 9). All the crowns of those equid teeth from the Pabbi Hills that were sufficiently complete and distinct showed the cusp morphology of *Equus*, and none showed a distinct protocone (see Fig. 9). It is possible that the specimen identified by Opdyke et al. (1979) as *Hipparion* was from an old individual, as MacFadden (1992, p. 109) notes that in old horses, the protocone may appear to be distinct as a result of wear. This may explain the anomalously late sighting of *Hipparion* by Opdyke et al. (1979). (Sadly, the specimen cannot now be traced).

3.7. Proboscidea

Proboscidean specimens were very common, but most (>2000) were molar plate and tusk fragments. Two types are represented: the first, and commoner, is *E. hysudricus*, found on units attributable to Sandstone 12 (1.2–1.4 Ma) or older, and the other is a species of *Stegodon,* found on deposits older than 1.4 Ma. There is no evidence of *E. planifrons*, which confirms earlier
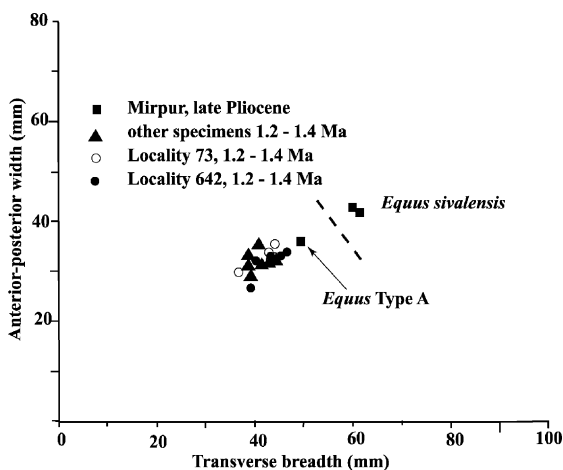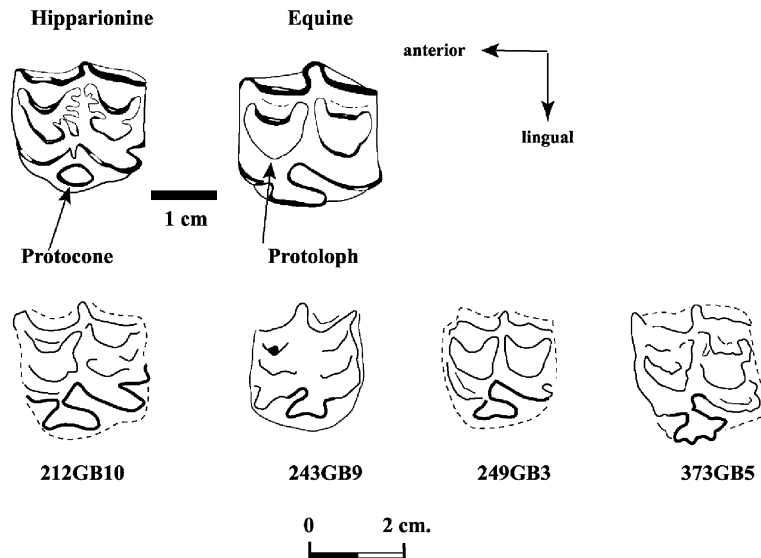
Fig. 9. Hipparionine and equine teeth (from MacFadden, 1992, Fig. 5.18), and equid specimens from the Pabbi Hills. Note the way the protocone is distinct in *Hipparion* but not in *Equus*. Specimen 212GB10 is 1.7–1.9 Ma; 243GB9 and 249GB3 are 1.4–1.7 Ma; and 373GB5 is 1.9–2.2 Ma.

suggestions by Hussain et al. (1992) that it may have become locally extinct by 2.7 Ma. The best specimen of *E. hysudricus* was 535GB1, a complete maxilla (1.9–2.2 Ma), and the best specimen of *Stegodon* was X507, a pair of mandibles of the same age. Comparable examples of *Stegodon* teeth are shown in Sahni and Khan (1988, Figs. 1, 8, 19, 22 and 23).

3.8. Anthracotheriidae

These are very rare in the Upper Siwaliks. Recently, Steensma and Hussain (1992) described a maxillary fragment of *Merycopotamus dissimilis* from Mangla–Samwal, dated as between 2.40 ± 0.20 and 2.65 ± 0. 21 Ma. This is the first well-dated specimen of this type, which is known from Pakistan, India, Burma and Java. Although no dental specimens of anthracotheres were found in the Pabbi Hills, a proximal metacarpal (529GB3) and a distal ulna (529GB16) (1.9–2.2 Ma) were identified by A. Currant (Natural History Museum, London) as anthracothere. These specimens thus extend the time-range of anthracotheres in South Asia towards the end of the Pliocene.

3.9. Hippopotamidae

Seventeen specimens were referred to this taxon, and in two cases (248GB8 and 347GB15), the identifications were confirmed in the UK against comparative material. All came from the early part of the sequence, and none was found in deposits younger than 1.7 Ma. It is likely that these belong to *Hexaprotodon*, a type

known elsewhere from the Upper Siwaliks (see e.g., Nanda, 1978b). This genus is identified chiefly from its six incisors, although Matthew (1929, p. 555) stated "I cannot see any very strong reason for according full generic status to *Hexaprotodon*. Except for the incisors, it is in no way different from the modern species" of hippopotamus. The genus has persisted as independent of *Hippopotamus*, however. *Hexaprotodon* is somewhat smaller, and probably related to the pygmy hippo, now found only in West Africa (Jablonski, 2004). According to Jablonski (2004, p. 121), the last definite appearance of *Hexaprotodon sivalensis* in the Pakistani Siwaliks is 3.5 Ma, although it may have persisted until 2.2 Ma (Barry et al., 2002). The above data indicate that it persisted longer, up to, but probably not beyond the Olduvai subchron (see also Dennell, 2004b).

3.10. Carnivores

Carnivore remains were rare, and only ca. 70 were found during the surveys. Several more were recovered during the excavations of localities 73, 362 and 642. The widest range of taxa was found at locality 73, at which *Crocuta*, *Pachycrocuta*, *Panthera*, an ursid and a herpestid were represented. Localities 362 and 642 contained a partial skeleton of a large canid, and some *Pachycrocuta* remains, respectively. Identifications were undertaken in comparison with other material from the Siwaliks and the collections of the Natural History Museum, London. Unfortunately, most of the older specimens from the region are in need of considerable taxonomic revision, and identifi-

cation of the newer fossils beyond the level of family is therefore often difficult. Material from the region in existing collections is usually poorly provenanced. The evidence summarised here therefore provides one very important bonus in establishing the presence of a number of species in the region within two very specific time bands. Full details are given in Turner (2004).

Crocuta crocuta Erxleben, 1777 was represented by two mandibular (73X GB56 and 73X GB57) and one maxillary fragment (73EX410) from locality 73, and a P4 (68B GB1034) from locality 68, both 1.2–1.4 Ma. All came from aged animals. Localities 68, 73 and 642 (all 1.2–1.4 Ma) and 214 (1.7–1.9 Ma) contained dental/mandibular specimens of *Pachycrocuta brevirostris* Aymard, 1846, commonly referred to as a gigantic hyaena. The main specimens were 68B GB314, a mandibular fragment; 73EX12, a left P_4; 214B GB19, a left P_3; 642GB1, a right mandible; 642EX1287, a left mandible; and 642EX1390, a left maxilla. A distal metapodial fragment (291GB9) and ca. 1.9–2.2 Ma was identified as *P. brevirostris* on the basis of its size. Several hyaenid specimens from other occurrences could not be identified to genus. These indeterminate hyaenid specimens come mostly from smaller animals. In terms of the listing of taxa provided by de Vos et al. (1987, p. 366), the most likely candidate, based on size and inferred stratigraphic range, is what the latter authors refer to as *Hyaenictis bosei* (following Matthew, 1929), and Werdelin and Solounias (1991) refer to as *Lycyaena bosei*. Examples are specimens 214A GB1, 315GB1/2 (both 1.7–1.9 Ma) and 437D GB26 (1.9–2.2 Ma).

Several mandibular (73EX58, 73EX238, 73EX568) and dental (73X GB51, 73B GB505, 73EX203, 73EX233, 73EX300, 73EX344, 73EX382 and 73EX420) specimens of a medium-sized, juvenile pantherine felid were found at locality 73 that were cautiously identified as *Panthera uncia*, the snow leopard. A right mandible 674GB21 (1.2–1.4 Ma) was identified as *Megantereon cultridens*. This specimen is similar in size to others from the Siwaliks in the Natural History Museum collections, and larger than most specimens from many other localities. The size differences have been the basis for specific differentiation of the Siwalik representatives (Petter and Howell, 1982), but there is no overwhelming argument for the existence of more than one widely distributed species (Turner, 1987).

Several other indeterminate felid specimens were also found, including at least one other larger taxon that does not appear to be *Homotherium*. In the Natural

History Museum collection are several fragmentary specimens, plus a complete felid skull, M32148 collected near Pinjor (but otherwise unprovenanced) and presented to the museum in 1977. With its flattened canines, shortened and wide muzzle, domed skull and short, wide zygomata, this specimen is clearly a species of *Dinofelis*, and Werdelin and Lewis (2001) have recently referred it to the species *D. cristata*.

Two types of canid were recognised. The smaller could not be identified to species level, and is referred to as cf. *Canis*. The larger type was represented by a semi-complete skeleton from locality 362 (1.7–1.9 Ma) preserving much of the dentition, vertebral material, a virtually complete front-limb, two lower rear-limbs and an *os penis* bone. The mandibular specimen (362X124) bears a considerable resemblance to material collected from the Siwaliks in the early 19th century and identified as *Canis cautleyi* Bose, 1880. The dental morphology is very similar to that of the Late Pleistocene and extant Holarctic *Canis lupus*. The relationship of *C. cautleyi* to other canids is currently unclear. European canids referred to the genus *Canis* are generally much smaller until the Upper Pleistocene (Turner, 1999), and the presence of such a large species in the Siwaliks at this time is clearly a matter for further investigation. So far as the smaller canid is concerned, Gaur (1987) refers to two small canid species, the already known *Sivacyon curviplatus* Falconer, 1868, and a newly identified species, *Canis pinjorensis* Gaur, 1987. In the absence of specimens for comparison, the fragmentary material available here cannot be referred with any confidence to either.

Two other types of carnivore were identified. The first was a herpestid, species indeterminate, represented by a mandibular fragment 73A GB52 from locality 73 which may have belonged to the common mongoose genus *Herpestes*. The second was an ursid, genus and species indeterminate, represented by an M_1 (73B GB515) and 703GB2, a calcaneum from occurrence 703; both specimens are ca. 1.2–1.4 Ma.

3.11. Molluscs

Samples of fossil molluscs were collected from several fossil occurrences, particularly in Kotha Kas in 1987 at localities ≥1.7 Ma. The commonest were *Lamellidens* and *Parreysia*, followed by *Bellamya*, *Indonaia* and *Viviparidea*. They are all typical of a large, slow-moving river with clean, shallow water, typically <5 m deep, and with abundant aquatic vegetation. It is unsurprising that turtle and crocodile remains were common at most of these occurrences.

4. Discussion

A number of issues are raised concerning continuity and extinction in the Pabbi Hills sequence, and its wider significance within the Upper Siwaliks of South Asia.

4.1. Continuity and extinction in the Pabbi Hills sequence

As stated earlier, approximately half the fossil material from the Pabbi Hills is derived from Sandstone 12-time (1.2–1.4 Ma), and the other half from deposits between 1.7 and 2.2 Ma. Each is roughly the same size (ca. 20,000 specimens), and sampled the same range of depositional environments: channel bars, abandoned channels, and overbanks. Consequently, the absence from one of these time bands of a taxon recorded in the other is likely to be genuine unless it was extremely rare, and is unlikely to be an artefact of inadequate sampling or small sample size. In contrast, the very limited amount of material from deposits between 1.4 and 1.7 Ma and 0.9–1.2 Ma means that the absence of a taxon from these units probably reflects the small amount of material relating to those time-bands. Further data collection could reasonably be expected to increase the range of taxa in these periods.

The main trends are summarised in Fig. 10. Overall, there appears to be a considerable amount of continuity in the range of large mammals in the Pabbi Hills between 2.2 and 1.2 Ma. The medium-sized bovid *D. palaeindicus*, and the equid *E. sivalensis* were the commonest ungulates. *R. sivalensis, E. sivalensis, E. hysudricus* and *Stegodon* were the only members of their genus, and there were probably two types of pig. The range of bovids has probably been under-estimated because of the limited number of well-preserved horn cores. In addition to *Damalops*, there were probably two others of the same size: an alcelaphine (seen at locality 610) and the bovid represented at locality 362. Additionally, there was a large bovid, *H. triqueticornis,* and a larger and much rarer one. The gazelle is probably under-represented because of its size and gracile skeleton, but the numerous post-cranial remains at locality 642 confirms its existence in the Upper Siwaliks as late as 1.2–1.4 Ma.

The main changes appear to be ones of extinction after 1.7 Ma. Although rare, *S. giganteum* is evidenced at several fossil occurrences in the Pabbi Hills, but all are between 1.7 and 2.2 Ma. Its remains are robust, and easily seen by virtue of their large size. Its absence from the whole of the Sandstone 12 assemblage (constituting ca. 50% of all the fossil material) is thus probably genuine, and it probably became locally extinct by 1.4 Ma, and perhaps shortly after 1.7 Ma. However, Ranga Rao et al. (1995) report *S. giganteum* from deposits dated to the early Brunhes Chron (<0.78 Ma) at Patiali Rao, Pinjor. This find appears very anomalous in the light of the data presented here, and further work is needed to resolve this discrepancy.

Other taxa known only in the early part of the Pabbi Hills sequence (i.e., 1.7–2.2 Ma) include anthracotheres, hippopotamids, and possibly the medium-sized bovid with twisted horns, known only from locality 362. Also evidenced before, but not after 1.7 Ma, was *C. cautleyi* (found in the excavated deposits of locality 362), and a small hyaenid (probably *Hyaenictis* or *Lycyaena*). All appear to have been extremely rare. *C. cautleyi* is represented only at locality 362 (1.7–1.9 Ma), at which several parts of one skeleton are preserved. Although carnivore remains are rare in the Pabbi Hills (with only ca. 120 specimens in total), over half were found at locality 73 (1.2–1.4 Ma), and the absence of this canid from this assemblage may be genuine. *Stegodon* may also have been extinct before Sandstone 12 time: its remains were very rare, and the youngest specimen (139GB56) is older than 1.4 Ma. According to Opdyke et al. (1979), however, at least one specimen of *Stegodon* is dated to the early Brunhes Chron, ca. 0.7 Ma, although no details are given about provenance or identification.

A few taxa are presented in assemblages between 1.2 and 1.4 Ma, but are absent from older ones. One is *C. crocuta*, which is evidenced at localities 68 and 73, both within the Sandstone 12 sequence. Others are an ursid and snow leopard, both represented at locality 73, and previously unrecorded in the Upper Siwaliks. As the teeth of these animals were found at locality 73, we can assume that they were autochthonous to the area, and not the result of down-stream transport from elsewhere. The significance of their presence in the Pabbi Hills area by 1.2–1.4 Ma is hard to assess. Both are usually associated with upland/montane regions. Their presence may indicate cooler conditions, or that the uplift and forefront advance of the Karakorum mountains had brought the Pabbi Hills within the annual migratory range of these animals.

By the time of the deposition of Sandstone 12, it is assumed that *S. giganteum, C. cautleyi, Hyaenictis* or *Lycyaena* (i.e., the smaller hyaenid), anthracotheres and hippopotamids, and possibly *Stegodon*, had become locally extinct. This may indicate the expansion of grassland at the expense of woodland. This assumes that *Sivatherium* and the very large bovid were browsers. Future research may test this hypothesis by, for
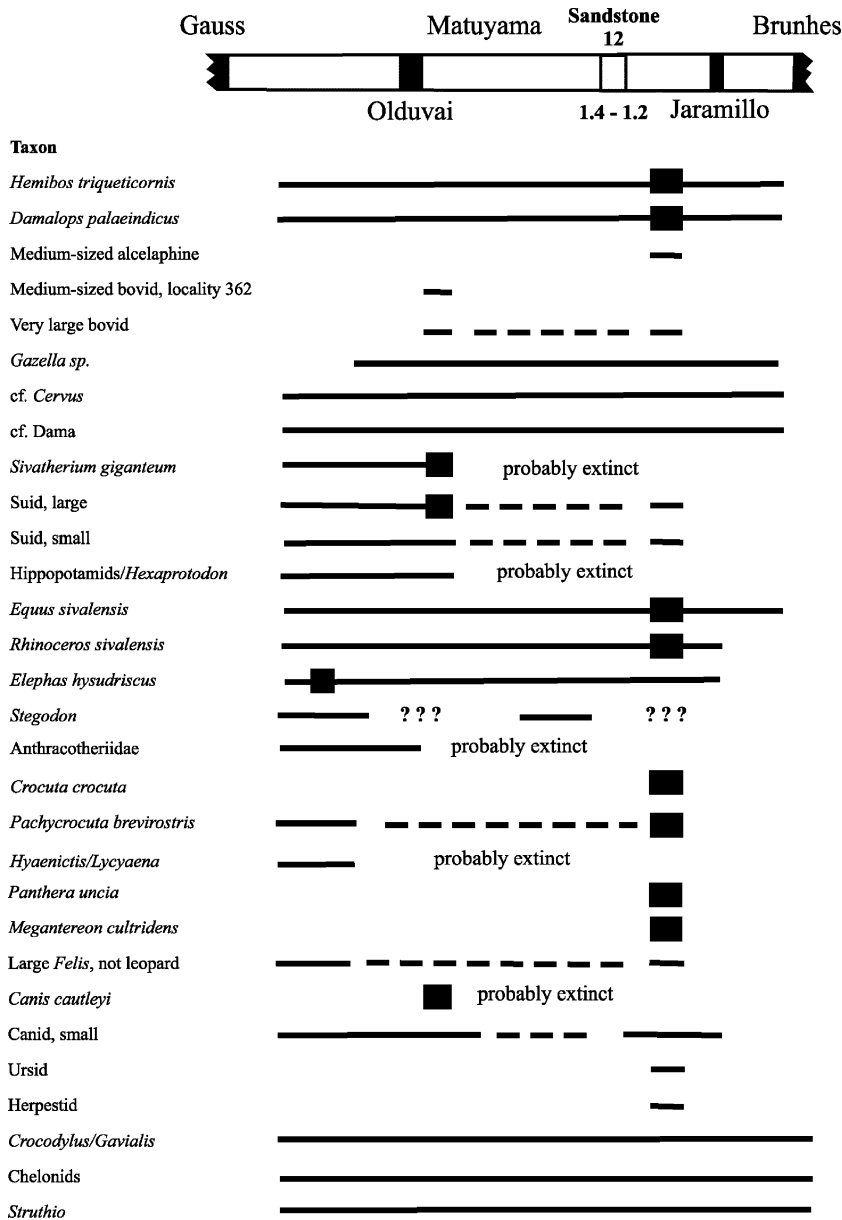
Fig. 10. Summary of the main biostratigraphic features of the Pabbi Hills. Solid squares denote particularly complete and/or in situ specimens.

example, examining the $C_3:C_4$ ratios in herbivore teeth. Another possibility worth exploring would be to see if gavials replaced crocodiles if the hot, swamp habitats preferred by the latter became rarer during the Early Pleistocene (see Patnaik and Schleich, 1993).

4.2. The Elephas hysudricus faunal zone

Earlier, we noted that Hussain et al. (1992) identified an *E. hysudricus* faunal zone, beginning at 2.7 Ma, but left open-ended as to duration or subsequent change. We suggest that this can be subdivided into an

E. hysudricus–Sivatherium part up to 1.7 Ma, which is defined by the local extinction of *S. giganteum*, hippopotamids, anthracoceres, and a large canid. The period between 1.7 and 0.9 Ma can be defined by *E. hysudricus–Crocuta–Ursus–Panthera*, although the FAD of both *Ursus* and *Panthera* may be extended back in time with further exploration. The LAD (last appearance datum) of *E. hysudricus* is currently unclear. In Middle Pleistocene times, it is replaced by the modern *E. namadicus*, the appearance of which may be part of the Galerian faunal turnover that affected Europe and southern Asia. According to Nanda

(1997), the end-point of *E. hysudricus* may be as late as 0.6 Ma.

4.3. Upper Siwalik biostratigraphy of Opdyke et al. (1979) reassessed

Opdyke et al. (1979) made a major contribution in attempting to establish a reliable biostratigraphy for the Upper Siwaliks that was based on specimens that could be dated by reference to a palaeomagnetic time-scale. Their work considered material from several sections in Pakistan from both the Tatrot and Pinjor stages. In considering the Pinjor Stage, their main attention was on the transition from the Tatrot, and the first appearance of key taxa such as *Equus* and *Elephas*. Since their investigations, important new material has been published from Mangla–Samwal, Mirpur, and our research in the Pabbi Hills has of course produced a great deal of new material. In the light of these new data, the following revisions and additions are proposed to the scheme they proposed in 1979, and summarised in Fig. 11.

Bovids: we propose that *D. palaeindicus* is substituted for the material they identified as *Proamphibos*, and *Hemibos* for *Bubalus*. This takes into account material published by Dmitrieva (1977) that was not mentioned by Opdyke et al. (1979), and the discovery of the *Hemibos* specimen H-GSP 16589 at Mirpur. We would also extend the range of *Damalops* (alias *Proamphibos*) from Mid- to Late-Matuyama time. The existence and time-range of *Gazella* is confirmed. Additionally, at least three other types of bovid are recognised: a medium-sized alcelaphine (locality 610, 1.2–1.4 Ma); a possible tragelaphine (locality 362, 1.7–1.9 Ma), and a very large bovid (1.2–1.9 Ma). *Cervids*: two types are recognised on the basis of their antler, and their time range is extended downwards slightly into the Late Matuyama. *Giraffids*: their presence in only the early part of the Pabbi Hills sequence is confirmed, with *S. giganteum* as probably the only member of this group. *Suidae*: new material from the Pabbi Hills supplements the very sparse record for Upper Siwalik suids presented by Opdyke et al. (1979). There are probably two types that may be *Sus*
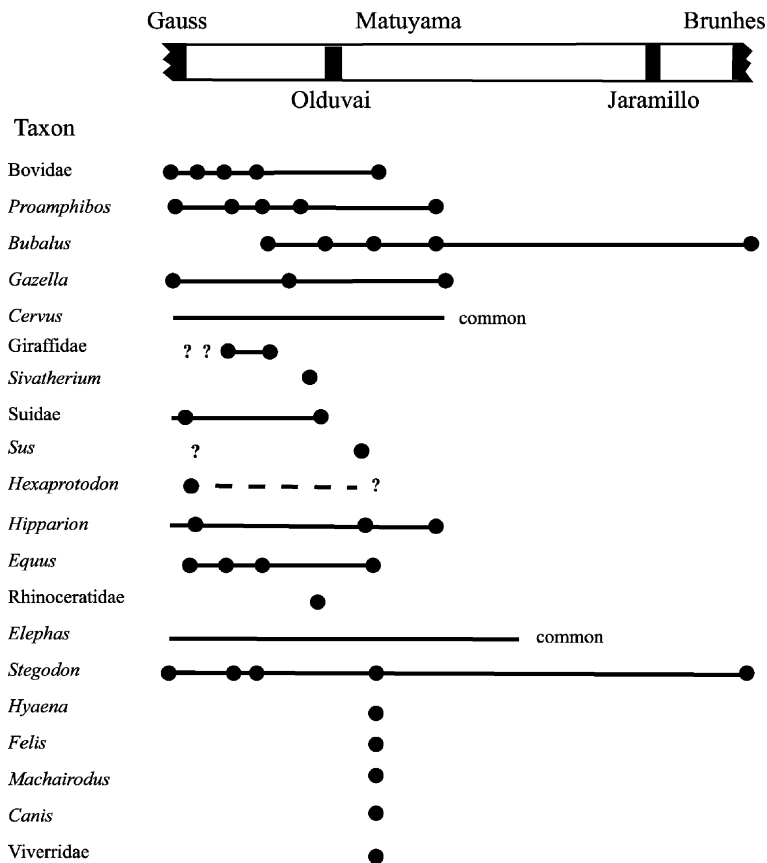

Fig. 11. Summary of the main biostratigraphic features of the Pabbi Hills and contemporaneous localities, as proposed by Opdyke et al. (1979, Fig. 21).

and *Potamochoerus*, but these need confirmation. *Equids*: the chronological range of *Equus* (probably *E. sivalensis*) is extended from Mid- to Late Matuyama time. More importantly, no evidence of *Hipparion* was found, and we consider it probable that it became extinct by 2.5 Ma; i.e., a million years earlier than indicated by Opdyke et al. (1979). *Rhinoceros*: its time-range is extended into Late Matuyama time. *Elephas*: the presence of one type of *Elephas* (*E. hysudriscus*) is confirmed, as is its time-range throughout the Matuyama Chron. *Stegodon*: our data indicate that it was present in the early, but not the later, part of the Pabbi Hills sequence. The persistence of *Stegodon* into the Middle Pleistocene, as suggested by Opdyke et al. (1979), needs confirmation. *Hippopotamids/Hexaprotodon*: in the scheme of Opdyke et al. (1979), its presence in the Matuyama Chron was very tentative. We confirm its presence in the Early Pleistocene prior to 1.7 Ma, but it is unlikely that it persisted long thereafter. *Anthracotheres*: these are very rare in the Upper Siwaliks, and were not reported by Opdyke et al. (1979). New data indicate that these persisted into the early Matuyama Chron, but were probably extinct by 1.9 Ma. *Carnivores*: these were very sparsely represented in the scheme of Opdyke et al. (1979). The new data indicate two types of hyaena (*Crocuta* and *Pachycrocuta*), not one, and possibly also *Hyaenictis* or *Leecyaena*. We suggest that *Panthera* should be substituted for *Felis*, and *Megantereon* for *Machairodus*. A third type (perhaps *Dinofelis*) may also be present. Two types of canid are recognised rather than one. The larger one (*C. cautleyi*) may have become extinct after 1.7 Ma. An ursid was also present in Late Matuyama time.

4.4. Regional differences within the Upper Siwaliks

The Pabbi Hills data reinforce the possibility that there are regional differences within the Upper Siwaliks across the Indian sub-continent. *Camelus* and cercopithecids, for example, are known from the Upper Siwaliks of India, but not Pakistan (Opdyke et al., 1979; Barry, 1987). Here, *Megantereon*, *Pachycrocuta*, *Ursus* and anthracotheres are recorded in the Pabbi Hills, but not at any other Upper Siwalik exposures in India. There may also be differences in the timing of regional extinctions. According to the data presented here, *Sivatherium* and *Hippopotamus* became extinct during or shortly after the Olduvai subchron, whereas *Sivatherium* is recorded as just above the Brunhes–Matuyama boundary by Ranga Rao et al. (1988), and hippopotamids persisted in the Deccan peninsula of India throughout the Pleistocene (Dennell, 2004b). These points imply that the term "Upper Siwalik" may mask subtle but important differences between and along the palaeo-Indus and -Gangetic drainage systems. Faunal immigrations and extinctions need therefore to be assessed in relation to the history and type of drainage basin in which they are found.

4.5. Faunal turnover in South Asia compared with that in East Africa

The East African faunal record (currently the best available for the period) indicates a series of complex, small and cumulative changes between 3.0 and 1.0 Ma ago. DeMenocal (1995) suggests there were three shifts towards more arid conditions, ca. 1.8, 1.7 and 1.0 Ma. In general, conditions in East Africa were more wooded before 1.6 Ma, and grasslands were commoner thereafter. The faunal record for the Late Pliocene and Early Pleistocene from Koobi Fora, Kenya, suggests a series of small, incremental changes that cannot be directly linked to the oceanic record, although grasslands appear to have increased after 1.8 Ma (Behrensmeyer et al., 1997).

The Pabbi Hills data generally support these conclusions. Overall faunal change between 2.2 and 1.2 Ma appears to have been slight, and many of the extinctions noted above may be attributed to a reduction of tree-cover. This is consistent with analyses of soil carbonates that show an overwhelmingly grassland environment in the Pabbi Hills after 1.7 Ma (Quade et al., 1993). What is perhaps surprising is the stability of the faunal communities and grassland-dominated landscapes in this region: despite at least a dozen glacial–interglacial cycles every 40 kyr during the Early Pleistocene, the overall characteristics of the landscape appear to have been very stable, apart from those associated with changes in tree-cover. This in turn suggests that climatic fluctuations evidenced in deep-sea cores and at high latitudes were more muted in terrestrial systems at lower latitudes.

5. Endnote

Fossil specimens were numbered as: fossil occurrence; GB (=Geological Survey of Pakistan–British Archaeological Mission to Pakistan); specimen number; an example is 30GB4. The largest fossil occurrences were subdivided into zones when collected, e.g., 489A-489E. Excavated material from localities 73 and 642 were recorded as 73EX or 642EX, followed by the specimen number; specimens excavated from locality 362 are indicated by X, as in 362X12.

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